

# Ideas in Ecology

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The word "ecology" means different things to different people. For example, during the last 25 years or so the word has been used to label attitudes, life-styles, consumer goods, political parties, and college courses. In the 1960s one university renamed its "Home Economics" course "Home Ecology." (But our own biology department reacted to the growing visibility of its conventional "Ecology" course by renaming it "Population Biology.") It is often said that Thoreau coined the word "ecology." He certainly ought to have done so, given the Rousseauesque yearnings that surround the word, and this may be why the myth lives on, even though it stems from a 1958 misreading of the word "geology" as "ecology" in one of his letters (James 1985). The German biologist Haeckel was actually the first to use the word "Oecologie," in 1866.

The scientific discipline called ecology is more coherent intellectually than the spectrum of popular movements of the same name, but in many ways it is even more diverse.

Here we make no attempt to give a balanced or comprehensive account of the many lines of inquiry that have been pursued during the last hundred years or so. Instead, we comment on some problems that have long been of central concern to workers in the field, and that are likely to remain so. Our remarks are organized under three headings that correspond to what we see as distinct approaches that have shaped the thoughts and research programs of ecologists.

First, we discuss an approach in which the world is seen to consist of diverse roles and relationships that are acted out by individuals and species. Then we examine a somewhat newer approach in which populations are thought of as mechanistic dynamical systems with char-

acteristic ways of reacting to disturbance. Finally, we look at a currently very fashionable approach that focuses on the unconscious motives and strategies of individual actors on the ecological stage.

## Roles and relationships

Fascination with the habits and life histories of individual creatures goes back at least to Aristotle, and continues to motivate a host of amateur naturalists, particularly in Britain. Gilbert White's *Natural History of Selborne* stands as a landmark in that it is arguably the first work to see individual plants and animals not simply as isolated curiosities, but rather as parts of a community of living organisms, interacting with the environment, with other organisms, and with human beings. Often thought of as the first book on ecology, *Selborne* was originally published in 1789. It is today the fourth most reprinted book in the English language.

Its roughly 200 different editions provide a capsule history of changing tastes in book illustration and design during two centuries of apparently unflagging curiosity about the countryside and its inhabitants.

