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ECOLOGY: AN IDIOSYNCRATIC OVERVIEW

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Ecology: An Idiosyncratic Overview

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Ecology is a word which conjures up disparate images in the minds of different people. It is part of the rhetoric of political parties, cries for salvation of dwindling species, attempts to increase utilization of renewable resources, determined efforts of scientists to understand our natural world, and blatant commercialism of products from laundry detergents to oil rigs. Aside from its use as an adjective to modify virtually every scientific research field, as the jargon "ecologically sound" it justifies a plethora of so-called development schemes from fragile wilderness areas to the urban metropolis. In daily usage it is regularly confused with environmentalism, and to those in the business community an ecologist may well be automatically considered an obstructionist. Despite all this misunderstanding of definitions, the concepts of ecology have had a major impact on the changing attitudes of humanity towards our world during the past two decades. Photographs of our glowingly beautiful orb as viewed from the moon notwithstanding, our conscious acceptance of the finiteness and interdependence of processes on this planet is, however, only slowly developing.

Some might well argue that the reduction of the startling complexity of our natural world to a system of scientific thought is a debasement of the beautiful intricacies that surround us. Certainly anyone only just slightly aware of the diversity of life that exists in even the most depauverate environments must have some feeling of awe towards this creation which we often take for granted. One of the major implications of modern ecological research is the immensity of the task before us, if we really wish to comprehend not just the structure of our natural world, but also the mechanisms that have caused that structure to evolve. Our ignorance is manifest. Acceptance of this ignorance, however, should not imply unwillingness to reduce its scope. In many ways, a scientific approach to studying the natural systems in which

we live not only increases our knowledge, and thus our ability to avoid mishandling the systems, but also develops our appreciation for its beauty.

What is it all about?

When discussing the science of ecology, it is quite important to properly limit the scope of the discussion. Indeed, essentially every field of biology could be considered a part of ecology. Medical science often deals with the environment internal to the human body and its effects on micro-organisms; agricultural science with the influence of environment on managed ecosystems; physiology and neurobiology with internal chemical environments and cellular response to them; while fields such as botany, zoology and psychology all include ecological components. One of the major impacts of ecology on scientific thought over the last several decades has indeed been the introduction of an ecological perspective to quite disparate fields. The importance of biotic interactions along with abiotic ones has been only gradually appreciated.

Given that ecology touches upon virtually every field of biology, and additionally requires knowledge of many non-biological sciences, how do we go about actually defining the field? Unfortunately, there are as many different definitions as there are textbook writers, a situation which is bound to discourage those with a mathematically-inclined penchant for exactitude. Historically, the term goes back to Henry Thoreau, though Ernst Haeckel first defined ecology as "Haushaltslehre de Nature" - the study of the economics of nature. See Krebs (1978) for a history of the term. Some examples of modern definitions of ecology are:

(i) the scientific study of the distribution and abundance of organisms (Krebs, 1978);

(ii) the study of the natural environment, particularly the interrelationships between organisms and their surroundings (Ricklefs, 1980);

(iii) environmental biology (Odum, 1971).

These differences in definitions are also backed up by the quite different viewpoints authors use in describing the subject. Krebs (1978) emphasizes distribution and abundance, Remmert (1980) puts more emphasis on physiological aspects, Odum (1971) pursues a systems-theory approach, while Emlen (1973) attempts a synthesis from an evolutionary perspective. Perhaps because of the highly diverse subject matter of the field and the non-agreement on a limiting definition, it has become common for ecology to be split up into a large number of subdisciplines. Some examples are physiological ecology, behavioral ecology, population ecology, human ecology, evolutionary ecology, systems ecology and hosts of others. Despite all this splitting, there is general agreement on the basic subject matter included in the field. For our purposes, I shall group this into four areas - physiological, population, community and ecosystem. Below, I give a brief overview of the questions addressed by each of these divisions. However, it should be kept in mind that these areas are in no sense independent - ecological research is highly interdisciplinary and often requires perspectives from different levels of the natural system under consideration.

