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Conservation biology: unsolved problems and their policy implications.

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Conservation biology: unsolved problems and their policy implications

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13.1 Introduction

A plot of the number of parks and other terrestrial protected areas established around the world over the past 100 years exhibits near-exponential growth (Figure 13.1), with marine parks following a similar trend. This is a testament to the growing recognition of the importance of sustaining natural systems worldwide. Yet, at the same time an expanding human population and the desire of all people for a more prosperous life have resulted in unprecedented rates of deforestation and habitat conversion. Accompanying these changes has been the spread of invasive, non-native species (including new disease organisms) to virtually all parts of the globe. With recent assessments placing 12% of the world's birds, 23% of mammals, and 32% of amphibians in danger of extinction (Baillie *et al.*, 2004), conservationists feel a justifiable sense of panic.

Any attempt to measure the full extent of the current biodiversity crisis is made immensely more difficult by our astounding lack of knowledge about the species that share this planet with us. For example, we do not know within an order of magnitude the number of species currently present on Earth (May, 1988, 1992; Novotny *et al.*, 2002); estimates range from 3 to more than 30 million species, of which only 1.5–1.8 million have been described to date. Not surprisingly, our inventory of the more charismatic groups of organisms, such as birds, mammals, and butterflies, is vastly more complete than our inventory of insects, arachnids, fungi, and other less conspicuous but no less important groups.

If we ask the logical follow-up question—what proportion of known (described) species is in danger of extinction?—we run into a similar barrier. While organizations like the World Conservation Union (IUCN) have prepared reasonably complete assessments for a few groups, notably the charismatic vertebrates, most species are too poorly known to assess. Even within the USA only about 15% of the species catalogued to date are sufficiently known to be given any sort of conservation rank, such as endangered or not endangered (Wilcove and Master, 2005); among invertebrates that value drops to less than 5%. Compounding this shortfall of data is an equally serious shortfall of money. Most conservation programs, especially those in developing countries, are woefully underfunded (Balmford *et al.*, 2003).

Under these circumstances, conservation must be efficient and effective. In this chapter, we explore several ways in which theoretical ecology is contributing to the efficiency and effectiveness of contemporary conservation efforts. We begin with a discussion of the challenges associated with determining what conservation measures (generally framed in terms of the amount and distribution of protected habitat) are necessary to ensure the long-term survival of an endangered species. We use as our example the case of the grizzly bear (*Ursus arctos*) in Yellowstone National Park, USA. Few endangered animals have attracted greater attention than this widely admired and widely feared species. We then consider the challenges associated with creating a network of reserves to protect multiple species of concern,

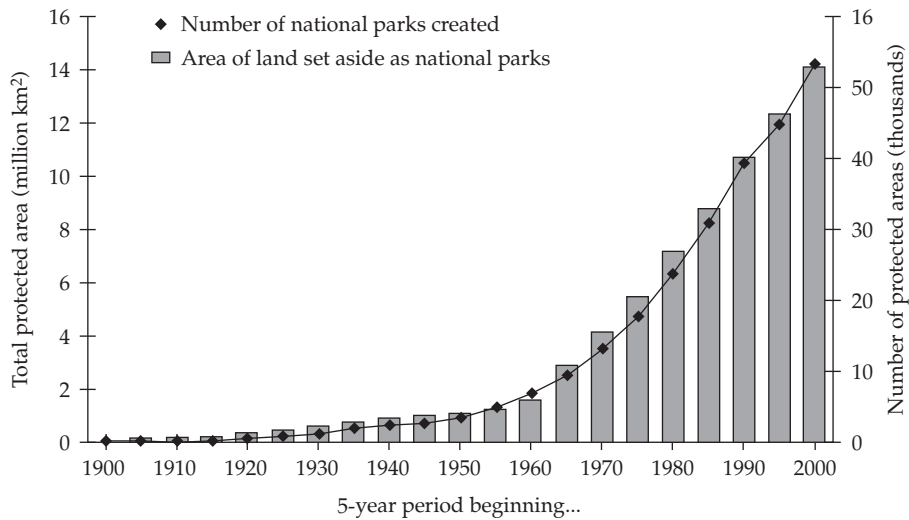


Figure 13.1 The total area of land set aside as national parks (bars) and the total number of national parks created in the time intervals shown (black diamonds). *Data from WDP A (2004).*

examining in detail some of the recent advances in the field of systematic reserve design. Having considered various theoretical challenges associated with protecting individual species or groups of species, we turn to the task of measuring and protecting the essential services provided by species, a subject of growing importance to conservation worldwide.

13.2 Protecting individual populations and species: the case of the grizzly bear

With varying degrees of enthusiasm and success, people have been trying to save populations of declining species for centuries. As far back as 1616, a rapid decline in the number of cahows (a type of seabird) prompted authorities in Bermuda to enact a proclamation prohibiting 'the spoyle and havock of the Cahowes, and other birds, which already wer almost all of them killed and scared away very improvidently by fire, diggeing, stoneing, and all kind of murderings' (Matthiessen, 1987). Nearly four centuries later, the cahow is still with us, although it remains one of the world's rarest birds, with fewer than 100 pairs nesting on a total of 1 ha of rocky islets off the coast of Bermuda (www.birdlife.org). The viability of this population is a function of many interacting factors, including the

amount, distribution, and quality of habitat, and community interactions between cahows and their prey, predators, competitors, and disease agents. These factors, in turn, are tied to a host of sociological issues that determine what is, and isn't, possible in terms of conservation.

A combination of direct persecution and habitat loss due to agriculture, logging, road building and oil and mineral exploration eliminated grizzly bears from most of their range in the western USA south of Alaska. In 1975, the US Fish and Wildlife Service declared the grizzly bear to be a threatened species in the coterminous USA. One of its last strongholds was in Yellowstone National Park and the surrounding national forests, but even here the population was small (~200 adults) and declining (Craighead *et al.*, 1995). Thirty years later, the Yellowstone population now hovers around 600, and the US Fish and Wildlife Service has announced its intention to remove the Yellowstone grizzlies from the list of endangered and threatened species. Are 600 grizzlies enough to ensure the long-term persistence of the species in Yellowstone? More generally, what constitutes a safe or viable population size for a species like the grizzly bear, and what factors other than the size of the population must be evaluated in deciding whether or not it has recovered? These are the

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sorts of questions that can be tackled via population viability models.

13.2.1 Population viability analysis

Our ability to model the dynamics of single populations and interacting sets of populations has grown enormously over the past two decades, providing conservation biologists with a set of powerful, new tools for developing conservation plans and designing nature reserves for endangered species. Indeed, population viability analysis has become an essential component of endangered species conservation efforts in many countries (Shaffer, 1990; Boyce, 1992; Burgman *et al.*, 1993). The most basic population-viability-analysis model simply considers the birth and death rates of the species deemed to be in danger of extinction. Thus, we could write a simple expression for the population B_t of Yellowstone's grizzlies over time as

$$B_{t+1} = sB_t(1 + b) = \lambda B_t \quad (13.1)$$

Where s is the annual survival of the bears, b is their annual fecundity, and λ is the annual rate of population increase. Determining the viability of the population essentially comes down to determining whether λ is greater than unity. Of course, the situation is more subtle than this because survival may vary from year to year and will also be different for older bears compared with cubs or yearlings. Because any variance in the birth and death rates will reduce the potential for long-term persistence, many early population viability analyses focused on obtaining accurate estimates of demographic rates and their underlying variability. However, these estimates of variability are confounded by statistical sampling procedures that, by definition, tend to give broad statistical confidence limits when data are scarce. This is often the case for rare and endangered species. With grizzly bears, several years may elapse before an individual enters sexual maturity, so a more detailed model would need to include a lag of several years in the birth term and perhaps also include some stochastic variation in birth and death rates.

More significantly, assuming that survival and fecundity are independent of climate and food

resources ignores the bear's dependence upon other species in its ecosystem and its vulnerability to variation in other environmental factors that determine the bear's survival and fecundity. Alternatively, fecundity and survival may decline as the bear population becomes inbred due to genetic isolation, a real possibility in the case of the Yellowstone grizzlies, which have been isolated from any other grizzly populations for nearly 50 years. (Indeed, the federal government is contemplating occasionally adding grizzlies from outside Yellowstone to reduce the effects of genetic isolation.) Population viability analyses include these additional details in a variety of ways, with the emphasis placed on each depending on the interests of the person running the analyses and the strident responses of people who review them.