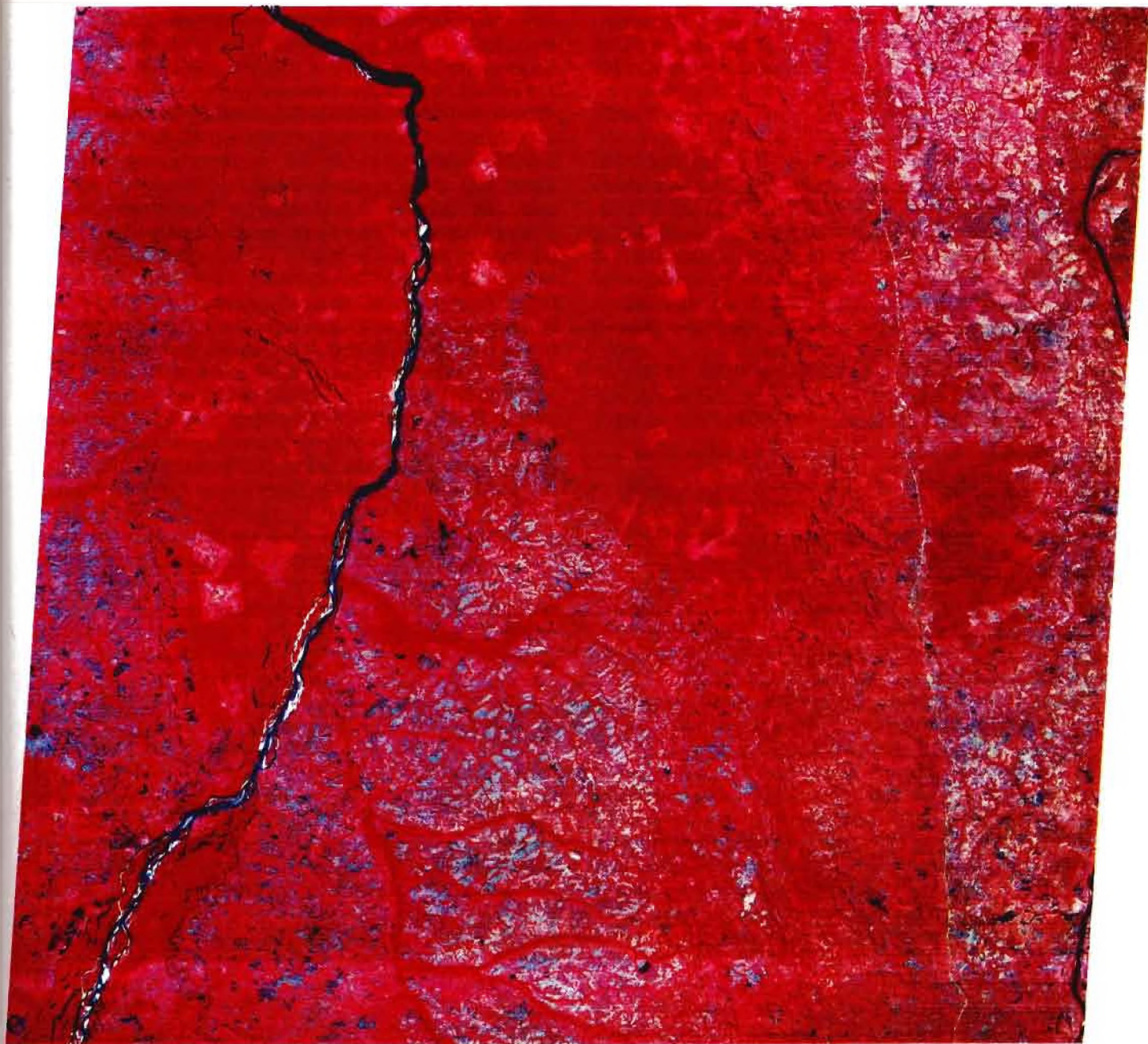
Darwin was a product of this tradition. Although the *Origin of Species* (1859) is primarily an evolutionary work, it also represents an advance in the definition of ecological questions. Darwin gives us the image of variously shaped wedges being pushed and hammered into a barrel as a metaphor for the way a set of species fit together to form a community. In outline this metaphor anticipates Hutchinson's definition (1957) of the niche as an abstract hypervolume situated in a space whose axes correspond to the biological and environmental variables affecting the organisms in question. The metaphor may also be taken to anticipate the still-unanswered questions of how communities are assembled and what controls the number of species/wedges we tend to find in a given environment/barrel. Elton's more concrete version (1927) of basically the same metaphor invokes the stylized village familiar to readers of Agatha Christie or Dorothy Sayers. Such a community is peopled with distinctive characters playing fixed roles—squire, doctor, lawyer, clergyman, postmistress, and so on—each role being in some way essential to the harmony and well-being of the entire community. The view that there exist fixed ecological roles is supported by the observation that ecological communities often bear striking resem-

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*Three complementary  
approaches have shaped the  
scientific discipline of  
ecology in this century*

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blances to each other even though their constituent species have very different evolutionary origins (Fig. 2).

The task of the research ecologist as it emerges from these earlier writings is to determine exactly which biological and physical factors characterize the niche occupied by a given species, and from this to build toward understanding how some combinations of species may persist together while others may not.

These issues were given sharp definition by Hutchinson in an influential paper entitled "Homage to Santa Rosalia, or Why Are There So Many Kinds of Animals?" (1959). What, Hutchinson asked, may be the limits to similarity among coexisting competitors? This question grew out of earlier work (discussed in the next section) suggesting that species with identical niche parameters could not persist together. As an example of the kind of answer that might emerge, Hutchinson noted that among some groups of competing species similar in all

Figure 1. A central problem in tropical ecology is to estimate the number of species likely to be permanently lost if deforestation continues at the current rate. This false-color Landsat image shows a mixture of tropical savanna and rain forest about 800 km south of Belém, Brazil. The area shown here is 185 km on a side.