It is worthwhile throughout this discussion to be aware that at this point in its development, the science of ecology has only one underlying paradigm - that of the theory of evolution. An evolutionary perspective, although often not explicitly stated, guides much of the current thinking on population and community structuring, organism adaptations to the environment, and ecosystem functioning. Although there are divergent opinions as to the mechanisms by which evolution acts (see for example, D.S. Wilson (1978) for one such alternative to the neo-Darwinian mechanisms of natural selection), this in no way reduces the importance evolutionary theory has in formulating and evaluating hypotheses about ecological phenomena. The laws of chemistry and physics are also fundamental to an understanding of many ecological processes, especially at the physiological level; however they do little to provide any overall structure to the field. In many respects, ecology

still lacks the capability to extend the results of a particular ecological study to similar systems in other regions of the world, or to species or conditions other than those investigated. Potentially, ecological theory may give us some indication as to how representative a particular observation or experiment is of the world in general. At present, except under fairly restricted circumstances, our theories simply cannot handle the complexities of the real world. The trade-offs between realism, precision, and generality (Levins, 1968)are particularly evident in ecology. There is certainly much room for improvement of the theories, but real advances in basic understanding will only be made through coupling theory with careful observation and experiment.

Physiological Ecology

Generally, physiological ecology refers to the study of the direct effects of the physical environment on individual organisms. Its emphasis is on how factors such as temperature, water availability, radiant energy, and wind affect the distribution of organisms, how the organisms adapt to variations in these factors within their lifespan, and how these factors have produced selective forces which bring about evolutionary change. Although abiotic factors are often the ones under study, organisms have the capability to modify their environment and thus biotic interactions also come into play. The structuring of the overstory in a forest canopy affects the environment of the understory and an animal may through movement modify its environment, an example being the shuttling behavior of lizards for the purpose of thermoregulation. It is this feedback between organism and environment, operating on time scales from fractions of seconds to years depending upon the organism and the particular process, which serves as the focus for much research in this area.

The maintenance of homeostasis, by which we mean that certain metabolic processes are regulated to stay within a range that the individual can tolerate, is a central problem that is faced by all lifeforms. Examples would be the maintenance of water saturated conditions within a leaf, proper osmotic potential in salt-water fish, or the relatively fixed body temperatures in homeotherms. One goal of research is to determine what physiological mechanisms limit the tolerance of individuals for environmental extremes and how these tolerance limits change due to genetic and developmental influences. Due to this interest in tolerance limits, a very common research tool is to study organisms in very harsh environments, in which the physiological constraints on the organism and the adaptations to cope with environmental extremes are quite evident. Examples would be the conditions at timberline (Tranquillini, 1979), or in hot, dry deserts (Osmond *et al.*, 1980). Homeostatic mechanisms ultimately have their origin in biochemical processes (Hochachka & Somero, 1973), and although this is recognized by ecologists, it is relatively rare for studies to be carried down to the biochemical level. The level of integration considered is the organ or whole individual.

To a great extent physiological ecology deals with biophysics. The reductionist approach to this area, in which all environmental influences acting on an organism are analyzed according to established laws of physics and chemistry, has been quite fruitful. See Campbell (1977) or Gates (1980) for a detailed analysis. Here for example, the heat and energy loads on an organism are analyzed by taking into account conduction, convection, radiation and evaporation. This leads to predictions based upon physical principles about which leaf sizes and shapes, how much fur or feathers, and what type of behavior are to be expected in particular environments. Another process which is heavily researched in this area is photosynthesis, with emphasis on how light, temperature, humidity, and atmospheric concentrations of carbon dioxide affect the capacity of a plant to transform solar energy into organic carbon compounds. A combination of laboratory and field observations are usually undertaken. Perhaps the most difficult aspect of biophysical work is dealing with the multiplicity of factors which often affect any particular physiological process. Establishing organism response to changes in any single environmental factor may be easily accomplished, but coupling this with responses to other factors requires assumptions about the additive or multiplicative effects of various inputs. Since real environments are quite dynamic on time scales within which physiological processes respond, the step of moving from experimentally controlled environments to those which organisms actually encounter is one in which mathematical modelling can be quite useful. See Hesketh & Jones (1980) for a detailed study of this approach to photosynthesis.

