

**"Fifth Course on Mathematical Ecology
including and introduction to Ecological Economics"**

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**BIODIVERSITY STATUS AND TRENDS.
WHY CONSERVE BIODIVERSITY?**

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Outline for talks at ICTP's
Fifth Course on Mathematical Ecology
Trieste, 6-10 March, 2000

Three talks:

- I) Monday, March 6, 1:30 pm: *Biodiversity status and trends. Why conserve biodiversity?*
- II) Tuesday, March 7, 2:30 pm: *Principles of conservation biology.*
- III) Wednesday, March 8, 10:30 am: In situ and ex situ approaches to the conservation of biodiversity.

I) Biodiversity status and trends. Why conserve biodiversity?

1) **What is biodiversity?**

Classic definition of biodiversity, following biological levels of organization: genes, individuals, populations, species, communities/ecosystems, biomes.

Begin with definition of species—basic unit of diversity measurement. Highlight that definition of species is not equally clear for all taxa.

Move up and down the hierarchy of the levels of organization to illustrate the other components of biodiversity: 1) from species “downward”: populations, individuals and genes; 2) from species “upward”: communities/ecosystems and biomes.

References:

- Harper, J. L. and D. L. Hawksworth (1994) Biodiversity: measurement and estimation. *Philosophical Transactions of the Royal Society of London B* 345: 5-12.
- Jenkins, M. (1992) Species diversity: an introduction. In: WCMC, Ed. *Global Biodiversity: Status of the Earth's Living Resources*, pp: 40-46. World Conservation Monitoring Centre (WCMC), Chapman and Hall.

2) **Global biodiversity patterns**

Maps of 1) latitudinal distribution of biodiversity and 2) megadiverse countries.

Origin of the term "hot spots". Megadiversity countries: seventeen of the world's countries (out of ~200) include between 60-70% of described species.

The paradox of biodiversity conservation: more resources where there are fewer species: 1) scientists per country (participants in UNEP's global biodiversity assessment), 2) per-capita GDP.

Discuss the idea that it is not only distribution but also abundance that matters. Most species are rare. Seven forms of rarity.

References:

Adams, J. M. (1989) Species diversity and productivity of trees. *Plants Today* 2: 183-187.

Myers, N. (1988) Threatened biotas: "hot spots" in tropical forests. *The Environmentalist* 8(3): 187-208.

Rabinowitz, D., S. Cairns and T. Dillon (1986) Seven forms of rarity and their frequency in the flora of the British isles. In: M. E. Soulé, Ed. *Conservation Biology: the Science of Scarcity and Diversity*, pp: 182-204. Sinauer Associates, Inc., Sunderland, Massachusetts, U.S.A.

3) How many species are there?

Classic estimates and controversy by Erwin, May and others.

References:

May, R. M. (1990) How many species? *Philosophical Transactions of the Royal Society of London B* 330: 293-304.

Pimm, S. L., G. J. Russell, J. L. Gittleman and T. M. Brooks (1995) The future of biodiversity. *Science* 269: 347-350.

4) Extinction rates past and present

Background extinction rates. Evidence from the fossil record. Extinction is part of the Earth's evolutionary history, but rates have changes. Contrast with current extinction rates. Present range of estimates—including the most extreme ones.

Current rates associated to impact of human activities. Examples: 1) earth from space, 2) habitat destruction rates; photographs of mahogany harvesting, deforestation in Amazonia. Rates of habitat conversion.

References:

- May, R. M., J. H. Lawton and N. E. Stork (1995) Assessing extinction rates. In: J. H. Lawton and R. M. May, Eds., *Extinction Rates*, pp: 1-24. Oxford University Press.
- Jablonski, D. (1995) Extinctions in the fossil record. In: J. H. Lawton and R. M. May, Eds., *Extinction Rates*, pp: 25-44. Oxford University Press.
- Bibby, C. J. (1994) Recent past and future extinctions in birds. *Philosophical Transactions of the Royal Society of London B* 344: 35-40.

5) What are we loosing?

Direct (e.g. biotechnology) and indirect (e.g. ecosystem services, ecotourism) benefits from biodiversity. Biophilia. Aspirin example from Lovejoy in *Biodiversity II*.

Direct use of biodiversity: bioprospecting. International legal framework provided by the Convention of Biological Diversity. Property rights, benefit sharing and technology transfer.

The value of biodiversity in pharmaceutical research. Costs and benefits of drugs derived from natural products. The random sampling approach vs. the ethnobiological research approach. Case studies: Costa Rica's INBIO and Shaman Pharmaceuticals.

Bioprospecting in the Third World: making the First World healthier? Outline research agendas for major pharmaceutical companies. Turning bioprospecting into a truly equitable enterprise.

References:

- Carlson, T. J., R. Cooper, S. R. King and E. J. Rozhon (1997) Modern science and traditional healing. *Royal Society of Chemistry Special Publication* 200: 84-95.
- Carlson, T. J., M. M. Iwu, S. R. King, C. Obialor and A. Ozioko (1997) Medicinal plant research in Nigeria: an approach for compliance with the Convention on Biological Diversity. *Diversity* 13(1): 29-33.
- King, S. R., T. J. Carlson and K. Moran (1996) Biological diversity, indigenous knowledge, drug discovery, and intellectual property rights. In: S. Brush and D. Stabinsky, Eds., *Valuing Local Knowledge: Indigenous People and Intellectual Property Rights*, pp: 167-185. Island Press.
- Simpson, R. D., R. A. Sedjo and J. W. Reid (1996) Valuing biodiversity for use in pharmaceutical research. *Journal of Political Economy* 104(1): 163-185.
- DiMasi, J. A., R. W. Hansen, H. G. Grabowsky and L. Lasagna (1991) Cost of innovation in the pharmaceutical industry. *Journal of Health Economics* 10: 107-142.

II) Principles of conservation biology.

1) **Definition of conservation biology**

Conservation biology is one of the fastest-growing fields of modern scientific research. It is an applied discipline that integrates principles of natural and social sciences with the objective of achieving the long-term persistence of biodiversity on Earth. The current global biodiversity crisis is the driving force behind the discipline's rapid growth, but its origins and practice are older. Formal recognition of conservation biology as an academic field dates back to the 1960s; since then, it has gradually acquired a character of its own which differentiates it from the many other disciplines it continues to borrow from, including: ecology, genetics, population biology, sociology, economics, and policy.

2) **Conservation biology as a crisis discipline**

Because conservation biology has grown in response to the extinction crisis, much of the attention of conservation biologists has focussed on dealing with problems of small, threatened populations. Genetics and population ecology have played a prominent role. Outline Caughley's "small population" and "declining populations" paradigms..

Restoration ecology, the cost of putting it back together.

Preventative conservation: the wave of the future?

3) **Using biogeographic and natural history data for planning wild species conservation**

Conceptual framework for using quantitative methods of conservation biology for large-scale (e.g. sub-national, national, regional) species conservation planning exercises. Three fundamental, consecutive questions provide structure to the process: 1) What to conserve?, 2) Where to conserve?, and 3) How to conserve?

The first question is answered using biological indicators, which help define the target of conservation action; for example: identify centers of endemism or areas of high diversity, monitor changes in habitat quality, or locate foci of human disturbance.

Once the target is established, the second question is approached using gap analysis in conjunction with algorithms for the optimal selection of nature reserve networks. This approach is aimed at maximizing the number of species included in protected area systems, while minimizing the amount of land needed to do so. Reserve selection algorithms.

The third question refers to the design of management plans either for single (or groups of) protected areas or individual (or groups of) species. An integration of the techniques of population viability analysis with the principles of adaptive management of natural resources allows for contrasting different management options, by weighing their benefits (e.g. reduced risk of extinction) against their costs (e.g. resources required to implement each option) over time.

References:

Bioindicators:

- Reid, W. V. (1998) Biodiversity hotspots. *Trends in Ecology and Evolution* 13(7): 275-280.
- Kremen, C., R. K. Colwell, T. L. Erwin, D. D. Murphy, R. F. Noss and M. A. Sanjayan (1993) Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* 7(4): 796-808.
- Pearson, D. L. and F. Cassola (1992) World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. *Conservation Biology* 6(3): 376-391.
- Rodríguez, J. P., D. L. Pearson and R. Barrera R. (1998) A test for the adequacy of bioindicator taxa: Are tiger beetles (Coleoptera: Cicindelidae) appropriate indicators for monitoring the degradation of tropical forests in Venezuela? *Biological Conservation* 83(1): 69-76.

Keystone and umbrella species:

- Simberloff, D. (1998) Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biological Conservation* 83(3): 247-257.

PVA:

- Possingham, H. P., D. B. Lindenmayer and T. W. Norton (1993) A framework for the improved management of threatened species based on population viability analysis (PVA). *Pacific Conservation Biology* 1: 39-45.

GAP analysis:

- Scott, J. M. and B. Csuti (1997) Gap analysis for biodiversity survey and maintenance. In: M. L. Reaka-Kudla, D. E. Wilson and E. O. Wilson, Eds., *Biodiversity II: Understanding and Protecting our Natural Resources*, pp: 321-340. Joseph Henry Press, Washington, D.C., U.S.A.

Reserve selection algorithms:

Csuti, B., S. Polasky, P. H. Williams, R. L. Pressey, J. D. Camm, M. Kershaw, A. R. Kiester, B. Downs, R. Hamilton, M. Huso and K. Sahr (1997) A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. *Biological Conservation* 80: 83-97.

III) In situ and ex situ approaches to the conservation of biodiversity.

1) Major threats to biodiversity

A few famous cases of extinct species: 1) the dodo, 2) passenger pigeon. Large population sizes are not necessarily enough.

Threatened species of the world, by taxonomic group.

Species' threats are not uniformly distributed, maps of 1) extinct species of the world, 2) hotspots of endangered species in the US.

Evolving threats for endangered species. Most extinct species due to overexploitation; most threatened species due to habitat destruction (Endangered Species Handbook).

Example from Venezuela to illustrate evolving threats.

Causes of threat in the US.

References:

Dobson, A. P., J. P. Rodríguez, W. M. Roberts and D. S. Wilcove (1997) Geographical distribution of endangered species in the United States. *Science* 275: 550-553.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips and E. Losos (1998) Quantifying threats to imperiled species in the United States. *BioScience* 48(8): 607-615.

2) Classifying endangered species

History of Red Data Books and red Lists. Evolution of endangered species classification systems. The 1994 IUCN Red List Criteria—assessing extinction risk. The difference between risk assessment and priority setting: national/regional conservation planning.

References:

Mace, G. M. (1995) Classification of threatened species and its role in conservation planning. In: J. H. Lawton and R. M. May, Eds., *Extinction Rates*, pp: 197-213. Oxford University Press.

3) What are we doing to conserve biodiversity?

Present definition of *in situ* and *ex situ* approaches (based on glossary in UNEP's *Global Biodiversity Assessment*). Emphasize that habitat conservation is the ultimate purpose.

Conservation not only limited to wild species. Brief introduction to germoplasm banks and botanical gardens. Value of domestic animal breeds.

4) Nature reserve design and management

Theory of island biogeography. Single large or several small (SLOSS) debate. Pros and cons of ecological corridors.

Ecotourism and charges for ecosystem services as mechanisms for funding protected areas; achieving self-sufficiency.

Nature reserves alone are not enough. Most protected areas are too small for long-term survival of large carnivores (Newmark's analysis of parks in the US and Tanzania). many species require habitat in private lands. Need to think more broadly—integrated large-scale management. Habitat Conservation Planning in the US.

References:

Wilcox, B. A. (1980) Insular ecology and conservation. In: M. E. Soulé and B. A. Wilcox, Eds., *Conservation Biology: an Evolutionary-ecological Perspective*, pp: 95-118. Sinauer Associates, Inc., Sunderland, Massachusetts, U.S.A.

Margules, C., A. J. Higgs and R. W. Rafe (1982) Modern biogeographic theory: are there any lessons for nature reserve design? *Biological Conservation* 24: 115-128.

Newmark, W. D. (1987) A land-bridge island perspective on mammalian extinctions in western North American parks. *Nature* 325: 430-432.

Simberloff, D., J. A. Farr, J. Cox and D. W. Mehlman (1992) Movement corridors: conservation bargains or poor investments? *Conservation Biology* 6(4): 493-504.

Aengst, P., J. Anderson, J. Chamberlin, C. Grunewald, S. Loucks, E. Wheatley and S. Yaffee (1997) Introduction to habitat conservation planning. *Endangered Species UPDATE* 14(7&8): 5-9.

5) Captive breeding for endangered species

Zoos and botanical gardens as a conservation tool. The evolution of zoos from collections of animals to conservation centers. Examples of species who have been saved by captive breeding. Problems with captive breeding: genetic, behavioral/social (e.g. adaptation to captivity), cost, lack of interinstitutional continuity and coordination. The value of captive breeding as an educational tool and for fundraising for wild population conservation.

References:

- Mench, J. A. and M. D. Kreger (1996) Ethical and welfare issues associated with keeping wild mammals in captivity. In: D. G. Kleiman, M. E. Allen, K. V. Thompson, S. Lumpkin and H. Harris, Eds., *Wild Mammals in Captivity: Principles and Techniques*, pp: 5-15. University of Chicago Press, Chicago, USA.
- Wiese, R. J. and M. Hutchins (1994) The role of zoos and aquariums in amphibian and reptilian conservation. In: J. B. Murphy, K. Adler and J. T. Collins, Eds., *Captive Management and Conservation of Amphibians and Reptiles*, pp: 37-45. Society for the Study of Amphibians and Reptiles, Ithaca, New York, USA.
- Snyder, N. F. R., S. R. Derrickson, S. R. Beissinger, J. W. Wiley, T. B. Smith, W. D. Toone and B. Miller (1996) Limitations of captive breeding in endangered species recovery. *Conservation Biology* 10(2): 338-348.

6) Reintroductions and translocations

When are reintroductions appropriate? Reintroductions as the last front in conservation action. The Margarita parrot: an example of a successful reintroduction; cost of each parrot.

References:

- Kleiman, D. G. (1996) Reintroduction Programs. In: D. G. Kleiman, M. E. Allen, K. V. Thompson, S. Lumpkin and H. Harris, Eds., *Wild Mammals in Captivity: Principles and Techniques*, pp: 297-305. University of Chicago Press, Chicago, USA.
- Sanz, V. and A. Grajal (1998) Successful reintroduction of captive-raised yellow-shouldered amazon parrots on Margarita island, Venezuela. *Conservation Biology* 12(2): 430-441.
- Griffith, B., J. M. Scott, J. W. Carpenter and C. Reed (1989) Translocations as a species conservation tool: status and strategy. *Science* 245: 477-480.

7) Additional bibliography

1) General reference

UNEP (1995) *Global Biodiversity Assessment*. United Nations Environment Programme, Cambridge University Press, Cambridge, UK.

WCMC (1992) *Global Biodiversity: Status of the Earth's Living Resources*. World Conservation Monitoring Centre, Chapman and Hall, London, UK.

Worldwatch Institute's *State of the World* annual reports

World Resources Institute's *World Resources* annual reports

2) Some recent textbooks

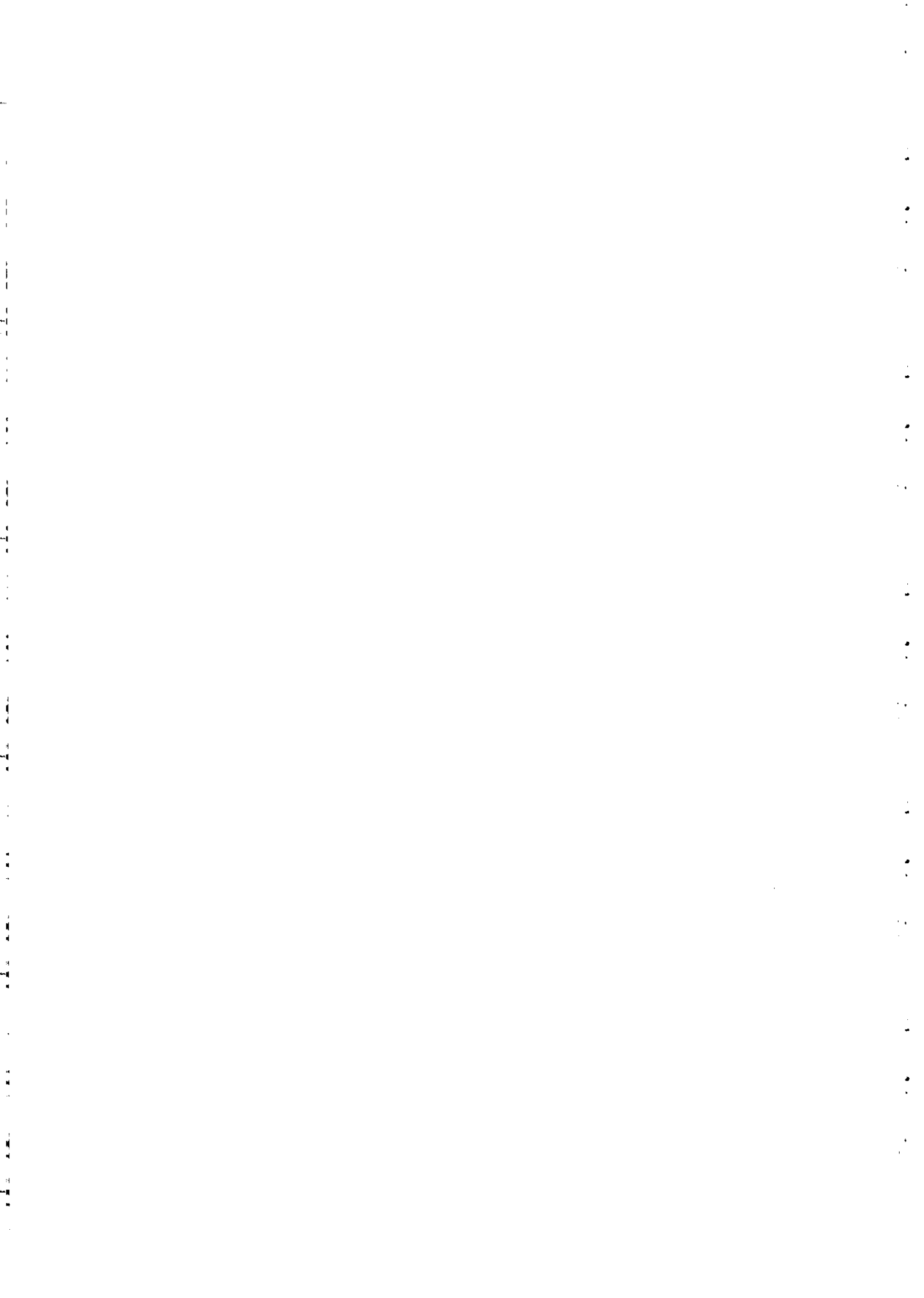
Caughley, G. and A. Gunn (1996) *Conservation Biology in Theory and Practice*. Blackwell Science, Cambridge, Massachusetts, USA.

Dobson, A. P. (1996) *Conservation and Biodiversity*. Scientific American Library, New York, USA.

Hunter, M. L. (1996) *Fundamentals of conservation biology*. Blackwell Science, Cambridge, Massachusetts, USA.

Meffe, G. K. and C. R. Carroll, Eds. (1997) *Principles of Conservation Biology*. Principles of Conservation Biology. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Primack, R. B. (1995) *A Primer of Conservation Biology*. Sinauer Associates Inc., Sunderland, Massachusetts, U.S.A.



Biodiversity: measurement and estimation

Preface

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CONTENTS

	PAGE
1. Introduction	5
2. What is 'biodiversity'?	6
3. Is biodiversity just the number of species in an area?	7
4. If biodiversity is more than the number of species how can it be measured?	8
(a) Taxic measures	8
(b) Molecular measures	8
(c) Phylogenetic measures	8
5. Are all species of equal weight?	9
6. Should biodiversity measures include infraspecific genetic variance?	9
7. Do some species contribute more than others to the biodiversity of an area?	9
8. Are there useful indicators of areas where biodiversity is high?	10
9. Can the extent of biodiversity in taxonomic groups be estimated by extrapolation?	11
10. Conclusions	11
References	11

SUMMARY

In introducing a series of 11 papers on the measurement and estimation of biodiversity, eight crucial questions are posed: What is 'biodiversity'? Is biodiversity just the number of species in an area? If biodiversity is more than the number of species how can it be measured? Are all species of equal weight? Should biodiversity measures include infraspecific genetic variance? Do some species contribute more than others to the biodiversity of an area? Are there useful indicators of areas where biodiversity is high? And can the extent of biodiversity in taxonomic groups be estimated by extrapolation? In addition, the modern concept of biological diversity is attributed to Elliot R. Norse and his colleagues.

1. INTRODUCTION

Within six years the word 'biodiversity' has exploded into the vocabulary of the popular press, governmental and intergovernmental reports, scientific papers and meetings. In the scientific literature the growth in usage of the term has been dramatic (figure 1).

It seems reasonable to ask of a word that is so widely used, just what is it supposed to mean. Is it just a new linguistic bottle for the wine of old ideas – a changed fashion label designed to attract funding – or does it refer to new and fundamental questions in science? Most especially, it seems sensible to ask whether 'biodiversity' is a property that can be measured and if so what is the most appropriate form that such measurement should take.

We may wish to ask such questions as: 'Does biodiversity confer stability?'; 'Does biodiversity confer productivity?'; 'Does biodiversity reflect sustain-

ability?'; 'Does biodiversity reflect the evolutionary time elapsed without major disturbance?'; alternatively, 'Does biodiversity reflect the frequency of major disturbance in ecological or evolutionary history?'.* We might reasonably expect to have some measure of this thing that we call biodiversity that we might use in a graphic plot or statistical analysis designed to answer these questions. In particular, we may wish to ask whether one species (or population, or community) is more or less diverse than another. Until we have decided how to measure 'biodiversity' we cannot begin to mobilize serious science into answering these questions and others posed in the 'research

* We might have mentioned 'ecosystem function' among those features that might be influenced by biodiversity. However, one of us finds the notion that an ecosystem might 'function' (verb) or 'have a function' (substantive) so incongruous that he has relegated the mention to this footnote (where it is even more likely to be noticed).

agenda for biodiversity' Solbrig 1991. But, 'The need for increased objectivity through measurement is not merely a scientific quest but can contribute to issues of topical concern at all levels of society' (Lovejoy, this volume).

In particular we need such a measure as part of the justification for spending limited financial resources on protecting, conserving, studying or exploring some communities and so denying the resources to do the same to others.

Of course, the collection of papers in this volume may reveal that the word 'biodiversity' means quite different things to different people. This would be a pity but better to be revealed and acknowledged than allowed to cause confusion.

This series of papers has been commissioned to encourage the scientific analysis of biodiversity, and particularly to force the question 'How do we best measure organismal biodiversity?' We are aware that the answer might simply be 'By counting the number of species', but it is clear from various papers contributed to this theme volume that there are deeper issues involved. There is also plenty of scope for controversy.

2. WHAT IS 'BIODIVERSITY' ?

'Biological diversity' has a long history of usage in a variety of contexts, but the start of its rise in the current senses can be traced to three publications which appeared in 1980: Lovejoy (1980a,b) did not provide a formal definition but used it essentially in the sense of the number of species present, and Norse & McManus (1980) employed it to include 'two related concepts: genetic diversity and ecological diversity'. The latter authors equated ecological diversity with species richness, 'the number of species in a community of organisms'. There were various usages in the United States in the early 1980s, mainly in connection with conferences with which Elliot Norse or his colleagues were involved, most notably the *U.S. Strategy Conference on Biological Diversity* in November 1981 (U.S. Department of State 1982). However, it was Norse *et al.* (1986, p. 2) who expanded this usage to refer unequivocally to biological diversity at three levels: genetic (within species), species (species numbers) and ecological (community) diversity.

The contracted form 'biodiversity' was evidently coined by Walter G. Rosen in 1985 for the first planning conference of what was to be a key meeting, the 'National Forum on BioDiversity', which convened in Washington, D.C. in September 1986. The proceedings of that forum, edited by Wilson (1988a) under the title *Biodiversity*, launched the word into general use. The term was defined only in as far as it 'represents, as well as any term can, the vast array of topics and perspectives covered during the Washington forum' Wilson 1988b, p. vi). Norse's seminal papers were not cited in any of the 57 contributions to that volume. The word 'biodiversity' first appears in the *Biological Abstracts* 'biosis' database in 1988 with four references, and by the end of April 1994 that number had escalated to 888 (figure 1).

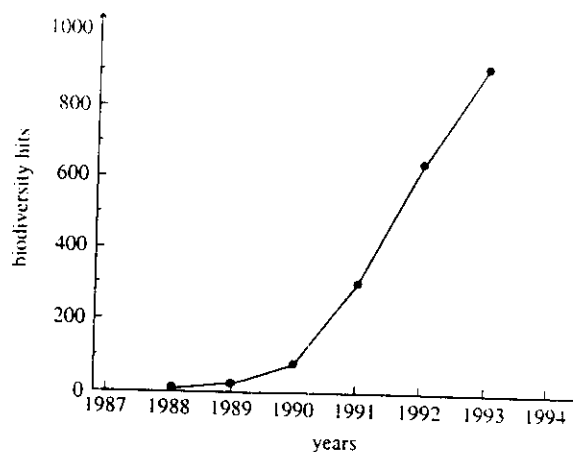


Figure 1. Growth of the number of hits for the term 'biodiversity' in the scientific literature as catalogued in BIOSIS File 5 (1969 onwards). This presentation is based on accumulating the number of hits within each year; the total of 921 at the end of April 1994 is an overestimate due to double-counting of citations with more than one year date; the actual number of single titles in the period was 888.

For practical purposes, 'biodiversity' can be considered as synonymous with 'biological diversity' as defined by Norse *et al.* (1986). This is reinforced by the official definition in Article 2 of the 'Convention on Biological Diversity', signed by 156 nations and the European Community at the United Nations Conference on the Environment and Development, 'The Earth Summit' in 1992 which closely mirrors the concept of Norse *et al.* (United Nations Environment Programme 1992, p. 27):

'"Biological diversity" means the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic systems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems [*sic*].'

These three levels are all considered in the *Global Biodiversity Assessment* currently being prepared by the United Nations Environment Programme with funding through the Global Environment Facility (GEF) administered by the United Nations Development Programme.

It is therefore essential that scientists, who use either the expanded or the contracted term in a technical sense that does not embrace all three levels, specify which level is intended. We therefore propose the use of the adjectives 'genetic', 'organismal', and 'ecological'. 'Organismal' is preferred to 'species' so as to embrace taxonomic categories above species rank. Eldredge (1992) used 'genealogical', 'phenotypic', and 'ecological' in a parallel manner, but we prefer 'organismal' to 'phenotypic' as its meaning is more transparent to a non-specialist. The usage of 'organismal' is also consistent with the need identified by Norse (1993) to view biological diversity at higher taxonomic levels.

We are unhappy with references to 'ecosystem' diversity and prefer 'community' or 'ecological'

diversity. Tansley (1935) introduced the word 'ecosystem' to refer to a community of organisms in the context of and including their physical environment. Clearly the physical environment does not have a biodiversity. Reference to 'the biodiversity of an ecosystem' devalues two useful concepts in the same phrase.

3. IS BIODIVERSITY JUST THE NUMBER OF SPECIES IN AN AREA?

Species can be counted and the number of species present at a site might seem to be a quantitative measure of its biodiversity and allow comparison with other sites. But this assumes that all species at a site, within and across systematic groups, contribute equally to its biodiversity.

This is clearly questionable as illustrated by the following hypothetical sites in all of which there are just two species present. One of the species present is a species of *Ranunculus* and the other is:

1. Another species of *Ranunculus* from the same section of the genus.
2. Another species of *Ranunculus* from a different section of the genus.
3. A species from a different genus in the same family (*Ranunculaceae*).
4. A species from a different family within the same order as the *Ranunculaceae*.
5. A species from a different family and in a different order (e.g. a grass).
6. A rabbit.
7. A fungus of the genus *Agaricus*.
8. A protozoan of the genus *Amoeba*.
9. An archaebacterium.
10. A eubacterium of the genus *Pseudomonas*.

This simple hypothetical series could easily be expanded, but is sufficient to make the point that any measure of biodiversity that described all of these sites as equal would be peculiarly uninformative. A measure of the biodiversity of a site ought ideally to say something about how different the inhabitants

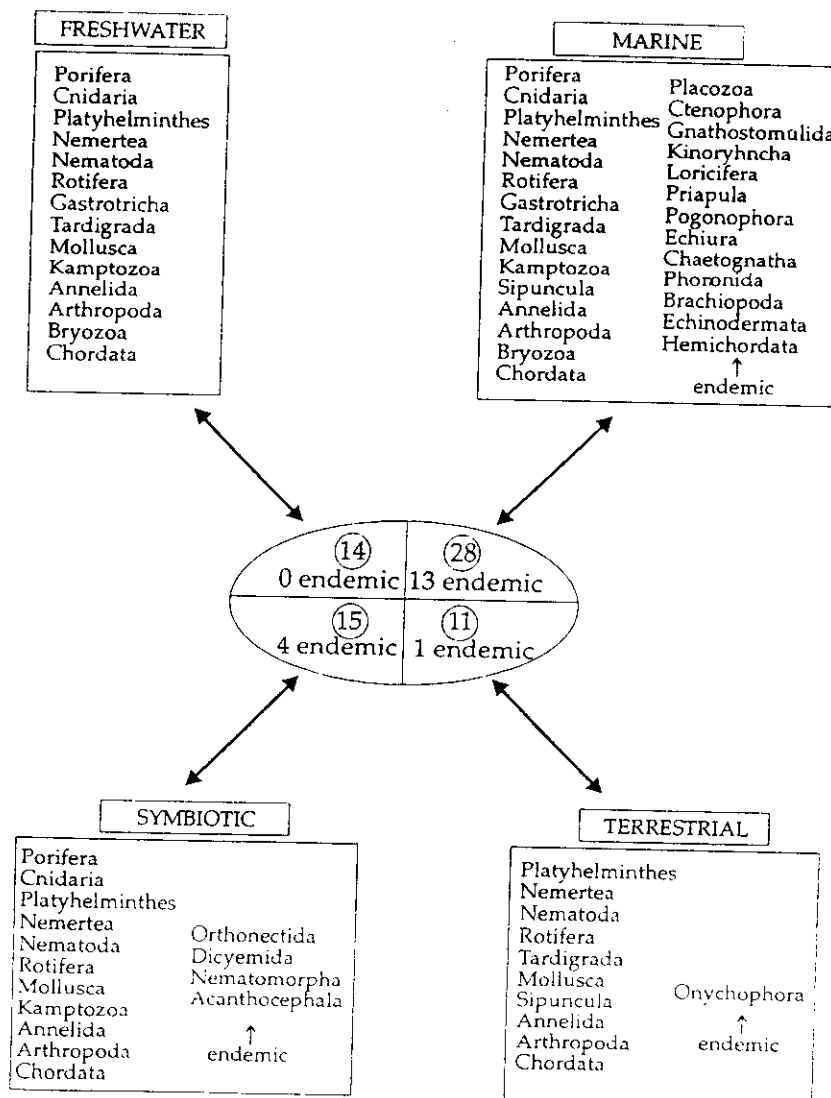


Figure 2. The distribution of phyla in the Animalia by habitat. Adapted from Grassle *et al.* (1991).

are from each other. A measure that reflects the increasing phylogenetic divergence of the organisms present at a site in the series progressing from case 1 to case (10) might be one promising possibility.

4. IF BIODIVERSITY IS MORE THAN THE NUMBER OF SPECIES HOW CAN IT BE MEASURED?

Three approaches are considered by contributors to this collection of papers:

(a) *Taxic measures*

Does the number of higher taxa, for example phyla, orders and families, provide a more appropriate measure of the biodiversity in a site than the number of species? In marine environments the number of phyla and higher taxa is substantially greater than on land (May, this volume); indeed 13 animal phyla are known only from marine environments whereas only one is exclusively terrestrial (Grassle *et al.* 1991; figure 2). For those concerned with the allocation of resources to the global conservation of life on Earth this statistic at least raises the question of whether the present balance of emphasis on terrestrial systems needs rethinking.

If the aim of conservationists is simply to conserve the maximum number of species we may ask whether the number of higher taxa present is a convenient quick estimator of the number of species in an area. Prance (this volume) finds that in the neotropics only 6.4% of the species belong to the approximately 40 exclusively or almost exclusively neotropical families. He argues that we need to focus our attention at the species level when assessing biodiversity for conservation planning. However, Williams *et al.* (1994) found a very close relationship between the number of families present in 0.1 ha plots and the number of species present (least squares regression $r^2 = 0.913$, $p < 0.001$). These authors point out that complete counts of organisms are impractical at present and that indirect solutions are needed that are both cheap and quick. They used data from families of seed plants to make world-wide maps of the regional distribution of family richness and endemism. The peak richness of families occurs in Cambodia which (if sampled first) contributes 53.67% of the total number of families. Mexico (Oaxaca), China (southern Sichuan) and Madagascar (north) add a further 11.65%, 5.82% and 4.81% respectively. The areas with peak richness of endemics are strikingly different with New Caledonia, south-west China and northern Australia contributing most.

If we planned to conserve those plant communities that could provide the richest diversity of pharmaceutical compounds, what measure of biodiversity would be the best guide? Either family richness or endemic richness might be good candidates but species richness itself could be dangerously misleading. The 242 species of *Hieracium* and 234 species of *Taraxacum* listed in the Norwegian flora (Lid 1952) are better indicators of taxonomic traditions than of

the scale of natural biological diversity. Pearson (this volume) considers the problems of using indicator taxa in the assessment of biodiversity.

In considering measurements through geological time, Niklas & Tiffney (this volume) concluded that the taxonomic level which yields statistically independent observations of sampling remained unresolved for vascular plants. They make the point that, as new evolutionarily successful characters arise within populations or species, they form the basis of radiations as the characters are incorporated in groups of increasing size and ultimately of higher rank. The community biodiversity that we are able to examine at any time may therefore contain differences between organisms that are comparable in magnitude but expressed at quite different systematic ranks. There is a frightening spectre that in some communities the relevant and comparable measure of biodiversity may be best expressed in some groups by the number of species, but in others by the number of genera or even of families.

(b) *Molecular measures*

An attractive possibility for the measurement of biodiversity is to use divergences in molecular characters, especially the percentage of either nucleic acid homology or base sequence differences. Unlike higher taxa which may be based on characters which are not necessarily directly comparable, the DNA and RNA found in all living cells can provide a basis on which to make direct comparisons between diverse organisms. There is a sense in which the biodiversity of a community is expressed as the sum of the variety of genetic information coded within the genotypes of the inhabitants. A biodiversity calculus could be envisaged for which we ask of the various species (and individuals) in a community how many new base sequences they each contribute to the genetic vocabulary of the whole. Embley *et al.* (this volume) demonstrate that the application of molecular technology to the study of biodiversity can destroy treasured icons. Some prokaryotic groups have proved so diverse at the molecular level, in comparison with eukaryotes, that new taxonomic hierarchies above the level of kingdom (e.g. 'domains') have had to be recognized properly to reflect the extent of their divergence.

(c) *Phylogenetic measures*

Cladistics can be used to give an objective measure of taxonomic distance or 'independent evolutionary history' (IEH) using methods pioneered by Vane-Wright *et al.* (1991). The technique has considerable promise (May, this volume), and is examined in depth by Faith (this volume). The approach provides information that is of especial value for the conservation of target groups (Vane-Wright *et al.* 1991) and in selecting areas appropriate for their conservation (Pressey *et al.* 1993) but it is difficult to see how sufficient phylogenetic data could be generated in the near future for this method to be used to compare the

diversity of whole countries. In the most speciose groups such as fungi and insects in which only 5–10% of the species on Earth may have been described, most of the species in an area will lack data suitable for phylogenetic analysis. Rather than progressing up from bumble-bees to Hymenoptera to Insecta and so on, an ideal index of biodiversity ought perhaps to be obtained by proceeding in the opposite direction, asking first the biggest question about diversity, 'How many kingdoms are represented on a site?', then 'How many phyla are represented per kingdom?', 'How many orders per phylum?', and so on. There is sufficient logic in this suggestion to elicit a wringing of hands and even apoplexy from those who might have to apply it.

5. ARE ALL SPECIES OF EQUAL WEIGHT?

The varying species concepts in different groups, and indeed often within a single group, are a major cause of uncertainty intrinsic to all aspects of biodiversity research that use the species as the 'standard' unit. If the unit of measurement is itself variable, conclusions based on it have necessarily to be treated with considerable caution. This applies equally to discussions of the relationship between biodiversity and community behaviour (Baskin 1994), to theoretical models (Lovelock 1992), and to indicators developed for policy makers (Reid *et al.* 1993).

The 'biological species' has been viewed as a comparable entity across groups as diverse as insects and fungi (Claridge & Boddy 1994), but how do such entities compare when examined by molecular or phylogenetic methods? How can biological species be recognized with confidence in the majority of organisms which are only known from preserved material? And how can a biological species concept be applied in groups that never undergo sexual reproduction or parallel exchanges of genetic material?

The species concept in bacteria is especially conservative at the molecular level in comparison with most other groups of organisms. Different strains placed within the single bacterial species *Legionella pneumophila* have DNA hybridization homologies as different as those characteristic of the genetic distance between mammals and fishes (May, this volume). Bacterial strains with 70% or more DNA–DNA relatedness are generally treated as belonging to the same species (O'Donnell *et al.*, this volume); on that basis, rather few species would be accepted in some macroorganism groups, and hominids with 98% homology would certainly be regarded as conspecific! We also wonder how many (or rather how few) 'species' of beetles could be sustained on the grounds that they possess less than 70% DNA homology! However, in DNA homology studies in particular, should not some allowance be made for the size of the genomes being compared?

Caution is clearly required when molecular data are used at or near the species level because of the discrepancies between DNA–DNA homology and rRNA sequence data for the same taxa (O'Donnell

et al., this volume). It would be rash to base far-reaching taxonomic decisions on a single type of molecular data at this time.

There is an urgent need for biologists working in different disciplines to move towards more comparable species concepts. Nowhere is this more important than in the treatment of apomictic 'species' of flowering plants in genera such as *Alchemilla*, *Hieracium*, *Taraxacum* and *Sorbus* which can grossly inflate measures of plant species richness in an area.

6. SHOULD BIODIVERSITY MEASURES INCLUDE INFRASPECIFIC GENETIC VARIANCE?

The genetic variation within species can be of major importance in identifying priorities for the conservation of crop plants and their wild relatives. These same measures can be useful in trying to judge which species have a sufficiently wide vocabulary of genetic information to allow them to respond to natural selection and evolve if the environment changes rather than become extinct.

Templeton (this volume) considers the possible ways of measuring genetic variation within species. These include the percentage of polymorphic loci, the number of alleles, heterozygosity, the average number of nucleotide differences, the number of segregating sites, and the construction of an allele or haplotype tree. Even within mammals the use of these measures shows that it is difficult to generalize about the size of the populations that might be required to maintain the genetic variation of the species.

Although it would clearly be desirable to include some measure of infraspecific biodiversity in the overall assessment of the biodiversity of a particular site, how this could be achieved for more than a handful of species in a locality at a time eludes us. However, the very act of thinking about the problem makes it clear that the concept of 'biodiversity' can mean all things to all people. To most geneticists it will seem absurd that any measure of 'biodiversity' should exclude infraspecific variance: the very stuff of the evolutionary process by which biodiversity is made.

7. DO SOME SPECIES CONTRIBUTE MORE THAN OTHERS TO THE BIODIVERSITY OF AN AREA?

The biological diversity of an area is much more than the number of species present, whether or not the species richness is discounted by measures of phylogenetic distance or relatedness. For an ecologist other dimensions of biodiversity are represented by the number of trophic levels present, the number of guilds, the variety of life cycles, and the diversity of biological resources. The presence of certain species makes a great contribution to overall species richness because, like the oak in Great Britain (Morris & Perring 1974), they provide specialist resources for a multiplicity of other species (nesting sites, gall-wasps, lepidoptera, mycorrhizal fungi, bark and leaf-

inhabiting fungi, pests and pathogens, bryophytes, lichens, other epiphytes, etc.). Trees, in general, contribute a wider range of biological resources to a site than annual or herbaceous plants. However, the role of organisms with less obvious 'keystone' roles, including pollinating insects, mutualistic symbionts and population-regulating pathogens and biocontrol agents can also have effects on the biodiversity of a site (Hawksworth *et al.* 1994; LaSalle & Gauld 1993).

Many individual species of marginal aquatic flowering plants contribute a diversity of leaf forms to a community. Batrachian species of *Ranunculus*, *Sagittaria sagittifolia*, and *Cabomba caroliniana*, bear distinct submerged and floating forms of leaf and a single species occupies two niches in a community that would commonly be occupied by two monomorphic species. In a similar vein, animal species with complex life-cycles contribute extra biological diversity to a site. Frogs, toads and other amphibians contribute to the species richness of a site as tadpoles in aquatic and as adults in terrestrial patches. In a sense each of these species contributes two doses of biological diversity to a community. Lepidoptera are also obvious examples of animal species that contribute more to the ecological diversity of a community than just a count of the species numbers would imply.

One biological measure of the diversity of a community must be the way in which it is sampled by different organisms that live in it (a worm's-, bird's-, or caterpillar's-eye view). During a single day a wood pigeon may experience the full above-soil biodiversity of a forest (fine-grained sampling) whereas the same forest, sampled by a caterpillar is experienced as the 'biomonotony' of a single leaf (coarse-grained sampling). The use of the concept of grain to describe an organism's eye view of the diversity of an environment is due to Robert MacArthur (e.g. MacArthur & Connell 1966). Even if we confine our measure of biodiversity to species richness and forget any discounting for differences in phylogenetic distances or ecological contribution there remains the fact that, at the 'grain' of community diversity sampled by us, some of the various species present in a community are abundant and others are very rare. This issue is especially acute for microbial groups; in most instances the largest numbers of individuals at a site will be the microorganisms which are not only unseen but often also unculturable (Embley *et al.*, this volume; O'Donnell *et al.*, this volume).

'Equitability' is therefore clearly an element of 'biodiversity' and is one aspect that has been built into formal mathematical indices, for example the Shannon Diversity Index and Simpson's Index that are defined and illustrated in ecological texts (e.g. Begon *et al.* 1990) e.g. Simpson's Index

$$D = \frac{1}{\sum_{i=1}^s p_i^2}$$

which is calculated by determining, for each species, the proportion of individuals or biomass that it contributes to the total in the sample, i.e. the

proportion is p_i . For the i th species where s is the total number of species in the community (i.e. its richness). The index suffers for some purposes because it is possible for a species-rich but inequitable community to have a lower index than one that is less species-rich but highly equitable.

Such an index, although it may be useful for a particular group (e.g. all vascular plants or all insect species at a site) is difficult to apply and perhaps largely meaningless if it were to be applied to the mixture of systematically diverse groups that forms most natural communities.

8. ARE THERE USEFUL INDICATORS OF AREAS WHERE BIODIVERSITY IS HIGH?

Although much is made of the need to focus nature conservation on areas of high biological diversity, choices are usually made on quite different grounds. Particular taxonomic groups appeal to the public and their conservation attracts political and financial support. The risk of losing a furry or feathery animal or a plant with appealing flowers will presumably continue to dominate most judgements about nature conservation rather than any formally considered scientific measures of biodiversity. This will certainly continue to be the case so long as science fails to develop appropriate measures for more rational (less emotional) decisions.

Ideally, comprehensive biological inventories of sites (ATBIS, see below), will be needed if full quantitative measures of biodiversity are to be used in making conservation decisions. However, these are unlikely to be obtained from more than a handful of sites in the foreseeable future. We need therefore to look for simpler yet objective ways of predicting where high biodiversity will occur. Are some taxa particularly good indicators of community biodiversity? Might it be that, by chance, those mammals, birds and plants (such as orchids) that appeal so strongly to the lover of wild-life happen to live in (and are therefore good predictors of) areas of particularly high biodiversity? Or are there other often unstudied yet easily observed groups such as the larger lichens that have the most potential in this regard? Pearson (this volume) considers the factors that could be used in selecting appropriate indicator taxa and Hammond (this volume) assesses the practical steps that can be taken to estimate biodiversity in the most speciose groups.

The most daunting problems arise in making any measure of biodiversity in the soil (O'Donnell *et al.*, this volume) where there may be more than 10^9 microorganisms per gram of soil, and in the sea where microscopic algae may have average densities of 10^6 cells per litre (Andersen 1992) and a 1 cm marine core may contain 4×10^{10} bacterial cells (Embley *et al.*, this volume).

Reid *et al.* (1993) discuss biodiversity indicators that may be of value to policy makers in establishing conservation priorities, but these have to be seen against the backcloth of questions raised here. The indicators so far proposed may be of value in the context of particular specified groups (e.g. wild plants

and their relatives, but are unlikely to reflect the total biodiversity in an area.

9. CAN THE EXTENT OF BIODIVERSITY IN TAXONOMIC GROUPS OR COMMUNITIES BE ESTIMATED BY EXTRAPOLATION?

A major challenge of biodiversity science is to develop firmer estimates of species numbers. May (this volume) considers the conceptual problems in current approaches to estimating the total numbers of species in different groups. The highest degree of probability exists where different approaches lead to broadly similar numbers, but insufficient data sets, especially from tropical and marine habitats are a major hindrance to progress in the development of protocols.

Theoretical aspects of the use of extrapolation to measure species richness are critically examined by Colwell & Coddington (this volume) with particular reference to the use of species accumulation curves, parametric models of relative abundance, and non-parametric methods. They also explore the problem of estimating complementarity from samples and propose a measure of this.

The companion contribution of Hammond (this volume) focuses on the practical aspects of the estimation of species diversity in speciose groups, and is based on extensive data sets from the U.K. and Indonesia. He concludes that simple ratios of species from taxon to taxon, focal group to inclusive group, site to site, sample to inventory, and across spatial scales provide the firmest base for extrapolation. The choice of both focal groups for extrapolative purposes and sampling methods to obtain reliable comparable data sets is critical, and there needs to be an awareness of, for example, the interplay between patchy distributions and sample dimensions.

A major stimulus to the improvement of the scientific base of extrapolative approaches would be the realization of Janzen's (1993) proposal to establish a series of sites which have an All-Taxon Biodiversity Inventory (ATBI). The efficacy of sampling and extrapolative procedures could be rigorously tested against known biota at such sites. The lack of a comprehensive inventory of all groups of the biota for any site in the world, even in the U.K., is a major obstacle to developing extrapolative methods. Yet it is just such methods that will have to become the norm in site assessments because of the impracticability of routinely attempting comprehensive inventories.

10. CONCLUSIONS

It will be evident from the questions we have raised and our comments on them, and also from many of the contributions to this collection of papers, that it is easier to identify the issues than to provide scientifically sound and testable answers. By openly posing basal questions, however, the challenges that need to be addressed are also brought firmly onto the scientific agenda. The issues identified need now to be confronted if the scientific foundation of the study of organismal biodiversity is to proceed on a firm basis.

There are two significant obstacles internationally to progress in the scientific study of biodiversity: (i) the inadequate size and inappropriate location of the workforce with the appropriate biosystematic skills; and (ii) the state and location of the collections and literature database (May, this volume). The mismatch between the magnitude and priority of the task and the resources available has to be addressed at the highest international levels (Janzen 1993).

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5. SPECIES DIVERSITY: AN INTRODUCTION

A BRIEF HISTORY OF DIVERSITY

Knowledge of the history of diversity through geological time is based on analysis of the fossil record. Because the fossil record gives only a very incomplete and highly biased view of the past history of life on earth, the reconstruction of that history has been, and continues to be, the subject of great debate. It is generally accepted that the fossil record can give a reasonable insight into past diversity in terms of taxonomic richness, particularly at higher taxonomic levels. However, it is far more difficult to derive other, more ecologically based, measures of diversity from it, as these require the reconstruction of palaeoenvironments, a far more contentious exercise than palaeotaxonomy.

While detailed patterns of taxonomic richness through the earth's history remain debatable, the overall outline is generally accepted. There are believed to have been relatively few species in total during the Palaeozoic and early Mesozoic; since then, that is for the past hundred million years, diversity has increased markedly. This recent diversification has passed through one major extinction event, at the Cretaceous-Tertiary boundary, and probably two minor events since then (see Chapter 16). Apart from these, the diversification appears to have continued more or less unabated, with the world apparently reaching its highest ever level of species richness during the Pliocene and Pleistocene, when climatic change and the advent of organised human activity finally halted the process. Significantly, however, diversity at higher taxonomic levels does not conform with this pattern, as evinced by the far higher number of animal phyla present in the early Cambrian than today (see below).

The early history of Life - the Precambrian

Recent consensus suggests that cellular life on the planet (in the form of procaryotes, at least some of which were probably very similar to living cyanobacteria) originated sometime between 3,900 and 3,400 million years ago (Mya). The origin of the earliest eucaryotes has proved difficult to establish, but it is generally accepted that the Precambrian microfossils known as 'acritarchs', which are recorded as far back as 1400 Mya, are almost certainly the cysts of marine algae and the earliest known eucaryotes. If this analysis is correct, then life on earth consisted only of procaryotes for at least 2,000 million years, or well over half its history. There is sufficient morphological variation in the fossil remains to permit some analysis of changes in diversity of these presumed early procaryotes in the late Proterozoic era. Vidal and Knoll (1983) have hypothesised a gradual increase in diversity from 1400 Mya to 750 Mya, when there was a peak of around 30 taxa in the fossil record, followed almost immediately by a sharp drop to around 10 taxa, possibly owing to a period of glaciation. After this there is an exponential increase in diversity, corresponding with the start of the Phanerozoic era.

The early Phanerozoic

For many years it was assumed that metazoans (multicellular organisms with internal organs) originated in

the Cambrian era at the base of the Phanerozoic. This is now known not to be the case, as a wide range of fossil metazoans is now known from well before this time, including recognisable arthropods and possibly echinoderms. Most fossils from this time, however, appear completely unrelated to extant forms, and consist mainly of enigmatic frond- and disc-shaped soft-bodied animals: the so-called Ediacaran fauna.

The lower Cambrian marks a dramatic change from this early fauna, with the sudden appearance in the fossil record of a wide range of metazoans, many with calcareous skeletons. It is generally accepted that this represents a genuine explosion of diversity which took place over only a few million years, and is not an artefact of the fossil record. The lower Cambrian thus represents the most important period of high-level diversification in the history of animal life on earth. Very many phyla may have existed at this time, no more than five of which have origins traceable to before the Cambrian-Precambrian boundary. These include every well-skeletalised animal phylum living today (with the possible exception of the Bryozoa), indicating that virtually no new animal phyla have appeared during the many subsequent evolutionary radiations. Perhaps most significantly, no new animal phyla appeared with the colonisation of land, some 50-100 million years after the Cambrian radiation.

The Cambrian appears to have represented not only a peak of diversification but perhaps also a peak of higher order taxonomic diversity, as suggested by the presence of many more animal phyla than the 35 or so now extant.

Changes in diversity of marine animal taxa through the Phanerozoic

Although the number of phyla has decreased markedly since the Cambrian, diversity at all lower taxonomic levels has either increased overall or in a few cases remained more or less level.

The number of orders (of marine animals) present in the fossil record climbed steadily through the Cambrian and Ordovician, levelling off towards the end of the Ordovician to a figure of between 125 and 140, which has been maintained throughout the Phanerozoic.

The diversity of families represented in the fossil record shows a similar pattern of increase through the Cambrian and Ordovician, levelling off at around 500, a figure which was maintained until the late Permian mass-extinction (see Chapter 16). This extinction event resulted in the loss of around 300 families; subsequent to this, family diversity has increased to the modern level, with a number of temporary reversals in the form of the series of extinction events outlined in Chapter 16.

The trend in number of species in the fossil record is even more extreme. From the early Cambrian until the mid-Cretaceous, the number of marine species remained low; since then, that is in the past 100 million years, it has probably increased by a factor of 10.

Diversity patterns in terrestrial animals

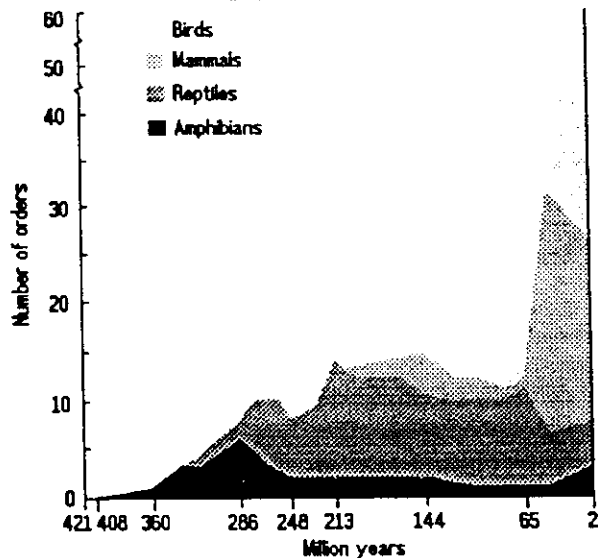
Colonisation of land by animals has occurred many times; although the oldest body fossils of terrestrial animals date from the early Devonian, it is generally accepted that the primary period of land invasion by animals was the Silurian.

The overwhelming number of described extant species of terrestrial animals are insects and arachnids. The fossil record for both these groups is generally scanty.

Some attempt has been made, however, to chart changes in insect diversity at the generic level. Insects first appear in the fossil record in the Carboniferous. The number of genera then increased through much of the Palaeozoic and first part of the Mesozoic, interrupted by a sharp drop coinciding with the late Permian mass extinction, and then levelling off during the late Triassic. Diversity then doubled during the Cenozoic or Tertiary, coincident with the radiation of the angiosperms.

The fossil record of terrestrial vertebrates is much better, particularly that of tetrapods. The bird record is much less substantial than that for other groups, probably because their light skeletons have been less frequently preserved. Terrestrial vertebrates first appear in the fossil record in the late Devonian. Diversity remained relatively low during the Palaeozoic, with around 50 families, and actually declined overall during the early Mesozoic. From the mid-Cretaceous the number of families started to increase rapidly, reaching a Recent peak of around 340. Diversity of genera follows this overall pattern in a more exaggerated form. These trends are shown in Fig. 5.1.

Figure 5.1 Fossil diversity: terrestrial vertebrates



Source: Adapted from Signor, P.W. 1990. The geological history of diversity. *Annual Review of Ecology and Systematics* 21.
 Note: Diversity is here measured in terms of number of taxonomic orders present.

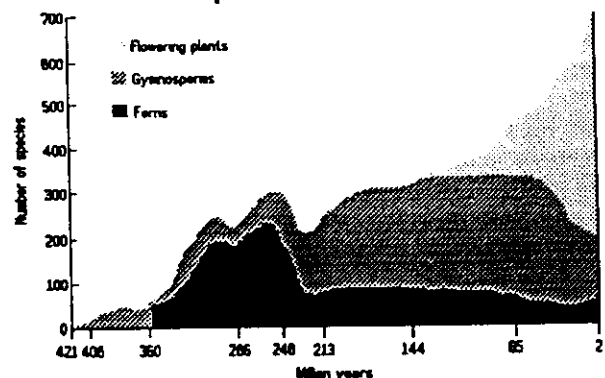
Diversity patterns in vascular plants

It is generally accepted that vascular terrestrial plants first

arose in the Silurian, although some palaeobotanists argue for a Late Ordovician origin. Diversity increased during the Silurian, and then more rapidly during the Devonian, owing to the first appearance of seed-bearing plants, leading to a peak of over 40 genera during the late Devonian. Diversity then declined slightly, but started to increase markedly during the Carboniferous, with at least 200 species recorded by the mid Carboniferous. Following this, diversity increased only slowly until the end of the Permian. There was a minor decrease in diversity at the end of the Permian, coinciding with or preceding the mass extinction of animal species, followed by a rapid rebound to previous levels. Diversity then continued increasing slowly, reaching around 250 species in the early Cretaceous. Starting at the mid-Cretaceous, diversity began increasing at an accelerating pace.

This overall pattern masks important changes with time in the composition of the flora, most notably in the relative importance of the three main groups of tracheophytes: the pteridophytes, gymnosperms and angiosperms. The Silurian and early Devonian are marked by a radiation of primitive pteridophytes. During the Carboniferous, more advanced pteridophytes and gymnosperms developed and underwent extensive diversification. Following the late Permian extinction event, pteridophytes were largely replaced (although ferns remain abundant) by gymnosperms which became the dominant group until the mid-Cretaceous. The dramatic increase in plant diversity since then is entirely due to the radiation of the angiosperms which first appeared in the lower Cretaceous. These trends are shown in Fig. 5.2.

Figure 5.2 Fossil diversity: terrestrial plants



Source: Adapted from Signor, P.W. 1990. The geological history of diversity. *Annual Review of Ecology and Systematics* 21.
 Note: Diversity is here measured in terms of number of species present.

MEASURING BIOLOGICAL DIVERSITY

A central problem in the maintenance of biological diversity is an assessment of the relative importance, in terms of diversity, of different areas, habitats or ecosystems. Only by understanding this can priorities in conservation efforts be usefully assigned. However, this importance can be assessed in different, though related, ways. The first, and most obvious, makes reference to its 'intrinsic' diversity, so that an area with higher diversity is deemed more important than one with lower diversity. The second attempts an

1. Biological Diversity

assessment of the contribution any given area makes to the overall diversity of a given geographic region, such as a country, continent or, ultimately, to the world overall. From this perspective, some areas with lower intrinsic diversity may be more important than others with higher diversity. This will be discussed further below; see also Chapters 2 and 15.

Assessments of diversity pose considerable problems, both practical and theoretical. In the first instance, the concept of diversity in an ecological context has to be made clear.

Local biological diversity

Species richness

Biological diversity measures for particular areas, habitats or ecosystems are often largely reduced to a straightforward measure of species richness. In its most ideal form this would consist of a complete catalogue of all species occurring in the area under consideration. In practice this is clearly unrealistic outside very small areas which will be of only limited interest in a global context. Even with small sites, a complete enumeration of all species will be impossible to carry out if micro-organisms are included.

Species richness measures will therefore in practice be based on samples. Such samples could consist of complete catalogues of all species in a particular, generally taxonomic, group (e.g. all birds, all ferns) or may consist of measures of species density (i.e. all the species in a sample plot of standard area) or of numerical species richness, defined as the number of species per specified number of individuals or biomass.

Although straightforward measures of species richness may convey relatively little ecologically important information, in practice because they are the most easily derived, they are perhaps the most useful index for comparisons of biological diversity on a large scale.

Species abundance

From an ecological viewpoint, simple species richness indices have limited value. More meaningful measures of diversity take into account the relative abundance of the species concerned. In general, the more equally abundant the species in the area or ecosystem under consideration are, the more diverse it is considered to be. A number of models have been developed which derive diversity indices from measures of species abundance. As different mathematical and biological assumptions are made in these models, they will often generate different diversity measures from the same sets of data. Thus there is no one authoritative index for measuring diversity.

Taxic diversity

Furthermore, weight can also be given to the relative abundance of species in various categories, for example in different size classes, at different trophic levels, in different taxonomic groups, or with different growth forms. Thus a hypothetical ecosystem which consisted only of several species of primary producers, such as photosynthesising plants, would be less diverse than one with the same number of species but which included herbivores and predators. Similarly, an ecosystem with representatives

from four different phyla would be more diverse than one with representative of only two.

Based on cladistic analysis, a number of taxonomic diversity indices have now been developed. Some of these give higher weight to so-called relict groups, that is taxonomic groups not closely related to other living groups and consisting of few species; others favour higher taxonomic groups with large numbers of species. The most complex measure so far developed is taxonomic dispersion, which endeavours to select an even spread of taxa in any given group.

Comparisons of different areas

Once a measure of diversity has been decided upon, it should be possible to compare the diversity of different areas. Such comparisons may not, however, be straightforward.

Diversity measures for ecological entities such as communities, habitats and ecosystems make the assumption that these entities are not site-specific, that is that they occur in essentially the same form over a wide area or in a number of different places. In practice, species composition and species abundance are very rarely constant either in space or in time; thus the existence of communities or ecosystems definable by species composition is seriously questioned by many ecologists. This therefore undermines the extent to which diversity measures derived from particular sites can be used as a basis for generalisation. Nevertheless, these ecological concepts still retain considerable force, even if they cannot be rigorously defined, and much discussion of biological diversity is couched in terms of comparisons between different habitats and ecosystems.

Species/area relationships

The relative diversity of different sites will often depend on the scale at which diversity is measured. Thus 1m² of semi-natural European chalk grassland will contain many more plant species than 1m² of lowland Amazonian rain forest whereas for an area of, say, 1km² or more this will be reversed. This is because as an area is sampled the number of species recorded increases with the size of the area, but this rate of increase varies from area to area.

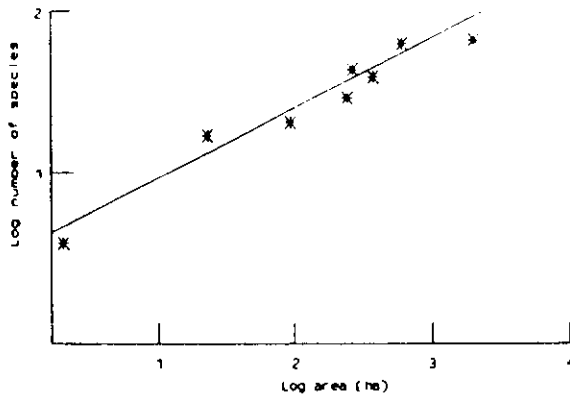
A wide range of observations has demonstrated that, as a general rule, the number of species recorded in an area increases with the size of the area, and that this increase tends to follow a predictable pattern, known as the Arrhenius relationship, whereby:

$$\log S = c + z \log A$$

where S = number of species, A = area and c and z are constants.

The slope of the relationship (z in the equation above) varies considerably between surveys, although is generally between 0.15 and 0.40, and some surveys do not fit the relationship at all. This relationship is shown graphically in Fig. 5.3.

Figure 5.3 A typical species-area plot



Note: The data are plotted on logarithmic axes resulting in a straight line graph, the slope of which (z) indicates the rate at which species number changes in step with changing area.

The most widely quoted generalisation from this finding is that a ten-fold reduction in an area (i.e. loss of 90% of habitat) will result in the loss of from c. 30% (with $z = 0.15$) to c. 60% (with $z = 0.40$) of the species present. This is often reduced to the rule-of-thumb that a ten-fold decrease in area leads to a loss of half the species present.

The causes of the species-area relationship appear to be relatively straightforward, and involve a combination of sampling effects and environmental heterogeneity. On a small scale, the increase in number of species with an increase in area is probably overwhelmingly a result of the former: that is, put very crudely, a given habitat in which species are randomly distributed will become increasingly more completely sampled as the area sampled increases. At larger scales, environmental heterogeneity will be more important: that is, as the area sampled increases, so different habitats with different species in them will be included in the sample.

Diversity at different scales

Thus the overall diversity of any given area will be a reflection both of the range of habitats it includes and the diversity of the component habitats. The greater the differences between the various component habitats in terms of species composition, then the greater the overall diversity will be. The differences between habitats are referred to as beta (β) diversity, while the diversity within a site or habitat is alpha (α) diversity. Thus an area with a wide range of dissimilar habitats will have a high β -diversity, even if each of its constituent habitats may have low α -diversity. Differences in site diversity over large areas, such as continents, are sometimes referred to as gamma (γ) diversity.

An area with relatively low species diversity may therefore still make an important contribution to the overall diversity of the larger region it is found in if it contains a significant number of species which do not occur elsewhere (endemics). Oceanic islands (see Chapter 14) and continental montane regions are examples of geographical entities which typically have comparatively low species diversity but high rates of endemism.

Assessing the relative importance of areas with high species diversity and low rates of endemism compared to areas with lower rates of diversity and high endemism remains an intractable problem. Attempts have been made to circumvent this by using somewhat different approaches, such as Critical Faunal Analyses, but these also generally do not generate unequivocal results (Chapter 15).

THE GLOBAL DISTRIBUTION OF SPECIES RICHNESS

Analysis of worldwide trends in biological diversity almost always treats this in terms of species richness, as this is the only indicator of diversity for which anything approaching adequate data is available on a global scale. Biological diversity is not evenly distributed around the globe.

Latitudinal gradients

The single most obvious pattern in the global distribution of species is that overall species richness increases with decreasing latitude. At its crudest this means that there are far more species per unit area and in total in the tropics than there are in temperate regions and far more species in temperate regions than there are in polar regions.

Not only does this apply as an overall general rule, it also holds within the great majority of higher taxa (at order level or higher), and within most equivalent habitats, although the most obvious and frequently cited are forests and shallow-water marine benthic communities, with, respectively, tropical moist forests and coral reefs being renowned for their remarkably high levels of species diversity.

This overall pattern masks a large number of minor trends where species richness in particular taxonomic groups or in particular habitats may show no significant latitudinal variation, or may actually decrease with decreasing latitude; nevertheless it remains a phenomenon of overwhelming biogeographical importance.

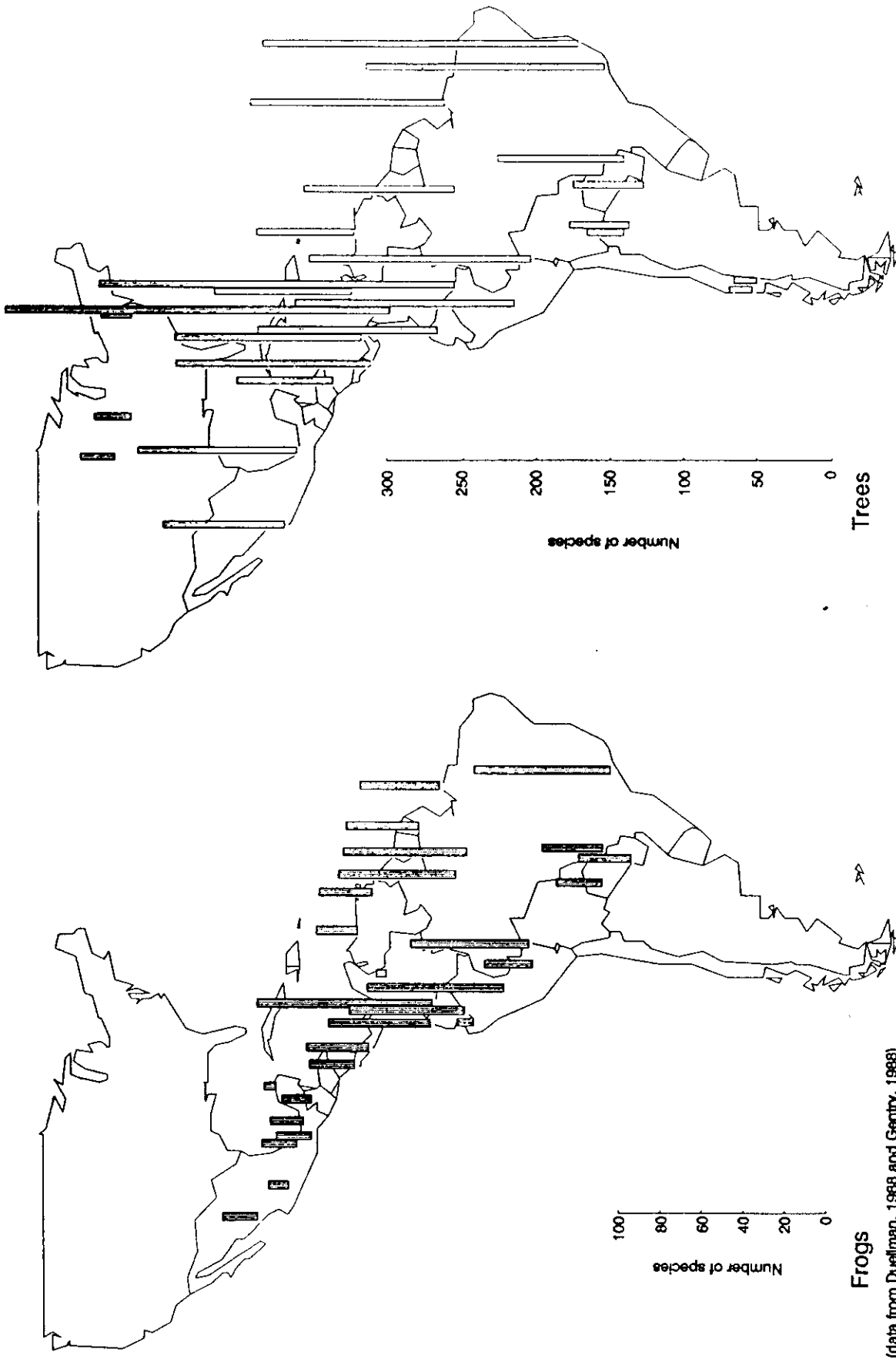
As well as latitude, changes in diversity can also be correlated with a many other variables, some of which are discussed briefly below. For some of these it is not easy to establish a significant relationship because there are often confounding variables, and because there are too few comparable datasets.

The maps in Fig. 5.4 demonstrate broad gradients in species richness in frogs (left) and trees (right) in the Americas (data extracted from Duellman, 1988 and Gentry, 1988). For these groups in this part of the world, climatic factors appear to play a large part in determining such gradients.

Elevational gradients

In terrestrial ecosystems, diversity generally decreases with increasing altitude. This phenomenon is most apparent at extremes of altitude, with highest regions at all latitudes having very low species diversity. There are fewer examples showing gradients of species richness with altitude, although amongst vertebrates this has been demonstrated for bird species in New Guinea (Kikkawa and

Figure 5.4 Gradients in species richness: frogs and trees in the Americas



Williams, 1971 cited in Brown) and on the Amazonian slope of the Andes in Peru (Terborgh, 1977). Gentry (1988) demonstrates it for woody plants in tropical forests, although notes that the data for upland sites are very incomplete. Suggestions have been made that, in tropical forests at least, diversity may be higher at mid-altitudes than in lower areas. However, there appear to be no substantiating data for this 'mid-altitude bulge' as a general phenomenon, although it has been noted in particular cases such as a desert mountain in Arizona where diversity at lower and higher altitudes is believed limited by aridity and low temperate respectively (Brown, 1988).

The decrease in straightforward species numbers with increasing altitude may in part be a reflection of species-area relationships, as available area generally decreases with increasing altitude, and number of species is closely related to area. Measurement of species numbers in standard-sized plots, such as those of Gentry (1988) take account of this, demonstrating that the relationship between altitude and species diversity is real, although not necessarily discounting the role that decreased available area may play in causing this phenomenon. It should also be noted that β diversity will often be higher in areas of varied topography because of increased environmental heterogeneity.

Precipitation gradients

Precipitation is generally believed to be an important factor governing terrestrial diversity. However, the relationship between precipitation and diversity is not straightforward, and it seems that seasonality in precipitation may be as important as absolute amount. As with altitude, the relationship between precipitation and diversity is most apparent at one extreme, as highly arid environments are well-known to be much less diverse than less arid, or more mesic, environments at similar altitudes and latitudes. There are, however, apparently few quantifiable data to demonstrate this. Gentry (1988) in his study of forest diversity, demonstrated a strong correlation between plant species richness and absolute annual precipitation. However, he notes that this correlation may not apply at all in the Palaeotropics, and that there were strong indications that the length and severity of the dry season were more important than absolute annual rainfall. In the Neotropics, there is a strong relationship between annual rainfall and strength of the dry season, which is much less marked in the Palaeotropics. The importance of seasonality was borne out by a preliminary study of a Brazilian site with a relatively low, evenly-distributed annual rainfall, which showed a much higher species diversity than would be expected from total rainfall measures alone. Moreover, there appears to be a marked tailing-off of increasing diversity with increasing rainfall at high rainfalls, with little or no increase in diversity once rainfall exceeded 4,000-4,500mm per year.

However, it should be noted that the limits on diversity may in fact represent a limitation of sampling technique: in the two most diverse sites sampled (in areas of year-round rainfall of 3,000-4,000mm p.a.), diversity was so high in the plots sampled (in one site 300 species \geq 10cm diameter out of 606 individual plants in one plot), that it seems likely that only by increasing the size of the survey plots would

any further trends be discerned (Gentry, 1988).

Nutrient levels

Although there are few studies of global trends in diversity and soil nutrients, the relationship between plant community richness and tropical soil nutrient levels has been the subject of considerable interest. The data that are available indicate that the relationship may not be straightforward. Studies in Southeast Asia indicate that diversity may be highest at intermediary levels of nutrition, with a decrease at higher levels, while in the Neotropics diversity generally seems to increase with increasing nutrient levels, being most strongly correlated with Potassium (K) levels. This overall trend is apparently also shown by a variety of other organisms, including bats, birds and butterflies. In general, however, diversity in tropical forest ecosystems seems much less strongly dependent on nutrient levels than other factors, notably latitude, altitude and precipitation (Gentry, 1988).

The relationship between nutrient levels and diversity in other ecosystems is also complex: declines in diversity with increasing nutrient levels of temperate freshwater habitats (eutrophication) and grasslands are well-documented, but it is difficult to draw general conclusions from these (Brown, 1988).