13.2.2 Simple models and confusing data

One might assume that the best-quality data available for a population viability analysis for grizzly bears are the data collected from radio-telemetry studies. This technique is widely used in wildlife research; indeed, it was first used by Frank and Lance Craighead to study grizzlies in Yellowstone (Craighead *et al.*, 1969, 1995). Radio-telemetry allows bears to be monitored with little human interference. It also makes it far easier for scientists to relocate females in order to monitor the number and survival of their cubs.

When these data were initially used to estimate the intrinsic growth rate of the Yellowstone grizzlies they presented a gloomy prognosis: the annual growth rate of the bear population was consistently less than unity, which suggested that the population was in a state of terminal decline following the closure of the garbage dumps where they had grown accustomed to feeding (Cowan *et al.*, 1974; Knight and Eberhardt, 1985; Eberhardt *et al.*, 1986). However, aerial surveys of grizzlies were also used to monitor the population, and they showed a consistent upward trend in grizzly numbers, particularly with respect to the key index of number of independent females with cubs (Figure 13.2a and b)—as well as an increase in litter size. Why, then, was the state-of-the-art radio-telemetry data giving a different answer than the

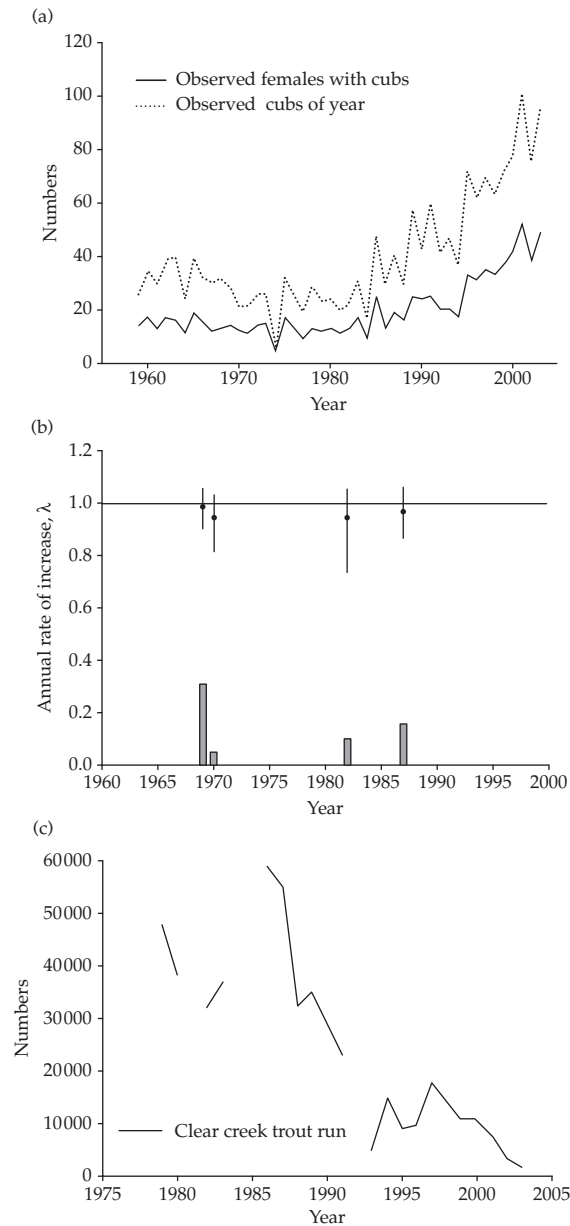


Figure 13.2 (a) The numbers of independent female grizzly bears and cubs counted in survey flights over the Greater Yellowstone ecosystem, 1958–2004. (b) Estimate of natural rate of population increase for grizzly bears using survival estimates based upon radiotelemetry data (after Dobson *et al.*, 1991). The upper points show the estimated annual rate of increase using demographic data collected at different time intervals, and the bars are the probability that the annual rate of increase is greater than unity. (c) Numbers of cutthroat trout counted in the Clear Creek trout stream in Yellowstone National Park, 1978–2003 (data from InterAgency Grizzly Bear Annual Reports; www.nrmcs.usgs.gov/research/igbst-home.htm).

more serendipitous survey data? Eventually researchers realized that very few of the females seen with cubs had radio collars; they lived in the more remote parts of Yellowstone and had very

little contact with humans. In contrast, there was a high proportion of ‘nuisance bears’ in the radiotelemetry sample; these were bears that had wandered into human areas and had become

acclimatized to the presence of humans. They suffer higher rates of mortality than the backwoods bears, largely because of road collisions and fatal interactions with hunters and property owners (Mattson *et al.*, 1996; Dobson *et al.*, 1997c; Pease and Mattson, 1999).

More recent work has shown that grizzly bears are intricately enmeshed with the Greater Yellowstone food-web. In spring a sub-population of bears focuses on catching cutthroat trout. Their ability to gain body fat after winter hibernation is highly dependent upon this food resource. Recent declines in Yellowstone's trout population have significantly reduced the fecundity of this section of the bear population (Figure 13.2c). Another crucial food resource for bears are the nuts of the white-bark pine, which the bears steal from red squirrels that cache them in convenient aggregations high on mountain slopes in the fall. Studies reveal that an abundance of white-bark pine nuts is crucial to grizzly over-winter survival (Mattson *et al.*, 1992; Pease and Mattson, 1999). Unfortunately, Yellowstone's white-bark pines are host to a pine blister rust that attacks their cambium, leading to reductions in cone production and increasing their susceptibility to attack by pine bark beetles (Kendall and Roberts, 2001). Climate warming has increased the speed at which the beetles reproduce, so the synergistic interaction between blister rust and bark beetle has caused white bark pines to decline throughout Yellowstone. Their demise could reduce over-winter survival of grizzly bears and bring the bears back to the edge of extinction.

The crucial point is that understanding grizzly bear population viability requires models that go beyond estimating simple birth and death rates and that examine the bears' interactions with other species in the ecosystem. These models will by necessity be simplifications, but they will provide important conservation insights. If we based decisions regarding the health of the bear population on data obtained purely from demographic studies (even seemingly robust studies involving radiotelemetry), we would miss details that are crucial to successfully managing the bears over the long term.

Despite the insights that models can provide in cases like the grizzly bear, their use can be

controversial. A bill to reform the Endangered Species Act that passed the US House of Representatives in September 2005 drew a distinction between empirical data and models, with the implication that the latter are somehow distinct from and inferior to the former. We presume this notion that data and models exist in separate realms stems from either ignorance about ecological models or a fear that the output of such models will be politically unpopular—or both. Yet without the use of models, it is all but impossible to make well-informed decisions about most aspects of endangered-species management.

13.3 Building a reserve network

Faced with limited resources, numerous species in need of assistance, and ongoing habitat loss, several methodologies have been developed to help determine global conservation priorities. Given that not all conservation organizations have precisely the same mission and objectives, it comes as no surprise that strategies for global prioritization differ (Redford *et al.*, 2003). Conservation International, for example, focuses on ~~selected~~ hotspots; regions that harbor large numbers of endemic species and have undergone substantial habitat loss ~~plus~~ a few additional, species-rich wilderness areas (Myers *et al.*, 2000; Mittermeier *et al.*, 2003). The World Wildlife Fund targets 238 terrestrial ecoregions, identified via a set of metrics related to species richness, endemism, presence of rare ecological or evolutionary phenomena, and threats (Olson and Dinerstein, 1998). The recently created Alliance for Zero Extinction targets the rarest of the rare: its goal is to protect approximately 600 sites, each of which represents the last refuge of one or more of the world's mammals, birds, reptiles, amphibians, or conifers (Ricketts *et al.*, 2005).