Inherent in the reductionist approach is that whole organism response can be deduced from analysis of the processes which make it up. In this view the whole is indeed the sum of the parts. An alternative approach is the holistic one, which implies that there are properties of natural systems - the jargon in ecology is "emergent properties" - which arise due to the structure of the system and could not be predicted from knowledge of the subcomponents alone. Although usually associated with ecological work at the community or ecosystem level, this concept comes into play at the physiological level, especially for evolutionary questions. It may be nigh impossible to consider all the environmental factors acting on an individual, and so concentration occurs on the one or two influences, called "limiting factors", which are found to have the most impact on the organism. The reductionist approach thus has its limitations, and an alternative is to consider phenotypic strategies for adaptation to environment. Here, within constraints set by the known biophysics, evolution is viewed as selecting individuals with phenotypes which are best suited for particular environments. A criterion for what is meant by best must be defined, some examples being net photosynthetic gains for a leaf, or rate of food intake by foraging animals. The optimum phenotype is then chosen according to this criterion, subject to physiological constraints, and then comparison is made with actual observations. The assumption is that there is sufficient genetic variation to enable evolution to bring about this optimum, and that you've chosen the proper criterion. This is subject to controversy (Lewontin, 1978), but the approach has led to a body of theory that some consider very useful (Pyke *et al.*, 1977). Certainly, the strategic approach serves as a way to tie together what we know about biophysics with the logical evolutionary consequences of that knowledge.

The results of physiological ecology find application to crop and forest growth analysis (de Wit & Goudriaan, 1978). Knowledge of plant response to environmental factors plays a major role in current research on such problems as assimilate partitioning, the effects of fertilization and irrigation, the energy potential of biomass, and the capacity of crop varieties to adapt to changing environmental conditions. Knowledge from the physiological level is critical to the construction of valid systems models of not only single-species crops, but also natural communities. Since physiological experiments are generally more readily carried out than those at the community level, in some senses we have a much better understanding of processes at the level of the individual than at that of the community. However, we are still far from a complete understanding of even the most basic physiological processes.

Population Ecology

At this level, the science investigates the dynamics and structure of populations of a given species. The definition of population depends upon the scale of interest. A field ecologist may study all the fish of a species within a particular lake, a system of lakes and rivers, or worldwide. In theoretical analyses, this variety of scales is often ignored, but they do lead to quite different assumptions about the mechanisms controlling population growth and decay. The chief questions of interest in population ecology concern how a population is structured, in terms of age, size and genotype, how this structure changes both temporally and spatially, and what factors external and internal to the population regulate this strucutre. For an excellent overview of the field, see Hutchinson (1978).

From the point of view of a field biologist who may be interested in establishing the size and structure of a population, a standard practice is to estimate the death and birth rates for individuals in different classes, the most usual being age classes. This allows the construction of a life

table, consisting of a number of variables as functions of age, including survivorship, mortality rate and expectation of further life, which describe the mortality schedule of the population. When combined with a fecundity schedule, it is possible to make predictions about future age structures, given an initial age distribution. The applicable techniques are the same as those in human demography (Keyfitz, 1968), the major difficulty being the statistical aspects (Poole, 1978). For plant populations, fecundity and mortality often depend more upon size than age, and although there are complications introduced due to non-linear relationships between these, size structured methods have been used (Caswell & Werner, 1978). The development rate of an individual may often be environmentally dependent, and thus transformations to such variables as degree days are common in studies of agricultural dynamics, along with other physiological time scales for insect development (Curry *et al*., 1978).