Salinity gradients

In aquatic ecosystems, salinity appears to act as a strong 'normalising' factor on diversity. Thus, in coastal areas, diversity almost invariably declines when salinity deviates from 'normal' sea water (i.e. 35 ppt), while in freshwaters diversity decreases when salinity increases above c. 2 ppt; this results in a bimodal distribution of diversity with increasing salinity (Brown, 1988).

Islands

The study of diversity on islands, both real and theoretical, has been an important factor in much of biogeography and conservation biology. In particular the equilibrium theories of island biogeography elaborated by MacArthur and Wilson (1967) have had an important influence on both disciplines. More recently discussion in this, as in many other areas of ecology, has tended to move away from assumptions of equilibrium to more realistic, but far more complex, non-equilibrium theories.

SPECIES AND ENERGY

The relationship between diversity and productivity has been the subject of long-standing debate in ecology. Recent studies have indicated that available energy is strongly correlated with species diversity on a large-scale, at least in terrestrial ecosystems. A study of North American tree species (Currie and Paquin, 1987) demonstrated that realised annual evapotranspiration, a measure of available energy, statistically explained 76% of the variation in species richness across the continent. Such recent studies have shown that diversity gradients in tree species are more closely related to indices of climatic productivity than to other geographical parameters, including latitude (Adams, 1989). These results could be used to predict accurately tree

1. Biological Diversity

species richness patterns in Great Britain and Ireland. Preliminary analysis of the diversity of terrestrial vertebrates in North America apparently yielded very similar results.

EXPLANATIONS AND HYPOTHESES

The explanation of geographic and temporal variation in species diversity is one of the central problems of biology. It has also proved one of the most intractable. The problem has generated an enormous amount of literature in which many different hypotheses have been proposed to attempt to account for it; these hypotheses often operate at different levels of explanation and much confusion has arisen as a result. It is beyond the scope of this report to attempt a thorough review of the subject, although, ultimately, an understanding of the importance of biological diversity should rest on an understanding of how and why it has the form that it does.

It is self-evident that, ultimately, all non-random patterns in species diversity must depend on past or present variations in the physical environment. How such variations result in the patterns observed is often far from clear. It is evident, however, that any complete explanation must involve both historical events and current ecological processes - the former implicit in any explanation of the *origin* of diversity, the latter in explanations of its *maintenance*, these being

two separate, although intimately linked, problems. The relative importance of these two factors in determining present patterns is still a subject of considerable debate.

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Chapter contributed by Martin Jenkins.



Species diversity and productivity of trees

J. M. ADAMS

The diversity of tree species found in natural forests varies between different parts of the world, and also on a local scale between different habitat types. Much of this variation in species diversity appears to be related to differences in the growth rate of vegetation (the primary productivity). Although many different explanations have been suggested, the ecological and evolutionary causes of this relationship remain unclear.

Biologists have long been fascinated by the ways in which the diversity of species can vary from one place to another. On a geographical scale, there is an overall decline in the numbers of plant and animal species between the tropics and the poles. Even on a very local scale, most groups of organisms are more diverse in some habitats than in others. Whilst these general patterns in diversity are often obvious, the underlying causes are not. Despite more than a century of thought, the question of how diversity trends have arisen is still one of the most controversial subjects in ecology.

Some of the most striking trends in species diversity are found in trees: a hectare of tropical rainforest (Fig. 1) will often contain more than a hundred species of trees, whilst

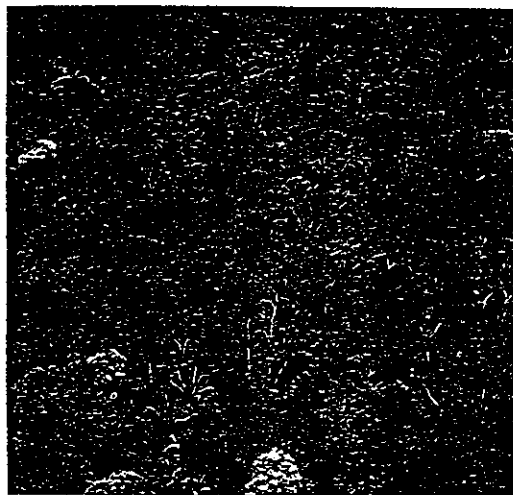
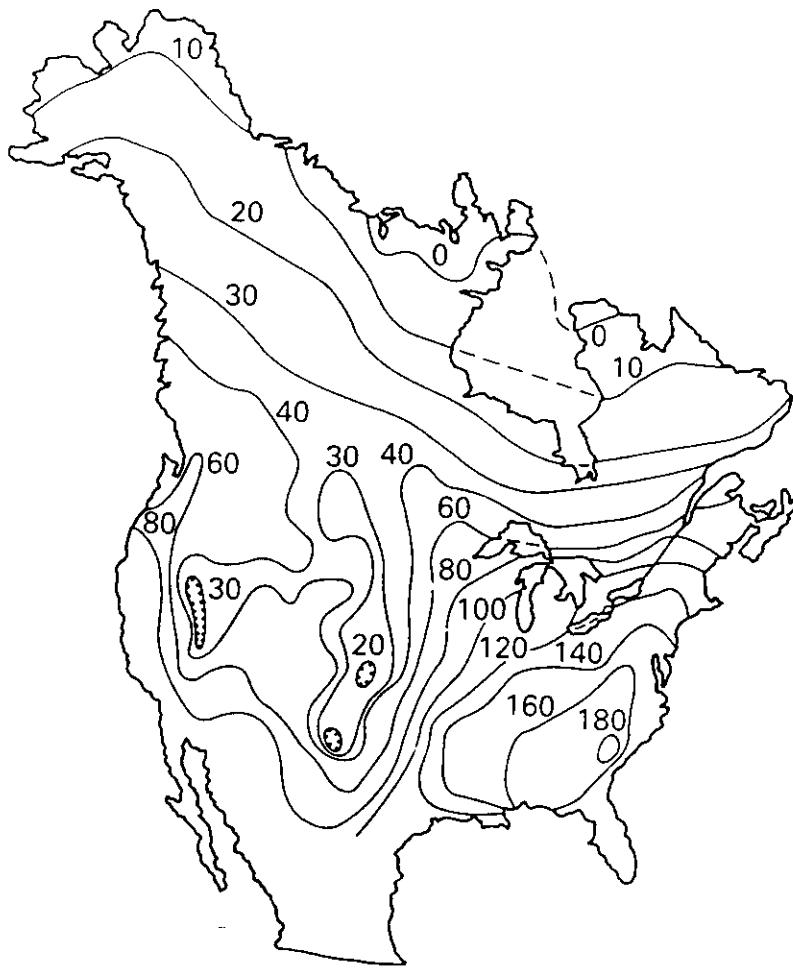


Fig. 1. A view across an area of tropical rainforest in the northern Amazon Basin. It is likely that there are hundreds of species of trees within this photograph alone.



▲ Fig. 2. Currie and Paquin recorded numbers of tree species (defining a tree as any woody plant reaching over 3m in height) occurring naturally within a grid of very large-scale quadrats, each with a mean size of around 70,000 square kilometres. The contours on this diagram represent the numbers of tree species occurring within each quadrat.

a similarly sized area of boreal forest may have no more than two or three species. The number of tree species found in a sample depends partly on the way in which the sample is taken, and different studies have used differing sample sizes and definitions for counting numbers of species. Nevertheless, there can be no doubt that trees show a general latitudinal diversity trend, as is found in so many other ecological groups. As the contour map (see Fig. 2 *Nature*, 329, 326–327, 1987) shows, this broad latitudinal trend is complicated by considerable longitudinal variations, with desert and semi-arid regions being relatively poor in species. On a more local scale, there is also a tendency for species diversity of forests to decrease up mountains, except where the lower slopes are arid and rainfall is relatively more abundant at higher altitudes.

Generally speaking, the warmer and rainier the climate, the more species of trees are found in the local flora. This trend in

diversity seems to parallel a general gradient in the growth rate of vegetation, known as the primary productivity. Recent studies have emphasized the closeness of this relationship in the tree floras of the northern temperate zone. Using data on the natural ranges of tree species, Currie and Paquin found that most of the variation in species diversity in North America is related to actual evapo-transpiration, which is a climatic index that shows a close relationship to primary productivity. Ian Woodward and I (Adams and Woodward, *Nature*, Vol. 339, pp. 699–701, 1989) carried out a broader study of tree species diversity trends in Europe, Eastern Asia and North America, and also found a strong relationship with a climatic predictor of productivity, the Chickugo Model, which incorporates data on net solar radiation and annual precipitation (Fig. 3). In each of these studies, diversity was much more closely related to climatic productivity indices than to a range of other geographical parameters, including latitude. It seems then, that we may be closing in on one of the underlying factors which cause latitudinal gradients in diversity to exist.

A similar trend may also exist within the World's tropical forests. Alwyn Gentry has compared data from various parts of the tropics, and found that variation in tree species diversity is closely related to annual rainfall, even within the tropical rainforests themselves. If we regard rainfall as a good general predictor of the favourability of conditions for growth of vegetation, it seems likely that here too we have a broad-scale relationship between species richness and productivity.

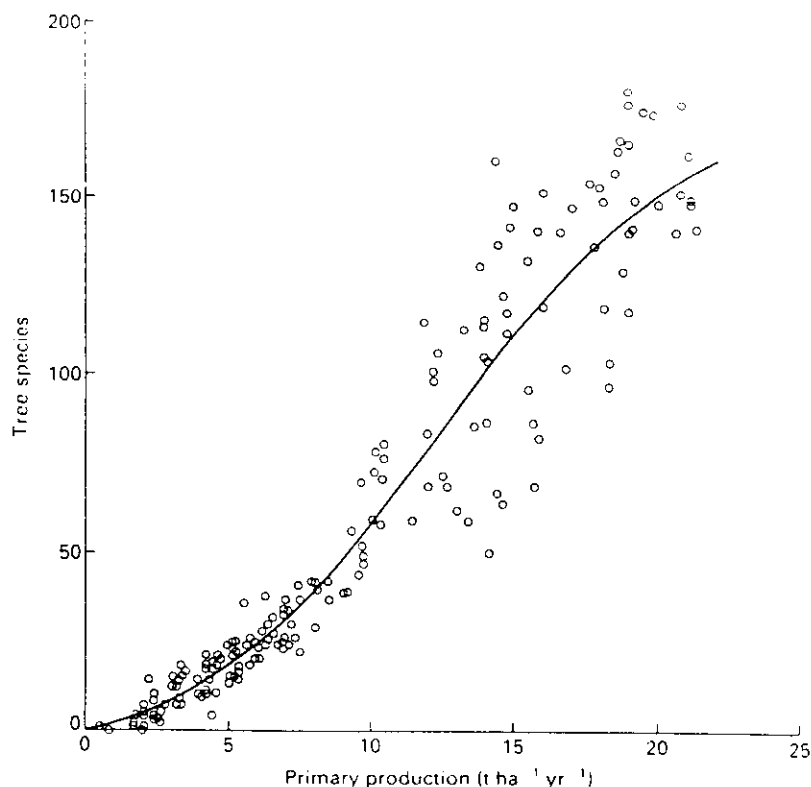
The general diversity-productivity relationship also seems to hold true when the variation in productivity is related to soil characteristics rather than climate. Within the temperate zone, the most diverse forest tree communities in both Europe and Eastern Asia are found on fertile river floodplains, rather than poorer soils of the valley slopes and uplands. This also appears to be the case within tropical forests, with sites on very nutrient-poor leached soils having fewer species of tree than nearby areas with richer soils. It seems that the highest species diversity of all is reached under conditions where both soil and climatic factors seem favourable to high primary productivity. The most species-rich forests so far discovered in the world (with over 300 species of tree per hectare) are found in the Peruvian area of Amazonia, where a combination of fertile alluvial soils, very high year-round rainfall and a warm climate appear to offer almost optimal conditions for growth of vegetation.

As with all patterns in ecology, there are certain exceptions to this trend. For example, redwood (*Sequoia*) forests show a high primary productivity and low tree species diversity. Swamp forests, despite having a higher productivity than some upland forests, also tend to be relatively poor in species. On a broad scale, some regions may be relatively depleted in species as a result of extinctions during the glacial phases of the Pleistocene. It is also quite evident that factors such as habitat heterogeneity are important; the effect of having a large number of altitudinal zones on a single mountain is one example. Nevertheless, the overall trend of rising richness with productivity remains very striking, and contrasts with the observations from local-scale studies on herbaceous plant communities which often show an initial rise in diversity from low levels of productivity, followed by a decline in diversity at higher productivity levels (the so-called hump-backed curve).

Whilst it seems clear that tree species diversity is closely related to primary productivity, this does not in itself provide an explanation for the trend. There must be some sort of ecological mechanism which allows more species to evolve and coexist in highly productive environments. To the layman, it seems intuitively reasonable that the more productive environments – with their lush vegetation and abundance of resources – should favour the existence of more species. However, this acceptance is based on vague, anthropomorphic feelings. The more thoroughly and rigorously we examine the problem, the more it becomes apparent that the actual mechanisms are poorly understood. Various types of mechanisms can be invoked to explain why diversity should follow productivity, and in the following sections I will discuss some of these.

Productivity and community structure

One view is that the abundance of resources under more productive conditions allows species to occupy more specialized ecological niches (Fig. 4). This may be because there is an evolutionary limit to specialization, imposed by the tendency of small or sparse populations to become extinct: when the 'cake' of productivity is bigger, species can survive on relatively narrow slices of the resource spectrum. This principle may well be correct for certain animal groups, but it is difficult to understand how it could work in the case of plants. Much of the difference in productivity between different plant communities and vegetation types results from

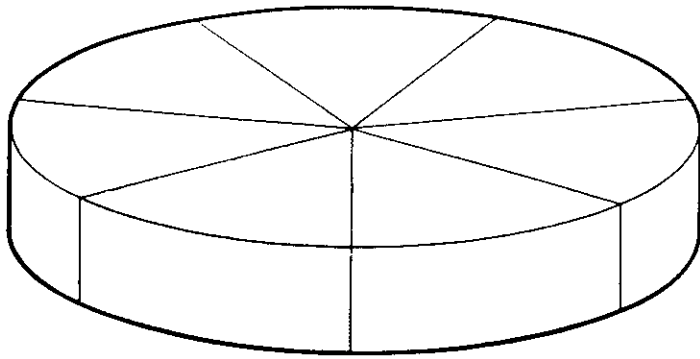


factors which cannot clearly be defined as resources. For instance, on a geographical scale, it is likely that differences in mean annual temperature are responsible for much of the variation in productivity (because plants photosynthesize and grow more rapidly under warmer conditions), and it is very difficult to imagine how heat could be competed for and partitioned. At a more empirical level, we should expect that if high-productivity conditions really do allow species to maintain viable population densities in narrower niches, then a high-productivity environment should have a greater total density of trees but the population density of each species should remain relatively constant. This is obviously not the case; although tropical forests do seem to have a slightly higher density of trees (of all species taken together) per hectare, the density of the population of each species is much lower in the tropics. Taken at its simplest, the resource-partitioning hypothesis obviously fails this test.

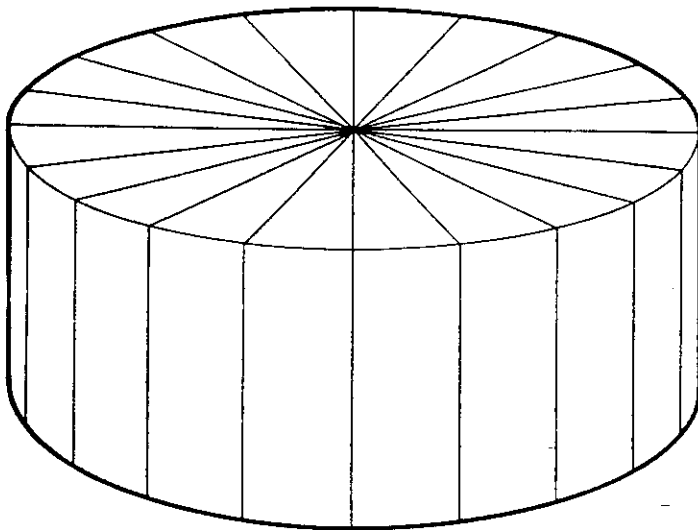
Many authors (e.g. Stevens) have suggested that the most important structural factor underlying geographical tree species diversity trends is not productivity *per se*, but seasonality, which generally tends to parallel it. The most productive tropical regions also

▲
Fig. 3. There appears to be a close relationship between geographical trends in tree species diversity and productivity in the temperate zone. This diagram shows numbers of tree species in a grid of large-scale quadrats (similar to those used by Currie and Paquin, Fig. 2), plotted against a climatic index of productivity based on net solar radiation and annual precipitation.

(a)



(b)



▲ **Fig. 4.** The supply of resources to a community may be regarded as a 'cake', from which each species can take a 'slice' according to ecological specialization. If a species takes too narrow a slice of resources, it will tend to go extinct. When the total 'cake' of resources is small (a), the 'slices' will have to be wider than when the cake is bigger (b). This type of principle has often been used to explain why so many plant and animal groups increase in diversity in parallel with primary productivity.

tend to be the least seasonal, and it may be that it is the degree of fluctuation in the environment which determines the micro-habitat niche width of trees which can exist. However, such explanations invoking seasonal fluctuations concentrate only on straightforward contrasts between the aseasonal tropics and the more seasonal zones at higher latitudes. They are less convincing as explanations of tree diversity trends which also exist within the seasonal temperate zones even though a marked dormant season exists throughout, and also on tropical mountains where there are no well-defined seasons. There is also the necessity of explaining differences between species diversity of habitats under the same climatic conditions but different soil nutrient levels.

Rather than an effect of productivity acting directly on the trees themselves, it is possible that the mechanism controlling diversity operates through some other group of organisms which interacts with the plants.

For example, Janzen has suggested that the intensity of predation exerted by herbivorous insects is a crucial factor in causing geographical trends in diversity of trees, because it may prevent exclusion of weaker competitors by dominant tree species. It may be that the evolutionary ecology and population biology of these insects is in some way different in high-productivity environments. Mutualists might also have a role in causing tree species diversity trends. For instance, Connell and Orians have suggested that fruit and pollen dispersers may be more sedentary in high-productivity environments. This may lead to more frequent speciation of the trees that they visit, as there is less gene flow between isolated populations. Another view is that the fruit dispersers and pollinators are able to become more specialized in high-productivity environments, leading to frequent speciation amongst trees and allowing each tree species to maintain a viable population at lower densities.

Many explanations involving herbivores or mutualists in tree diversity trends invoke an important role for seasonality in the detailed evolutionary and population biology level aspects of their explanations. In these cases, the average level of productivity may be less important than the stability of productivity throughout the year, with a dormant season bottleneck in food supply preventing specialization by herbivores, pollinators and fruit-dispersers. However, such ideas suffer from the same problems as those which invoke seasonality as a direct effect on niche-specialization of tree species.

Whilst mechanisms involving productivity effects (acting through other trophic levels) do sound promising, the ideas are still somewhat vague and need to be tested thoroughly using observational sources of data. It may be that they operate only at the geographical scale, and are not involved in more local-scale productivity relationships.

Harshness of low-productivity environments

Rather than a direct effect of productivity on community structure or functioning, it is possible that productivity indicates the general physiological suitability of an environment for plants to survive and reproduce. Along a gradient of increasingly harsh conditions, successively more complex physiological adaptations are required if plants are to be able to survive, so the probability of an evolutionary lineage having acquired such adaptations may decrease. This hypothesis relies fundamentally on the idea that the angiosperms (which constitute

most species of trees) originated in fertile, moist tropical conditions and only later radiated outwards into other environments. Palaeontological evidence does appear to be consistent with this view, in that the earliest angiosperm fossils appear in river floodplain sediments deposited under warm climatic conditions.

A complementary view is that low-productivity environments have somehow offered less of a target for evolution, in the sense that they have occupied relatively small areas during the geological past. Partly because of their rarity, such areas may also have provided a less stable set of conditions for those species which have colonized them, so there may have been a higher probability of extinction. Certainly, moist tropical climates were very widespread during most of the Tertiary (65–2 Myr ago), with large areas of cool and dry climate only appearing towards the end of this period.

Relatively infertile soil conditions may also be regarded as extreme in the sense that they occupy small areas. However, by this token one might also expect that the most highly fertile soil conditions must also be regarded as extreme, as they too are likely to be relatively rare and ephemeral in geological time, even though they tend to have more diverse tree floras.

Historical arguments of this type sound reasonable, although they are more difficult to test than ideas which invoke community structure and interactions as a cause of diversity trends. One observation which might be taken to conflict with a purely historical explanation of this sort, is the close convergence in tree species diversity between corresponding regions which have been separated for tens of millions of years. If communities have accumulated species independently of the richness level already reached, we might expect that different areas under similar productivity levels will have diverged in diversity. However, Gentry has reported that samples of forest taken under similar climatic conditions, but from different regions of the tropics, tend to have similar levels of diversity. Another example appears to be the New Zealand tree flora, which shows a similar diversity to northern temperate floras at corresponding predicted productivity levels. Convergence of this sort may be taken to indicate that there is some capacity to the numbers of tree species present in forest communities, which is related to the level of productivity. Further

studies are necessary to determine whether this convergence is a general phenomenon.

Conclusion: the enigma remains

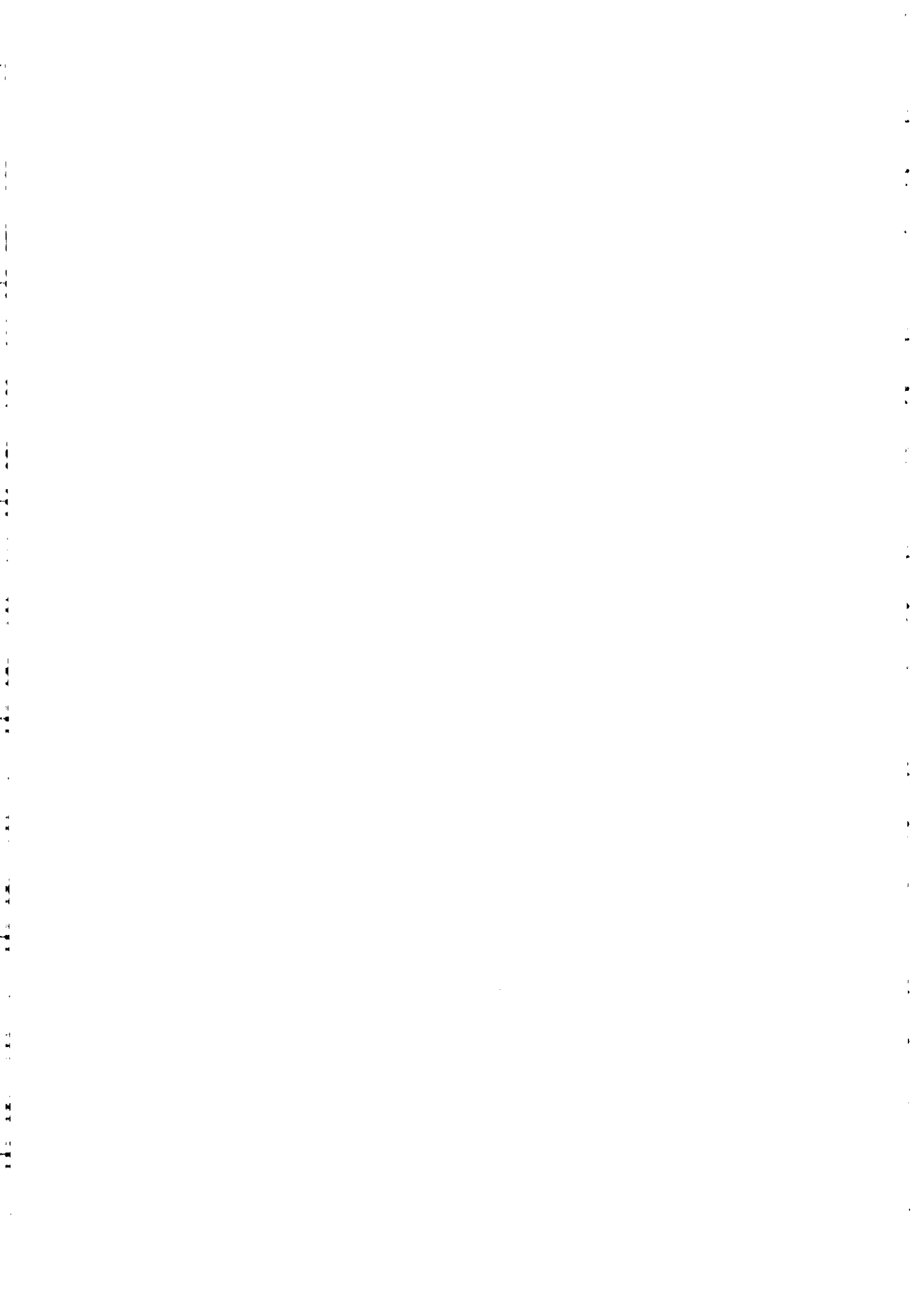
The causes of the productivity diversity relationship of trees remain a tantalizing enigma. Several different hypotheses can be invoked to explain this trend, but it is very difficult to know which, if any, of these is correct. A simple resource-partitioning mechanism seems unlikely, but there are all manner of other complex ways in which a similar system might operate. The physiological harshness hypotheses sound fairly plausible, although the apparent convergence of diversity levels between climatically corresponding regions might be taken to indicate that there is actually some structural mechanism at work as well.

A basic problem is that it is very difficult to test hypotheses which invoke subtle ecological and evolutionary processes acting over millions of years. Our understanding of community interactions and evolution is still too sketchy even to guess at some of the mechanisms which might have operated. It is quite possible that there is no single process underlying all productivity-diversity relationships; rather it may be a combination of several very different processes tending to act in parallel, and varying in relative importance from one place to another and from one spatial scale to another. We can only hope that, as knowledge slowly accumulates, further clues to the mechanisms behind diversity trends will emerge.

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Threatened Biotas: "Hot Spots" in Tropical Forests

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Summary

The mass-extinction episode underway is largely centred on tropical forests, insofar as they contain at least half of all Earth's species and they are being depleted faster than any other biome. But species distributions and depletion patterns are anything but uniform throughout the biome. This paper identifies 10 areas that, a) are characterised by exceptional concentrations of species with high levels of endemism and b) are experiencing unusually rapid rates of depletion. While these "hotspot" areas comprise less than 3.5 percent of remaining primary forests, they harbour over 34 000 endemic plant species (27 percent of all plant species in tropical forests and 13 percent of all plant species worldwide). They also feature 700 000 endemic animal species and possibly several times more. Unfortunately, they appear likely to lose 90 percent of their forest cover as soon as the end of the century or shortly thereafter, causing the extinction of almost 7 percent of Earth's plant species and at least a similar proportion of animal species, this occurring in only 0.2 percent of Earth's land surface. By concentrating on such areas where needs are greatest and where the pay-off from safeguard measures would also be greatest, conservationists can engage in a more systematised response to the challenge of large-scale extinctions impending in tropical forests.

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The Environmentalist

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Introduction

There are many prognoses (Ehrlich and Ehrlich, 1981; Myers, 1987a; Raven, 1987; Western and Pearl, 1989; Wilson, 1988) of a mass extinction of species during the next few decades, notably in tropical forests. This paper proposes that we can identify a number of localities in tropical forests that:

- a) feature exceptional concentrations of species with exceptional levels of endemism, and that,
- b) face exceptional degrees of threat.

These "hotspot" areas, 10 of which are identified in this paper, total only 292 000 km² (3.5 percent) of a biome of 8.5 million km² of primary forest remaining. But they feature a large proportion, possibly a majority, of the 125 000 higher plant species, both local endemics and wide-distribution species, that exist in tropical forests overall. Moreover, the areas are exceptionally rich in animal species too. If present exploitation trends persist in these forests (they are likely to accelerate), there may be little left of the hotspot areas, except in severely degraded form, by the start of the next century or shortly thereafter.

Thus, there appears to be a major extinction spasm impending in these areas alone. Conversely, of course, if conservationists can identify key localities of biotic richness under acute threat, they can determine their conservation priorities in a more informed and methodical manner than has often been the case to date.

Right from the start, however, the analysis is bedevilled by lack of basic data. We know all too little about the numbers of species, especially of

animal species, in hotspot areas. In tropical forests overall, defined here as forests with a mean annual rainfall of 1500 mm or more, and a mean monthly minimum of 100 mm, there could be anything from 2.5 million to 30 million (conceivably 50 million) animal species (Erwin, 1988), yet to date we have identified little more than 0.5 million of them. So for the purposes of this paper, attention will be confined to species of vascular plants, also known as "higher plants" of which flowering plants comprise 88 percent, and henceforth referred to simply as plant species.

This is not to leave animal species entirely out of account. Species-area inventories in diverse sectors of tropical forests suggest there are at least 20 animal species for every one plant species, assuming a minimum planetary total of all species of 5 million. This means that if the hotspot areas feature, say, half of all plant species in tropical forests, viz. about 62 500 species (the true total could be a good deal greater), they presumably contain at least 1.25 million animal species, though as noted, the actual figure for animal species could be far higher, indeed several times higher.

Biotic Richness of Tropical Forests

The abundance of tropical-forest species is well documented. In the central portion of the La Selva Forest Reserve in Costa Rica, totalling only 13.7 km², there are almost 1500 plant species, more than in the whole of Great Britain with its 243 500 km². In the Reserve there are 388 bird species (spanning 56 families and 273 genera), 63 bat species (9 and 37), 42 fish species (13 and 17), 122 herptile species (23 and 63), and 143 butterfly species (11 and 59). These totals are to be compared with species numbers for the continental USA: 650 birds, 40 bats, 775 fish, 455 herptiles and 415 butterflies.

As an example of an entire country, Ecuador contains an estimated 20 000 plant species, the bulk of them in its forests and at least 4000 of them endemic. By contrast, the temperate zone state of Minnesota, twice the size of Ecuador, has 1700 plant species, only one of them endemic (Gentry, 1986a). Ecuador harbours more than 1300 known bird species, or almost twice as many as in the USA and Canada combined.

Moreover, tropical forests feature much higher levels of plant endemism than regions elsewhere; for details see the descriptions of hotspot areas below. Similarly, endemism among

birds is pronounced; in tropical forests of South America, 440 species of birds, about 25 percent of the total, have ranges of less than 50 000 km², by contrast with 8 species, or 2 percent of the total, that have similarly restricted ranges in the USA and Canada (Terborgh and Winter, 1983).

Plainly, endemic species are extremely vulnerable to extinction when their localised habitats are deforested. Not so plainly, the ecological specialisations of many tropical-forest species, such as sensitive positions in complex food webs, leave them subject to summary demise when their support ecosystems are merely destabilised through forest disturbance and degradation (Gilbert, 1980; Janzen, 1975; Terborgh, 1986). In particular, the marked phenomenon of outbreeding among tropical-forest plants means that when they are reduced to small populations, they become specially susceptible to sudden extinction.

Hot Spot Areas: Quality of Data

Now to consider 10 discrete areas in tropical forests that rank as "hot spots" by virtue of their floristic richness and deforestation rates. See Fig. 1 for their location and Table 1 for summarised data; and Table 2 for a comparison with other parts of the world. Since the critical data are presented in compressed form, the accounts are supported with numerous references. Where no reference is given, the information derives from the author's own experience while working intermittently in the countries in question over a period of 17 years.

In a broad-ranging review of this sort, the data are bound to vary considerably in quality. In many instances the statistical information is considered accurate to within 5 percent or better. In many others it is sufficiently accurate to rank as sound support for "working estimates". In some it is regarded as qualitatively correct, even though the quantitative data are deficient: indicative information and best-judgement appraisals have their role to play in a paper such as this, provided their constraints are recognised. In a few further instances, which are identified as such, the information base is so poor that we have nothing better than "educated assessments", even rough-and-ready estimates that occasionally amount to little more than guesstimates, albeit carefully conservative.

The author believes that this overall approach, uneven as it is, is justified in an analytical

TABLE 1 "Hotspot" Areas in Tropical Forests.

Area	Extent of forest (km ²) Original	Present (primary)*	Plant species in original forests	Number of endemics in original forests (percentage)	Original endemics as proportion of Earth's plants total (percent)	Present forest area as proportion of Earth's land surface (percent)
Madagascar	62000	10000	6000	4900 (82)	1.96	0.00675
Atlantic coast Brazil	1000000	20000	10000	5000 (50)	2.00	0.0135
Western Ecuador	27000	2500	10000	2500 (25)	1.00	0.0017
Colombian Chocó	100000	72000	10000	2500 (25)	1.00	0.0486
Uplands of Western Amazonia	100000	35000	20000	5000 (25)	2.00	0.0236
Eastern Himalayas	340000	53000	9000	3500 (39)	1.40	0.0358
Peninsular Malaysia	120000	26000	8500	2400 (28)	0.96	0.0175
Northern Borneo	190000	64000	9000	3500 (39)	1.40	0.04
Philippines	250000	8000	8500	3700 (44)	1.48	0.0054
New Caledonia	15000	1500	1580	1400 (89)	0.56	0.001
Totals	2204000	292000	**	34400	13.8	0.2
For comparison:						
Hawaii	14000	6000	825	745 (88)	0.30	0.004
Queenland	13000	6300	1165	435 (37)	0.17	0.004

* Some, though not many, primary forests species can survive in degraded forests.

** It is unrealistic to sum total these figures for plant species, on the grounds that there is some overlap between adjacent regions, e.g. some plants occur in Peninsular Malaysia, Northern Borneo and the Philippines.

Note: There is a great range of accuracy in these figures (and many are rounded anyway). At one end of the range, some figures are thoroughly well documented and can be generally considered accurate to within 5 percent or better. At the other end of the range, they are little more than "informed assessments" or even "educated guesstimates". The rest fall between these two extremes, with more of them clustered towards the "accurate" end of the range than the "imprecise" end.

Sources: numerous, as cited under the area reviews in the text.

TABLE 2 Plant Species World-wide: Areas, Species Concentrations and Endemics. In the tropical countries listed, most species occur in forests.

Country/region	Area (km ²)	Plant species	Endemism (percent)
Costa Rica	50899	8-10000	15
La Selva Reserve	13.7	1500	
Panama	78513	8500	14
Barro Colorado Island	15.6	1369	
Colombia	1138914	45000 or so	
Chocó Department	47200	10000 or so	25
Ecuador	461477	20000 or so	20
Rio Palenque Research Station	1	1250	4
Peru	1285215	20000 plus	
Manu National Park	18000		
Tambopata Reserve	55	(215 tree species listed)	
Madagascar	587041	10000 plus	80 plus
India	3166828	15000	33
Sri Lanka	65610	3365	27
Borneo	757000	10000 plus	34
Philippines	299498	8500	44
New Guinea	875821	11000	90
New Caledonia	19154	3138	75
For comparison:			
Continental USA	9337532	16500	
California Floristic Province	324000	4452	48
Minnesota	219000	1700	0.06
Hawaii	16641	1100	90
Europe (outside Soviet Union)	5680000	11300	
British Isles	302470	1822	0.8
Soviet Union	22400000	21100	
Australia	7682300	25000	
South Africa			
Cape Floristic Kingdom	18650	8579	68

Source: Davis *et al.*, 1986, and numerous references cited in text.

exercise that seeks to delineate the conservation challenge of a mass-extinction episode in its full scope. Moreover, in cases where there is inadequate documentation of a quantitative sort, one should not be preoccupied with what can be counted, if that is to the detriment of what also counts. After all, to decide that an area should not be evaluated because we lack a conventional degree of accurate data is effectively to decide that its conservation needs cannot be evaluated either, in which case its cause tends to go by default.

A further brief point arises. In many instances a patch of primary forest may be grossly disrupted without being destroyed outright. Or, when an area cleared of its forest regenerates the result is secondary forest, with species

complements that differ markedly from the original primary forest. But this paper confines itself to primary forest cover for two reasons. First, only primary forest contains the high species diversity that characterises the biome. Secondly, the biome features only small amounts of secondary forest, whereas "conversion" of primary forest generally results in total and permanent elimination of forest cover. In any case, there is little overlap in species composition between primary forest and secondary forest. In Rondonia State in Brazilian Amazonia, for instance, secondary vegetation as much as 15 years old shows little regeneration of primary forest species, even though the new vegetation is structurally similar to the original forest (Lisboa *et al.*, 1988).

TABLE 3 Three Critical "Hotspot" Areas: Madagascar, Atlantic Coast Brazil and Western Ecuador.

Area	Original forest (km ²)	Remaining primary forest in 1987 (km ²)	Total of original plant species	Total of original plant endemics (percentage of original species)	Total of plant species eliminated or on the verge of extinction	Remaining forest area as proportion of Earth's land surface	Total of original plant species as proportion of all Earth's plant species (percent)
Madagascar	62000	10000	6000	4900 (82)	2450 ³	0.00675	2.4
Atlantic Coast Brazil	1000000	20000	10000	5000 (50)	2500	0.0135	4.0
Western Ecuador	27000	2500 at most	10000	2500 (25)	1250	0.0017	4.0
Totals	1089000	32500	26000	12400	6200	0.02	10.4

Notes:

1. In the light of the findings of the theory of island biogeography.
2. The number of animal species in a similar situation can be roughly estimated by multiplying the number of plant species by 20, thus supplying a minimum estimate. According to the calculations presented here, the total number of animal species in question is 124 000. The actual could be several times higher.
3. That is, when remaining Madagascar primary forest declines to 10 percent of original extent, which is likely within the next decade at most.

Sources: See references cited in text.

Ten "Hotspot" Areas

1. Madagascar

This ancient island is famous for its unique biota. Yet nationwide, only 5 percent of the original vegetation remains (Guillaumet, 1984; Jenkins, 1987; Jolly *et al.*, 1984; Leroy, 1978; Lowry, 1986; Mittermeier, 1986). Fortunately, the situation is somewhat better in a strip of moist forest along the island's eastern side, where more than 6000 plant species occur of which 4900 (82 percent) are endemic. Virtually all of the narrow coastal plains and the lower slopes have been deforested, but on the higher slopes some tree cover persists, amounting today (early 1988) to rather less than 20 000 km² (32 percent of the original 62 000 km²) (Sussman *et al.*, 1988). Around half of these relict patches have been degraded through intensive slash-and-burn cultivation, which is now eliminating 1000-1500 km² of forest per year. The forest remnants that feature greatest species diversity and endemism, notably in the northern part of the strip, are precisely those forest tracts under most pressure from agricultural settlers.

Thus there is little hope that more than 10 percent of original forest will survive beyond the end of the century. Madagascar's population growth remains high at 2.8 percent per year. Rural poverty is pervasive. Existing farmlands are among the most eroded anywhere; and because they are generally unable to support the rural population, growing throngs of peasants seek new lands to cultivate, notably in the forests.

2. Atlantic Coast Brazil

Along its Atlantic coast, Brazil possesses a discontinuous strip of remnant forest. This strip, floristically far different from Amazonia, once featured about 10 000 plant species, with an endemism level around 50 percent (53 percent for trees, 64 percent for palms) (Boom *et al.*, 1983; Fonseca, 1985; Mori, 1988). From the onset of Portuguese colonisation, the forest has been heavily and repeatedly logged for timber and charcoal. Worse, extensive sectors have been cleared for plantations of sugar-cane, coffee, cocoa and other cash crops. Of the original 10 000 km² of forest, only 5 percent remains today, a mere 2 percent in primary form, and less than 0.1 percent is protected as parks and reserves.

3. Western Ecuador

The lowland wet forest of western Ecuador, once

covering 27 000 km², and now reduced to 2500 km² at most, shows some floristic affinity with the Colombian Chocó (see next item), but its many unique features, e.g. its abundant endemic epiphytes, allow it to rank as a distinct phytogeographic zone. It once contained some 10 000 plant species, around 2500 of them endemic to the area (Dodson and Gentry, 1978). The original forest was almost completely converted to cash-crop plantations and other non-forest uses within just 12 years from 1960 onwards.

An idea of the former biotic diversity may be gained from the Rio Palenque Science Center at the southern tip of the area, where less than 1 km² of primary forest survives. In this fragment there are 1200 plant species, 25 percent of them endemic to western Ecuador (Dodson and Gentry, 1978). As many as 100 of these Rio Palenque species have proved to be new to science; 43 are known only from the site, and a good number exists in the form of just a few individuals, some as a single individual.

About 8 km east of Rio Palenque is the Centinella Ridge, isolated from the main Andean range. Some 600 m high, and measuring only 20 km long by 1 km wide, the ridge formerly supported almost 100 endemic plant species (Gentry, 1986a). Between 1980 and 1984 it was cleared for settlement agriculture and its native vegetation, including its endemic species, was eliminated. Several dozen other semi-isolated ridges along the base of the Andes could well show similar species richness and high endemism, but they remain little explored botanically. If they prove to match the floristic richness of the Centinella Ridge, they could well contain at least 1000 undiscovered species, many of them endemic. Around half have recently been cleared for agriculture (Gentry, 1987).

Western Ecuador, and the other two areas described above, rank as the hottest of hot spots insofar as they are the richest and the most threatened of all the areas considered in this paper. In these three areas together there must have already occurred a mini-spasm of extinctions. In the light of the data presented, it is realistic to suppose that until recently they supported a total of 26 000 plant species, together with well over 500 000 animal species, indeed many more animal species if original numbers were proportionally higher than postulated on the basis of a minimum planetary complement of 5 million species. Endemism levels ranged from 25

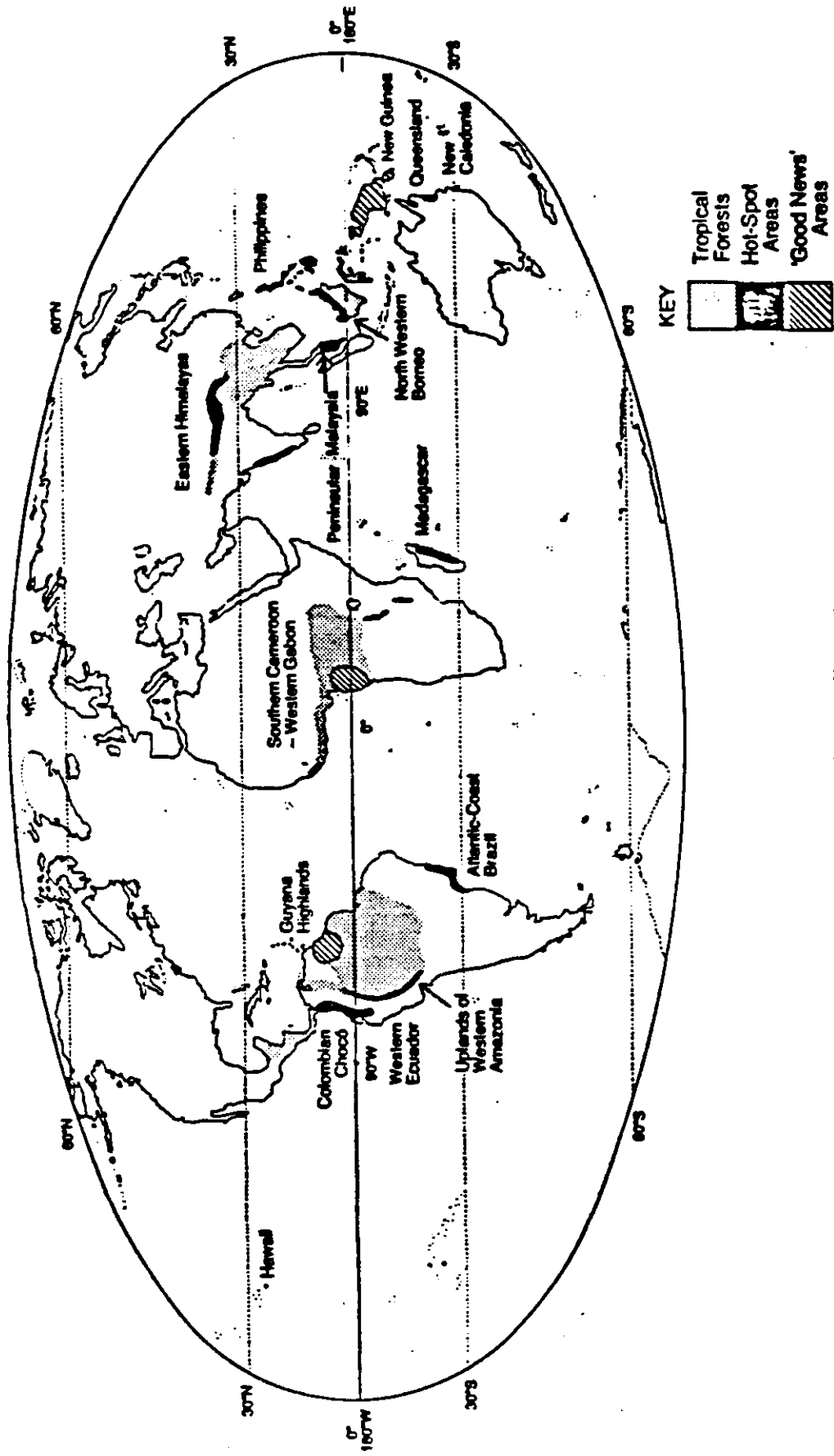


Fig.1. Tropical Forests: Hotspot Areas.

to 82 percent. In each area less than 10 percent of original vegetation remains today, or is likely to last beyond the end of the century. According to the well-established theory of island biogeography (MacArthur and Wilson, 1967), when a habitat loses 90 percent of its original extent it can no longer support more than 50 percent of its original species. In these three areas alone, then, recent or near-future extinctions could well total some 6200 plant species and at least 124 000 animal species. Alternatively stated, a collective area of originally 1 089 000 km² of tropical forest, amounting to only 0.74 percent of Earth's land surface, formerly supported 10.4 percent of Earth's plant species; and it is now surely experiencing the extinction of almost 2.5 percent of Earth's plant species and at least a similar share of animal species. See Table 3 for a consolidated summary.

Let us suppose, moreover, that the great majority of these extinctions will have occurred during the last 50 years of this century (much deforestation overtook Madagascar and Atlantic coast Brazil before 1950, whereas western Ecuador did not start deforestation until 1960). The calculations above indicate that in these three areas alone an average of one plant species will have been eliminated every three days, and several animal species, possibly as many as five species, every day.

Of course these are crude calculations. They are advanced solely as a preliminary exploration of a mass-extinction episode already underway: no more, no less.

4. *The Colombian Chocó*

The Colombian Chocó is an expanse of mainly coastal-plain forest, extending from the Panama border right through to the Ecuador boarder, and formerly comprising almost 100 000 km² of forest. While only a little more than 3500 plant species have been recorded, there are probably at least 8000, and possibly 9000, in just the Chocó Department, with a total of at least 10 000 in the whole of the Chocó region. Of these, 25 percent are believed to be endemic (Gentry, 1982a, 1982b; Forero and Gentry, 1987). Similarly high rates of endemism apply to birds (Terborgh and Winter, 1983) and butterflies (Brown, 1982).

Since the beginning of this century there has been a steady stream of settlers spreading out along the rivers, drawn by the timber stocks and mining potential, and pushed by socio-economic problems, such as land hunger in the Colombian

highlands (Gentry, 1987; Kirkbride, 1986). In 1980, two-thirds of rural households were either landless or they worked insufficient land to sustain themselves (Sinha, 1984); and today the mal-distribution of farmlands has become still more skewed. Moreover, there are growing throngs of workless people. Of a labour force of 9 million people in 1984, unemployed and under-employed amounted to 40 percent; and increasingly these impoverished people seek to support themselves through settlement agriculture in the Chocó and in Amazonia (see next item).

Since the early 1970s, deforestation has proceeded apace. The northern part of the Chocó has virtually all been deforested by logging and the spread of agriculture. In much of the central Chocó, forest accessible from rivers, including tributaries, has been all but eliminated, apart from a few remote localities. In the southern sector adjoining the Ecuador boarder, forest has given way to oil-palm plantations (Gentry, 1987). All in all, undisturbed forest in 1979 amounted to less than 80 000 km², meaning that roughly 20 percent of the forest cover had already been removed (Gentry, 1987). Today there is probably no more than 72 000 km² left and deforestation is proceeding faster than ever.

5. *Uplands of Western Amazonia*

This area includes upland sectors between 500 and 1500 m of the Andean slopes that border Western Amazonia, with high rainfall year-round and fertile soil. It comprises a belt mainly 50 km wide, sometimes only 25 km. It extends about 2200 km from the southern part of Colombian Amazonia, through Ecuador, and right along the Amazonian fringe of Peru. Thus it encompasses no more to than 100 000 km². Not only is it extremely rich in species, it is probably undergoing more forest depletion than is occurring in the 15 times larger Brazilian State of Amazonas.

Western Amazonia as a whole, i.e. lowlands as well as uplands, is surely the richest biotic zone on Earth (Brack, 1987; Caballero, 1981; Gentry, 1986a, 1988a; Parker, T.A., 1987; Remsen, 1987; Stark and Gentry, 1988; Terborgh, 1987). Indeed it deserves to rank as a kind of global epicentre of bio-diversity (Munn, 1987). In south-eastern Peru, the forests of the 15 000 km² Manu Park contain at least 8000 described plant species, or almost half as many as in the 520 times larger USA. There are also 200 animal species, or more than in the USA and Canada, and 900 bird

species, or more than 10 percent of all those on Earth. *Manu* extends from the Amazon plain far up in the Andean slopes and, as elsewhere along the fringes of Western Amazonia, much of the flora and fauna of the lowlands are found in the "upper tropics" as well. But the converse does not apply to the same extent. Of 1200 bird species in Peruvian Amazonia, 75 percent of the country's total, there are many more above the 1000 m line than below; and of 160 tanagers in the whole of Amazonia, more than 120 occur in the upper tropics (Parker, T.A., *et al.*, 1982; see also Haffer, 1985 and Terborgh *et al.*, 1984; for similar findings in Colombia and Ecuador, see Cracraft, 1985; Hilty and Brown, 1984).

Despite the extreme biotic richness of this part of Western Amazonia, we know all too little about the flora of the area. We cannot even advance a substantiated estimate of the total number of plant species. Of an estimated 10 000 plant species awaiting discovery in the Neotropics, many are surmised to be in Western Amazonia (Gentry, 1988b). There are reputed to be 4000 species in the relatively small Ecuadorian sector alone (Balslev, 1988). For the purposes of this paper, and on the basis of comparative assessments (Gentry, 1987), we can hazard an "informed assessment to the effect that Western Amazonia may well support 20 000 plant species.

More important still, there is a higher level of endemism in the uplands than in the lowlands (Brack, 1987; Dourojeanni, 1986; Duellman, 1987; Gentry, 1986a; 1988a; 1988b; Gentry and Dodson, 1987a; 1987b; Patton, 1987; Remsen, 1987). This probably occurs, in part at least, because the Andean slopes are divided by deep valleys. In just eight valley systems of eastern Peru, several as small as 5000 km² in extent, there are 65 endemic bird species (Parker, T.A., *et al.*, 1982). For vertebrate species generally in five separate drainages, the endemism level appears to be of the order of 30 percent (Parker, T.A., 1987; Terborgh, 1987). While the level of plant endemism is little documented, we know from other biotically rich areas in tropical forests of South America that endemism among plants often matches that of animals (Gentry, 1987). So it is realistic to suppose that the endemism level for plant species in the area could well be 25 percent, if not higher, and this figure is accepted for the purposes of this paper.

Throughout much of the area there has been extensive road building for at least two decades.

This fosters the spread of subsistence farming and plantation agriculture (coffee, tea, cocoa, coca) in the area with its rich soils. The result has been large-scale conversion of forest, both by outright deforestation and by gross disruption of forest ecosystems. In the Colombian sector, the influx of new settlers in the late 1970s was eliminating between 1500 and 2000 km² of forest per year and degrading a good deal more (Marsh, 1983). According to scattered reports and the author's own field findings in south-eastern Colombia, the amount of land deforested and otherwise converted so far could well amount to 10 000 km², viz. virtually the entire upper tropics zone.

In the Ecuador sector there were only 45 000 people in 1950, but almost 300 000 today (Salari, 1986). Since the late 1960s, the sector has been Ecuador's most important source of petroleum, which has been paying for a large share of the national budget. There has been not only much road building and settlement but also rapid conversion of forest into oil-palm plantations; Ecuador has high hopes that palm-oil will join petroleum as a major source of foreign exchange for its ailing economy (Bromley, 1981; Hiraoka and Yamamoto, 1980; Rudel, 1983). The amount of forest converted to date could well be as much as 15 000 km², again almost all the remaining forest being in the upper tropics zone.

As for Peruvian Amazonia, the largest and biotically the richest part of the area, forest depletion is proceeding widely and rapidly, but because the upper tropics zone is much more extensive here than in Colombia and Ecuador, the forest has not yet been eliminated so widely. In the late 1970s, almost 30 000 additional people were entering Amazonia each year, mostly into the upper tropical zone (Dourojeanni, 1979; Myers, 1980). They were arriving primarily in response to land hunger in traditional farming areas of western Peru, where landlessness and near-landlessness amounted to 75 percent of small-scale farmers (Durham, 1979; Sinha, 1984). By 1979, lands under effective agricultural use in Peruvian Amazonia, mostly in the uplands, amounted to 13 200 km², with a further 37 400 km² of abandoned farmlands (Myers, 1980). Today, the total is put at more than 70 000 km², in the uplands and lowlands combined, with an annual deforestation rate of almost 3000 km² (Dourojeanni, 1988; Salari *et al.*, 1988).

In summary, and according to recent observers (Gentry, 1987; Munn, 1987; Parker, T.A., 1987; Patton, 1987; Salari *et al.*, 1988;

Terborgh, 1987), almost the entire upper tropics zone has been deforested in Colombia and Ecuador, while in Peru, the same applies at least from the Rio Marañon in the north to the Rio Apurimac in the south. This means that, roughly estimated, some 65 000 km² (65 percent) of the area's forest has already been cleared or otherwise converted. Moreover, deforestation is proceeding ever more rapidly. There is a progressive build-up of land hunger pressures in traditional farming territories of all countries concerned; and these pressures are being compounded by faltering economies and population growth. In addition, each of the governments in question perceives an incentive to speed up settlement of Amazonia as a means to assert sovereignty over the area with its abundant mineral resources. Given the accelerating deforestation trends of the past two decades, it is not unrealistic to surmise that at least 90 percent of forest will be converted by the year 2000, if not sooner, meaning that 50 percent of the species of the area will have disappeared or be on the point of elimination.

6. Eastern Himalayas

Phytogeographically, the Eastern Himalayas form a distinct floral region (Maheshwari, 1980; Ohashi, 1975; Palliwall, 1982; Polunin and Stainton, 1984; Sahni, 1979; Takhtajan, 1986). The area comprises Nepal, Bhutan and neighbouring states of northern India, plus a contiguous sector of Yunnan Province in south-western China. Although some Himalayan forests occur at altitudes of 1800 to 3500 m, where their physiognomy, structure, etc., make them more akin to temperate zone forests, and they all lie well north of the Tropic of Cancer, they will be considered here as tropical forests since they occur largely within the climatic tropics.

The Eastern Himalayas feature ultra-varied topography, a factor that fosters species diversity and endemism. Many deep and semi-isolated valleys are exceptionally rich in endemic plant species. In Sikkim, in an area of 7298 km², of 4250 plant species, 2550 (60 percent) are endemic (Palliwall, 1982).

In India's sector of the area some 5800 plant species occur, roughly 2000 (36 percent) of them being endemic (Jain and Mehra, 1983; Jain and Sastry, 1982; Maheshwari, 1987; Nair, 1987; Ramakrishnan, 1985; Rao, 1980; Nayar and Sastry, 1987). In Nepal there are an estimated 7000 plant species, many of which overlap with those of India, Bhutan and even Yunnan (totals for

the Eastern Himalayas). Of these plant species, at least 500 (almost 8 percent) are thought to be endemic to Nepal (Hara *et al.*, 1978-82; Shrestha *et al.*, 1986). Bhutan possesses an estimated 5000 species, of which as many as 750 (15 percent) are considered to be endemic to the Eastern Himalayas (Grierson and Long, 1983).

As for China, it harbours an estimated 15 000 plant species in its tropical regions, which comprise some areas additional to the main locality in Yunnan (Anon., 1985; Hou, 1983; Takhtajan, 1986; Zheng-Yi, 1980). Yunnan alone, with its centres of exceptional endemism (Tsun-Shen and Zhi-Song, 1984; Zalfu, 1984; Zang, 1987; Zhenzhou, 1987), is believed to possess almost 12 000 species, mostly in its tropical forest zone that now covers only 10 percent at most of the 436 200 km² province. Plant endemism rates range from 10 to 34 percent according to locality. But regrettably, no good data are available for species numbers and distribution. For the purposes of this paper and its attempts to come up with "working estimates" of species totals, let us consider an informed and strictly conservative assessment, based on the author's communications with Chinese botanists (Youxu, 1987; Zang, 1987; Zhenzhou, 1987): Yunnan's tropical forest plants total 7000 species, some overlapping with territories to the west; at least 1000 (14 percent) of them being endemic.

In summary then, in that portion of the region within the Indian sub-continent, i.e. excluding south-western China, there are an estimated 8000 plant species, some common to the Indian sub-continent, at least 1000 of them endemic. So a conservative estimate for the whole of the Eastern Himalayas can be set at 9000 species, with 3500 (39 percent) of them being endemic.

Early in this century, forest cover in the entire Himalayan range was still extensive, especially in the eastern portion. Today, much has been eliminated altogether, and most of the remainder is degraded (Gupta and Bandhu, 1979; Myers, 1986; Singh and Kaur, 1985). In the Indian sector of the eastern portion of the range, there is virtually no forest left below 2000 m, and in the next zone up to 3000 m it has declined from about 35 percent in 1950 to 8 percent or less today (Haig, 1984; Lall and Moddie, 1981; Maheshwari, 1987; Rao, 1987). The total can be tentatively put at 57 000 km², and as much as 66 percent is biologically depauperate. Population pressures are already acute: 70 percent of smallholdings in the Indian sector of the Eastern Himalayas are less

than 1 ha each.

In Nepal, forest cover declined by 1982 to less than 25 000 km² (Bajracharya, 1983; Malla, 1986). Of today's forest, estimated at a little over 21 000 km², 33 percent is considered degraded to such an extent that it no longer retains more than a fraction of its biological productivity and biotic richness. If current rates of deforestation continue in Nepal, there will be virtually no forest left by the end of the century (Martens, 1982; Wallace, 1985). As for Bhutan, at least 23 000 km², or 50 percent of national territory, are still forested, but only 22 percent features closed or partially closed forest (Sargent *et al.*, 1985). Moreover, many forest tracts, especially those that are richest biotically, have been severely disrupted through logging and expanding agriculture (Sargent, 1985).

In the case of Yunnan, there is scant information available except that tropical forests are reported to have declined since 1950 from 55 to 21 percent of their former extent, i.e. to roughly 9000 km², due principally to heavy pressures from agricultural settlement (Chamberlain, 1987; Smil, 1985; Youxu, 1987; Zaifu, 1984; Zang, 1987; Zhang, 1986; Zhenzhou, 1987). Much of the remaining forest is degraded.

According to these data and best information available from recent researchers in the region, we can conclude, albeit tentatively, that former forest in the Eastern Himalayas as a whole was once some 340 000 km², but is reduced today to 110 000 km² at most, only 53 000 km² of that being primary forest.

7. Peninsular Malaysia

The Malaysia Peninsula features at least 8500 plant species in its 131 000 km², virtually all in the tropical forests which once covered pretty well the entire Peninsula (Aiken and Leigh, 1986; Ashton, 1982; Soepadmo, 1987; Whitmore, 1984). Of 2400 tree species, 654 (27 percent) are endemic; and this paper assumes a similar rate of endemism among all plants, for a total of 2,395 species. Of the endemic tree species, 343 (52 percent) are endangered; and of 66 such species recorded only in the State of Perak, many of them in tin-rich areas that have been heavily mined, the majority have not been seen since 1940 (Zakaria, 1987). Much the same appears to apply to all other endemic tree species in the Peninsula: according to two experts on the endemic species in the Peninsula (Ng and Low, 1982, "Their fate hangs in the balance".

Specially important are limestone outcrops. Totalling only 269 km², these outcrops feature 1,216 plant species of which 261 (21 percent) are endemic (Kiew, 1983). Virtually all outcrops are severely threatened by quarrying, mining and agriculture.

Ten years ago, only 53 500 km² of Peninsular Malaysia remained forested and of this, only 28 000 km² ranked as primary forest (Aiken and Leigh, 1985; Davison, 1982). Today, hardly any lowland forest, viz. the richest forest type, remains except in degraded form. Peninsular Malaysia has recently become a net importer of hardwood timber, a situation that directs still greater exploitation pressure at remaining upland forest.

8. Northern Borneo

The 757 000 km² island of Borneo contains at least 11 000 plant species, around 34 percent of them endemic, making it the richest of the Sunda islands (Davis *et al.*, 1986). As in the case of Peninsular Malaysia, virtually all the species occur in forests which constitute the overwhelmingly dominant type of vegetation on the island. That part of Borneo with the greatest species diversity by far is the northern sector that comprises most of Sarawak, the mini-state of Brunei and Sabah, totalling 175 000 km², or 23 percent of the island in terms of original forest areas (Takhtajan, 1986; Veldkamp, 1987). In this northern sector, a 10 hectare aggregate of forest can support 700 tree species, or as many as in the whole of North America (Ashton, 1977). Of Borneo's 267 dipterocarp tree species, 250 (94 percent) occur in Sarawak and Brunei, 68 of them (27 percent) being endemic (Ashton, 1982; see also Anderson, 1980; Chai and Choo, 1983). In Sabah there is a major centre of diversity at Mount Kinabalu, with its 4500 plant species, 700 to 1000 of them being orchids, or at least 25 percent of all orchids in South-east Asia (Luping *et al.*, 1978). Of Borneo's 135 fig tree species, 75 appear on Mount Kinabalu, 13 of them (17 percent) being endemic; while of the 100 or more *Ericaceae* species (rhododendrons and associates), 43 percent are endemic (Cockburn, 1980; Luping *et al.*, 1978). According to best-judgement, albeit little documented, estimates of experienced observers, northern Borneo, as defined here, is estimated to contain 9000 plant species of which at least 3500 species (39 percent) are believed to be endemic to the area.

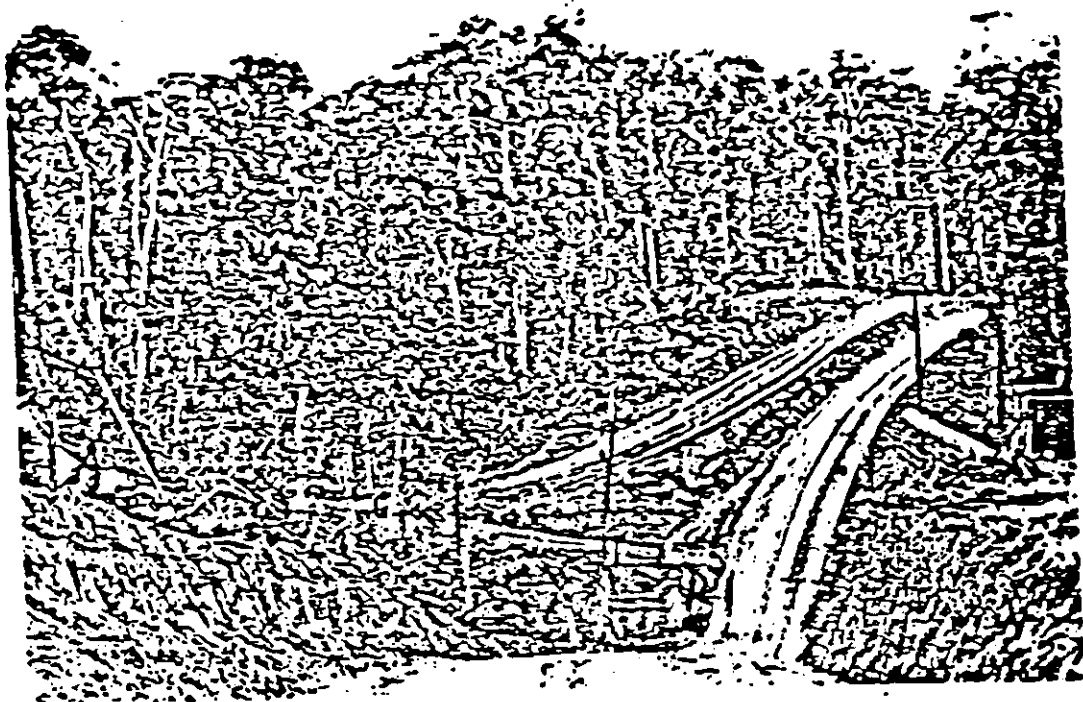


Fig. 2. Logging Road through Tropical Rainforest, Borneo

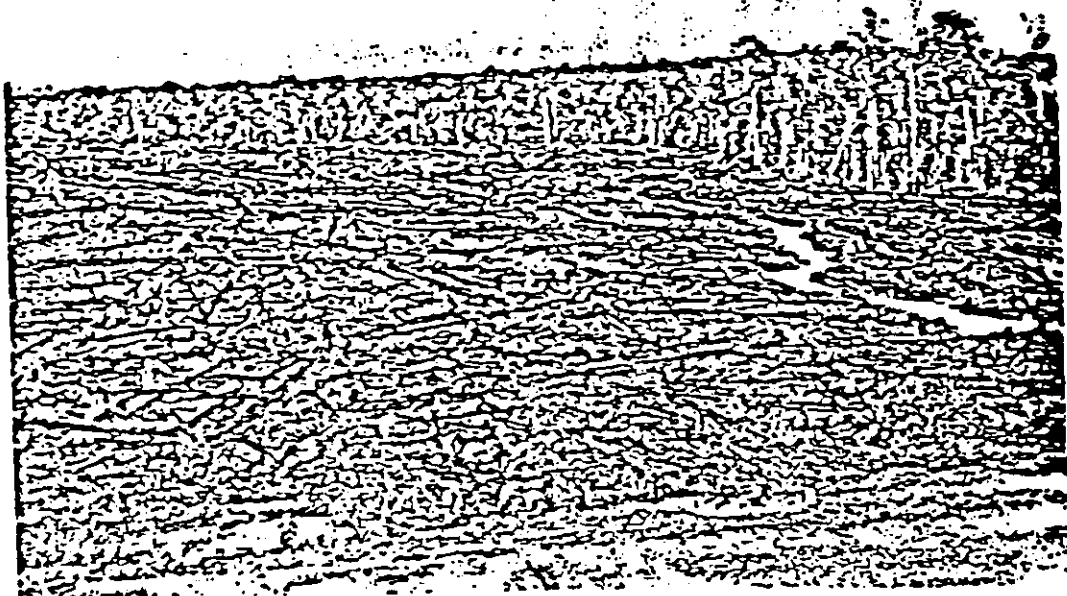


Fig. 3. Large area of Tropical Rainforest cleared, Malaysia

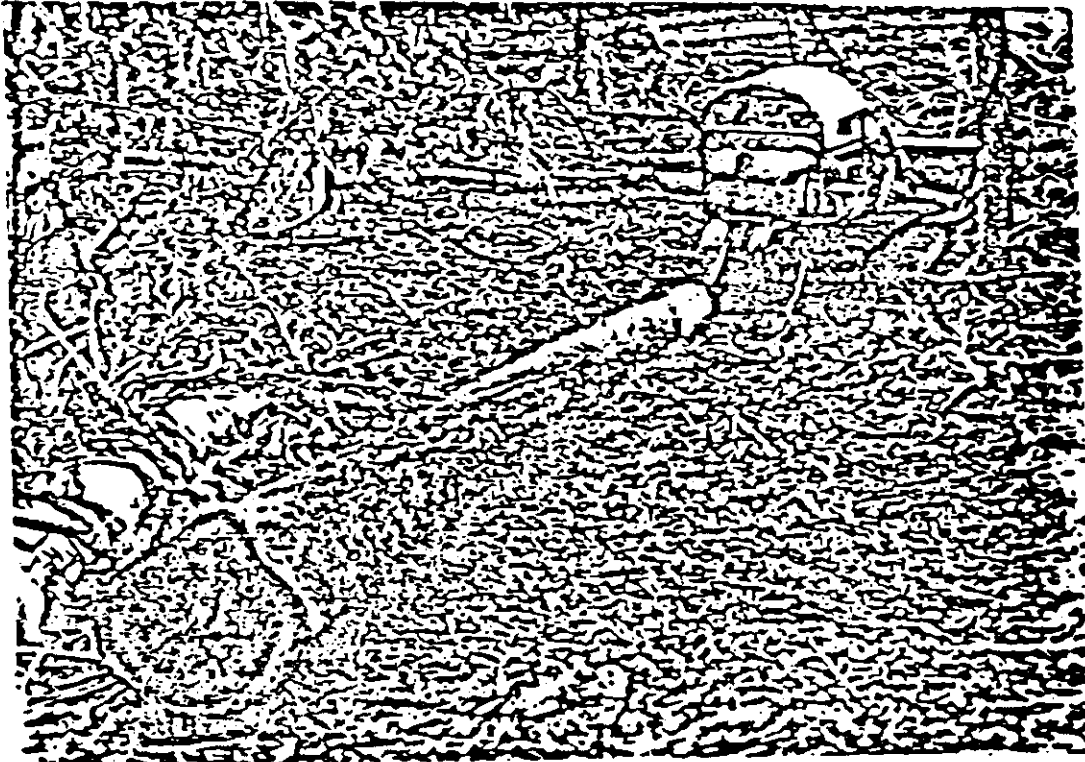


Fig. 4. Logging in progress. Digger dragging log. Borneo

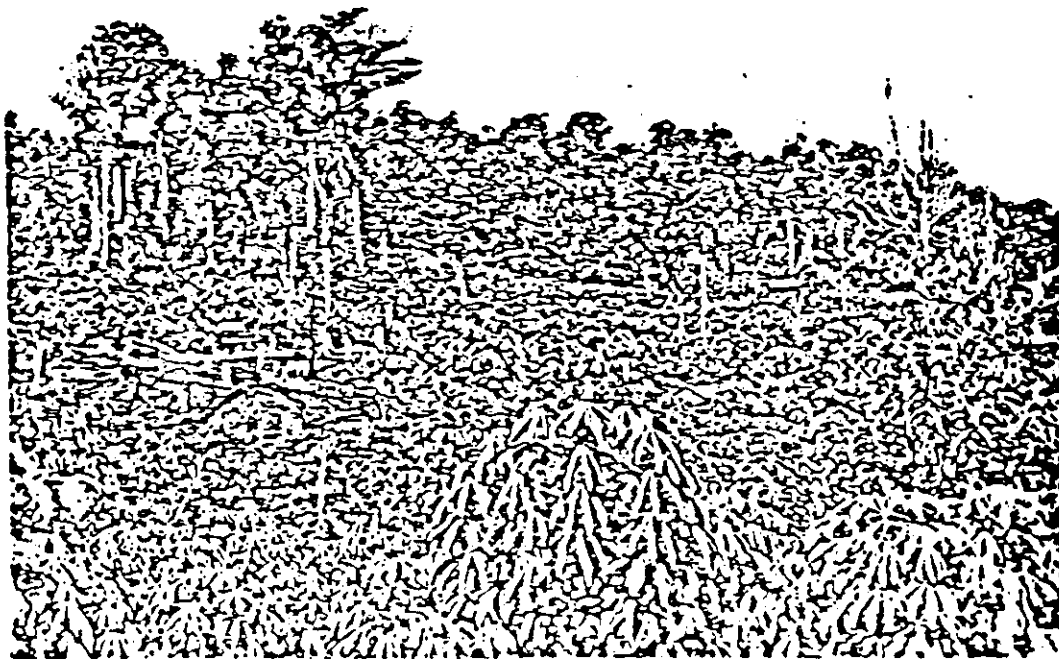


Fig. 5. Shifting cultivation of Tapioca, Malaysia

The forests of the area are being depleted quite fast. In Sarawak, logging proceeds apace and there remains a maximum of 75 000 km² of forest in the State territory of 125 000 km² (Caldecott, 1986; Hong, 1987; Lee *et al.*, 1986). No more than 50 percent of this is considered to rank as primary forest; almost all remaining forest tracts in Sarawak have been given out to timber concessions, and the entire expanse could well be logged by the year 2000, if not earlier. In addition, the State government considers that a large portion of forest lands, as much as 27 000 km², are suitable for conversion to permanent agriculture.

In Sabah, 61 500 km² (87 percent) of the State were still under forest cover of one type or another in 1980, around 50 percent having been disrupted and degraded (Myers, 1980). Today the amount of primary forest is reputed to be no more than 24 000 km² (Marsh, 1987). Almost 21 000 km² of forest are considered by the government to offer agricultural potential and are scheduled for eventual conversion to agriculture and agro-industry. Forest Reserves, which permit logging, comprise another 24 000 km². Forest protection areas amount to less than 5000 km². Through a recent shift in policy, the forests are being rapidly felled with the aim of maximising immediate revenues.