Continuous forest appears intensely red, low vegetation is paler, bare ground is white, and water is blue-black. The Rio Araguaia, at the left, flows north toward the mouth of the Amazon River. The thin white line at the right is the Belém-Brasília highway, which was built in the late 1950s, opening this area for development. By 1973, when this image was made, several enormous rectangular ranches had already been carved out of the forest. Cleared land supports cattle ranching or other forms of agriculture for only a few years, because the thin soils quickly lose their fertility and erode. Worldwide, about 100,000 km<sup>2</sup> of tropical forest is felled every year. This is 2 to 3% of the remaining total, or about four times the entire area shown here. Tropical forests are by far the most biologically diverse places on earth, yet most of their millions of species of plants and animals remain undescribed and unstudied. (Reproduced by permission of EOSAT.)



respects except in the average sizes of prey taken, successive species differ by a factor of around 2 in average weight, or around 1.3 in linear dimensions. This suggestion has an appealingly quantitative air to it, and it is not surprising that the next ten years saw other examples of "1.3 ratios" added to Hutchinson's list, mainly from birds and predatory invertebrates. Co-occurring species of fruit pigeons in New Guinea provide some striking instances of this pattern (Diamond 1973). Other studies of the limits to similarity among coexisting competitors reformulated the question, going beyond morphological differences to ask more generally how much niche overlap is consistent with coexistence, or how much of their "niche hypervolume" co-occurring species may share.

Building on these ideas, Diamond (1973, 1975) and others looked at the patterns of presence and absence of individual bird species among the islands of archipelagos

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### *What, Hutchinson asked, may be the limits to similarity among coexisting competitors?*

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(mainly in the Pacific), and sought to deduce heuristic "assembly rules" governing the construction of bird communities: if species A and B are present, then species C is not; any one of species D, E, and F is likely to be present, but never any two; species G may be found in early stages of colonization of volcanic islands, but never later. These assembly rules were deliberately conceived as empirical precursors to a more fundamental understanding of the interactions that produced them, just as the phenomenological rules about "allowed" and "forbidden" lines in atomic spectra preceded a more fundamental explanation based on the quantum states of electrons.

Over the last ten years or so, Simberloff, Strong, and others have helped to set more rigorous standards in this search for community patterns (see Strong et al. 1984). It seems likely, for instance, that the 1:3 size ratio arises partly because sequences on this scale obtrude themselves, while significantly finer (or coarser) graduations are unconsciously dismissed. This notion receives oblique support from Horn and May's observation (1977) that we can readily find other collections of "competing" objects that obey the rule—skillets, recorders, the violin family, instars of children's bicycles, and so on. Arguments about the reality of apparently nonrandom size ratios stimulated Schoener (1984) to undertake a massive computational study in which the distribution of size differences between randomly chosen pairs (or triplets, or quartets) of hawk species is compared with the actual distribution of size differences between pairs (or triplets, or quartets) that coexist in the real world. Schoener finds significantly greater average size separation between species actually occurring together than is expected from his examination of the universe of all conceivable comparisons.

More generally, Simberloff and others have urged

that inferred patterns in community structure should always be tested against "null models" that describe what might be expected if communities were randomly assembled by sampling species from some larger pool. This is sound counsel, and is essentially what we do every time we assign a confidence level to a regression line. The special difficulty for community ecology lies in generating the hypothetical or "null" expectation. In principle, one could reshuffle the data themselves at random, as in Schoener's study. This method is closely related to recent "bootstrap" techniques in statistical hypothesis testing (Diaconis and Efron 1983; Efron and Gong 1983). But if the limited ecological data are indeed strongly conditioned by competitive or other biological interactions, then the randomly reshuffled universe may remain far from "neutral" (Colwell and Winkler 1984; Harvey et al. 1983).