Population biology is perhaps the most mathematically developed area of ecology, with a long history of interest by mathematicians in the problems associated with the dynamics of populations. Early studies of the population fluctuations of small mammals and a variety of organisms studied in the laboratory lent themselves well to a mathematical formulation. Far and away the greatest emphasis has been on animal populations, leading to the development of fairly sophisticated models in both discrete and continuous time (Freedman, 1980), with and without delays due to maturation times (Cushing, 1974), along with stochastic models (Ludwig, 1974). A great deal of recent research deals with the effects of spatially non-uniform environments (Levin, 1976) and the diffusive spread of organisms (Okubo, 1980). Despite all the theory which has been developed, it is unclear how predictive the models are for situations other than the laboratory (Nisbet & Gurney, 1982). Part of the reason for this is the temporal heterogeneity associated with any natural environment. There is a long-standing controversy within population biology regarding whether populations are mostly regulated by density-independent factors (often considered abiotic) or density-dependent ones (often due to biotic interaction). The theories go a long way towards analyzing the effects of density-dependent factors, but provide much less information on abiotic factors, due to their complexity and variability. It is at this point that input from the physiological studies is needed to construct realistic theories of population structure. This combination of physiological ecology with demography serves as the focus of the rapidly growing study of plant population biology (Harper, 1977), a field which has developed relatively slowly in comparison to animal ecology at this level.

Another area of great current interest is the study of life histories, by which is meant the reproduction, growth and senescence patterns exhibited by a population, which determine its long-run behavior. In a similar manner to the strategic approach to studying physiological adaptations mentioned earlier, the idea here is to consider such factors as time of first reproduction, number of offspring per clutch, number of reproductive phases per lifespan, and energy expended per offspring as variables under genetic control. It is then assumed that evolution acts to maximize some measure of population growth, for example the mean population fitness. Predictions may then be made about the circumstances in which certain life histories are to be expected. See Stearns (1976) for a review. Again, this approach can be subject to the criticism levelled at optimization in evolutionary theory, but it can be tied into a population genetics framework (Roughgarden, 1979) and has proved very useful in deriving hypotheses about ecological phenomena which are subject to testing.

Behavioral ecology is another field which has become intensively studied in recent years, the goals being to analyze specific behavioral traits of animals in light of ecological constraints. The evolution of co-operation within social groups, territoriality, parental care, and dominance hierarchies may be viewed from a game theory perspective, leading to the theory of evolutionarily stable strategies (Maynard Smith, 1982). Conflicts of interest (as measured in terms of an organism's fitness) are settled in this theory through an evolutionary dynamics towards a Nash equilibrium solution of a game, meaning a solution which is stable under perturbations of the strategies played. Again, controversy has arisen regarding how appropriate this solution is to evolutionary biology (Lewontin, 1978), but it can often be demonstrated analytically that this solution is consistent with calculations from population genetics which track the full genetic trajectory of the situation (Maynard Smith, 1982).

The approaches of population biology have great applicability to wildlife management practices, especially regarding the problem of setting harvesting levels so as to attempt to maintain optimum yield (Clark, 1976). Models of population dynamics are central to the understanding and application of optimal control techniques for containing pest outbreaks (Vincent, 1981). Large portions of the sciences of forestry, fishery biology, and wildlife management rest upon the theories of population structuring, so that improvements in our theories will hopefully lead to better resource utilization.

Community Ecology

When all the populations of species within a prescribed region are considered as an interacting unit, we call this a community. Although intuitively it is relatively easy to perceive different communities, such as prairie grassland, mixed-deciduous forest, or ephemeral pond, the actual classification of community types historically involved vast effort on the part of many ecologists, often with quite a bit of acrimony. Part of the contention involved whether a community should be perceived as a "super-organism" with its own emergent properties not derivable from those of the populations which make it up. The debate is hardly settled, but it is probably fair to say that most ecologists view the superorganism concept as generally untenable, though there are indeed properties of a community, such as succession, which are inherent in the interactions between populations, and not in the populations themselves. For a discussion of the history of classification, see Whittaker (1962), or Golley (1977). A wide variety of methods are regularly used by ecologists especially analysis of species changes along an environmental gradient and numerous multivariate statistical techniques (Gaugh, 1982), in attempts to elucidate correlations between compositional changes and environmental variations within the community.

The central problems of modern community ecology are the studies of diversity and stability, trophic structure, and community dynamics. In all of these, it is common to consider just isolated parts of a particular community. Thus in a predator-prey system such as the lynx-hare, effects of the hare on grass or of lynx droppings on fly populations are ignored. This reduction of a real world community to an isolated portion is utilized in field, laboratory, and modelling studies. Its justification is based upon the assumption that the major impacts on the populations you consider occur completely within the sub-system chosen. This very much depends upon the scale of the problem under investigation, for if other biotic influences change on a slow time scale relative to the populations you are considering, then they may be viewed as fixed. For example, in models of spruce-budworm outbreaks, the response of the trees is much slower than the insects, and thus the dimensionality of the problem is reduced (Ludwig *et al.*, 1978).