Fortunately, Brunei still features around 3600 km² of forest in little disturbed state.

9. The Philippines

There are some 8500 plant species in the Philippines, occurring almost entirely in tropical forests that covered most of the archipelago as recently as the start of this century (Madulid, 1982, 1987; Quisumbing, 1967; Revilla, 1986). Some 3700 plant species (44 percent) are endemic (Heaney, 1986). Many of the endemic plants have been collected only once or twice, and despite recent efforts by botanists to re-collect them in their original forest habitats, many have not been found and are presumed to be extinct.

Species richness and endemism have been promoted by the fact that the Philippines comprises more than 7000 islands. Some islands are strictly oceanic, others are fragments of once larger islands, and still others have had recent land-bridge connections to the Asian mainland. As a result, islands with quite distinct flora and fauna are separated by only short distances (Heaney, 1986). Of 628 terrestrial vertebrates, 229 (37 percent) are single-island endemic,

making them all the more vulnerable to summary extinction (Hauge *et al.*, 1987). A similar degree of highly localised endemism applies to plants (Madulid, 1987; Tan *et al.*, 1986).

Remaining forests cover no more than 55 000 km² (18 percent of the country), mostly in disturbed and degraded form. Old-growth dipterocarp forests in primary status, viz. the richest forests in both biotic and commercial senses, have been reduced to only 8000 km² at most, and they are expected to be logged out well before the year 2000 (Revilla *et al.*, 1987). Yet the principal factor in forest depletion is no longer the loggers. It is the slash-and-burn cultivators who occupy much of the country's uplands where most of the remaining forests are located, and who often feature population densities of 200 persons or more per km², i.e. far more than can be sustained by shifting cultivation of a traditional type (Cruz, 1986). These forest-land farmers now total at least 14.4 million. They mostly comprise subsistence peasants who, finding themselves landless in the country's lowlands, migrate to remaining forest lands. Given the current population growth rate nationwide of 2.8 percent (no significant decline since 1980), and the closing of the agricultural frontier in the lowlands, this migratory trend is likely to accelerate until virtually all remaining forest of whatever sort has been eliminated within another two decades (Myers, 1988a).

10. New Caledonia

In the island's forests there are 1575 plant species of which nearly 1400 (89 percent) are endemic (Cherrier, 1986; Holloway, 1979; Lowry, 1986; Morat *et al.*, 1984). Even before Europeans arrived there was much burning of forests, and during the period 1870-1940 the best timber stands were logged. By the middle of this century many forest areas with the greatest biotic diversity had been either burned or logged, and by 1970, only 2000 km² at most, out of a total of 3740 km², could be considered to feature undisturbed forest (Thomson and Adloff, 1971). By today, the amount has declined still further to 1500 km² (Morat *et al.*, 1984).

According to the Forestry Department, certain of these primary forests, together with secondary forests, many of them degraded to savannah woodlands, continue to recede under the impact of over-exploitative logging, mineral extraction and wild fires (Boulet, 1987; Cherrier, 1986; Dahl, 1984). Much of the forest remaining is on

steep slopes, so is less accessible to commercial logging, but the few remaining timber companies are still trying to harvest some last patches of primary forest (Dahl, 1984; Spiers, 1985). Moreover, all forests remain vulnerable to mining activities and frequent bush fires.

These, then are the 10 "hot spot" areas of special importance. In addition, there are several other, though smaller and less rich areas also under severe threat. They include the Mosquitia forest of Honduras and Nicaragua; the Darien Gap in Panama; five centres of diversity in Brazilian Amazonia; the south-western part of the Ivory coast; the "eastern arc" forests of Kenya and Tanzania; the Western Ghats of India; south-western Sri Lanka; southern Thailand; and Sumatra. Altogether, these areas possibly support as many as 5000 endemic plant species, by contrast with 34 200 in the hotspot areas.

Comparisons: Hawaii and Queensland

For comparison, let us briefly consider two hot spot areas in the developed world where conservation resources are much more plentiful than in the developing world, and where extinction threats can be much more readily reduced.

1. Hawaii

Covering only 16 707 km², the islands harbour at least 1100 native plant species, some 990 (90 percent) of them being endemic and nearly half of them threatened (Carlquist, 1980; Mueller-Dubois *et al.*, 1981; Stone and Scott, 1985). At least 75 percent of plant species and an estimated 825 of endemic species occur in the island's forests, which are now reduced to well under 50 percent of their original extent. Deforestation continues in response to a tax system which encourages forest clearing for agricultural expansion.

A comprehensive conservation strategy has recently been formulated (Nature Conservancy of Hawaii, 1987). Of roughly 150 ecosystem types, the bulk of them in the forests, 88 are considered so endangered that they will certainly be eliminated within another two decades unless they are protected forthwith. At least 30 of these ecosystems, representing 33 percent of the critically imperilled communities, could be saved for a cost of \$10 million, while the rest could be

secured for a further \$150 million.

2. Queensland

In northern Queensland, another developed-world area, there are 6300 km² of wet forest remaining out of some 13 000 km² half a century ago. In this tiny tract, less than 0.1 percent of the surface area of Australia and actually a patchwork of forest remnants, there are at least 1165 plant species, of which 435 (37 percent) are endemic to the area (Aiken and Leigh, 1987; Keto, 1984; Parker, P.K., 1987; Rainforest Conservation Society of Queensland, 1986; Tracey, 1982). As in many tropical areas, some plant species are so restricted that they occur in a single valley or on a single hilltop. Moreover, of the world's 19 primitive flowering-plant families, 13 occur here, two of them endemic to the area, giving the area the highest concentration of such plant families anywhere.

Yet despite the scientific value of the area, it continues to be logged, with support from the Queensland Government in the form of abundant subsidies. The area has been designated by the Government of Australia as a candidate for World Heritage Listing, a move that is being legally contested by the Queensland Government.

"Good News" Areas

Fortunately, there are a number of tropical forest areas with unusual concentrations of species, including many endemic species, and where there are few threats of imminent depletion. An instance is the Guyana Highlands, covering the south-eastern half of Venezuela and extending into Guyana, and a little into Brazil, amounting to 500 000 km². The area contains more than 400 endemic species described, out of a predicted flora of about 8000 species (Davis *et al.*, 1986; Maguire, 1970; Steyermark, 1984). Human populations are sparse and there seems little prospect that primary forests will be modified within the foreseeable future.

Another such area comprises southern Cameroon and western Gabon, extending into parts of Congo and covering roughly 300 000 km² (Brenan, 1978; Catinot, 1978; Hamilton, 1976; Letouzey, 1976; Stuart, 1987). Southern Cameroon supports probably the richest flora in continental tropical Africa, though statistical evidence is regrettably sparse. Gabon, while little explored botanically, is reputed to harbour around 8000 plant species of which 1750 (22 percent) are

endemic. Congo contains an estimated 4000 plant species, 880 (22 percent) of them endemic; and the western portion of Congo's northern forests is considered to be one of the most species-rich areas in the entire Zaire Basin. With human populations in Gabon and Congo totalling only 3 million people in 610 000 km², and no more than 5 million in southern Cameroon, population pressures on the forests are slight, though in Gabon there is some threat from logging interests.

New Guinea also ranks as a good news area for the most part. In the Papua New Guinea (PNG) portion there are more than 350 000 km² of forest left, covering about 75 percent of the country; and a roughly similar amount exists in the Irian Jaya sector of Indonesia, which is slightly smaller. These 700 000 km² of forest contain the great majority of the island's 11 000 plant species, 90 percent of them endemic (Gressitt, 1982; Morauta *et al.*, 1982; Pajmans, 1976). While 40 percent of the forests of PNG have been disturbed or destroyed through slash-and-burn farming, outright clearing amounts to only about 3000 km² per year. Broadly similar figures apply to Irian Jaya, where the government plans to devote about 20 percent of the territory to protected areas of various sorts. PNG contains only 3.5 million people and Irian Jaya 1.2 million, so population pressures are slight so far.

The forests of these three areas could well contain as many as 15 000 endemic plant species.

The Role of Parks and Reserves

Parks and reserves can play only a limited role in preserving species in hot spot areas, even though certain areas, notably Western Amazonia and Peninsular Malaysia, feature several protected areas of good size. The cost of establishing a network of parks and reserves, i.e. sufficient to safeguard a representative array of high-value forest ecosystems, would be high. A recent assessment (World Resources Institute and World Bank, 1985) estimates that to establish an adequate, though less than comprehensive, system of protected areas throughout the biome might require an outlay of \$800 million over 5 years.

In any case, there are severe limitations to protected areas as a long term safeguard strategy, due to the "islandizing effect". This occurs when a patch of habitat becomes a park and its environs are given over to alien activities, leaving the park as an isolated patch of habitat. For the park to serve as a viable ecological entity that can

safeguard 50 percent of its original species complement, it must generally constitute at least 10 percent of the original expanse of habitat, which is hardly ever the case. As a consequence of the "islandizing effect" and the processes of "ecological equilibration", there ensues a delayed fallout of species. Even in the best managed park, delayed fallout eventually causes the species complement to decline to less, often a good deal less, than before the islandization occurred.

The same process applies to those many forest areas that do not become parks, but are islandized through fragmentation of forest tracts. The remnants of primary forest in the Philippines have almost all become far smaller than 10 percent of their original extent. This means that they are too small already to constitute independent eco-units with full panoply of species in perpetuity, even if they were to be protected as parks forthwith. Much the same applies to large parts of remaining forests in Madagascar, Atlantic-coast Brazil, the Eastern Himalayas, Peninsular Malaysia and New Caledonia, where most of the remaining forests have been reduced to relict eco-islands. Indeed, in these six hot spot areas there must have been a sizeable fallout of species already.

For a graphic illustration of delayed fallout, consider Amazonia. According to Simberloff (1986), if deforestation continues at present rates until the year 2000 (and it is likely to accelerate), but then halts completely, we should anticipate an eventual loss of about 15 percent of the plant species of Amazonia. Were the forest cover to be ultimately reduced to those areas now set aside as parks and reserves, we should anticipate that 66 percent of plant species will eventually disappear, together with almost 69 percent of bird species and similar proportions of other major categories of animal species.

The Climate Connection

In any case, the best protected areas may shortly suffer severely through climatic disruptions. In Amazonia it is becoming apparent that even if sizeable amounts of forest cover were to be safeguarded but the rest were to be "developed out of existence", there could soon emerge a hydrological feedback effect that would allow a good part of the region's moisture to be lost to the ecosystem (Salati and Vose, 1984). In turn, this could impose a steady desiccatory process on the remaining forest until it became more like a woodland; with all that would mean for the

species communities that are adapted to forest habitats. Even with a set of forest safeguards of exemplary type and scope, Amazonia's remaining biotas would be more threatened than ever.

There are other climatic changes impending, with potential impact on tropical-forest biotas that could prove yet more pervasive and profound. By the end of the century or shortly thereafter, a planetary warming will surely be emerging, caused by a build-up of carbon dioxide and other "greenhouse gases" in the global atmosphere (Bolin *et al.*, 1986). In addition there will be some redistribution of rainfall patterns, with disruption of monsoon systems and other seasonal rainfall patterns (Davis, 1986; Emanuel, 1987; Myers, 1988b; Zong-Ci Zhao and Kellogg, 1988). Among hotspot areas that could be vulnerable to this form of perturbation are Eastern Himalayas, Philippines and New Caledonia (also Hawaii and Queensland).

Equally to the point, these climatic changes could work in amplificatory accord with other factors, such as deforestation and ecological sensitivity of species, to deplete species communities more than would be the case if they worked in isolation from one another. These synergistic responses could serve to impose a still greater scale of extinctions, and do so more rapidly, than is sometimes anticipated (Myers, 1987b).

Analysis and Summary Assessment

The findings presented in this paper indicate that unless far more vigorous conservation measures are instituted in the 10 areas in question, we can anticipate the extinction of a sizeable number of plant species by the end of the century or shortly thereafter. Assuming that endemic plants in these areas total rather more than 34 200 (Table 1), and assuming that their habitats are reduced to 10 percent or less of their original extent within the foreseeable future, there will ensue, according to island biogeography, the extinction of half these species, or more than 17 000 species. This extinction spasm, accounting for more than 13 percent of all plant species in tropical forests, will occur in a total area of only 292 000 km² or 3.5 percent of remaining tropical forests. These calculations also mean that almost 7 percent of Earth's plant species are now at terminal risk in 0.2 percent of Earth's land surface.

As for animal species, the number in danger is 350 000, assuming a minimum planetary total

of 5 million species. The true total could well be several times higher.

Furthermore we should not think only in terms of sheer numbers of species. There is a qualitative aspect to biotic depletion. In some cases there will be elimination of taxa beyond the species level. For instance, in the forests of Madagascar four or five families of plants are endemic to the area; and in New Caledonia, five families. In all of the hot spot areas, many plant genera are endemic. This makes the extinction spasm underway a yet more impoverishing phenomenon than is suggested by a simple count-up of species.

There is yet a further repercussion for the plant kingdom. Large plants have existed on land for the last 430 million years; and by 65 million years ago, flowering plants (the great majority of the plants considered in this paper) totalled somewhere between 100 000 and 150 000 species, constituting about 75 percent of all plant species on land. Today there are 220 000 such species, or 88 percent of 250 000 species (Knoll, 1986). But during the late Cretaceous mass-extinction episode, plant life on land seems to have escaped with moderate losses at most, possibly with only a few losses, as compared with animal life. Thus the impending depletion of the plant kingdom in hot spot areas alone seems set to match the worst mass extinction during the entire history of vascular plants; and it will surely prove greater than any other such episode. Alternatively stated, of the 15 million (maximum estimate) vascular plant species that are thought to have existed during the past 400 million years, 14.75 million have become extinct through natural, *i.e.* non-human caused, reasons. This works out at a very crude average of 1 species every 27 years (more in recent times, as the standing stock of species has increased). During the next 25 years or so, we can expect that the extinction rate in 10 hot spot areas alone may well average almost 2 per day, or almost 20 000 times the "background" rate.

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Post-publication note It now turns out that certain of the above findings are on the low side. For one thing, deforestation in many if not most of the hot-spot areas has been proceeding faster than thought. For a second and more important thing, the application of island biogeography theory in the calculations is unduly cautious and conservative. The basic assertion, viz. that when a habitat loses 90 percent of its original extent it can still support 50 percent of its original species, depends critically on the status of the remaining 10 percent of habitat. If this remaining portion is split into many small pieces of habitat (as is the case with virtually all the hot-spot areas described), then a further "islandizing effect" comes into play, reducing the stock of surviving species still further. It is not known how severe this additional depletion can be: informed estimates suggest the 50 percent figure could readily be reduced to (roughly) 40 percent, more generally to 30 percent, sometimes to 20 percent, occasionally even to 10 percent. Moreover isolated remnants of forest become prone to additional depauperizing processes such as "edge" effects, also to desiccating effects due to local climate change. So the calculations presented above for extinction rates, based on the 50-percent survivorship rate, should be considered as minimum estimates. The "true" extinction figures could well be a good deal higher.

In: Soule, M.E. (ed.) 1986. Conservation Biology: the Science of Scarcity and Diversity. Sinauer Associates, Inc.

SEVEN FORMS OF RARITY AND THEIR FREQUENCY IN THE FLORA OF THE BRITISH ISLES

Deborah Rabinowitz, Sara Cairns
and Theresa Dillon

A central concern of conservationists is the protection of rare species. Our colloquial notion of "rarity" brings to mind organisms that are uncommon or unusual, and these rare creatures sometimes take on connotations of being particularly fragile, precious, or valuable. Indeed, many biologists contend that rare species are more susceptible to extinction than common ones for a variety of reasons (Terborgh and Winter, 1980). The most pressing reason for concern is the presumed impending extinction of many species due to the destruction of tropical forests (Myers, 1984 and Chapter 19), but various taxa throughout the world are threatened as well.

However astute their natural history may be, biologists and conservationists lump together many kinds of organisms under the term "rare," possibly because English does not have a rich lexicon of words to describe rarity. This lack of precision obscures much interesting biology for a very heterogeneous group of organisms. Clearly, before we can effectively protect rare species, we must understand what kinds of rarity exist and in what important ways rare species differ from one another. Let us illustrate with two examples.

Argyroxiphium macrocephalum A. Gray (Compositae), the Haleakala silversword (Figure 1), is an extremely restricted endemic, found only in the "crater" of Haleakala Volcano on the Hawaiian island of Maui (Degener et al., 1976). Approximately 47,000 individuals exist, and within its tiny range, it is surprisingly common. Nonetheless, this is a plant that clearly merits the judgment of being rare on the basis of its restricted geographic range.

But some plants with very broad distributions are also justifiably termed rare. *Setaria geniculata* (Lam.) Beauv. (Gramineae)—knotroot bristlegrass—has a huge geographic distribution, from Massachusetts to California in North America, and southward through tropical America to Argentina and Chile (Hitchcock and Chase, 1950). This grass is not selective about the habitats in which it grows but it is never found in large local populations. That is, *S. geniculata* is chronically sparse, and is rare in the sense that it is never common anywhere.

The issue we are addressing is the kinds of rarity that plants can exhibit and we focus on three questions:

1. Can we clarify the concept of rarity? Are there distinct kinds?
2. If so, how frequent or unusual are the different forms of rarity?
3. What are the consequences of such a classification for conservation biology?

Thomas and Mallorie (1985) address similar issues with reference to the conservation of Moroccan butterflies, and Hubbell and Foster (Chapter 10) consider forest dynamics and conservation of tropical tree species.

KINDS OF RARITY

Naturalists have noted that plants may be rare in several ways. They may occur only in rare habitats, they may be very localized in a small area, or they may have few individuals. We begin by distinguishing three traits that all species possess.

1. *Geographic range*: Whether a species occurs over a broad area or whether it is endemic to a particular small area.
2. *Habitat specificity*: The degree to which a species occurs in a variety of habitats or is restricted to one or a few specialized sites.
3. *Local population size*: Whether a species is found in large populations somewhere within its range or has small populations wherever it is found.

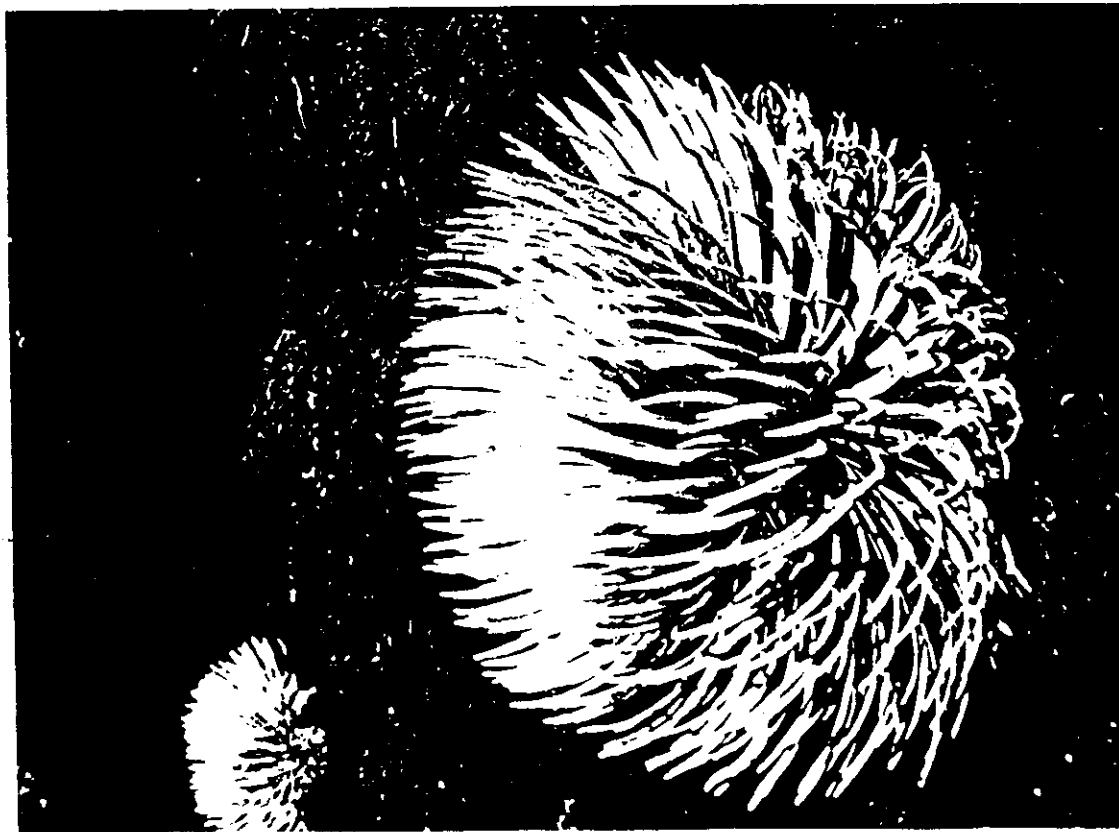


FIGURE 1. *Argyroxiphium macrocephalum*, the Haleakala silversword, on Maui in the Hawaiian Islands.

Of course, these three traits are really continuous variables, but for convenience, we can dichotomize them into an eight-celled $2 \times 2 \times 2$ table (Table 1; see also Rabinowitz, 1981). Only one of these eight categories contains species which are really common in the ordinary sense—plants with wide ranges, many habitats, and large population sizes. *Chenopodium album*, lamb's quarters or fat hen, is an example.

Endemics such as *Argyroxiphium macrocephalum* are species with small ranges and restricted habitats. *Lloydia serotina* provides a striking example (Woodhead, 1951). In Britain, it is found only in Snowdonia, in tiny vertical fissures on almost sheer cliff faces. The plants are often solitary and never common, making the alpine lily rare in each of the three dimensions. These are the classic rare species that attract biologists' attentions (Stebbins and Major, 1965; Kruckeberg and Rabinowitz, 1985). In contrast, sparse species such as *Setaria geniculata* are particularly inconspicuous; they illustrate the distributional form opposite to endemics: wide range in numerous habitats, but small populations.

Plants restricted to specific habitats but with broad geographic range, such as mangroves (*Rhizophora mangle*) and salt marsh species, usually can easily be found since these plants are generally as predictable as their habitat. An interesting example in the British flora is *Draba muralis*, wall whitlow grass, a small herb in the mustard family. Native only to shallow immature soils of carboniferous limestone, it is widely scattered over England in populations where it is never common (Ratcliffe, 1960). Curiously, as an introduced species, *D. muralis* is capable of spreading as a garden weed. The remaining

TABLE 1. Seven forms of rarity, based on three traits.

Habitat specificity	Geographic distribution			
	Wide		Narrow	
	Broad	Restricted	Broad	Restricted
Somewhere large	<i>Chenopodium album</i> , lamb's quarters	<i>Rhizophora mangle</i> , red mangrove	<i>Primula scotica</i> , Scottish bird's-eye primrose	<i>Argyroxiphium macrocephalum</i> , Haleakala silversword
Everywhere small	<i>Setaria geniculata</i> , knotroot bristlegrass		<i>Draba muralis</i> , wall whitlow grass	<i>Lloydia serotina</i> , alpine lily

(Adapted from Rabinowitz, 1981)

two categories have narrow geographic range but broad habitat specificity. Botanists have difficulty citing examples of these types of rarity, but one interesting case is *Primula scotica*, Scottish bird's-eye primrose, confined to the extreme northeast coast of Scotland and Orkney. Within its tiny range, it is found in populations of hundreds of individuals in a variety of habitats as variable as maritime cliffs, dune slacks, and pastures (Ritchie, 1954). The geographic limitation of such species is particularly puzzling.

Armed with this system of classification, we can determine the frequencies of different forms of rarity in a flora. To do so, we need both a data base (a flora with sufficient information to give us data on the three traits independently) and a method to assign species to the eight categories in an unbiased manner.

We ideally wish to consider commonness and rarity of a large number of species from data collected over their entire ranges, but flora inventories are not extensive enough to permit us to do so. The two studies in this volume that examine rarity from large data sets, ours and the study on the trees of Barro Colorado Island in Panama by Hubbell and Foster (Chapter 10), are perforce geographic samples of larger "universes." Hubbell and Foster census a 50-ha plot and find that many trees which are rare within their area of concern are common in nearby portions of the forest. We use the flora of the British Isles as our data base and find similarly that species with geographically restricted distributions in Britain may have much larger distributions when viewed on a global scale. *Thymus serpyllum*, for example, is confined in Britain to a tiny area of dry sandy soil on the breckland of East Anglia, but its range extends through European Russia to Siberia and China (Pigott, 1955). This change in status for rarities as geographic area increases is not really a drawback of these two studies, but it emphasizes that rarity must be considered on a variety of spatial scales, and in particular in delimited samples versus "global" censuses. Conservationists face similar decisions when they deal with whether to protect geographic outliers of species with vast populations in other areas, for instance prairie plants which extend into the eastern United States.

THE BIOLOGICAL FLORA OF THE BRITISH ISLES AS A DATA BASE

The British flora, one of the best known in the world, is our data base. The *Biological Flora of the British Isles*, published in the *Journal of Ecology*, is a series of articles each containing detailed information on habitat distribution and abundance for particular species. A total of 177 native species or 9.7 percent of the native flora have been described

in the *Biological Flora* as of early 1985. The *Atlas of the Flora of the British Isles* (Perring and Walters, 1976; Perring and Sell, 1978) was the source for a dot map of geographic range for each species on a 10-km grid (Figure 2). In addition to providing sufficient information to document the three traits of interest, there are two other important advantages of this data set. The flora of the British Isles corresponds to a natural geographic area, and the *Atlas*' dot maps are based on an aerial grid of equal-sized entries (Stott, 1981). There are many excellent floras containing dot maps which do not lend themselves to quan-

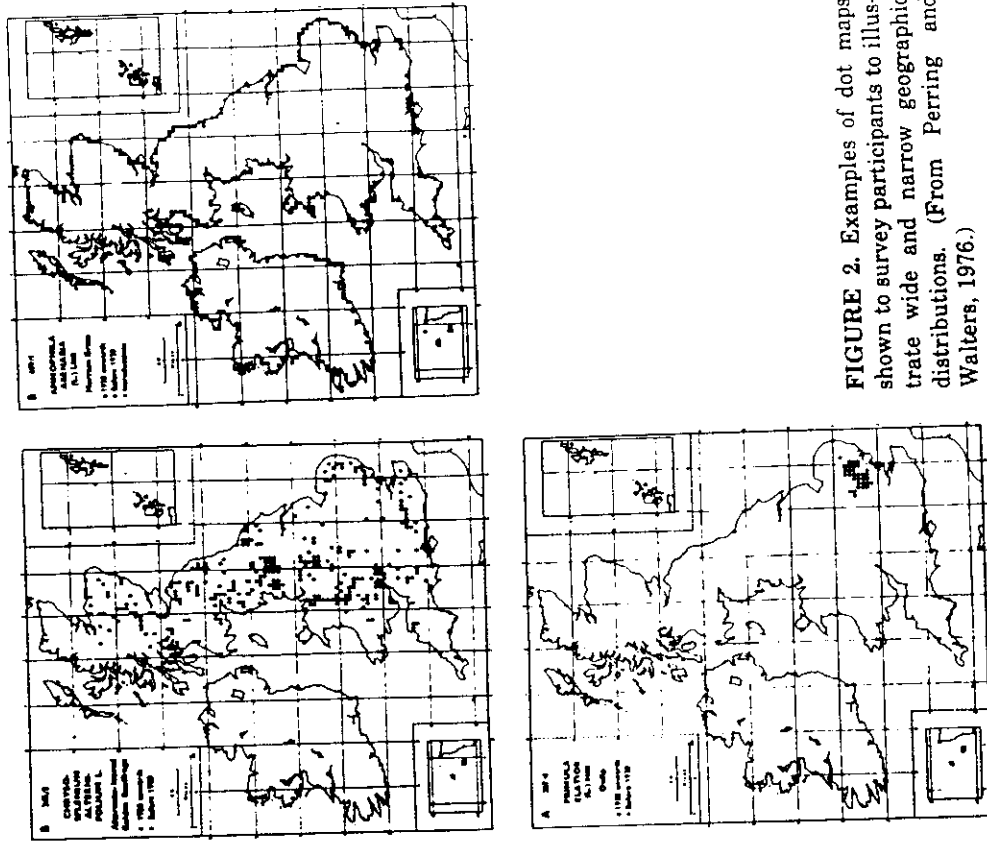


FIGURE 2. Examples of dot maps shown to survey participants to illustrate wide and narrow geographic distributions. (From Perring and Walters, 1976.)

titative analyses because they are either based on arbitrary political boundaries (for example, Pennsylvania; Wherry et al., 1979) or the aerial units are unequal (such as counties in the United States; Great Plains Flora Association, 1977).

What historical forces have shaped the flora of the British Isles and how does their island nature influence our study? Even for islands, the British Isles have a depauperate flora and a low level of endemism. The former is because of repeated glaciation and the latter because the British Isles have only recently become separated from Europe, about 5500 years ago (Pennington, 1974). Because they are islands, they possess a long coastline and consequently well-developed maritime habitats. Members of these communities are habitat specialists to a large degree—for instance, *Ammophila arenaria*, marram grass (Figure 2). The British flora, of course, is in a dynamic state and is pervasively influenced by human activity (Perring, 1974).

BIAS IN SPECIES SELECTION FOR THE BIOLOGICAL FLORA

Since the *Biological Flora* is a subset of the entire British flora, we need to know (1) how its entries were selected, and (2) whether they are a biased set from our perspective. The entries to the *Biological Flora* are contributed on a voluntary basis by taxonomists and ecologists (British Ecological Society, 1975). If these biologists have a tendency to select rarer species (because they attract attention) or common species (because they are easier to work with), then our frequencies of the seven forms of rarity will be influenced. Probably both kinds of bias have operated during different periods (P. Grubb, editor of the *Biological Flora*, personal communication). Earlier contributions (1940s and 1950s) were from naturalists and taxonomists who were interested in "unusual" species. In the 1960s and 1970s, as demographic analyses became popular under J.L. Harper's influence, entries in the *Biological Flora* were selected primarily for their experimental tractability. Thus they tended to be common species.

The net effect of these biases can be quantified in two ways with the dot maps. In the *Atlas*, each species in the entire flora is marked with an A, B, or C, depending on the number of vice-counties in which it is found (Figure 3). We can compare these frequencies in the flora as a whole with the frequencies in the subset in the *Biological Flora*. The species occurring in the fewest counties (A) are in the same proportions on both lists, but widespread species (C) are overrepresented in the *Biological Flora* and intermediate species (B) are underrepresented (G -test; $G = 7.10$, $0.025 < p < 0.05$; Sokal and Rohlf, 1981).

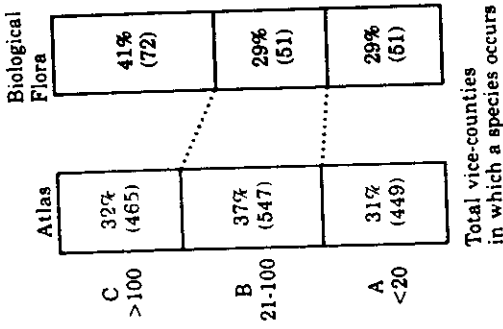


FIGURE 3. The total number of vice-counties in which a species is found. Sample sizes are 1461 for the *Atlas of the British Flora* (not including the *Supplement*) and 174 for the *Biological Flora of the British Isles* (3 of the 177 total native species in the survey do not have an ABC designation in the *Atlas*).

A second means of assessing bias in species selection is to compare the distribution of number of dots on the maps for species in the *Biological Flora* with those from the *Atlas*. Each dot in the maps represents the occurrence of the species in a 10 km² area. Total dot counts per species thus measure the total geographical area in which the species is found.

Of the 177 species in the *Biological Flora*, 80 were selected at random and their total dots counted from the maps printed in the *Atlas*. Similarly, total dot counts were obtained for 80 species chosen at random from the 1822 species in the *Atlas* (introduced species and subspecies were not included). The distribution of the total dot counts for the sample from the *Atlas*, representing all the British flora, was highly non-normal, being skewed to the right (Figure 4). The square root transformation commonly used for count data did not normalize the distribution, but did make it less skewed. The species in the *Biological Flora* show a more uniform distribution.

The random samples from the *Atlas* and the *Biological Flora* were compared using the Kolmogorov-Smirnov Two-Sample test (Sokal and Rohlf, 1981), and were significantly different ($D = 0.30$, $p < 0.01$). Inspection of Figure 4 confirms the finding that moderately widespread species are underrepresented, widespread species are overrepresented, but infrequent species are present in their actual proportion. The *Biological Flora* is in fact a biased subset of the British flora, at least in terms of geographical range.

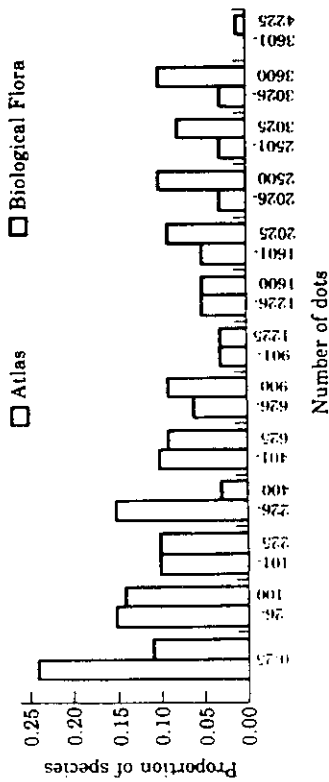


FIGURE 4. Histogram of the frequency of total dot number on distribution maps for species in the *Atlas of the British Flora* and in the *Biological Flora of the British Isles*. The ABC analysis (Figure 3) was based on the number of vice-countries in which a species occurred. Although this measure is correlated with total dot counts, the two are not identical measures; total dot counts for species classified as "A" in the two samples ranged from 1 to 182, those classified "B" from 71 to 2094, and "C" from 392 to 3745. Moreover, the ABC classification necessarily uses arbitrary cutoff values in dividing a continuous variable into discrete categories.

ASSIGNMENT OF SPECIES TO RARITY CATEGORIES

Our second requirement for estimating the frequencies of the forms of rarity in a flora was a method of assigning each species to one of the eight cells in an unbiased fashion. If one person were to classify all the species in the *Biological Flora*, the results would reflect that person's biases and preconceptions about rarity, albeit based on much field experience with rare plants. Since there were no objective boundaries between, for instance, wide and narrow geographic distributions, our judgments about assigning species to categories were necessarily subjective, but we hope not arbitrary. Our approach was to use a survey format and ask a number of biologists to classify each species. We specifically did not tell our participants what criteria to use in making their choices. Our classification of species therefore rests on educated opinion rather than on objective, arbitrary criteria. We are not advocates of the idea that science is an objective and impersonal march toward truth and reality. Science is a human, socially contingent activity (Gould, 1981), and there is a large, generally accepted role for informed opinion in scientific inquiry. We are simply utilizing it more systematically here.

Dot maps from the *Atlas* were used to indicate geographic range, and quotes were extracted from the *Biological Flora* to describe habitat

specificity and local abundance. For geographic distribution, our judges were asked to decide whether the distribution was "Wide" or "Narrow." For habitat specificity, the choices were "Broad" or "Restricted," and for local abundance "Somewhere Large" or "Everywhere Small." Before filling out the survey, participants were shown unambiguous examples of species belonging to each of the two choices available for the three traits. Maps (Figure 2) were used to demonstrate two types of wide geographic distribution, and we emphasized that only total range, not density, of dots should be considered. For example, *Chrysopolitanum alternifolium*, golden saxifrage, shows wide geographic distribution over most of the interior of Britain, but *Ammophila arenaria*, marram grass, has a wide geographic distribution along the coast. The map of *Primula elatior*, oxlip, was given as an example of a species with narrow geographic distribution. Examples given for the other two traits are shown in Table 2. For habitat specificity, the first quotation is an example of broad specificity, the next two quotes are examples of narrow restriction. The second quote illustrates different descriptions of a single habitat. For local population size, the first two quotes are examples of species that should be scored as having populations that are somewhere large, the last as a species which has populations that are everywhere small.

In the survey itself the three traits were in separate sections, each in a different random order. The dot maps for the geographic distribution section were presented four to a page with the species names removed. Tables 3 and 4 give examples from the sections on habitat specificity and local abundance. Each of the three traits was thus judged independently and without reference to species identity. Each choice always included a category of "can't tell," which participants

TABLE 2. Examples shown to survey participants to illustrate the kinds of habitat specificity and local abundance.

HABITAT SPECIFICITY

1. "Marshes, fens, heaths, woodlands, and waste ground. A common weed of arable land."
2. "Edges of roads, along paths and cart-ruts, and along ridges in woods."
3. "Restricted to soil-filled crevices in scree slopes."

LOCAL POPULATION SIZE

1. "In favorable situations, it forms large clumps or pure stands which may cover considerable areas."
2. "Locally abundant."
3. "Scarce when present. Occurs as widely scattered individuals."

TABLE 3. Sample page from survey administered to participants, describing habitats of individual species from the *Biological Flora of the British Isles*.

Wide	Narrow	Can't tell	472.1 ¹	Open grassland where the herbage is short. Gateways, lanes and roadsides. A nuisance in lawns.
Wide	Narrow	Can't tell	669.4	Banks of slow-flowing rivers and canals with inorganic substratum. Almost or completely stagnant ponds and dykes, ungrazed marshland in river floodplains, peat basins with strongly tidal water.
Wide	Narrow	Can't tell	166.3	Chalk and limestone grassland, occasionally found on alkaline sandy soils. Restricted to exposed, unshaded sites.
Wide	Narrow	Can't tell	678.1	Hedges, dry banks, sides of dykes, sea cliff tops, pastures, hedgerows, meadows, rough grassland.
Wide	Narrow	Can't tell	123.7	Rock ledges, in crevices, on screes and mountain-top detritus, and on sea cliffs.
Wide	Narrow	Can't tell	55.1	A member of the floating leaf community of still, or slowly flowing, fresh waters. Usually occurs in water 2-10 feet deep over mud, silt, or peat, rarely over shingle.

¹Numbers are codes from the *Atlas of the British Flora* for identification of the species.

were encouraged to use in instances of ambiguous data. This procedure helped to eliminate the effects of preconceptions of how species "ought" to behave, and so the process was desirably "blind."

Consistency of judges' decisions

The 15 judges were ecologists and systematists, all members of the Cornell academic community. Fourteen were North Americans with little direct experience with the British flora; the single Briton was a lepidopterist. How closely do the judgments among these scientists agree? Consistency among judges was examined in two ways. The first was to look at scores for each judge over all three traits and to compare between judges. Judges were quite consistent in deciding the proportion of all species considered to have a "wide" geographic range (Table 5). They were less consistent about habitat specificity and local abundance, and their written comments on the survey indicated that these were the more difficult decisions to make.

To quantify the degree of agreement between judges, we calculated a species-by-species Spearman rank correlation (corrected for ties as

in Siegel, 1956) between all possible pairs of judges by coding "wide" decisions as 1, "narrow" as 3, and "can't tell" as 2. Thus a disagreement between "wide" and "narrow" would have the largest magnitude ($3 - 1 = 2$). With this coding, judges' choices were highly correlated for geographic distribution (average correlation = 0.80, range 0.63-0.94), less so for habitat (average correlation = 0.58, range 0.45-0.73) and local abundance (average correlation = 0.54, range 0.31-0.75). An oblique principal components analysis (VARCLUS procedure in SAS; SAS Institute, 1982) showed that there were no grounds for splitting the judges into discrete clusters. That is, there are no distinct "schools of thought" among the participants.

The second analysis of the judges' consistency was based on the fact that the dot maps of four species selected as being particularly ambiguous were put into the survey twice (mixed randomly with the other maps). Within-judge consistency was then tested by examining how frequently judges changed their minds. Seventy percent of the 60

TABLE 4. Sample page from survey administered to participants, describing the local abundance of individual species from the *Biological Flora of the British Isles*.

Somewhere large	Everywhere small	Can't tell	600.1 ^o	Many form pure societies on patches of sand in woodland. Frequent and often locally dominant constituent of oak and beechwood.
Somewhere large	Everywhere small	Can't tell	715.1	Dominance in many moorlands, generally abundant in the north and west of British Isles.
Somewhere large	Everywhere small	Can't tell	58.4	Never abundant anywhere, usually only a few scattered individuals are found. Seldom, if ever, found in large populations.
Somewhere large	Everywhere small	Can't tell	61.1	Moderately common and locally extremely abundant.
Somewhere large	Everywhere small	Can't tell	176.1	In the island scrub it may attain subdominance. Sometimes locally abundant as a subordinate tree layer in mature beechwood.
Somewhere large	Everywhere small	Can't tell	158.1	Occurs as scattered individuals or more frequently in colonies.
Somewhere large	Everywhere small	Can't tell	685.3	Tends to form pure stands, particularly if left undisturbed. A common component of lightly grazed grassland communities.

^oNumbers are codes from the *Atlas of the British Flora* for identification of the species.

judgments were consistent. Of the 18 inconsistent decisions, 83 percent (15 of 18) changed from or to the "can't tell" category. Only 18 percent (3 of 18) reversed a judgment from "wide" to "narrow" or vice versa.

In summary, the judgments of participants were moderately correlated with one another for habitat specificity and local abundance and highly correlated for geographic range; judges were remarkably consistent when asked to make the same difficult decision twice.

Data analysis: assignment of species to categories of rarity

After collecting data from the participants, each species was assigned to one cell of the eight-celled table. We performed two analyses, one using conservative criteria, the other using liberal criteria. For the conservative analysis, if three people disagreed or if there was a consensus that the data were ambiguous for any one of the three traits, a species was excluded from the tabulation. This resulted in 128 exclusions, leaving a sample of 49 species. For the liberal analysis, a simple plurality (six respondents in agreement) was considered adequate to classify a species. This technique produced a sample size of 160, with only 17 species excluded. Species excluded from consideration had 6:6 ties or a plurality of "can't tells."

Some examples will clarify this procedure (Table 6). *Deschampsia cespitosa*, tufted hair-grass, was included in the tabulations according to both the conservative and liberal criteria because there was very close agreement on all three traits. For the conservative analysis, *Agrostis setacea*, bristle-leaved bent, was omitted because five judges disagreed on geographic range, but it was included in the liberal analysis because more than six agreed for each trait. Similarly, *Draba muralis*, wall whitlow grass, was included in the liberal but not the conservative analysis. *Myosotis alpestris*, alpine forget-me-not, was excluded from both analyses because there was no consensus on any trait and because a plurality agreed that the geographic and local population data were ambiguous.

The final step in classifying the species is to place each species in the appropriate cell and tally up the total frequencies; Table 6B shows the categories of the species in the example. *Deschampsia cespitosa* falls into the common category in the upper left cell—wide geographic range, broad habitat specificity, and large local populations. *Agrostis setacea* falls into one of the endemic categories, with narrow geographic range, restricted habitat specificity, but large local populations. *Draba muralis* falls in a third cell; it is a species with wide geographic distribution but restricted to particular habitats, within which it is never common.

TABLE 5. Decisions of judges from the survey.

Judge	Geographic range			Habitat specificity			Local population size		
	Wide	Narrow	Can't tell	Restricted	Broad	Can't tell	Somewhere large	Everywhere small	Can't tell
1	146	26	5	28	28	110	39	163	13
2	154	16	7	85	15	78	14	144	15
3	142	24	11	26	6	77	74	149	24
4	156	15	6	77	58	58	42	137	35
5	124	31	22	69	22	74	34	128	40
6	143	21	13	59	13	81	37	109	50
7	134	36	7	65	7	96	16	145	18
8	154	17	6	75	6	94	8	137	30
9	151	16	10	83	10	90	4	161	7
10	121	24	32	44	32	85	48	153	20
11	150	26	1	101	1	72	4	158	12
12	152	14	11	24	11	104	49	154	20
13	145	26	6	56	6	86	35	135	39
14	150	23	4	79	4	83	15	149	15
15	124	31	22	74	22	69	34	121	36

Results of the conservative and liberal analyses were similar (Table 7). The proportion of species which had broad versus restricted habitat specificity was compared for those species which had both large local abundance and wide geographic distribution (the two categories with the most species to test whether the two analyses gave different results). Of 129 such species, 58 (45 percent) had wide habitat specificity under the liberal criterion, while 6 out of 20 (30 percent) had wide habitat specificity under the conservative criterion. The 95 percent confidence intervals are 34-54 percent and 12-54 percent respectively. Since the two intervals completely overlap, the different percentages (45 percent versus 30 percent) under the two different criteria can be accounted for by the variability expected in smaller samples, and there is no evidence that the different criteria led to different proportions of species being assigned to these two categories. Thus, for the remainder of the discussion, we restrict our attention to the larger data set of the liberal analysis.

Independence in the liberal data

The test for independence of the three traits was performed using the general loglinear model described in Fienberg (1981). The results indicate that the model of complete independence of the three traits adequately fits the data ($G^2 = 5.9047, p < 0.10$). This is an interesting result because it tells us that geographic range, habitat specificity, and local population size are three independent variables in the British flora. Thus each variable supplies information on rarity not provided by the other two.

This conclusion might seem to contradict the views held by many ecologists that generalists are widespread and that abundance is positively correlated with range (Brown, 1984). This is not the case, however. Even though local abundance is independent of geographic range and habitat specificity in our contingency table, we still might find a correlation for a collection of species between total number of individuals for each species and the total area it occupies.

Naturally, we have no idea whether the independence of the three traits is universal, since this is the first test of its existence (but see Thomas and Mallorie, 1985). Again, the issue of scale emerges as critical (Hubbell and Foster, Chapter 10). Were the global ranges of the species considered, rather than simply their occurrence in the British Isles, particular species would shift among the eight categories, but perhaps the proportions in each would remain similar. As yet, we do not know.

B. Placement of species in categories.

Species	Geographic range			Habitat specificity			Local population size		
	Wide	Narrow	Can't tell	Broad	Restricted	Can't tell	Somewhere	Everywhere	Can't tell
<i>Deschampsia cespitosa</i>	15	0	0	15	0	0	14	0	1
<i>Agrostis setacea</i>	2	10	3	0	15	0	15	0	0
<i>Draba muralis</i>	14	0	1	1	9	5	2	9	4
<i>Myosotis alpestris</i>	1	6	8	1	8	6	4	5	6

Habitat specificity	Geographic distribution		Local population size
	Broad	Restricted	
<i>Deschampsia cespitosa</i> , tufted hair-grass	Broad	Restricted	Somewhere large
<i>Draba muralis</i> , wall willow grass	Broad	Restricted	Everywhere small
<i>Agrostis setacea</i> , bristle-leaved bent	Broad	Restricted	Can't tell

TABLE 6. Assignment of species to categories of rarity. A. Survey results for four species.

These plants will be as frequent in their occurrence as is their habitat. *Ammophila arenaria*, marram grass (Figure 2), is a good example from the British flora (Huiskes, 1979). Often the only species present on semi-fixed and mobile sand dunes along most of the coastline, this maritime species is abundant in a frequently encountered habitat. *Limonium humile*, lax-flowered sea lavender, a resident of muddy substrates in salt meadows, also has a wide geographic distribution and occurs in locally large populations (Boorman, 1967). But in contrast to *A. arenaria*, the habitat appropriate to *L. humile* is curiously infrequent, and as a result, the lavender is quite a rare plant.

The second most numerous form of rarity (14 species) is the classic restricted endemic: habitat specialist, small range, but common when you find it (Table 7). Such rarities have been the object of study by biogeographers and evolutionists for decades (Cain, 1944; Kruckeberg, 1954; Stebbins and Major, 1965). The British flora contains numerous interesting cases of this form of rarity, but especially striking is *Orchis purpurea*, lady orchid. Confined to chalk coppice and beechwoods in extreme southeast England, the lady orchid is "still locally plentiful" (Rose, 1948).

As both Robert Whittaker and Ledyard Stebbins have suggested, there seems to be a cell in this table that is impossible or nearly so. Plants with narrow range, small populations, but broad habitat specificity seem not to exist in the British flora, at least when one samples from 177 species. It is interesting to note that Thomas and Mallorie (1985) found a single butterfly species (out of 39) in this category in the Atlas Mountains, *Gonepteryx cleopatra*. Here we return to the issue of bias in selection of species for inclusion in the *Biological Flora*. For this and the following forms of rarity, inconspicuous or pedestrian species of intermediate abundance or range are underrepresented because they do not attract the notice of biologists. We hope that our classification will bring these species to the greater attention of researchers.

Truly sparse species (the opposite of endemics), with large ranges, many habitats, but chronically low local population sizes, are infrequent. We sampled only two from a population of 177 species. This result surprised us, but perhaps sparse species are especially underrepresented in Britain or in the *Biological Flora*. An interesting case is *Hypochoeris maculata*, spotted cat's ear, a composite with a scattered distribution in Britain and the Continent, found in habitats as varied as "chalk grassland, ancient earthworks, old quarry workings, blown sand and maritime cliffs on calcareous and serpentine-derived soils" (Wells, 1976). Yet it is not particularly common anywhere. The remaining three categories are infrequent as well, for reasons

TABLE 7. Results of the liberal (boldface) and conservative (parentheses) analyses.^a

Habitat specificity	Wide		Narrow	
	Broad	Restricted	Broad	Restricted
Somewhere large	58 (21)	71 (23)	6 (0)	14 (4)
Everywhere small	2 (0)	6 (0)	0 (0)	3 (1)

^aNumbers are species counts out of a total of 160 for the liberal and 49 for the conservative analysis.

Frequencies of the marginal totals and cells

Most species are common somewhere (Table 7), as Brown (1984) on regional and continental scales and Shmida and Ellner (1984) on a within-habitat scale have recently argued. In the British Isles, 149 species out of 160 have large populations somewhere within their ranges, but only 11 have chronically small populations. Many more species (137) have wide geographic ranges than narrow ones (23). A slight majority of the species have restricted habitat specificity (94), but many (66) occur in a variety of habitats.

Again we have an apparent but not actual contradiction with the ecological generalization of the lognormal distribution of species abundance (May, 1975). Within a single site, very few species have large populations, and most species are represented by only a few individuals. That is, locally most species are rare. Our results say that most species are common somewhere within their ranges, but it may be that most species have locally small populations throughout the majority of the sites where they occur.

Species of wide geographic distribution, restricted habitat, but high local population size are the most numerous category of plants in our sample of the British Isles (71 species; Table 7), even more numerous than ordinary common species (58 species). These plants are predictable habitat specialists—for example, sand dune, marsh, bog, and fen species, or forest floor species under particular canopies. Plants in this category may be especially numerous in Britain due to its long coast and predominance of maritime species. Nearly one-third (30 percent) of the 71 species have exclusively coastal distributions.

CHAPTER NINE / RABINOWITZ, CAIRNS & DILLON

we don't understand. We have already discussed instances of these rarities (Table 1). *Draba muralis* has a wide geographic distribution but is habitat-restricted in small populations. *Primula scotica* grows in several habitats in considerable populations, but its range is tiny. And *Lloydia serotina* is rare on all three fronts. It is important to recognize the existence of such species and to determine in the future whether they are truly unusual distributional forms in other floras as well and if so, why this might be true.

IMPLICATIONS FOR CONSERVATION BIOLOGY

The seven forms of rarity give us some recommendations and justifications for conservation practice. How one goes about protecting a species will hinge on the dimension in which it is rare, and it is useful, perhaps necessary, to specify precisely what kind of rarity one is dealing with. For example, for a rare plant such as *Primula scotica*, with a tiny range in northeastern Scotland, its large populations in several habitats suggest that the species possesses substantial ecological plasticity and tolerance for a variety of environmental conditions. This form of rarity indicates that there probably is available uncolonized but suitable habitat where the species does not occur and that transplant experiments stand a good chance of success. In contrast, the large range and patchy restriction of *Limonium humile* to large populations in a narrow habitat suggest that in the past, dispersal has "sampled" a wide variety of maritime habitats, and colonization has already occurred on the patches that are suitable in some subtle way we cannot detect. Transplants as a method of conservation have less likelihood of being successful in such a species, and protection of reserves against environmental perturbation is probably critical. The primrose and lavender are thus likely to be endangered by very different forces. On the other hand, there are some rare species such as *Hypochoeris maculata* which, despite small local populations, occur over a wide geographic range in a variety of habitats. Such sparse species are unlikely to be endangered except by massive habitat destruction. In a triage system for rare species, they can be left to look after themselves and may even provide us with clues on how to protect close relatives in more precarious states.

Rarity thus comes in a variety of forms, and our results are a first attempt at determining how frequent these are, based on a method applicable to any well-studied flora on a local, regional, or continental scale. An interesting second step would be to compare the distribution of endangered species or extinct species with species as a whole in a flora. This examination would tell us whether endangered species were a random subset of floras or whether they were drawn from particular

sorts of rarity. The exercise might suggest the causes of the endangered state.

The British flora shows that the preponderant attention which conservationists pay to endemic species is well justified (Kruckeberg and Rabinowitz, 1985). We already knew that these plants of small range and narrow habitat specificity, such as *Orchis purpurea*, are easily threatened or extirpated by habitat destruction. Our results show that they are a numerically important part of the flora, not just isolated cases.

Findings for both endemics and species of wide geographic range underscore that most species occur in restricted habitats. Conserving and studying habitats is probably the most effective means of conserving such species (Thomas and Mallorie, 1985), in much the way that the reserve in Snowdonia protects *Lloydia serotina*.

These data do give us a hopeful indication that we can move from our colloquial notions of rarity to a concept based on a solid quantitative footing. The independence of geographic range, habitat specificity, and local abundance tell us that conservationists concerned with rare species need to pay attention to all three traits. The consistency of our judges' decisions is an encouraging sign that observers converge in their notions of rarity. So conservationists can "objectify" what has previously been the exclusive province of "natural history." Our results bode well for the possibility of advancing the conservation of rare species to a discipline based on sound ecological principles.

SUGGESTED READINGS

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APPENDIX

Species from the *Biological Flora of the British Isles* included in the survey and the category into which each fell.

A note about error. Since our approach is statistical, misclassification of particular species are inevitable, especially considering the absence of a standard list of habitats in the *Biological Flora of the British Isles*. For example, *Senecio jacobaeae* occurs in large populations (C. Thomas and H. Robertson, personal communication), yet it fell into the category of "everywhere small"

for local population size based on quotes from the *Biological Flora*. There are undoubtedly other errors of this sort. If they are random with respect to category, the tallies for the eight cells will not be biased, but we have no way to assess whether this is the case.

**WIDE Geographic Distribution
BROAD Habitat Specificity**

SOMEWHERE LARGE Local Population Size

Acer campestre L.
Agropyron repens (L.) Beauv.
Arrhenatherum elatius (L.) J. & C. Presl
Arum maculatum L.
Calluna vulgaris (L.) Hull
Catapodium rigidum (L.) C.E. Hubbard
Chenopodium album L.
Chenopodium rubrum L.
Dactylis glomerata L.
Deschampsia cespitosa (L.) Beauv.
Deschampsia flexuosa (L.) Trin.
Eleocharis unguiculata (Link) Schult.
Endymion non-scriptus (L.) Garcke
Epilobium angustifolium (L.) Scop.
Erica cinerea L.
Eriophorum angustifolium Honck.
Galeobdolon luteum Huds.
Holcus lanatus L.
Holcus mollis L.
Hypochoeris radicata L.
Ilex aquifolium L.
Juncus conglomeratus L.
Juncus effusus L.
Juncus inflexus L.
Lolium perenne L.
Menyanthes trifoliata L.
Narcissus pseudonarcissus L.
Nardus stricta L.
Papaver argemone L.

WIDE Geographic Distribution

RESTRICTED Habitat Specificity

SOMEWHERE LARGE Local Population Size

Allium ursinum L.
Alnus glutinosa (L.) Gaertn.
Alopecurus myosuroides Huds.
Ammophila arenaria (L.) Link
Anthemis cotula L.
Aster tripolium L.
Atropa bella-donna L.
Carex arenaria L.
Carex flacca Schreb.
Chrysanthemum segetum L.
Cirsium acaulon (L.) Scop.
Cladium mariscus (L.) Pohl
Colchicum autumnale L.
Corynephorus canescens (L.) Beauv.

Halimione portulacoides (L.) Aell.
Helianthemum canum (L.) Baumg.
Helianthemum chamaecistus Mill.
Hippocrepis comosa L.
Hippophae rhamnoides L.
Hornungia petraea (L.) Rehb.
Hymenophyllum tunbrigense (L.) Sm.
Hymenophyllum wilsonii Hook.
Juncus acutus L.
Juncus squarrosus L.
Juncus subnodulosus Schrank
Lathyrus japonicus Willd.
Limonium humile Mill.
Limonium vulgare Mill.
Lobelia dortmanna L.
Mertensia maritima (L.) S.F. Gray
Narthecium ossifragum (L.) Huds.
Nuphar lutea (L.) Sm.
Nuphar pumila (Timm) DC.
Nymphaea alba L.
Papaver rhoeas L.
Plantago coronopus L.
Plantago major L.

WIDE Geographic Distribution

BROAD Habitat Specificity

EVERYWHERE SMALL Local Population Size

Hypochoeris maculata L.
Senecio jacobaea L.

WIDE Geographic Distribution

RESTRICTED Habitat Specificity

EVERYWHERE SMALL Local Population Size

Draba muralis L.
Papaver hybridum L.
Papaver fecogii Lamotte
Saxifraga cespitosa L.
Silene acaulis (L.) Jacq.
Subularia aquatica L.

NARROW Geographic Distribution

BROAD Habitat Specificity

SOMEWHERE LARGE Local Population Size

Arbutus unedo L.
Lobelia urens L.
Melampyrum cristatum L.
Pinus sylvestris L.
Polemonium caeruleum L.
Primula scotica Hook.

NARROW Geographic Distribution

RESTRICTED Habitat Specificity

SOMEWHERE LARGE Local Population Size

Agrostis setacea Curt.
Corrigiola litoralis L.
Daboecia cantabrica (Huds.) C. Koch
Draba aizoides L.
Dryopteris vittarii (Bell) Woyнар
Erica mackenzii Bab.
Frankenia laevis L.
Helianthemum apenninum (L.) Mill.
Linum anglicum Mill.
Orchis purpurea Huds.
Saxifraga rosacea Moench
Spartina maritima (Curt.) Fernald
Suaeda frutescens Forsk.
Thymus serpyllum L.

Plantago media L.
Poa annua L.
Polygonum hydropiper L.
Quercus petraea (Mattuschka) Liebl.
Rorippa microphylla (Boenn.) Hyland
Rorippa nasturtium-aquaticum (L.) Hayek
Rubus chamaemorus L.
Saxifraga hypnoides L.
Saxifraga oppositifolia L.
Schoenus nigricans L.
Sinapis arvensis L.
Sonchus oleraceus L.
Spartanium erectum L.
Spartina x townsendii H. & J. Groves
Suaeda maritima (L.) Dum.
Tamus communis L.
Tuberaria guttata (L.) Fourreau
Viola lactea Sm.
Vulpia membranacea (L.) Dum.
Zostera angustifolia (Hornem.) Rchb.
Zostera marina L.

NARROW Geographic Distribution
 BROAD Habitat Specificity
 EVERYWHERE SMALL Local Population Size
 No species in this category

NARROW Geographic Distribution
 RESTRICTED Habitat Specificity
 EVERYWHERE SMALL Local Population Size
Saxifraga hartii D.A. Webb
Arabis stricta Huds.
Lloydia serotina (L.) Rehb.

CANT TELL for at least one of the three categories
 (Geographic Distribution, Habitat Specificity, and/or Local
 Population Size)

Allium vineale L.
Anemone pulsatilla L.
Anthemis arvensis L.
Arum italicum Mill.
Chrysanthemum leucanthemum L.
Gentiana verna L.
Hypericum linariifolium Vahl
Juncus filiformis L.
Myosotis alpestris F. W. Schmidt
Oxalis acetosella L.
Phyllodoce caerulea (L.) Bab.
Ranunculus bulbosus L.
Senecio integrifolius (L.) Clairv.
Sibbaldia procumbens L.
Thymus pulegioides L.
Vaccinium vitis-idaea L.
Viola lutea Huds.

How many species?

ROBERT M. MAY

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SUMMARY

This paper begins with a survey of the patterns in discovering and recording species of animals and plants, from Linnaeus' time to the present. It then outlines various approaches to estimating what the total number of species on Earth might be: these approaches include extrapolation of past trends; direct assessments based on the overall fraction previously recorded among newly studied groups of tropical insects; indirect assessment derived from recent studies of arthropods in the canopies of tropical trees (giving special attention to the question of what fraction of the species found on a given host-tree are likely to be 'effectively specialized' on it); and estimates inferred from theoretical and empirical patterns in species-size relations or in food web structure. I conclude with some remarks on the broader implications of our ignorance about how many species there are.

1. INTRODUCTION

Earlier papers in this volume have surveyed our growing understanding of the factors that govern the population densities of individual species. Later papers have gone on to consider the dynamics of single populations in relation to the systems of interacting species in which they are embedded (Godfray & Blythe; Sugihara *et al.*), to their genetic structure (Travis), and to past (Valentine) and present (Hubbell; Lawton) patterns of relative abundance of species within communities. Ideally, this final paper should build on this foundation to arrive at an analytic understanding, as distinct from a mere compendium, of how many species of plants and animals we may expect to find in a given community or in a particular region. Ultimately, such analyses could aim to pyramid toward a fundamental understanding of why the total number of species on our planet is what it is, and not grossly more or less.

Needless to say, we are a long way from this goal. This paper, therefore, focuses on the plainly factual question of how many species of plants and animals there are on earth, a number currently uncertain to within a factor 10 or more, and does not ask about the underlying reasons. The paper thus differs from an earlier review with a similar title (May 1988), in which I dealt mainly with basic factors that may influence species diversity, both locally and globally.

My paper begins with an account of those species that have been named and recorded. Amazingly, this current total is not known, because there is no central catalogue or list of named species; a good estimate may be around 1.8 million (Stork 1988). I then discuss a variety of ways in which the total number of plant and animal species on earth today may be estimated: by extrapolating past trends of discovery within particular groups; by inferences from detailed studies of the arthropod canopy fauna in tropical trees; by direct

estimates of the proportion of new species in studies of groups of tropical insects (often different from extrapolating past trends, which come predominately from temperate regions); from species-size relations; and so on. Different approaches yield global totals as small as 3 million or as large as 30 million or more. A penultimate section raises some broader questions about species diversity that are prompted by such estimates of local or global totals. I conclude with subjective thoughts on why it is important to know how many species there are.

2. HOW MANY RECORDED SPECIES?

It is noteworthy that Linnaeus' pioneering codification of biotic diversity came a century after Newton, in the mid-1700s. Whatever the reason for this lag between fundamental studies in physics and in biology, the legacy lingers. Today's catalogues of stars and galaxies are effectively more complete (by any reasonable measure), and vastly better funded, than catalogues of Earth's biota. And this certainly is not because stellar catalogues offer more opportunity for commercial application than do species catalogues.

The 1758 edition of Linnaeus' work records some 9000 species of plants and animals. Table 1 summarizes estimates of the numbers recorded since then up to 1970, for different groups. Table 1 also gives the time it took to record the second half of the total number of species (up to 1970) in each group, and the era when new species within each group were being discovered at the fastest rate (from Simon 1983). The table gives a sense of the differences in the attention paid to different groups, with half of all known bird species already recorded in the century after Linnaeus, while half the arachnid and crustacean species known in 1970 were recorded in the preceding 10 years; contrast figure 1 and figure 2.

The furies and featheries are, of course, very well

Table 1. *Taxonomic activity, from 1758 to 1970, for different animal groups, as revealed in patterns of recording new species (after Simon 1983)*

animal group	estimated number of species recorded up to 1970	length of time years, prior to 1970, to record the second half of the total in the previous column	period of maximum rate of discovery of new species
Protozoa	32000	21	1897-1911
'Vermes'	41000	28	1859-1929
Arthropoda (excluding insects)	96000	10	1956-1970
Arthropoda (insects only)	790000	55	1859-1929
Coelenterata	9600	58	1899-1928
Mollusca	45000	71	1887-1899
Echinodermata	6000	63	1859-1911
Tunicata	1600	68	1900-1911
Chordata			
Pisces	21000	62	1887-1929
Amphibia	2500	60	1930-1970
Reptilia	6300	79	1859-1929
Aves	8600	125	1859-1882
Mammalia	4500	118	1859-1898

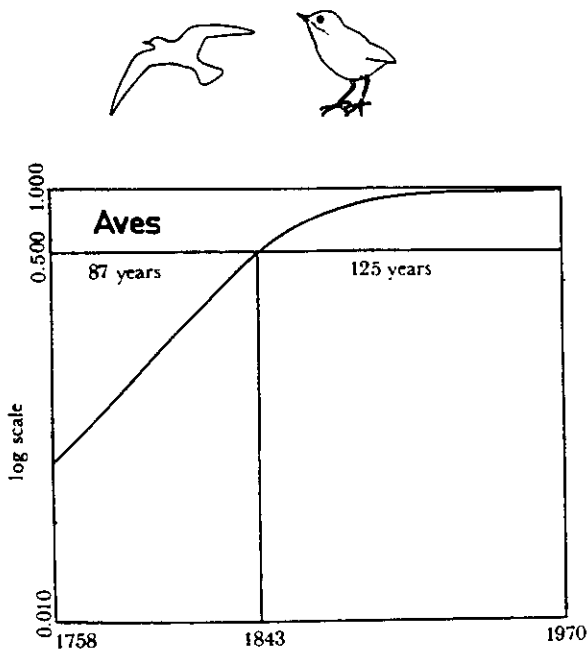


Figure 1. The curve shows the rate of discovery of bird species, from the time of Linnaeus (1758) up to 1970. Numbers of known species (expressed as a fraction of those known in 1970, on a logarithmic scale) are plotted against time. The vertical and horizontal lines show the point (1843) when half the 1970 total of species had been discovered. After Simon (1983).

known by now. As reviewed in detail by Diamond (1985), only 134 bird species have been added to the total of just over 9000 since 1934, representing a rate of discovery of around three species per year since 1940 (most of them small, brown tropical birds). Rates of discovery are somewhat higher for mammals, with 134 of the current total of 1050 genera added since 1900, at a rate of about 1 genus per year since 1940 (most of them tropical bats, rodents or shrews, or small

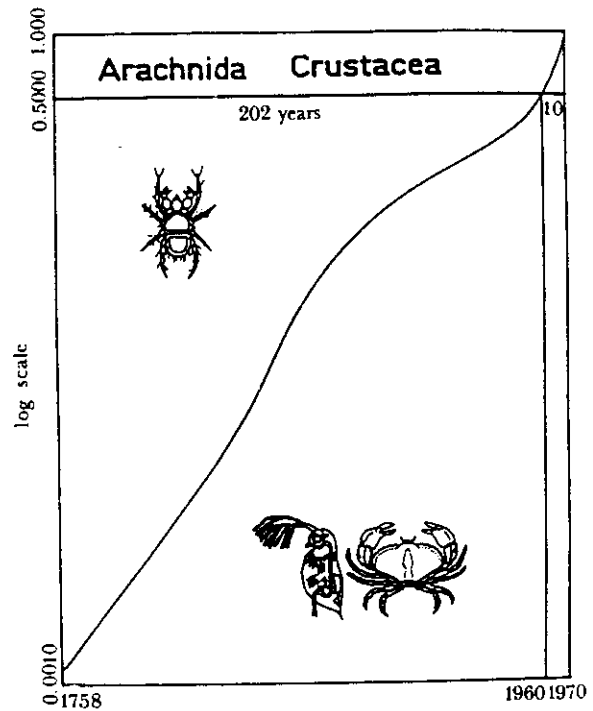


Figure 2. As for figure 1, but now showing recorded numbers of Arachnid and Crustacean species (essentially, arthropods excluding the Insecta) over time. The pattern of discovery is very different from that for bird species, with half of the total up to 1970 being recorded since 1960. After Simon (1983).

marsupials). As we shall see below, however, the story is altogether different for insects and other smaller creatures.

Publication rates provide another measure of the differential attention paid to different groups (see table 3, May 1988). Of papers listed in the *Zoological Record* over the past few years, mammals and birds average about 1 paper per species per year, reptiles, fish and amphibians about 0.5 papers per species per year.

Table 2. Estimated numbers of canopy beetle species that are specific to the host tree species *Luehea seemanii*, classified into trophic groups after Erwin 1983.

trophic group	number of species	estimated fraction host-specific %	estimated number of host-specific species
herbivores	682	20	136
predators	296	5	15
fungivores	69	10	7
scavengers	96	5	5
Total	1100+	--	160

whereas insects and other groups average from 0.1 to 0.01 or fewer papers per species per year.

Even within a given class, or order, different families can show different patterns in the study they have received. Thus, looking at different families of insects, Strong *et al.* (1984) show that recorded species of whiteflies (Aleyrodidae: Hemiptera) and phytophagous thrips (Thripidae: Thysanoptera) increased dramatically this century with a peak around 1920–40; weevils (Curculionidae: Coleoptera) show a gradual rise since Linnaean times, again peaking around 1920–40; whereas the papilionoid and danaid butterflies (Papilionodea and Danainae: Lepidoptera) are more like birds, with broad peaks in recording rates in the second half of the 19th century.

Such patterns in rates of recording new species can be projected forward, group by group, by standard statistical techniques. In this way, we can obtain an estimate of the eventual global total of species of plants and animals. As mentioned earlier, however, the records of named species are scattered, so that estimates of the total number actually named by a given date are themselves insecure (three frequently cited estimates are 1.5 million (Grant 1973), 1.4 million (Southwood 1978), and the more current 1.8 million (Stork 1988)). Projected totals are correspondingly subject to wide fluctuations, depending on the views taken of trends in particular groups and the statistical procedures used. Simon (1983, table 31) surveys several estimates arrived at by these methods, which range from concluding that essentially all species have already been named(!) to Simon's own estimates of around 6–7 million animal species in total. Grant's (1973) projection of 4–5 million is often referred to, but it is essentially based on the crude procedure of multiplying the recorded total number of insect species (which he put at 0.75 million in 1973) by 5. It must be emphasized that all the estimates based on projecting rates of discovery pre-date the dramatic studies of tropical insects discussed in §3 and §4.

A cruder, but intuitively satisfying, estimate that the global total lies in the range of 3–5 million species has been provided by Raven (1985) and others. This estimate rests on two observations. First, among well-studied groups such as birds and mammals there are roughly two tropical species for each temperate or boreal species. Second, the majority of species are insects, for which temperate and boreal faunas are much better-known than tropical ones; overall,

approximately two thirds of all named species are found outside the tropics. Thus if the ratio of numbers of tropical to temperate and boreal species is the same for insects as for mammals and birds, we may expect there to be something like two yet-unnamed species of tropical insects for every one named temperate or boreal species. This carries us from the recorded total of 1.4–1.8 million species to the crude estimate that the grand total may be around 3–5 million.

3. QUESTIONS RAISED BY STUDIES OF TROPICAL CANOPY FAUNAS

Recent studies of the arthropod faunas of tropical trees raise serious doubts about the validity of the above estimates, based as they are on projecting forward from past trends of discovery and recording. The essential point is that all the past trends are dominated by temperate-zone invertebrate groups, especially insects, whereas the recent work (surveyed in this section and the next two) suggests that tropical insect faunas may have very different patterns of diversity.

One frequently quoted upward revision to a global total of 30 million species or more comes from Erwin's (1982, 1983; Erwin & Scott 1980) studies of the insect fauna in the canopy of tropical trees. By using an insecticidal fog to 'knock down' the canopy arthropods, Erwin concluded that most tropical arthropod species appear to live in the treetops. This is not so surprising, because the canopy is where there is most sunshine as well as most green leaves, fruits and flowers.

Specifically, Erwin's original studies were on canopy-dwelling beetles (including weevils) collected from *Luehea seemanii* trees in Panama, over three seasons. As summarized in table 2, he found more than 1100 species of such beetles, which he partitioned among the categories of herbivore, predator, fungivore and scavenger.

To use the information in table 2 as a basis for estimating the total number of insect species in the tropics, one first needs to know what fraction of the fauna is effectively specialized to the particular tree species or genus under study. Unfortunately, there are essentially no systematic studies of this question even for temperate-zone trees, much less tropical ones. Erwin guessed 20% of the herbivorous beetles to be specific to *Luehea*, in the sense that they must use this

tree species in some way for successful reproduction. As shown in table 2, his overall answer is more sensitive to this estimate than to the corresponding figures of 5%, 10%, and 5% for predator, fungivore, and scavenger beetles, respectively. In this way, Erwin arrived at an estimate of around 160 species of canopy beetles effectively specialized to a typical species of tropical tree.