A deliberately oversimplified example that illustrates this possible dilemma is as follows. Consider two species, A and B, which are distributed throughout an archipelago of  $n$  islands in such a way that every island contains either species A or species B—never neither, and never both. The simple view is that such a "checkerboard" pattern is manifest evidence for competition between A and B. A seemingly more critical way to approach these data is to construct a null model by randomly reshuffling the data. But if such rearrangement is subject to the constraints that there be two species and  $n$  islands, that each species be on as many islands as in the observed data, and that each island have one species on it, then all we have done, in effect, is to rechristen the islands; the checkerboard pattern remains. It would be absurd to conclude that the observed biogeographical pattern is therefore indistinguishable from a random assembly. Rather, we need a better null model, which in this simple case may be obtained by supposing species A to be present on any given island with probability  $p$ , equal to the fraction of islands actually inhabited by A, and likewise species B with its corresponding probability  $q$ . The null hypothesis would then have some islands empty, some with one species, and some with both. If  $n$  is not small, the observed checkerboard pattern will stand out as significantly different from a randomly colonized archipelago.

This example is grossly more simple than cases that typically arise in practice, but it illustrates the essentials. We need to be sure that apparent patterns are truly significant, but appropriate statistical tests and null hypotheses may be very hard to construct.

The search for limits to similarity among coexisting competitors has been further clouded by the realization that most species (and certainly most invertebrate species) live in a world that is heterogeneous in both space and time. For species that compete for patchy and ephemeral resources, questions of relative mobility are as important as relative success when the species meet on the same patch. If a competitively dominant species exhibits sufficient clumping in its pattern of egg-laying or other uses of resources, inferior competitors may persist even without any compensating advantages in superior mobility (Atkinson and Shorrocks 1981; Ives and May 1985). This may be an important reason why there is such a high diversity of species in the tropics. Seasona-

lity or environmental unpredictability can further complicate competitive interactions in a variety of ways (Chesson 1985).

The current state of play is well summarized in two recent reviews, one by Schoener (1983) and one by Connell (1983). Schoener analyzed 164 field studies on interspecific competition, in which population densities of one or more species were manipulated and the response of other species was measured. He concluded that competition demonstrably occurred between species in 90% of the studies, and that competitive interactions were present at essentially all times in most of the studies. Connell imposed stricter criteria for including manipulative field experiments on competition in his synoptic list, and ended up with 72 studies (most of which were also in Schoener's list of 164). Like Schoener, Connell found evidence for competition between species in a very high proportion—83%—of the studies in his survey. Unlike Schoener, he found the strength of

interspecific competition to be variable in more than half the studies, waxing and waning in response to environmental changes. Both Schoener and Connell found the competitive effects to be asymmetrical in most instances, with the effects of species A on species B typically being stronger or weaker than the effects of B on A. Such pervasive asymmetry was also found in a more restricted review of evidence for competition among insect species by Lawton and Hassell (1984).

Schoener concludes that interspecific competition is more firmly evidenced, and typically stronger, among primary producers (that is, plants that compete for space, light, and nutrients) and carnivores (themselves usually relatively free from predation) than among herbivores. This is what most theorists would expect. But Connell's smaller sample of studies did not clearly suggest that competition was more pervasive at the bottom and the top of food chains than in the middle. Schoener found that the evidence for his bottom-and-top pattern was stronger in terrestrial and freshwater communities than in marine systems. Connell may not have observed the pattern because marine systems form a larger fraction of his list of 72 studies than they do of Schoener's list of 164 studies. Both reviews emphasize that in most cases there is clear evidence that competition between individuals is stronger within species than between them, which again is what most theorists would expect.