A large theory of community dynamics has developed through the analysis of systems of ordinary differential equations to describe population density changes caused by competition, commensalism, and predator-prey types of interactions. The theory for two-species systems is quite well developed, though higher order systems involve considerably greater complications and it isn't clear how results from two-species systems carry over to multi-species situations. Although full dynamic solutions can be derived for many two-species cases, often in higher dimensions one is limited to an analysis of the equilibria. Thus there has been great emphasis placed on studying the local asymptotic stability of these equilibria. The biological relevance of this definition of stability is quite debatable (Lewontin, 1969), although due to ease of analysis, it is often the only form of stability investigated. A number of other measures of stability have been suggested and investigated, including the persistence of the system (no species approach extinction) and resilience (time constant for return to equilibrium following a perturbation). See Maynard Smith (1974).

Associated with investigations of stability is the question of whether stability is enhanced by higher diversity, meaning the number of species in a community. A typical example of this would be the decrease in diversity as one moves away from the tropics. Results from certain multi-species models indicate that stability may be decreased by increased diversity (May, 1973), although the area is still quite murky, partially due to the quite different definitions of stability used by various investigators (Robinson & Valentine, 1979).

The manner in which multi-species assemblages are structured as a hierarchy of energy flows within the system revolves around its trophic structure. This is based upon who eats whom, and the relative proportions of the populations which are plants, herbivores, carnivores, omnivores and detritivores. Within any community the trophic interactions form a complex pattern, often more of a web than the classical food chain. Analysis of the structure of these food webs (Cohen, 1978; Pimm, 1982) has led to some generalizations about them, such as the ability to represent them as an interval graph. The analysis of such webs is closely related to theoretical studies of niche partitioning, meaning the manner in which limiting resources are partitioned among populations, each of which has their own functional roles, or niches, within the community. See Whittaker & Levin (1975) for an exposition of the niche concept.

Results from community ecology can play a major role in settling such issues as the proper site and pattern of wildlife refuges in order to preserve endangered species (Terborgh, 1975). In this view, the results of island biogeography, which attempts to relate species diversity to such factors as island or refuge area, and inter-island distances (MacArthur & Wilson, 1967), provides a framework for the analysis of this problem. Although arguments can be made about the limitations of our current ability to apply such theories (Simberloff & Abele, 1976), the theory serves a focal point for further analysis. Community theory may be ultimately quite useful also in providing predictive estimates of the potential for pest outbreaks (Conway & Murdie, 1972), an area of great importance in agriculture.

Ecosystems

An ecosystem may be defined as the collection of communities within some region, taken together with the environmental influences upon them. Thus the communities contained within a certain watershed, bay, or old field could all be considered as ecosystems, particularly if the emphasis of their analysis concerns biotic-environment interactions and feedbacks throughout the system. Major questions of interest in ecosystem studies concern the flow of nutrients, energy, and biomass through the system. Coupled with this are the patterns of successional change in the system through time, and how these affect such factors as primary and secondary production by the system. Here primary production refers to the energy content of materials produced by plants from solar energy inputs, while secondary production refers to energy obtained by consumers from plants used for growth and reproduction. See Whittaker (1970) for estimates of the productivity of a variety of ecosystems.