Several other assumptions and guesses are needed to go from this estimate of 160 host-specific species of canopy beetles per tree to 30 million species in total. Slightly simplified, the argument runs as follows. First, Erwin noted that beetles represent 40% of all known arthropod species, leading to an estimate of around 400 canopy arthropod species per tree species. Next, Erwin suggested that for every two insect species in the canopy there may be one species elsewhere on the tree or the immediately neighbouring forest-floor, increasing the estimate to around 600 arthropod species effectively specialized to each species or genus-group of tropical tree. Finally, by using the estimate of 50000 species of tropical trees, Erwin arrived at the possibility that there are 30 million tropical arthropods in total.

As Erwin emphasizes, this chain of argument does not give an answer, but rather an agenda for research. Setting aside the question of whether *Leuhea* (along with its ensemble of associated lichens, vines, bromeliads, etc.) is a typical tropical tree, there are at least four areas of uncertainty: (i) what fraction of the beetle (or other) fauna on a given tree species are effectively specialized to it; (ii) do beetle species constitute the same fraction of insect faunas in the tropics as they do in better-studied temperate regions; (iii) for each insect species in the canopy, how many other species are found elsewhere or in or around a tree, and (iv) how do we scale up from the number of insect species associated with a given tree species in a given place to a global total? These four links in Erwin's chain of argument serve to organize the remainder of this section.

(a) What fraction of the fauna is 'effectively specialized' to a given tree species?

Suppose a given region contains 100 different tree species, and a total of 1000 different species of canopy beetles. At one extreme, all the beetles may be complete generalists, so that (setting aside sampling problems) all 1000 species could be found on any one tree species. At the opposite extreme, it could be that all beetles were complete specialists, with the total of 1000 made up by each of the 100 tree species contributing its particular 10 species of beetles. Now turn this around, and suppose that in a region where there are 100 tree species we find 100 species of canopy beetles in exhaustive sampling from just one tree species. How many beetle species are there likely to be in total? The above argument suggests that, if the studied tree is indeed representative, the total number of canopy beetle species lies somewhere between 100 (all generalists) and 10000 (all highly specialized).

Suppose we are investigating a region containing a total of M different tree species. The above issues can now be made precise by formally defining $p_k(i)$ to be

the fraction of canopy beetles (or other insects) found on the tree species labelled k ($k = 1, 2, \dots, M$), which utilize a total of i different tree species (including the one labelled k). Further, let N_k denote the total number of canopy beetles (or other insects) found on tree species k . Then, of the beetles found on tree species k , $N_k p_k(1)$ are found only there, $N_k p_k(2)$ are found on k and on only one other tree species, and so on. The total number of distinct canopy-beetle species, N , in the region is then given by the sum:

$$N = \sum_{k=1}^M \sum_{i=1}^M (1/i) N_k p_k(i). \tag{1}$$

That is, we sum the numbers of beetle species over all tree species, discounting each tree by the factor $1/i$ for those of its beetle species found on i tree species.

The 'effective average' number of beetle species per tree species, or overall average number of beetles 'effectively specialized' to each tree species, is then N/M , with N given by equation (1). For the tree species labelled k , the proportion of its beetle species that are 'effectively specialized' to it, f_k , is given by

$$f_k = \sum_{i=1}^M (1/i) p_k(i). \tag{2}$$

The corresponding overall proportion of beetle species 'effectively specialized', averaged over all tree species, is denoted by f :

$$f = N / \sum_k N_k. \tag{3}$$

Here N is given by equation (1). Equation (3) says that the overall average fraction of beetle species 'effectively specialized' to each tree species, f , is given by the total number of different species divided by the sum of the totals from each tree species, without discounting for overlaps.

Unfortunately, there is to my knowledge not a single systematic study of the distribution functions $p_k(i)$ for the apportionment of any faunal group among any group of plant or tree species. At best there are some studies, essentially all for temperate communities, which distinguish among monophagous, oligophagous, and polyphagous insects (roughly, those feeding on a single species or genus, on a family, or more generally, respectively). The assumptions codified in table 2 correspond to assuming that f_k is 0.20, 0.05, 0.10, 0.05 for herbivore, predator, fungivore, scavenger beetles in the canopy of *Leucea*, respectively; but these are guesses.

Although quantitative studies are lacking, the formal definitions embodied in equations (1-3) can at least alert us to some of the pitfalls in intuitive estimates of the proportion of beetle species that are 'effectively specialized'. Suppose, for example, that for a given group of insects in a particular tree species (labelled 1) the distribution function, $p_1(i)$, has the geometric-series form $p_1(i) = c\alpha^i$ (with $\alpha < 1$). This says that the fraction of species utilizing i tree species decreases geometrically as i increases. The normalization constant, c , ensures that $\sum p_1(i) = 1$ (if the total number of tree species is large, $M \rightarrow \infty$, then $c \rightarrow (1-\alpha)/\alpha$). In this event, the fraction of the insect species on tree species 1 that are effectively specialized to it, f_1 , can be seen to be given

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Table 3. A very preliminary study of the distribution of beetle species among four species of British oaks, to show ideas about the distribution function, $p_k(i)$, and definitions of 'effective specialization' from unpublished data provided by T. R. E. Southwood

oak species	number of beetle species found on a given oak species, N_k	number of beetle species found on a given oak species, that are found on a total of i of the 4 oak species (proportion found on i species, $p_k(i)$)				proportion of beetle species effectively specialized on this oak species, f_k , from eqn (2)
		$i = 1$	2	3	4	
<i>cerris</i>	28	5 (0.18)	8 (0.29)	7 (9.25)	8 (0.29)	0.48
<i>ilex</i>	47	20 (0.43)	10 (0.21)	9 (0.19)	8 (0.17)	0.64
<i>petraea</i>	48	14 (0.29)	15 (0.31)	11 (0.23)	8 (0.17)	0.57
<i>robur</i>	50	15 (0.30)	15 (0.30)	12 (0.24)	8 (0.16)	0.57
totals	173	54	24	13	8	average, $f = 0.57$

(in the limit of very large M) by $f_1 \approx [(1-\alpha)/\alpha] \ln[1/(1-\alpha)]$. But an estimate of f_1 based on biological intuition might simply ask about the 'monophagous' fraction, that are found only on that tree species or genus-group; this would lead to the estimate $f_1 \approx p_1(1) = 1-\alpha$. Suppose that in fact $p_1(1)$, the fraction monophagous within this distribution, is 20% (that is, $\alpha = 0.8$). Then in this illustrative example the fraction 'effectively specialized' is $f_1 = 0.40$, which is twice as large as might be guessed on intuitive grounds.

What are needed, of course, are not speculative abstractions, but analytic studies of the distribution functions $p_k(i)$ for particular floral and faunal communities. By way of illustration, table 3 shows a very preliminary analysis of the distribution of beetle species among four species of oak trees, *Quercus cerris*, *Q. ilex*, *Q. petraea* and *Q. robur* in Wytham Wood, Oxford (data provided by T. R. E. Southwood). The data in table 3 represent the species 'knocked down' by insecticidal fog (specifically, from 6 foggings per tree species in the months of May and June). On this basis, the four above-mentioned oak species show totals of 28, 47, 48 and 50 beetle species, respectively, for a gross total of 173 species. But in fact only 99 distinct beetle species are present, with the pattern of overlap as shown in table 3. The table also shows that, for this example, the fraction of the beetle species that are 'effectively specialized' to a given oak species (as defined by the formulae above) is roughly around 60%. It must be emphasized that this example is presented for illustrative purposes, to make the above ideas more concrete; it is a very crude and preliminary analysis of a fragment of a much larger data set.

The definition of the distribution function $p_k(i)$ was made on biological grounds, based on the number of tree species whose resources are utilized in some way by a particular insect species. The data in table 3 are, however, surely dominated by sampling considerations. A few of the beetle species in table 3 are represented by only one individual, and many of the species that utilize these oaks are absent from the samples altogether. Moreover, the table does not distinguish between species that are known to utilize a given tree, and those that accidentally happen to be on it when the sample is collected by fogging (Moran & Southwood's (1982) 'tourist' species). In this respect the data presented in table 3 are similar to those likely to be collected in most studies of canopy and other faunas: the patterns of distribution of insect species

among tree species will be a mixture of the underlying biological patterns of resource use (and of specialization and generalization), clouded or often dominated by sampling effects. I believe there is a need here both for theoretical studies (clarifying the interplay between sampling effects and the underlying distributions of resource utilization, among other things) and for empirical investigations. Such work will ultimately illuminate fundamental aspects of the structure of ecological communities, and will contribute to more reliable estimates of the global total of species. My aim in this sub-section, which obviously provides questions not answers, is to stimulate such further work.

The coarse and conventional division of phytophagous insects into monophages, oligophages and polyphages may be sharpened somewhat for the phytophagous beetles on oak trees in Southwood's study. By using standard handbooks (Fowler 1913; Joy 1931; Portevin 1935), it is possible to determine: (i) what fraction of the approximately 100 species are restricted to oaks (that is, to the genus *Quercus*); (ii) what fraction to the family Fagiaceae, or (iii) the order Fagales, as opposed to (iv) those found generally on angiosperms, or (v) even more broadly. A tentative analysis of Southwood's data suggests the proportions of phytophagous beetle species in the five categories thus defined are 0.10, 0.03, 0.06, 0.77 and 0.04, respectively.

If these exceedingly rough figures were taken as representative, they would suggest that Erwin's estimate that 20% of herbivorous canopy beetles are host-specific be replaced by a figure of 10% or less (remember, the 10% above is for the oak genus, not for a particular species). This would halve the estimated global total, to 15 million species or fewer. And if tropical beetles are typically less specialized than temperate ones, as they may need to be in response to the much patchier distribution of a vastly greater diversity of tree species, then the percentage that are host-specific (and thence the estimated global species total) could be smaller yet. On essentially these grounds, Stork (1988) had suggested that the effective fraction of host-specific beetle species in tropical canopies may be closer to 5% or less than to 20% (with a corresponding global total of 7 million or fewer species); see also Beaver (1979). There is clear need both for more theory (dealing with f_k and the way sampling and other effects influence it), and for more facts.

(b) In particular settings, what proportion of insect species are beetles?

Although roughly 40% of all recorded insect species are beetles, the existing handful of detailed studies suggest that beetle species constitute a smaller fraction of insect faunas collected by fogging tropical or temperate trees.

Southwood *et al.* (1982) sampled the invertebrate fauna (essentially all of which were insects) of six tree species in both Britain and South Africa, by using pyrethrum knockdown. In Britain, the total number of invertebrate species on the different tree species varied from 176 to 465, and the beetle species constituted, on average, 7% of the total (ranging from a low of 5% on *Salix* to a high of 11% on *Quercus*; see table 1 in Southwood *et al.* (1982)). The corresponding species totals on South African trees ran from 105 to 300, of which an average of 19% were beetle species (ranging from a low of 15% on *Salix* to a high of 23% on *Erythrina* and *Quercus*). Of the roughly 2800 species represented in the 24000 arthropod individuals collected in fogging samples from 10 trees in Borneo by Stork (1988, figure 3), approximately 30% were beetles.

These numbers have led Stork to speculate that beetles may more typically constitute around 20% of the insect species found in tree canopies, rather than the 40% that is characteristic of beetles more generally. All other things being equal, such a revision to this link in Erwin's chain of argument would double the global total number of species. My view is that these different results from different studies speak to the complexity and contingent nature of the underlying questions. Until such time as we have a better understanding of why beetles (or any other group) make up such different fractions of the species totals in different trees at different places, I would be inclined to stay with the overall average figure of 40% beetle species when making global estimates by 'scaling up' local studies.

(c) What is the ratio of canopy insects to all insects on a tree?

There are no studies of all the arthropod species found on the various parts of a tropical tree, but there are some studies of how the numbers of individuals are distributed.

Stork (1988) used a range of techniques to sample the fauna from each of five parts of trees in the lowland rainforest of Seram in Indonesia: canopy; tree trunk; 'ground vegetation' (from 0 to 2 m above the forest floor); leaf litter; and soil (the first few cm). In this site, Stork estimates there were approximately 4200 individuals per square metre, distributed among the five categories listed above as 1200, 50, 10, 600 and 2400. Roughly 70% of all individuals are found in the soil and leaf litter, mostly springtails (Collembola) and mites (Acarina). In the canopy, which contains about 14% of all individuals, ants are the most abundant arthropods (constituting roughly 43% of the individuals). If numbers of species bore a direct relation to numbers of individuals, we can see that Erwin's

estimate of one insect species elsewhere on the tree for every two species in the canopy would be out by almost a factor 10. But although ants tend to be more abundant than beetles in tropical canopies, they contribute significantly fewer species. The same seems likely to be true for the springtails in the soil and leaf litter. I have serious doubts, however, whether it is also true for the mites (moreover, the number of individual mites in the soil and leaf litter is typically an order-of-magnitude larger than the number of beetle individuals in the canopy).

Adis and colleagues (Adis & Schubart 1984; Adis & Albuquerque 1989) have made similar studies of the arthropod faunas of seven different types of Amazonian forests and plantations, using soil cores (0–7 cm), ground and arboreal traps of various kinds, and canopy fogging. Like Stork, they found the majority of individuals were Collembola and Acarina in the soil and leaf litter (with two thirds or more of these in the top 3.5 cm of the soil). The main difference between these Amazonian studies and the Indonesian ones is in the total numbers of individuals, which ranged as high as 30000 or more per square metre at some Amazonian sites. But the divisions of numbers of individuals among canopy, trunk, ground vegetation, leaf litter and soil are broadly similar in all the studies, as are the broad apportionments of individuals among taxonomic groups.

Understandably but unfortunately, all of these studies are of numbers of individuals in the different parts of the tree, not of the numbers of species. Until more is known, a consensus guess may be that for every insect species in the canopy there is one elsewhere in the typical tropical tree (rather than Erwin's 0.5). But this could lead to a serious underestimate of the global total, if the mites turn out to be as surprisingly diverse as the tropical canopy beetles.

(d) How do we scale up from insect species per tree to a global total?

Even if we knew how many insect species were effectively specialized to a truly representative species of tropical tree at a particular place, there remain serious difficulties in scaling this up to the roughly 50 000 species of tropical trees. The reason that we cannot simply multiply the number of species per tree by the number of tree species is twofold: on the one hand, the same tree species may play host to different insects in other parts of its range (so that simple multiplication underestimates the global total); on the other hand, the same insects may be effectively specialized on other tree species in other regions (so that simple multiplication could lead to overestimation).

Ward's (1977) study of Juniper in Britain is an example of the first of these two complications. Looking at each one degree band of latitude in the range of Juniper, from 50° N to 59° N, she found the recorded numbers of species of arthropods varied from 5 to 20. The total number of species associated with Juniper in Britain in this study is 27, which is larger by a factor 1.4–5.0 than the total that might be inferred from any one regional study.

The converse phenomenon, the same species specialized to different plants in different places, is shown by Thomas's (1990) analysis of the *Passiflora-Heliconius* system in South America. For this unusually well-studied association, Thomas averages over 12 sites to find a mean of 7.2 *Passifloraceae* species and 9.7 *Heliconiinae* species per site (he uses families or subfamilies, because a few *Heliconiinae* are not in the genus *Heliconius*, and likewise a few *Passifloraceae* are not in the genus *Passiflora*). The total number of recorded *Passifloraceae* species in the neotropics is 360. A naive scaling up may therefore suggest 360 times $(9.7/7.2) \approx 485$ *Heliconiinae* species. But this total is in fact only 66 species. The complicating factor is, of course, that these relatively specialized butterflies use taxonomically different (although ecologically similar) species of *Passifloraceae* in different parts of the neotropics, with the result that simple multiplicative estimates are an order-of-magnitude too high. There are further complications and caveats here. For one thing, it could be that, to some extent, systematists have tended to split the *Passifloraceae* and lump the *Heliconiinae* (Gilbert & Smiley (1978) refer to one downward revision from 70 to 7 species of *Heliconius*). For another thing, only some 100–150 species of *Passifloraceae* are found below 1500 m, which represents an upper limit to the range of *Heliconiinae* species (Gilbert & Smiley 1978), so that simple multiplication might more properly suggest 135–200 *Heliconiinae* species. This is still significantly larger than the 66 that exist.

The essential point is that the simple procedure of multiplying the average number of species per tree by the number of tree species can be misleading for those insect species with ranges significantly larger than that of the host-tree species in question, and conversely for tree species whose ranges exceed that of the insects in a given region. We cannot begin to resolve these problems until we have a better understanding of the patterns in the distributions of geographical ranges for plant and animal species.

Despite some pioneering efforts (Rappoport 1982; Hanski 1982; Brown 1984; Root 1988), little is yet known about range-size patterns for individual species, much less for joint distributions of, for instance, herbivorous insects and their host plants. Figure 3 summarizes one recent analysis of the distributions of range sizes for all North American mammals, showing that most species have relatively restricted ranges (the median range size is about 1% of the area of North America), but that there is considerable variability. On the whole, it seems likely that for tree species with below-average ranges, we may need to acknowledge that many of the insects that are effectively specialized to them range more widely, using other trees in other places (so that Erwin's simple multiplicative procedure may overestimate totals). Conversely, trees with above-average ranges may embrace different faunas in different places, resulting in underestimated totals if one location is treated as definitive. Ultimately, such questions of range-size and geographical distribution shade into larger questions of how we define commonness and rarity, and how patchiness and regional

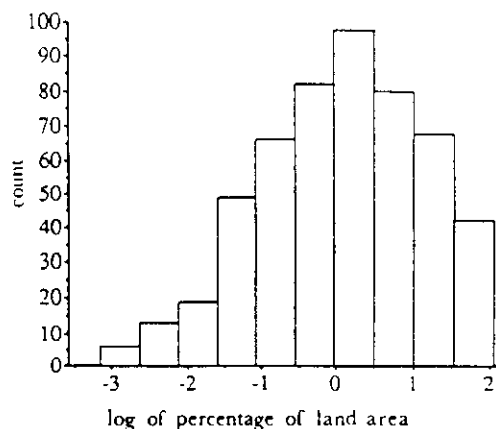


Figure 3. Histogram of the logarithms of the sizes of species' geographical ranges for 523 species of North American non-aquatic mammals. The range size is expressed as a percentage of the total land area of North America. The distribution is roughly lognormal in shape, with the proportion of species in the different (logarithmic) range-size categories falling away roughly symmetrically on either side of the median value of around 1%. After Pagel *et al.* (1990).

differentiation affect extinction probabilities (Rabinowitz *et al.* 1986; Pagel *et al.* 1990; Hubbell, this symposium).

I end this section by circling back to Erwin's method of estimating the total number of species on Earth. Suppose we accept a total of 1200 beetle species in the canopy of a tropical tree species as typical. Further assume there are 2.5 other canopy insect species for each beetle species (40% of insects are beetles), and one species elsewhere on the tree for each one in the canopy. Suppose a fraction, f , of this fauna is effectively specialized to the tree species in question. Finally, assume we can simply multiply the effective number of insect species per tree species by the number of tropical tree species (50 000) to arrive at the grand total. This total is then $(300f)$ million. If, overall, 10% of the insects are effectively specialized to a given tree, we recover Erwin's 30 million. To reduce an estimate along these lines down to the previously-conventional figure of around 3 million, we need to assume that only 1% of the insect species are effectively specialized, which seems a bit low. I return to this below.

4. DIRECT ESTIMATES OF GLOBAL TOTALS

Hodkinson & Casson (1990) have presented a very direct way of estimating species totals, based essentially on determining what fraction of a thoroughly sampled group, in a particular region, have previously been described.

Specifically, they use several methods to sample the bug (Hemiptera) fauna of a moderately large and topographically diverse region of tropical rainforest in Sulawesi, in Indonesia, over a one-year period. Hodkinson & Casson (1990) estimate that their samples represent the bug fauna on the roughly 500 tree species in their study sites in Dumoga Bone

National Park in Sulawesi. They found a total of 1690 species of terrestrial bugs, of which 63% were previously unrecorded (this proportion of undescribed species is weighted according to the number of species per family within the group).

If the bugs in Sulawesi are representative of tropical insects more generally, then we may say that the total number of recorded insect species (approximately 1 million) represents 37% of the real total, leading to an estimated 2.7 million insect species in total. Hodkinson & Casson give a somewhat more detailed argument, with several intermediate steps, to reach an estimated total of 1.8 to 2.6 million, but I believe the more direct approach outlined above contains the essentials.

Hodkinson & Casson also use their data to give a different derivation of the global total number of insects. First, if they find roughly 1700 bug species on 500 tree species, we might expect 170000 bug species on the tropical total of 50000 tree species. Second, bugs comprise approximately 7.5% of all described insects (Southwood 1978), so we can estimate a grand total of 2.3 million insects (again, Hodkinson & Casson's somewhat more detailed estimate gives a total of 1.9–2.5 million). This second estimate is surprisingly close to the first, and much more direct, estimate of 2.7 million. This rough coincidence between the two estimates is not trivial or tautological; it can be seen to arise essentially because the factor of 100 in the ratio between tree species globally and in Dumoga Bone Park is roughly cancelled by the factor of 109 in the ratio between all known bug species and the number of known species in their study (or 114 if aquatic bugs are included in the global total).

This is a brief summary of an important study. There is obviously an enormous amount of work in completely sampling and classifying any group of tropical insects, and one must always worry whether the group or site is representative of more general patterns. But I see this as the simplest and most direct route to estimates of global totals. When other taxa are added, Hodkinson & Casson's estimate of insect species totals carries us back to the previously conventional global total of 3–5 million species. On the other hand, to reconcile Hodkinson & Casson's estimate with Erwin's data, we need to assume that over 400 of his roughly 1200 beetle species in the canopy of *Leuhea* have been described and recorded, which seems unlikely to me.

5. SPECIES TOTALS FROM SPECIES-SIZE RELATIONS

An altogether different approach to estimating how many species there are derives from examining patterns in the numbers of terrestrial animal species in different body-size categories (May 1978, 1988). Very roughly, as one goes from animals whose characteristic linear dimension is a few metres down to those of around 1 cm (a range spanning many orders-of-magnitude in body weight), there is an approximate empirical rule which says that for each tenfold reduction in length (1000-fold reduction in body weight) there are 100 times the number of species.

This empirical relation begins to break down at body sizes below 1 cm in characteristic length. As the relation itself is not understood, this break-down may mean nothing. But the break-down may plausibly be ascribed to our incomplete record of smaller terrestrial animals, most of which may be unrecorded tropical insects. If the observed pattern is arbitrarily extrapolated down to animals of characteristic length around 0.2 mm, we arrive at an estimated global total of around 10 million species of terrestrial animals (May 1988).

This frankly phenomenological estimate would be more interesting if we had a better understanding of the physiological, ecological or evolutionary factors generating species-size distributions (Lawton, this symposium).

6. SOME MORE GENERAL CONSIDERATIONS

This section touches briefly on some more general questions that are prompted by the above discussion.

(a) *Different patterns for different groups?*

We have seen that Hodkinson & Casson's direct estimates of global species totals, based on the fraction of bug species in their Sulawesi samples that were previously known, agree with estimates of around 3 million species of insects that earlier were obtained by projecting past trends of discovery. But conservative reappraisals of Erwin's estimate, based on beetle species in tropical canopies, suggest totals of at least 7 million and possibly more. To produce a total of as little as 3 million insects from Erwin's or other similar data requires that we assume only 1% of the beetle fauna are effectively specialized to a given tree species, or that more than 400 of the beetle species found in the canopy of *Leuhea* have been previously recorded; these assumptions seem a bit extreme.

One way of squaring this circle is to recognize that very different patterns may pertain to different taxonomic groups, or in different settings. We have already seen hints of this in the canopy fauna. Tobin's preliminary analysis of data from tree canopies in Manu National Park in Amazonian Peru suggests ants constitute 70% of the individuals and beetles less than 10%, but that there are many more beetle species than ant species (May 1989). Similarly, Stork's fogging samples from 10 Bornean trees were dominated by ants (4489 individuals), but they only contributed 99 of the total of 2800 species; one family of beetles contributed 1455 individuals but 739 species. In tropical canopies generally, ants contribute many individuals, typically half or more, but relatively few species, while beetles contribute relatively few individuals but many species. It seems likely to me that patterns of 'effective specialization' will also vary greatly from group to group, so that we need a much better understanding of the ecology of specific communities of organisms, before we can draw general conclusions about species diversity from limited studies of particular groups in particular places.

(b) Food web structure and species totals

Studies of the structure of food webs are beset with many difficulties of biases and inconsistencies in the way data are assembled. Provocative generalizations are nevertheless emerging (Cohen *et al.* 1990; Yodzis 1990; Nee 1990; Lawton 1989). One of these is the suggestion by Lawton and co-workers (for example, Strong *et al.* (1984)) that there may typically be something like 10 species of phytophagous insects for each plant species. Applied globally, and given that there are at least 300 000 recorded species of higher plants, this would put a lower limit of around 3 million on the number of insect species. However, Lawton's ratios come mainly from studies of temperate-zone plants, and corresponding ratios may be higher for tropical plants (which would tend to support higher estimates of the global total).

Similar arguments about food web structure suggest there could be, on average, as many as five species of parasitoids (parasitic wasps and flies that lay their eggs on or in larval or pupal stages of other insects) for each phytophagous insect species, in both tropical and temperate regions (Hawkins 1990). Applied generally, this estimate could clearly escalate the global total to very high levels (Hochberg & Lawton 1990). I think such estimates are probably too extravagant, although they do suggest that closer studies of tropical hymenoptera may produce surprises to match Erwin's work on beetles.

Such estimates of global species totals, based on the number of plant species combined with the structure of food webs, are akin to the estimates in § 5 based on species-size relations. They provide independent lines of attack upon the problem, related only obliquely to direct estimates based on counting species.

(c) Microbial diversity

Throughout this chapter, I have followed the usual practice of assuming species diversity to mean the numbers of animal species, or sometimes plant and animal species. More precisely, five kingdoms are usually recognized, distinguished by different levels of cellular organization and modes of nutrition. Two of these kingdoms, the prokaryotic monerans and the eukaryotic protists, comprise microscopic unicellular organisms, and together they account for something like 5% of recorded living species. The fungal and plant kingdoms represent roughly another 22% of species. The animal kingdom thus does comprise the majority (more than 70%) of all recorded living species. The extent to which these recorded numbers of species in the different kingdoms accurately reflect their relative diversities is, however, open to question. As one moves down the size-spectrum of organisms, from the romantic large mammals and birds, through nondescript small arthropods, on down to protozoan, bacterial and viral species, not only does concern for diversity and conservation fall away, but it even changes sign. In the Smithsonian Institution in Washington, a touching label attached to Martha, the

last passenger pigeon, laments her death in 1914, but no-one mourned the passing of the last smallpox virus.

Regardless of the amount of study they have received, the microorganisms that act as decomposers in the soil and leaf litter are crucial to the functioning of ecosystems. Recent work has, moreover, revealed that the diversity in natural populations of microbial organisms is far greater than that found in conventional studies of laboratory cultures (Olsen 1990). Ward *et al.* (1990) examined the ribosomal RNA sequences from a well-studied photosynthetic microbial mat from a hot spring in Yellowstone National Park, and found eight distinct sequence types, none of which were the same as any of the 12 laboratory-cultured prokaryotes believed to be characteristic of this mat. More surprisingly, only one of the eight sequences bears any close resemblance to a recognized bacterial 'phylum'. Broadly similar results were obtained by Giovannoni *et al.* (1990) from studies of ribosomal RNA gene sequences of microorganisms from samples of ocean water. These studies of natural populations of microorganisms, as distinct from laboratory cultures, are, in their own way, even more astonishing than Erwin's and others' revelations about tropical canopy faunas. They mark the advent of a new stage in our understanding of microbial ecology and diversity. We have not yet begun to address the questions that such studies of naturally occurring microbial diversity raise, for example, for the release of genetically engineered organisms.

(d) What is a species?

Up to this point, I have deliberately avoided any definition of what is meant by a species, nor will I pursue it in detail here. But a few remarks should be made.

First, some researchers recognize more species than others, even within well-studied groups. This is particularly noticeable for asexually reproducing organisms. For examples, some taxonomists see around 200 species of the parthenogenetic British blackberry, others see only around 20 (and a 'lumping' invertebrate taxonomist may concede only two or three). Some strongly inbreeding populations are almost as bad, with 'splitters' seeing an order-of-magnitude more species than do 'lumpers'; *Erophila* and *Arabidopsis*, British plants in the mustard family, are notable examples.

Second, and more fundamentally, studies of nucleotide sequences show homologies of less than 50% (as revealed by DNA hybridization) for different strains of what is currently classified as a single bacterial species, *Legionella pneumophila* (Selander 1985). This is as large as the characteristic genetic distance between mammals and fishes. Relatively easy exchange of genetic material among different 'species' of microorganisms could mean that basic notions about what constitutes a species are significantly different for vertebrates than for bacteria.

Third, the increasing armamentarium of techniques for exploring the genetic structure of populations is uncovering further complexities in what we mean by a species. For example, *Neomachilellus scandens*, a member

of the Meinertellidae, is found in inundation forests in the Rio Negro valley (which are flooded for 5–6 months each year), and in primary and secondary dryland forests near Manaus. Ecological studies show the species to be univoltine in inundation forests, with a defined reproductive period, but polyvoltine in dryland forests. These two ecologically distinct forms of *N. scandens* are effectively indistinguishable on morphological grounds, and traditional taxonomy would at most recognize them as 'biotype-specific races'. But protein analyses by Adis (1990), using electrophoresis to test 15 enzymes, shows that there is no gene flow between the univoltine and polyvoltine populations, even when the typical spatial separation is less than 50 m. Adis (1990) proposes that on ecological and genetic grounds we should recognize two species here, and that this situation may be much commoner in the tropics than is currently recognized. If so, we could be dealing with even more species than suggested by Erwin.

(e) *Are some species more equal than others?*

Human activities are destroying natural habitats, and the associated biota, at rates that are probably without precedent in the history of life on Earth. In particular, the clearance and burning of an area of tropical forest roughly the size of Britain each year is surely contributing to accelerating losses of tropical arthropods and other animals. Against this background, we need to go beyond knowing how many species there are, and to use this knowledge to optimize conservation efforts (either in planning National Parks and other protected regions, or in devising strategies that reconcile sustainable exploitation of resources with preservation of an appreciable fraction of the original fauna).

Such conservation efforts will pose increasingly difficult choices. Should all species be treated as equal? Or should we take the view that, for conservation purposes, a species not closely related to other living species is more important than one with many widely distributed congeners? And if the answer to this latter question is yes, how do we quantify the relative importance of different species?

Vane-Wright *et al.* (1990) have made a beginning of this task, showing how taxonomy and systematics can build from species lists toward assessment of the relative distinctness of different species and, ultimately, communities. At one extreme, we could of course regard all species as equally important. At the opposite extreme, we could take a phylogenetic or cladistic tree, which represents the hierarchical relations among the constituent species, and measure taxonomic distinctness by weighting each group equally with respect to the summed weights of their terminal taxa. This scheme has the merit of recognizing taxonomic distinctness, but it has the fault that taxonomic rank overwhelms species numbers: on this basis, the two Tuatara species would be seen as equal to all 6000 other reptile species taken together. Vane-Wright *et al.* propose an intermediate scheme, which quantifies the amount of information contained in a given hierarchical classi-

fication. Their method gives answers that depend on the topology of the hierarchy (even for a fixed number of terminal taxa), and that recognize the importance of, for example, Tuataras without amplifying it out of all proportion (see May 1990).

My purpose here is not to dwell on the details of these pioneering efforts, but rather to emphasize that a more complete understanding of how many species there are is only a first step. More and more, conservation efforts will be faced with difficult choices. It will be helpful to be guided by quantitative measures of distinctness that are based on systematic understanding of the phylogenetic relations among species.

7. CONCLUDING REMARKS

Why should we care how many species there are? One line of argument is narrowly utilitarian. Thus, for instance, essentially all modern medicines and other pharmaceutical products have been developed from natural products, and so it would seem sensible to be looking at the other shelves in the larder rather than destroying them. The triumphs of intensive agriculture have been accompanied by progressive narrowing of the genetic diversity of the plants we exploit. The likelihood of global changes in climate gives fresh emphasis to the desirability of conserving existing gene pools and exploring the possibility of utilizing new plants.

Important though such considerations are, I think a more pressing and more basic utilitarian reason for studying and cataloguing diversity is because it is a prerequisite to understanding how biological systems work. The scale and scope of human activity are now so large that they rival the natural processes that created and maintained the biosphere as a place where life can flourish. Current rates of input of carbon dioxide, chlorofluorocarbons and other gases are beginning to disturb the balance of the biosphere. Most of our uncertainties about the long-term consequences stem from uncertainties about how physical and biological processes are coupled. We need to understand the structure and functioning of ecosystems, particularly tropical ecosystems, much better than we do. And we cannot hope to do this if we do not even know what is there, and why tropical diversity is what it is.

Beyond these practical motivations, I believe we need to understand the diversity of living things for the same reasons that compel us to reach out toward understanding the origins and eventual fate of the universe, or the structure of the elementary particles that it is built from, or the sequence of molecules within the human genome that code for our own self-assembly. Unlike these other quests, understanding and conserving biological diversity is a task with a time limit. The clock ticks faster and faster as human numbers continue to grow, and each year 1–2% of the tropical forests are destroyed. Future generations will, I believe, find it incomprehensible that Linnaeus still lags so far behind Newton, and that we continue to devote so little money and effort to understanding and con-

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erving the other forms of life with which we share this planet.

I have been helped by Paul Harvey, Michael Hassell, Ian Hodkinson, John Lawton, Nigel Stork, Chris Thomas and many others. I am particularly grateful to Sir Richard Southwood for letting me use his unpublished data. This work was supported, in part, by the Royal Society and by NERC (through its Interdisciplinary Research Centre at Silwood Park).

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Discussion

R. J. H. BEVERTON - *Montana, Old Roman Road, Gwent, U.K.*
The 'target' of the total number of species is not, of course, static because species are continually being lost by natural

and man-made processes and added by speciation. Could Professor May say something about these rates of change, and how they compare with the overall picture of species diversity?

R. M. MAY. It is true that throughout most of the recorded history of life on Earth, species have been going extinct and new species have been appearing. The next half-century or so is, however, likely to be singular in two respects. First, there is the scope and timescale of impending extinctions in relation to speciation. For most of the time, extinction rates and speciation rates have been roughly in balance, and both

have been on geological timescales: *something like* half the species currently extant appeared *over the past* 50-100 million years or so. Over half are likely to *become* extinct over the next 50-100 years. Thus rates of disappearance or extinction and rates of appearance or speciation are likely to be out of balance by a factor of a million! This clearly is not what has been going on over most of geological time. Secondly, most past 'extinctions' see the basic lineage continued (at least since the Cambrian); likely current rates of extinction in the tropics will see lineages ended, not transformed.

The Future of Biodiversity

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Recent extinction rates are 100 to 1000 times their pre-human levels in well-known, but taxonomically diverse groups from widely different environments. If all species currently deemed "threatened" become extinct in the next century, then future extinction rates will be 10 times recent rates. Some threatened species will survive the century, but many species not now threatened will succumb. Regions rich in species found only within them (endemics) dominate the global patterns of extinction. Although new technology provides details of habitat losses, estimates of future extinctions are hampered by our limited knowledge of which areas are rich in endemics.

Debates about the consequences of human population growth are not new. Our numbers have increased dramatically since Malthus but so has our technology (1). Will technical ingenuity keep pace with increasing population problems? Ingenuity can replace a whale-oil lamp with an electric light bulb, but not the whales we may hunt to extinction. Species matter to us (2). How fast we drive them to extinction is a matter of our future. Critics consider high estimates of current and future extinction rates to be "doomsday myths," contending that it is the "facts, not the species" that are endangered (3). Here, we review these estimates.

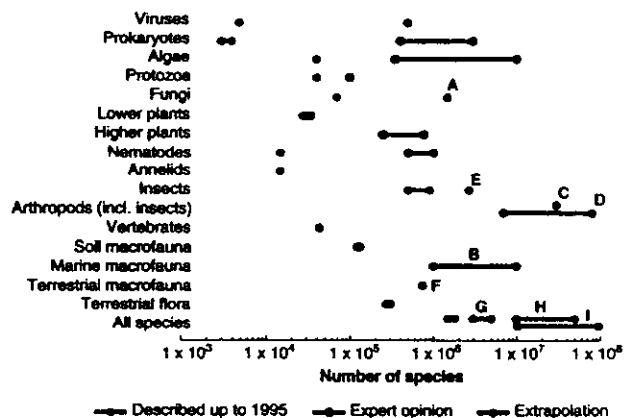
Extinctions have always been a part of Earth's history. So what is the background rate of extinction: how fast did species disappear in the absence of humanity (4)? A summary of 11 studies of marine invertebrates suggests that fossil species last from 10^6 to 10^7 years (5). For ease of comparison, we use the number of extinctions (E) per 10^6 species-years (MSY) or E/MSY . If species last from 10^6 to 10^7 years, then their rate of extinction is 1 to 0.1 E/MSY .

These estimates derive from the abundant and widespread species that dominate the fossil record. The species most prone to current extinction are rare and local. Moreover, we emphasize terrestrial vertebrates in our discussions of current extinctions. There are only two studies of their fossils (5), and these suggest high background rates ($\sim 1 E/MSY$). Interestingly, we can supplement these estimates from our knowledge of speciation rates. These could not be much less than the extinction rates, or the groups would not be here for us to study.

Molecular phylogenies are now produced rapidly and extensively. There is one for 1700 bird species (6). Using the relative time axis of molecular distances, we can

elucidate the patterns of species formation. Models in which every lineage has the same, constant probability of giving birth to a new lineage (speciation) or going extinct (death) permit estimation of the rate parameters (7). The rich details of this approach offer hope in testing for important factors controlling the relative rates of background speciation and extinction. Obviously, absolute rates require accurately dated events, such as the first appearance of a species or genus in the fossil record. There are genetic distance and paleontological estimates of divergence times for 72 carnivore and 14 primate species or subspecies (8). Given their importance as a benchmark

Fig. 1. Numbers of described species and estimates of species numbers, including expert opinions of taxonomic specialists (12) and various extrapolations (26). (A) The British ratio of 6 fungi species:1 plant species and a world total of 2.5×10^6 plant species suggests ~ 1.5 million species of fungi worldwide. (B) A world total of 10^6 to 10^7 species of marine macrofauna comes from the accumulation of new species along sample transects. (C) A large sample of canopy-dwelling beetles from one species of tropical trees had 163 species specific to it. There are 5×10^4 tree species, and so $163 \times 5 \times 10^4 = 8 \times 10^6$ species of canopy beetles. Because 40% of described insects are beetles, the total number of canopy insects is 2×10^7 . (D) If only 20% of canopy insects are beetles, but there are at least as many ground as canopy species, then the grand total is 8×10^7 . (E) Some 63% of the 1690 species on ~ 500 Indonesian tree species were previously unrecorded. The $\sim 10^6$ described insect species thus suggest a total of 2.7×10^6 species. (F) Across many food webs, there are roughly three times as many herbivores and carnivores combined as there are plants. This resulting estimate of terrestrial animal species, $\sim 7.5 \times 10^5$, is certainly too low, because published food webs omit many species. (G) There are about two tropical bird and mammal species for each temperate or boreal species. Yet, of the $\sim 1.5 \times 10^6$ described species, about one-third is tropical. The prediction of 3×10^6 species is an underestimate, because not all temperate species are described. (H) There is a linear increase in species numbers with decreasing body size. Below a threshold level, however, the numbers drops, perhaps because of sampling bias. If the true pattern remained linear, there would be 1×10^7 to 5×10^7 species. (I) We added the more detailed estimates for the numbers of species in the largest groups.



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against which to compare modern extinction rates, we plead for more absolutely timed accounts.

How Many Species Are There?

Any absolute estimate of extinction rate requires that we know how many species there are. In fact, we do not. May (9) shows that the problems of estimating their numbers are formidable. Only $\sim 10^6$ species are described and $< 10^5$ —terrestrial vertebrates, some flowering plants, and invertebrates with pretty shells or wings—are popular enough to be known well. Birds are exceptional in that differences in taxonomic opinion [~ 8500 to 9500 species (6)] far exceed the annual descriptions of new species (~ 1). Most species are as yet undescribed in every species-rich group (Fig. 1). Major uncertainties lie in those groups in which we have scant or conflicting evidence of very high diversity. There are $\sim 10^6$ described insects, yet estimates range from $\sim 10^7$ to nearly 10^8 species. Some potentially rich communities, such as the deep-sea benthos, have been sparsely sampled.

How can we be confident in our extrapolations of extinction rates from the $< 10^5$ well-known species to the $\sim 10^6$ described, or to the conservative grand total of $\sim 10^7$ (5)? If extinction rates in diverse taxa and regions are broadly similar, then they are

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likely to be representative. If we understand the underlying mechanisms, we may find they operate universally.

The Past as a Guide to the Future

Unambiguous evidence of human impact on extinction comes from before-and-after comparisons of floras and faunas (10). Polynesians reached the planet's last habitable areas—Pacific islands—within the last 1000 to 4000 years. The bones of many bird species persist into, but not through, archaeological zones that show the presence of humans. No species disappeared in the longer intervals before the first human contact. Adding known and inferred extinctions, it seems that with only Stone Age technology, the Polynesians exterminated >2000 bird species, some ~15% of the world total.

We must infer extinctions, because we will not find the bones of every now-extinct species. From the overlap in species known from bones and those survivors seen by naturalists, sampling theory infers that ~50% of the species are still missing (10). Faunal reconstruction affords a second inference. For example, Steadman (10) contends that every one of ~800 Pacific islands should have had at least one unique species of rail. A few remote islands still have rails. Others lost theirs to introduced rats in the last century. Large volcanic islands typically lost several species of rails. Accessible islands lost their rails earlier, for every survey of bones from islands now rail-free has found species that did not survive human contact.

High extinction rates also followed the Pacific's colonization by Europeans. Since 1778, the Hawaiian islands have lost 18 species of birds; the fate of 12 more is unknown (10). Nor are birds unusual. Of 980 native Hawaiian plants, 84 are extinct and 133 have wild populations of <100 individuals (11). Across the Pacific, a predatory snail introduced to control another introduced snail ate to extinction hundreds of local varieties of land snails (12).

Nor are Pacific islands unusual: of 60 mammalian extinctions worldwide, 19 are from Caribbean islands (12). In the last 300 years, Mauritius, Rodrigues, and Réunion in the Indian Ocean lost 33 species of birds, including the dodo, 30 species of land snails, and 11 reptiles. St. Helena and Madeira in the Atlantic Ocean have lost 36 species of land snails (12).

Importantly, extinction centers are not necessarily on islands nor only in terrestrial environments. The fynbos, a floral region in southern Africa, has lost 36 plant species (of ~8500); 618 more are threatened with extinction (12). Extinctions of 18 (of 282) species of Australian mammals rival those

from the Caribbean; 43 more are threatened (12). In the last century, North American freshwater environments lost 21 of 297 mussel and clam species (120 are threatened) and 40 of ~950 fish species (12). This world tour of extinction centers has remarkable features (12). Recent extinction rates are 20 to 200 E/MSY (Fig. 2)—a small range given, among other things, the uncertainties of whether to average rates over a century or a shorter interval that reflects more recent human impacts. We find high rates in mainlands and islands, in arid lands and rivers, and for both plants and animals. Although we know less about invertebrates, high rates characterize bivalves of continental rivers and island land snails. There is nothing intrinsic to the diverse life histories of these species to predict their being unusually prone to extinction.

What obvious features unite extinction centers? We know the species and places well—as did naturalists a century ago. Importantly, each area holds a high proportion of species restricted to it. Such endemics constituted 90% of Hawaiian plants, 100% of Hawaiian land birds, ~70% of fynbos plants, and 74% of Australian mammals (12). In contrast, only ~1% of Britain's birds and plants are endemics (12). Remote islands are typically rich in endemics, but so are many areas within continents (13). Past extinctions are so concentrated in small, endemic-rich areas that the analysis of global extinction is effectively the study of extinctions in one or a few extinction centers (12). Why should this be?

Random extinction is the simplest model. Some species groups and some places will suffer more extinctions than others, but generally the more species present, the more there will be to lose. This model does a poor job of predicting global patterns. If island birds were intrinsically vulnerable to extinction, then Hawai'i and Britain with roughly the same number of species of breeding land birds (~135) would have suffered equally. Hawai'i had >100 extinc-

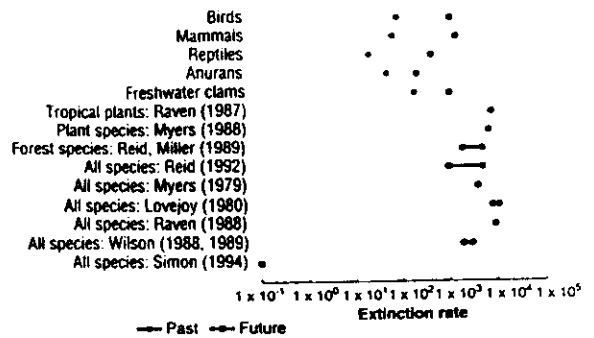


Fig. 2. Estimates of extinction rates expressed as extinctions per million species-years. For birds through clams, we derive past rates from known extinctions in the last 100 years; we derive future rates by assuming that all currently threatened species will be extinct in 100 years. The latter rates are much higher than the former but are still far too low. The remaining estimates are previously published (1, 16, 27). Myers (1979) (27) assumes an exponential increase in the number of extinctions. Myers (1988) (16) assumes the loss of a small number of areas rich in endemics. With the exception of Simon, the rest are estimates based on the relation between habitat loss and species loss. Simon's claims (1) of one (or a few) species per year (out of a conservative total of 10^7 species) are not scientifically credible.

tions, Britain only 3 (12). Nor is the number of species an area houses a good predictor of the total extinctions. Islands house few species and suffer many extinctions.

Imagine a cookie-cutter model where some cause destroys (cuts out) a randomly selected area. Species also found elsewhere survive, for they can recolonize. But some of the endemics go extinct, the proportion depending on the extent of the destruction. We do not assume that island biotas are intrinsically more vulnerable than mainlands. For random species ranges, the number of extinctions correlates weakly with the area's total number of species, but strongly with the number of its endemics. By chance alone, small endemic-rich areas will contribute disproportionately to the total number of extinctions.

This model is consistent with known mechanisms of extinction. Habitat destruction cuts out areas, as the model implies. Introduced species also destroy species regionally. Species need not be entirely within the area destroyed to succumb to extinction: The populations outside may be too small to persist (14). Moreover, across many taxa, range-restricted species have lower local densities than widespread species (15). The former are not only more likely to be cut in the first place, but their surviving populations will have lower densities and thus higher risks of extinction than widespread species. This entirely self-evident model emphasizes the localization of endemics—Myers' "hot spots" (16)—as the key variable in understanding global patterns of recent and future extinctions.

Predicting Future Rates of Extinction

Projecting past extinction rates into the future is absurd for no other reason than that the ultimate cause of these extinctions—the human population—is increasing exponentially. For vertebrates, we have worldwide surveys of threatened species

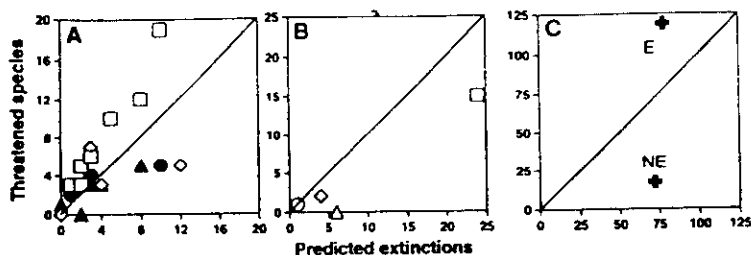


Fig. 3. The numbers of species currently threatened with extinction plotted against the numbers of species predicted to become extinct. Squares, Philippines; circles, North Wallacea; diamonds, Greater Sundas; triangles, Lesser Sundas. The predictions use satellite estimates of remaining forest cover and the relation between species numbers and area. (A) For the subset of species endemic to single islands, these numbers match; they straddle the graph's diagonal. (B) For the subset of species that are endemic to several islands within each region, the predicted extinctions consistently exceed the numbers of threatened species. (C) When we combine the species found on one or several islands (E) across the entire region, the predictions based on forest losses (78) are slightly smaller than the number of threatened species (119). The remaining subset comprises widely occurring species (NE). Their predicted extinctions (72) far exceed the few (17) actually threatened with extinction. Predictions of extinctions from habitat loss must be scaled to the number of endemics the area contains (23).

(12). Is it reasonable to assume that all these species will be extinct in <100 years, thus making future rates 200 to 1500 E/MSY (Fig. 2)?

Some threatened species are declining rapidly and will soon be extinct. Others, not so obviously doomed, have small numbers (<10²). They risk the demographic vagaries of sex (all the young of a generation being of the same sex) and death (all the individuals dying in the same year from independent causes). For these, both models and empirical, long-term studies of island populations suggest times to extinction on the order of decades (17). Population fluctuations, and the environmental vagaries that cause them, drive the extinction of larger populations (>10²) (14). Over 20 years, bird densities can vary 10-fold, and insect densities 10,000-fold (14). Ecologists have been slow to combine models and data. Yet even in the absence of a formal analysis, such fluctuations can obviously doom even quite large populations.

Our predictions may err because some threatened species will survive the century (18). The more serious problem with our predictions is that species not now threatened will become extinct. For birds—the one group for which we have detailed lists of the causes of threats—limited habitat is the most frequently cited factor, implicated in ~75% of threatened species (18). Increasingly well documented studies (19) show that habitat destruction is continuing and perhaps accelerating. Some now-common species will lose their habitats within decades.

Interestingly, accidentally or deliberately introduced species are blamed for only 6% of currently threatened birds (18). Yet introduced species, and the predation, competition, disease, and habitat modification they cause, are the most frequently cited

factors in all the extinction centers we discussed above (12). Undoubtedly, many species will be lost to introduced species in ways that we cannot now anticipate. For example, no one considered the birds on the island of Guam to be in danger 30 years ago, but an introduced snake has eliminated all the island's birds since then (14). Were this predator to reach Hawai'i, all its birds would be at risk.

Calibrating Species Loss from Habitat Loss: A Tale of Two Forests

So far, we have sampled well-known, but disparate species whose high extinction rates probably typify the unknown majority. We now consider a typical mechanism of extinction: habitat loss. Can we predict species losses from estimates of habitat losses? The function $S = cA^z$ relates the number of species counted (S) to the area surveyed (A); c and z are constants (20). If the original habitat area, A_o , is reduced to A_n , we expect the original number of species, S_o , to decline eventually to S_n . Now $S_n/S_o = cA_n^z/cA_o^z$ or $(A_n/A_o)^z$ —an expression that is independent of c . Across different situations, z varies from 0.1 to 1.0, but it is often taken to be ~1/4 (20). This value is typical of islands isolated by sea-level changes, a process that may be the best model for large habitat fragments isolated by deforestation (20, 21).

This recipe forms the basis of the predictions of 1000 to 10,000 E/MSY shown in Fig. 2. To challenge these estimates, critics point to the few bird extinctions after the clearing of North America's eastern forests (3). Is the recipe flawed? Only if interpreted naively are these results a poor model for what happens elsewhere.

An extinction "cold spot." European col-

onists cut >95% of the eastern forests of North America, but not simultaneously. Locally, forests reclaimed abandoned fields, and regionally forests recovered in the Northeast as settlers moved westward. Of the region's 2.87×10^6 km² area, forests always covered >50% (21). So 16% (= $0.5^{0.25}$)—or 26 of the ~160 forest species—should have gone extinct. Only 4 did so (21). Yet, such predictions are naive. Not enough time may have elapsed for the extinctions to occur. However, all but 28 of these species occur widely across North America. They would have survived elsewhere even if all the forest had been permanently cleared. The cookie-cutter model restricts the analysis to the region's 28 endemics, whence the predicted and observed number of extinctions correspond (4 ≈ 16% of 28).

Simply, this region has very few endemics and so few species to lose. In contrast, tropical moist forests may hold two-thirds of all species on Earth (22). Despite inevitable differences in their definition, satellite imaging yields detailed and rapidly changing estimates showing their rapid depletion (19). The forests' global extent is variously estimated at 8×10^6 to 12.8×10^6 km² and their rate of clearing as 1.2×10^6 to 1.4×10^6 km² per decade (19).

An extinction "hot spot." The 1.47×10^6 km² of forests in the Philippines and Indonesia (excluding Irian Jaya) hold 545 endemic bird species—20 times the number in America's eastern forest in half the area (23). Only 0.91×10^6 km² of forest remains, and ~10% of the original area is cleared per decade. Using current satellite-based estimates of forest cover, the species-area recipe adequately predicts the number of species endemic to single islands that are currently threatened (Fig. 3A). The recipe, however, overestimates the numbers of currently threatened species that are found on several islands (Fig. 3B) and greatly overestimates the number of currently threatened species that are widespread (Fig. 3C).

Estimates of extinctions from habitat losses (Fig. 2) use an area's total number of species, not its smaller number of endemics. Does this reliance on such totals inflate these rates? In general, it does not, because many tropical areas are unusually rich in endemics (13). For example, 18 areas worldwide are so rich in endemics as to encompass ~20% of the known species of flowering plants in a total area of 0.74×10^6 km² (16). A larger area than this was cleared from the eastern American forests in the 19th century. The fate of these areas obviously dominates the calculations of future extinction rates. Details of land use changes in these areas are critical, but the details are not sufficient in themselves. We also need the detailed patterns of endemism.

Unfortunately, we know the geographical ranges of only a small proportion of the already small proportion of species for which we have names. We do have a comprehensive understanding of the geographical patterns of species richness (20). Its lessons are not encouraging. First, we cannot extrapolate from one species group to the next. For instance, across a continent species richness in frogs may not correlate with the species richness in birds (24). Worse, the direction of the correlation—positive or negative—may differ between continents (24). Second, areas rich in species are not always rich in endemics (24). Simply, our understanding of endemism is insufficient for us to know the future of biodiversity with precision (25).

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Assessing extinction rates

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1.1 Introduction

In this opening chapter, we review what we see as some of the major themes, and major questions, which emerge from the data presented in the subsequent chapters, all of which are empirically-oriented.

We also sketch the essential elements of three different theoretical approaches to estimating likely future rates of extinction. The first, and by far the most familiar, uses species-area relations in combination with current or projected rates of tropical deforestation. The second method provides a very rough estimate, based on the current rates at which species in better-studied groups (specifically, birds, mammals, and palm trees) are 'climbing the ladder' of the International Union for the Conservation of Nature and Natural Resources' (IUCN) categories of threat, from 'vulnerable' to 'endangered' to 'probably extinct' to certified extinction. The third method is a new one, presented here in Chapter 13 by Georgina Mace; it uses the estimated probabilities of extinction, as functions of time, which underpin the IUCN categories of threat for individual species. In reviewing these three approaches, which give surprisingly concordant answers, we emphasize the many uncertainties and other problems associated with them. We also discuss the discrepancies between rates of documented extinction over the past century or so, and the roughly hundredfold higher rates of projected future extinctions.

Our chapter concludes with some comments on the implications for conservation of biological diversity which emerge from the later chapters, and from other recent work on patterns of commonness and rarity among different groups and different places.

1.2 Extinction rates in the fossil record

Biological diversity has been increasing from at least 3.5 billion years ago (3.5×10^9 ya), the date assigned to the oldest objects that are probably microbial fossils (Awramik *et al.* 1983). There is as yet no agreed explanation of why multicellular organisms apparently did not begin to diversify until around 1.4 billion years ago (Walter *et al.* 1990), nor why multicellular animals initiated their explosive diversification in the Early Cambrian, some 600 million years ago (600 mya). Plants and animals did not invade the land and begin their pattern of terrestrial diversification until somewhat later still, around 450 mya. That is,

these latter three milestones—the beginning of diversification of multicellular organisms, multicellular animals, and terrestrial plants and animals—fall around 60%, more than 80%, and almost 90% along the road from the beginning of life on earth to the present, respectively. As Sepkoski (1992) emphasizes: 'The basic observation here is that diversification has not been continuous. This is not a conclusion that could easily be reached from first evolutionary principles'.

In dealing with past extinction rates, our attention—both in this opening chapter and throughout the book—is confined almost exclusively to the plant and animal kingdoms, as revealed by the fossil and other records since the Cambrian. We recognize that communities of soft-bodied multicellular organisms undoubtedly pre-date the Cambrian, but it is difficult to estimate their diversity. We also recognize that arguably the most important and interesting phase in the evolution of life on earth was the first two billion years or so, from the emergence of simple self-replicating molecules to the first prokaryotes. Last and perhaps most important, we recognize that microorganisms, representing five to seven recognized kingdoms of organisms, and including viruses, bacteria, protozoans, and algae, created the planet's oxygen-rich atmosphere, and that the 'ecosystem services' they provide today as decomposers, soil maintainers, and so on, underpin all other living things. Be all this as it may, our focus is on only two kingdoms, plants and animals, over the past 600 million years.

Table 1.1 summarizes a variety of estimates that have been made of the average lifespan of a species in the fossil record, from origination to extinction. Many of these estimates were collected together by Raup (1978), whose own assessment of around 11 million years for the average lifespan of invertebrate species is based on computer analysis of some 8500 cohorts of fossil genera. The other estimates summarized in Table 1.1 are of varying degrees of sophistication; some of the subtleties and difficulties in such analyses are discussed in more detail in Chapters 2 and 11. All in all, Table 1.1 suggests the average species has a lifespan of around 5–10 million years.

It follows that, if the average species lives 5–10 million years, and the duration of the fossil record we are considering is around 600 million years, then—all things being equal—the Earth's current tally of plant and animal species represents about 1–2% of all those that have ever lived.

Of course, all things are not equal. Figure 1.1 shows the numbers of families of marine animals as a function of time, throughout the Phanerozoic (which is essentially the 600 million year span we are focused on). As Sepkoski (1992) emphasizes, the patterns in diversity at the level of families seen in Fig. 1.1 are broadly in agreement with the corresponding patterns at higher (orders) and lower (genera, species) taxonomic levels; in particular, they correlate well with underlying species diversity (Sepkoski *et al.* 1981; Bambach and Sepkoski 1992). Moreover, similar 'stair-step' patterns have been documented—although with different time axes—for terrestrial plants (Niklas *et al.* 1983; Knoll 1986), tetrapod vertebrates (Benton 1985, 1990), and possibly for terrestrial arthropods (Sepkoski and Hulver 1985; Labandeira and Sepkoski 1993; see Fig. 1.2 and further discussion, below). Figure 1.1 thus suggests that the diversity of life-forms

Table 1.1 Estimates of species' lifespan, from origination to extinction

Taxon	Source of estimate	Species' average lifespan (mya)
All invertebrates	Raup (1978)	11
Marine invertebrates	Valentine (1970)	5–10
Marine animals	Raup (1991)	4
Marine animals	Sepkoski (1992)	5
All fossil groups	Simpson (1952)	0.5–5
Mammals	Martin (1993)	1
Cenozoic mammals	Raup and Stanley (1978)	1–2
Diatoms	Van Valen (1973)	8
Dinoflagellates	Van Valen (1973)	13
Planktonic foraminifera	Van Valen (1973)	7
Cenozoic bivalves	Raup and Stanley (1978)	10
Echinoderms	Durham (1970)	6
Silurian graptolites	Rickards (1977)	2

in the sea—measured at taxonomic levels ranging from orders to species—rose abruptly throughout the Cambrian, to attain a rough plateau toward the end of the Ordovician; this plateau continued, albeit with significant fluctuations, until the great wave of Permian extinctions (which marked the end of the Palaeozoic), since when there have been fluctuations about a roughly steady upwards trend. Sepkoski (1992) concludes that present marine diversity is roughly twice the average level over the entire span of the Phanerozoic (and that the biases introduced by better knowledge of more recent events and records is not a significant factor in this conclusion).

Today, however, only about 15% of recorded species are found in the sea; the majority are terrestrial (Barnes 1989, May 1994). If this ratio of recorded species accurately reflects reality (and some would argue it does not: Grassle and Maciolek 1992, but see Hammond 1992 and May 1992, 1994), and if it has been roughly thus since the land was colonized, then we must focus primarily on terrestrial patterns. As noted by Sepkoski (1992) and others (see the preceding paragraph), terrestrial diversity of plants and animals, again measured at taxonomic levels ranging from species to orders, shows patterns very roughly similar to those in Fig. 1.1, but on a shorter timescale of around 450 million years. Terrestrial diversity rose steadily throughout the Devonian, to level out in the Carboniferous and Permian; the trends since the Triassic, accentuated in the Tertiary, have been toward increasing diversity (owing, in part, to the Earth's land masses becoming more fragmented and dispersed toward the end of the Tertiary than at any other point in the Phanerozoic; the degree to which this helps explain corresponding increases in marine diversity is less clear). In short, Sepkoski's (1992) rough rule, that the current marine diversity is about twice the Phanerozoic average, also suggests that the larger terrestrial diversity today is about twice the average over the 450 million year history of life on land.

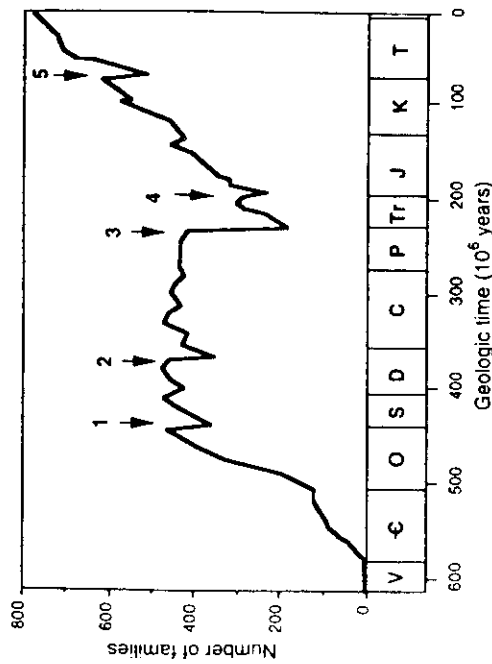


Fig. 1.1 The history of the diversity of marine animal families throughout the Phanerozoic, as a function of time. The curve connects 77 discrete data points, each showing the total number of well-skeletonized families known from a particular stratigraphic stage. The arrows labelled 1 to 5 identify the five major events of mass extinction: 1, end Ordovician (O); 2, late Devonian (D); 3, end Permian (P); 4, end Triassic (Tr); 5, end Cretaceous (K). The durations of the various geological periods are indicated on the time axis. In addition to the five just given, the abbreviations for the remaining periods are: V, Vendian; ε, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; T, Tertiary. (After Sepkoski 1992.)

Putting all this together (and recognizing that the difference between 600 and 450 million years is relatively insignificant, given the accuracy of our estimates), we double our 'all things being equal' estimate, to conclude that today's species of plants and animals constitute roughly 2–4% of the total there have been.

These figures, of course, are sensitive to our estimates of the average species' lifespan inferred from the fossil record. But the actual numbers of fossil species that have been named and recorded (as distinct from the numbers inferred from our more-complete knowledge of higher-order taxa, such as families and orders) is a small sample of the actual total. Basing his analysis on an earlier one by Raup (1976), Sepkoski (1992) estimates that some 250 000 species of fossil marine animals have been documented. This is roughly equal to his estimate of 200 000 for the number of animal species in the ocean today. Hence, by essentially the same arguments as we have just used to assess the fraction of all species that are alive today, Sepkoski concludes that the known fossil record of marine species represents a sample of only 2–4% of the total (in fact, he obtains 2%, because he takes the average species' lifespan to be 5 million years, at the lower end of our 5–10 million year range).

Actually, the overall sample is worse than this. Around 95% of all fossil species

are marine animals (Raup 1976), partly because a lot of them are shallow-sea creatures that dwell in the kinds of environments which produce rich beds of fossils. But we just noted that around 85% of today's recorded plant and animal species are terrestrial. If a similar proportion of species were terrestrial over a reasonable fraction of the Phanerozoic, then documented fossil species are unlikely to represent as much as a sample of 1% of the true total.

They are, moreover, a heavily biased sample, being predominantly species of marine invertebrates. Estimated average species' lifespans, however, vary significantly among groups, as Table 1.1 shows (and as is discussed more fully in the next four chapters). In particular, the average lifespan of mammal species in the fossil record is around 1 (or possibly 2) million years, which is an order-of-magnitude less than the roughly 10 million year estimate by Raup (1978) for invertebrates (essentially all of which are marine). Even among marine invertebrates, there are substantial differences from group to group, with Mesozoic ammonoids, for example, having average species' lifespans of only 1–2 million years (Kennedy 1977). Conversely, there are indications (in Chapter 4 by Coope, and in Fig. 1.2 below) that insect species may be unusually long-lived, at least in north-temperate regions. In addition, Labandeira and Sepkoski (1993) have suggested that the record of insect diversification is one of roughly linear increase from low levels around 300–400 mya; today, insects account for 56% of all named and recorded species (indeed, to a first approximation, all contemporary species are insects). Such a combination, for insects, of relatively long species' lifespan and numerical preponderance within recent species totals could seriously undercut all the above estimates. Even if we make the modest assessment that the total number of insect species on Earth today (recorded plus yet-unknown) is only around 3 million or so, it is conceivable that 10% or more of all plant and animal species ever to have lived are with us today, and they are terrestrial insects.

Finally, notice that our 'all things being equal' estimate implies that, on average, the plant and animal species living at any one time during the Phanerozoic represent 1–2% of the overall total. The five great 'spasms' of extinction in the fossil records are indicated in Fig. 1.1. Those which marked the ends of the Ordovician, Devonian, Triassic, and Cretaceous (marked 1, 2, 4, 5, respectively, in Fig. 1.1) eliminated 65–85% of animal species in the ocean, while that at the end of the Permian (marked 3 in Fig. 1.1) extinguished 95% or more of marine species. These five mass extinctions differed from each other, and each one affected different taxonomic groups differently (Benton 1986); for example, insect diversity was particularly affected by the extinction event at the end of the Permian (marked 3). Nevertheless, if we assume that terrestrial extinction levels very roughly paralleled marine ones, we conclude that the total fraction of all plant and animal species eliminated by the five mass extinction events (the 'Big Five') is 1–2% multiplied by $(4 \times 0.75 + 0.95)$, or roughly 4–8%. This accords with Raup's (1986, 1992) more detailed estimates that 90–96% of all extinctions occurred outside these major episodes.

This section has dealt exclusively with *proportions* of species to have become

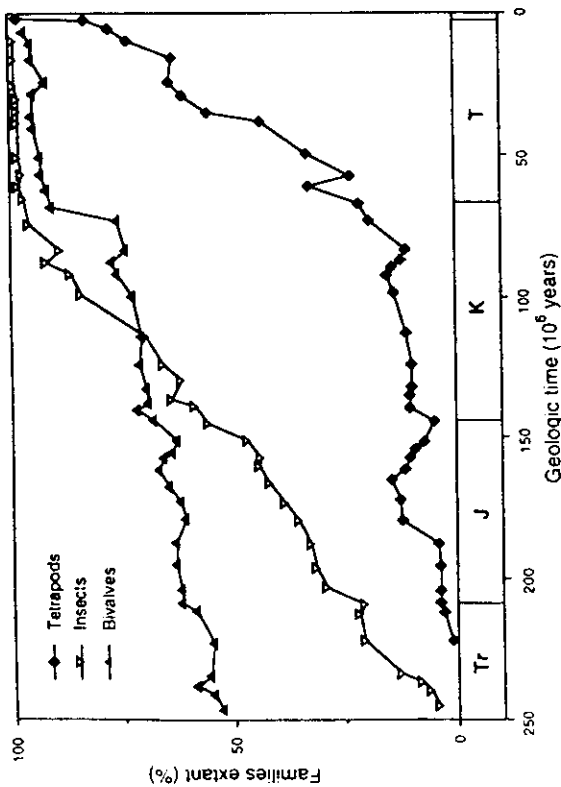


Fig. 1.2 These curves show currently-extant families as a proportion of the total number of families found in the fossil record, at various times over the past 250 million years. The curves are for insects, marine bivalves, and terrestrial vertebrate tetrapods, as indicated. The data are plotted for discrete stratigraphic stages, and the abbreviations for the geological periods are as in Fig. 1.1. The main features of these three different curves are discussed in the text (notice that the curves need not be monotonic, because radiations of short-lived families can temporarily depress the fraction that survive into the present). In particular, these data suggest that essentially no insect families have become extinct over the past 100 my or so. (After Jabloncki and Sepkoski 1993.)

extinct, and so on. Any assessment of *absolute* rates of species extinction requires an estimate of the total number of plant, animal, and other species currently extant, and thence (by the kinds of arguments used above) ever to have lived. A full discussion of guessimates for such species totals, and in particular any discussion of recent (and sometimes dramatic) suggestions for upward revisions for particular groups, would require its own chapter (for a short summary, see May 1990a, 1994; Hammond 1992; or Stork 1988). We content ourselves with the estimate of 5–10 million species currently alive. Combined with the estimate of 5–10 million years for the average species lifespan, this gives a very rough estimate for the 'background' extinction rate in the fossil record of one species per year (but it could easily be at least a factor two bigger or smaller).

1.3 Ecological and evolutionary factors affecting past extinctions

The following chapters discuss some of the patterns discernible in which species survive, and which do not, at various times in the fossil record.

Jablonski and Jackson both survey evidence in support of the view that species which are fairly widely dispersed, and particularly those that achieve this by wide dispersal of larval stages, are more likely to survive extinction events (both the 'Big Five' and the many smaller events, on nested hierarchies of scales), than are more sessile or range-restricted species. This is, indeed, the prevailing view (e.g., Diamond 1984; Simberloff 1986a), although counter-examples can be found. Vermeij (1993), for instance, examined a collection of 15 marine species (1 gastropod, 1 coral, 3 mammals, 10 birds) that have disappeared during the human-dominated post-Pleistocene period: although 9 of these did have narrow ranges (being known from a single island or a single marine biogeographical province), at least 5—one-third of the total—have large ranges, embracing parts of two or more marine biogeographical provinces. On balance, we believe the conventional generalization is valid, although it must be applied with caution to specific cases.

This generalization has recently received theoretical support, which goes beyond the commonsense observation that you are obviously better off if you are widespread and abundant than if you are localized and rare. Tilman *et al.* (in press) have generalized earlier studies by Nee and May (1992), to examine multispecies metapopulations in which a number of species can persist together in an environment where there are many habitat patches: metapopulations of each species maintain themselves by a balance between local extinctions and colonizations; there is a hierarchy of competitive ability, so that competitively superior species exclude competitively inferior ones from co-occupied patches; and inferior competitors persist by virtue of higher colonization rates and/or lower patch-mortality rates. This system has complicated dynamics, and exhibits inherent 'limits to similarity' (manifested through the colonization and mortality parameters, and not arbitrarily imposed as in many older studies of this subject). If this metaphorical system is stressed by environmental events which reduce the total number of habitat patches, or which reduce the overall biomass in the system, it is the superior competitors (often the most abundant species) which tend to be lost, while the superior dispersers survive. This is, admittedly, an oversimplified metaphor, but it has interesting implications (Tilman *et al.* in press).

Another theme which emerges in several of the later chapters of this book is that environmental changes—human-related or otherwise—are likely to have less effect on floras and faunas which have undergone similar stresses in the not-so-far-distant past. Thus, Jackson shows the onset of glaciation in the northern hemisphere around 2 mya caused dramatic extinctions among species of molluscs, corals, and planktonic foraminiferans throughout tropical America, whereas subsequent cycles of glaciation, temperature fluctuations, and sea-level changes have had comparatively little effect. Pimm, Moulton, and Justice show that, for birds, there are fewer recent extinctions, and fewer currently-endangered species, on the islands of the western Pacific (which were colonized by humans some 3000–5000 ya) than on the more recently colonized Hawaiian and other eastern Pacific islands. Greater compares records of recent plant extinctions for 'Mediterranean' floras in the actual Mediterranean, South America, California,

and Western Australia. These extinction rates are lowest (around 0.1%) for the Mediterranean, where human impacts are oldest, and highest (around 1%, and possibly higher) in Western Australia, where they are most recent. All this points to the conclusion that species assemblages which have been winnowed by relatively recent vicissitudes (on timescales from thousands to millions of years) are likely to suffer less from subsequent impacts of the same general kind. Expressed this way, the conclusion is unsurprising. But taken in isolation, the relatively low rate of recent extinction, and perhaps even of current endangerment (around 15%), for the flora of the Mediterranean littoral—one of the world's most human-impacted regions—is surprising.

Various other suggestions have been made about factors which may predispose particular species or groups to extinction. For several of these factors, no clear message emerges from the data surveyed in the book. Thus, Jablonski finds that, over the fossil record, position in the trophic hierarchy does not correlate clearly with extinction; top predators do not appear to have generally higher extinction rates. Lawton shows that the effects of body size upon extinction rates are complex, with no simple rules.