All of these strategies strive for efficiency, aiming to protect the largest number of conservation targets in the fewest sites or at the lowest cost (Possingham and Wilson, 2005). In the context of species conservation, that efficiency is largely a function of the degree to which species' distributions overlap: the greater the number of targeted species that co-occur, the smaller the amount of land that must be secured on their behalf. This

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rather obvious point has a number of important ramifications for conservation planning, stemming from the fact that species' distributions can be measured at various spatial scales, from a coarse-grained measurement of how species' ranges are distributed across space (extent of occurrence, *sensu* Gaston, 1991) to finer-grained measurement of how the populations of species are distributed within their respective ranges (area of occupancy, *sensu* Gaston, 1991). The degree of overlap (or lack thereof) at each scale fundamentally influences the efficiency of conservation.

At the broadest scale, that of whole ranges, there is often considerable overlap between species; this is demonstrated by the existence of centers of endemism for particular groups of organisms. The degree to which these centers of endemism overlap *between* groups is an issue of considerable importance to conservation practitioners; unfortunately it appears to vary geographically. Myers *et al.* (2000), for example, reported a high degree of congruence between endemic plants and endemic terrestrial vertebrates within hotspots such as Madagascar (594 000 km²) and the tropical Andes (1 258 000 km²). On the other hand, the Cape Floristic Province (74 000 km²) and the Mediterranean Basin (2 382 000 km²) each contained large numbers of endemic plants but relatively few endemic vertebrates.

Prioritization at the global scale can help efficiently allocate conservation resources by adding coherence to conservation efforts. Yet most conservation action necessarily takes place at a much finer scale (Dinerstein and Wikramanayake, 1993). Species, including threatened species, are concentrated in different areas within regions (Dobson *et al.*, 1997b). Many decisions about site protection and management must be made in the context of local conservation priorities for biodiversity targets and funding (Jepson, 2001), and global political agreement on any one comprehensive plan is unlikely. Moreover, to date, data necessary for the actual implementation of conservation at individual sites has been unavailable over a global extent. Thus, the development of global strategies over the past two decades has been accompanied by the parallel, but largely separate, development of theory and tools for the selection of ~~regional~~ protected and managed areas.

13.3.1 Systematic reserve design

The problem of selecting sites within regions addresses the central issue of efficiency in conservation planning: select the set of sites that protects the greatest number of conservation elements (e.g. species, habitat types) for the lowest cost. Early approaches tackled this problem with stepwise algorithms (Kirkpatrick, 1983; Margules *et al.*, 1988). Later workers framed the question as an optimization problem (Cocks and Baird, 1989; Camm *et al.*, 1996). In its simplest form, the problem is one of identifying the smallest number of sites or 'minimum set' that includes all species on at least one site. Minimize

$$\text{cost} = \sum_{i \in I} x_i \tag{13.2}$$

subject to

$$\sum_{i \in I} p_{ik} x_i \geq 1 \quad \forall k \in K \tag{13.3}$$

where i and I are, respectively, the index and set of sites, k and K are, respectively, the index and set of species, x_i is an indicator variable equal to 1 if and only if site i is included in the reserve network, and p_{ik} is an indicator variable equal to 1 if and only if species k is present in site i . Eqn 13.2 minimizes the number of sites in the reserve network, whereas eqn 13.3 ensures that the reserve network includes each species in at least one site. This formulation is a binary integer program which can be solved with optimization software.

Not surprisingly, these optimal formulations outperform a variety of heuristic methods (algorithms whose solutions are not provably optimal) ~~in practice~~ (Csuti *et al.*, 1997; Rodrigues and Gaston, 2002a), including, among others, various stepwise approaches. But several assumptions of these simple formulations—for example, that all sites have equal cost or that any one site is sufficient to protect a species—make them trivial for most conservation purposes. Fortunately, optimization methods can produce more relevant solutions by incorporating additional factors into the above models. Additional complexities include site-specific costs; weights so that some species are more 'valuable' than others, minimization of

networks of individual protected

boundaries so that contiguous sites are preferred, and specifications of areas of suitable land required for each species rather than their simple presence or absence (Rodrigues *et al.*, 2000; Fischer and Church, 2005). These fuller descriptions of the desired properties of a reserve network can be much more difficult to optimize. Heuristic methods such as simulated annealing are potentially applicable to larger data-sets and problems of greater complexity than are optimal methods (Pressey *et al.*, 1996). However, identification of optimal solutions using mathematical programming remains the preferred method for problems of manageable size (Csuti *et al.*, 1997), since results of optimization methods are either provably optimal, or, if solutions are not found in a short-enough time frame, the distance from optimality can be quantified. (Although the notion of knowing how far one is from an unknown optimal solution is somewhat counterintuitive, this can be achieved by solving the problem to optimality under relaxed constraints; the distance to the relaxed optimum is then an upper bound on the degree of actual suboptimality.) Moreover, optimal techniques are increasingly applicable to a broader number of complex problems (e.g., see Rodrigues and Gaston, 2002a), and even when optimal solutions are not feasible within time constraints, best solutions found under truncated solution times (e.g., 2 min; Fischer and Church, 2005) have been shown to outperform simulated annealing solutions to the same site-selection problems.

13.3.2 Site-selection algorithms meet real-world complexities

The potential advantage of optimal sets of sites is straightforward: by definition, acquiring all sites in such a set is the most efficient means to satisfy conservation objectives subject to the constraints and criteria used. Traditionally, theoretical work on site selection assumes a static world: a reserve network is identified, and then all sites in that network are acquired for protection simultaneously. In practice, however, reserve networks are often acquired over a period of ~~some~~ years (Pressey and Taffs, 2001). During this time unanticipated complications can wreak havoc with

what had once been an optimal solution. Simply recomputing the optimal solution based on updated data each year cannot overcome these shortcomings (Turner and Wilcove, 2006).

If acquisition is not instantaneous and uncertainty exists with respect to when sites become available for acquisition, if unprotected sites become unsuitable over time, or if budgets fall short of those initially envisioned, even optimal portfolios may perform poorly (Faith *et al.*, 2003, Drechsler, 2005). Simulation of site acquisition under such uncertainty has revealed that optimal solutions to the minimum-set problem may be outperformed by several heuristic methods (Meir *et al.*, 2004). Among these is a 'greedy' algorithm which simply purchases those sites adding the most additional targets to the existing network at any given time. The problem is that, when many sites are available, the chances are good that most of the sites in a single optimal set can be acquired. But when site availability is limited, such an approach is handicapped by its narrow focus on a few key sites, many of which may never become available. Thus the simpler greedy algorithm, which considers sites outside of a fixed initial portfolio, is able to fare better, even under uncertainty. On the other hand, this potential benefit brings with it opportunity cost: when site availability is high, considering more sites (i.e. lower-quality sites) for acquisition may result in a reserve network more costly than necessary to meet targets. Furthermore, conservation planners do not always know in advance what site availability will be, making it difficult to identify a decision rule for reserve acquisition that will perform well in a given situation.

Adaptive decision rules (Turner and Wilcove, 2006) offer one approach to address these uncertainty issues. Adaptive decision rules combine the relative strengths of the minimum-set approach (optimum cost efficiency when sufficient sites are available) and heuristic rules (ability to create networks that meet more targets when site availability is lower). The best-of-both-worlds (BOB) rule is an adaptive rule that proceeds as follows. During each year, first compute the mean number of sites that must be acquired per year to exhaust the budget at the end of the multiyear acquisition

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period. Then acquire any available sites that appear in the current optimal solution. If the number thus acquired in a given year falls short of the mean number needed per year, use the greedy rule as a backup to make up the difference. This is repeated for each successive year.

The key innovation of BOB as a decision rule for acquisition is that it adapts to uncertainty or variation in availability. In years in which the optimal algorithm falls short due to low availability of sites in the optimal portfolio, BOB attempts to correct the shortfall immediately with a backup method (the more aggressive, greedy method). Adaptive rules such as BOB outperform non-adaptive rules such as the minimum-set approach or existing heuristic methods on a variety of data-sets and under a broad range of availability rates (Figure 13.3), degradation rates, and overall acquisition budgets (Turner and Wilcove, 2006).