It is perhaps worthwhile noting at this point that the division between ecosystems and community ecology is not a sharp one and some authors would include most of the topics mentioned in the above paragraph as being community metabolism (Krebs, 1978). Despite this, I choose to make this a separate category of ecological research because the approach to answering the above questions is mostly that of systems analysis. By this I mean that the system is broken down, sometimes quite arbitrarily, into a set of compartments, for example primary producers, consumers, and detritivores in a simple ecosystems model. The flows of the currency of interest, such as energy, between compartments are then estimated, and a model constructed. The model is analyzed, tested against an independent set of data, and then utilized to answer questions of interest. This approach served as the basis of the International Biological Program, which attempted to collect immense quantities of data on particular ecosystems around the world, utilize computer-based systems models to collate all this information, and then use the model to analyze the system. Although the IBP definitely aided our understanding of many natural systems, the original hopes of realistically simulating a system via a computer were generally unrealized. Even the simplest natural systems are far too complex for the interactions to be suitably well understood to meet the demands of model construction. Even if adequate data were available to specify the functional forms for the interactions in the models, the enormous number of parameters necessary are quite difficult to specify even approximately with the available data. There is thus the danger that virtually any result desired can be obtained from the models, just by choosing appropriate parameter values. Despite this, IBP resulted in a collection of very fascinating studies, for example on the convergence of form and structure in mediterranean-type ecosystems around the globe (Miller, 1981). Systems approaches have been quite useful tools in forming an underlying structure for the study of a wide variety of ecosystems problems. See the series of books by Patten (1971).

Despite the difficulty imposed on ecosystem studies due to the great complexity of the interactions involved, it is at this level that the great number of public policy questions concerning human acitivities and their ecological impacts must be answered. The effects of environmental toxicants, construction of power plants which use rivers and lakes for cooling, mining in wilderness areas, and hosts of other actions of society pose challenging questions for ecologists. Unfortunately, the answers are required now and there is rarely time for adequate background research to be undertaken. There is probably some doubt that we shall ever be able to completely understand even a single natural system, but it is clear that with adequate time for study we shall be able to give, if not perfect, then at least rough estimates as to the effects of particular human activities on natural systems. One example is that of clear cutting a forest, the effects of which only become apparent after many years of study (Bormann & Likens, 1979). No matter how complex a computer model is constructed, it is worthless without the understanding of the underlying processes that can only be determined from field and laboratory studies.

Conclusions and the Role of Mathematics

The above review is ideosyncratic in that I have purposely emphasized some areas and left others virtually unmentioned. I have definitely slanted my remarks towards theoretical ecology, and have not discussed field techniques and statistical methods. There is certainly no lack of fascinating statistical problems which crop up in ecological studies, but I consider them to be a part of statistics, not ecology. I have not tried to give anything like a complete overview of the subject, but wished only to briefly mention those areas which I consider essential and that a theoretician should be informed about. My own biases have certainly crept in, and one should keep in mind that ecology is a highly contentious field. Others will undoubtedly argue with my choice of topics and my comments.

I view mathematical modelling as having three potential uses, not necessarily independent, in any field. A model may be descriptive, in the sense that it synthesizes the available information on a process with no real attempt to explain the underlying mechanism. An example would be a regression fit to data, a model in the statistical sense. A model could also be explanatory in that it makes certain underlying assumptions about the process under study, and derives the logical implications of those assumptions. An example would be the effect of heat loading on a leaf in which the physics of conduction, convection and evaporative heat loss are applied to explain leaf temperatures. Thirdly, a model may be constructed for the purpose of predicting the response of the system to factors which haven't been observed. An example would be determining the effects of the rise in temperature in a lake, caused by a power plant, on fish populations. All of these uses come into play in ecological applications, though I think it is fair to say that it is the explanatory and predictive aspects that are potentially the most important. To date, most models are explanatory and often through their construction, they point out to us areas which need further study. This tendency for the process of model construction to display clearly our ignorance of a certain aspect of the system under study is very useful. For example, the most complex physiologically-based crop growth models still cannot compete with relatively simple regression models in terms of their ability to forecast yields. However the mechanistic models have clearly aided our understanding of crop systems merely by focussing our attention on certain processes - respiration is one - which require more study.