On the other hand, some kinds of trophic links do have implications for extinction processes. In Chapter 9, Bond examines the ways in which plant species can be put at risk by loss of pollinators or seed dispersers. He considers the trade-offs among different categories of risk, and shows that plants often compensate for high risk in one aspect of their relation with a mutualist by low risk in another aspect. For example, self-incompatible plants with specialized pollinators that are rare often have vegetative propagation. Bond notes that some systems—including the South African Cape flora and lowland tropical rainforests—lack this kind of compensation, and are thereby especially vulnerable to 'knock-on' extinctions when mutualists are lost. This analysis raises subtleties that go well beyond the simple observation that if one partner in an obligatory dyad is extinguished, the other is doomed (even though it may take time to disappear if it is a long-lived tree: Janzen's 'living dead').

Some clear-cut co-extinction events do, however, go unnoticed, largely because little things in general, and parasites in particular, elicit scant concern. For instance, Stork and Lyal (1993) note that the mournful label attached to Martha, the last passenger pigeon, in the Smithsonian Institution's Natural History Museum makes no mention of at least two species of obligate ectoparasite, the lice *Columbicola eximicus* and *Campanulotes defectus*, which accompanied her into oblivion, nor does the World Conservation Monitoring Centre (WCMC 1992) list any species of Phthiraptera (lice) or Siphonaptera (fleas) as extinct. This kind of selective attention has larger implications (Gaston and May 1992).

1.4 Differences in extinction rates among groups

Coope's main theme, highlighted in his title for Chapter 4, is that species of northern insects in general, and British beetles in particular, have shown

remarkably few extinctions over the past few million years. He suggests that this may be because the mobility of most insects allows them to track environmental changes, shifting their ranges as climate alters. One slight problem here is that, as Nix (1986), Busby (1986), and others have shown, climate changes do not always cause a species' range (as defined by physiological and other constraints) to move smoothly and continuously across the map; the result is often discontinuous fragmentations and saltatory jumps in a mosaic of potentially suitable habitat. Coope himself emphasizes that such environmental 'tracking' will not be possible if changes are too fast, too extreme, and/or on too large a scale, and he suggests this may reconcile the constancy he sees in the Pleistocene insect fauna of Britain with the list of recent losses (and the larger list of impending losses) surveyed by Thomas and Morris in Chapter 8.

The fact remains that, in this book, there is a notable difference between the patterns of relatively low extinction rates seen for northern insects by Coope and for 'Mediterranean' floras by Greuter, versus the relatively high rates documented for birds by Pimm *et al.* and by Bibby. Mammalian extinctions in the late Pleistocene, although not discussed elsewhere in the book, also tell a story different from Coope's insects: about 40% of the genera of large mammals in Africa, and more than 70% in North America, South America, and Australia, were extinguished over the past 100 000 years or less (the timescales are correlated with human arrivals in Australia and the New World: see Martin and Klein 1984).

These differences among different groups are writ larger in the estimates of the characteristic lifespans of species, from origination to extinction, summarized in Table 1.1 above. Figure 1.2 suggests the differences among groups may be even greater than indicated in Table 1.1 (Labandeira and Sepkoski 1993). This figure shows the families of insects, marine bivalves, and terrestrial vertebrate tetrapods that are alive today, as fractions of all families (in each group) found in the fossil record as we reach back over the past 250 million years or so. Admittedly most insect families are more speciose than vertebrate ones, and thereby possibly more resistant to extinction if species lifespans are comparable (see Jablonski, Chapter 2), but even so the differences seen in Fig. 1.2 are remarkable. The differences between the average family lifespans of bivalves and tetrapods accords with the order-of-magnitude differences in species' lifespans between the two groups indicated in Table 1.1 (roughly 10 my versus 1 my). As mentioned earlier, Fig. 1.2 suggests that, over the past 100 my or so, the average lifespan of an insect species could be well in excess of 10 my.

Such differences among groups prompt questions about whether we are applying the same taxonomic criteria to all groups. There are problems with 'taxonomic inflation' over the years; what was a genus to Linnaeus might be a family, or even higher, today (Sepkoski 1992). These instabilities, applying differently to different groups and dependent to some degree on the amount of attention given to different groups, create problems when we try—as we have been doing above—to draw inferences about the history of particular groups of species from their superspecific taxonomy (Patterson and Smith 1989). Such

methodological differences among taxonomic groups show up in other fundamental ways: for example, Selander (1985) has observed that different strains of what is currently classified as a single bacterial species, *Legionella pneumophila*, have nucleotide sequence homologies (as revealed by DNA hybridization) of less than 50%; this is as large as the characteristic genetic distance between mammals and fishes.

All this being said, the balance of current evidence suggests there are real differences in characteristic extinction rates among different groups, possibly grounded in systematic ecological differences (some of which may be caricatured as the differences between 'r-selected' and 'K-selected' species, to use a metaphor which has been much abused). But we must be wary about applying any such tentative generalizations to current situations. In particular, most of our knowledge of Palaeozoic insects comes from what was then in the tropics (the Dominican amber samples insects of the subtropics, as do the Cretaceous ambers of Mexico), whereas most of our detailed knowledge of late Cenozoic insects is for non-tropical faunas (Coope, this volume).

Against this background of past events, we now turn to recent and likely future events.

1.5 Current and recent extinction rates

As discussed in more detail in Chapters 7 and 13, by Bibby and Mace, respectively, the information we have about documented extinctions of animal species since around 1600 has been drawn together by the IUCN (1990) and the WCMC (1992). The IUCN/WCMC Red Data Books also list species under various categories of extinction threat: 'possibly extinct', 'endangered' (survival unlikely if causal factors continue), 'vulnerable' (likely to become 'endangered' if current trends continue), along with 'rare' (but not necessarily threatened), 'status unknown', and 'not [or no longer] threatened'. A more analytic account of these categories, and of attempts to give greater precision to them over recent years, is in Chapter 13 (see also Mace 1994; and Mace and Lande 1991). The WCMC database also provides information about seed-bearing plants threatened with extinction, using comparable categories of threat.

Table 1.2 summarizes these data, showing both the absolute numbers and the proportions of major animal and plant taxa that have become extinct since 1600, or that are currently threatened. Roughly half these recorded extinctions of 485 animal and 585 plant species have taken place this century (Smith *et al.* 1993b). Many authors, including Bibby and Mace in this book, have emphasized the many difficulties and shortcomings in the database summarized by Table 1.2. We outline some of these problems, because several raise interesting and wider questions.

First, notice that documented extinctions among insect species are two orders-of-magnitude less (as a fraction of their recorded fauna) than among vertebrates, over the past 400 years or so. This ratio is, of course, even smaller if one recognizes that the true number of insect species is almost surely at least 3 million,

Table 1.2 Species in major taxa that have become extinct since 1600 or are threatened with extinction. (After Smith *et al.* 1993a.)

	No. of species certified extinct since 1600	No. of species listed as threatened* (in thousands)	Approx. total of recorded extant species (in thousands)	Approx. total extinct (%)	Approx. threatened (%)
<i>Animals</i>					
Molluscs	191	354	100	0.2	0.4
Crustaceans	4	126	40	0.01	0.3
Insects	61	873	1000	0.006	0.09
Vertebrates	229	2212	47	0.5	5
Fishes	29	452	24	0.1	2
Amphibians	2	59	3	0.1	2
Reptiles	23	167	6	0.4	3
Birds	116	1029	9.5	1	11
Mammals	59	505	4.5	1	11
<i>Total</i>	485	3565	1400	0.04	0.3
(animals)					
<i>Plants</i>					
Gymnosperms	2	242	0.8	0.3	30
Dicotyledons	120	17474	190	0.06	9
Monocotyledons	462	4421	52	0.9	9
Palms	4	925	2.8	0.1	33
<i>Total</i> (plants)	584	22137	240	0.2	9

*Threatened here includes IUCN categories of 'vulnerable', 'endangered', 'probably extinct', but does not include other categories of concern, such as 'rare' or 'insufficiently known'

and possibly much higher. Although we have argued, in the preceding section, that the average insect species' lifespan in the fossil record might be an order-of-magnitude longer than those of tetrapods, there is no suggestion of a disparity as great as seen in Table 1.2. Rather, the differences among taxa in the proportions listed as extinct or threatened result primarily from differences in the attention paid to them. For one thing, the ratio of taxonomists to numbers of species is roughly 100 times greater for vertebrates than for invertebrates, and 10 times greater for vertebrates than for vascular plants (Gaston and May 1992). For another thing, this differential attention is seen in the rates at which new species are recorded, and in the completeness of collections, for different groups: new bird species are found at the rate of around 3-5 per year (or 0.03-0.05% of the total in the group); tropical botanists can expect to find roughly one new plant species per 100 species collected (G.T. Prance, pers. comm.); but collections of insect species, or fungi, or marine macrofauna from previously unstudied locations have shown proportions of new species ranging from 20% to 50-80%.

and occasionally even more (May 1990a, 1994; Hawksworth 1991; Poore and Wilson 1993). In short, some of the groups in Table 1.2 are much better-studied than others.

Second, even for the comparatively well-known groups, such as birds and mammals, the documented extinctions are surely underestimates (Diamond 1989; Pimm *et al.*, Chapter 5). The stringent IUCN criteria required to be listed as 'extinct' in Table 1.2 are not easily satisfied by animals and plants in remote places. Diamond (1989), for example, studied the bird fauna of the Solomon Islands, where 164 species have been recorded; 12 of these have not been seen since 1953 or earlier, nor could he find them. These 12 bird species are almost certainly extinct, yet only 1 is so certified. Among vertebrates, freshwater fish species almost surely are proportionately the most endangered, as a result of pollution of rivers (although introduced species are also causing major problems, of which those in Lake Victoria may be the best known). One indicative recent four-year search for the 266 species of exclusively freshwater fishes recorded last century in lowland peninsula Malaysia found only 122 (Mohsin and Ambok 1983). Yet relatively few fish species show up as extinct or threatened in Table 1.2 (Wilson 1992).

These problems are exacerbated by so many species being known from only a single collecting site. Stork and Hine (in press), for example, estimate that such is the case for about 40% of the estimated 400 thousand recorded species of beetles. Under these circumstances, it is difficult to assess anything other than local extinctions.

Third, rates of documented extinction and threat vary among geographical locations (Smith *et al.* 1993b; Mawdsley and Stork 1994). Some of these patterns may reflect reality, but others surely do not. An example of a real pattern is that roughly 61% of the animal extinctions (but only 27% of the plants) in Table 1.2 come from island endemics, mainly in the Pacific Ocean (58% and 72% of all island extinctions for animals and plants, respectively). The differential vulnerability of previously-isolated island endemics to all four of Diamond's (1989) 'evil quartet'—habitat destruction and fragmentation, introduced species, over-exploitation, and chains of extinction or 'knock-on' effects—has been much discussed; the numerical preponderance of Pacific islands is probably because there are more of them. An example of an artefactual pattern is that about two-thirds of the recent animal extinctions recorded on continents are from North America and the Caribbean, and about one-fifth from Australia. The relative paucity of recorded animal extinctions from South America, Africa, and Asia surely reflects less knowledge and less recording effort from these species-rich regions (the recent discovery of three new species of primates in Brazil, and of a new bovid in Vietnam, highlights this; Mawdsley and Stork 1994). Similarly, roughly two-thirds of recorded continental plant extinctions are from North America and Australia. All 45 extinctions in sub-saharan Africa are from the Cape flora of South Africa; as Bond's Chapter 9 makes clear, this comparatively well-studied flora may have particular vulnerability, but it seems unlikely that no other African floras have suffered losses.

These various problems in the database summarized by Table 1.2 show up clearly—even laughably—when we look closely at its 61 extinct insect species (Mawdsley and Stork 1994). Of this 61 species, 33 are lepidopterans. The remaining 28 species are distributed among orders in rough proportion to the specificity of orders, but the over-representation of lepidopterans in general, and butterflies in particular, most likely derives from their status as 'honorary birds'. Looking from another perspective, it is perhaps reasonable that 51 of the 61 species are island endemics. But 42 of this 51 are from Hawaii. Of the 10 continental extinctions, 9 are from North America (specifically, the United States), 1 from Europe (specifically, Germany). Again, this speaks eloquently of where the researchers, rather than the endangered species, live.

It is illuminating to observe that for the insect and other invertebrate fauna of Britain, which is better-known than that of any other country, the rates of extinction and endangerment (within Britain) are comparable to those for birds and mammals (more generally) in Table 1.2. The British Red Data Books for insects (which covers some 14 000 of Britain's estimated 22 000 insect species) and for other non-marine invertebrates are summarized in Table 1.3. From these data, we see that roughly 1% of Britain's insects have been extinguished this century (although essentially all survive, and many are thriving, elsewhere), and 6% are currently threatened. Although there is only one recorded extinction among Britain's other invertebrates, a similar fraction, 7%, are listed as threatened. These proportions among a comparatively well-known invertebrate fauna are similar to the fraction of the world's birds and mammals on Red Lists of threatened species, strengthening the argument that many of the entries in Table 1.2 reflect lack of knowledge, not lack of endangerment.

Finally, we note that, for the comparatively well-studied birds and mammals, roughly 100 of the documented extinctions in Table 1.2 took place this century. There are around 14 000 species of birds and mammals in total, so this represents documented extinction of about 1% of these species over the past 100 years. Such a rate translates to an expected lifespan, before extinction, of around 10 000 years for the average bird or mammal species. Although this may seem long, it is 2 to 3 orders-of-magnitude shorter than the average species lifespan of 1–10 my deduced from the fossil record.

1.6 Estimated future extinction rates from species-area relations

Essentially, all projections of impending rates of extinction are based on species-area relations, combined with estimated rates of loss of habitat ('area') due to deforestation or other processes. There have been many such projections (for reviews, see the papers in Whitmore and Sayer 1992), but they all have the same simple basis.

The species-area relation is an empirical rule, based on a variety of studies of how the number of species, *S*, of a particular taxonomic group (beetles, birds, vascular plants, etc.) found on individual islands within an archipelago depends

several ecological or evolutionary factors is likely to lead—via the central limit theorem applied to multiplicative random factors—to a lognormal distribution, and for $N \gg 1$ this will tend to give $S \approx bN^z$, with z indeed in the range around 0.2–0.3 and b some constant (May 1975). Second, if we assume that the total number of individuals of the group in question is roughly proportional to the area occupied, we have $N = aA$, with a being a proportionality constant. These rough theoretical arguments thus lead to eq(1), with z in the empirically-observed range.

Suppose we now assume that eq(1) applies to the kinds of species reduction resulting from deforestation or other processes which reduce habitat area. Let the proportional reduction in area (expressed as a fraction or as a percentage) be represented by ΔA . If ΔA is small ($\Delta A \ll 1$), the corresponding proportional reduction in species numbers, ΔS , is then simply

$$\Delta S = z \Delta A. \quad (2)$$

We can now estimate the eventual loss of species consequent upon any particular annual rate of deforestation, ΔA , assuming z indeed is around 0.25. In particular, current rates of tropical deforestation have been variously assigned values in the range of 0.8–2% per year (see, e.g., Reid 1992, table 3.3; and Groom and Schumaker 1993, fig. 2). This immediately translates into a corresponding fraction of 0.2–0.5% of the species in them committed to extinction each year. If sustained, this annual extinction rate is equivalent to an average species' lifespan of around 200–500 years.

To translate any such estimate into a statement about the numbers of species committed to extinction by deforestation obviously requires that we specify the number of species in the group under consideration. If we apply the estimated loss of 0.2–0.5% per year to a conservatively-estimated global total of 5 million species, we arrive at 10–25 thousand species each year, or 1–3 species per hour. This assessment depends not only on our estimates of z and ΔA , but also on our guesstimate of total species numbers; the estimated 200–500 year species' lifespan depends only on z and ΔA .

There are, however, problems with applying such species area relations to estimated extinction rates. Equation (1) was originally deduced from observations on species distributions among real or virtual islands. If instead applied simply to numbers of species found in areas of different sizes on a continent, eq(1) often does apply, but with z -values more typically in the range of 0.1–0.2 (Diamond and May 1981). As eq(2) makes clear, such a low z -value would imply a lower rate of species' loss for any given rate of loss of habitat area. Probably more important are questions about the extent to which the effects of habitat fragmentation, especially in the tropics, are described by the species-area relations of 'island biogeography'. Simberloff (1992), for example, points out that the forests of the eastern United States were reduced, over two centuries, to fragments totalling only 1–2% of their original extent, yet only three forest birds went extinct.

More generally, the species' lifespans of 200–500 years projected by the

Table 1.3 Insect and other non-marine invertebrate species that have become extinct, or are threatened with extinction, within Britain. (After Shirt 1987; Bratton 1991; Hyman and Parsons 1992, 1994.)

	Extinct: formerly native to Britain, but not recorded since 1900	Threatened: species listed as 'vulnerable' or 'endangered'	Estimated no. of species surveyed
<i>Insects</i>			
Coleoptera	63	247	3900
Diptera	3	496	6000
Lepidoptera (butterflies)	16	49	2500
Hymenoptera	(3)	(5)	(56)
Trichoptera	18	49	580
Heteroptera	2	13	199
Orthoptera	6	20	540
Odonata	—	5	30
<i>Total</i>	108	885	14 000
<i>Other invertebrates</i>			
Mollusca	—	17	c. 202
Arachnida	—	53	647
Crustacea	1	3	c. 70
Myriapoda	—	—	c. 92
Others ^b	—	1	c. 41
<i>Total</i>	1	74	c. 1050

^a For Lepidoptera, includes a few subspecies of macro-moths
^b C. celerentata, Nemerita, Bryozoa, and Annelida

on the area of the island, A . The islands may be real islands in the sea, or virtual islands, such as freshwater lakes or isolated mountain tops. Very often, log-log plots of S against A show a straight line, so that the relation can be written

$$S = cA^z. \quad (1)$$

Here, c is a constant, and the parameter z has values in the rough range $z \sim 0.2-0.3$ (MacArthur and Wilson 1967; Diamond and May 1981). This rough rule is often expressed by saying that if the area of suitable habitat is reduced to 10% of its pristine value, the number of species will be halved.

Although less commonly appreciated, the rule also has a theoretical foundation. First, within particular taxonomic groups, the distribution of individuals among species (or 'species-relative abundance') often obeys a so-called 'canonical lognormal distribution' (Preston 1962; MacArthur and Wilson 1967). Such a distribution implies that the total number of individuals, N , is related to the number of species, S , by the power law $S \approx bN^{1/4}$, provided S is reasonably large (May 1975). More generally, a multiplicative interplay among

species-area methods are much shorter than the lifespans of around 10 000 years deduced earlier for birds and mammals, on the basis of documented extinctions over the past century. Setting aside the fact that these documented extinctions are surely underestimates (so that true lifespans are less than 10 000 years), the discrepancy largely disappears if we are more careful in recognizing that species-area estimates are projected numbers of species that, on current trends of habitat destruction, are 'committed to extinction'. Loss of, say, 90% of habitat will, on this basis, eventually lead to loss of around half the species in it, but the time taken to attain this new, impoverished state is not specified, and will depend on details that vary from place to place and species to species. In general, the notion of 'committed to extinction' recognizes that extinction is a gradual process on an uncertain timescale, but that the endpoint is nevertheless certain once a species' demographic and genetic base has been sufficiently eroded by habitat destruction or other processes (Heywood and Stuart 1992).

For example, Simberloff (1986b) used a species-area approach to estimate that some 1350 species of birds would be committed to extinction by the year 2015. If this figure were misinterpreted as the predicted number actually to go extinct between 1986 and 2015 (which was not Simberloff's intent), it would imply an average of 45 extinctions per year, which seems implausibly high. A more empirical approach is to examine the 1029 entries in Collar and Andrew's (1988) list of threatened bird species. Interpreting 'committed to extinction' as referring to any species whose populations in the wild are no longer viable and will inevitably become extinct, unless major conservation actions reverse current trends (by habitat restoration, elimination of introduced predators, captive breeding and re-introduction, and so on). Heywood and Stuart (1992) estimate that 450 bird species will be committed to extinction by 2015, with 27 of these already probably extinct (in addition to the 12 listed as almost certainly extinct). Whilst this empirically-based estimate is still one-third the theoretically-based one, the disparity is not the worrying factor of 20–50 noted above.

1.7 Estimated future extinction rates from IUCN Red Lists

An alternative approach to estimating impending extinction rates is to look, not at the entries in the IUCN/WCMC database as such, but rather at their recent patterns of change. Specifically, Smith *et al.* (1993a) have analysed the changes in the IUCN Red Lists for animals in 1986, 1988, and 1990, and in the WCMC Plants Database between 1990 and 1992. The numbers of animal species listed as threatened have increased by more than 30% between 1986 and 1990. Over this interval, only 15 vertebrate species (and 33 animal species in total) satisfied the stringent criteria for addition to the list of recorded extinctions; this rate, if sustained, would take about 7000 years to extinguish half the 47 000 or so vertebrate species. Similarly, between 1990 and 1992, 163 plant species were added to the database of recorded extinctions; this corresponds to about 3000 years for extinction of half the planet's quarter million or so plant species.

We can, however, make a better—although still extremely crude—guess at how extinction rates might currently be accelerating, by examining how fast the status of species on these lists is changing. Smith *et al.* (1993a) take the conventional categories of the IUCN lists, and assign them values of 0 for the bottom rung of the ladder (rare, status unknown, or not threatened), 1 for 'vulnerable', 2 for 'endangered', 3 for 'probably extinct', and 4 for 'extinct'. Any species whose status has changed during the time-frame of the analysis is given a score, according to the size and direction of its movement on this ladder. Thus, a change from 'vulnerable' to being 'probably extinct' would score +2. The median score for all species in a taxon is then determined; this is a very small number, because the majority of species, even in well-studied groups, are not on any such lists (i.e., have status unchanged at 0). The median time to extinction for species in the group is then computed by dividing the number of status changes required for extinction, starting from unthreatened (viz, +4), by the median status change per species per year. For insects, most plants, and other poorly-studied groups, rates of status change tell us more about lack of information and rates of data entry than about extinction. But for birds and mammals, and for the comparatively well-studied palms, they possibly provide a crude guide. For birds and mammals, this approach implies extinction of half the species within roughly 200–300 years, and for palms it suggests 50–100 years.

In Chapter 13, Mace outlines a third, independent way of estimating impending rates of extinction. This again is based on the IUCN categories of threat. However, it uses recent refinements whereby, for some better-known species, these categories are based on species-by-species assessments of extinction probability distributions as functions of time (Mace 1994; Seal *et al.* 1993). Mace calculates the expected times when half the species in each of 10 vertebrate taxa will probably be extinct (3, 4, 3 orders or families of reptiles, birds, mammals, respectively). These 10 average extinction times range from 100 to 1000 years, but are characteristically 300–400 years for mammals and birds.

In this section, we have been estimating the rough times for extinction of half the species in particular taxonomic groups. Given the highly approximate nature of all such estimates, it makes sense to regard them as equivalent to estimates of the projected average lifespan of individual species, until extinction (more strictly, average species' lifespans would differ from the half-life of the entire group by a factor $\ln 2 \approx 0.7$ if individual extinction was a Poisson process; for a more general discussion of these niceties, see Raup 1978).

It must be emphasized that the data in the Red Lists, upon which both the estimates of Smith *et al.* (1993a) and of Mace (Chapter 13) are based, have been compiled opportunistically rather than systematically. They may tell us more about the vagaries of sampling efforts, of taxonomists' interests, and of data entry than about real changes in species' status. Bibby and Mace further underline and document this point in Chapters 7 and 13, respectively. These IUCN category-based approaches nevertheless have potential merit in suggesting new lines of investigation of the dynamics of species extinction. (For instance, Mawdsley and Stork (1994) have taken advantage of the relatively well-documented state of the

British fauna to make analytic comparisons between insects and birds, both for rates of extinction, and for proportions listed in various categories of threat).

In short, all projected extinction rates are beset by many uncertainties. But for birds and mammals, three different approaches—one based on species-area relations, one on IUCN 'category ladder-climbing', one on IUCN estimates of probability distributions—give roughly concordant answers, with projected species' extinction times of around 200–400 years. The situation is less clear for plant species, and even less clear for invertebrates. Moreover, the genetic erosion of plant and other species is a major concern, yet is usually overlooked in extinction debates.

1.8 Extinction rates and conservation planning

The information about extinction processes presented in this book has many implications for conservation planning. In this concluding section, we focus on a few main points.

In the mass extinctions seen in the fossil record, species with limited ranges have, on the whole, tended to suffer most. So it is perhaps not surprising that so many of the threatened species on the IUCN/WCMC lists have very limited ranges. As Bibby discusses more fully in Chapter 7, this suggests we should give priority to identifying and protecting 'hotspots' of endemism, where disproportionate concentrations of threatened plants and animals with restricted ranges are found. Bibby and the International Council for Bird Preservation (ICBP 1992) have noted that 27% of the world's bird species have breeding ranges of less than 50 000 km², and that these restricted-range species account for 77% of all threatened birds. They identify an efficient set of 221 Endemic Bird Areas—of which 168, or 76%, are in the tropics—which cover about 5% of the Earth's land area, and yet accommodate 95% of all restricted-range bird species (including 90% of threatened such birds, or 70% of all threatened bird species). This ICBP analysis was prompted, in part, by Myers' (1988) identification of 18 plant 'hotspots', mainly in tropical forests, which in total contain around 20% of all vascular plant species within 0.5% of the world's land surface.

Underlying such focus on particular groups of restricted-range species is the thought that 'hotspots' for, say, birds will also generally be important for plants and other animals (ICBP 1992, p.2). But Thomas and Morris in Chapter 8, for example, show that the factors which endanger British insects vary from group to group, and from habitat to habitat (see also Mawdsley and Stork 1994). In different forms, this theme recurs throughout the book. Particularly telling is the recent analysis by Prendergast *et al.* (1993) of the distribution patterns of five groups—birds, butterflies, dragonflies, aquatic plants, and liverworts—in Britain. Using the detailed (10 km² grids) range maps that are available for so many groups in Britain, they found that the 'hotspots' of species-richness for these five different groups did not overlap significantly more than would be expected by chance alone. Even more strikingly, Prendergast *et al.* (1993) showed that, for any one group, the majority of rare species were not to be found in the

species-rich places; in these five cases, protecting 'hotspots' would not protect rare species.

In short, endangerment and protection—like commonness and rarity (Rabinowitz *et al.* 1986)—are multidimensional concepts.

Ehrlich's concluding Chapter 14 looks toward a sustainable future, provided we can make monumental changes in the way people live. But even in Ehrlich's most optimistic scenario, we will have enormous impacts on the environment, and upon plant and animal communities, before the rising tide of human numbers levels out and perhaps begins to ebb. Much of the diversity we inherited will be gone before humanity sorts itself out. Under these circumstances, it will be increasingly necessary to make choices about how to optimize what we can save.

In Chapter 12, Margules and Austin show how well-designed surveys and appropriate analysis can provide accurate estimates of the spatial distribution patterns of species. Such databases then allow us to make an efficient choice among potential reserves or protected areas, so as to optimize biological diversity, subject to any given set of constraints (such as total area, and so on). Pressey *et al.* (1993) outline some of the criteria upon which such choices may be based. The simplest such criterion is to preserve the largest number of species from variously-defined pools of candidates.

As Vane-Wright *et al.* (1991) first emphasized, however, not all species are equal. The tuatara, for example, is a large, iguana-like reptile which is the sole survivor of a group that flourished in the Triassic. Today it survives as two species on a few islets off the coast of New Zealand. The tuatara branched off from the main stem of the reptiles' phylogenetic tree so long ago, and is so distinctive, that it comes close to being a two-species sub-class of its own (Daugherty *et al.* 1990). How do we value the tuatara against any other species of reptile? At one democratic extreme, we could regard all species as equally important, each a unique evolutionary product; in this view, the tuatara is no more important than any other among the roughly 6000 species of reptiles. At the opposite extreme, we might give equal weight to each 'sister group' in the phylogenetic tree of reptiles; on this basis, the two species of tuatara would be weighed equally with the sum of all 6000 other reptile species. Vane-Wright *et al.* (1991) propose a sensible middle way, based on the topology of the phylogenetic branching diagram, which seeks to value species according to some rough measure of their evolutionary uniqueness, and which gives results intermediate between the two extremes just outlined (the tuatara, on this scheme, would represent something like a few per cent of the taxonomic distinctness found among reptiles, intermediate between the 0.03% of the democratic extreme and the 50% of the opposite extreme; May 1990b).

Various refinements of these basic ideas are being actively pursued (Faith 1992, 1993; Williams *et al.* 1991; Crozier 1992). Ideally, if we had some quantitative measure of the branch lengths within the phylogenetic tree of the group in question, we could unambiguously quantify the amount of 'independent evolutionary history' (IEH) vested in a species, by adding up the lengths of the branches which connect it to the base of the tree and appropriately discounting

all shared branches (Faith 1992, 1993; May and Nee in prep.). If we could preserve only, say, half the species in the group, the optimum choice would then be found by maximizing the summed branch length that was preserved. But, generally, we have only the topology of the tree, without quantitative measures of the various branch lengths; in this case, the best procedure would be to assign the branches the lengths that are, on average, most likely for this particular topology, and then go forward on this basis. Such a procedure will, of course, often in fact be sub-optimal, because the underlying evolutionary tree differs from the statistically 'expected' one. In general, however, extensive theoretical simulations of choices made on a topological basis, from artificially generated trees whose underlying branch lengths are known, suggest that values assigned in this way are close to the 'true' ones (May and Nee in prep.). Ultimately, our question is how much of the IEH within a group will be preserved if we can only save, say, 10 of 20 species? The simulations referred to above suggest that, for the 10 of 20 case, we can on average preserve 82% of the group's IEH if we have quantitative information about branch lengths, 77% if we have only topological information about the branching structure of the phylogenetic tree, and 63% if we must choose at random (May and Nee in prep.). Real situations will obviously involve many other important considerations, including other measures of the relative values of species (in preserving 'ecosystem services', for example), and political and economic constraints on which areas may be preserved. But there is no doubt that, increasingly, agonizing choices will have to be made. More and more, such choices will be best made if they can be based on a 'calculus of biodiversity', along the lines just sketched.

Some may ask why be so fussed about impending extinctions. After all, there have been great waves of extinction in the past, and yet diversity has recovered or even rebounded to greater heights. Others will take little comfort from the previous spans of some 10–100 million years for such recovery. Whatever view one takes, the impending sixth mass extinction will be unique in the history of the planet, being the first to result not from environmental changes as such, but rather from the extraordinary population growth and associated activities of one single species. As Ehrlich emphasizes in Chapter 14, *Homo sapiens* now sequesters for its own use somewhere between 25% and 50% of all terrestrial net primary productivity. This state of affairs is without precedent, and in this sense makes the coming extinction spasm qualitatively different from all previous ones.

Summary

The average lifespan of animal species in the fossil record, from origination to extinction, is around 10^6 – 10^7 years (with the higher number being more typical). For the comparatively well-studied birds and mammals, rates of documented extinction over the past century correspond to species lifespans of around 10^4 years. And three altogether different methods for projecting impending extinctions—each one of which has serious shortcomings—concur in suggesting a lifespan for bird and mammal species around 200–400 years, if current trends

continue. These numbers are likely to be broadly representative of plants and other groups of animals; impending extinction rates are at least 4 orders-of-magnitude faster than the background rates seen in the fossil record.

Such rough estimates are a useful point of departure. As the subsequent chapters make clear, however, what is now needed is a more richly textured understanding of how observed extinction rates differ among taxonomic groups and among geographical locations, and of the underlying causes. Effective conservation action depends upon such understanding.

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- 22 Robert M. May, John H. Lawton, and Nigel E. Stork
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Extinctions in the fossil record

David Jablonski

2.1 Introduction

The October 1993 mailing for The Nature Conservancy (US) opens unequivocally: 'Right now, today, species are becoming extinct at a rate *faster* than any time in the Earth's history—one species per day.' Most of the contributors to this volume assess present-day extinction rates, but I am going to address the palaeontological half of that statement. The fossil record provides an enormous database on extinctions, and I will briefly review the fossil record of extinction, how it is quantified and the potential sources of error, and outline some implications for today's biota. Because of significant differences in scale, resolution, and taxa under study, I will argue that the statement quoted above is unjustified, and that profitable comparisons between ancient and ongoing extinctions are less likely to be based on absolute rates than on relative extinction intensities among taxa or regions, on relative recovery rates, or on the biogeographic and evolutionary behaviour of taxa during past intervals of global climate change.

2.2 Global compilations

Most large-scale analyses of extinction in the fossil record rely on synoptic compilations of geologic ranges for genera and families. The fossil record at the species level is very incomplete and especially subject to sampling and preservational biases, and so more inclusive taxa are nearly always used for work at the global scale, particularly over large blocks of geologic time (see Raup 1979a). These synoptic time series are most useful for recognizing episodes of unusual extinction intensity, and for quantifying overall biotic losses. They are less effective in resolving the details of timing or geography for any given extinction event, a research problem requiring an intricate interplay between detailed, local time series, and global compilations (not discussed here; see Raup 1989; Koch 1991; Marshall 1991; Sepkoski and Koch 1994).

As many authors have noted, the fossil record of shelly marine invertebrates is the most complete and reliable for global biodiversity analysis (Benton 1989; Signor 1990 for reviews). Broadly speaking, this is because marine environments provide for more continuous and extensive sedimentation than the terrestrial environment, and shelled invertebrates are both extremely abundant and

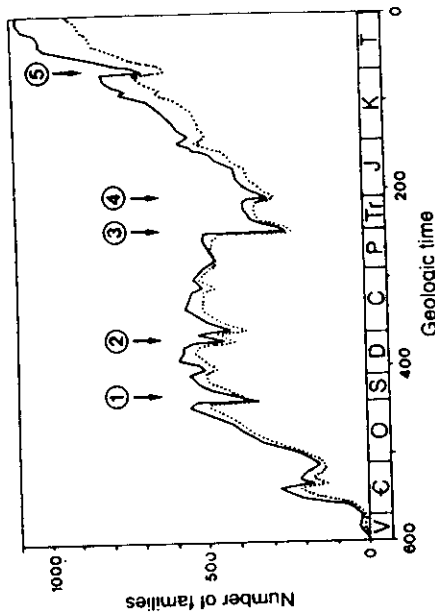


Fig. 2.1 The diversity history for marine animal families through the Phanerozoic, including the 'Big Five' mass extinctions. Solid line, 1992 data; dashed line, 1982 data. Major extinction events: 1, end Ordovician; 2, late Devonian; 3, end Permian; 4, end Triassic; 5, end Cretaceous. Geologic periods along the horizontal axis: V, Vendian; C, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; T, Tertiary. (After Sepkoski 1993.)

these events as seen both in Sepkoski's revised database (Sepkoski 1993) and in a semi-independent compendium by Benton (1993, marshalling an army of taxonomic experts). A host of lesser extinction events are also known; these form local maxima in extinction time series but are not necessarily of the requisite scale geographically (e.g., the early Toarcian; Hallam 1987) or taxonomically (e.g., the late Pleistocene megafauna; Barnosky 1989; Stewart 1991). Some of these local maxima, however, such as the mid Carboniferous extinction pulse, do appear to be genuine but less severe global events (Raymond *et al.* 1990; Sepkoski 1994).

Many taxonomic problems remain in the large databases, of course, and phylogenetic analysis will clarify many of the details of clade survivorship and recovery around extinction events. The inevitable inclusion of paraphyletic taxa, not defined according to strict cladistic principles, is sometimes seen as seriously compromising the entire enterprise (see Smith and Patterson 1988). However, paraphyletic taxa are probably not a major liability at this scale of analysis. Some argue this on biological grounds: the loss of a paraphyletic genus or family often reflects the disappearance of a distinctive mode of life or an ecologically meaningful suite of traits (Van Valen 1984, 1985; Valentine 1990). Sepkoski (1987a, 1989, 1992b) and also Fisher (1991) argue from the topology of evolutionary trees: except for true gradualistic transformations of monospecific taxa, the loss of a paraphyletic genus or family must signal the extinction of at least one species and thus is a useful, if damped, proxy for species-level biodiversity dynamics (Sepkoski and Kendrick 1993 reinforce this point in an elegant simulation study). Similarly, the use of higher taxa in Linnaean rank-based classifications may seem

Table 2.1 Extinction intensities (percentage extinction, $E: D \times 100$) at the five major mass extinctions in the fossil record. Genus- and family-level values based on Sepkoski's compendia (Sepkoski 1994), with binomial standard errors calculated following Raup (1992a); species-level estimates based on Raup's (1979b) reverse rarefaction technique. Note the agreement between the two estimates of species losses for each extinction episode

Mass extinction	Families		Genera	
	Observed extinction (%)	Calculated species loss (%)	Observed extinction (%)	Calculated species loss (%)
End Ordovician (439 mya)	26 ± 1.9	84 ± 7	60 ± 4.4	85 ± 3
Late Devonian (367 mya)	22 ± 1.7	79 ± 9	57 ± 3.3	83 ± 4
End Permian (245 mya)	51 ± 2.3	95 ± 2	82 ± 3.8	95 ± 2
End Triassic (208 mya)	22 ± 2.2	79 ± 9	53 ± 4.4	80 ± 4
End Cretaceous (65 mya)	16 ± 1.5	70 ± 13	47 ± 4.1	76 ± 5

mya, million years ago; ages from Harland *et al.* (1990)

intensively studied for economic purposes. Sepkoski's (1992a) *A compendium of marine animal families* has been a boon to all interested in such analyses. Datasets that focus on particular groups, regions or time intervals can be more accurate and more precise, and thus useful for a different and perhaps broader range of questions, but they inevitably lack the sample sizes and temporal sweep of Sepkoski's compendium. Similar databases exist for terrestrial vertebrates and insects (Benton 1989; Maxwell and Benton 1990; Labandiera and Sepkoski 1993); Niklas *et al.* (1985) analysed the plant record at the species level but have not yet published their data. The terrestrial vertebrates and plants exhibit perturbations that correlate, at least roughly, with the major mass extinctions detected in the oceans, but the magnitude and timing of land-based extinctions relative to the marine ones is still controversial (see McGhee 1989; Johnson and Hickey 1990; Sweet and Braman 1992; Benton 1991; Maxwell 1992; Weems 1992; Erwin 1993).

Synoptic compendia have been the basis of a wide array of intriguing analyses, but here I concentrate on the five major mass extinctions detected for marine invertebrates (Table 2.1). Mass extinctions can be taken as substantial biodiversity losses that are global in extent, taxonomically broad, and rapid relative to the average duration of the taxa involved (Jablonski 1986a). The 'Big Five' extinctions have been confirmed in several generations of family- and genus-level databases (Newell 1952; Valentine 1969; Sepkoski 1994) (Fig. 2.1). The past decade of particularly intensive work, with many additions, corrections, and reinterpretations of taxonomy and stratigraphy have served only to sharpen

dangerously arbitrary (Smith and Patterson 1988; Doyle and Donoghue 1993). However, under realistic sampling conditions for most groups, even arbitrary higher taxa may provide a more robust portrait of biodiversity changes than will any tabulation of the relatively short-lived and undersampled species themselves (Valentine 1974; Raup 1979*a*; Gilinsky 1991; Sepkoski and Kendrick 1993). Thus, although a fully resolved phylogenetic analysis is essential for some kinds of problems, such as the diversity histories of specific groups, it is not an absolute prerequisite for reconstructing the broad history of global biodiversity or recognizing the major biotic upheavals in Earth history.

2.3 Extinction metrics

Quantifying extinction intensity has other pitfalls, however, and each of the standard extinction metrics has drawbacks (see Sepkoski and Raup 1986; Raup and Boyajian 1988; Raup 1991*a*; Gilinsky 1991; Sepkoski and Koch 1994; Foote 1994; for discussions; and Van Valen 1984; Gilinsky and Good 1991, for additional metrics). For example, the raw number of extinctions in a time interval, E , has a simple error term but does not take into account the number of taxa at risk: the loss of 100 families is clearly a more significant event when global diversity (D) totals 200 rather than 600 families. The proportion of taxa becoming extinct (E/D) is intuitively a more satisfying metric but introduces additional uncertainty because estimates of global diversity also have an associated error (Gilinsky 1991).

Extinction rates (E/t) have often been used to take into account the possibility that longer intervals can accumulate more extinctions, but distortions enter owing to uncertainties in geologic time estimates (Sepkoski and Raup 1986; Raup and Boyajian 1988; Gilinsky 1991). For example, the Cretaceous, the shortest stage of the Cretaceous, can exhibit an extinction peak in time series analyses (e.g., Sepkoski and Raup 1986; Hubbard and Gilinsky 1992) depending on the timescale used, but exhibits unexceptional turnover under detailed study. More generally, Sepkoski and Koch (1994) show that recent estimates for the duration of stratigraphic stages in the Devonian differ by 26–33% of mean stage length; this uncertainty in the denominator yields alarmingly large error terms. In a simulation study, Foote (1994) found that rate metrics tend to be negatively correlated with interval length under the majority of realistic extinction models. Further, rate metrics assume that extinctions are evenly or randomly distributed through the time interval, which seems not to be true for several of the stratigraphic stages associated with mass extinctions (Raup 1986; Ward 1990; Gilinsky 1991; Foote 1994). Per taxon extinction rates (E/Dt) may have the strongest theoretical appeal (Gilinsky 1991), but they compound these uncertainties and thus yield even larger potential error.

The statistical properties of the extinction metrics are still poorly understood, not least because taxonomic databases are not strictly random samples of either diversity or extinctions. Extinction intervals, for example, are often poorly sampled owing to sea-level drops or other environmental changes that reduce the volume of fossiliferous rocks available for study, and rare taxa are themselves under-sampled

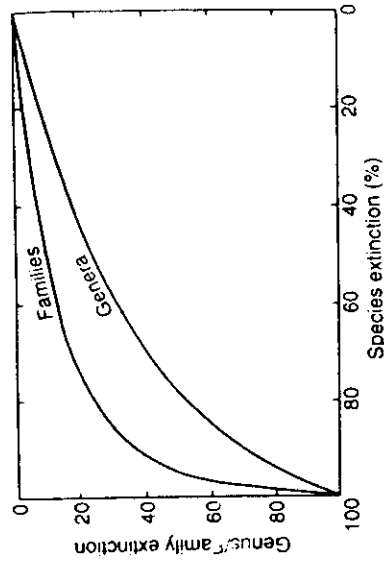


Fig. 2.2 The magnitudes of species-level losses during mass extinctions are estimated using Raup's method of reverse rarefaction. The curves are used to estimate the proportion of species extinction required to account for observed extinctions at the genus or family level. (After Raup 1979*b*.)

but may be more extinction-prone than common taxa. Two principal strategies have been used to minimize these problems: (1) use several metrics to test for sensitivity of interesting features to different error sources (e.g., Van Valen 1984, 1985; Sepkoski and Raup 1986); or (2) use stratigraphic intervals of approximately equal length, combining short intervals and subdividing long ones to reduce variance (e.g., Sepkoski 1989; Raup and Boyajian 1988; Sepkoski and Koch 1994). Confidence intervals are calculated as binomial standard errors. These assume random sampling and thus are inexact, but are useful as measures of relative uncertainty (Raup 1991*a*; Sepkoski and Koch 1994).

2.4 Estimating species-level extinction

Extinction intensities at the species level are estimated from the distribution of species within present-day families and genera (Raup 1979*b*). This 'reverse rarefaction' technique (Fig. 2.2) carries several assumptions. First is the assumption that extinctions are temporally concentrated and not spread through a geologic stage or longer interval. As already noted, some evidence supports this view, but the effects of relaxing this assumption have not been explored systematically. Raup's (1979*b*) estimates were based on the distribution of species within genera and families of present-day echinoids, under the assumption that these distributions were representative of the biota as a whole; this need not be true, particularly in Palaeozoic faunas (see Valentine 1969, 1974; Van Valen 1985). This issue deserves more investigation, but convergent estimates of species losses from both generic or familial data suggests that the echinoid data do provide a reasonably good proxy (see Table 2.1).

Reverse rarefaction also assumes that species survival is uncorrelated with

David Jablonski

Table 2.2 Extinction events and taxa in which species-richness was not a buffer against extinction

Cambrian trilobites	Westrop (1989)
End Ordovician bryozoans	Anstey (1978)
Late Devonian corals	Sorauf & Pedder (1986)
Late Devonian ammonoids	House (1985)
End Permian brachiopods	Carlson (1991)
End Cretaceous echinoids	McKinney (1988)
End Cretaceous bivalves and gastropods	Jablonski (1986b, 1989)
Exception: End Permian gastropods	Erwin (1989, 1993)

membership in a particular higher taxon. However, related species tend to be clumped ecologically, and in some instances at least (e.g., reef dwellers), their shared risk probably exceeds the random expectation. Species losses would then be overestimated, because it would take fewer non-random species extinctions to remove a given number of genera (see Simberloff 1986, p. 170; Raup 1991b, p. 73). The assumption that species loss is randomly distributed among higher taxa also implies that species-poor genera and families should be at greater risk than species-rich ones, which was evidently not the case for many mass extinctions (Table 2.2; but see Erwin 1993 for an exception). This implies that the loss of a genus or family is more likely to involve a species-rich taxon than the random expectation, so that reverse rarefaction might then underestimate species loss. A conservative interpretation of the agreement in Table 2.1, therefore, might be that *genera* are lost randomly with respect to family membership, so that extrapolation from observed extinction at both taxonomic levels yields comparable species-level values.

How far reverse rarefaction distorts true species extinction intensities is unknown. They are probably not severely inaccurate: most studies show species richness to be ineffective rather than actively selected against during mass extinctions, for example. The genus-level extinction data might provide an empirical lower bound for percentage species loss for each event: the loss of a greater proportion of genera than species is unlikely under realistic conditions (D. M. Raup, pers. comm. 18 November 1993). Unusual circumstances could confound such an estimate, however: imagine losing 9 monospecific genera but allow one 10-species genus to survive unscathed, and genus extinction is 90% but species extinction is 47%.

2.5 Comparisons to present-day extinction

Palaeontological extinction data are extremely difficult to compare to present-day extinction rates. As already noted, the most robust palaeontological data, and most analyses on ancient extinction intensities and selectivities, deal with marine invertebrates. The conservation status of today's marine biodiversity is woefully under-documented compared even to our incomplete knowledge of most terrestrial organisms, and only a handful of extinctions are known—

reflecting perhaps both our ignorance and the greater inertia of marine systems (Winston 1992). Human impacts are increasingly severe, however, from over-exploitation to pollution to introduction of exotics, and clearly the marine fossil record can provide useful insights for conservation. The larger problem, however, is how to generalize from the marine-biased history of global biodiversity to today's situation, where most data and the most rapid and extensive species losses are terrestrial.

Even in the marine record, fossil species and higher taxa are not random samples of the biota, or even of the biota with durable skeletons. The taxa in palaeontological databases—marine and terrestrial alike—are skewed towards the more abundant, widespread, and geologically long-lived species, which will have the greatest total number of individuals and occur in the greatest number of localities and rock types, and so are most likely to be preserved and recorded (Raup 1979a; Koch 1991). Moreover, the best time resolution consistently achievable in the pre-Pleistocene fossil record is c. 10^3 – 10^4 years, due to gaps in the record and time-averaging of successive populations (Kidwell and Behrensmeier 1993). This does not mean that the *relative* abundances, geographic ranges, and geologic durations of fossil taxa are irretrievable or hopelessly distorted—quantitative analyses of sampling densities and preservation biases have verified that a strong biological signal comes through in many instances (e.g., Paul 1989; Jablonski and Valentine 1990; Marshall 1991; Kidwell and Bosence 1991). But the very nature of the fossil record suggests that palaeontological estimates should be applied to present-day situations with extreme caution, because palaeontological extinction data almost exclusively involve taxa drawn from the extinction-resistant tail of the entire biota! Palaeobiologists continue to debate the kinds of perturbations required to eliminate hundreds or thousands of species with subcontinent-scale geographic ranges (see Jablonski 1991 for examples), and it is not at all clear that the majority of tropical species whose losses are inferred by extrapolation of local surveys—mainly rare, extreme endemics—would be palaeontologically detectable (Jablonski 1991).

Present-day extinction is usually expressed as a simple rate (E/t) rather than as a proportion (E/D) (see Myers 1993 and references therein). However, given the enormous differences in sampled or estimated diversities for extant and fossil biotas, comparisons are only feasible after normalization according to the size of the taxon pool. Smith *et al.* (1993a) tabulated the percentage species loss recorded for different animal and plant groups since 1600, and found none greater than 1.3%. Species threatened by extinction in well-known groups, however, constitute a significantly higher proportion, for example, 32% for gymnosperms and 33% for palms. With some assumptions about extinction probabilities of such groups, these data imply 50% extinction within 50–100 years (Smith *et al.* 1993b). This does approach the intensities required to generate a genus-level extinction on the scale of the 'Big Five' mass extinctions. Still uncertain, of course, is whether these numbers are representative of the entire biota, and how they should be scaled against palaeontological data. The next step might be to develop correction factors for more rigorous comparisons to the fossil record, by estimating for each group the

proportion of species whose original abundance and distribution was on a scale commensurate with potential fossilization and palaeontological discovery. This can be done directly using taxa with well-studied fossil records, for example > 77% of shelly marine mollusc species off the California coast occur as Pleistocene fossils (Valentine 1989), and comparable figures could be probably obtained for temperate plant and arthropod species.

2.6 Taxon-specific rates

In the fossil record, species or genus durations within higher taxa vary by more than an order of magnitude even during times of background extinction away from the 'Big Five' mass extinctions, so that computation of a grand mean is not very informative (although broad rate differences do exist among major groups; cf. Stanley 1979; Valentine 1990). Not only is the variance enormous, it is strongly right-skewed: most taxa within a major group tend to be geologically short-lived but the frequency distribution usually includes a tail of long-lived taxa (e.g., Stanley 1979). Some of the observed variation is due to sampling and other artefacts, but data on a wide variety of higher taxa show biological factors to be important in determining extinction rates for species and genera in the fossil record (reviews by Stanley 1985, 1990a). For example, molluscan species durations are positively correlated with geographic ranges (Jablonski 1986b, 1987; Marshall 1991; also Jackson *et al.* 1985 on corals and bryozoans). Stanley (1990b) found body size to be a more important determinant of survivorship in Late Cenozoic bivalves in the northern Pacific. His attribution of the inverse relation between body size and species survival to differences in population size makes intuitive sense and may well be correct, but needs to be tested more directly. Body size is a poor predictor of species abundances (Blackburn *et al.* 1993), with population densities in marine communities, for example, ranging over 2–4 orders of magnitude for a given body size except at extreme values (e.g., Marquet *et al.* 1990).

Whatever the precise causal links or focal level of selection (cf. Jablonski 1987; Williams 1992), the clear differentials in species survivorship detected in many fossil groups are a rich source of empirical data on variations in extinction risk among taxa (from protozoans, e.g., Norris 1991, to mammals, e.g., Van Valkenburgh and Janis 1993). The list of factors reported to affect extinction probabilities in the fossil record will come as no surprise to the biologist: geographic range, niche breadth, mobility in larval or adult stage, abundance, and population growth rates, etc. The fossil record does more than confirm the role of various attributes, however: it permits the ranking of different factors, providing empirical data on what circumstances erase the benefits of broad geographic range in favor of, say, stable resources—and how large and in what direction the differentials will be among related taxa. Under background extinction, for example, larval ecology is a better predictor of gastropod species survivorship than phylogenetic affinity or adult trophic group (Jablonski 1986c) (Fig. 2.3). Regions, habitats, and taxa should be targeted for palaeobiological

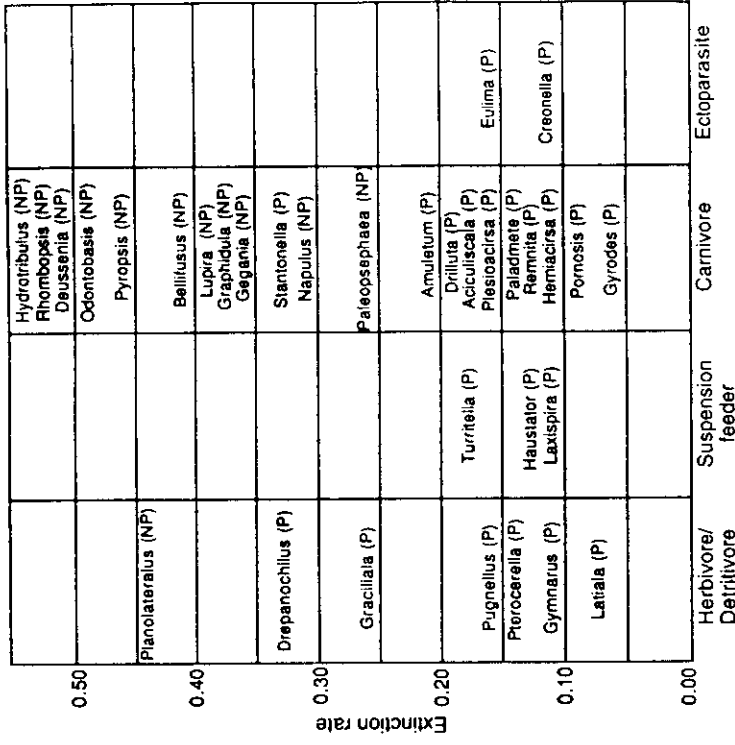


Fig. 2.3 Background extinction rates in Late Cretaceous marine gastropods are more closely related to modes of larval development (P, planktotrophic; NP, non-planktotrophic) than to the adult feeding categories listed along the bottom of the figure. These significant differences in extinction rate are probably the result of the broader larval dispersal ability, and thus broader geographic ranges, typical of species having planktotrophic larvae ($P < 0.001$, Mann-Whitney U -test) (see Jablonski 1986a, and in prep.). Extinction rates calculated as a per-species rate per million years.

studies designed explicitly to address conservation issues; palaeobotanical analyses along these lines are sorely needed, for example.

It may be surprising that I advocate palaeontological analyses of background extinction as a tool in assessing present-day extinction risk, given data suggesting that background rules of survivorship are disrupted during the major mass extinctions (e.g., Jablonski 1986b, 1989, 1991; Westrop 1991) (Table 2.2). I am not belittling the magnitude of today's problems, nor do I deny the potential for long-term losses of similar scope and evolutionary impact to the major mass extinctions of the fossil record (cf. Simberloff 1986). Background extinction patterns may nevertheless provide clues to how the present-day biota will respond to anthropogenic disturbances, for at least three reasons:

1. It is not clear that present-day disturbances, although undeniably extensive,

patterns to perturbations of various magnitudes—particularly those short of the 'Big Five' events—are still unclear.

3. The great majority, probably > 90%, of species extinctions in the fossil record occur outside the five major extinction events (Raup 1986, 1991c): mass extinctions have such profound biological consequences because they bite deep into standing diversity and disrupt background selection regimes, not because they account for most species terminations. In fact, extinction magnitudes for the stratigraphic stages of the Phanerozoic form a continuous distribution. Some impressive extinction pulses fail to stand significantly above background variance, and data from those intervals should be used to advantage as long-term records of taxon selectivity.

Geographic patterns

For present-day biotas, extinction risk is not spread evenly over the globe. Some regions are suffering greater encroachment than others, and some regions are known to be exceptionally species-rich so that their disruption will be especially costly in terms of biodiversity. The biogeography of ancient mass extinctions has been relatively neglected, perhaps because such data are not reliably recorded in synoptic databases, but a few general patterns emerge.

Most striking is the disruption of reef and related communities on tropical carbonate shelves: each mass extinction brings a major reorganization of these taxon-rich habitats, with once-dominant taxa eliminated or relegated to secondary roles (Copper 1988, 1989; Talent 1988; Kauffman and Fagerstrom 1993). Alternative hypotheses for these spectacular collapses include: (a) tropical biotas in general are fragile because their species are adapted to a narrow range of climatic and other conditions; (b) tropical biotas contain a large proportion of extinction-prone endemics, so that losses are strong here owing to biogeographic structure; (c) reef communities are such a tightly woven network of biological interactions that the initial removal of the same proportion of species as were lost at high latitudes could be more disruptive; (d) the favoured habitat of reef communities, low-sedimentation and low-nutrient shallow-water platforms or ramps, is itself easily disrupted. Some support exists for the biogeography- and habitat-based hypotheses. First, interprovincial variation in mass extinction intensities within latitudinal belts tend to be positively related to the proportion of endemic genera in the pre-extinction biota (Jablonski 1989; Sheehan and Coorough 1990; Westrop 1991). Second, a global analysis of end-Cretaceous extinction in marine bivalves found that tropical settings outside of the carbonate platforms suffered no greater losses than did extratropical faunas (Raup and Jablonski 1993). The dissection of these alternative mechanisms for the repeated demise of reef communities, indeed for any major community type, could have valuable applications to present-day biodiversity.

As discussed above, marine extinctions are remarkably sparse over the past 2 million years, even for reef taxa, despite massive fluctuations in sea-level and other environmental variables as global climate oscillated between glacial and

Table 2.3 Extinction events and taxa in which broad geographic range at the genus level enhanced survivorship

Late Cambrian trilobites	Fortey (1983); Westrop (1989, 1991)
End Ordovician bivalves	Bretsky (1973)
End Ordovician brachiopods	Sheehan & Coorough (1990)
End Ordovician bryozoans	Anstey (1986)
End Ordovician trilobites	Robertson <i>et al.</i> (1990)
Late Devonian bivalves	Bretsky (1973)
End Permian bivalves	Bretsky (1973)
End Permian gastropods	Erwin (1989, 1993)
End Triassic bivalves	Bretsky (1973)
End Cretaceous bivalves and gastropods	Jablonski (1986b, 1989)

are on a par with those that drove the major mass extinctions. If we could apply all the appropriate correctives, present and near-future extinctions may or may not fall quantitatively within palaeontological background rates but there is little evidence that the qualitative change in survivorship such as seen at the Cretaceous-Tertiary boundary has occurred today. So far as they are known, today's extinction patterns conform mainly to intensified versions of background expectations, with losses concentrated in endemic species and subspecies. The major mass extinctions operated on a different scale: genera endemic to single subcontinental provinces were lost preferentially, regardless of the geographic ranges of their constituent species (Jablonski 1986a, 1989, 1991) (Table 2.3).

2. Even if selectivities of present-day extinctions were congruent with those seen during the ancient mass extinctions, not all background patterns of survival are overturned under the mass extinction regime, and some evolutionary continuity exists even across the most severe events (Jablonski 1986d, 1989). The persistence of survival advantages may be clade- or event-specific, as in the presence of a resting cyst in the life cycles of high-latitude phytoplankton during the end Cretaceous event (Kitchell *et al.* 1986; see also Norris 1991 on continuity in planktic Foraminifera). In other instances, enhanced survivorship under both mass and background regimes may represent the long-term effects of previous mass extinctions. For example, severe extinction in the bivalve order Pholadomyoida during the end Permian extinction but not during the succeeding end Triassic event may reflect the purging of vulnerable members of the clade followed by re-radiation from survivors that happened to retain extinction-resistant features. Similarly, the remarkably low extinction rates in shallow-water molluscs during the huge Pleistocene climate and sea-level fluctuations (references in Valentine and Jablonski 1993) have been linked to Pliocene turnover events that may have already eliminated the most vulnerable species (Stanley 1990b; see also Jackson, Chapter 3). Because we are just beginning to explore the factors that allow clades or trends to prevail under both background and mass extinction regimes, the limits to the relevancy of background extinction

interglacial states. Local extinctions were legion, but few taxa disappeared entirely because species were able to adjust geographic ranges in response to dramatic shifts in climate and shoreline—an option increasingly unavailable, I might add, given human encroachments (review in Valentine and Jablonski 1993). The same phenomenon has been superbly documented for terrestrial animals and plants (see Graham and Grimm 1990; Webb and Bertlein 1992; Coope, Chapter 4) and has immediate implications for the design of biological reserves. Reserves must be sufficiently large and environmentally complex to accommodate the array of disparate geographic range shifts that any climate change will evoke from the resident species (Graham 1988; Hunter *et al.* 1988). Reserves that are environmentally homogeneous or constructed tightly around the present distribution of a cluster of high-priority species will see their subjects melt away species by species in response to climate changes. This disassembly process has occurred not only in the temperate latitudes that bore the brunt of Pleistocene glaciations, but in tropical settings as well (marine, Paulay 1990; terrestrial, Bush *et al.* 1992).

2.7 Biodiversity and biodiversity

Other palaeontological approaches can be used to explore the effects of extinction, such as quantifying the loss of morphological variety rather than taxonomic diversity *per se*. The ecological or evolutionary impact of an extinction event resides not simply in the number of taxa lost, but in the loss of what could be termed (with some trepidation) *biodisparity*, the range of morphologies or other attributes within a clade or within a local or regional subsample of a clade. Neither the will nor the resources exist to save every endangered species in today's biosphere, and when priorities are set, biodiversity should probably enter into the equation. Phylogenetic information is also important in many conservation contexts; some workers have proposed metrics for phylogenetic distinctness, for example, based on depth of branch-points in a phylogeny or number of species relative to sister taxa (reviewed by Nixon and Wheeler 1992).

A drawback of phylogenetic metrics is their requirement of detailed cladistic analyses; time is not available for such analyses for all potentially endangered plants and animals. Further, consistency indices decline and the number of alternative or slightly less parsimonious phylogenetic trees expands with the number of taxa analysed, so that subgroups can radically change their conservation status with alternative interpretations of character state distributions, or with a glance at those trees that are one or two steps longer than the shortest phylogeny. Genealogy is extremely important in understanding biodiversity, but it should not be the only basis for weighing biological 'quality' against 'quantity'. If we are concerned with avoiding the loss of particular functional groups, or with maximizing the potential source pool for evolutionary recovery, then biodiversity measures may provide a more appropriate assessment, beyond sheer numbers of taxa, of how priorities should be set.

A variety of methods are available for quantifying biodiversity, ranging from

ecomorphological studies that test for convergence or displacement of species morphologies within and among communities (e.g., Winemiller 1991) to the construction of theoretical or empirical morphospaces used to track clades through geologic time (see McChes 1991 and Foote 1991, 1993). Most of the palaeobiological work has focused on radiations, particularly the relation between taxonomic and morphologic diversification during the Cambrian Explosion, but background and mass extinction could be analysed in the same fashion. At present, we know little of how taxonomic losses impinge on patterns of morphospace occupation in ancient or present-day biotas. As Foote (1992) points out, if extinction is effectively random with respect to morphology, a disproportionately large number of extinctions is required to reduce morphological variety substantially. On the other hand, extinctions might be selective in morphospace just as they are taxonomically. This has not been explored, however, and we do not know if taxa lying in different regions or densities of morphospace vary predictably in risk. For example, are there kinds of perturbations (density-dependent versus density-independent?) that tend to concentrate losses in the core morphospace or around the morphospace periphery? Do different higher taxa or extinction intensities exhibit characteristic loss patterns of morphospace?

Biodisparity analyses should not be seen as a new way to identify morphological outliers that can serve as flagship species for biological preserves. Instead, they can quantify real or potential losses in a region's or community's relative biological wealth in terms of morphologies rather than species, potentially even in the absence of detailed formal taxonomy (cf. Foote 1993).

2.8 Rebounds

Evolutionary rebounds after mass extinctions are an important component of macroevolution (reviews by Jablonski 1986b, c; Benton 1987). The recovery of both biodiversity and biodiversity in the aftermath of mass extinctions is rapid by geological timescales, often accompanied by significantly accelerated evolutionary rates (Hallam 1987; Miller and Sepkoski 1988; Sheehan and Coorough 1990; Sepkoski 1992b), but it is extremely slow by human timescales. Refurbished reef communities, for example, emerge only after a 5–10 million year lag following each of the major mass extinctions (Copper 1988, 1989; Kaufman and Fagerstrom 1993) (Fig. 2.4). Talent (1988) argues that this delay stretches far beyond the offset of the environmental stresses that eliminated the preceding community. This has significant implications for restoration ecology, as it implies some other constraint on the evolution of species or the assembly of communities capable of occupying these habitats; the community ecology of rebounds from past extinction events should be a focus for future research. In addition, recoveries from global events need not be geographically homogeneous. For example, the post-Cretaceous rebounds in molluscan faunas differ significantly in Europe and North America despite the lack of geographic variation in end-Cretaceous extinction intensities (references in Raup and Jablonski 1993).

2.9 Conclusion

The mass extinctions of the fossil record are, if nothing else, cautionary tales. They show unequivocally that marine and terrestrial biotas are not infinitely resilient, but have breaking points that have been exceeded repeatedly in the past, with extreme and long-lasting biological consequences. The fossil record of extinction can yield more specific insights, however, even though estimates of present-day extinction are difficult to compare directly with those calculated for past mass extinctions. Raw numbers aside, the fossil record provides our only empirical data on what happens when biological communities collapse or disassemble, when increased extinction rates impinge on taxa of different relative vulnerabilities, when global warming or cooling occurs faster than species can adjust to local conditions, when ecological stresses ameliorate after prolonged or severe episodes, and so on. All of these are situations that we may face in the coming century, and it is in these more circumscribed questions that the fossil record may provide the most insight and has the greatest predictive power.

Summary

Direct comparison of ancient extinctions to the present-day situation is difficult, because quantitative palaeontological data come primarily from marine invertebrates, fossilized species are usually drawn from the more abundant and widespread taxa, and time resolution is rarely better than 10^3 - 10^4 years. A growing array of techniques permits quantitative error estimates on some of these potential biases, and allows calculation of species extinction intensities from genus-level data, which are more robust. Extensive as today's species losses probably are, they have yet to equal any of the 'Big Five' mass extinctions. Background extinction patterns are potential sources of insight regarding present-day biotic losses; over 90% of past species extinction has occurred at times other than the 'Big Five' mass extinctions. Mean durations of fossil species vary by more than an order of magnitude even within clades, rendering uninformative any global average for background extinction. Taxon-specific variation is evidently related to intrinsic biotic factors such as geographic range and population size. Approaches to extinction analysis and prediction based on morphological variety or *biodisparity*, rather than biodiversity, should be explored as an adjunct or alternative to taxon inventories or phylogenetic metrics. Finally, rebounds from mass extinctions are geologically rapid but ecologically slow, and biodiversity recovery and the reestablishment of some communities typically requires 5-10 million years.

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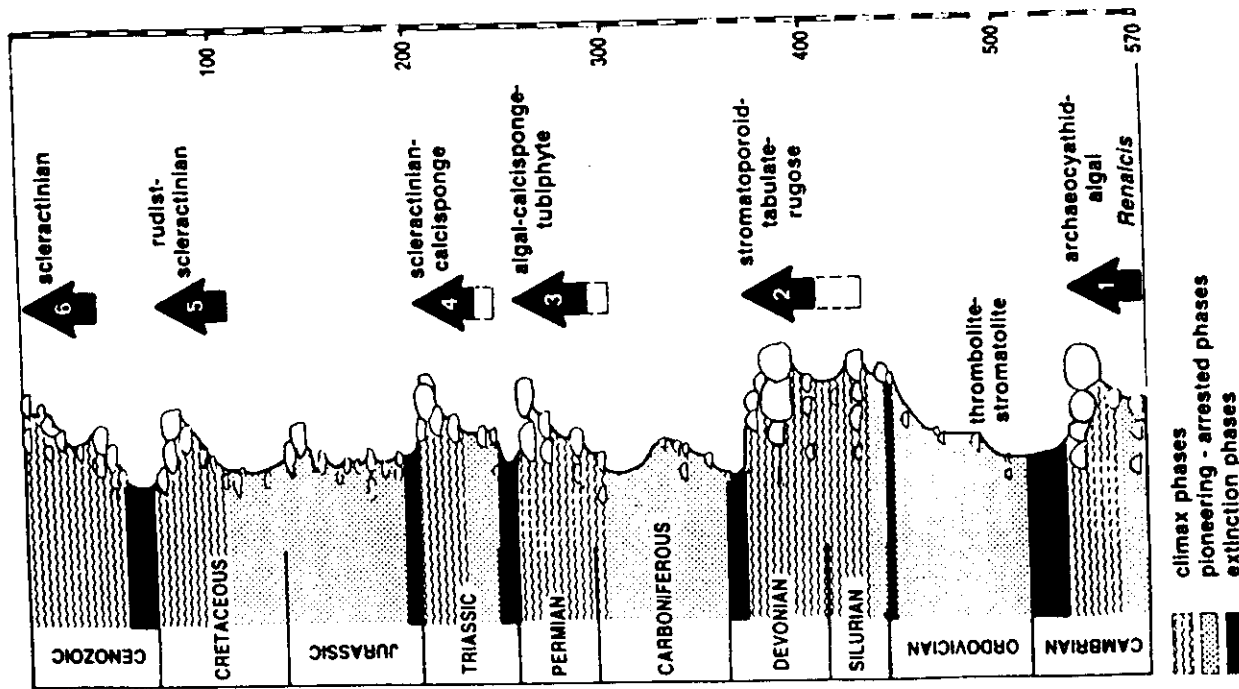


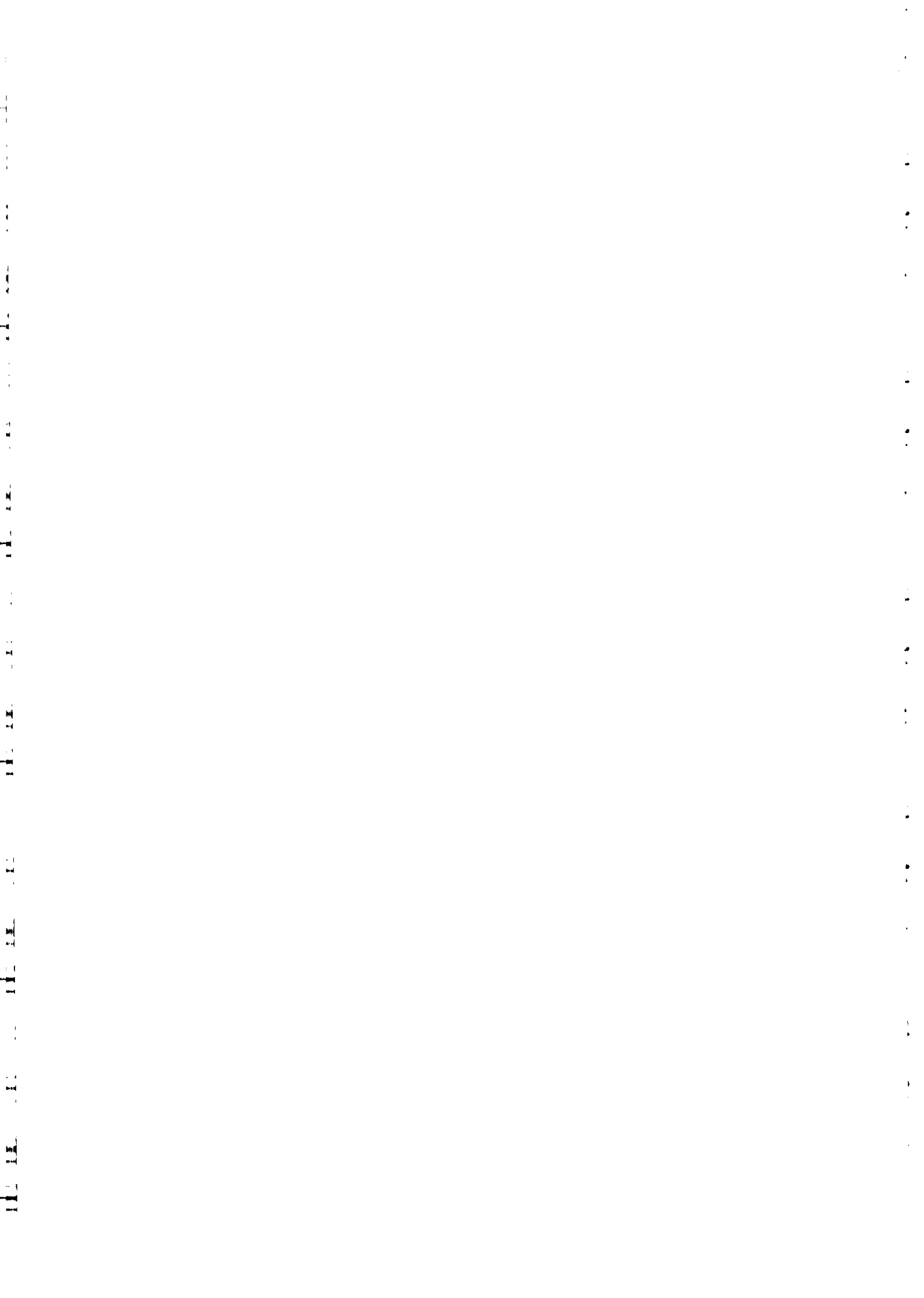
Fig. 2.4 The geologic history of reef and carbonate platform faunas. Six major associations are recognized, all but the present scleractinian-dominated one terminated by an extinction event, followed by a protracted interval lacking reefs. (From Copper 1988, by permission of the author and the Society for Sedimentary Geology.)

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Recent past and future extinctions in birds

Colin J. Bibby

7.1 Introduction

As a class, birds are second only to terrestrial molluscs in the number of known extinctions in the past few centuries (Jenkins 1992). If we understood extinction processes, we might be able to predict probabilities of future extinctions and target applied research and conservation work. Knowledge of recent past losses of species, either globally or locally, offers some understanding of extinction. Population modelling may give a more rigorous route to insight.