Adaptive rules attempt to address real-world challenges (i.e. the dynamic, uncertain nature of reserve implementation) by linking the processes of conservation planning and reserve acquisition under a single model. They thus require tight coordination and feedback between biological planners (the prioritization phase) and acquisition personnel (the acquisition phase). Biological data and up-to-date information on the success or failure of site acquisitions, at a minimum, must be fed back into a single comprehensive model (BOB or something similar) for these approaches to work. These methods are new, and it remains to be seen to what extent this institutional coupling of biological prioritization and acquisition can work in practice.

An alternative approach is to recognize the more disjunct institutional structure (less-tightly coupled biological prioritization/acquisition teams or phases) that exists in many situations and ask,

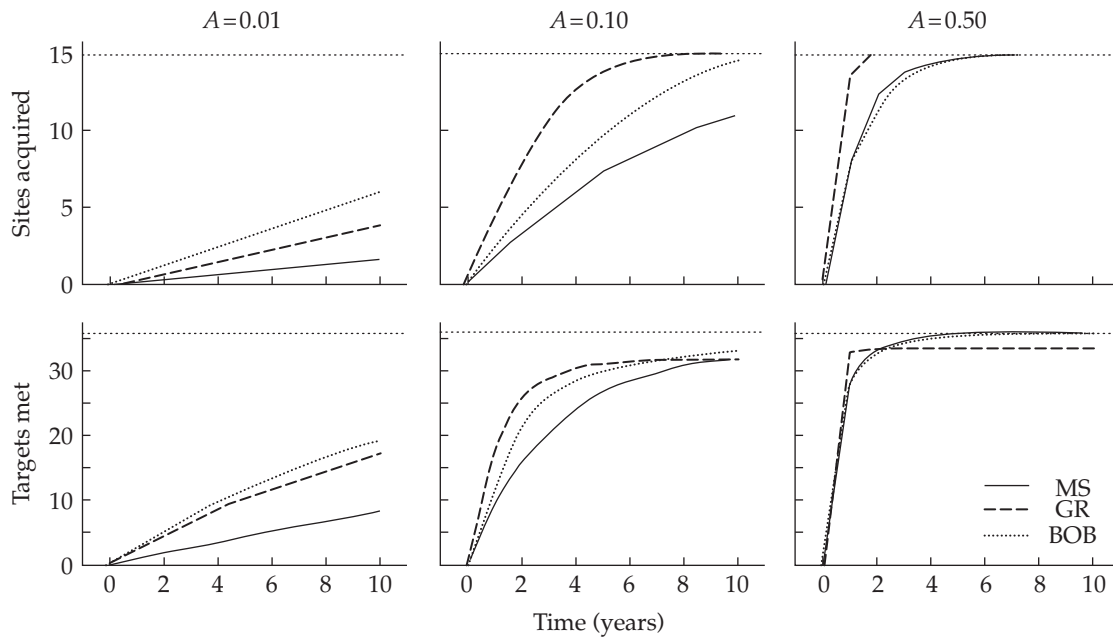


Figure 13.3 In reserve acquisition, adaptive decision rules generally meet more targets more efficiently than existing methods under conditions of uncertain or incomplete site availability. The annual probability of each site becoming available, A , strongly affects performance of decision rules over the course of reserve acquisition. Results are shown for 36 species of the Lake Wales Ridge ecosystem in Florida, USA, with targets of three sites/species and a budget of 15 sites. Upper and lower rows of graphs show the number of sites acquired and number of targets met, respectively, with horizontal lines indicating the initial minimum set size and maximum possible targets met, respectively. Acquisition-decision rules include an improved rule based on the optimal minimum-set (MS) algorithm, a greedy richness-based (GR) algorithm, and the best-of-both-worlds (BOB) adaptive rule.

what potential products from the prioritization phase will be most useful to the acquisition phase under the broadest range of realistic scenarios? The principle of irreplaceability, which values sites according to the likelihood that their protection will be required for the reserve network to meet or maximize conservation objectives, appears particularly well suited to this task. It may be used to create products that are robust to unknown conditions, yet may be tailored to those conditions which are known (e.g. total budget; Turner *et al.*, 2006). However, one drawback with irreplaceability scores is that they are at present a means to rank sites but are not themselves a prescription for the identification of a full reserve network. Indeed, for this reason an irreplaceability-based acquisition rule failed to protect as many biodiversity targets in simulations as the adaptive rule BOB (Turner and Wilcove, 2006).

13.4 Habitat destruction

The need to create networks of reserves stems primarily from the rapid rate at which natural habitats are being converted to other uses. These habitats are most often converted from their pristine or near-pristine state into agricultural land, and then into either degraded land, if they fail to sustain agriculture, or into housing developments, golf courses, or cities (Turner *et al.*, 1990; Tilman *et al.*, 2001b). In some cases, conversion to agriculture (and pastureland) is at least partially reversible. In the eastern USA, for example, forests were converted to farmland in the eighteenth and nineteenth centuries. After many of these farms were abandoned in the late nineteenth and early twentieth centuries, forests regenerated over substantial areas.

13.4.1 A model of land-use change

Models with similar structure to those developed to examine the dynamics of infectious diseases and forest fires can provide insights into the dynamics of land-use change (Dobson *et al.*, 1997a). In essence these models consider pristine land to be equivalent to a susceptible population of hosts, which is then colonized (or infected) by humans

who use the land for agriculture. The land is then either farmed in perpetuity or until the time when it is no longer productive, when it is abandoned and left to recover slowly through succession, until it is once again susceptible to colonization for agriculture. The relative duration of time it takes to recover and the duration of time it lasts under agriculture are equivalent to the durations of infectivity and resistance in standard SIR (susceptible, infectious, and resistant) models; here they determine the equilibrium amount of land under agriculture, A , in recovery, U , pristine (and recovered), F , and the size of the human population supported by agriculture, P .

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$$\frac{dF}{dt} = sU - dPF \quad (13.4)$$

$$\frac{dA}{dt} = dPF + bU - aA \quad (13.5)$$

$$\frac{dU}{dt} = aA - (b + s)U \quad (13.6)$$

$$\frac{dP}{dt} = rP \frac{A - hP}{A} \quad (13.7)$$

The model assumes that land is viable for agriculture for a period of time $1/a$ years. The land is then abandoned and slowly returns to the original habitat type by a successional process that takes $1/s$ years. Abandoned land may also be returned to agricultural use at a rate b . The model assumes a human population birth rate r (around 4%) and that each human requires h units of land to sustain them. Each of these parameters can be quantified for different habitats and historical levels of food productivity. The system settles asymptotically to the following equilibrium conditions:

$$\begin{aligned} A^* &= hP^*; U^* = \frac{aA^*}{(s+b)}; \\ F^* &= \frac{ah}{d} \left(\frac{s}{s+b} \right); \\ P^* &= \frac{F_0 - \left(\frac{ah}{d} \right) \left(\frac{s}{s+b} \right)}{h \left(\frac{a}{s+b} + 1 \right)} \end{aligned} \quad (13.8)$$

where F_0 is the original extent of the forest (or savanna).

We can also derive an approximate expression for the initial rate of spread of agriculture, equivalent to the R_0 of epidemic models. For this system $R_0 = rdF_0/a$, suggesting that agricultural development will expand at a rate determined by human population growth, the efficiency of habitat conversion, and the duration of time over which the land supports agriculture.

This simple approach is insightful in that it suggests counterintuitive results. For example, the longer land is viable for agriculture, the less of it will remain in a pristine state (Figure 13.4). This occurs because large amounts of agricultural land support an increasing human population that constantly demands more land. When agricultural land is productive for only a short period of time, as is typical of slash and burn (swidden) systems, humans are constantly forced to move on, resulting in a mosaic of patches in different stages of succession. Echoes of this simple theoretical prediction are seen in the patterns of land-use change in Puerto Rico, the Philippines, and the USA (Figure 13.4). In particular, as land use tends to decline with altitude and the time to succession is positively correlated with duration of time for which land is used, then this can produce a

changing mosaic of land-use patterns across altitudinal locations and soil types.