In my view, there are two different possible attitudes towards applying mathematics to biological problems. In one of these, a model already constructed is either analyzed further or extensions made to it, such as considering time-dependent solutions or adding stochastic variation. The emphasis is mathematical with little or no attempt to tie together the mathematical results with biological observation. It is essentially a mathematical exercise, with a bit of biological justification. I refer to this as biomathematics, though I realize there are many biomathematics departments in which this is not the approach. In comparison, consider the situation in which a biological problem is investigated with mathematical tools, but the mathematics is considered of purely secondary interest, as a means to an end. Here the mathematical techniques which are utilized are not specified beforehand by the expertise of the researcher, but are chosen as appropriate for the particular biological problem. The objective is to derive biological conclusions which are testable, not to develop elegant mathematics, though that may indeed occur. This I refer to as mathematical biology. A great deal of mathematical work in ecology has been biomathematics and, although the results can be fun mathematics, too often they are either irrelevant to biological problems, or completely outside the realm of real-world testability. Very few ecological models can stand up to intense scrutiny of their assumptions, simply because of our lack of knowledge. If the models are constructed with a firm basis in biological fact, however, there is the likelihood that their analysis will lead to results which are testable. Good applied mathematics is also good science.

Given that one is mathematically trained, and the objective is to do mathematical biology rather than biomathematics, how does one proceed? In my experience, there are two routes: either learn the necessary biology, or find a biologist who is willing to collaborate. Each path has its advantages, and to be truly successful, a bit of both is undoubtedly best. Becoming an expert in a certain biological discipline can be extremely time-consuming, but it is probably the best way to ensure that any modelling efforts undertaken are firmly rooted in observation. By immersing oneself in a field, it also becomes apparent what the major open questions are, and the biological intuition developed will certainly aid the rather iterative process of model construction. Collaboration has the benefit of not requiring as much time spent learning the biology, but to be effective, a certain minimum effort on the mathematician's part to learn at least the basics is necessary. As there are few who have the ability or desire to become biologists (in my definition a biologist is someone who can come up with a real-world counterexample to any statement a theoretician makes), collaborative work is essential, even for those with biological expertise in one discipline. Happily I have found a very positive attitude growing among biologists, especially ecologists, towards the utility of mathematics in aiding our understanding of ecological systems. This can certainly be enhanced by further efforts on the part of theoreticians to learn the relevant biology and view modelling as a path to a biological end, not a mathematical one.

References

Bormann, F.H. & G.E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, N.Y.

Campbell, G.S. 1977. An introduction to environmental biophysics. Springer-Verlag, N.Y.

Caswell, H. & P.A. Werner. 1978. Transient behavior and life history analysis of teasel (Dipsacus sylvestrus Huds.). Ecology 59: 53-66.

Clark, C. 1976. Mathematical bioeconomics. Wiley-Interscience, N.Y.

Cohen, J.E. 1978. Food webs and niche space. Princeton Univ. Press, Princeton, N.J.

Conway, G.R. & G. Murdie. 1972. Population models as a basis for pest control. P. 195-213 in J.N.R. Jeffers (ed.), Mathematical models in ecology. Blackwell, Oxford.

Curry, G.L., R.M. Feldman & P.J.H. Sharpe. 1978. Foundations of stochastic development. J. theor. Biol. 74: 397-410.

Cushing, J.M. 1974. Integrodifferential equations and delay models in population dynamics. Springer-Verlag, Heidelberg.

de Wit, C.J. & J. Goudriaan. 1978. Simulation of ecological processes. Centre for Agric. Publ. & Docum., Wageningen.

Emlen, J.M. 1973. Ecology: an evolutionary approach. Addison-Wesley, Reading, Mass.

Freedman, H.I. 1980. Deterministic mathematical models in population biology. Marcel-Dekker, N.Y.

Gates, D.M. 1980. Biophysical ecology. Springer-Verlag, N.Y.

Gaugh, H.G., Jr. 1982. Multivariate analysis in community ecology. Cambridge Univ. Press, Cambridge.

Golley, F.B. (ed.) 1977. Ecological succession. Dowden, Hutchinson & Ross, Stroudsburg,P.A.

Harper, J.L. 1977. Population biology of plants. Academic Press, London.

Hesketh, J.D. & J.W. Jones (eds.) 1980. Predicting photosynthesis for ecosystem models. Vol. I & II. CRC Press, Boca Raton, Florida.

Hochachka, P.W. & G.N. Somero. 1973. Strategies of biochemical adaptation. Saunders, Phila. PA.

Hutchinson, G.E. 1978. An introduction to population ecology. Yale Univ. Press, Provincetown, RI

Keyfitz, N. 1968. Introduction to the mathematics of population. Addison-Wesley, Reading, Mass.