In this chapter, I will examine the extent to which practical guidance for future actions can actually be given on the basis of these approaches.

7.2 Predicting future extinctions

Recent extinctions

About one hundred bird species, or 1% of all birds, are believed to have been lost since 1600 (Temple 1985). Roughly 90% of these were island species. (King 1985; Johnson and Stattersfield 1990). As reviewed by Pimm, Moulton, and Justice in Chapter 5, still more species were lost in the earlier history of human settlement before naturalists ever saw or documented them (see also Diamond 1982; Olson 1989). Milberg and Tyrberg (1993) describe over 200 extinct island species known from sub-fossil remains in spite of the large numbers of islands yet to be explored.

Factors salient in the extinction record on islands include human predation (especially of large flightless species), introduced predators (cats, rats, dogs, mongooses, monkeys, etc), habitat loss due to direct human impact or introduced grazers and browsers (goats, pigs, cattle, and rabbits), and introduced diseases. Species which evolved in the absence of natural predators on remote oceanic islands have often become flightless (Diamond 1981), apparently tame, and otherwise lacking in predator avoidance. Such species may also be vulnerable to introduced disease as suggested on Hawaii (Ralph and van Riper 1985). Often, island species are further vulnerable by virtue of small populations and ranges. The relatively uniform habitats on islands lower the chances of population refugia surviving and recolonizing (Frankel and Soule 1981). While many oceanic island species are already gone, a highly vulnerable class survives

on those islands which have not yet been colonized by alien predators (Atkinson 1985; Moors *et al.* 1992).

Local losses from habitat islands

Comparable losses have yet to occur amongst continental species although they are widely predicted to be imminent (e.g., Ehrlich 1986; Myers 1989). Many species have small total ranges (about 27% of all birds have total ranges below 50 000 km², ICPB 1992). Large areas of natural habitat, most strikingly tropical forests, have been cleared in many countries. As a result, an increasing number of continental species with naturally small ranges are now isolated in shrinking habitat islands (Terborgh 1974). Factors leading to loss of local populations may not be the same as those causing global extinctions (Soule 1983). On the other hand, many currently threatened birds are confined to dwindling numbers of local populations (e.g., Collar *et al.* 1992). In such cases, global extinction would merely be the last of a series of losses of local populations.

Island biogeographic theory has been used to infer that fragmented habitat patches will lose species. Direct observation of this phenomenon has been made in Brazilian coastal forests (Terborgh and Winter 1980), on the artificial island of Barro Colorado (Karr 1982), and in experimentally created fragments in Brazil (Bierregaard *et al.* 1992).

Salient predictors of extinction in small habitat patches include initially small population size, vulnerability to predators, membership of specialist guilds (such as large predators, army-ant followers or other mixed species flocks), dependence on variably available diets (such as fruits or nectar), larger members of guilds, and local catastrophes (such as hurricanes). Vulnerability to predators is often exacerbated by the disappearance of the largest species, which in general do not prey on birds but often kill smaller predators. In their absence, smaller predators with differing diets, including birds, may become more abundant (Terborgh 1988).

Small population models

Empirical observations are of limited use in making predictions because so many species share some of the factors known to have been associated with global extinction or local losses (Simberloff 1986). It is likely that factors acting in combination will be more lethal, but how do we pick the species which, in the absence of intervention, would actually head the list of extinctions in this century?

Population viability analysis (PVA) is a process which might help (Green and Hirons 1991). Indeed, new proposals for categorizing threatened species are based on categories of probability of extinction over given time periods (Mace, Chapter 13; see also Mace and Lande 1991, Mace *et al.* 1993). The interpretation of model outputs is open to various criticisms (Boyce 1992). The process requires ecological and life-history data, a reasonable model, and insight into the factors which might change in the future, either naturally or within a management

regime. For such models to be of practical use, we usually require data about reproductive rates and their variances, survival rates and their variances, density dependence relationships for survival and reproduction, frequency of catastrophic events and their impact, carrying capacities of habitats and their variances, and dispersal rates between sub-populations.

There is a serious practical difficulty in obtaining many of these measures, especially if the species is endangered and urgency precludes long-term study. Variance estimates can only be acquired over a run of time which may simply not be available. Catastrophes, which may be devastatingly quick in their effect, can easily be imagined. But how do you estimate the probability of a cat being landed on a particular small island in the next five years?

This is not to suggest that PVAs are worthless. The PVA process entails bringing experts and managers together to agree on the meaning of available information and on likely management options and to explore possible consequences. The prospect of a continuous process of modelling, management, and observation supports the ideal notion of management regimes being adaptive to changing knowledge and circumstances. The majority of conservation decisions are still taken in the absence of formal population viability analysis and this is likely to continue to be the case. A move to greater formality would be a great aid in focusing scientific attention on the kinds of data most urgently needed to improve the chances of success of a management plan.

7.3 Red Data Books

The basis of Red Lists for birds

As discussed in more detail by Mace in Chapter 13, one approach to predicting which species are at risk of extinction has been the IUCN-promoted Red Lists. These have reached their greatest elaboration for birds, which are the only class amongst which all species have been reviewed and classified as 'threatened', 'near threatened' or 'safe' (Collar and Andrew 1988). In the case of Africa (Collar and Stuart 1985) and the Americas (Collar *et al.* 1992), extensive literature reviews have been published. We might ask how accurate these lists are in predicting future candidates for imminent extinction. A more practical question might be to ask what conservation biologists should next be doing to help.

Threatened species of the Americas, including the near Pacific islands and the Caribbean, have been listed five times (Anon. 1964; Vincent 1966-71; King 1981; Collar and Andrew 1988; Collar *et al.* 1992). Over the last 30 years, the list has expanded fivefold (Table 7.1) with most of the growth being in continental South America.

By 1988 the list for the Americas had grown to 360 species. This list was reviewed in greater depth leading to the 1992 publication. These two most recent reviews differ by 141 species (Table 7.2). Some (24) of the changes were due to taxonomic alterations or discoveries. In general, the consultative process producing the 1988 list tended more towards precautionary listing of species than

Table 7.1 Numbers of threatened bird species listed for the American region at various dates. The area covered has been standardized to that in Collar *et al.* (1992). (Sources are given in the text.)

	1964	1971	1979	1988	1992
North America	10	6	7	13	12
Pacific islands	9	10	4	19	15
Caribbean	18	13	16	31	37
Latin America	31	27	62	297	263
<i>Totals</i>	68	56	89	360	327

Table 7.2 Changes of classification of threatened species in the Americas between 1988 and 1992 and their causes

	No. of species
Listed in 1988	360
Listed in 1988 but not 1992	-87
Listed in 1992 but not 1988	+54
Listed in 1992	327
<i>Deletions from the 1988 list</i>	
6 species no longer regarded as valid	
76 species regarded from new knowledge as 'near threatened'	
5 species regarded from new knowledge as 'safe'	
<i>Additions in the 1992 list</i>	
6 species newly discovered since 1988	
20 species newly erected by taxonomic split or clarification	
11 species missed from earlier review	
18 species reassessed as a result of better knowledge (of which 14 had been listed as 'near threatened')	

to omission of candidates found, on fuller study, to be valid (Collar, pers. comm.). Of 29 species entering the threatened list for the first time in 1992, 14 had previously been indicated as near threatened and only 15 had been inappropriately, as revealed by fuller review, omitted or overlooked.

The general similarity of these two most recent listings suggests a convergence of opinion on which the threatened species are. The very process of reviewing and listing species with documentary evidence can help to promote and target further study. Ideally, knowledge gaps would be indicated and people would be stimulated to fill the most urgent in a continuous process of discovery and review. There is some evidence that this has actually happened.

Table 7.3 Quality of knowledge of birds of the Americas listed as threatened in 1992

	No. of species
<i>Trend in the last 50 years</i>	
(0) Unknown	121
(1) Inferred downwards because of habitat loss	133
(2) Inferred downwards from decrease in numbers of records	50
(3) Quantified in the last 20 years	23
<i>Numbers</i>	
(0) Totally unknown	76
(1) Inferred rate from few records or small range	173
(2) Some counts or densities	41
(3) Total population estimate	37
<i>Range</i>	
(0) Virtually unknown no pattern, few recent records	37
(1) Some pattern with gaps—few known current sites	121
(2) Fairly well known in several to many current localities, but new discoveries likely	110
(3) Formerly bounded, potentially measurable, new localities unlikely	59

Errorous judgement is clearly less likely if population parameters of species are adequately documented (King 1987). The degree of knowledge of range, population, and trend of threatened species listed in 1992 is indicated in Table 7.3. In spite of a huge upsurge of ornithological interest in Latin America, the state of knowledge of many birds remains poor, as shown by Green and Hirons (1991).

Of the three parameters considered, range tends to be best known, but many species have been recorded from rather few localities and can only be presumed to be likely to occur in nearby areas of similar habitat (if there are any surviving). Less than a quarter of threatened species have been subject to any formal counting. The majority are inferred to be rare because they have infrequently been seen within what are often known or inferred to be very limited ranges. Not surprisingly, formal estimates of population trend are still less common because even fewer species were counted 20 years ago. The most frequent pattern of trend is that numbers are inferred to be declining because of habitat loss which has often been very extensive within known ranges.

There is some relationship between quality of knowledge and category of threat (Table 7.4). A slightly higher proportion of endangered species are relatively well known, but this is primarily because of the inclusion of some very thoroughly studied North American species. On the other hand, 10 endangered species are virtually unknown. Species categorized as rare are often better known but the causation may be that they have to be reasonably well known before they can be classified as rare rather than insufficiently known.

Table 7.4 Distribution of quality of knowledge of threatened species in the Americas (1992) in relation to threat class. Degree of knowledge for each species is the sum of three scores (0-2) shown in Table 7.3

Class of threat	Quality of knowledge					Mean	n
	0	1-3	4-6	7-9			
Endangered	10	32	36	18		4.1	96
Vulnerable	4	24	21	3		3.4	52
Vulnerable/rare	1	35	37	6		3.8	79
Indeterminate	10	26	12	2		2.6	50
Rare	1	4	8	6		5.2	19
Insufficiently known	2	20	8	1		2.6	31
<i>Total</i>	28	141	122	36			327

Table 7.5 Frequency of classes of recommendations made for the conservation of 327 threatened bird species in the Americas

Action	No. of species
Secure sites	241
Locate new sites	214
Estimate populations in sites	197
Study ecology	164
Manage sites	91
Control taking	49
Educate people	44
Captive management	23
Taxonomic study	8
Other	14

Recommendations from Red Data Books

The recommended actions from *Threatened birds of the Americas* (Collar *et al.* 1992) are summarized in Table 7.5. Within the divisions made, there are, in total, 1045 recommendations for 327 species. A high proportion (71%) concern a set of four site-specific actions, (find new sites, protect sites, manage them and enumerate populations within them). For only five species do the recommendations include no site-based actions. Species were classified according to degree of threat and reasons for the assessment (see Collar *et al.* 1992). Recommended actions tend to be rather similarly distributed according to threat class ($\chi^2 = 77.0$; d.f. = 55).

The cause of such results is that the most frequent pattern for threatened birds

in Latin America combines limited distribution, dramatic habitat loss, and limited protection of representative areas of the habitat. Minimum conservation measures in such circumstances entail finding populations if the locations of few (or none) are known, followed by protection of viable populations in representative sites. Since numbers are so rarely known, there is a major challenge to survey the threatened species in protected areas as a first step towards establishing whether populations are likely to be viable. Ecological study might assist the management process in protected areas by diagnosing causes of decline and suggesting remedies.

The tropical pattern of risk of extinction differs from that in northern temperate latitudes where, both absolutely and relative to the smaller avifaunas, fewer species are globally at risk. The few that are globally threatened have often been recorded as declining over long periods of time.

7.4 Biodiversity approaches

The fact that so many threatened species have very limited ranges leads to the obvious priority for identifying and protecting the uniquely important sites where they occur (Terborgh and Winter 1982). In a global study (ICBP 1992), we have shown that 27% of all birds on Earth (2609 species) have breeding ranges of less than 50 000 km². There is a high degree of overlap among these ranges which have been classified into 221 distinct areas of endemism, each with at least two unique restricted-range species. By this definition, endemic bird areas (EBAs) embrace about 5% of the Earth's land surface and uniquely accommodate 2484 (9.5%) restricted-range birds.

In the continental Americas with their nearby islands (the same area as covered by Collar *et al.* 1992), 81 EBAs occupy just over 3 million km² embracing the full range of 999 bird species. Of these restricted-range species, 253 are listed as threatened. This amounts to 77% of the threatened birds of the region.

In addition, a further 52 threatened species with ranges greater than 50 000 km² also occur in EBAs (Table 7.6). Thus the future of 90% of the threatened birds of the Americas could largely be determined by the sustained existence of sufficient natural habitat in these EBAs. Of the species not embraced by EBAs, 17 have limited ranges not co-incident with other such species and 4 are sea birds in need of protection at their limited breeding sites. Thus, these 21 species could also largely be safeguarded by appropriate actions in very limited areas. Of just 16 remaining widespread and threatened species, 7 occur in the United States.

The potential efficiency of managing threatened species by conservation policy in EBAs can be illustrated by the areas involved. If attention was given to threatened species, all 253 are confined to 2.2 million km² but 309 to only 1 million km² (Fig. 7.1).

The extent to which individual threatened species with restricted ranges are found in protected areas is one measure of the degree to which their poor conservation status has been recognized and acted upon. On the other hand, if

Table 7.6 Occurrence of threatened birds in the Americas in relation to range and endemic bird areas (EBAs)

Distribution	No.
Restricted-range and solely in EBAs	237
Restricted-range occurring singly	18
Range > 50 000 km ² but occurring in EBAs	52
Others (4 sea birds, 7 US, and 9 South American species)	20
<i>Total</i>	<i>327</i>

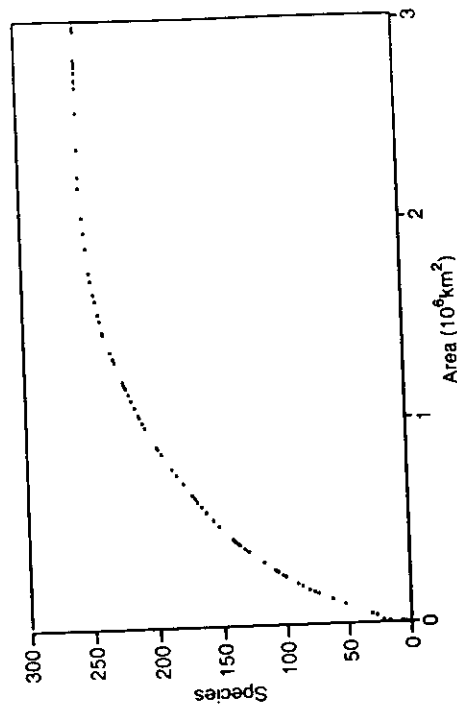


Fig. 7.1 Numbers of threatened species in relation to land area in 81 endemic bird areas (EBAs) in the Americas. Species number and land area are summed cumulatively across EBAs ranked in order of declining numbers of species per unit area.

such species do not occur in protected areas, it is very likely that other elements of biodiversity, both species and communities, will also be unprotected. Knowledge of the distribution of threatened species can thus be used to assess the degree to which they are threatened and also the adequacy of existing networks of protected areas.

An example is shown in Fig. 7.2. The Albertine Rift mountains in Central Africa have 41 endemic birds and can be divided into 12 separate areas of surviving forest, of which 7 enjoy some formal protection. Not surprisingly, the 15 threatened species are still less widespread than the other local endemics, occurring, on average, in only two areas each. At the moment, 9 threatened species do not occur in a protected area at all. Had the protected areas been chosen differently, a set of five would have been sufficient to secure at least one

The coincidence in range of many rare species argues strongly for the identification, designation, and adequate protection of representative areas. Systematic review of the threatened birds of the Americas (Collar *et al.* 1992) provides a very clear indication of priority species and places to start such a search. A further analysis (Wege and Long 1994) portrays these priorities with a clearer geographic rather than species-based emphasis.

Evidence reviewed by Thirgood and Heath (1994) points to the strong likelihood that centres of endemism for birds will be centres of endemism for other taxa at a broad scale. There is a striking, but not complete, similarity between the formally identified endemic bird areas and centres of plant diversity which have been identified semi-formally (Anon. 1992; Davis and Heywood in prep.). While we might hope for a great increase in knowledge of bird species in the next few years, this is optimistic for the majority of the world's other species which may not be identified for a few hundred years. The use of indicator species from other taxa would be a prudent approach to identifying gaps in protected area coverage missed by ornithologists.

Although the majority of species which have so far been driven to extinction would always have been relatively rare by virtue of limited range and particularly vulnerable because threats could have operated throughout their small ranges, some spectacularly abundant species (e.g., passenger pigeon *Ectopistes migratorius* and Carolina parakeet *Conuropsis carolinensis*) have also been exterminated. Concentration on species at risk of extinction also ignores the progressive erosion of biodiversity represented by reduction of range and numbers of many species. Imboden (1987) and Diamond (1987) have therefore proposed the green listing of those species which are ubiquitous and tolerant of habitat modification.

Such an approach has been taken in Europe where nearly half of all species have an unfavourable conservation status, although rather few of them are currently at risk of global extinction (Tucker *et al.* 1994). It would be wise to review the conservation status of all the world's birds and draw attention to widespread declines as well as risk of extinction.

Summary

Most recent extinctions of birds have been caused by habitat loss or by human or introduced predators and have been on islands. Local losses of species in habitat patches are particularly prevalent amongst various specialist feeders and species occurring in small numbers. Future candidates for global extinction are hard to pick from lists of species with indicators of susceptibility. Population modelling should help, but data are generally lacking.

Review of threatened birds in the Americas shows that declines and rarity are often inferred from habitat loss and infrequent records, in the absence of quantitative data. The most threatened species often occur in very few places, where their future is likely to be determined. Safeguarding protected areas within centres of endemism offers a pragmatic response for a high proportion of globally threatened birds and probably other taxa as well.

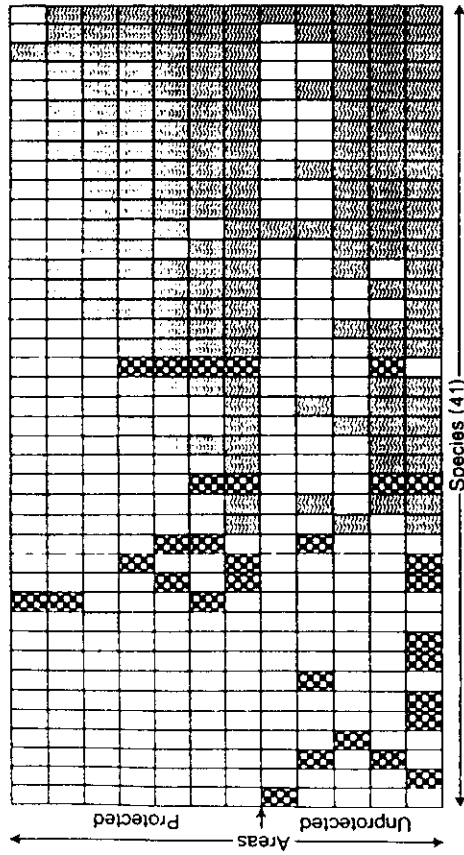


Fig. 7.2 Occurrence of 41 species endemic to the Albertine Rift mountains (Central Africa) in relation to 12 subdivisions of the region. Threatened species are hatched in bold.

place of occurrence for all the threatened species. Four of these five are the unique locations for one threatened species each and are not currently protected.

7.5 Discussion

Evidence from previous extinctions, losses from habitat fragments, and population modelling all point to small populations and losses of habitat as recurring themes on the road to extinction. Birds with these features can be identified fairly readily and include about 10% of all the world's species. The impact of stochastic variation on extinction risk is clear from modelling and from observed losses from habitat fragments. It is rather unclear how vulnerable most particular species or habitats are to stochastic variation beyond the observation that fruit and nectar feeders are vulnerable. Both modelling and observation point to the devastating potential of catastrophic events. With the exception of hurricanes, it is difficult to see how to anticipate the identity of most possible catastrophes, let alone their probability. This is most evident in the case of islands. If the predator-vulnerable species still survive, there is a perpetual risk of accidental introductions. The impact of an alien snake on Guam (Savidge 1987) shows how steep the slope to extinction can be. In less than 40 years, the island lost 7 of its 25 species, 4 survive in small numbers, and 7 more have declined. The Guam flycatcher *Myiagra freycineti* declined from 450 individuals in 1981 to extinction by 1984 (Engbring and Pratt 1985). This is the fastest rate of decline of any threatened species for which such an estimate could be made (Green and Hirons 1991). Only perpetual precaution and vigilance can lower the chances of such disaster and warn of the need for urgent action should it occur. Clearly, the warning time can be very brief.

Acknowledgements

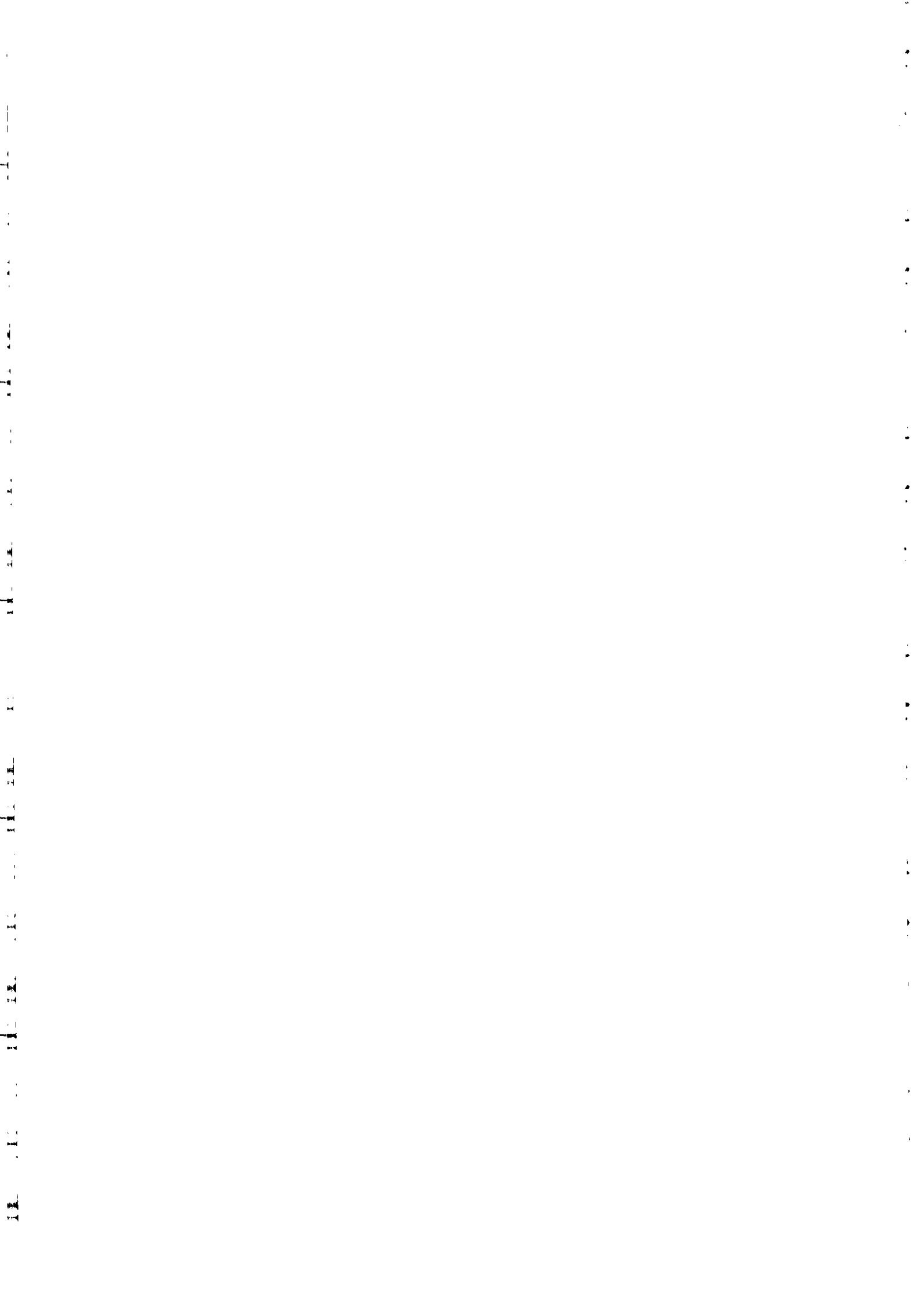
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Modern Science and Traditional Healing

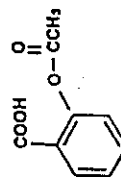
Thomas J. Carlson, Raymond Cooper, Steven R. King and Edward J. Rozhon

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1 HISTORICAL PERSPECTIVE

The pharmaceutical industry clearly has a goal and a challenge to discover, develop and deliver novel chemical and biological entities for the treatment of human diseases; and natural products have played, and will continue to play, an important role in this process. Tropical forest plant species have served as a source of medicines for people of the tropics for millennia. Many medical practitioners with training in pharmacology and/or pharmacognosy are well aware of the number of modern therapeutic agents that have been derived from tropical forest species. In fact, over one-hundred and twenty pharmaceutical products currently in use are plant-derived, and some 75 per cent of these were discovered by examining the use of these plants in traditional medicine.^{1,2} Of these, as shown in Table 1, a large portion has come from tropical forest species. Three examples of plants are presented that (1) present a rich ethnomedical history, (2) offer a basis in ethnomedicine and traditional healing, and (3) have become the basis for multimillion-dollar drugs.

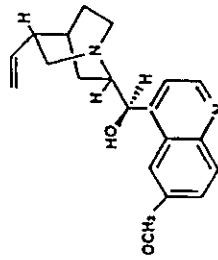
First is the willow, the botanical "parent" of aspirin. The willow (*Salix alba*) is a tree that grows in low-lying damp areas and along rivers in many European countries. The bark of this plant has been used for centuries by people in Europe to treat inflammation, pain and fever. In the 18th century, the information was formally documented with the Royal Chemical Society, and clinical administration of extract to people having the 19th century, developments in the German chemical industry led to the chemical and synthetic strategies for making today's aspirin based on the chemical found in the bark. Bayer Chemical Co. thus became the first to commercialize a synthetic drug based on an herbal remedy; this remains the largest selling drug of all time.



Aspirin From: Willow tree bark
 Utilities: Anti-inflammatory, analgesic, antifebrile, prevention of heart attack

Table 1. Examples of clinically useful drugs from tropical rain forest plants and currently in use in the U.S.A.

Compound	Plant	Clinical Use
Bromelain	Ananas comosus (L.) Merrill (Bromeliaceae) (Pineapple)	Anti-inflammatory; Proteolytic
Camphor	Cinnamomum camphora (L.) Nees & Eberm. (Lauraceae) (Camphor tree)	Rubefacient
Chymopapain	Carica papaya L. (Caricaceae) (Papaya)	Proteolytic; Mucolytic
Cocaine	Erythroxylum coca Lam. (Erythroxylaceae) (Coca)	Local anesthetic
Deserpidine	Rauvolfia tetraphylla L. (Apocynaceae) (Snakeroot)	Antihypertensive; Tranquilizer
L-Dopa	Mucuna deeringiana (Bort.) Merrill (Leguminosae) (Velvet Bean)	Antiparkinsonism
Emetine	Cephaelis ipecacuanha (Brot.) A. Richard (Rubiaceae) (Ipecac)	Anticidic; Emetic
Ouabain	Strophanthus gratus (Hook.) Ball. (Apocynaceae) (Twisted flower)	Cardiotonic
Papain	Carica papaya L. (Caricaceae) (Papaya)	Proteolytic; Mucolytic
Physostigmine	Physostigma venenosum Baill. (Leguminosae) (Ordeal Bean)	Anticholinesterase
Pilocarpine	Pilocarpus jaborandi Holmes (Rubiaceae) (Jaborandi)	Parasympathomimetic
Quinidine	Cinchona officinalis L. (Rubiaceae) (Yellow cinchona)	Antiarrhythmic
Quinine	Cinchona officinalis L. (Rubiaceae) (Yellow cinchona)	Antimalarial; Antipyretic
Reserpine	Rauvolfia serpentina (L.) Benth. ex Kurz (Apocynaceae) (Indian snakeroot)	Antihypertensive; Tranquilizer
Tubocurarine	Chondrodendron tomentosum R. & P. (Menispermaceae) (Curare)	Skeletal muscle
Vinblastine, Vincristine	Catharanthus roseus (L.) G. Don (Apocynaceae) (Madagascan periwinkle)	Antitumor and Antileukemic agents

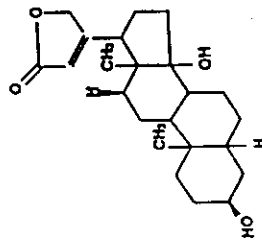


Quinine From: *Cinchona* spp.
 Utility: Antimalarial

As a second example, extracts from *Cinchona calisaya* and *C. officinalis* containing the antimalarial drug quinine have been known to healers in South America for hundreds of years. The cinchona bark was brought back to Spain in the 1500's, and an original sample has been preserved and is permanently on display at the Royal Pharmacy Museum in Madrid. The plant has been extensively studied by

phytochemists, leading to the identification of the active constituent. Quinine and its derivatives have been and continue to be a major drug of choice in the fight against malaria.

Third, European herbalists were well acquainted with the properties of the digitalis plant (*Digitalis lanitana*, and *D. purpurea*, commonly known as foxglove). This plant has been used for a long time to treat heart conditions. Digoxin is the main component prescribed for the treatment of congestive heart failure.



Digoxigenin (Aglycone of Digoxin)

From: Foxglove

Utility: Treatment of congestive heart failure

2.2 An Ethnobotanical Approach

2.2.1 Philosophy

A different approach to new drug discovery involves a collection program for medicinal plants, with primary emphasis on the use of plants by indigenous people in the tropical regions of the world.^{3,4} This approach, utilized by Shaman Pharmaceuticals since its inception, integrates a philosophy of looking for plant leads that already have been shown to be efficacious in humans. By isolating the biologically active compounds from these plants we thereby shortcut the long and expensive screening phase of drug discovery used by the conventional industry. It should be noted that the plant selection is very focused, based on ethnomedical use for a select disease target.

The two described approaches are shown in Figure 1. On the right-hand side, in a high-volume approach, crude extracts and samples are most often tested *in vitro*, using enzyme- and cell-based assays. *A priori*, no initial *in vivo* information is known. By contrast, in Shaman's approach (at left in Figure 1), the plants have already been used in humans, so a high percentage of the select number of actives is effective in animal models at the outset of the discovery process.

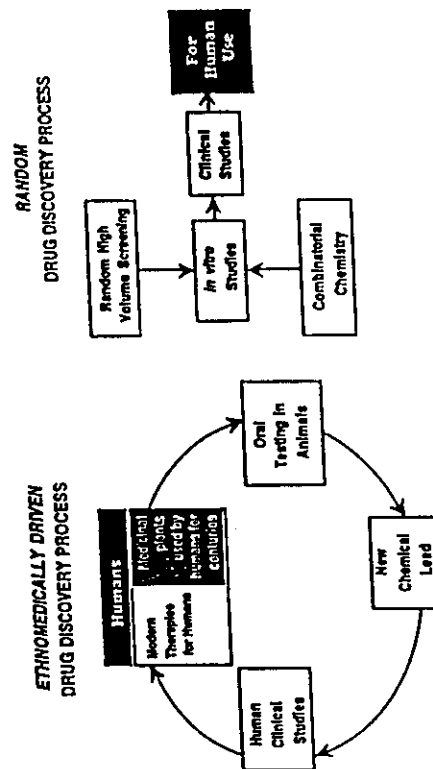


Figure 1. Different approaches to the drug discovery process

2 SCREENING APPROACHES

2.1 High throughput screening

The pharmaceutical industry is aggressively seeking new bioactive entities to treat the numerous disease targets. Tremendous investment is being pumped into this effort, particularly into research and discovery. Modern approaches to drug discovery include random high-volume screening of thousands of chemical entities. These are generated from chemical libraries, combinatorial approaches and natural products, all of which feed into various test systems. The technological advances of robotics for high-throughput, random screening in the 1980's gives the industry an ability to handle very large numbers of samples. This technology advance is now coupled with expanding the sources of screening entities. Thus one consequence has been a renewed interest in including novel and biodiverse tropical species; and this in turn has stimulated a renaissance of activities in the areas of plant natural product chemistry, pharmacognosy, and ethnomedical research. This approach includes the classic random collection of plants that are incorporated into the high throughput screening programs using a variety of mechanism-based assays with specific applications to numerous therapeutic areas. Any positive "hits" typically are subjected to an initial *in vitro* evaluation before proceeding along the chain of development. This methodology, that requires screening of tens of thousands of natural products and chemical entities, is well-suited to the infrastructure and philosophical approach to drug discovery of traditional, yet highly successful pharmaceutical companies.

2.2.2 Plant Collection

The plant collection process is conceived over many months of planning, and by assessing those areas that may yield opportunities for collaboration with local traditional healers. We have a unique ethnomedical field research program that uses an ethnobotanist - physician team. Many weeks and months are spent with the local healers to understand their ways, their approaches and applications. A key phase early in our process takes place in the healer's village, where our ethnobotanist - physician team carefully observes the craft of the healer, the choice and harvesting of the plant part and the way the healer prepares it. This phase is crucial to our own selection process and subsequent in-house extraction activities. We prepare our extract to closely resemble those preparations made by the healer. Many of the traditional preparations are water extractions.

2.2.3 Confirmation of Activity

In essence, the rain forest, its associated ethnomedical history, and the field research prioritization serve as the initial biological screen. The next step in our drug discovery process is to bring the plant in-house and confirm the pharmacological activity of the plant using an animal model that closely simulates the human disease for which the plant was selected. Using this *in vivo* testing approach, we have been able to rapidly identify active lead extracts and compounds for several important diseases in humans. In the diabetes program, for example, this approach has allowed us to efficiently find orally active preclinical candidates, and we have confirmed activity in over 50% of the plant extracts that have been selected for diabetes, by demonstrating blood glucose lowering activity in a diabetes mouse model. The most promising plant leads are then subjected to *in vivo*-guided fractionation campaigns, whereby natural products chemists use state-of-the-art chemical separation techniques to isolate the chemical entity responsible for the observed activity from its inactive components. We begin this campaign using a traditional healer's preparation or a classic organic extract preparation. Modern spectroscopic techniques are then used to elucidate the chemical structure of the active compound.

3 TARGET DISEASES

3.1 Diabetes

One of our targeted disease areas is diabetes, specifically type II non-insulin-dependent diabetes mellitus (NIDDM). We have selected this disease target because, first, it presents opportunities for improved drugs to better meet therapeutic demands; second, we can obtain valuable knowledge from traditional healers on plants they use to treat diabetes in their communities; and

third, we have established an *in vivo* animal model to discover orally active molecules that lower blood glucose. Genetically modified mice (db/db and ob/ob mice) are used as animal models for NIDDM. The mice are dosed orally, and we monitor the effects of these extracts by measuring the blood glucose at various time intervals. Usually we administer extracts and pure compounds to mice by oral gavage and if necessary continue dosing at select intervals for 1-3 days. As a supplement to this *in vivo* approach, we also examine glucose transport through the use of a cellular *in vitro* assay based on 3T3-L1 adipocytes.⁵

3.2 Virology

Another program at Shaman which relies on the ethnomedical approach to new drug discovery is the antiviral program. We have focused on viral diseases that generally are inadequately treated with existing therapies; examples include respiratory syncytial virus disease, influenza, and several herpesviruses. As in the diabetes program, plants are selected and prioritized based on their use by the indigenous peoples for treating various symptoms of viral infection (e.g., for respiratory viral infections, runny nose, pharyngitis, cough, difficulty in swallowing and fever). Upon arrival at Shaman, plants are subjected to chemical extraction and the resulting extracts are tested for antiviral activity in *in vitro* (cell culture-based) and *in vivo* (animal-based) systems.

4 FIELD DATA AND LABORATORY CONFIRMATION OF SELECTED PLANTS

4.1 Diabetes

The genesis of the diabetes program relies on ethnobotanical data from the field. Our ethnomedical field research methodology includes discussing medical case presentations with healers. To gain a better understanding of the efficacy of these botanical medicines and how these plant extracts are effectively prescribed, our colleagues in a variety of host countries have conducted studies to measure blood glucose levels in patients with NIDDM who are treated with a botanical medicine. An example of one of these patients is given in Graph 1. All data points in this graph represent morning fasting blood glucose levels. Normal morning fasting blood glucose levels are 75 - 115 mg/dl. The patient in Graph 1 is a 47-year-old Latin American male who was diagnosed with NIDDM by a medical physician from his host country. Days 1-3 represent pre-treatment. On days 4-8 the patient was being treated. The introduction of the botanical medicine resulted in a significant drop in morning fasting blood glucose levels. By day 8, there was a drop of 90 mg/dl of blood glucose compared to the pretreatment levels on days 1, 2 and 3. Similar studies have also been conducted by tropical country colleagues that involve 6-10 patients. It should be noted that in these examples the patient's weight did not change significantly throughout

Table 2. Correlation between ethnomedically ranked plants for respiratory virus disease and activity against respiratory syncytial virus in the plant extract

RANK	ETHNOMEDICAL INDICATION	% MEETING ACTIVITY CRITERIA*
1.0-1.3	High-Medium Priority Viral Respiratory Infection	20
1.5	Low Priority Viral Respiratory Infection	15
2.0	Non Respiratory Viral, but Possibly Other Viral Indications	8
3.0	Non-viral Ethnomedical Use	8

* Antiviral activity, ED₅₀ = 83 µg/ml & selectivity index ≥ 10.

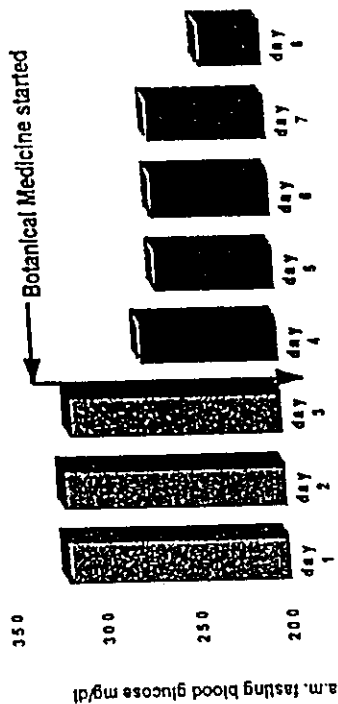
We have also compared the frequency of isolating lead antiviral compounds from plants using Shaman's ethnobotanically driven approach and the high volume, random screening approach (Table 3, part 1). In this analysis, isolation of pure antiviral lead compounds, from plants indicated for three viruses, shows isolation frequencies ranging 1.6 to 8.2%. Compared to the frequency of isolating lead compounds from a fourth virus using the random screening approach (Table 3, part 2), the ethnomedically driven approach is 125 to 630 times more efficient (depending on which virus is used for comparison).

Table 3. Comparison of frequencies of isolating lead compounds using Shaman's approach and the random screening method

PART 1: SHAMAN'S EXPERIENCE			% Isolation Frequency
Area	Number of Plants Tested	Number of Active Compounds Isolated	
RSV	97	8	8.2
FLU	123	2	1.6
CMV	231	5	2.2

PART 2: GENERAL INDUSTRIAL EXPERIENCE			% Isolation Frequency
Area	Number of Natural Products Tested	Number of Active Compounds Isolated	
HSV	15,000	2	0.013

the treatment period. These human data help prioritize the plants on which to focus pre-clinical and clinical studies.



Graph 1. 47-year-old Latin American male with NIDDM

4.2 Virology

The direct assessment of the effects of antiviral plants on tropical patients is more difficult than the evaluation of the effects of antidiabetes plants. When evaluating viral infections, the field research physician is able to make a clinical diagnosis and follow the patient in the field throughout the treatment. In many instances, our field teams are able to assess whether or not a plant is efficacious in the patient. Selection of antiviral plants is based on discussions with the traditional healer as well as direct evaluation of their patients being treated with botanical medicines. Thus, from these discussions, interactions and observations, potential antiviral plants are assigned a priority value based on the research of the ethnobotanist-physician team (Table 2). Using an *in vitro* antiviral assay test the inhibitory effect of these plants against respiratory syncytial virus (RSV) at Shaman, a direct correlation is observed between priority and activity. Plants in the highest priority categories (1.0-1.3) exhibit the greatest percentage of active plants, whereas plants in the lowest category, 3.0, exhibit the lowest frequency of active plants (Table 2). This correlation not only supports the ethnomedical approach to discovering new antiviral leads, but also confirms that the process for selection and prioritization of plants has significant benefit by directing our efforts to those plants that have the highest probability of containing antiviral compounds.

4.3 Frequency of confirming biological activity

Another recent analysis was to compare the frequencies for confirming antiviral activity using *in vitro* and *in vivo* primary assays for plants which were selected based on ethnomedical criteria. Using RSV again as the example, we found that we were more efficient in confirming the antiviral potential of a plant using the *in vivo*, animal-based assay than by using the *in vitro* assay (Table 4). Given that mice more closely resemble humans biologically than cell cultures, and that the animal model at least partially mimics human RSV disease, this finding seems sensible. Moreover, the criteria for selecting potential antiviral plants in the first place is based on a history of activity in humans, not cell culture systems. Similarly, the diabetes program was also more efficient when animal-based assays, rather than *in vitro* assays were used as the primary assay to confirm glucose lowering activity of plants (Table 4).

Table 4. Experimental frequencies for confirming biological activity in ethnomedicinally indicated plants

	Cellular	Animal
Antiviral	20%	29%
Diabetes	39%	57%

5 DEVELOPMENT OF ACTIVES

To date, several different classes of compounds have been isolated and their structures determined. Primary study of these compounds indicates significant lowering of blood glucose but the mechanism of action is not known at this time. Medicinal chemistry and synthetic efforts support these natural product leads in the event that the isolated natural product is available in a low yield and/or the plant source is not amenable to sustainable harvesting. In this situation, when feasible, a synthetic approach to the natural product is considered. An equally important medicinal chemistry mission is to use the isolated natural product as a template for further structural modification to reduce toxicity and/or improve potency. As a result of this process, new chemical leads can be generated from the initial orally active natural product lead. The medicinal chemistry program has been highly successful: two total syntheses originating from an antifungal natural product isolated from *Tribachia alata* and *Antholectia djalonensis* were completed and have been published⁶⁷, and a structural modification study originating from a natural product isolated from *Ambrosia charmissonis*⁶⁸ has been achieved.

6 SHAMAN'S RECIPROCIITY STRATEGIES

Many modern medicines are plant-derived, but the origins of these pharmaceutical agents and their relationship to the knowledge of the indigenous people in the tropical forests is usually omitted.

The idea of compensating indigenous people for the use of knowledge about biological diversity is one based on fairness and equity. A logical means of compensating indigenous peoples for their role in a drug discovery process would be to accord them a share of the profits from the drug, once it is commercialized. However, because of the long period of time needed for commercial drug discovery and development (often ten years or more), such a mechanism for reciprocity requires a long waiting period before any benefit is realized by the indigenous peoples. Furthermore, in most instances, the indigenous knowledge gathered may not lead to a commercial product and thus, no benefit of any kind would come to the local people. From its inception, Shaman has been committed to the concept of reciprocal benefits: to developing new therapeutic agents by working with indigenous and local peoples of the tropical rain forests and, in the process, contributing to the conservation of biological and cultural diversity, or "biocultural diversity".⁹⁻¹³

Shaman, at its inception, founded the Healing Forest Conservancy as a nonprofit organization. The Healing Forest Conservancy is dedicated to conserve cultural and biological diversity and to sustain the development and management of the natural and biocultural resources that are a part of the heritage of native populations. The Conservancy was founded because no governmental organization existed to provide a formal and consistent process to compensate countries and communities for ethnobotanical leads which subsequently are developed into commercial product. The Conservancy ensures a mechanism for the species-rich tropical countries and the small-scale indigenous communities in tropical forests to be equitably compensated for their participation in the development of therapeutic agents. A number of pilot programs has been initiated and described in recent publications.^{10,14-16}

7 CONCLUSION

Shaman Pharmaceuticals embraces the idea of creating an efficient drug discovery process through the integration of ethnobotany, modern medicine and natural products chemistry. Our approach integrates traditional healer information in the field followed by direct application of this knowledge base in our modern lab facilities. We believe we can continue to derive plant chemical entities using the knowledge of the traditional healer. To translate indigenous healing lore into modern medicinal science, we implement a valid methodology for adapting local use of medicinal plant preparations. Thus we combine the attributes of traditional and current knowledge, by choosing only those plants

Phytochemical Diversity: A Source of New Industrial Products

selected by traditional healers, then using state-of-the-art technology to isolate and purify the active principal and verify its activity in our in-house animal model.

Shaman has developed a pioneering technology platform, integrating the sciences of ethnobotany, ethnomedicine, medicine, modern separation science, medicinal chemistry, and primary *in vivo* screening. The process has led to the discovery of multiple orally active antihyperglycemic leads in our antidiabetes discovery program that are currently undergoing preclinical evaluation. We are currently entering Phase II clinical trials with Provir™, an oral product for the treatment of secretory diarrhea, and beginning pivotal Phase III clinical studies on Virend®, a topical antiviral agent for the treatment of genital herpes simplex virus.

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Medicinal Plant Research in Nigeria: An Approach for Compliance with the Convention on Biological Diversity



by T.J. Carlson, M.M. Iwu, S.R. King,
C. Obialor, and A. Ozioko

The following case study is of particular interest as the United Nations prepares to review progress achieved towards global implementation of the Convention on Biological Diversity (CBD) and other agreements resulting from the 1992 Rio Earth Summit. This case study describes one private company's activities—some of which actually predate the Biodiversity Convention by years—that incorporate many of the CBD's guiding principles and mandates.

An estimated one in four prescription drugs is derived at least in part from plants, many of them found in developing nations. Because natural products are an important source of medicinal compounds, their value to the \$60 billion-a-year U.S. pharmaceutical industry is considerable. With investments of this magnitude, the private sector has a significant stake in the Convention on Biological Diversity (CBD),

which encourages "cooperation between government authorities and the private sector in developing methods for sustainable use of biological resources" and calls for the equitable sharing of benefits resulting from the use of genetic resources through appropriate access to genetic resources, transfer of relevant technologies, and funding that appropriately acknowledges rights over resources and technologies.

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The most culturally and biologically diverse, species-rich, floristic, and traditional botanical medicine systems in the world are located in rain forests of tropical countries, while technological infrastructure, expertise, and financial resources to study these tropical medicinal plants are mainly located in temperate countries. This leads to an increasingly frequent situation in which plants are collected in the tropics and then studied by academic institutions and private companies in the United States, Europe, and Japan. Such an imbalance between accessors and owners of indigenous knowledge raises a wide range of political and ethical issues, many of which are addressed in the CBD through legal mechanisms for implementation and enforcement required of the 165 nations which have, to date, ratified the Convention. Signatories to the CBD are searching for working examples to aid them in developing their own country strategies to implement the Convention's requirements.

Compliance with CBD objectives also falls to companies and nonprofit scientific researchers who study, and hope to utilize, biological resources. The recent resurgence in interest on the part of industry in evaluating plants for pharmaceutical development has motivated many major companies, including Merck, Glaxo, and Bristol Myers Squibb, to upscale or initiate natural products programs (see Belson, p.18). This renewed enthusiasm is prompted by several factors: revived interest in using the ethnobotanical approach to identify plant leads

for evaluation; developments in natural products chemical methods; and the demand for new and unusual compounds in the pharmaceutical development pipeline. Table 1 summarizes a variety of guidance documents and policies relating to preservation of biodiversity and cultural knowledge within research protocols.

Shaman Pharmaceuticals strives to incorporate these principles in its strategies, plans, and programs by involving indigenous peoples to maintain cultural diversity as well as biological diversity. The company recognizes that community-based projects and the inclusion of host country expertise are essential to the successful development, evaluation, and monitoring of national plans. In a statement by Lisa Conte, founder and CEO of Shaman Pharmaceuticals, Inc., to a 1994 U.S. Senate Foreign Relations Committee hearing regarding U.S. ratification of the CBD, she asserted:

The Convention is critical to Shaman's operations and philosophy because it defines not only biodiversity conservation, but also the sustainable use of biodiversity and of the equitable sharing of benefits that arise out of that use. As the name of my company implies, Shaman Pharmaceuticals integrates the ancient knowledge of indigenous peoples' use of medicinal plants with the modern technology of the pharmaceutical industry to create a more timely and less costly method for drug discovery. This unique method focuses on the isolation of active compounds from tropical plants

that have a history of medicinal use in indigenous societies and has enjoyed an unprecedented success rate.

The collaborative relationships established by Shaman Pharmaceuticals with local communities, traditional healers, and scientific institutions in Nigeria could provide a working model for those nations and private companies that are seeking creative, equitable, potentially lucrative ways to comply with the CBD.

Nigeria's Geography and Culture

Nigeria is one of a number of tropical countries in Africa, Asia, and Latin America that collaborate with Shaman Pharmaceuticals. With an estimated population of 88.5 to 119 million and high levels of both biological and cultural diversity, Nigeria is an ideal country in which to study medicinal plants. Over 70% of the population is rural and 250-400 ethnic groups are recognized, with nearly 60% of the total population comprised of the Yoruba in the southwest, the Igbo in the southeast, and the Hausa and Fulani in the north.

Shaman's collaborative effort focused mainly on the healers of the cultural groups of Igbo, Efik, and Doko-uyanga in the states of Imo, Anambra, Abia, Enugu, Ebonyi, and parts of Bendel and Rivers southeast Nigeria, an area referred to as Igboland with an estimated 10 million people. The predominant colonial religions are the Catholic and Anglican churches which coexist with the traditional religions of the region. Historically, each Igbo village com-

TABLE 1. GUIDELINES AND RESEARCH PROTOCOLS

Organization	Document	Policies and Practice
Association of Systematics Collections	ASC Guidelines for Institutional Database Policies	The document discusses the ethical way to share, collect, and conserve systematic collections among large institutions, but does not mention any involvement with local communities.
Center for Plant Conservation	Genetics and Conservation of Rare Plants	The guidelines consist of recommendations for collecting genetic variation and rare plants, but does not mention collaboration with local communities.
International Society of Ethnobiology	Covenant Between a Responsible Corporation, Scientist, or Scientific Institution and an Indigenous Group	The covenant lists specific responsibilities required in the partnership between researchers and indigenous peoples for the culture, community, society, environment, region, and nation/state.
National Cancer Institute	Letter of Collection	This agreement acknowledges intellectual property rights and compensation for product development between accessors and owners of biodiversity.
Pew Conservation Fellows	Biodiversity Research Protocols	The protocol suggests a framework to promote good ethical, responsible research between communities and institutions which access biodiversity.
Shaman Pharmaceuticals	Agreement of Principles	This agreement emphasizes prior informed consent and compensation to host countries, cultures, and local communities.
University Research Expeditions Program	Scientific Code of Ethics	The code specifically suggests how researchers can work with, involve, and compensate local communities.
WWF, IUCN, WHO Conservation Strategy of Medicinal Plants	The Guidelines on the Conservation of Medicinal Plants	This document does not discuss the relationship between researchers and local communities.

Data compiled in this table are from:

- Churcher, T. 1996. Directory Partial of Guidance Documents Relating to Biodiversity and Cultural Knowledge Research and Prospecting. Berkeley: Compiled for the Biodiversity and Ethics Working Group of Pew Conservation Fellows, 1996.
- Churcher, T., and Nielschmann, B. 1994. Biodiversity Rights: Paper presented at Pew Conservation Fellows Annual Conference, 1994, Tucson, Arizona. Berkeley: Compiled for the Biodiversity and Ethics Working Group of Pew Conservation Fellows.



Dr. Anumba, a Nigerian medical doctor, talking with Ester Madu, a traditional healer, about plants used to treat Type II diabetes. (©Steven R. King)

munity, or village state, is autonomous with its own chief and government.

The uneven distribution of modern medical facilities in Igboland provides, not unexpectedly, much higher accessibility to the higher socioeconomic groups in urban areas than to the people living in rural communities. Indigenous medical systems thrive along with Western medical facilities, and both are used simultaneously and consecutively.

An estimated two-thirds of the health care practitioners in Nigeria are traditional healers of one sort or another. In 1980, Nigerian law integrated herbalists and "spirit mediums" into the state-run national health service. In 1995, the government of Nigeria officially granted further recognition of traditional healers as health care providers within the country.

Traditional healers in Nigeria fall into several categories, including traditional birth attendants, herbalists, traditional pharmacists, traditional bone setters, traditional psychiatrists, clairvoyants, diviners, and oracles. Categories may overlap and a healer may be, for instance, a traditional herbalist/psychiatrist or diviner/herbalist. Furthermore, many village people who are not recognized as healers have knowledge of a significant number of widely used medicinal plants.

A Case Study in Collaboration

In this Nigerian setting, Shaman Pharmaceuticals established a collegial research relationship and collaboration with a number of stakeholders, including scientific institutions, scientists, village communities, traditional healer organizations, and traditional healers. Shaman's compensation to these stakeholders is stated in the company's "Agreement of Principles" (see Table 1).

The relationship between Shaman Pharmaceuticals and its Nigerian counterparts has been in place since 1990, and four ethnobotanical research expeditions have been conducted in Igboland in 1993, 1995, and 1996. Collaborators with Shaman include Western-trained scientists located at the University of Nigeria at Nsukka; Biore-sources Development and Conservation Program (BDCP), a Nigerian non-govern-mental organization; village communities; and traditional healers and their organiza-tions. Such collaborations can advance dis-cussions of mutually beneficial partnerships with a pharmaceutical company in a tropi-cal country. Integral to these collaborative research relationships is the distribution of immediate, medium-term, and long-term benefits to the stakeholders.

Prior Informed Consent Prerequisite to Research

In accord with the CBD, all Nigerians with whom Shaman collaborated were informed of the activities and philosophy of the company before it conducted ethnobotanical research expeditions, recog-nizing the right of host country scientists, traditional healers, and community mem-bers to decide whether they will collabo-rate and provide information on medicinal plants. It is important to note that a number of the Nigerian healers read, write, and speak English. To ensure prior informed consent, Shaman discussed such issues as:

the intentions and goals of the project; how and where the plants would be analyzed; the potential for commercialization of any pharmaceutical that is developed; issues of compensation and benefit sharing for col-laborators; and the potential for immediate, medium-term, and long-term benefits.

The Nigerian scientists, with Cosmas Obialor and Maurice Iwu, proposed the initial discussions with healers and traditional leaders. They visited the communities that had participated in several years of research collaboration, which included the villages where Iwu and Obialor were born and still periodically spend time.

Objectives of the research project, potential commercialization of products, and compensation were discussed with the community and the healers. It was clearly stated that an average of 10 years of research and development are required before a product is commercialized. The community decision-making process was consistent with the traditional governing customs of this area and included the vil-lage chief, his advisors, traditional healers, and village elders. Groups are predomi-nantly male with typically 20-30% of the members female. After all parties came to a mutually beneficial agreement, Shaman began its ethnomedical research collabora-tion. The steps taken during this negotiat-ing process and the time frame involved are described in Table 2.

The Shaman field research methodolo-

TABLE 2. STEPS TO ESTABLISH PRIOR INFORMED CONSENT

Step	Dates	Project Duration
1. Shaman communicates with scientists at the University of Nigeria at Nsukka and prior informed consent regarding Shaman's objectives and commitments is discussed	1990	start
2. Shaman brings Nigerian scientists to visit its laboratories in California	1990	1st year
3. Shaman contributes financially to the scientific capacity building at the University of Nigeria at Nsukka (a governmental institution) and the Biore-sources Development and Conservation Program (BDCP), a nongovernmental organization established in 1991, prior to any ethnobotanical research	1990 1991 1992	1st-3rd years
4. Nigerian scientists visit village communities and establish prior informed consent of Shaman's objectives and commitments and proposed collaboration with BDCP and Shaman	1992	3rd year
5. Interested communities invite Shaman research team to visit	1993	4th year
6. Shaman obtains research and plant export permits from Nigerian government	1993	4th year
7. Shaman research team (with Nigerian western-trained scientists) visits village community and discusses issues to ensure prior informed consent for Shaman's objectives and commitments and propose collaboration	1993	4th year
8. A mutual agreement is established between the Nigerian scientists, village community, BDCP, and Shaman	1993	4th year
9. The ethnobotanical research proceeds in combination with capacity building and technology transfer	1993 1995 1996	4th,6th,7th years

Source: Shaman Pharmaceuticals, Inc

gy included an ethnobotanist-physician team working at times with an ethnopharmacologist and a phytochemist. All data collection forms included the name and location of the healer who provided the information. After botanical voucher specimens were collected and copied, the botanical and ethnomedical data were deposited in two Nigerian institutions—the University of Nigeria, Nsukka, and the Bioresources Development and Conservation Program (BDCP). Bulk botanical collections of 1-40 kgs of selected medicinal plants were compiled later by the Nigerian field research team and/or the traditional healer, for which the collector was paid a set amount per dried kilogram of plant. Collaborating traditional healers and community members were paid for the number of days they worked on the project, based on the local norm for daily wages. Imme-

diated reciprocity was also provided for the benefit of the whole community based on proposals put forth by the traditional community governing bodies.

An important medium-term benefit is to communicate laboratory results back to the participating communities, which is done routinely, and general literature is published on medicinal plants from Nigeria. Shaman maintained a fundamental philosophy and procedures to equitably compensate indigenous societies for their intellectual contributions to the identification of useful products in the drug discovery process, even prior to the inclusion of such requirements in the Biodiversity Convention. The company had developed a compensation program designed to provide immediate, medium-term, and long-term compensation to indigenous peoples. To implement long-term compensation, Shaman founded a

nonprofit organization, the Healing Forest Conservancy, to funnel a percentage of the profits from commercialized products to countries and communities that have participated in Shaman's drug discovery process. It provides indigenous communities with validation and economic benefits for their knowledge, innovations, and practices.

Collaborators and Partners Ensure Program Viability

While most healers and villagers were not readily satisfied with the prospect of receiving benefits as much as 10 years in the future, they were interested in immediate and medium-term benefits. Shaman made it clear, however, that when these long-term resources were made available to the village, the decisions of the people of the region would determine the use of the resources for projects that would benefit them.

TABLE 3. COMPLIANCE BY SHAMAN PHARMACEUTICALS WITH CONVENTION ON BIOLOGICAL DIVERSITY (CBD)

CBD Principles [Articles]	Shaman's Compliance
Preamble	
<ul style="list-style-type: none"> <i>In situ</i> conservation of ecosystems and natural habitats, recovery of viable species populations Equitable sharing of benefits arising from use of traditional knowledge, innovation, and practices 	<ul style="list-style-type: none"> Recognized importance of indigenous and local people and their traditional knowledge in <i>in situ</i> conservation; desire and intent to collaborate Provided US\$2,000 in 1994 to community and traditional healers' organization in Umobi Community, Umukabia Village, Imo State, for community-based medicinal plant forest reserve
Articles 8(a) and 8(j)	
<ul style="list-style-type: none"> Protected areas or special measures to conserve biological diversity Respect, preserve, and maintain knowledge, innovations, and practices of indigenous and local communities embodying traditional lifestyles 	<ul style="list-style-type: none"> Sponsored two workshops in 1993 and 1996 on ethnomedicine, botany, and conservation for Nigerian botanists, ecologists, conservation officers, chemists, pharmacologists, and physicians. All Shaman ethnomedical and botanical field research documents given to participants Sponsored three ethnobotany and conservation training programs, in Nigeria (1993, 1996) and Cameroon (1994) Co-sponsored workshop on 'Ecology, Cultural Transition, and Human Health' at International Society of Ethnobiology (ISE) annual meeting in Nairobi, September 1996. Conducted in three villages, designed for host country western-trained scientists, local community members, and traditional healers to acquire skills integrating biological ecology, anthropology, and public health Workshop sponsored by Healing Forest Conservancy and BDCP at ISE annual meeting to develop code of ethics
Article 12(a)	
<ul style="list-style-type: none"> Scientific and technical education and training in biological diversity for needs of developing countries 	<ul style="list-style-type: none"> Provided \$8,000 to support 1995 BDCP conferences and ethnobotany workshops in Limbe and Douala, Cameroon Financial support for two Cross River State villages to supply village schools with books, table and chairs, and fund for paying school teachers \$5,000 to support Nigerian scientist attendance at six-week course in biodiversity monitoring at Smithsonian Institution, U.S. Shaman and BDCP sponsor training course on 'Ethnobiology and Field Taxonomy' at Limbe Botanic Garden, Cameroon, October 1995
Article 9(b)	
<ul style="list-style-type: none"> Establish and maintain <i>ex situ</i> conservation, preferably in country of origin 	<ul style="list-style-type: none"> Contributed resources and botanical collection supplies to help establish herbarium at BDCP office Funded and worked with Enugu State Herbarium, Department of Forestry, Enugu State
Article 11	
<ul style="list-style-type: none"> Adopt economic and social incentives for biodiversity conservation, sustainable use 	<ul style="list-style-type: none"> Provided ethnomedical field research materials to BDCP-Nigeria scientists to study malaria, leishmaniasis, and trypanosomiasis to better understand treatment through plant medicines Treated traditional herbalist's husband for malaria with mefloquine Paid for hospitalization of three sick children from Cross River State
Articles 15.5 and 15.6	
<ul style="list-style-type: none"> Prior informed consent of parties providing access to genetic resources Full participation in scientific research 	<ul style="list-style-type: none"> Shaman established prior informed consent with scientists at University of Nigeria at Nsukka, appropriate government agencies, and village communities. Ethnobotanical research proceeds after mutually agreed-upon relationship established
Article 18.1	
<ul style="list-style-type: none"> Promote international technical and scientific cooperation in conservation and sustainable use of biodiversity 	<ul style="list-style-type: none"> Three Nigerian scientists visited Shaman Pharmaceuticals laboratories Nigerian scientist in natural products chemistry at Shaman January 1994-March 1995 to learn modern analytical techniques

Shaman's program further incorporated principles later stated specifically in the Biodiversity Convention by reinvesting in host-country activities and supporting local populations to develop and implement remedial action in degraded areas where biological diversity has been reduced. From 1990 to 1996, resources totaling over US\$210,000 in compensation and reciprocity have been provided to Nigeria from Shaman Pharmaceuticals.

Phytotherapy Research Laboratory, University of Nigeria, Nsukka—As a demonstration of its commitment to host-country capacity building, Shaman Pharmaceuticals provided \$20,000 in 1990, \$10,000 in 1991, and \$10,000 in 1992 to the Phytotherapy Research Laboratory at the University of Nigeria at Nsukka to enhance research on the pharmacology, chemistry, and botany of medicinal plants. The funds were used to support a pharmacognosy lab; assist several graduate students in the Department of Pharmacognosy; provide chemical and pharmacological reagents and equipment; establish biological assays for a variety of microbial pathogens; and acquire botanical herbarium and collection supplies.

Bioresources Development and Conservation Program—In 1991, Nigerians representing a variety of cultural groups established a non-governmental organization, the Bioresources Development and Conservation Programme (BDCP). Since its inception, Shaman Pharmaceuticals has provided financial support to strengthen its infrastructure and facilitate its activities, which have included:

- establishing collaborative relationships with traditional healers' organizations;
- strengthening traditional botanical medicine and traditional healers within Nigeria;
- conducting educational workshops with western-trained scientists and traditional healers as participants;
- establishing BDCP offices in Lagos, Nsukka, Owerri;
- constructing a two-level facility in Nsukka equipped with office space, meeting rooms, facsimile equipment, a librarian, computers, a botany lab and herbarium, chemistry labs, pharmacology labs, and biology labs;
- conducting research on plants that treat parasitic diseases prevalent in West Africa; and
- developing strategies to best utilize traditional botanical medicines to meet health care needs of African countries.

The BDCP is now expanding to other African countries such as Cameroon and Guinea where host-country scientists and traditional healers manage similar organizations.

A Novel Approach to Benefit Sharing

Shaman pioneered these concepts, which essentially converted Biodiversity Convention principles into practice, by working through its nonprofit foundation, the Healing Forest Conservancy, whose purpose is to work with local, indigenous Shaman collaborators to distribute benefits after a product is commercialized. In the long term, Shaman will return a percentage of its profits to all the indigenous communities and countries with which it has worked, regardless of where the actual plant sample or traditional knowledge originated.

Pilot Projects Foster Better Understanding of Compensation Options

The Healing Forest Conservancy has successfully sought additional support for compensation pilot projects from foundations, nonprofit groups, and environmental organizations that view compensation programs as having merit as stand-alone conservation programs. Pilot programs were developed through input from three sources: (1) indigenous federations and their declarations; (2) international conventions, such as the CBD, signed by governments of species-rich countries, and (3) professional associations that have or are developing codes of conduct for ethnobiological research, such as the Society for Applied Anthropology, the International Society for Ethnobiology, and the Pew Biodiversity Research Protocols.

All of these programs recognize the importance of prior informed consent, compensation, and the creation of mutually beneficial relationships between Western-trained scientists and researchers working with traditional rural healers in Nigeria in the face of a variety of ethical, scientific, and traditional resource rights challenges. Shaman Pharmaceuticals scientists cultivate such relationships through discussions and clear communication before, during, and after research expeditions, particularly in establishing collegiality, trust, and fluent communication with local healers. Transfer of technology to the host country, reciprocity, and benefit sharing from research collaboration also are encompassed by Shaman's philosophy. Such exchange of resources begins when the research relationship is initiated with a

host country and continues throughout the duration of the collaboration, regardless of whether a commercialized product is ever developed from the research.

If a marketable product is developed from plants collected from Nigeria, the Healing Forest Conservancy will work with the BDCP and the Fund for Integrated Rural Development and Traditional Medicine to maintain longitudinal dialogue and distribute these resources to local communities to help conserve their biological and cultural diversity.

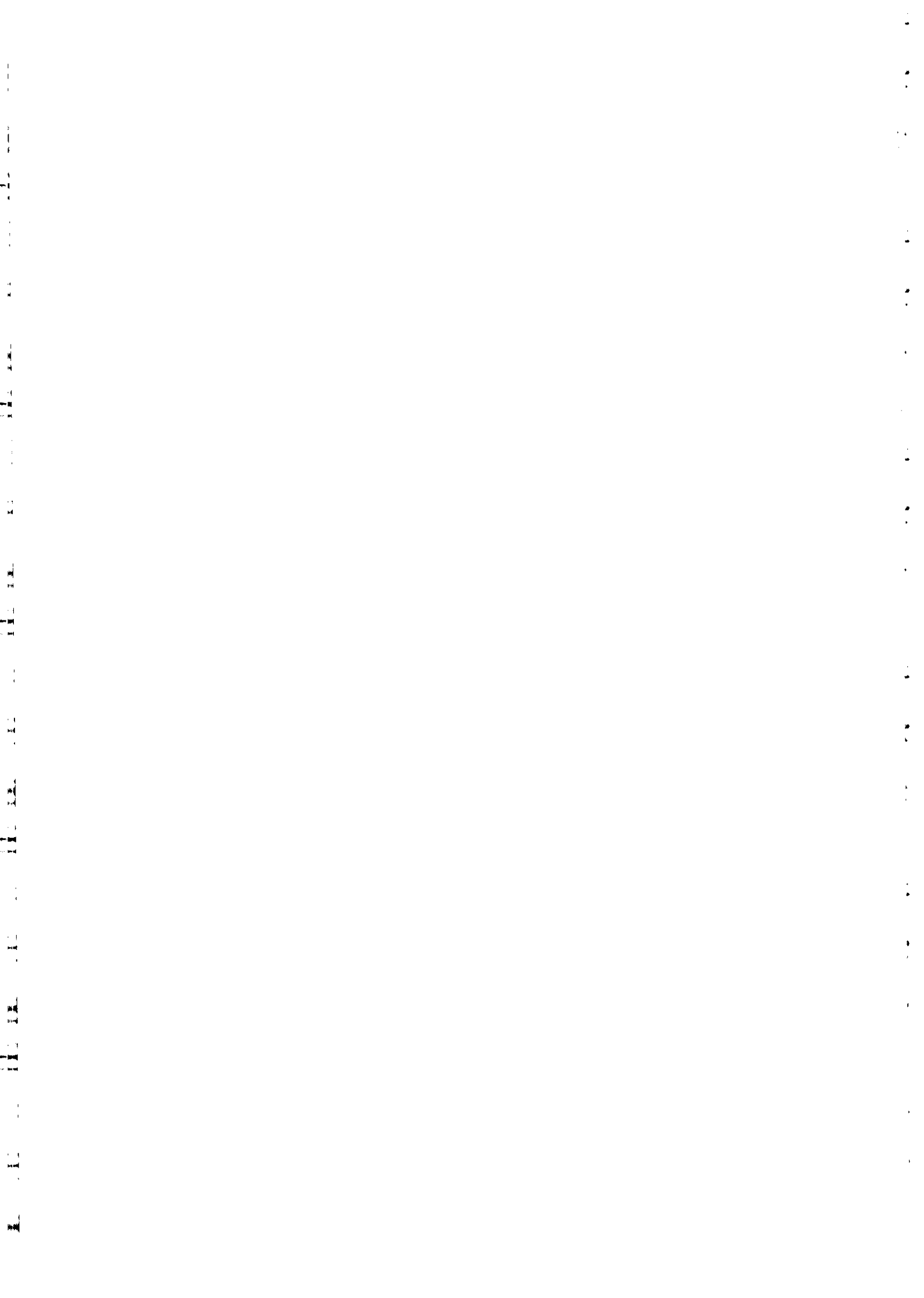
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Further Reading

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Chapter 8

Biological Diversity, Indigenous Knowledge, Drug Discovery, and Intellectual Property Rights

Steven R. King, Thomas J. Carlson, and Katy Moran

Shaman Pharmaceuticals, Inc., has pioneered the direct utilization of indigenous knowledge in the drug-discovery process. They are also attempting to pioneer compensation strategies different from traditional postcommercialization profit sharing. Steven King and his coauthors describe here some of the compensation strategies being used by the pharmaceutical company itself during the drug-discovery process, as well as attempts to funnel resources to partner communities through an independent nonprofit organization, the Healing Forest Conservancy.—Eds.

The idea of compensating indigenous people for the use of knowledge about biological diversity is one based in equity and fairness. It is hard to make an argument that an exchange of resources or reciprocal action is not needed. But it is also exceedingly difficult to find the proper means of exchange. A logical means of compensating indigenous people for their role in the drug-discovery process would be to accord them a share in the profits from the drug, once it is commercialized. However, this not only requires a five- to ten-year waiting period and research conducted in any given village in any country may never lead to a commercialized product. In these instances, no benefits of any kind would come to the local people. The most challenging and difficult issue we are confronted with, then, is how to provide reciprocal benefits, and through what types of mechanisms, so that communities may receive appropriate, and appropriately timed, compensation. We are

presently exploring ways to provide reciprocity, in addition to profit-sharing means and programs that provide communities with immediate and medium-term benefits. We describe in this chapter a number of different approaches and concrete reciprocal benefits conferred on the communities with whom we work.

In the drug-discovery process at Shaman Pharmaceuticals, we utilize indigenous knowledge of medicinal plants during the prescreening of rain forest plants. This knowledge greatly reduces the number of plants that we screen intensively and increases our potential for success. We place a high value on the knowledge that we receive from our collaborators, and for this reason feel it absolutely necessary to reciprocate the contribution to our drug-development process.

There is another reason to demonstrate to the world our commitment to reciprocity and the value we place on indigenous knowledge. To preserve the rain forest without preservation of shamanic knowledge of the plants in the forest would be to cut ourselves off from cures for present and future diseases. In order to preserve that knowledge and ensure that it is passed on from generation to generation, we must also preserve cultural diversity. An explicit goal of our program is to find ways to preserve not only the rain forest plants, but the indigenous knowledge and cultural uses of those plants (King 1991).

It is important that we begin to acknowledge the benefits that native people provide to the world in the form of their historical and contemporary management of global genetic resources, and the different types of relationships between indigenous and outside organizations or governments that can be formed to preserve these benefits. We should view the indigenous knowledge of these people as a highly valuable human cultural resource that should be carefully safeguarded and considered. In explicitly recognizing the expertise of these individuals, we reinforce its importance by according adequate compensation for their intellectual property.

Reciprocity Strategies

As already mentioned, reciprocity may take many forms. In the first section, we describe briefly the methods we use to confer the more conventional type of reciprocity, long-term benefits. We then describe our activities over the past four years to return tangible and explicit immediate and medium-term reciprocal benefits to the people and places where we have worked. We provide descriptions of various means we use to provide reciprocal benefits in the form of medicine and public health projects. We also describe activities of both Shaman Pharmaceuticals and the Healing Forest Conservancy that we hope will help to maintain and enrich biological and cultural diversity in our partner communities.