The efficiency with which land is used for agricultural production has led to a heated debate in conservation biology, where again theoretical insights have proved important. There is instinctive gut reaction among many environmentalists that genetically modified food and big agriculture are bad for biodiversity. Certainly, the massive expansion of industrial agriculture in the twentieth century has converted many natural habitats into fields and orchards. (One of the first books to consider conservation as a topic for valid scientific study was Dudley Stamp's *New Naturalist* volume, which focused on how loss of hedgerows due to agricultural expansion was having major impacts on British farmland birds; Stamp, 1969). However, the Millennium Ecosystem Assessment (MEA) provides an important counter example. Land-use changes in the Far East over the last 40 years have been driven dramatically by the need to feed the area's rapidly growing human population. Industrialization, in turn, has hugely increased the region's wealth and food purchasing power. In the early 1960s about 35% of the available land was already converted to agricultural production; if

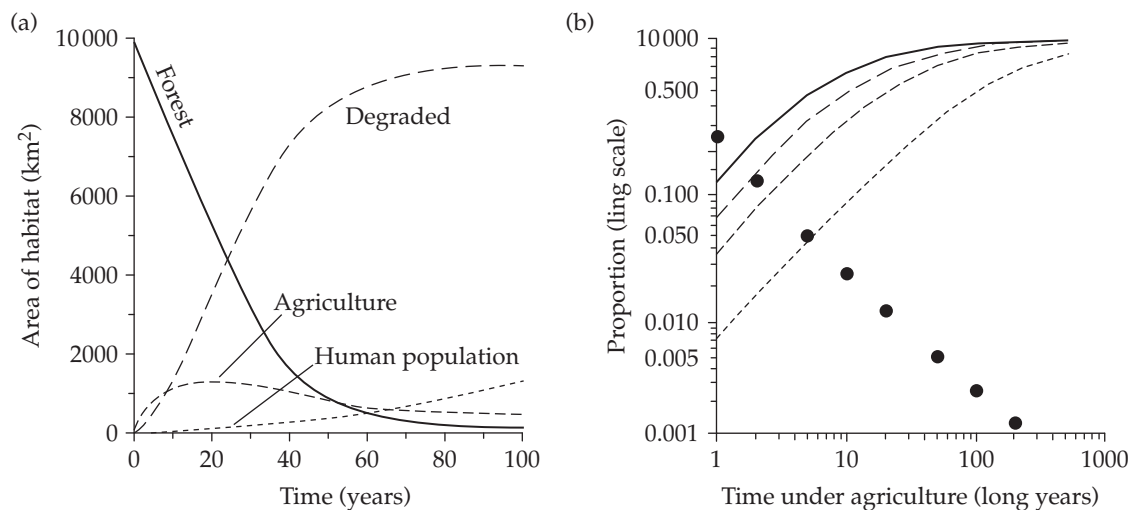


Figure 13.4 (a) Temporal change of land use based on a simple SIR forest fire model of land-use change. (b) Equilibrium proportions of land remaining as undisturbed forest (black dots) and as agricultural land (lines). The land retained under agriculture is depicted for four different rates of recovery of abandoned land: 5 years (solid line); and 10, 25, and 100 years (highest to lowest dashed lines). From Dobson *et al.* (1997a).

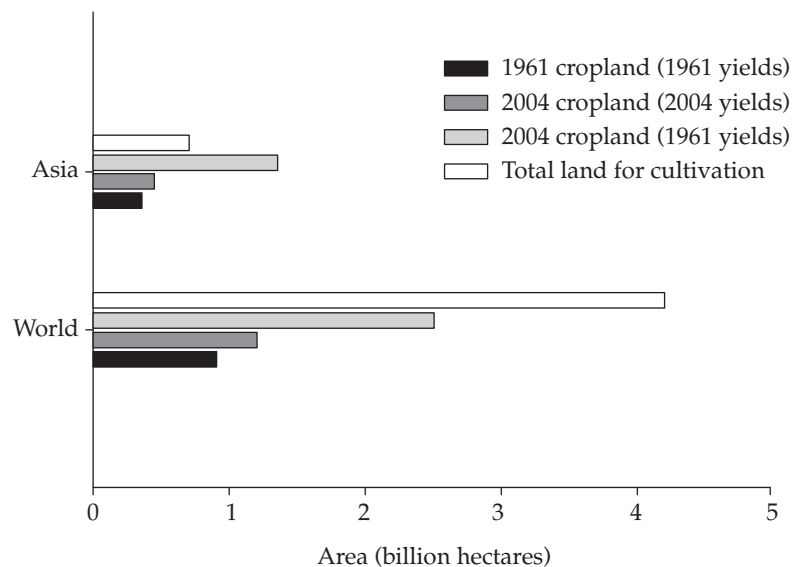


Figure 13.5 Land use and agricultural intensification. The graph shows the areas of land needed to feed the population of Asia (upper bars) and the world (lower bars) in 1961 and 2004. In each case the top bar gives the total land area available for cultivation (excluding mountains and cities), the lowest bar gives the total area of land under cultivation in 1961, the bar above this gives the land under cultivation in 2004, and the green bar gives the area of land needed to produce 2004 agricultural yield if agricultural efficiency had remained at 1961 levels (that is, with no Green Revolution). After Wood *et al.* (2006).

there had been no advances in agriculture, then all of the remaining land and a significant portion of Africa would be needed to feed the current population of the Far East (Figure 13.5).

However, increases in agricultural efficiency, particularly the development of high-yield varieties of rice and grains (see Chapter 12 in this volume; Conway, 1997), have allowed rates of land conversion to proceed at a much lower rate. In the terms of this model, high-yielding agriculture acts to decrease h , the amount of land needed for each human. Ironically this increased agricultural efficiency comes with an increased dependence upon water for irrigation, and this, in turn, may provide a further motivation to conserve habitats such as forests that store water and regulate its flow across the landscape. In the following section, which discusses models of ecosystem services, we describe how this model can be adapted to include a relationship representing support for the human population, P , from the pristine land, F (eqn 13.9; see below).

More general explorations of this effect have been examined in a series of models developed by

Green *et al.* (2005; but see Vandermeer and Perfecto, 1995, 2005). These models suggest that the best type of farming for the persistence of other forms of biodiversity is dependent both upon the demand for agricultural products and on how the population densities of sensitive species change with agricultural yield. If species are highly sensitive to reductions in pristine habitat, then intensive agriculture may be a better option, as it minimizes the land used for any level of agricultural productivity. In contrast, wildlife-friendly agriculture may require a much larger area of land under cultivation to achieve similar levels of food productivity, and this could be much more detrimental to species that are unable to use land that has been partially converted for agricultural use.

13.4.2 Habitat loss, species extinctions, and extinction debts

Conservation biologists have long wrestled with how to link loss of a habitat to loss of the species it contained. Initial work in this direction focused on using the species area curves of MacArthur and

Wilson (1963, 1967) to extrapolate from loss of habitat to loss of biodiversity (Diamond and May, 1981; Reid, 1992; Simberloff, 1992). This in turn led to the SLOSS (single large or several small) debate (Gilpin and Diamond, 1980; Higgs and Usher, 1980; Wilcove *et al.*, 1986), which focused on ascertaining whether two small reserves were more effective than one large reserve in conserving a maximum number of species.

Whereas some uses of the species-area extrapolation have been successful in predicting the expected number of extinctions for birds in the eastern USA (Pimm and Askins, 1995) and in southeast Asia (Brooks *et al.*, 1997), the approach has been less successful for other taxa (Simberloff, 1992). This may be because the basic species area curve assumes that both species and habitat loss occur at random, and when they are non-random and correlated then species may be lost at a faster rate than is predicted (Seabloom *et al.*, 2002). There may also be a considerable lag before habitat loss leads to species loss from the landscape. Tilman and colleagues (Tilman *et al.*, 1994) have suggested that because of this time lag the conversion of forests, savannas, and other natural habitats into agriculture creates an extinction debt. That is, in the absence of intervention, extinctions will continue to occur after habitat destruction has ceased. These extinctions are predicted to occur among the species persisting in the remaining, isolated patches of natural habitat in a fashion largely determined by the dispersal and competitive strategies of each species still present in the community (Nee and May, 1992). Two different management approaches can be adopted to reduce the rate of extinction: where possible patches in the landscape may be reconnected by protecting land that might serve as corridors for the dispersal of key species that would otherwise go extinct. Alternatively, habitat loss may be reduced by explicitly recognizing the dependence of the human economy upon the services provided by natural habitats.