Krebs, C.J. 1972. Ecology: the experimental analysis of distribution and abundance. Harper & Row, N.Y.

Levin, S.A. 1976. Population dynamic models in heterogeneous environments. Ann. Rev. Ecol. System. 7: 287-310.

Levins, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton, N.J.

Lewontin, R.C. 1969. The meaning of stability. Brookhaven Symp. Biol. 22: 13-24.

______________ 1978. Fitness, survival and optimality. P. 3-21 in D.H. Horn, R. Mitchell, & G.R. Stairs (eds.), Analysis of ecological systems. Ohio St. Univ. Press, Columbus, OH.

Ludwig, D. 1974. Stochastic population theories. Springer-Verlag, Heidelberg.

Ludwig, D., D.D. Jones & C.S. Holling. 1978. Qualitative analysis of insect outbreak systems: the spruce budworm and forest. J. Anim. Ecol. 47: 315-332.

MacArthur, R.H. & E.O. Wilson. 1967. The theory of island biogeography. Princeton, Univ. Press, Princeton, N.J.

May, R.M. 1974. Stability and complexity in model ecosystems. Princeton Univ. Press, Princeton, N.J.

Maynard Smith, J. 1974. Models in ecology. Cambridge Univ. Press, Cambridge.

________________ 1982. Evolution and the theory of games. Cambridge Univ. Press, Cambridge.

Miller, P.C. (ed.) 1981. Resource use by chapporal and mattoral. A comparison of vegetation function in two mediterranean type ecosystems. Springer-Verlag, N.Y.

Nisbet, R.M. & W.S.C. Gurney. 1982. Modelling fluctuating populations. Wiley, Chichester.

Odum, E.P. 1971. Fundamentals of ecology. Saunders, Phila. PA

Okubo, A. 1980. Diffusion and ecological problems: mathematical models. Springer-Verlag, Heidelberg.

Osmond, C.B., O. Bjorkman & D.J. Anderson. 1980. Physiological processes in plant ecology - toward a synthesis with Atriplex. Springer-Verlag, N.Y.

Patten, B.C. 1971-76. Systems analysis and simulation in ecology. Vol. I - IV. Academic Press, N.Y.

Pimm, S.L. 1982. Food webs. Chapman & Hall, N.Y.

Poole, R.W. 1978. The statistical prediction of population fluctuations. Ann. Rev. Ecol. System. 9: 427-448.

Pyke, G.H., H.R. Pulliam & E.L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 52: 137-154.

Remmert, H. 1980. Ecology. Springer-Verlag, Berlin.

Ricklefs, R.E. 1980. Ecology. Nelson and Sons, Middlesex.

Robinson, J.V. and W.D. Valentine, 1979. The concepts of elasticity, invulnerability and invadeability. J. theor. Biol. 81: 91-104.

Roughgarden, J. 1979. Theory of population genetics and evolutionary ecology. MacMillan, N.Y.

Simberloff, D.S. & L.G. Abele. 1976. Island biogeography theory and conservation practice. Science 191: 285-286.

Stearns, S.C. 1976. Life-history tactics: a review of the ideas. Quart. Rev. Biol. 51: 3-46.

Terborgh, J. 1975. Faunal equilibrium and the design of wildlife preserves. P. 369-380 in F.B. Golley & E. Medina (eds.), Tropical ecological systems. Springer-Verlag, N.Y.

Tranquillini, W. 1979. Physiological ecology of the alpine timberline. Springer-Verlag, Berlin.

Vincent, T.L. 1981. Proc. of a workshop on control theory applied to renewable resource management and ecology. Springer-Verlag, Heidelberg.

Whittaker, R.H. 1962. Classification of natural communities. Bot. Rev. 28: 1-239.

______________ 1970. Communities and ecosystems. MacMillan, N.Y.

Whittaker, R.H. and S.A. Levin (eds.) 1975. Niche : theory and application. Dowden, Hutchinson & Ross, Stroudsberg, PA.

Wilson, D.S. 1978. The natural selection of populations and communities Benjamin/Cummings, Meulo Park, Calif.