Long-Term Reciprocity Strategies

Shaman plans to provide a portion of the profits of any and all products to all of the communities and countries in which we have worked. This spreads out the risk to communities of being involved with a financially unpredictable industry and assures a more rapid return of resources for all of our collaborators. Potential profits to be shared would include a portion of those profits derived from a product that may enter the company through a separate route, including a product licensed from another company.

Shaman channels a percentage of product profits, or compensation, equally to each indigenous group—at the federation or collective organization level—that represents people with whom Shaman has collaborated in the drug-discovery process. We do this through an independent nonprofit foundation, founded by Shaman Pharmaceuticals, called the Healing Forest Conservancy. Compensation will be delivered in the form of projects that help to conserve biocultural diversity, largely framed through consultation with representatives of collaborating countries and indigenous organizations.

A second component of our strategy to return long-term benefits to the communities we work with involves the creation of new sustainable natural-product supply industries in the countries in which we work. The development of new sustainable supply industry in tropical countries is considered to be a vital part of economic development by the governments and local people and many countries throughout the tropics (Bennet, 1992; Reid et al. 1993). We are attempting to establish supply relationships with a number of indigenous groups in Latin America. Our research and development work with indigenous federations is described in a separate publication (King 1994).

Short-Term Strategies

Ethnobiologists and numerous international professional societies such as the Society of Economic Botany, the International Society of Ethnobiology, and American anthropological associations have emphatically stated the importance of ethical reciprocal conduct by all people doing research of any type with local and indigenous people (Boom 1990 a, b; Cox and Balick 1994; Cunningham 1991, 1992; Elisabetsky 1991). We believe this should include making a commitment to provide immediate reciprocity by developing projects that help to enhance the health and welfare of the forest people. We advocate a system in which researchers provide for some of the immediate needs of communities. To do this, an organization must ask the people with whom they work what their immediate needs are. Contribution of short- and medium-term reciprocal benefits based on the requests of local people is a model strategy that could be followed by all individuals, organizations, or corporations studying and using local people's traditional knowledge. The fol-

lowing paragraphs detail many of our successful attempts to provide these shorter-term reciprocities to our partner communities.

Integrating Public Health and Ethnobotany Projects

As forest ecosystems are damaged, wild food supplies and traditional agricultural systems are disrupted, leading to a reduction in the nutritional status of food provided. Increased consumption of introduced processed foods and a more sedentary lifestyle result in increased incidence of Type 2 *Diabetes mellitus* (Ali et al. 1993; King et al. 1984; Ramachandran et al. 1992). Microbial pollution of water and a more sedentary lifestyle contribute to an increased intestinal parasite load in village populations. Gold-mining by-products (e.g., mercury) and oil-drilling effluents contaminate water and food supplies in villages near these operations. Logging, oil-drilling, and gold-mining projects can also result in the introduction of new infectious disease strains (e.g., drug-resistant strains of tuberculosis and malaria). A salient example is the epidemic of drug-resistant *Falciparum malaria* that was introduced into Yanomami Indian villages in Brazil by invading gold miners. Effective public health programs can complement forest conservation projects through improving the health status of forest-dwelling people.

Historically, ethnobotany and forest conservation projects have not been conducted in coordination with public health and medical projects. Projects that merge these fields can be mutually beneficial and enhance the efficacies of the individual projects. Shaman routinely uses physicians on expeditions to aid in determination of medicinally active forest plants. Ethnobotanical research is enhanced because a physician can diagnose the diseases seen and/or discussed with the local herbal healers. This helps to streamline the pharmacological analysis of medicinal plants being used. However, the physician can also play a very important role in the provision of direct medical care and facilitation of public health projects. We have established a division of ethno-biomedical field research within our botany department, the purpose of which is to develop and implement the medical and public health components of ethnobotanical field research expeditions.

In providing medical assistance to indigenous communities, it is important to emphasize to the people of those communities that we respect their traditional botanical medicine and recognize its effectiveness in the treatment of many of their diseases. The ethnobotanist should always set the tone and guide the physician's interaction with the local people. When providing medical care it is important that the village herbal healer not be upstaged and that the culture's confidence in their traditional botanical medicine not be weakened. The relationship between the physician and shaman should be re-

spectful and never competitive. Western medicine should be administered in a culturally sensitive fashion as a supplement to traditional medicine, not a replacement.

Community-based public health workshops and conferences can be organized and supported to demonstrate the interrelationship between the stability of forest ecology and the health status of the forest people. Two of the authors of this chapter recently organized and contributed to a three-week course with community-based forest conservation workers. Public health issues for the forest village people were discussed in the context of forest conservation. Collaborative projects with public health workers and physicians working with ethnobotanists and forest conservationists are presently active in Madagascar (Quansah 1992), Peru (Hansson et al. 1992), and the Caribbean basin. Shaman has and will continue to generate and support these and other collaborative efforts to link health care with biodiversity conservation.

Offering Direct Medical Care

We have found that the most effective medical projects are those that are locally based and emphasize both preventative (e.g., clean water projects) and primary health care. Certain diseases (e.g., introduced drug-resistant strains of tuberculosis and malaria) continue to cause significant morbidity and mortality in tropical villages. These illnesses that are not well-treated by traditional medicine should be the focus of Western-trained physicians.

We take a number of steps in providing health care to our partner communities. Contact is made with physicians, nurses, and public health workers at the regional and local clinics and hospitals in the area where field research is conducted. These medical personnel are interviewed to discuss the main diseases in the villages. This information is used to supplement the epidemiological literature survey. It is also important for identification of the resources of local facilities, and lack of resources, hence needs (e.g., books, medicines, equipment, etc.). Based on this information, the physician can donate medical materials, provide technical assistance, and work in the clinics. Some specific examples of our mutual medical exchange and support are described here:

- While conducting ethnobotanical research in Papua New Guinea, one of the authors developed a dermatitis from contact with a species in the *Anacardiaceae* plant family. The dermatitis was very uncomfortable due to the hot humid tropical environment. The Papua botanical healer working with us saw the arm and immediately pointed out the plant that caused

the dermatitis. He then collected the vine of another plant and applied its stem sap on the skin of the author, which resulted in immediate relief of itching. Later in the day we were in the healer's village and he requested that we evaluate some of the elderly people in the village with a variety of illnesses. The sense of sharing knowledge and health care was very natural.

- Another Papua collaborator is one of the most knowledgeable field botanists from the Lae Herbarium. This botanist had been poked in the eye with a thorn six months before while doing his botanical field work. This resulted in a cataract, which made him blind in that eye. On our evaluation of this man, we determined that his sight could be restored with routine cataract surgery and placement of an intraocular lens implant. As our colleague did not have money to afford this surgery, we paid for all his surgical and travel fees. His sight was restored, and he could better work with his valuable knowledge about the plants of Papua New Guinea. While the support of projects to improve the long-term public health of an area is crucial, to be able to provide short-term, immediate health care benefits is also important.
- While working with an Igbo woman herbalist in South Eastern Nigeria, we were introduced to her husband, who was ill with *Falciparum malaria*. He had recently been treated at a nearby allopathic clinic with chloroquine, but his symptoms did not improve. With the agreement of the man and his wife (the herbalist), we treated him with the antimalarial mefloquine, which resulted in an improvement of his condition.
- In 1992, one of us was approached at a scientific meeting by an anthropologist, who made a request for antimalarial medications that could be utilized to help the Yanomami Indians in the Northern Brazilian Amazon. These people were dying from a chloroquine-resistant strain of malaria which was introduced by the gold miners. On behalf of the Yanomami, we contacted Roche Labs, the manufacturer of mefloquine, an effective treatment for this type of malaria, and requested a donation of the medicine. Shortly thereafter, we received the first 500 doses of mefloquine for these people and sent them to the Commission for the Creation of a Yanomami Preserve (CCYP) offices in Sao Paulo, Brazil, who delivered them to treat the most critical malaria cases among the Yanomami. Shaman is not presently working with the Yanomami, but we feel there is a moral obligation to provide support to any indigenous people facing a health crisis.
- On a recent expedition in East Kalimantan, Indonesia, one of the villages we worked in requested that their people be evaluated for tuberculosis and be treated appropriately. It was determined that 17 people in the village had active tuberculosis, and Shaman arranged to have enough antituberculosis medicines sent to treat them all for nine months.

- During our research expedition to Ecuador, at the village's request, we conducted medical clinics and made house calls in the village. The shaman accompanied us into some of the homes, and we functioned as his consultant. One of the patients was a respected elder in the village whose son was the apprentice to the shaman. The shaman told us that the plant medicine being administered was not curing the elder man's skin disease. He presented the patient to us and asked if we had any medicines that would heal the problem. On our physical examination the patient was found to have early developing pyomyositis of the back and chest. This disease is an infection of the skin and subcutaneous tissue that extends into the underlying muscle and causes abscesses. Pyomyositis is a well-recognized cause of morbidity and mortality in the Ecuadorian Amazon (Kerrigan and Nelson, 1992), and is caused by *Staphylococcus* or *Streptococcus*. In advanced stages, people can develop infection of the bloodstream, resulting in death from bacterial sepsis. We were fortunate to be able to provide an oral antibiotic that cured his infection and healed his skin lesions. The village and the elder man's family were appreciative that he was treated effectively and cured. The shaman was not threatened, but rather delighted that his patient and friend was feeling better.
- While in Ecuador in October 1992, in addition to listening to and recording the spontaneous requests by local people for assistance, we also had a village meeting to give everyone the opportunity to identify ways we could contribute to the welfare of the village. One suggestion was the treatment of their intestinal worms. The next day we provided worm medicine to everyone in the village and developed an arrangement with a collaborator from Ecuador to offer worm medicine to the village every three to six months. Responding to another village request, Shaman committed to funding the visit of an Ecuadorian physician and dentist to the village every three months. We also strongly emphasized the value of using their traditional botanical medicine. We supplied each household in the village with an Ecuadorian-produced book on the botanical medicine of their culture. It has become standard procedure to acquire and leave data on local medicinal plants to stimulate and strengthen cultural health care independence.

Establishing Infrastructure for Ongoing Public Health Programs

Offering direct medical care to local people is a way to contribute immediate benefits on each ethnobotanical research expedition. However, when the physician leaves, often no infrastructure is left behind to maintain public health improvements. The programs that have the greatest impact on the health status of the collective population are public health projects (e.g., pre-

ventative medicine and clean water projects). The efficacy of public health projects can be dramatic; simply having clean drinking water in a village can result in a dramatic reduction in the infant mortality rate and incidence and prevalence of infectious diseases in all age groups. Even in the United States, it was the public health measures in the 1920s and 1930s that reduced the infant mortality rate, not the advent of antibiotics and other modern medicines. Based on the request of an Ecuadorian Amazon Quichua village, we are currently supporting a project that will pipe fresh spring water throughout the village, including into the schoolhouse. The indigenous village people are integrally involved in the creation and maintenance of this project, thus making it a self-sufficient system.

On a recent research expedition in East Kalimantan on the island of Borneo, the Kenyah Dayak village we worked with reported they had developed a system to pipe water to one-third of the homes in the village, but they ran out of pipe. They specified the diameter, total length, and type of pipe they needed to provide clean water to the remaining two-thirds of the village. They even told us where we could buy the pipe. The town where it could be purchased was five days away by canoe, so a person from the village accompanied us to Tarakan, where we purchased the pipe. The village representative then took it back to the village to be assembled.

Public health programs should establish infrastructures that facilitate continuous long-term improvements of the population's health status. Through working with regional health-care professionals, local people can be trained to be village health-care workers. Long-term benefits of such projects can be assured by integrating the local people into the planning and implementation of these health-care projects. In addition to conducting clean water and preventative medicine projects, this infrastructure could also be used to administer medicines for treatment of tuberculosis and malaria. When these projects are integrated thoughtfully, they can complement the existing indigenous medical systems.

Community Requests for Immediate and Medium-Term Reciprocity

In October 1992, Shaman conducted a research expedition in Amazonian Ecuador. Prior to our expedition's arrival, the community decided that they were in need of an expanded airstrip, as planes were only capable of taking one passenger at a time. This meant that emergency evacuated medical cases often had to take young children or adults without family members to the regional hospital in Puyo, Ecuador. Shaman complied with this request and provided \$1,500 for the purchase of supplies, material, and labor to lengthen the airstrip for this community. This was completed several months before our arrival.

Medium-Term Strategies

Shaman focuses our medium-term efforts on providing benefits that may not be immediately apparent, but that will nonetheless accrue to the community before profit-sharing might, such as through increasing its scientific and research capability. Some specific examples of medium-term reciprocity have involved providing chemical reagents, high-pressure liquid chromatography (HPLC) equipment, software for scientific data analysis, books, and other critical resources for training to help improve the capacity of local country scientists. These types of benefits have been provided in particular to scientists working within a nongovernmental organization and Malagasy scientists, traditional healers, university students, and other nonprofit organizations.

Scientific Support and Exchange

Shaman has provided direct support for laboratories in developing countries working on traditional medicine. Resources for laboratory materials and scholarships for study have been provided each year to a Nigerian research laboratory that is working on plant treatments for malaria and other diseases prevalent in the tropics of West Africa. We have also provided a year-long fellowship for a Mexican research scientist working in a traditional medicine research institution. This fellowship enables a scientist to direct full-time and continual efforts to traditional medicine and plant research without having to resort to alternative wages to support a family. This scientist was brought to our laboratory for several weeks to work directly with our scientists on techniques and methodologies for the development of central nervous system medicinal plants. Another scientist from Papua New Guinea worked in our labs for three months in late 1993. We also provided support for the purchase of an HPLC device for the chemists' laboratories in Papua New Guinea. This is part of our commitment to provide for technology transfer and exchange. Finally, we have provided opportunities for scientists to come and participate in an intensive biodiversity conservation monitoring course at the Smithsonian Institution in Washington, D.C.

Funding a Shamanic Apprenticeship

On spending time with the family of the sick village elder in Ecuador, we were told that the son (the shaman's apprentice) needed to leave the village periodically and work on a tea plantation to earn money for the family. This unfortunately has interfered with his apprenticeship. We then provided immediate and long-term funding for both the apprentice and the shaman so that they could continue their working relationship full-time. Now the young apprentice does not have to leave the village and go out to seek wages, as he can earn them as part of his apprenticeship with the most specialized healer

in the village. This support will help assure that this valuable shamanic knowledge will be passed on to another generation.

Sustainable Harvesting Studies

Other forms of medium-term reciprocity include the commissioning of sustainable harvesting studies of plant species that are important for local traditional medicine and also of interest to Shaman Pharmaceuticals. Thirteen distinct studies have been commissioned, produced, and distributed in four different Latin American countries on various fundamental aspects of the ecology, distribution, production, and management of several species widely used in traditional medicine in Latin America. These studies, fully commissioned and paid for by Shaman Pharmaceuticals, have been distributed to indigenous groups, nongovernmental conservation organizations, and government institutions within these Latin American countries. By supporting these studies and their distribution, Shaman is assisting the development of the scientific infrastructure and knowledge base of critical biological medicinal plant resources. This helps to create an increased expertise and knowledge of how to manage the important genetic resources of the collaborating countries.

Projects Addressing Conservation of Biocultural Diversity—The Work of the Healing Forest Conservancy

The independent, nonprofit Healing Forest Conservancy was founded in 1989 with a donation by Shaman Pharmaceuticals, Inc. The conservancy was created to provide a mechanism to return short-, medium-, and long-term benefits to people living in tropical forest countries. One of the goals of the conservancy is to return a portion of profits from commercialized products to all of the indigenous groups, communities, and countries with whom we have worked. The conservancy works to support solutions to secure the long-term survival of biological and cultural diversity of tropical forests, with a particular emphasis on preservation of knowledge of medicinal plants and traditional medical practices using plants.

The conservancy works to conserve biocultural diversity through alliances with other nonprofit groups and tropical forest people's organizations in designing and implementing programs with the following objectives: to strengthen indigenous people's organizations and foster communication between indigenous groups and the outside world; to integrate local people into programs for species collection, identification, and inventory of local genetic

resources by merging indigenous and modern scientific methods; to promote sustainable, ecologically sound development through local harvesting of products from forests so as to prevent forests from being cleared for timber extraction; to link public health groups and forest conservation groups; and to support programs and policies that foster the health and welfare of indigenous cultures and tropical forests. The following information is an account of several of the activities of the conservancy.

Medicine Woman Program

A high priority in the implementation of the Convention on Biological Diversity (UNEP, 1992) that entered into force on December 29, 1993, will be to stimulate technical training in the sustainable development of biological resources at local, national, and bioregional levels in species-rich countries and geographical regions. Tropical countries have varying capacities to both conserve and develop their biodiversity; at the local level, most of the small-scale communities that live near and interact daily with flora and fauna lack the technical training to add value to their biological resources. Local capacity-building, through training and education for skills in technical jobs to collect, identify, inventory, and screen the biological assets housed within tropical forests, supplies income-producing incentives to communities living near biological resources and thus best located to protect those resources. On a routine basis it could provide people with technical jobs and/or the ability to market knowledge and information to a broad spectrum of interested partners or companies, both nationally and internationally.

The Medicine Woman program provides for education and training to add value locally to medicinal plant resources, emphasizing the participation of indigenous women. If training, education, or employment opportunities are available to women, ecological impacts may be magnified. Studies demonstrate that women who have the option of a job or another child typically choose the former, effectively lessening population pressures on natural resources. Few programs specifically offer women this type of opportunity, though indigenous women have specialized knowledge of medicinal plant use for contraception, abortion, pre- and postnatal care, and other health and nutrition-related treatments. With support from the Rex Foundation, the International Society of Ethnobiology, and others, The Healing Forest Conservancy has established this program to provide small grants to indigenous women in communities where technical training to add value locally to medicinal plants is culturally appropriate and suits local needs.

Technical training can be valuable to local communities at many levels, but choice as to which level of training sophistication is pursued should be deter-

mined by the communities. Plant collection, biological inventories, chemical screening, and biological assays are types of analysis that can be done at the local level; each is a more sophisticated technique than the previous one. Technical skills in collection include how to make and use a plant press, plant-drying methods, care and storage of dried plants, and simple laboratory techniques for collections. Skills in collecting can be learned to supplement local systems of plant use, to enhance employment opportunities with national governments that are responsible for completing country biodiversity inventories, or with foreign employers interested in developing biological resources commercially. Local participation in the collection process supplies communities with greater control over the use of their biological resources and serves as the basis for more advanced training procedures such as biological inventories and screening.

Before countries can systematically conserve and utilize their biological diversity, inventories are necessary to chronicle the present state of diversity. An inventory supplies a catalogue of a country's biological resources, measures amount, variation, and uniqueness of species, and describes how species are distributed and their status, all of which helps to determine how to manage them. Inventories can also record local uses of indigenous plants.

Screening at local laboratory facilities entails the proper scientific collection and documentation of forest plant material with associated information on its use, preparation, and therapeutic benefits. Screening is labor-intensive, yet does not require the destruction of large amounts of plant samples. In this way, it can generate jobs and be compatible with local conservation programs.

More sophisticated training could include training in biological assay (bioassay) methods. Bioassays are tests in which chemical extracts of, in this case, plant material, are assessed for their effects on selected organisms, cell cultures, or other target systems. Conduct of biological assays involves scientific procedures to process, with locally available and appropriate solvents and reagents, material for toxicity, safety, and efficacy screening. Technicians conduct tasks such as adding extracts of traditionally made medicinal plants to indicator organisms such as brine shrimp, or basic phytochemical screening, perhaps in search of members of a particular class of compounds. These tasks are a form of chemical inventorying to determine the potency or biological activity of compounds and should be incorporated as part of the cataloging process.

National governments stand to benefit from a trained domestic workforce in a number of ways. In addition to an initial fee for use of the country's biological diversity, governments can earn revenue from the sale of information generated through inventories, screens, and assays. Additional revenues may allow debt-ridden nations to forgo the short-term monetary gains associated with destructive practices such as logging, cattle grazing, and monoculture of

cash crops, and focus instead on conservation-related activities. Regional medical needs can be met through increased knowledge to conserve the plants that form the basis of traditional health-care systems. Also, this type of training can set a foundation for the development of a national infrastructure for science, commerce, jobs, and taxes.

A Medicine Woman Pilot Project

In 1994 the Healing Forest Conservancy funded a nine-day Medicine Woman pilot course in Lucknow, India. The course was timed and located to coincide with the Fourth International Congress of Ethnobiology, which students were also able to attend. The purpose of the course was to increase and diffuse knowledge of ethnobiology among the participants. Another important reason for this pilot course in India was to encourage conservation of the nation's rich biocultural diversity, with over 400 unique ethnic groups (75 percent tribal) and 45,000 species of plants. The course covered basic technical skills, as well as created a forum for informed participation in applied ethnobiology through discussion on ethical issues and other professional dialogue with those practicing ethnobiology around the world.

The conservancy, in cooperation with the Asia Foundation and the National Botanical Research Institute of India, supported participation by 28 trainees, over half of whom were tribal women and, as such, the primary managers of natural resources in their communities. Due to their roles of attending to the everyday needs of children and household, and the outmigration of men from their communities, they have acquired an intimate knowledge of local resources and their use, as illustrated partly by home gardens. The tradition of home gardens, tailored to family use, provides considerable variation in plants among individual gardens. Consequently, the gardens serve as botanical refuges for less-common and nondomesticated plants. Home gardens are "research and development" laboratories where different plants are experimented with and adapted for food, fodder, fiber, medicines, religious, ceremonial, and other subsistence uses. They increase the probability that varied and less-common plants will be maintained over time.

On the first day of the course, students were asked what type of information they could best benefit from, given the brevity of the pilot course. Responses included:

- How can communities benefit from their plant resources while maintaining traditional systems?
- What steps must be taken to commercialize plant resources? How can overexploitation of resources be prevented?

- What primary processing can be done at the field level to add value to resources? Basically, students wanted more information and skills to increase their capacity to sustainably develop their biotic resources.

Mornings were spent in classes discussing methods in ethnobiology with varied international specialists in the natural and social sciences who had arrived early for the congress, in order to participate as course instructors. Afternoons were spent in the field, for technical training in collection methods, such as how to make and use a plant press and methods of drying plant material. During a visit to an herbarium, procedures such as care and storage of dried plants and simple herbarium laboratory techniques were demonstrated. Evening discussions focused on ethical issues in applied ethnobiology, such as intellectual property rights.

The brief but intense pilot project, as well as roundtables and discussions with professionals at the following international congress of ethnobiologists, supplied many opportunities to address the questions of the first day. Future Medicine Woman projects worldwide of varying length and depth will offer specific information and training to respond to local needs.

Terra Nova

Traditional territories and resources are the basis of the livelihood, social organization, and cultural identity of indigenous communities. A critical step in the conservation of biocultural diversity is to recognize important cultural links with resource-rich areas, and to preserve both the resource and the culture. Terra Nova is a pilot project to demarcate and manage plant resources, led by local healers who have formed an association for that express purpose. It is a joint partnership between the government of Belize and the Belize Association of Traditional Healers.

The government of Belize has designated a 6,000-acre tract to establish what many believe to be the world's first ethnobiomedical plant reserve. To impede recent poaching and logging, management of the reserve was awarded to The Belize Association of Traditional Healers (BATH), composed primarily of Maya traditional healers. The BATH was formed in 1992 and is an example of communal management of resources, uniting traditional people's use of plants with their sustainable extraction. The land, named Terra Nova, near the Cayo District of Belize, has terrain ideal for many types of Maya medicinal plants integral to Central American traditional healing. The reserve is a nursery for "orphaned" species—medicinal plants rescued from construction bulldozers and transplanted to a safe location. Terra Nova also offers a means to train and pass on the healing forest legacy to future generations of healers. Future plans, supported by the Healing Forest Con-

servancy, the New York Botanical Garden's Institute of Economic Botany, and the Rex Foundation, include making Terra Nova a self-supporting extractive reserve by creating a for-profit factory producing Mayan herbal remedies.

The Usko-Ayar Amazonian School of Painting

The Usko-Ayar Amazonian School of Painting in Pucallapa, Peru, is much more than an art school. Students learn the names and uses of the rain forest plants they paint and, through art, record the myths and traditional knowledge of their elders. While many students become accomplished artists whose paintings capture scenes from the rain forest in stunning detail, they also learn about themselves, their culture, and the natural world of the Amazon.

Since the nonprofit school was founded in 1988, it has taught more than 600 children from working-class families in rural areas of the Ucayali River in the Peruvian Amazon. Usko-Ayar, meaning "Spiritual Prince" in Quechua, offers classes free of charge and provides art supplies for promising students. Paintings from the school have earned acclaim at international art exhibits, particularly the collection of the works of Pablo Amaringo, founder of the school. Amaringo, who has Lamista, Cocama, and Piro Indian ancestors, was awarded the United Nations Global 500 Award in recognition of his protection of the environment through the school's work. The Healing Forest Conservancy currently supports expansion of the present one-room school by selling the children's paintings at Shaman's corporate headquarters and, along with other environmental organizations, features the school in art exhibits in the United States and Europe.

The Richard Evans Schultes Award

To foster and encourage professionalism in the expanding applications of ethnobotany, the Healing Forest Conservancy presents an annual award to a scientist, practitioner, or organization that has made an outstanding contribution to ethnobotany or to indigenous people's issues related to ethnobotany. The award is in the name of Richard Evans Schultes, widely recognized as the father of ethnobotany, with many distinguished academic and applied accomplishments. Schultes earned his Ph.D. in biology from Harvard, where he now serves as Professor Emeritus, and is an internationally renowned specialist in the botany of rubber trees, medicinal plants, and hallucinogens. He has published over 400 technical papers and nine books, including *Plants of the Gods* (1979), *Where the Gods Reign* (1988), and with Robert Raffauf, *The Healing Forest* (1990) and *Vine of the Soul* (1992). The Healing Forest Conservancy was named after their 1970 book.

Schultes' deep respect for the Indians of the Northwest Amazon is legendary, but best related in his own words:

The accomplishments of aboriginal people in learning plant properties must be a result of a long and intimate association with, and utter dependence on, their ambient vegetation. This native knowledge warrants careful and critical attention on the part of modern scientific methods. If phytochemists must randomly investigate the constituents of biological effects of 80,000 species of Amazon plants, the task may never be finished. Concentrating first on those species that people have lived and experimented with for millennia offers a short-cut to the discovery of new medically or industrially useful compounds (Schultes 1988).

The first Richard Evans Schultes Award was presented during the June 1993 Society for Economic Botany meeting, of which Schultes is a founding member. Dr. Calvin R. Sperling, of the National Germplasm Resources Laboratory at the U.S. Department of Agriculture, was recognized for his comprehensive work as a field ethnobotanist in the preservation of genetic resources and the ethnobotany of economic plants. The 1994 award was presented to Professor Hernando Garcia Barriga from Bogota, Colombia, primarily recognizing his life work, *Flora Medicinal de Colombia*. The annual award features a cash prize of \$5,000 donated by Shaman Pharmaceuticals and Conservation International.

Summary

We have outlined in this chapter some of the approaches that we as a company are taking to provide immediate and medium-term reciprocal benefits to the communities in which we work. While there has been a tremendous amount of interest and discussion regarding the importance of intellectual property rights with a strong emphasis on royalties, we feel that immediate benefits are as important to local people as potential long-range benefits. We feel as well that the obligation to provide such benefits extends well beyond the commercial or industrial sector and applies to any type of research, be it academic, corporate, professional, or otherwise.

We advocate that tangible, concrete benefits be reciprocated to all people with whom research is conducted, regardless of the end product. The reciprocal benefits should commence when a project begins and continue throughout its duration. We suggest that all grants for research in developing countries, regardless of the size, include a portion of the research or resources that will be reciprocated to the people in that country.

In fulfilling these ethical obligations, companies must consider and solicit the expressed desires of the people themselves. We have found that the most common forms of reciprocal requests are resources for health care, schools and education, and new markets based on sustainable harvesting of nontimber forest products. There have been centuries of inequitable exchange between local people and outside businesses or research entities. It is time for the ethnobotanical, academic, and industrial research communities to set and maintain new precedents for ethical and reciprocal relationships with local people in tropical forest regions.

There is much faith today in the ability of market forces to "save" the rain forest. While it is useful to link economics and environment, a third 'e' representing equity is a critical component for sustainable development of biodiversity. Indeed, market forces can be a double-edged sword when Western concepts such as markets are introduced into nonmarket groups. Maintaining equity in the process creates a balance of power among participants interested in developing biocultural diversity: species-rich but cash-poor tropical countries, small-scale indigenous communities that have discovered and nurtured their knowledge system of the use of medicinal plants, and the institutions and commercial enterprises of industrialized countries that possess the resources and the technical means to develop biocultural diversity.

Equity means not only compensation but, more importantly, equal standing among participants in making decisions about what form compensation should take. For example, compensation for some countries can mean technical assistance to write and implement national laws that prevent the unregulated use of tropical species. Uppermost, compensation must localize the value of biocultural diversity. This is a unique challenge for which no formal, inclusive, or consistent process currently exists. However, if we are serious about the conservation and sustainable development of biocultural diversity, fair compensation must be the principle to guide it.

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Valuing Biodiversity for Use in Pharmaceutical Research

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Resources for the Future

"Biodiversity prospecting" has been touted as a mechanism for both discovering new pharmaceutical products and saving endangered ecosystems. It is unclear what values may arise from such activities, however. Evidence from transactions is incomplete and existing theoretical models are flawed. We calculate an upper bound on the value of the "marginal species." Even under favorable assumptions this bound is modest. Slightly modified assumptions lead to drastically lower estimates. We extend our findings to the value of the marginal hectare of habitat and find that the incentives for habitat conservation generated by private pharmaceutical research are also, at best, very modest.

1. Introduction

There has been considerable recent interest in "biodiversity prospecting," the search for chemicals produced by wild organisms. In nature, these compounds are employed to escape predators, capture prey, enhance reproductive success, and fight infection. These chemical compounds might be of considerable commercial value if adapted to industrial, agricultural, and, particularly, pharmaceutical applications.

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Biodiversity prospecting has also been touted as a tool for conservation. It has been argued that incentives for the preservation of areas in which biological diversity is greatest, particularly tropical rain forests, might be increased if landholders could be compensated for the values generated by endangered organisms used in new product research (this argument has been made by, among others, Farnsworth and Soejarto [1985], Principe [1989], Wilson [1992], Reid et al. [1993], and Rubin and Fish [1994]).

In order to determine the strength of such conservation incentives, we would need to know the value of the "marginal species" in biodiversity prospecting. A number of studies, including those of Farnsworth and Soejarto (1985), Principe (1989), McAllister (1991), Harvard Business School (1992), Pearce and Puroshothaman (1992), Aylward (1993), and Artuso (1994), have adopted a straightforward approach to valuing biodiversity for pharmaceutical research. These authors have multiplied an estimate of the probability of discovering a commercially valuable substance by the value of a discovery. Results of these exercises range from as little as \$44 per untested species in situ (Aylward 1993) to as much as \$23.7 million (Principe 1989).

The more careful of these studies are useful in that they incorporate detailed treatments of the benefits of new product discovery. We believe the method underlying all these studies to be flawed, however. Existing work takes little account of scarcity. Redundant resources are not scarce and hence do not have great value. By multiplying the probability with which an organism sampled at random contains *some* chemical compound of commercial value—whether unique to that organism or not—by the expected value of a successful commercial product, earlier researchers have failed to recognize the *possibility* of redundancy among natural compounds.

Our approach is more closely related to that of Brown and Goldstein (1984): we value the marginal species on the basis of its incremental contribution to the probability of making a commercial discovery. Our work is also related to that of Weitzman (1992, 1993), Solow, Polasky, and Broadus (1993), and Solow and Polasky (1994). In these papers the authors measure biological diversity in terms of the genetic "distance" between related species;¹ in fact, Weitzman (1992) and Solow and Polasky (1994) show how their proposed measures of diversity can be related to the incremental probability of discovering commercially valuable compounds. In each of these papers, however, the authors are attempting to describe a *measure* of biodiversity, that is, a ranking by which one collection of organisms

¹ See Weitzman (1992) for an explanation of how distance may be measured by matching DNA.

may be said to be more or less diverse than another.² In our work, we accept current taxonomic practice as the appropriate measure; we suppose that all species within a particular taxon are "equally different." We then ask by how much *value* is augmented by increasing the number of species that may be tested in new drug research.

Valuation methods based on the work of these other authors will prove more useful as better information concerning the genetic compositions of species becomes available. Our simplest approach is closer to practical application, however. Biologists estimate there to be between 10 million and 100 million living species. Of these, only about 1.4 million have been described (Wilson 1992) and a far smaller number have been subjected to chemical or genetic analysis (Farnsworth 1988). The types of measures suggested by Weitzman and Solow et al. simply cannot be performed on a broad scale with existing data and computational limitations. In our work we treat each species to be evaluated as an independent Bernoulli trial with an equal probability of yielding the commercial product for which it is being tested. Since much of the literature on biodiversity preservation emphasizes the importance of saving as yet unknown species as genetic insurance against as yet unidentified diseases, our approach seems appropriate.

We provide some background information on biodiversity prospecting in Section II. We then turn in Section III to a discussion of possible sources of redundancy in biodiversity prospecting. Our main results are presented in Sections IV–VI. We present a simple model in which discoveries may prove redundant. We are able to derive an upper bound on the value of the marginal species and, by extension, on the marginal hectare of habitat on which it exists. We demonstrate that this upper bound is relatively modest even under very optimistic assumptions and that the value of the marginal species falls off very rapidly if the probability of discovery differs from the one that maximizes the marginal value. Any model that purports to measure something as speculative as the value of a species for its pharmaceutical research potential must be built on a number of simplifying assumptions. We discuss these assumptions and their implications in Section VII, but we can summarize here by saying that we do not believe that a more realistic treatment would change our results much.

We state our conclusions in Section VIII, but we should emphasize one point now. This paper is concerned solely with pharmaceutical researchers' willingness to pay for biodiversity as an input into com-

² A more recent paper by Polasky and Solow (in press) does deal with valuation issues. That paper does not address values on the margin, however, and does not incorporate any costs of prospecting. It also appears to have been written in part to address perceived omissions in earlier versions of our work.

mercial products.³ Biodiversity may give rise to a number of other ecological, moral, and aesthetic values that are not captured in market transactions. Our point is not that biodiversity is not valuable. If biodiversity is determined to have great value, however, the international community should be seeking other mechanisms to finance its conservation.

II. The Use of Biodiversity in Pharmaceutical Research

Natural organisms' genetic codes contain the "recipes" for chemical compounds of potential value in pharmaceutical products. These recipes can be exploited for commercial purposes by acquiring a breeding stock of the organism that produces the desired compound, transplanting genes, or using the naturally occurring compound as a model for the synthesis of the same or related compounds. Pharmaceutical research on natural products is more often intended to develop "leads" than to identify natural products that can be used in an essentially unmodified form. Leads are promising molecules: blueprints of compounds that must be modified to increase efficacy or reduce side effects. Part of the reason for the increased recent interest in natural products research is a renewed appreciation of the importance of natural leads. While considerable efforts at "rational design" of drugs from inorganic materials continue, researchers have also come to recognize that nature has perfected chemicals that synthetic chemists might never dream up (Reid et al. 1993).

These considerations indicate that genetic resources are nonrival goods. Property rights in them have typically not been well established (see Sedjo 1992; see also Chichilnisky 1993; Vogel 1993). The seminal contributions of Coase (1960) and Demsetz (1967) (see also Barzel 1989) suggest that property rights will come to be established either *de facto* in the form of contracts between parties or *de jure* when the benefits of defining property rights exceed the costs of their enforcement. The legal and institutional treatment of indigenous genetic resources is, in fact, changing. The Biodiversity Convention (United Nations Environment Program 1992) prepared for the 1992 United Nations Conference on Environment and Development in Rio de Janeiro and recently signed by the United States guarantees states

³ We emphasize here that we are considering private, rather than social, incentives to engage in biodiversity prospecting. While we shall consider the implications of broadening our focus later in the paper, we devote most of our attention to private incentives. Much of the conservation advocacy literature promotes the establishment of private biodiversity prospecting schemes; an important policy issue is, then, whether such schemes are likely to generate much money for conservation.

sovereignty over their genetic resources and forbids their appropriation without prior informed consent. Organizations in many countries are now entering into commercial agreements with foreign pharmaceutical researchers. The most noted of these agreements is probably the one signed between Merck and Company, a large U.S. pharmaceutical firm, and Costa Rica's Instituto Nacional de Biodiversidad (INBio). This agreement calls for a fixed payment of some one million dollars and promises of substantial royalties in the event of new product discovery (Sittenfeld and Gámez 1993).

While institutional developments are indicative of a new enthusiasm and optimism concerning the value of indigenous genetic resources, they provide little evidence concerning the value of unimproved genetic resources *in situ*. Markets for transactions in indigenous genetic resources are just beginning to emerge. While payments of between \$50 and \$200 per kilogram for samples have been reported (Laird 1993), the interpretation of fixed payments for samples as a measure of the value of resources *in situ* is suspect for at least two reasons. The first is suggested by our discussion above: it is not entirely clear whether collectors have (or should have) legal title to the samples they sell. Observed prices might, then, be misleadingly low.

The second reason why observed prices may be misleading is that they generally also reflect a measure of compensation for collection and processing effort and expertise. Sample collection is typically a much more difficult process than it may seem. It is important that collection be undertaken by trained taxonomists; appearance and location must be carefully recorded so that funds will be replicable. Samples are next dried and ground. While these processes may sound straightforward, they must also be performed to tight tolerances. The next step is typically to extract active compounds with a chemical solvent. Extracts are then tested to determine activity for certain purposes. Some or all of these steps are now performed by sellers of samples. Payments made for samples may, then, reflect compensation for collection and processing and taxonomic expertise rather than rents for the materials themselves.⁴

Compensation for access to samples is often not made in the form of simple cash transactions, however. Many agreements specify royalty provisions rather than up-front payments. Inasmuch as the terms of these provisions are generally secret and the parties' estimation of

⁴ The Merck-INBio agreement illustrates this point. Of the million dollar up-front payment, less than 10 percent was designated for conservation activities. The remainder went for equipment purchases and to defray INBio's expenses (Sittenfeld and Gámez 1993).

both the probability of discovery and the payoff in the event that a valuable discovery is made are unknown, little can be inferred about the value of resources *in situ* from public information concerning these contracts. Moreover, it can take 10 or more years from the time a useful lead is identified until commercial sales of a resulting product begin, so there is little evidence of the outcomes of existing arrangements. For these reasons, most attempts to estimate the value of biodiversity for pharmaceutical research have been based on inferences from indicators other than observed transactions.

III. Value and Redundancy in Indigenous Genetic Resources

In this paper we seek to determine the value of biodiversity *in situ* for pharmaceutical research and, by extension, the incentives that might be created by pharmaceutical research for the preservation of undisturbed habitat. We derive a demand curve for indigenous genetic resources and then determine from this demand curve the willingness to pay for the "marginal species"⁵ and, by extension, the marginal hectare of threatened habitat.

In deriving this demand curve, we must consider the likelihood not only that useful products will be found in one sample but that they will be duplicated by other finds. The marginal value of genetic information for medicinal purposes is measured by its contribution to the improvement of available health care. For example, the value of a new cancer treatment is determined by its capacity to improve remission rates, reduce side effects, lower costs, and so forth. A new drug that may be effective but is identical or inferior to an existing treatment has little value. While the discovery of a novel compound may not often prove completely superfluous, it is often the case that one product will largely duplicate another or that discovery of one effective compound will reduce the urgency of continuing research on others.

The essence of the argument we shall make below is that *regardless* of the probability with which the discovery of a commercially useful compound may be made, if the set of organisms that may be sampled is large, the value of the marginal species must be very small. We shall treat these issues more formally below; we note in passing, however, that there are several reasons why genetic resources may be

⁵ For want of a better index, we shall treat "species" as the basic units of genetic differentiation. It would be inaccurate to suppose that all species are separated by the same degree of genetic variation. It is common, however, to consider the species as the basic unit of both biological diversity (Wilson 1992) and economic value.

VALUING BIODIVERSITY

relatively redundant. First, the same species may be found over a wide range. If all representatives of a species produce a particular compound, individuals in excess of the number needed to maintain a viable population are redundant. Second, there are numerous instances in which identical drugs, or drugs with similar clinical properties, have been isolated from different species (Farnsworth 1988). To give a recent example, the discovery of the anticancer drug taxol in the Pacific yew of western North America has set pharmaceutical researchers looking for similar compounds in its old-world relatives (see, e.g., Chase 1991). It may also be the case that there are a host of other sources of common compounds that remain undiscovered because current sources are adequate. Given the numerous examples of parallel morphological development in the evolution literature, it should not be surprising to find that different organisms that have evolved in similar ecological niches have developed similar chemicals.

Finally, there is a dimension of what we might call medicinal redundancy. Different therapeutic mechanisms may be effective in treating the same symptoms. Moreover, while the inventiveness of nature in developing useful compounds is much extolled as a factor in the increased demand for natural products for pharmacological research (Reid et al. 1993), synthesis from inorganic sources may also yield substitutes for natural product leads.

IV. A Simple Model

In this section we derive a simple demand function for biodiversity in pharmaceutical research, determine the willingness to pay for the "marginal species," and consider the sensitivity of the value of the marginal species to the probability of discovery and assumptions concerning overall profitability. The intuition behind our results is easily grasped by considering extreme cases. If all species are promising sources of leads, most would be redundant and the marginal species close to valueless. If no species are likely sources of leads, it is unlikely that two or more will prove redundant but also unlikely that any species will prove to have value. Increasing the likelihood of success with any species has two offsetting effects on the value of the marginal species: it increases the expected payoff in the event the species is tested, but it also decreases the expected payoff inasmuch as it is more likely that another equally valuable species is discovered first. By identifying the probability of success at which these effects are balanced, we can derive an upper bound on the value of the marginal species. As the number of species available for testing increases, this upper bound declines.

We begin with a very simple model. Suppose that medical research-

ers have identified a need for a new product. A new product, if successfully developed, will earn net revenue of R . Revenue R is assumed to be net of production, advertising, and marketing costs but gross of any costs of product research and development (i.e., costs of determining whether or not a natural material will in fact lead to a commercially successful product). These costs of R & D will be denoted by c .

Suppose that there are n species of organisms that may be sampled in the search for the new product. Suppose further that p is the probability with which any species sampled at random yields a successful commercial product. We treat each new sampling as an independent Bernoulli trial with equal probability of success. Testing for a particular application ends with the first success; once a successful product is found, further discoveries would be redundant. Thus the value of the entire collection of n samples is

$$V(n) = pR + c + (1-p)(pR + c) + (1-p)^2(pR + c) + \dots + (1-p)^{n-1}(pR + c) \quad (1)$$

$$\frac{pR + c}{p} [1 - (1-p)^n]$$

That is, with probability p , the first organism tested yields a commercially successful product and the search ends. With probability $1-p$, the first organism tested does not yield a successful product and the second organism is tested, and so on. If none of the n organisms tested yields a commercially successful product, search ceases.

What is the value of the marginal species? In other words, how much does total expected value increase with the addition—or decrease with the loss—of a species that could be tested? The increase in total value to be realized by the preservation of an additional species is

$$\begin{aligned} V(n+1) - V(n) &= \frac{pR + c}{p} [1 - (1-p)^{n+1}] \\ &= \frac{pR + c}{p} [1 - (1-p)^n] \\ &= (pR + c)(1-p)^n. \end{aligned} \quad (2)$$

We shall abbreviate this expression for the value of marginal species as $v(n)$ in what follows. Note the straightforward intuition underlying expression (2): the value of the marginal species is the expected payoff in the event it is sampled, $pR + c$, times the probability with which search is unsuccessful in the set of n other species, $(1-p)^n$. Obviously, we must have $pR + c > 0$ if any sampling is deemed

worthwhile; on the other hand, as p becomes larger, the magnitude of $(1-p)^n$ declines more quickly than that of $pR + c$ increases. In what follows, we describe how the value of the marginal species varies with the probability of success in any given trial. We derive two main results in this section. First, one must make optimistic assumptions in order to believe that the value of the marginal species is very large even if the probability of success in each trial were the one that maximizes the value of the marginal species. Second, the function relating the value of the marginal species to the probability of success in any given trial is sharply peaked. With large numbers of organisms from which to sample, not only is the maximum possible value of the marginal species low, but the value also falls off steeply if the probability of success differs even slightly from the maximizing probability.

Differentiate (2) with respect to p to find that

$$\begin{aligned} \frac{\partial v}{\partial p} &= -n(pR + c)(1-p)^{n-1} + R(1-p)^n \\ &= [R - c - (n+1)(pR + c)](1-p)^{n-1} = 0 \end{aligned} \quad (3)$$

when p is chosen to maximize $v(n)$. Heuristically, the first term to the right of the equal sign in the first line of (3) reflects the loss in marginal value associated with the increased likelihood that a successful test will be conducted before the last species is tested. The second term reflects the gain in value associated with the increased expected payoff from testing the last available species, conditional on no earlier discovery.

The second-order condition for a maximum requires that

$$\begin{aligned} \frac{\partial^2 v}{\partial p^2} &= -(n-1)[R - c - (n+1)(pR + c)](1-p)^{n-2} \\ &\quad - (n+1)R(1-p)^{n-1} \leq 0. \end{aligned}$$

As the satisfaction of the first-order condition requires that the expression in brackets is zero at the maximum, the second-order condition is satisfied. It is also easy to see that there is only one extreme point on the interval $[0, 1]$, so the probability that maximizes the value of the marginal species is unique.

The first-order condition may now be expressed as $p^*R + c = (R - c)/(n + 1)$, or

$$p^* = \frac{R + nc}{(n + 1)R} = \frac{1}{n + 1} + \frac{n}{n + 1} \frac{c}{R} \quad (4)$$

The restrictions that $p^*R + c > 0$ and $p^* < 1$ are both satisfied if $R > c$.

Using (4), we can derive the maximum possible value of n , which we shall call n^* :

$$v^* = v(n)|_{p^*} = \frac{R - c}{n + 1} \left(\frac{R - c}{R} - \frac{n}{n + 1} \right). \quad (5)$$

The approximation $[n/(n + 1)]^n \approx 1/e$ (where e is the base of the natural logarithm, approximately 2.718) is very accurate for values of n on the order of those we are considering for wild species. Incorporating this approximation, we have

$$v^* \approx \frac{R - c}{(n + 1)e} \left(\frac{R - c}{R} \right). \quad (6)$$

Expression (6) still involves a number of variables concerning whose magnitudes and relative magnitudes we have not yet said anything. At this point we can see, however, that the *maximum possible* value of the marginal species could be insubstantial. As n grows large, v^* will be small for even relatively small values of c . This is true for two reasons. The first is the $n + 1$ in the denominator of (6). The second is that $(R - c)/R$ is raised to the n th power in (6); for large values of n , this expression will become quite small for even moderate values of c relative to R .

It is also revealing to express (6) in another way. From (1), we can define the expected revenues of a program searching for a particular product as $\Pi = R[1 - (1 - p)^n]$ and the total expected costs as $K = (c/p)[1 - (1 - p)^n]$. We can then rewrite

$$\frac{R - c}{R} = 1 - \frac{pK}{\Pi}.$$

Using (4) to evaluate this expression at p^* , we find

$$\left(\frac{R - c}{R} \right)^n = \left[\frac{(n + 1)(\Pi - K)}{(n + 1)\Pi - nK} \right]^n.$$

For large n , we have approximately

$$\left(\frac{R - c}{R} \right)^n \approx e^{-K/(n \cdot K)},$$

and the maximum value of the marginal species is approximately

$$v^*(n) \approx \frac{R - c}{n + 1} e^{-\Pi/(n \cdot K)}. \quad (7)$$

As K approaches Π , $v^*(n)$ again approaches zero. In short, the value of the marginal species can be high only if the expected aggregate

gate profitability of the research venture is high. In figure 1 we illustrate this relationship.⁶

It also bears mentioning both that the marginal species takes on its maximum value at a probability relatively close to the one at which prospecting "breaks even" and that the value of the marginal species declines relatively rapidly with respect to probability after having reached a maximum. Recall that prospecting is profitable in expectation only if $pR - c > 0$, that is, $p > c/R$. Our statements about relative closeness may be made more concise if we define a basic unit

$$\mu = p^* - \frac{c}{R} = \frac{1}{n + 1} \frac{R - c}{R}. \quad (8)$$

Note that μ is necessarily less than $1/(n + 1)$.

If we now consider v , the value of the marginal species, as a function of p , the probability of success in any given trial (fixing n), it follows that $v(p^* + \mu) = 0$. More generally,

$$v(p^* + m\mu) = (m + 1) \frac{R - c}{n + 1} \left(\frac{n - m}{n + 1} \frac{R - c}{R} \right)^m \quad \text{for } 1 \leq m \leq \frac{1}{\mu} p^*.$$

For large n , the approximation

$$v(p^* + m\mu) \approx \frac{R - c}{n + 1} \frac{e^{-m + 1} \left(\frac{R - c}{R} \right)^m}{e^{-m}}$$

is very accurate. Thus, to a very close approximation,

$$v(p^* + m\mu) \approx \frac{m + 1}{e^{-m}} v(p^*). \quad (9)$$

The shape of this function is illustrated in figure 2; it is, of course, the same as the graph of $(pR - c)(1 - p)^n$. Note the extreme concentration at the function's peak. Recall that $\mu < 1/(n + 1)$; thus, on an interval of length less than $10/(n + 1)$, $v(n)$ varies from zero to its maximum value to $10e^{-9} = 0.0012$ times its maximum value. The probability p^* is greater than $1/(n + 1)$. If, as seems likely, a researcher cannot predict the probability with which she anticipates success in any given sample evaluation within an order of magnitude ex ante, her expectation of the value of the marginal species is likely to be very low.

⁶ The curve in fig. 1 quickly approaches a linear relationship, recall from (7) that

$$v^*(n) \approx \frac{R - c}{n + 1} e^{-\Pi/(n \cdot K)}$$

For $\Pi \gg K$, the exponential expression asymptotes to e^{-1} .

V. Some Specific Examples

It is impossible to estimate the value of the marginal species with any precision. Even deriving an estimate for its maximum possible value is a highly speculative exercise. We can, however, get some idea as to the magnitudes involved by using some data from the pharmaceutical industry. While our estimates are necessarily imprecise, there are reasons to believe that even our upper-bound estimates will be optimistic.

In order to relate our model to real-world data, we must aggregate over all possible discoveries. Some of what we believe to be the excessive enthusiasm for the potential of biodiversity prospecting as a conservation strategy stems from an unrealistic view of the number of products to be generated from prospecting activities. One rarely finds things for which one does not look. Genetic prospectors subject samples to a limited series of tests at any given time. While the history of science records many serendipitous discoveries, they are the exceptions. It would be difficult to come up with a figure for the number of applications for which species are tested;⁷ whatever that number, however, we do have statistics on the numbers of new products developed. We should require as a reality check that the probability of discovery times the number of applications for which tests are performed not vastly exceed current numbers of new products developed.

We shall suppose that there exists a series of "potential products" that might be derived from genetic resources. Potential products might be regarded as cures for diseases. The demand for them may arise as new infectious diseases become widespread, as demographic characteristics change and the health needs of certain groups become more important, or as new technologies are developed. We label these as potential products since there is no assurance that solutions to newly identified needs can actually be found. It is not unreasonable to suppose that new potential products are generated by a Poisson process with parameter λ . Then, in expectation, λ potential new products will be identified every year. We shall suppose that λ remains constant over time: potential new products are identified at a more or less constant rate.

We might suppose that each new potential product j identified at time t would have a stream of revenues net of R & D costs denoted by R_{jt} . Similarly, we could say that the cost of evaluating the potential of the i th species for its use in deriving the j th potential product at time t is a random variable c_{ijt} . It is not unreasonable to assume, at this level of detail, that all the R 's and c 's are statistically independent

⁷ Conversations with researchers suggest that 100 or fewer tests are typically done on species for their pharmaceutical potential.

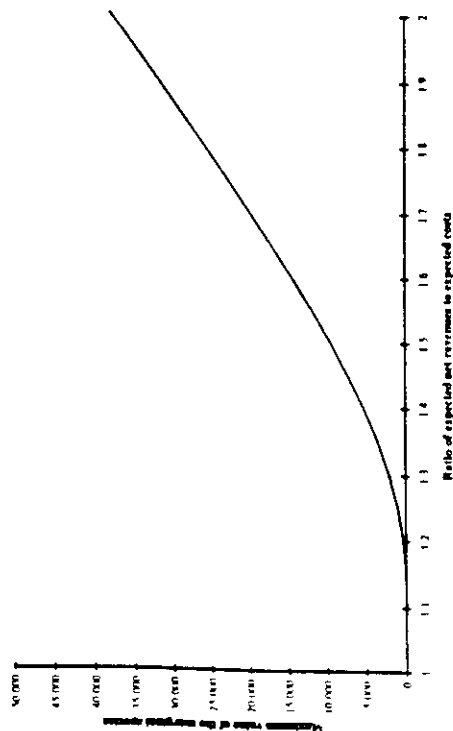


FIG. 1.—Maximum value of the marginal species as a function of the ratio of expected revenues to expected costs in a new product research program.

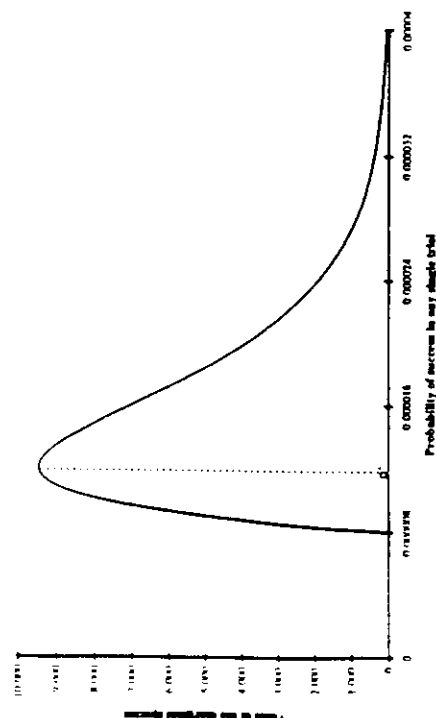


FIG. 2.—Value of the marginal species as a function of the probability of success in any single trial.

and denote the expectation of each as R and c , respectively. If future returns are discounted at a constant rate r , the expected value of the marginal species is simply

$$\sum_{t=0}^{\infty} \lambda(1+r)^t (pR - c)(1-p)^t = \frac{\lambda}{r} (pR - c)(1-p)^n. \quad (10)$$

As was noted above, if we are considering extremely large numbers of species, the value of any one species must be negligible. While biologists are unable to specify the number of living species to within even an order of magnitude, a reasonable lower bound would be 10 million species. The "base case" estimate we report below would have been reduced by 41 orders of magnitude if we had assumed that all 10 million species were equally likely to yield a successful product.

Let us therefore narrow the range of species over which we consider searching. Some have argued that phytochemicals—compounds produced by higher plants—have exceptional pharmaceutical potential (see, e.g., Joffe and Thomas 1989). These compounds may be unlikely to be produced by other types of organisms and may have substantial pharmaceutical value. Aspirin, quinine, and the anticancer drugs vincristine, vinblastine, and taxol are all derived from higher plants. There are estimated to be at least 250,000 species of higher plants (Myers 1988; Wilson 1992).⁸

Between 1981 and 1993 the U.S. Food and Drug Administration approved an average of 23.8 new drugs per year (annual reports of the Pharmaceutical Manufacturers Assoc., 1982–94). This rate was relatively stable (see table 1), varying between 14 in 1983 and 30 in 1985 and 1991. There is no discernible trend in the data. As new drug applications include compounds first approved in the United States and subsequently sold to the rest of the world, as well as drugs already sold elsewhere but just being approved in the United States, we take these figures to be representative of world discovery rates.

About one-third of all prescription drugs are derived from higher plants (Chichilnisky 1993); we shall assume that 10 new drugs per year are expected to be discovered from investigating higher plants. The expected number of new products developed per year is the expected number of new potential products identified, λ , times the probability with which a successful commercial product is developed, $1 - (1 - p)^n$.

DiMasi et al. (1991) estimate pharmaceutical R & D expenditures per successfully derived product to be \$231 million. A recent report

⁸ Fairweather (1988) places the number at between 250,000 and 750,000, so our estimates of the value of the marginal species should again be biased upward.

TABLE 1
NEW DRUG APPROVALS

Year	Number of Approvals
1981	27
1982	28
1983	14
1984	22
1985	30
1986	20
1987	21
1988	20
1989	23
1990	24
1991	30
1992	26
1993	25

Source: U.S. Food and Drug Administration.

suggests that "a reasonable upper bound" on the figure is \$359 million (Office of Technology Assessment 1993). We shall assume a value of \$300 million for our calculations. In our notation, the expected R & D cost per successful product developed would be expressed as

$$\frac{c}{p} = \frac{\lambda}{1 - (1 - p)^n}$$

We shall adopt what seems to us a generous assumption, that the expected return to a new product research effort is 50 percent.⁹ If the expected cost per successful product developed is \$300 million, then we shall suppose that the expected net revenue is $R = \$450$ million. Finally, we shall suppose that pharmaceutical firms discount future returns at 10 percent per year.

The results of an exercise based on expression (6) and these assumptions are summarized in table 2. Our assumptions imply that the probability of hitting on any given species for any given potential product that maximizes the value of the marginal species would be about 12 in a million. Over an entire collection of 250,000 species from which to sample, the probability of making a hit is slightly over 95 percent. The expected cost of evaluating a sample is around \$3,600. The maximum possible value of the marginal species is slightly less than \$10,000.

⁹ This assumption seems a generous estimate on the basis of reported revenues, costs, and R & D expenditures of major pharmaceutical firms, although these data are admittedly difficult to interpret.

TABLE 2
PARAMETER VALUES AND RESULTANT VALUE OF THE
MARGINAL SPECIES FOR THE BASE SCENARIO

Number of species	250,000
Expected number of new products	10
Cost of developing a new product	\$300,000,000
Revenue to cost ratio	1.50
Discount rate	.10
Revenue	\$450,000,000
c	\$3,600
p^*	.000012
Probability of a hit	.9502
λ	10.52
Value of the marginal species	\$9,431.16

NOTE: Variables are defined in the text.

We must emphasize that these estimates are extremely sensitive to changes in assumptions, however. Recall that we have evaluated the marginal species at the probability of success that maximizes its value. The results reported in table 2 indicate that $p^* = .000012$. If we continue to assume that $c = \$3,600$ and $R = \$450,000,000$ but allow p to vary, we may get very different results. We must have $p \geq .000008$ in order to have the expected value of conducting any test be positive. From that level, however, the value of the marginal species quickly increases to the peak at \$9,431. If p were to increase further, to .000030, the value of the marginal species declines to only about \$67. If p were an order of magnitude greater than p^* —but still only on the order of 10^{-4} —the value of the marginal species would plummet to less than \$0.00000005!

The second assumption that can make a great deal of difference in our results concerns the relative magnitude of net revenues and costs. In our base case scenario we assumed that expected net revenues exceed expected research costs per successful new product derived by 50 percent. If we assumed instead that expected net revenues exceed expected costs per successful product by 25 percent, the value of the marginal species would be only \$1,017.53; if expected net revenues exceed expected costs per successful product by 10 percent, the value of the marginal species would be \$2.20.¹⁰

¹⁰ These examples beg the question of what would happen if the margin were higher than 50 percent. One answer is that returns are ultimately limited by demand, and even if evaluation costs were negligible relative to revenues in the event of a new product discovery, the upper bound might well still be modest given the number of species available for testing. Another consideration is that, in the interest of brevity, we have not modeled investments in processing capacity and the timing of R & D. If we were to do so, we would expect that high expected returns to prospecting activities would not exist: a firm—in its competitors—could hasten the research process by making new investments in testing capacity.

We shall see in the next section that even numbers on the magnitude of \$10,000 may translate into very limited incentives for the preservation of threatened habitats. It is worth emphasizing again, however, that we have generated values of that magnitude only under what we regard as generous assumptions. We do not claim to have proved that the marginal species necessarily has negligible value; extremely fortuitous circumstances may combine to create greater values. Our results do suggest, however, that only very optimistic researchers might demonstrate a substantial willingness to pay.

VI. Incentives for the Conservation of Endangered Habitats

We have concentrated to this point on efforts to evaluate the worth of the "marginal species." We are, perhaps, past due in defining this concept and justifying its importance. Economists should be familiar with the notion of valuing resources on the margin but may be uncomfortable with applying marginal analysis in an ecological context. How can one identify the marginal element of a large and complex ecosystem?

Much of the current concern with respect to the extinction of species arises from the destruction of habitat. There is an extensive literature on the relationship between habitat area and the richness of species. We shall employ a widely used model in the ecological literature, advanced by Preston (1960, 1962) and incorporated by MacArthur and Wilson (1967) in their influential theory of island biogeography. Because habitat disturbances may not be as devastating as island biogeography implicitly assumes (see, e.g., Lugo, Parrotta, and Brown 1993), the model is likely also to incorporate an upward bias in estimates of value.

The theory of island biogeography predicts that the number of species, n_i , in a particular taxon found in an area of size A_i , is given by

$$n_i = \alpha_i A_i^z, \quad (11)$$

where α_i is a constant that measures the species richness potential of an area and z a constant whose value is approximately 0.25 (see, e.g., Preston 1962; MacArthur and Wilson 1967; Wilson 1988).

To infer the maximum possible value for the marginal hectare of land for biodiversity prospecting, then, we can differentiate $V_i/\alpha(A_i)$ with respect to A_i to find that

$$\frac{\partial V_i}{\partial A_i} = \frac{\partial V_i}{\partial n_i} \frac{\partial n_i}{\partial A_i}.$$

$\partial n_i / \partial A_i$, can be found by differentiating (11) with respect to A_i :

$$\frac{\partial n_i}{\partial A_i} = Z \alpha_i A_i^{-1} = Z \frac{\alpha_i A_i}{A_i} = Z D_i \quad (12)$$

where D_i is the species density, that is, the number of species per unit area.

We can combine expression (12) with our earlier results presented in table 2 to estimate the conservation incentives that would arise in particular threatened habitats. If we accept the figure of \$9,431 for the value of the marginal species of higher plant, we can translate this number into a figure for a pharmaceutical company's maximum willingness to pay to conserve a marginal hectare. In table 3 we have entered data on Myers's (1988, 1990) 18 biodiversity "hot spots." We find that the greatest willingness to pay might be on the order of \$20 per hectare in western Ecuador. In other areas with less genetic diversity, the willingness to pay would be considerably lower, on the order of a dollar per hectare or less. Again, it should be emphasized that even these very low estimates arise under optimistic assumptions concerning the probability of discovery and expectations of profitability. Equally plausible conjectures concerning these parameters would yield radically lower values.

VII. Caveats and Extensions

It is, of course, impossible to derive precise estimates of the values arising from an activity as speculative as biodiversity prospecting. Our simple model does not begin to do justice to the real-world complexities involved. On balance, however, we believe that it is reasonable to argue that a consideration of such complexities would, if anything, lower our upper-bound estimates. Consider, for example, the omission of discounting from our model. In a world in which it might take years, or even decades, for the marginal species to become the subject of testing, values might be considerably lower. Similarly, an incorporation of Bayesian updating might drive the value of the marginal species to zero: researchers might well quit in discouragement after testing hundreds of thousands of species with no success.

The most obvious omissions of our model concern heterogeneity of species and statistical dependence between tests. Incorporating these features would require the solution of difficult search models, but we doubt that our results would change much if we adopted a more sophisticated procedure. It is, of course, true that pharmaceutical researchers do not generally conduct random searches; rather, they begin searching in the most promising taxa. We might simply regard part of the "testing" process as determining whether or not potential

TABLE 3
MAXIMUM WILLINGNESS TO PAY TO PRESERVE A HECTARE OF LAND IN 18 BIODIVERSITY HOT SPOTS

Hot Spot	Present Forest Area (1,000 ha)	Number of Plant Species	Proportion of Plant Species Endemic to Region	Species per Hectare	Maximum Willingness to Pay
Western Ecuador	250	3,750	25	.00875	\$20.63
Southwestern Sri Lanka	70	1,000	30	.00714	\$16.84
New Caledonia	150	888	89	.00527	\$12.43
Western Ghats of India	800	3,550	82	.00291	\$6.86
Madagascar	800	4,050	40	.00203	\$4.77
Philippines	400	3,595	44	.00198	\$4.66
Atlantic Coast Brazil	2,000	7,500	50	.00188	\$4.42
Uplands of western Amazonia	3,500	15,383	25	.00110	\$2.59
Tanzania	600	1,600	33	.00088	\$2.07
Cape Floristic province of South Africa	4,900	8,600	73	.00071	\$1.66
Peninsular Malaysia	2,600	3,799	28	.00062	\$1.47
Southern Australia	3,470	3,630	74	.00052	\$1.22
Ivory Coast	400	2,770	67	.00048	\$1.14
Northern Borneo	6,400	6,856	59	.00042	\$0.99
Eastern Himalayas	5,300	5,655	59	.00042	\$0.98
Colombian Choco	1,200	2,212	35	.00032	\$0.75
Central Chile	4,600	2,900	30	.00032	\$0.74
California Floristic Province	21,600	4,450	48	.00009	\$0.29

SOURCE — Myers (1988, 1990) and authors' calculations.

samples are in promising taxa, however. With respect to statistical dependence, results in the limiting case are obvious. If the efficacy of any two species were perfectly correlated, they would be redundant. More generally, some species may constitute "guideposts" pointing toward promising relatives. It may well be the case, however, that if any substantial number of species are closely enough related to be useful guideposts, researchers would be unlikely to regret the loss of any one species.

Two other issues merit consideration. The first concerns option value. It is well known (see, e.g., Pindyck 1991) that, under uncertainty, irreversible (dis)investments should not be made until the expected value of their exercise exceeds the opportunity cost by a positive margin. The extinction of a species is an irreversible event. If we consider the overall stochastic variability of new product demand, however, we doubt that option considerations would substantially increase what are, in all likelihood, very small values.¹¹

Our final remark relates to the distinction we mentioned above between private and social benefits from biodiversity prospecting. As we said above (n. 3), we have concentrated on private incentives since many policy issues involve defining and exploiting the willingness of private companies to pay for access to biodiversity for new product research. Social incentives for biodiversity preservation might be considerably greater: consumer surplus from new product development could well exceed profits by a large margin. Even if this is the case, however, values on the margin will still be low if the number of candidate species is large. We regard our example in the section above as a *reductio ad absurdum*, a demonstration that even under extraordinarily optimistic assumptions, private willingness to pay will be, at best, modest. A consideration of social willingness to pay for the marginal species when there are tens of millions of possibilities for search, alternative avenues of pharmaceutical investigation open, a positive cost of sample evaluation, and some uncertainty with regard to the probability of success in any individual test could well yield negligible estimates of marginal value to society even when overall demand is great.

¹¹ Another consideration concerns advances in science. The invention of processes that radically reduce sampling costs might increase our upper-bound estimates of value considerably. At the same time, however, such scientific advances might well increase the range of living organisms over which biodiversity prospecting could be conducted (consequently reducing the value of the marginal species) and enhance the capabilities of synthetic chemists to develop products without reference to natural leads (we are grateful to an anonymous referee for noting these implications).

VIII. Conclusions

We have developed a simple model of the demand for biological diversity for use in pharmaceutical research. We have demonstrated that the upper bound on the value of the marginal species—and, by extension, of the "marginal hectare" of threatened habitat—may be fairly small under even relatively favorable assumptions. Moreover, the value of the marginal species may be a very sharply peaked function of the probability with which any species chosen at random yields a commercially valuable discovery. Finally, we have argued that our model, even though it is very simple, may yet offer some important insights into the real values that biodiversity prospecting might generate for conservation.

It is true that by making very generous estimates of the profitability of the industry and supposing very fortuitous realizations of the probability of discovery, one might postulate moderate values for the conservation incentives provided by biodiversity prospecting. One would have to take a very rosy view to suppose that the probabilities of discovery happen to be precisely those that generate the maximum possible value for the marginal species. If one takes the more reasonable perspective that researchers have some subjective probability distribution over the probability with which individual species sampled will yield commercial products, it seems quite likely that the perceived value of the marginal species will be minuscule. This view seems to be consistent with information concerning observed transactions. This subject should be studied further, but we would not expect a reversal of the conclusion of our analysis: the private value of the marginal species for use in pharmaceutical research and, by extension, the incentive to conserve the marginal hectare of threatened habitat are negligible.

We should emphasize again in closing that none of our conclusions implies that we should not be concerned with the problems of declining biodiversity. Our point is, rather, that if the international community values biological diversity, it should be actively seeking other alternatives for financing its conservation.

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Cost of innovation in the pharmaceutical industry*

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The research and development costs of 93 randomly selected new chemical entities (NCEs) were obtained from a survey of 12 U.S.-owned pharmaceutical firms. These data were used to estimate the pre-tax average cost of new drug development. The costs of abandoned NCEs were linked to the costs of NCEs that obtained marketing approval. For base case parameter values, the estimated out-of-pocket cost per approved NCE is \$114 million (1987 dollars). Capitalizing out-of-pocket costs to the point of marketing approval at a 9% discount rate yielded an average cost estimate of \$231 million (1987 dollars).

1. Introduction

Product innovation in the pharmaceutical industry is risky and time-consuming, with research and development (R&D) costs representing a high

*We are indebted to Gene Trimble who selected our sample of investigational drugs from a Center for the Study of Drug Development database and assisted in preparing our questionnaire. We are also grateful to Marianne Uliczka for assistance with data entry. In addition, we wish to thank the Bradley Policy Research Center at the William E. Simon Graduate School of Business Administration of the University of Rochester and Duke University's Program in Pharmaceutical and Health Economics for partial support of expenses incurred by Ronald Hansen and Henry Grabowski, respectively. Finally, we thank the surveyed firms for providing proprietary data, and a number of individuals in those firms who graciously gave of their time when we requested clarification of responses.

The output from our work can be applied to these various issues in subsequent research.

The approach to estimating an average pre-tax cost of new drug development used in this paper follows, for the most part, that found in Hansen (1979). Micro-level data on the cost and timing of development were obtained through a confidential survey of U.S. pharmaceutical firms for a random sample of NCEs first investigated in humans from 1970 through 1982. Reported development expenditures run through 1987. For every NCE that is approved, several others are abandoned at some point in the development process. Consequently, we associate the costs of failed projects with expenditures capitalized to the point of marketing approval.

In this paper, we examine the sensitivity of R&D costs to various parameters such as the clinical success rate and the economic discount rate. We also consider the sensitivity of R&D costs in reductions in Food and Drug Administration (FDA) regulatory review times and the lengths of various phases of NCE development. In addition, results are presented for the costs of developing approved new drugs categorized by an FDA measure of a new drug's medical significance.

The remainder of this paper is organized as follows: section 2 contains an outline of the new drug development process, which serves as background for the rest of the paper; section 3 provides a review of the literature on the cost of drug development; the cost estimation procedures we employ are described in section 4; a description of our sample data and the population from which they were drawn is given in section 5; baseline results on the average cost of NCE development are presented in section 6, while results for subsamples are given in section 7; section 8 contains an analysis using published aggregate pharmaceutical industry R&D data that serves as an external check on some of our baseline results; and some conclusions and prospects for future research are offered in section 9.

2. The new drug development process

New drug development is typically a sequential process. At several points in the process a pharmaceutical firm will review the status of testing on a drug and make a decision on whether to continue with its development.² In general, the decision depends on potential therapeutic benefits, the expected frequency and severity of adverse reactions, projected additional development, marketing, distribution, and production costs and estimates of a future revenue stream.

²The number and timing of these critical points in the life of an investigational drug vary by firm. See Wiggins (1981) for a discussion of when these decisions are usually made and what considerations are used in making them.

proportion of sales revenues.¹ Although other forms of pharmaceutical innovation exist, new chemical entity (NCE) development is, on the whole, the most therapeutically and economically significant.^{2,3} Typically, the R&D process for NCEs is spread over many years, and only a small proportion of these new drugs are eventually approved for marketing.

Empirical analyses of the cost to discover and develop NCEs are interesting on several counts. First, knowledge of R&D costs is important for analyzing issues such as the returns on R&D investment.⁴ Second, the cost of a new drug has a direct bearing on the organizational structure of innovation in pharmaceuticals. In this regard, higher real R&D costs have been cited as one of the main factors underlying the recent trend toward more mergers and industry consolidation.⁵ Third, R&D costs also influence the pattern of international resource allocation, and hence, international competitiveness.⁶ Finally, the cost of R&D has become an important issue in its own right in recent policy deliberations involving regulatory requirements and the economic performance of the pharmaceutical industry.⁷ In this paper we confine our analysis specifically to the study of R&D costs.

¹The Pharmaceutical Manufacturers Association (PMA) Statistical Fact Book (1987) reports that, for member firms, U.S. pharmaceutical expenditures expressed as a percentage of U.S. pharmaceutical sales was 15.0% in 1986, up from 10.2% in 1965.