13.5 Ecosystem services

A significant number of conservation studies over the last 10 years have focused on the importance of

ecosystem services, defined as those goods and services that are provided by nature but not necessarily valued in the marketplace (Costanza *et al.*, 1997; Daily, 1997; Daily *et al.*, 2000; Balmford *et al.*, 2002). Examples of such services include pollination of crops, production of water, climate amelioration, erosion control, and aesthetic enjoyment. The rest of this chapter focuses on some of those studies as we explore how ecosystem services can be monitored, how consideration of ecosystem services might be incorporated into models for land-use change, and how simple models can help us understand what patterns of change in ecosystem services we might expect as land use grows.

13.5.1 Monitoring economic goods and services provided by natural ecosystems

Ecologists and economists have spent much of the last decade wrestling with how to quantify the goods and services provided by natural ecosystems (Daily, 1997; Daily *et al.*, 1997, 2000). At one extreme this discussion has focused on attempting to quantify the net annual economic benefit provided to the human economy by natural ecosystems (Costanza *et al.*, 1997). However, such studies do not address a number of important practical issues. For example, few ecologists (or ecologically informed economists) would disagree with the assertion that the world's wetlands provide a large number of vital ecosystem services. But for a particular marsh at a particular site, what are the consequences to ecosystem services of filling 1, 5, or 10 acres? What is the impact of losing a particular species in that marsh (e.g. an endangered bird) or of a change in the composition of the dominant vegetation (for example, replacement of sedges by cattails)? Knowing the overall value of wetlands does little to inform these sorts of everyday decision. ~~There has been~~ a heated discussion among ecologists regarding the dependence of ecosystem function upon species diversity (Tilman *et al.*, 1997; Chapin *et al.*, 2000; Kinzig *et al.*, 2001; Loreau *et al.*, 2001; Bond and Chase, 2002).

The recently completed Millennium Ecosystem Assessment has adopted a classification of

This led to

ecosystem services that provides a useful way of framing a discussion about how we might measure changes in the rates at which they are delivered. The Millennium Ecosystem Assessment divides these services into supporting services and provisioning, regulating, and cultural services. Quantifying ecosystem services on a species-by-species basis is clearly an impossible task, particularly as many of the most important services are undertaken by microscopic species whose taxonomic status is unclear (Nee, 2004). Nevertheless, it is likely that different types of service will predominantly be undertaken by species on different trophic levels. For example, regulating services, such as climate regulation and water regulation and purification will be predominantly undertaken by interactions between species at the lowest trophic levels. In contrast, cultural services, such as recreation and tourism, as well as aesthetic and inspirational services, will often require ecosystems that contain a near-complete suite of large mammals, raptors, and other charismatic species; this requires that the upper trophic levels remain intact. Thus the trophic diversity of ecosystems can provide important information on their ability to provide different types of services. Ultimately, a key index of the health of an ecosystem might be some measure of trophic diversity, such as food-chain length, or the standard deviation of trophic position for all the species in a food-web of the region (Dobson, 2005). This index could provide a potentially important indication of the diversity of ecosystems services supplied by the system.

13.5.2 Models of ecosystems services and land-use change

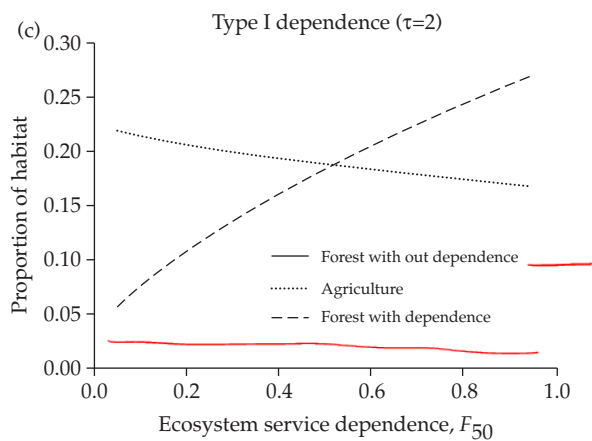
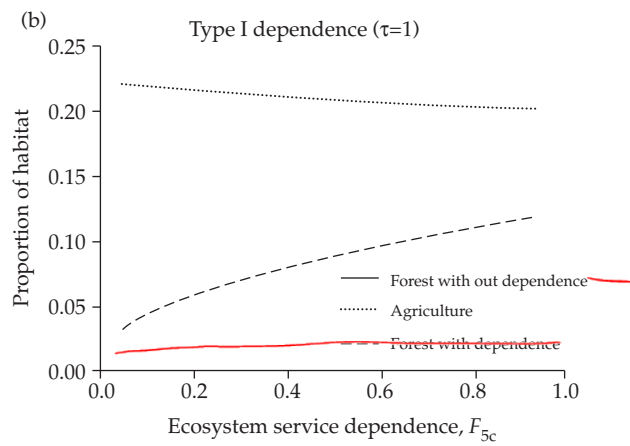
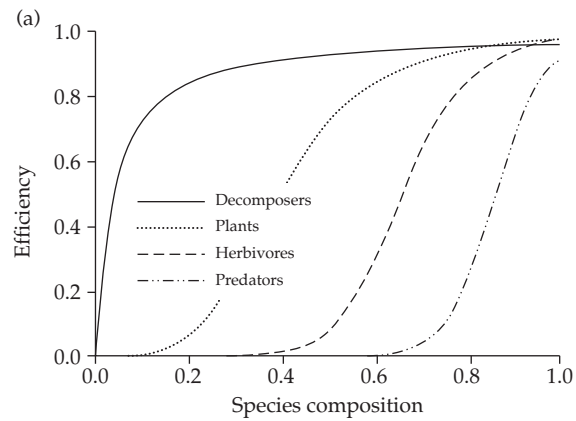
Although hard to measure, ecosystem services are an important factor in considering the impact of land-use change. In this section we present a model that explores how consideration of the economic value of pristine land changes our expectation of the growth of converted land. Let us initially consider a simple modification of the model described above for the dynamics of land-use change (eqns 13.4–13.7). One way to incorporate ecosystem services would be to include an

additional expression for the dynamics of an ecosystem service that is supplied by the forest to the converted land, for example, provision of water for crops and sanitation. Here we will assume that agriculture and human well-being are fundamentally dependent upon the presence of water (which is certainly true), but that the volume of water available is a function of the area of land still maintained as natural forest (or savanna). Madagascar's Ranomafana National Park provides a classic example of this effect. Although the park is justly famous for containing the world's highest diversity of lemur species, as well as numerous endemic bird and plant species, the main reason it was protected is because it contains a hydroelectric dam whose efficiency is determined by a steady stream of water from the forested watersheds that form the national park. The dam is not especially intrusive, but its turbines are dependent upon the forest retaining water and releasing it at a steady and continuous rate. This dam supplies most of the electrical energy for the major city of Antananarivo. Water from the park is also vital for the agriculture that covers the coastal plain between the park and the Indian Ocean. The potential of the forest to store and maintain a steady supply of water for electrical power and irrigation is a classic example of an ecosystem service in action. We can readily include this effect into our model of habitat conversion by assuming that the rate of food production on the land converted to agriculture is a simple Michaelis–Menton-type function of the area of land retained as pristine forest (e.g. $A \sim AF/(F + F_{50})$, where F_{50} is the area of pristine land at which agricultural productivity drops to half its maximum level). The expression for human population growth is the only equation that needs be modified. It now becomes

$$\frac{dP}{dt} = \frac{rP(A - hP(1 + F_{50}/F))}{A} \quad (13.9)$$

This simple modification has a number of important consequences. Most notably, the system now settles to a new set of equilibria. The expressions for abandoned land remains unchanged from above, $U^* = \frac{aA^*}{(s+b)}$, but the agricultural land, forest, and human population settle to new levels:

$$\frac{aA^*}{(s+b)}$$



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Figure 13.6 (a) The phenomenological relationship between the efficiency with which ecosystem services are undertaken and species composition (as a proportion of original intact community). The curves are drawn for services that are predominantly driven by species on specific trophic levels (e.g. ecotourism may be highly dependent on top carnivores; soil productivity and photosynthesis are dependent upon bacteria and plant diversity). They assume that a Michaelis–Menten type function can be defined for a 50% level of ecosystem service efficiency at some level of species diversity (after Dobson *et al.*, 2006). (b and c) Equilibrium proportion of land under agriculture and retained as ‘natural habitat’ when agricultural land has a dependence upon services supplied by the ‘natural habitat’. In each case the x axis describes the position of the 50% ecosystem service efficiency inflexion point, the solid line indicates the area of pristine land in the absence of any recognition of dependence of agriculture on ecosystem services, the dashed line indicates the area of land retained in its pristine, forested form as the dependence of agricultural productivity increases, and the dotted line is the area under agriculture. In (b), we have assumed that the slope of the agricultural dependence on pristine land is unity ($\tau = 1$) at the inflexion point, in (c) we assume the slope is 2; thus (b) phenomenologically corresponds to ecosystem services produced by species at the lowest trophic levels (e.g. bacteria, soil micro-organisms) and (c) corresponds to services produced by species at low to intermediate trophic levels (e.g. plants). As the slope of the dependence increases (corresponding to higher trophic levels) it is possible to get multiple-stable states (A.P. Dobson, unpublished work).

$$\begin{aligned}
 A^* &= hP^* \left(1 + \frac{F_{50}}{F^*} \right) \\
 F^* &= \frac{1}{2}c_1 \pm \frac{1}{2}(c_1^2 + 4c_1F_{50})^{1/2} \text{ where } c_1 = \frac{sal}{d(b+s)} \\
 P^* &= \frac{F^*(F_0 - F^*)}{h(F_{50} + F^*) \left(\frac{a+b+s}{b+s} \right)} \quad (13.10)
 \end{aligned}$$

The primary effect of including this phenomenological form of ecosystem service is to reduce the amount of habitat that is converted to agricultural land. This, in turn, reduces the size (and density) of the human population supported by the agricultural land; more explicitly it accurately recognizes that the size of the human population that can be supported is not solely dependent upon the land converted to agriculture but also upon the land remaining as forest; this slows future demands for habitat conversion (Figure 13.6). It is a relatively trivial exercise to modify eqn 13.9 so that the term in F_{50}/F is raised to the power of τ (Figure 13.6b and c illustrates the case for $\tau = 1$ and 2); this will correspond to increasingly strong (steep) dependence of agriculture on the remaining forest land. As the value of τ increases, the system now has the potential to settle to either of two (or more) alternative states (A.P. Dobson, unpublished work). These results echo the earlier work of May (1977c) and the more recent explorations of others (Carpenter and Cottingham, 1997; Scheffer *et al.*, 2001). Plainly, the results are dependent upon the functional forms we have chosen to represent the dependence of agriculture on water and the efficiency with which increased agricultural production translates into increased human population or increased demand for resources. Notice also that the larger the dependence of agriculture on pristine habitat, the greater the proportion of forest that is retained. We suspect that these are all functions that could be measured for different crops, habitats, and human culture.

The main point of this exercise is to illustrate that once we recognize a dependence of the human economy on services provided by natural resources, we begin to see changes in the predicted rate at which we convert natural habitats. Notice too that an interesting psychological switch has occurred in the motivation to conserve wild areas

such as Ranomafana. Initially the land was set aside for purely utilitarian reasons. Once the area's biological wealth was appreciated, this became an equally important justification for protecting the area. If the principal way to protect biological diversity is to set aside land in nature reserves, we will be more successful if we can identify and quantify the diversity of utilitarian services provided by different types of natural ecosystems in addition to their value as reserves for imperiled species.

13.5.3 How will the value of ecosystem services change as habitat is converted?

This initial consideration of ecosystem services assumes that the converted land is entirely dependent upon the non-converted land for services. In most cases, however, the converted land will not only provide new services of its own (e.g. farm crops, retail outlets, golf courses) but also will continue to provide a significant number of the services that the land provided prior to its conversion. The new set of plants will also photosynthesize and create and retain soil. (Indeed, some invasive plant species do so at a more efficient rate than the native species they displace.) We therefore need to develop frameworks that consider how different ecosystem services change as we modify the proportion of converted and pristine land in the landscape.

A handful of studies have examined the relationship between economic goods and services provided by natural systems and the services supplied in adjacent, or equivalent, modified systems (Peters *et al.*, 1989; Bonnie *et al.*, 2000; Kremen *et al.*, 2000; Balmford *et al.*, 2002). Cost-benefit analyses of these studies suggest that in most cases the net economic value of habitat that is totally converted declines by an average of around 50%, and the benefit/cost ratio of conserving the remaining unconverted habitats may be as high as 100:1 (Balmford *et al.*, 2002).

The essentials of these phenomena have been examined in a general model of land-use change (Dobson, 2005). The principal objective of this terse model of the services provided by pristine and modified environments is to examine the underlying

factors that confound our ability to detect changes in the rate at which ecosystem services are supplied.

Let us assume that the net production of ecosystem services can be characterized by the net relative value (NRV) of the goods and services produced by both the pristine and converted habitat. Let us then consider the situation where a proportion, p , of habitat has been converted from its pristine state into agriculture, mining, or some other modified use. We will define the current value of the total landscape as a simple sum of the converted and unconverted portions, relative to its initial value of unity in its pristine state when all it supplied were indirect services to the human economy. Doing so naively assumes we have some way of quantifying this value when, at present, all we really know is that we tend to undervalue it (Daily, 1997; Daily *et al.*, 1997; Balmford *et al.*, 2002).

The model is developed in three steps. The first is to define how the goods and services produced by the pristine land decline as the amount of pristine habitat shrinks. The second is to describe how the modified portion of the landscape produces goods and services. The total goods and services produced, NRV, is then the sum of these two parts.

Let s' be the value of the goods and services produced by a unit area of pristine land, a function of three parameters: p the proportion of land converted; ES_{50} the proportion of land converted at which ecosystem services produced decline to half of their maximum, pristine, value; and τ , a shape parameter describing how sharply goods and services derived from pristine land fall as the amount of remaining pristine land shrinks. The first step in the model is to define s' , goods and services provided by the remaining area of pristine land as:

Goods and services from a unit area of pristine land

$$= s' = ((1 - p)/p)^\tau / (ES_{50} + (1 - p)/p)^\tau \quad (13.11)$$

In Figure 13.7 the solid lines show the quantity $(1 - p)s'$, which is the goods and services produced by all of the remaining pristine land. The second stage in developing the model is to define how the converted land produces goods and service. This falls into two parts: ~~that~~ produced by the

converted land independently of the pristine land, s , and ~~that~~ produced by the converted land using services from the pristine land, sds' . Here d represents the degree of dependence of converted land on pristine land. For example, pollination of farm crops may be strongly dependent upon the diversity and abundance of pollinators in the remaining patches of natural habitat (Kremen *et al.*, 2002; Ricketts *et al.*, 2004).

~~Thus~~ Goods and services ~~supplied~~ from a unit area of converted land = $s + sds'$ (13.12)

In Figure 13.7 the dotted lines show the quantity $ps(1 + ds')$, which is the goods and services produced by all of the converted land. The final step is to add these two terms together to give the NRV of the goods and services produced by the total habitat (converted and pristine):

$$NRV = (1 - p)s' + ps(1 + ds') \quad (13.13)$$

Figure 13.7 illustrates how this value, the service supply rate, can change as a function of p , the amount of land converted. Notice in particular how an ecosystem where the modified land is heavily dependent on the pristine land and the pristine land fails to provide goods and services at high p leads to a situation where total goods and services are high for all low and intermediate values of land use, but fall precipitously as the proportion of land used approaches 1.

The key point is that if we are to monitor declines in ecosystem functions as changes in the net value of goods and services they supply, then we need to know more about the shapes of these curves. This is principally because our ability to detect changes in the economic value of natural habitats will be a subtle function of the relative value of services supplied by the pristine and modified habitats as well as the dependence of the services provided by the modified landscapes on the presence of unmodified habitat.

A handful of simple messages emerge from the model. We usually undervalue the economic services supplied by the natural environment as we are able to put a quantitative economic value on only a subset of the services provided by the natural habitat (Balmford *et al.*, 2002). If the value of

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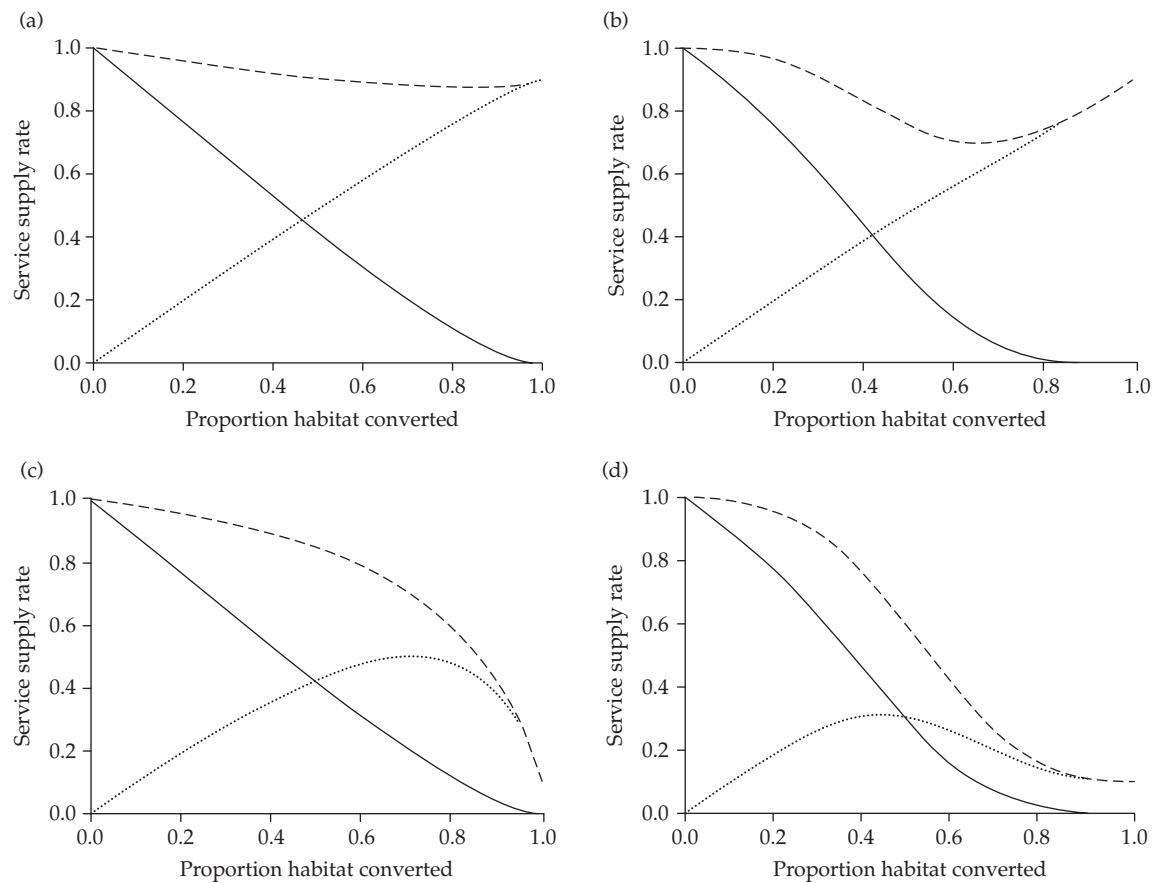


Figure 13.7 Net services produced by simple mixtures of converted and pristine habitat (y axis); in all cases the x axis is the proportion of habitat converted from pristine habitat to agricultural land, the solid line illustrates the declining rate of production of ecosystem services (to converted habitat) as pristine land is converted, the dotted line is the value of services produced in the converted (agricultural) habitat, and the broken line is the sum of the services produced in the mixture of two habitats at this level of conversion (eqn 13.10 in the text). We have illustrated four different scenarios that reflect all four combinations of high/low dependence and fast/slow rates of ecosystem service decline. (a) Weak dependence of agriculture on pristine land ($d=0.1$) and services decline slowly ($ES_{50}=0.5$) as habitat is lost. (b) Weak dependence of agriculture on pristine land ($d=0.1$) and services decline rapidly ($ES_{50}=0.2$) as habitat is lost. (c) Strong dependence of agriculture on pristine land ($d=0.9$) and services decline slowly ($ES_{50}=0.5$) as habitat is lost. (d) Strong dependence of agriculture on pristine land ($d=0.9$) and services decline rapidly ($ES_{50}=0.2$) as habitat is lost.

the services provided by the modified habitat are assumed to be similar to or less than those provided by the pristine habitat, then we will be able to detect changes in the value of these services only when the modified habitat's value is highly dependent upon the area of pristine habitat. When the services provided by the modified habitat are largely independent of the pristine habitat, the rate of change of land value may be too shallow to be detected as more of the pristine habitat is

degraded or converted. In many cases, the initial decline in land value will be reversed as the new land use comes to dominate the landscape. Unfortunately, mistakes are costly; doubly so as the cost of restoration may take many years to be recovered. If developers discount the future, services supplied by pristine habitats may never be recovered once conversion has proceeded beyond a critical economic threshold where the cost of restoration exceeds their future discounted potential value.

13.6 Conclusions

Our goal in writing this chapter has been to illustrate and suggest emerging areas in conservation biology where theory can provide valuable insights into real-world problems. The problems we explored ranged from the very specific (e.g. is the grizzly bear population around Yellowstone National Park in danger of extinction?) to the very general (e.g. what is the relationship between land-use change and the loss of ecosystem services?). This is significant, for it indicates the breadth of opportunities awaiting theoreticians interested in tackling applied problems. Indeed, we note with pleasure that a large fraction of the students applying to graduate programs in ecology today do so with an avowed interest in conservation biology.

It is also worth emphasizing that many of the most interesting examples discussed in this chapter involve the integration of the social sciences, especially economics, into solutions to ecological problems. Examples include the incorporation of cost constraints into the selection of reserve networks (a problem that also requires one to delve into operations research) or linking rates of deforestation to the values of ecosystem services produced by pristine and disturbed lands. Economic considerations have been a part of some ecological models (e.g. fisheries) for decades, but on the whole, the social sciences have yet to be incorporated into much of the theoretical research now underway in conservation biology. We predict (and hope!) this will change, given that a viable solution to an environmental problem must make sense not only from a scientific perspective but also from a socio-economic one.

There is no reason why advances in applied fields cannot yield insights relevant to more academic disciplines, and this is certainly true in the case of conservation biology. The population viability models used to guide policies for imperiled species continue to shed light on the structure and functioning of metapopulations. Conversely, metapopulation theory has been enormously influential in conservation biology. Thus, one is tempted to conclude that the distinctions between theory and practice, or pure and applied, are illusory to a large degree. For aspiring theoreticians, we offer this advice: Pay attention to applied problems, for they offer plenty of theoretical challenges as well as practical benefits. And for conservation practitioners, we suggest that theory (in its many forms) will play an increasingly valuable role in the search for solutions to real-world problems.

Of course, the conservation of biodiversity will depend ultimately upon the preservation of natural habitats, the restoration of degraded ones, and the discovery of new ways to maintain important ecosystem services on lands largely devoted to activities such as farming and energy generation. Our major worry, therefore, is that whatever scientific progress we are making occurs against a backdrop of a worldwide series of uncontrolled experiments, involving the destruction of wildlands, extinction of species, changes in nutrient cycles, and even changes in the Earth's climate. If we may offer a final, whispered word of advice to the upcoming generation of theoretical ecologists and conservation biologists, it is simply this: hurry!



Add reference

WDPA - World Database on Protected Areas (2004)
 2004 World Database on Protected Areas. CD-ROM.
 IUCN World Commission on Protected Areas, UNEP
 World Conservation Monitoring Center, Washington, D.C.