²An NCE is defined here as a new molecular compound not previously tested in humans. Excluded are new salts and esters of existing compounds; surgical and diagnostic materials; certain externally used compounds such as disinfectants, antiperspirants, and sunscreens; nutritional compounds such as natural forms of vitamins and sweetening agents; and certain biological compounds such as vaccines, antigens, antisera, immunoglobulins, or purified extracts of existing drugs.

³Data in the PMA Annual Survey Report, 1987-1989, indicate that 82.9% of member firm company-financed human and veterinary use R&D expenditures in 1987 were spent on research for the advancement of scientific knowledge and development of new products and related services. The remainder was spent on research oriented to significant improvements and/or modification of existing products. This percentage has not varied much over the last few decades. The reason why such a high proportion of R&D is spent on new drugs is that a compound patent can usually be obtained covering the active ingredient. This patent confers protection from competition from any generic version of the drug.

⁴The two most recent rate of return analyses in the economics literature use cost estimates in Hansen (1979, 1980), Joglekar and Paterson (1985) estimates an after-tax rate of return for a hypothetical NCE first investigated in 1976. Grabowski and Vernon (1990) provides rate of return estimates for NCEs first marketed in the U.S. in the 1970s. The cost estimates used are applicable to NCEs first investigated in humans during the period 1963-1975. Future studies can benefit from cost estimates relevant to a later period.

⁵Within the past few years, there have been several major mergers and acquisitions in the pharmaceutical industry including SmithKline Beecham, Bristol Myers Squibb, Eastman Kodak-Sterling Drug, Merrell Dow Marion Laboratories, and American Home Products. Robins

⁶For studies of competitiveness in pharmaceuticals, see the analyses presented in the National Academy of Engineering (1983), Grabowski (1989), and especially Thomas (1990).

⁷In particular, Congressional concern has been focused on increases in relative drug prices and the role of increased R&D costs in explaining higher prices [U.S. Congress (1985, 1987, 1989)].

For drugs that make it all the way through to the point of FDA marketing approval, the sequence usually runs as follows. Prior to synthesis considerable discovery research is undertaken by chemists and biologists to develop concepts for new compounds. Once a new compound has been synthesized it will be screened for pharmacologic activity and toxicity *in vitro*, and then in animals. If, at this point, the drug is still considered a promising candidate for further development, the firm will file with the FDA an Investigational New Drug Application (IND).⁹ Unless the FDA places a hold on this application, the firm may begin clinical (human) testing 30 days after filing. Clinical testing normally occurs over three distinct phases, each of which contributes different amounts and types of information on safety and efficacy.

Phase I testing is performed on a small number of (usually healthy) volunteers. These trials are conducted mainly to obtain information on toxicity and safe dosing ranges in humans. Data are also gathered on the drug's absorption and distribution in the body, its metabolic effects, and the rate and manner in which the drug is eliminated from the body.

In the second phase of human testing, phase II, the drug is administered to a larger number of individuals. The groups selected consist of patients for whom the drug is intended to be of benefit. Under the 1962 Amendments to the Food, Drug, and Cosmetics Act of 1938 (FD&C), substantial evidence of efficacy in the intended use of the drug is required before marketing approval can be granted. When successful, phase II trials usually provide the first significant evidence of efficacy. Additional safety data are also obtained during this phase.

The third, and final, premarketing clinical development phase, phase III, involves large-scale trials on patients. Additional evidence of efficacy is sought during this phase. The larger sample sizes increase the likelihood that actual benefits will be found to be statistically significant. Because many patients are typically enrolled in the trials, phase III testing is also useful in detecting adverse reactions that occur infrequently in patient populations. In addition, this testing may more closely approximate the manner in which the drug would be utilized after marketing approval.

Although extensive toxicology experimentation on animals occurs during the preclinical period, to detect teratologic and carcinogenic effects firms usually perform long-term animal testing concurrent with phases II and III. Long-term stability testing, and sometimes additional dosage formulation work and process development for manufacturing the compound in sufficient quantities for clinical testing, also occurs during the clinical period.

Once the clinical development phases have been completed and the firm believes that it has sufficient evidence for approval, it will submit a New

⁹See Marfisi et al. (1988) for analysis of trends in the number of INDs filed by U.S. firms.

Drug Application (NDA) to the FDA for review. Marketing for approved uses may begin upon notification from the FDA.¹⁰

We designed our procedures for estimating average costs to utilize this categorization of drug development by phase. Not all new drug testing fits neatly into this framework, but the firms were able to allocate clinical costs satisfactorily to phases.

3. Previous estimates of new drug R&D costs

A number of studies, covering various time periods, have attempted to provide estimates of at least a portion of the R&D expenditures required to bring new drugs to market. Although comparing results from studies with differing methodologies is risky, taken as a whole these analyses point to rising real R&D costs over time.

Table I presents the main results from these studies, the nature of the data analyzed, and the periods covered. Schnee (1974), Sarett (1974), and Clymer (1970) used out-of-pocket development cost data on limited groups of NCFs. Clymer's estimates for the late 1960s, exclusive of the costs of unsuccessful products, range from \$2.5 to \$4.5 million. This may be compared to Schnee's estimate of \$0.5 million. If both estimates are correct, then R&D costs increased dramatically from the 1950s to the late 1960s.¹¹

Mund (1970) and Baily (1972) used annual U.S. industry R&D expenditures and NCF introductions to estimate average costs, and also found a substantial increase in costs over time. An advantage to using aggregate data is that estimates will be based on information from a large group of firms. A serious disadvantage, though, is that aggregate expenditures cannot be associated in any precise manner with particular NCFs.¹²

Figure 1 shows the time pattern between 1963 and 1989 of annual U.S. pharmaceutical industry R&D expenditures and U.S. NCF approvals. As this figure shows, NCF approvals have changed only moderately over time, while real dollar pharmaceutical outlays have increased several times over this 25 year period. Aggregate industry data are therefore strongly suggestive of sharp increases in R&D cost over time, and this upward trend seems to have intensified in the 1980s. There are a number of difficulties, however,

¹⁰This contrasts with subsequent FDA approval of additional indications, dosage strengths, dosage forms, and delivery systems for the new drug. Further testing is required to obtain approval for such changes in the drug's labelling.

¹¹Sarett's estimate for 1967 is also consistent with the Clymer range. A plausible hypothesis for explaining at least part of the large observed post 1962 change is that more extensive testing was required for approval following the implementation of the 1962 Amendments to the FD&C.

¹²Mund utilizes a simple 5-year fixed lag approach. Baily relates the average of aggregate R&D expenditures lagged 4 to 6 years to NCF introductions using a regression analysis framework. In computing the Baily cost estimates in table I, we employ actual values of his independent variables, as opposed to the 'steady state' equilibrium value used in his article. The former is more appropriate for comparative purposes.

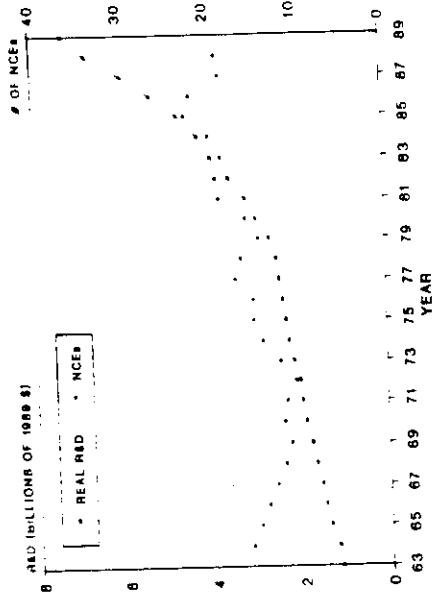


Fig. 1 Annual US pharmaceutical industry real R&D expenditures and US NCE approvals for the period 1963-1989. Expenditures are for PMA member firms and are indexed using the 1963 implicit price deflator. The NCE approval line is constructed from 3-year moving averages of annual approvals.

in using aggregate data to obtain precise estimates of R&D cost per approved NCE over particular subperiods. First, one must specify a lag structure between R&D inputs and output. This lag has been lengthening over time. Second, aggregate industry data cover compounds licensed from abroad, in addition to those that are U.S.-discovered. These two categories of drugs are likely to have vastly different R&D cost expenditure patterns within the United States.¹¹ For these reasons, R&D cost studies based on micro data at the individual project level are likely to produce much more accurate cost estimates.

The only prior R&D cost study that utilized multi-firm project level data for new drugs is Hansen (1979). Data were obtained from 14 firms on a large randomly selected group of NCEs first tested in humans during the period 1963 to 1975. Information was requested from surveyed firms on NCEs originated and developed by those firms. Time and cost data by development phase were gathered so that average phase lengths and costs could be computed. Costs of projects that were abandoned at some point in the clinical testing period were included and R&D was treated as an investment

¹¹For example, the aggregate industry R&D cost data available from the FDA do not include the R&D expenditures performed abroad for licensed compounds originating in foreign countries. As we show later in the paper, where aggregate data are employed as a check on our results, average U.S. R&D costs for foreign licensed compounds are estimated to be small compared to the self-originated NCEs of U.S. firms. Of course, license fees account for much of the difference in R&D costs, but they are not publicly available.

Table 1
Prior R&D cost studies

Author	Sample	Notes
Schnee	17 approved NCEs Single drug firm Successful NCEs	Discover costs and unsuccessful NCEs ignored; no capitalization
Sarret	Single drug firm	Discover costs and unsuccessful NCEs ignored; no capitalization
Clymer	New drug candidates Single drug firm	Discover costs ignored; no capitalization
Mund	Aggregate industry data on R&D and NCEs	Five-year lag assumed between R&D and new drug introductions; no capitalization
Baily	Aggregate industry data on R&D and NCEs	Fixed lag regression analysis approach; no capitalization
Hansen	Representative sample of drugs tested in humans, 1963-1975	Includes discovery and development costs capitalized to date of marketing introduction
Wiggins	Aggregate industry data on R&D and NCEs approved 1970-1985 (by therapeutic class)	Fixed lag regression analysis approach; also uses selective parameter estimates from Hansen
	(A) Partial cost studies	
	(B) Full cost studies	
	1.2 mil, 1962	Discover costs and unsuccessful NCEs ignored; no capitalization
	3.0 mil, 1967	Discover costs and unsuccessful NCEs ignored; no capitalization
	11.5 mil, 1972	Discover costs ignored; no capitalization
	10.5 mil, late 1960s	Discover costs ignored; no capitalization
	1.5 mil, 1950s	Five-year lag assumed between R&D and new drug introductions; no capitalization
	10-20 mil, 1960s	Fixed lag regression analysis approach; no capitalization
	2.3 mil, late 1950s	Fixed lag regression analysis approach; no capitalization
	21.8 mil, late 1960s	Fixed lag regression analysis approach; also uses selective parameter estimates from Hansen
	34 mil, 1976 dollars	Includes discovery and development costs capitalized to date of marketing introduction
	225 mil, 1986 dollars	Fixed lag regression analysis approach; also uses selective parameter estimates from Hansen

with returns delayed until marketing approval. Hansen's R&D cost estimate of \$54 million (in 1976 dollars) was larger than those of prior studies, but it was also more complete in the sense that it took account of discovery as well as development costs, the costs of failed projects, and the time value of funds invested in R&D.

The most recent drug R&D cost study is Wiggins (1987). It employs industry aggregates calculated at the therapeutic class level to compute an 'R&D production function'. Regression coefficient estimates are then used to infer an R&D cost value. This methodology is similar to that employed in Baily (1972). For NCEs approved during 1970-1985, Wiggins found an uncapitalized cost per NCE of \$65 million in 1986 dollars. Wiggins then used the time profile for new drug development estimated in Hansen (1979) to provide capitalized cost estimates. For his base case, Wiggins used Hansen's preferred discount rate of 8% to determine capitalized cost to be \$125 million in 1986 dollars. Woltman (1989), however, has pointed out that the Wiggins capitalized value should only be \$108 million, given a proper analysis of the time profile utilized in Hansen (1979).¹⁴

When compared to Hansen's results, the corrected estimates reveal a relatively small real cost increase. General price inflation accounts for 80% of the increase in estimates (\$54 million in 1976 dollars translates to \$97 million in 1986 dollars). However, the time periods considered in the two studies also do not differ very much. Wiggins used data that were meant to be relevant to 1970-1985 NCE approvals. Given his imposed lag structure, R&D expenditures included run from 1965 through 1982. Hansen's R&D expenditures run from 1963 to the mid-1970s, with expenditures more concentrated in the latter half of this period.¹⁵

Even for identical periods, however, results from these two types of studies may not be comparable. Wiggins employed data that are a mixture of both licensed and self-originated NCEs, and this is likely to produce a lower R&D cost estimate than from a sample consisting of only U.S. self-originated NCEs.¹⁶ In addition, Wiggins' (and Baily's) estimates, which are obtained from an R&D production function type analysis, are really marginal costs. They are estimates of the additional cost that would have been incurred if one more NCE had been approved during the sample

¹⁴Wiggins obtained capitalized costs. Wiggins multiplied his \$65 million uncapitalized cost estimate by the ratio of capitalized to uncapitalized costs in Hansen (1979). Uncapitalized costs per marketed NCE are not presented in Hansen (1979), but can be determined from other data therein. Wiggins claimed that this figure is \$28 million. The correct amount, however, is \$32.5 million. This changes the Wiggins base amount to \$108 million.

¹⁵Hansen's data are for a sample of NCEs first investigated in humans during 1963-1975. Some of the NCEs first investigated in the early part of this period had long development times with significant expenditures incurred late in the period.

¹⁶As noted in footnote 11, licensed compounds originating from foreign countries tend to have much lower U.S. costs than compounds originating in the U.S. from U.S.-owned firms.

period. Hansen's results, and those of the other studies listed in table 1, are average cost estimates. Unless constant returns to scale with respect to R&D effort exist at the industry level (at or near average expenditure levels for the sample period), marginal and average costs differ.

In summary, results from the studies discussed above suggest that new drug R&D costs have risen over time, at least relative to the pre-1962 Amendments period. However, only Hansen's study employs micro data, and none of the studies includes much data from the 1980s, a period during which real industry R&D expenditures have risen rapidly (fig. 1).¹⁷ This study, like Hansen's, employs project level data, and a significant amount of the data used was taken from this recent time period.

4. Estimating the average cost of new drug development

We use project level data to obtain an estimate of the clinical period average cost per NCE tested in humans. A majority of these NCEs will not be approved for marketing. Our approach uses an estimated clinical approval success rate to link the R&D costs of failed projects to the costs of those NCEs that obtain marketing approval. A representative time profile for an NCE progressing through all testing phases to the point of marketing approval is also estimated and used to capitalize R&D expenditures. Preclinical discovery and development costs are accounted for and treated in a more refined manner than was the case in Hansen (1979).

Since the full R&D costs for licensed or acquired NCEs are not typically reflected in R&D budgets of the firms that acquired them, we restricted our analysis to self-originated NCEs. The various steps we use to determine an estimate of the total cost per approved self-originated NCE (inclusive of unsuccessful efforts, preclinical expenditures, and the opportunity cost of funds invested) are formally described below.

4.1. Expected out of pocket costs

Let h be the clinical period development cost of a randomly selected NCE tested in humans. This can be decomposed into a sum of random variables. Specifically, $h = \lambda_1 I + \lambda_2 V_1 + \lambda_3 V_2 + \lambda_4 V_3$, where $\lambda_1, \lambda_2, \lambda_3$, and λ_4 represent the NCE's development costs for phases I, II, and III, respectively, and V_1 is its long-term annual testing cost. If the project was terminated prior to entering a phase, then the random variable for that phase assumes the value zero. The expected value of clinical period costs is then $E(h) = p_1 \lambda_1 I_1 + p_2 \lambda_2 V_2 + p_3 \lambda_3 I_3 +$

¹⁷Data from the PMA Annual Survey Report, 1987-1989, can be used to compute growth rates for real pharmaceutical R&D expenditures for different time periods. From 1963 to 1979 real R&D expenditures grew at a 5.7% compound annual rate; from 1980 to 1989 expenditures grew at a 10.7% compound annual rate.

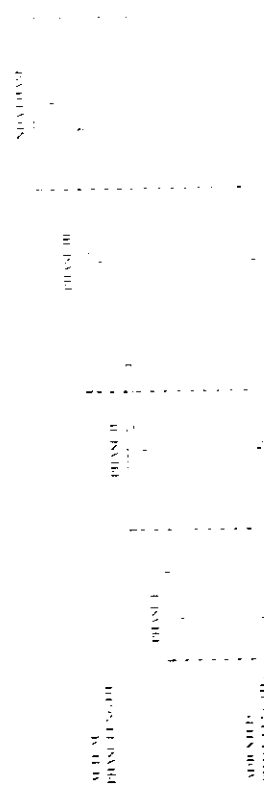


Fig. 2. Representative time profile for an NCE passing through all clinical development phases.

specific NCEs in a precise manner. Consequently, we use reported aggregate annual firm R&D expenditure data for the preclinical and clinical periods, and our previously estimated cost per approved NCE estimate, C_a , to derive P_a , the uncatalyzed preclinical cost per approved NCE. Specifically, we use aggregate data to estimate the ratio of preclinical period to total expenditures, λ . We then estimate P_a from the identity $\lambda = P_a / (C_a + P_a)$, or $P_a = \lambda / (1 - \lambda) C_a$. Estimated total uncatalyzed cost per approved NCE is given as $C_a + P_a$.

4.2. Expected capitalized costs

To include the opportunity cost of funds invested in NCE R&D for a full cost estimate, we capitalize the mean phase costs to the point of marketing approval using a representative time profile for an NCE: passing through all clinical period testing phases; use of a representative time profile yields a lower bound on costs. Weighted mean phase lengths, t_i , are calculated for our survey NCEs in the same manner as weighted mean phase costs.

It is generally not the case that a phase will begin exactly when the preceding phase ends. In many instances there is a significant overlap for successive phases. There can also be gaps between phases. To construct a time profile we reduce each calculated mean phase length by the weighted average overlap of that phase with the next (or add to the phase length for a gap).¹⁶ Figure 2 depicts a hypothetical time profile. The adjusted mean phase lengths, t_i , are used to determine where in the time profile phase costs begin. Hence, the time from the start of phase 1 to NDA approval, T , is given as $T = t_1 + \sum_{i=2}^n t_i$, where t_n is average NDA review time. We measure the time from the start of a phase to the expected approval date, T_i , as $T_i = \sum_{j=i}^n t_j$, with $t_0 = 0$.

Mean long-term annual testing time, t_A , is calculated in a manner identical

¹⁶gap or phase III the succeeding phase is the period during which the NDA is under review.

P_A/A_{1E} , where P_1 , P_{II} , and P_{III} are the probabilities that a randomly selected NCE tested in humans will enter phases I, II, and III, respectively. P_A is the probability that long-term animal testing will be done, and μ_{1E} , $\mu_{II E}$, $\mu_{III E}$, μ_{A1E} , and $\mu_{AII E}$ are conditional expectations. Specifically, μ_{1E} , $\mu_{II E}$, $\mu_{III E}$, and μ_{A1E} are the population mean costs for phases I, II, III, and long-term animal testing, respectively, for those NCEs that enter the respective phase.

The proportion of NCEs tested in humans that are taken through the various clinical period testing phases diminishes with each successive phase. As will be shown below, only a small minority undergo all testing phases. Thus, a simple random sample of this population will likely contain a good deal of information about NCEs that do not last very long in testing and little information about NCEs that reach the point of NDA submission or approval. Furthermore, we expect phase costs to be more variable for later testing phases. The later clinical trials are larger, last longer, and should be more subject to variability in size and duration depending on the type of drug tested and the condition it is meant to treat.

Therefore, to reduce overall sampling error, we grouped NCEs into strata according to the time spent in active testing if research was abandoned, whether research was still in progress, and whether an NDA had been submitted or approved. Successful NCEs were deliberately oversampled and unsuccessful NCEs lasting only a short time in active testing were under-sampled. The sample percentage distribution for the strata was specified before sample selection. In preparing our estimates, we reweighted the responses to replicate the population.

The population from which our sample was selected consisted of a subset of the investigational NCEs contained in a Center for the Study of Drug Development (CSDD) database. The proportions of population NCEs that fall in our strata can be determined from information in this database. Thus, we were able to define a set of weights to be applied to the sample data that transform the sample from one that is unrepresentative with respect to the strata to one that is perfectly representative. Mean phase cost (in constant dollars), γ_i , and the probability that an NCE tested in humans will enter a phase, γ_i , can then be estimated from the weighted sample (see appendices A and B for computational details). The expected clinical period cost per new drug tested in humans can be expressed as $\bar{E} = \sum_{i=1}^n \gamma_i t_i + \sum_{i=1}^n \gamma_i \gamma_i t_i$.

To estimate the expected cost per approved drug, C_a , one needs to multiply \bar{E} by the ratio of the number of drugs taken into humans, n_1 , to the number approved, n_2 (i.e., $C_a = \bar{E}(n_1/n_2)$). Alternatively, C_a can be expressed as \bar{E}_s/s , where s is the successful rate for NCEs tested in humans (the ratio of NCEs for the survey firms can be used to estimate s).

The final step in estimating R&D costs is to incorporate preclinical expenditures. Firms are generally not able to allocate all preclinical costs to

to that used for the actual mean durations of the clinical trial phases. The length of this phase, however, is not adjusted for an overlap (or gap) with other phases. We need to determine, though, how this testing fits into our representative time profile. The weighted mean time from the start of phase I to the start of long-term animal testing, t_{IA} , can be calculated. We then consider long-term animal testing costs to begin t_{IA} units of time after the start of phase I.

Phase costs are assumed to be distributed uniformly over actual mean phase lengths and capitalized at the discount rate r . Specifically, capitalized mean phase costs, c_j , are determined as follows, where the index values 1, 2, and 3 refer to phases I, II, and III, respectively:

$$c_j = \int_{t_{j-1}}^{t_j} (c_j / t_j) e^{-rt} dt \quad \text{for } j = 1, 2, 3. \quad (1)$$

Capitalized long-term animal testing costs, c_A , can be found in a similar fashion.¹⁹

An estimate of expected capitalized clinical period cost per NCF (tested in humans, \bar{c}) can be obtained as $\bar{c} = \sum_{i=1}^n P_i c_i / \sum_{i=1}^n P_i c_i \bar{c}_i$. Transforming this into a cost per marketed NCF, C_A , requires only the approval success rate. In particular, we have $C_A = \bar{c} / \bar{c}_A$.

Eq. (1) implies continuous compounding. The discount rate estimates we use are based on discrete compounding. It is possible, though, to find a continuous rate, r , that is equivalent to any discrete rate (with regard to monetary value after the same amount of time).²⁰

Preclinical costs can be capitalized to the point of marketing approval in the same way that phase costs are in eq. (1). The average duration of the preclinical period, t_{PC} , can be estimated using data on preclinical development times from a CSDD database on approved NCFs. Capitalized preclinical cost per approved NCF, P_A , can then be given as

$$P_A = \int_0^{t_{PC}} (P_A / t_{PC}) e^{-rt} dt. \quad (2)$$

4.3. Cost of capital for pharmaceutical R&D

In selecting a baseline cost of capital for this analysis, we sought a

¹⁹Specifically, capitalized long-term animal testing costs can be computed as

$$c_A = \int_0^{t_A} (c_A / t_A) e^{-rt} dt, \quad \text{where } t_A = t_{IA} \text{ and } t_A' = t_A' - t_{IA}$$

²⁰For example, if the relevant discrete rate is 10%, we use $r = 0.095$.

representative value for the pharmaceutical industry over the period spanned by the development of the drugs in our study. Our sample includes NCFs first tested in humans between 1970 and 1982. The marketing approval dates for this sample centers around the mid 1980s, with a few compounds still in active research. Hence, we want a cost of capital measure that essentially covers the period between 1975 and 1985 where the bulk of the expenditures are concentrated.

Our baseline analysis employs a 9% real cost of capital. This value is based on a recent study on R&D returns [Grabowski and Vernon (1990)]. The study applied the capital asset pricing model (CAPM) to a portfolio for a representative sample of pharmaceutical firms for each of the years from the mid 1970s to the mid 1980s. Over this period, the equity cost of capital for this representative group of firms clusters around 9%.²¹ The capital structure of the pharmaceutical industry is overwhelmingly equity financed (in excess of 90%). Hence, their estimated 9% cost of equity capital offers a good proxy for the overall cost of capital.²²

Hansen (1979) utilized an 8% cost of capital. That study focused on an earlier time period (i.e. R&D expenditures in the 1960s and 1970s). Although the 8% value was not based explicitly on a CAPM analysis, it is generally consistent with the values emerging from analyses for the relevant period of that study [see, e.g., Statman (1983)]. The slightly higher cost of capital utilized in the present study essentially reflects the trend toward higher real interest rates during the past decade [Feldstein (1988)]. Although a 9% real cost of capital measure is employed as our preferred estimate in the baseline analysis, we also perform sensitivity analysis using values significantly above and below this value.²³

5. Data

Twelve U.S.-owned pharmaceutical firms agreed to participate in their self study and provide, on a confidential basis, information on their self

²¹An analysis of investment riskiness for this portfolio of pharmaceutical firms was undertaken and indicated that pharmaceutical firms generally had comparable riskiness to the market over the period (i.e. betas approximately equal to one). Long term estimates on risk free rates and market rates were obtained from Ibbotson Associates [Grabowski and Vernon (1990) p. 806].

²²One can compute a weighted cost of capital taking account of how much debt relative to equity is held by pharmaceutical firms, as well as the tax deductibility of debt compared to equity [see Statman (1983)]. Since the percentage of capital held in the form of debt is minimal over this period, this does not change the computed 9% value in an appreciable manner.

²³An alternative approach for estimating the cost of capital would be to utilize the arbitrage pricing model (APM). Some preliminary analysis applying the APM to the pharmaceutical industry by one of the authors suggests higher values for the cost of capital than that obtained from the CAPM. The hurdle rates employed by pharmaceutical firms also tend to suggest somewhat higher values for the cost of capital [Grabowski and Vernon (1990)].

originated NCE development activities (a copy of the questionnaire is available upon request).²⁴ These firms include a number of the largest in the U.S. pharmaceutical industry, as well as some that are small in size. From 1980 to 1986, these firms accounted for approximately 40% of U.S. industry R&D expenditures on ethical pharmaceuticals.²⁵

We limited our study to self-originated NCEs since the full research and development expenditures for licensed and acquired NCEs would not be reflected in the acquiring firm's R&D accounts. The NCEs included in the study were first tested in humans during the period 1970-1982. Most of the NCEs from this period that eventually emerge as approved drugs will have entered the market in the 1980s or early 1990s. We did not extend the sample past 1982 since many of the later NCEs would still be in early testing at the time of the survey.

To construct a representative sample of NCEs tested during this period we used information from a CSDD database on investigational NCEs. This database, obtained from a triennial survey of the U.S. pharmaceutical industry,²⁶ provided us with information on the origin, therapeutic area, and development status of NCEs first tested in humans during the period 1970-1982. This information allowed us to identify the survey firm NCEs that met our study inclusion criteria (i.e. self-originated NCEs first tested in humans during the period 1970-1982), and to select a random sample of survey firm NCEs.²⁷ Detailed information was requested from each firm for the NCEs that we selected.

The firms provided data on 93 NCEs, or 19% of all NCEs in the CSDD database that met inclusion criteria. The NCE therapeutic class distributions for the sample and population are nearly identical. For the NCEs selected, firms provided clinical period phase beginning and ending dates, costs by year of clinical testing, and the date testing was suspended on those NCEs for which research was abandoned.

Aggregate pharmaceutical R&D expenditure data for the years 1970-1986 were also provided by the survey firms. The firms reported total annual pharmaceutical R&D expenditures broken down into expenditures on self-originated NCEs, on licensed or otherwise acquired compounds, and on existing approved products. For firms as a whole during the period 1970-

²⁴A number of these firms had several major pharmaceutical divisions. Counting these as separate units, data were obtained from 15 divisions.

²⁵One of the survey firms was not able to break out pharmaceutical R&D from total R&D expenditures for the 1970s. The industry level is the aggregate of PMA member firm real pharmaceutical R&D expenditures over the period 1980-1986 (computed from data in PMA Annual Survey Report, 1987-1989).

²⁶At the time the sample was selected, 43 firms were included in the database, 34 of them U.S.-owned.

²⁷The eligible NCEs were first stratified as described in section 4, and a random sample was selected from each strata.

Table 2

Average out-of-pocket clinical period costs for NCEs tested in humans (in thousands of 1987 dollars).^a

Testing phase	Mean cost	Standard deviation of phase costs	Median cost	N ^b	Probability of entering phase (%)	Expected cost
Phase I	2,134	4,519	960	87	100.0	2,134
Phase II	1,954	5,230	2,175	70	75.0	2,966
Phase III	12,801	13,974	7,888	46	36.2	4,634
Long term animal	2,155	2,411	1,336	49	56.1	1,209
Other animal	618	1,183	139	15	15.8	102
Total						11,015

^aAll costs were deflated using the GNP Implicit Price Deflator. Weighted values were used in calculating means, standard deviations, medians, and the probability of entering a phase.

^bN = number of NCEs with full cost data for the phase.

1986, 73.7%, 16.3%, and 10.0%, of total pharmaceutical R&D expenditures were spent on self-originated NCEs, existing approved products, and licensed and acquired compounds, respectively. Annual total expenditures for self-originated NCE R&D were further broken down according to whether they were incurred during the preclinical or clinical periods (since firms are generally unable to allocate all preclinical costs to individual NCEs, data were not obtained on preclinical expenditures for specific NCEs).

The firms did not provide full phase cost data for every NCE that entered a given phase, either because that phase was ongoing on the survey date or records were incomplete. Costs were not included in computations if the phase was ongoing or cost data were missing. Only nine NCEs were continuing in research on the survey date, and for each of them complete information is available for some phases.

6. Baseline cost estimates

6.1 Clinical cost per investigational NCE

Using the weighting procedure described in section 4, mean phase costs were calculated and are presented in table 2. All costs were deflated using the GNP Implicit Price Deflator and are given in 1987 dollars.²⁸ Since a

²⁸The GNP Implicit Price Deflator measures changes in the prices of the nation's output. Ideally, we would want to use an index based on pharmaceutical R&D input prices. No such index, however, exists. Other indices which we considered were judged to be less appropriate than the GNP Implicit Price Deflator. The Producer Price Index is determined solely by manufacturing output prices. Mansfield (1987) develops an R&D input price index applicable to a number of industries for the years 1969-1983. The closest match to the pharmaceutical industry is the chemicals and of category. Only a few pharmaceutical firms, however, were

number of firms reported clinical period animal testing other than the long-term animal tests, we reported their costs as other animal costs. On average, however, they constitute a very small portion of total costs.

The phase to phase attrition rates in column 6 of table 2 are roughly consistent with alternative estimates in an FDA study [Tucker et al. (1988)]. That study used FDA records to follow the progress of the new molecular entities (NMEs)²⁹ for which INDs were filed during the years 1976-1978. Based on their records and a mathematical model to project future outcomes, they found 70% of the NMEs entering phase II and 33% entering phase III.

Average costs vary substantially by clinical development phase. Phase II costs are nearly twice as large as phase I costs. The large-scale clinical trial costs of phase III are about six times as large as phase I costs. These are averages, however, and the third column of table 2 reveals substantial variation in individual NCE testing costs for each phase. The phase cost distributions are also positively skewed, as indicated by the differences between mean and median costs.

Since there is substantial attrition of NCEs prior to the more expensive phases II and III, expected phase costs rise less steeply than mean costs. For example, expected phase III costs are only slightly more than twice as large as expected phase I costs. Our estimate of the expected clinical period cost for NCEs tested in humans is \$11.0 million in 1987 dollars.

6.2. Capitalized clinical cost per investigational NCE

To calculate the capitalized value of clinical period expenditures, we computed adjusted phase lengths and constructed a representative develop-

²⁸footnote 28 continued

included in the sample. We deemed the chemicals and oil index too broad based to use extrapolation of the index through 1987 would also have been necessary. We also considered an index developed for biomedical R&D [U.S. Bureau of Economic Analysis (1986)], but judged it to be too dependent on the university research sector. However, we did apply alternative price indices to our cost data and found the following to be the case in general: The Producer Price Index resulted in overall cost estimates that were roughly 10% lower than those obtained with the GNP Deflator. We regressed Mansfield's chemicals and oil index on the GNP Deflator to obtain predicted Mansfield index values for 1983-1987. Applying the expanded Mansfield index resulted in overall costs that were approximately 10% higher than the GNP Deflator estimates. Use of the biomedical R&D index resulted in about a 10% increase in costs relative to those for the Mansfield index.

²⁹The FDA definition of an NME differs somewhat from our definition of an NCE. One difference is that the FDA includes diagnostic agents and we do not. Another difference is that we include a few therapeutically significant biologics, whereas the FDA does not include any. Aside from the fact that we study a longer time period, an additional reason why the FDA study results are not precisely comparable to ours is that their drugs include some that were licensed or acquired. Presumably these drugs were prescribed to some extent, and so we might expect them to have success rates higher than those for self-originated new drugs. The impact of the other differences, however, is unclear.

Table 3

Average phase lengths and clinical period capitalized costs for NCEs tested in humans (in thousands of 1987 dollars)^a

Testing phase	Mean phase length (months) ^b	Mean phase length (adjusted) ^b	Time from phase start to approval ^c	Capitalized mean phase cost ^d	Capitalized expected phase cost
Phase I	15.5	16.2	98.9	4.103	4.103
Phase II	24.3	22.5	82.7	6.564	4.924
Phase III	36.0	29.9	60.2	17.370	6.283
Long-term animal	33.6	33.6	78.7	3.366	1.889
Other animal	33.6	33.6	78.7	3.012	1.89
Total					13.63

^aAll costs were deflated using GNP Implicit Price Deflator

^bMean phase lengths and the time from the beginning of a phase to NDA approval are given in months. Weighted values were used in calculating mean phase lengths.

^cThe NDA review period was estimated to last 3 months. Animal testing was estimated to start 4.0 months into phase II.

^dCosts were capitalized at a 9% discount rate.

ment time profile as described in section 4.2. The actual and adjusted phase lengths presented in table 3 indicate, on average, a very small gap (0.7 months) between the end of phase I and the beginning of phase II, and an overlap of phase III with both phase II (1.8 months) and the NDA review phase (6.1 months). The mean NDA review time for self-originated NCEs first tested in humans during 1970-1982 by U.S.-owned firms (30.3 months) was determined from a CSDD database. Long-term animal testing began, on average, 20.2 months after phase I testing commenced.³⁰ Our estimated time profile has a length of 98.9 months from the initiation of clinical testing to NDA approval. The time from the start of phase I testing to NDA submission is 68.6 months.

The expected capitalized cost per NCE tested in humans for the entire clinical period is \$17.3 million in 1987 dollars. Of that amount, 36% is accounted for by interest costs.

6.3. Clinical costs per approved NCE

To relate costs to the number of approved NCEs, we need a clinical period approval success rate estimate. While phase success rates could only be obtained from information in our cost survey, approval success rate estimates can be obtained using a broader sample contained in CSDD databases on investigational and approved NCEs. Our methodology for estimating the

³⁰Other animal testing sometimes occurred before long-term animal testing, sometimes after it and at still other times both before and after it. No tendency in relation to the timing of long-term animal testing was apparent. As an approximation, then, we distributed other animal costs over the long-term animal testing period.

approval success rate is similar to that used in Sheek et al. (1984) and is described in appendix B. Evidence that the predictive power of our model is quite high is presented in the appendix.

The base clinical success rate for the cost survey firms (23%) is utilized to determine clinical cost per approved NCF from our prior estimates of clinical cost per investigational NCF presented in tables 2 and 3. In particular, dividing our prior cost estimates by the success rate of 23% yields estimates of clinical costs per approved NCF. Utilizing a 9% discount rate, the capitalized clinical cost per approved NCF is estimated to be \$75 million, while the uncanceled cost per approved NCF is \$48 million. This contrasts with estimates of \$17.3 and \$11 million for capitalized and uncanceled cost per investigational NCF, respectively.

6.4. Preclinical costs

In the preceding sections we reported expected clinical period development costs calculated from project specific data. Many costs incurred during the preclinical period cannot be directly assigned to specific NCFs. Moreover, some specific development projects are abandoned prior to reaching the clinical stage. The activities in the preclinical period are essential to the eventual development of NCFs and the expenditures during this period should be allocated to approved NCFs to determine the total cost of developing a new pharmaceutical.

The activities during the preclinical period lead to a flow of NCFs into clinical testing. As described in section 4.1, we use the ratio of uncanceled preclinical to clinical expenditures and our estimate of the uncanceled preclinical period cost per approved NCF to allocate preclinical costs to approved NCFs. In order to estimate λ , the preclinical period portion of total R&D costs, we need to confine our analysis to those expenditures that involve self-originated NCFs. Therefore, in our survey we requested annual expenditures on self-originated NCF R&D by preclinical and clinical periods for each of the survey firms for the years 1970-1986.

In the aggregate, 66.1% of total self-originated NCF R&D was spent during the preclinical period. Both the preclinical and clinical expenditure series, however, tend to increase in real terms over the survey period. Since clinical period expenditures lag behind preclinical costs, the ratio of preclinical period real R&D expenditures to total real R&D expenditures overestimates the true preclinical period contribution to the total. A lag structure for the aggregate data, based on average lengths of the preclinical and clinical periods, can be imposed to better estimate λ .

The mean length of the preclinical period for self-originated NCFs of US-owned firms first tested in humans during 1970-1982 was estimated from data in a CSDD database on approved NCFs to be 42.6 months. Our

Table 4

Expected phase costs per marketed NCF (in millions of 1987 dollars)^a

Testing phase ^b	Uncapitalized expected cost	Mean phase length (actual)	Capitalized expected cost
Preclinical	65.5	42.6	155.6
Phase I	9.3	15.5	17.8
Phase II	12.9	24.3	21.4
Phase III	20.2	36.0	27.1
Long-term annual	5.3	33.6	8.2
Other annual	0.4	33.6	0.7
Total	113.6		230.8

^aAll costs were deflated using the GNP Implicit Price Deflator. A 2% clinical approval success rate was utilized.

^bThe NDA review period was estimated to last 40 months. Annual testing was estimated to start 4.0 months into phase II.

^cCosts were capitalized at a 9% discount rate.

representative time profile suggests a clinical period duration (inclusive of phase III testing after NDA submission) of 74.7 months. We approximate the lag between preclinical and clinical period aggregate expenditures by computing the time between the midpoint of the preclinical period to the midpoint of the clinical period.¹¹ Thus, our base case lag is 5 years and the corresponding value of λ is 0.577. Hence, our previously estimated uncanceled clinical cost is multiplied by a factor of 1.36 to obtain an estimate of uncanceled preclinical cost ($P_n \{ \lambda (1 - \lambda) C_n \}$).

Using the 5 year lag, uncanceled and capitalized preclinical costs are \$66 and \$156 million, respectively. For lags of 4 and 6 years (adjusting at the same time the assumed duration of the preclinical period), the uncanceled costs are \$69 and \$63 million and the capitalized costs are \$152 and \$166 million, respectively. Thus, our preclinical cost estimates are not very sensitive to reasonable variation in the lag.

6.5. Total expected cost per approved NCF

Given the preferred 5 year lag, discount rate of 9% and clinical success rate of 23%, total capitalized cost per approved NCF is shown in table 4 as \$230.8 million. Preclinical research activities, because they occur much earlier in time, entail significantly greater interest costs than do clinical activities. In particular, interest costs represent 58% of preclinical costs (\$90 million of

¹¹Survey data on phase costs were provided by year of clinical testing. Computing costs by year from the start of phase I testing revealed that the midway point of the clinical period (37.35 months) corresponds roughly to the time of maximum expected cost per NCF tested in humans.

Table 5

Preclinical, clinical, and total capitalized expected costs per marketed NCE, at alternative approval success rates and discount rates (in millions of 1987 dollars)^a

	Capitalized costs				
	0%,	5%,	8%,	9%,	10%, 15%
(A) Success rate: 25%					
Preclinical	61	98	131	144	156
Clinical	44	57	66	69	73
Total	105	155	197	213	229
(B) Success rate: 23%					
Preclinical	66	107	142	156	170
Clinical	48	62	72	75	79
Total	114	169	214	231	249
(C) Success rate: 20%					
Preclinical	76	123	163	179	196
Clinical	55	71	83	86	91
Total	132	194	246	265	287

^aAll costs were deflated using the GNP Implicit Price Deflator (clinical period expenditures were assumed to represent 42% of total R&D expenditures). The corresponding assumed preclinical phase length is 42.6 months.

\$156 million), whereas they represent only 36% of clinical costs (\$37 million of \$75 million).

Table 5 allows us to examine how sensitive our estimate of total R&D cost per approved NCE is to variations in two key parameters—the clinical success rate and the discount rate. If we take as plausible ranges on these parameters a discount rate of 8 to 10% and a clinical success rate of 20 to 25%, the corresponding range in R&D cost per approved NCE is between \$197 and \$287 million. This provides some bounds around our estimate of \$231 million per approved NCE by allowing for uncertainty in the values of these important parameters.

6.6. Comparison with Hansen's analysis

It is interesting to compare our base case average cost estimates with the preferred estimates in Hansen (1979), and measure the contribution to the apparent increase in costs of changes in several factors. In 1987 dollars Hansen's total capitalized cost estimate is \$100.5 million, while his clinical period capitalized cost estimate is \$39.2 million. Thus, in real terms, total capitalized costs are about 2.3 times larger here than in Hansen; clinical

period capitalized costs are about 1.9 times larger. Assuming both sets of estimates are correct for their respective covered time periods, we can examine how much of the cost increases are due to differences in a given determinant of cost, holding all other determinants fixed.

Ignoring second-order interaction effects we may state the following. Table 5 reveals that the higher opportunity cost of capital used here (9%, as opposed to 8%) results in an increase in cost amounting to 13.0% of the measured increase in total cost between the two studies.

R&D and regulatory review times are somewhat longer here. Our results show essentially no difference in phase II duration, but there is a 7.1 month increase in phase I duration and a 7.3 month increase for phase III. Regulatory review time and the preclinical period are 6.3 and 6.6 months longer here, respectively. Our longer development and regulatory review times result in total cost increases amounting to 23.9% of the measured increase in total costs.

The effects on total costs of changes in the discount rate and phase development times, taken together, constitute the change in time costs between the two studies. The residual proportion of the measured increase in total costs (63.1%) can be viewed as that part of the change in measured total costs that is due to changes in out-of-pocket costs. Out-of-pocket costs are dependent on the clinical approval success rate, the probabilities of entering the various phases, and the mean uncapitalized phase costs.

Mean uncapitalized preclinical period and clinical phase costs are substantially higher here and account for the bulk of the increase in out-of-pocket costs. In constant dollars, phases I, II, and III mean uncapitalized costs are 3.9, 1.4, and 2.5 times larger here than in the Hansen study. Similarly, long-term animal and preclinical costs are 1.6 and 3.7 times larger here, respectively. The phase-to-phase success rates estimated here are higher than those reported by Hansen,³ but their cost increase effect is more than offset by the cost reducing effect of a higher clinical approval success rate.

6.7. Reductions in development and review times

Since our estimates of the full cost of developing a new pharmaceutical include an implicit interest charge, changes in the timing of expenditures will affect the full cost. Firms may be able to shorten development times by doing parallel, rather than sequential, studies. Clinical trial phase lengths may also

³ Fewer drugs are screened out in phases I and II here relative to the earlier study. The probability of reaching phases II and III are 25% and 36% in this study and 50% and 19% in the Hansen study, respectively. The probability of approval conditional on reaching phase II has increased from 25% to 31%, but the approval probability conditional on entering phase III has remained virtually unchanged (65% previously vs. 64.5% currently).

Table 6

Impact on capitalized expected costs per marketed NCI of one-year reductions in average phase lengths (in millions of 1987 dollars).^a

One-year reduction	Total capitalized expected cost ^b	Reduction in total cost
Preclinical	224	8
Phase I	218	13
Phase II	245	16
Phase III	213	18
NDA review	212	19

^aAll costs were deflated using the GNP Implicit Price Deflator A 2%: clinical approval success rate was utilized.

^bCosts were capitalized at a 9% discount rate.

be shortened if the conferences now held between the FDA and sponsor firms during the development period provide firms with a better understanding of what will be necessary for approval. Reductions in the average length of the NDA review phase would shorten the time between R&D expenditures and marketing approval and so lower total costs.

In table 6 we present estimates of the effects of a 1-year reduction in phase duration (holding mean phase costs constant). The largest cost reduction (\$19 million or 8.2% of total cost) is for a 1-year reduction in the NDA review phase. The reason the NDA phase carries the greatest impact is that a reduction in any phase length decreases the capitalized cost for that phase and for all prior phases.

Since preclinical costs are a large portion of the total cost, even a 1-year reduction in phase I produces savings of \$13.5 million per approved NCI. Approval rates during the 1980s have averaged 19 per year. Thus, our results suggest that 1-year reductions in the clinical development or regulatory review phases would, holding all else constant, produce annual savings of \$257 to \$361 million in 1987 dollars.¹³

The activities required to shorten development times may require additional out-of-pocket costs. For example, doing studies in parallel may result in performing tests that would not have been performed had the results of the other tests been known. Shortening the NDA review period may require additional resources for the FDA. The cost of achieving a reduction in development times must be compared to the estimated savings in implicit interest costs. Within a broader context, one should also consider the effects on product lifetimes and associated sales revenues from having earlier marketing dates, and the benefits to society from having effective medications available for patient use sooner.

¹³It is worth noting that the entire FDA budget for fiscal year 1988 was \$478 million, with \$169 million spent on salaries and expenses for the human drugs and biologics divisions [U.S. Department of Health and Human Services (1990)].

7. Cost estimates for subsamples

7.1. Within sample period effects

We examined whether it is possible to discern time trends in our data. The sample did not contain enough information to investigate costs on a year-to-year basis, so we divided the sample into two time periods (NCIs first tested in humans during the periods 1970-1976 and 1977-1982). The distribution of population NCIs over the strata used in the weighting scheme for the full sample differed by period. Consequently, we reweighted NCIs for each period according to the sample and population strata proportions for that period.

Mean phase III development time and cost are significantly lower for the more recent period, but these data are not complete. In particular, NCIs with long development times will be underrepresented in the late period. At this point, meaningful comparisons across periods of phase III costs cannot be undertaken. However, counting only phase I and phase II costs, the 1977-1982 period uncaptialized costs are 100.5% higher than those for the 1970-1976 period. This suggests a strong upward time trend in out-of-pocket clinical costs.

7.2. Clinical period costs for approved NCIs

The cost of development may differ between successful and unsuccessful projects. To investigate this, we examined costs for the approved NCIs in our sample. We had complete cost data on 22 of the 27 NCIs that had obtained marketing approval as of October 31, 1990. One of the 22 NCIs is an extreme outlier with respect to cost and was removed from the approved NCI subsample.¹⁴ It was retained for the full sample results. Given the much larger sample size and the small weight this NCI received in the weighting scheme used for the full sample, its impact on the full sample results is minor.

Table 7 offers a comparison between mean phase costs and lengths for the approved NCIs and those for all sample NCIs. Development times are very similar. However, except for early clinical testing (phase I), phase costs are significantly higher for the approved NCIs. This may reflect a tendency to direct more resources, perhaps through conducting more studies concurrently, to the NCIs that early clinical testing suggests have the greatest promise of approval. Table 7 also shows that, as is the case for the full

¹⁴Both the uncaptialized and capitalized clinical costs of the outlier are roughly double those of the approved NCI with the next highest clinical costs.

Table 7

Clinical period average phase costs and phase lengths for approved NCEs, and for all sample NCEs (in thousands of 1987 dollars)*

Testing phase	Approved NCEs ^b				Full sample ^c			
	Mean phase cost	Standard deviation of phase costs	Mean phase length (actual)	Mean phase cost	Standard deviation of phase costs	Mean phase length (actual)	Mean phase cost	Standard deviation of phase costs
Phase I	2,475	2,957	140	2,134	4,519	155		
Phase II	5,629	4,138	259	3,954	5,270	243		
Phase III	30,023	14,016	368	12,801	13,974	360		
Long-term annual	3,646	3,065	374	2,155	2,411	336		
Other annual	1,777	2,200	374	648	1,183	336		

*All costs were deflated using the GNP Implicit Price Deflator.

^bEstimates for approved NCEs are based on data for 21 of the 93 sample NCEs.

^cWeighted values were used in calculating means and standard deviations for the full sample estimates.

sample, substantial variation exists in the costs of individual approved drugs for each phase.

The uncapitalized mean clinical period cost for the approved NCEs is \$31.9 million; the median cost is \$31.0 million. The 95% confidence interval for mean out-of-pocket clinical period cost is \$31.9 ± 7.7 million.³⁵ Since we have approval dates for these drugs, it was not necessary to use a representative time profile; costs were capitalized to the point of actual marketing approval. Mean capitalized clinical period cost for approved NCEs is \$43.0 million; median capitalized cost is \$40.9 million. The 95% confidence interval is \$43.0 ± 11.3 million.^{36, 37}

The FDA rates new drugs according to whether the drug represents an important therapeutic gain (A), a moderate therapeutic gain (B), or little or no therapeutic gain (C) over existing therapy. To get a sense for whether the cost of developing NCEs is related to their therapeutic importance, we

³⁵A chi-squared goodness-of-fit test was used to compare the sample frequency distribution of uncapitalized clinical period costs to a normal probability distribution. The hypothesis of no difference in distributions could not be rejected. Hence, we used a *t* distribution in constructing the confidence interval.

³⁶As is the case with uncapitalized costs, the hypothesis that the capitalized costs were taken from a normal population cannot be rejected.

³⁷Given the right-censored nature of the data, approved NCEs with very long development times may be somewhat under-represented in the sample. We found a moderate positive correlation between capitalized clinical period cost and the time from the start of clinical testing to NDA approval (Spearman rank correlation coefficient: 0.666). Thus, reported costs for the approved NCEs may be somewhat biased downward.

computed costs for approved NCEs according to their therapeutic ratings.³⁸ Mean and median capitalized clinical period costs for the A and B rated approved NCEs are \$51.7 and \$41.5 million, respectively.³⁹ Costs for the C rated approved NCEs are somewhat lower—mean and median capitalized clinical period costs are \$36.5 and \$36.2 million, respectively.

8. An external check on the results

As an external check on our results, we analyzed the R&D performance of the U.S. pharmaceutical industry to see if it was consistent with our analysis. In particular, our approach is to relate industry R&D expenditures to the NCF introductions of U.S. firms (see fig. 1) using the same lag structure and time period in our study. However, since our study focuses on the self-originated NCEs of U.S.-owned firms, it is necessary to make various transformations of the publicly available industry data before meaningful comparisons can be undertaken.

For the cost survey firms, we determined the proportions of their aggregate pharmaceutical R&D expenditures that were spent on self-originated NCEs (73.7%) and on licensed or acquired NCEs (100%). Published PMA industry R&D expenditure data, however, do not distinguish between what firms spend on self-originated NCEs and what they spend on licensed or acquired NCEs. The procedures we employ to estimate annual industry self-originated NCF R&D expenditures and how they can be related to annual NCF approvals are described in appendix C.

We averaged both lagged R&D expenditures and the number of approvals over the period 1979–1989.⁴⁰ Using an average of 7.3 industry self-originated approvals per year for this time frame, we found uncanceled and capitalized cost estimates of \$138 and \$270 million, respectively. In 1983 there was only one approval of a self-originated NCF from a U.S.-owned firm. Excluding this outlier year yields 7.9 as an average annual number of

³⁸Although the FDA gives an initial rating to investigational NCEs shortly after IND filing we have information only on the final ratings for the approved NCEs in our sample. The FDA rating system must be viewed with caution when considered as a measure of therapeutic benefit since the FDA has rather limited information when it assigns the ratings. The ultimate clinical significance of some drugs may not become apparent until the drugs have been in widespread use for a number of years for the original approved indications, or until their effectiveness for additional indications has been noted in clinical practice.

³⁹The A and B rated drugs were combined since there is only one A rated drug in the subsample of the remaining 20 approved NCEs, eight are B rated and 12 are C rated.

⁴⁰Year-to-year cost estimates using aggregate data are highly variable because they are extremely sensitive to the denominator (number of self-originated NCF approvals) used for the calculations. Thus, to reduce variability in the estimate, we used average values for the numerator and denominator, as opposed to an average of the annual ratios of lagged expenditures to current approvals.

approvals, and reduces the uncatalyzed and capitalized cost estimates to \$127 and \$250 million, respectively. Hence, our estimate of \$231 million is comparable to what one obtains from a comprehensive aggregate analysis.

9. Conclusions and prospects for future research

We have estimated the average cost of new drug development from a large sample of self-originated NCEs that were first tested in humans during 1970-1982. Data were obtained from a confidential survey of 12 U.S.-owned firms. The average cost of NCE development was estimated to be \$231 million in 1987 dollars (with \$114 million of that paid out-of-pocket). A representative time profile for an NCE, passing through all phases of development from synthesis to marketing approval extended nearly 12 years.

Cost estimates are substantially higher here than in previous studies; some of which, however, did not measure R&D cost fully or adequately. Our period of analysis is also more recent than the periods used for these other analyses. In particular, this study is the only one to date that has reflected its estimates much of the sharp increase in pharmaceutical R&D expenditures that occurred during the 1980s.

The most recent study on the cost of new drug development [Wiggins (1987)] used R&D expenditure data that covered the period 1965-1982, but with full weight placed only on expenditures from 1967 to 1980. This can partially explain why costs in that study are much lower than those found here. Another, perhaps more important, reason is that Wiggins used expenditure and approval data for all NCE approvals. In particular, he did not differentiate between self-originated and licensed or acquired NCEs. The R&D expenditures incurred on new drugs up to the point of licensing or sale will not be included in U.S. industry (PMA) data if the drug originated from an overseas operation of a foreign firm. Our analysis of industry data revealed substantially lower company expenditures per new drug on licensed or acquired NCEs than is the case for self-originated NCEs.

When results here are compared to those of a previous study [Hansen (1979)] with a similar methodology, total cost is seen to have increased 2.3 times in real terms. Development times are longer and a higher discount rate is used. The bulk of the increase in cost per approved NCE, however, can be attributed to large increases in out-of-pocket costs.

That clinical trial costs have risen sharply in recent years is attested to in F. D. C. Reports: The Pink Sheet (1989), where an executive of a major pharmaceutical firm reports that the information required to support NDAs has increased dramatically. Clinical trials for one of the firm's anti-infective NCEs approved in 1979 used 1,493 patients; the trials for a related anti-infective that the firm is currently developing will require testing on 10,000

patients. Also mentioned as factors leading to rising costs are the complexity and scope of the research required and the adoption of expensive new technologies. Another factor often suggested to explain increased costs is that firms are now focusing development more on treatments for chronic and degenerative diseases, which typically require longer and more expensive testing.

In many applications that utilize pharmaceutical R&D cost estimates, the relevant concept is the after-tax cost (e.g., rate of return analyses). R&D is typically expensed immediately, rather than depreciated during the life of the marketed product. If the firm has sufficient profits against which to expense the R&D, the net cash flow required to finance the R&D will be reduced by the amount of the tax savings. However, in contrast to an investment in an asset such as a building, which can be depreciated over its useful life for tax purposes, the investment in R&D necessary to bring a product to market cannot be depreciated during the years in which sales occur. Thus, the effect of expensing rather than depreciating R&D is one of changing the time at which the deduction occurs.

The R&D tax credit, enacted in 1981, was in effect for only part of our study period. Depending on changes in firm spending levels, the credit had differential impacts across firms. In aggregate, though, the impact of the credit on our cost estimates is likely to be minor.⁴¹ Since we were only interested here in estimating social cost, rather than rates of return, we did not adjust for the timing of taxes or the extra credits.⁴²

Further research on the cost of new drug development could profitably be directed at a detailed analysis of differences in costs across therapeutic classes. We will address this issue in future research. Another interesting topic for future research is whether trade-offs exist on the margin between clinical trial expenditures and NCE failure rates.

Our analysis has been directed to the R&D cost of self-originated NCEs from U.S.-owned firms. In future research it would be interesting to analyze the R&D costs of NCEs originating in other countries. This would be especially the case for Japan. Aggregate data suggests that R&D costs per

⁴¹ If we use U.S. pharmaceutical industry R&D expenditure data, we can obtain a rough upper bound estimate of the effect of the R&D tax credit. Under the Tax Reform Act of 1986, the annual credit was 25% of the increase in covered R&D expenditures over the average of R&D expenditures for the previous three years. The Tax Reform Act of 1986 reduced the credit to 20%. Nominal U.S. pharmaceutical industry R&D expenditures grew at an 11.7% compound annual rate of growth from 1978 to 1986. This implies a 6.8% subsidy if all expenditures are covered and the credit is 25%. Much of our clinical cost data and the bulk of the related preclinical expenditures, though, predate the credit. Thus, the tax savings relevant to our study are likely much less than 6.8% of total expenditures.

⁴² The impact of the tax rate on rate of return studies may not be substantial. Grubowski and Vernon (1989) found their results little affected when sensitivity analysis was conducted on the tax rate parameter.

Appendix A

Estimated weighted mean phase cost, v_p , is determined as follows (where the index values 1, 2, 3 and A refer to phases I, II, III and long-term annual testing, respectively):

$$v_p = \sum_{t=1}^n w_t v_{tp} \quad \text{for } t = 1, 2, 3 \text{ and A.} \quad (A.1)$$

where

- n = number of NCTs in the sample;
- w_t = ratio of the n_t of population NCTs to the n of sample NCTs for the stratum in which NCT t falls;
- v_{tp} = $\left\{ \begin{array}{l} \text{ } \end{array} \right\}$ j th NCT phase t cost if the j th NCT has phase t costs, 0 otherwise;
- b_{tp} = $\left\{ \begin{array}{l} 1 \end{array} \right\}$ if the j th NCT has phase t costs, 0 otherwise.

For phases I, II, and III the estimated probability of entering a phase, θ_{tp} , is the product of the estimated conditional probability that the NCT will undergo testing in the phase given that the previous phase was entered, and the estimated probability of entering the preceding phase. For long-term annual testing, the estimate, θ_{tp} , is a weighted proportion of the sample NCTs that underwent that type of testing. Specifically, we have:

$$\theta_{tp} = \left(\sum_{g=1}^G \theta_{tp}^g v_{pg} \right) v_{pg} \quad \text{for } t = 1, 2, 3 \quad (A.2)$$

$$v_{pg} = \sum_{a=1}^A \theta_{tp}^a v_{pa} \quad \text{for } t = 1, 2, 3 \quad (A.3)$$

where

- θ_{tp} = ratio of the n_{tp} of population NCTs to the n of sample NCTs for stratum g ;
- v_{pg} = number of sample NCTs in stratum g that entered phase t ;
- v_{pa} = number of sample NCTs in stratum g ;
- v_{pg} = 1;
- δ_{tp} = δ_{tp} .

With (A.1) and (A.2) an estimate of expected clinical period costs for a randomly selected NCT, tested in humans, \bar{c}_p , can be expressed as $\bar{c}_p = \sum_{t=1}^n v_{tp} b_{tp} v_{tp}$. Given that the sample strata are prespecified the

NCT originating in Japan are significantly lower than those in the United States [Grabowski (1990)]. At the same time, pharmaceutical R&D in Japan has different characteristics from that undertaken in the United States, and has produced significantly fewer NCE introductions in major markets outside of Japan. Given the increased policy interest in international competitiveness, the cost and determinants of R&D performed in different countries is likely to be an important question for future research.

It would also be instructive to compare the total costs for U.S. firms of originating a new drug in-house versus licensing or acquiring one externally. Our survey data indicate that the R&D costs incurred by U.S. firms for a self-originated compound is several times what they spend for a licensed or acquired NCE. This raises the issue of whether the licensing fees and other costs for externally acquired compounds exactly offset the higher R&D costs of self-originated NCEs. This is what would be expected in equilibrium, if the market for licensed and acquired NCEs is perfectly competitive. Whether this in fact has been true of recent experience in the pharmaceutical industry is an interesting topic for future research.

Another important topic for future work is the effect of firm size and the scale of R&D activities on the costs of new drug introductions. This topic is also likely to have significant policy interest, given the recent tendency toward increased consolidation of the pharmaceutical industry. In this regard, it would be useful to know whether this consolidation is motivated in part by higher real R&D costs or potential R&D scale economies.

Our R&D cost estimates should be a useful input to studies of the returns to current new drug introductions. It should be emphasized that rising real R&D costs do not necessarily represent a problem for pharmaceutical innovative activity. In particular, if the higher costs are reflective of higher probabilities of commercial success and/or higher average sales per new drug introduction, then strong incentives to undertake pharmaceutical R&D can be maintained even in the face of rising R&D costs. Hence, it will be important in future research to examine trends in innovative output and sales revenues, as well as R&D costs.

Finally, it should be emphasized that while our estimates are presented in 1987 dollars, they are not estimates of the cost of developing a new drug in 1970 and 1982, and many of the successful candidates from this sample are entering the market in the 1980s and 1990s (the mean approval date for approved drugs in the sample was in early 1983, with future approvals expected to raise the mean to early 1984). However, the expected cost of developing a new drug for which testing begins in the late 1980s or the 1990s will be affected by changes in the process which have occurred since our sample period. The trends suggest that the cost will be higher than our estimate.

weights, w_i and θ_i are not random variables. We can see, then, that x_i and s_i are unbiased estimates of the population mean phase i cost and the population proportion of NCEs entering phase i , respectively. There is no reason to expect that the weighted mean cost for a phase and the weighted proportion of NCEs entering that phase are correlated across independent samples. Under the assumption that s_i and x_i are stochastically independent, it can easily be shown that \bar{E} is an unbiased estimate of $E(h)$.

Appendix B

The problem of estimating an approval success rate for the population of cost survey firm NCEs that meet survey inclusion criteria is modelled in two stages. Since the ultimate fate of some NCEs first tested in humans from 1970 to 1982 is, to our knowledge, not yet determined, survival analysis should prove useful [see Cox and Oakes (1984)].

In the first stage we estimate the distribution of times that the NCEs are in residence. For NCEs that have either been abandoned or approved by the end of 1986, we define residence time to be the time from first testing in humans to either research abandonment or NDA approval. Some NCEs are being continuing in research as of the end of 1986. Data for such NCEs are right-censored. Survival analysis techniques utilize the information provided by censored observations.

In the second stage of the model, we estimate the probability that an NCE will meet a given fate (research abandonment or NDA approval) as a function of residence time. Thus, the cumulative probability of success (NDA approval) as a function of residence time, t , can be given as

$$S(t) = \int_0^t f(u)P(u)du, \quad (B.1)$$

where $f(u)$ is the probability density function for residence time, and $P(u)$ is the probability that an NCE with a residence of u receives NDA approval at that time. The density function can be estimated by a nonparametric product-limit technique.

The data on approvals at various residence times indicate that the process may be adequately approximated by a sigmoidally shaped distribution. Thus, we applied the logit and probit models to estimate $P(u)$. Both the logit and probit models provided good fits and, in fact, were virtually indistinguishable from one another.⁴³ Computed values of the likelihood ratio index deve-

⁴³The transformation suggested in Amemiya (1981) for comparing coefficients in logit and probit models showed very small differences in the coefficients. The results on cumulative success rates are also virtually the same when logit and probit specifications for $P(u)$ are used.

loped in McFadden (1974) shows the probit model to have a slightly superior fit, and so the success rate estimates utilize the probit specification for $P(u)$.⁴⁴

The cost survey firms investigated in humans 279 NCEs that met cost survey inclusion criteria.⁴⁵ As of December 31, 1989, 17.2% of these NCEs had been approved. Our model predicts that approximately 23% of the population NCEs will have been approved 14 years after first testing in humans. By the end of 1986 only four NCEs had been in residence longer than 14 years, and information obtained in the cost survey indicated that two of these NCEs had been abandoned. We use 23% as our base case clinical approval success rate.

Evidence of the predictive power of eq. (B.1) can be obtained by focusing on one subclass of NCEs. Taking note of dates of research abandonment obtained from the cost survey and approvals after 1986, we were able to completely characterize the fate of all anti-infective NCEs. The model (using data through 1986) predicted an approval success rate of 31.7%, for this class, which compares very well with the actual final cumulative success rate of 31.0%.

Appendix C

The PMA publishes R&D expenditure data for its member firms (PMA Annual Survey Report, various years). From these data it is possible to extract annual expenditures for human use ethical pharmaceuticals. These expenditures, in real terms for the years 1967-1987, are given in the first column of table C.1.

At our request, we also obtained information from the PMA on the percentage of total R&D expenditures accounted for by U.S.-owned member firms. The PMA had such data only for recent years. We utilized the 1987-1988 percentage (84.3%) to estimate annual R&D expenditures by U.S.-owned firms (column 2 of table C.1). There is some evidence of a slight decrease in this percentage over time. Given the downward trend in this percentage, the values in column 2 are likely to be conservative estimates.

We next subtract foreign expenditures from the values of U.S.-owned R&D expenditures to obtain their domestic R&D expenditures (column 3 of table C.1). We include only domestic expenditures in our analysis under the assumption that the foreign expenditures of U.S.-owned firms will be directed

⁴⁴Specifically, we used an iteratively reweighted non-linear least squares routine to estimate $P(u) = F(\alpha + \beta u)$, where u represents residence time in months and $F(\cdot)$ is the cumulative distribution function of the standard normal random variable. The maximum likelihood estimates of α and β are -2.3329 and 0.0244, respectively.

⁴⁵The information needed to conduct the survival analysis was available for 276 of these NCEs.

Table C1

U.S. pharmaceutical industry real human use R&D expenditures 1967-1987 (millions of 1987 dollars)

Year	(1) All PMA firms	(2) U.S.-owned PMA firms ^a	(3) U.S. R&D of (2) ^b	(4) Self-originated R&D of (3)
1967	1,163	1,149	972	670
1968	1,400	1,180	1,058	729
1969	1,492	1,258	1,135	782
1970	1,583	1,334	1,203	829
1971	1,663	1,402	1,264	871
1972	1,684	1,470	1,251	863
1973	1,785	1,505	1,247	883
1974	1,870	1,576	1,282	922
1975	1,928	1,635	1,318	922
1976	1,989	1,677	1,367	912
1977	2,061	1,737	1,393	960
1978	2,123	1,790	1,468	1,011
1979	2,275	1,918	1,501	1,034
1980	2,549	2,149	1,593	1,098
1981	2,762	2,328	1,771	1,220
1982	3,100	2,613	2,047	1,410
1983	3,362	2,918	2,321	1,601
1984	3,726	3,141	2,513	1,731
1985	4,142	3,492	2,721	1,911
1986	4,703	3,965	3,101	2,137
1987	5,310	4,476	3,508	2,417

^a Expenditures on R&D for ethical pharmaceuticals intended for human use were obtained from the PMA Annual Survey Report (various years) and deflated using the GNP Implicit Price Deflator.

^b The expenditures for all firms in a year were reduced by the average percentage of member firm R&D expenditures accounted for by U.S.-owned firms for 1987 and 1988 (source: Gary Persinger, PMA).

^c Computed based on U.S.-owned firm aggregate expenditure levels, and data contained in the PMA Annual Survey Report (various years).

primarily to non-U.S. introductions. This assumption will also tend to produce conservative estimates, since at least some of the foreign expenditures of U.S.-owned firms are obviously directed towards approval of new drugs in the United States and other major world markets.⁴⁰

The last step in the analysis is to determine the percentage of R&D that is devoted to self-originated NCEs by U.S.-owned firms. In particular, we need to separate such R&D expenditures from those on licensed or acquired NCEs and on R&D for improvements in existing products. It would be

⁴⁰ Although some of the domestic R&D expenditures of U.S. firms may be targeted specifically to products only introduced abroad, our approach will produce a conservative estimate so long as these outlays are smaller in value than the foreign R&D expenditures of U.S. firms that are related to domestic introductions. This appears to be a reasonable presumption given the tendency of U.S. firms to present compounds abroad for the U.S. market.

Table C2

New chemical entity approvals in the United States, 1979-1989

Year	Total NCEs	U.S.-owned PMA member firm NCEs	Self-originated NCEs of U.S.- owned PMA firms ^a
1979	13	13	9
1980	11	9	6
1981	23	15	6
1982	22	18	11
1983	12	6	1
1984	21	15	8
1985	26	16	12
1986	20	13	8
1987	18	13	10
1988	16	8	5
1989	21	10	4

^a Information on the origin of compounds was obtained from a Center for the Study of Drug Development annual survey of firms with U.S. NCE approvals and supplemented, when necessary, with published sources.

inappropriate to assume that the firms who did not participate in our survey have the same pattern of R&D allocations as our survey firms. NCE output data show that non-survey U.S.-owned firms are somewhat more reliant on licensed or acquired NCEs.⁴¹ We assume that the R&D effort necessary to produce a self-originated NCE relative to a licensed or acquired NCE is the same for the survey and non-survey firms.⁴² Using this approach, we estimate that the non-survey U.S.-owned firms devoted 60.6% of their pharmaceutical R&D to self-originated NCEs. Given this estimate, and the fact that our cost survey firms account for 48.3% of the total pharmaceutical R&D expenditures of all U.S.-owned firms, we can compute a weighted

⁴¹ For the cost survey firms, 66.7% of their NCE approvals during the period 1979-1989 are self-originated. For the same period, only 48.1% of the approvals of other U.S.-owned firms are self-originated.

⁴² In particular, the ratio of expenditures on self-originated NCEs per approval of NCEs of this type to the expenditures on licensed or acquired NCEs per approval of such NCEs was estimated to be 1.7 for firms in our survey. In other words, it takes nearly four times the R&D outlays to produce a self-originated NCE compared to the R&D necessary for a licensed or acquired NCE for our survey firms (ignoring licensing and acquisition fees). We assume that this ratio is the same for the U.S.-owned firms that are not in our survey sample. We also assume that the group of foreign-owned PMA member firms spent the same proportion of their U.S. pharmaceutical R&D on new products as did the survey firms. We then used information available in the PMA Annual Survey Report (various years) to estimate that non-survey U.S.-owned firms spent 78.1% of their pharmaceutical R&D on new products. Using these two estimates, together with information on the breakdown of NCE approvals between self-originated and licensed or acquired NCEs for non-survey U.S.-owned firms, we estimated that these firms spent 60.6% of their pharmaceutical R&D for self-originated NCEs.

average estimate of the percentage of pharmaceutical R&D performed by U.S.-owned firms for self-originated NCEs (66.8%) and apply it to the previously calculated values in column 3 of table C.1.

We also performed a parallel analysis for the U.S. NCE approvals between 1979 and 1989. These results are presented in table C.2. We first separated total NCE approvals into those emanating from U.S.-owned PMA member firms and all other firms. The NCEs from U.S.-owned PMA firms (shown in column 2) were then further subdivided into self-originated versus licensed or acquired NCEs. To classify NCEs into these sub-categories, we used the CSDD annual survey of NCE approvals together with information from related sources. For the 1979-1989 period, the last column of table C.2 shows the annual number of self-originated NCEs accounted for by U.S.-owned PMA member firms. We found that approximately 39% of all U.S. NCE approvals for this period were for self-originated NCEs of U.S.-owned PMA firms.

For a lag structure, we use the phase time profile and cost levels found in this study. This implies that approvals in one year should be associated with R&D expenditures lagged 2 to 12 years. Monthly expenditures were calculated and spread over this period according to the phase time profile.⁴⁹ Weights to be attached to each of the lag years can then be determined, and used to estimate uncapped cost per approval. Given the time profile, weights for capitalized cost estimates can also be calculated.

⁴⁹Data from a CSDD database were used to determine that NCEs approved over the last 15 years received their approvals, on average, eight months into the year of approval. This was used to establish the endpoints of the time profile.
⁵⁰If approval occurs in year t , then the weights for years $t-5$ to $t+2$ are 0.038, 0.075, 0.083, 0.072, 0.058, 0.105, 0.163, 0.163, and 0.020, respectively. These weights represent the proportions of out-of-pocket expenditures incurred in the years prior to approval.

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Canadian medical malpractice liability: An empirical analysis of recent trends*

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The determinants of the frequency of Canadian malpractice claims, the proportion of claims that result in payment, and the severity of these claims are examined. Inter-specialty variation in the frequency of malpractice claims is almost entirely related to the differential performance of major surgery. Various legal doctrines concerning both compensation and liability appear responsible for approximately half of the upward trend in the propensity to initiate malpractice litigation. We believe that the remaining explanations for growth in claims frequency are changes in social attitudes toward risk-bearing, increasing social distance between patients and physicians, and innovations in medical technology.

1. Introduction

In recent years, there has been a growing perception among Canadian physicians that they are facing a malpractice 'crisis'. This perception has been influenced by the trends in malpractice claims, by the level of fees paid by physicians for protection against such lawsuits, and by the introduction of differential malpractice fees reflecting the different loss experiences of different specialties.

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