We have chosen to dwell on competitive relations because the issues have exercised North American ecologists for the past several decades. But we do not share the belief of some ecological researchers that "competition was the only game in town" in the 1960s and 1970s (see

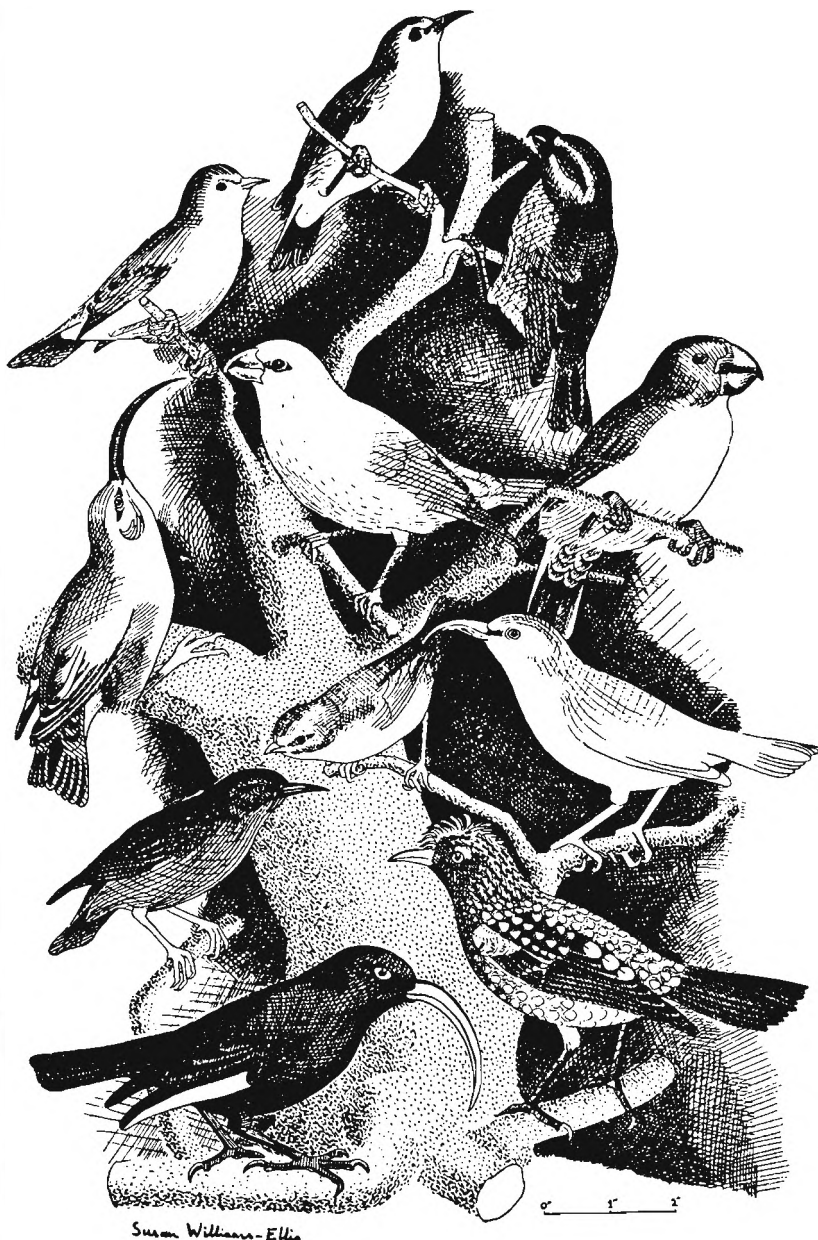


Figure 2. The idea that particular sets of interlocking ecological "roles" tend to appear again and again is strongly supported by adaptive radiations like that seen in the Hawaiian honeycreepers, shown here. All these birds are believed to be descended from a single ancestral species that arrived in the Hawaiian Islands only a few million years ago. Forms rapidly evolved to fill the niches usually occupied on the continents by parrots, hummingbirds, finches, flycatchers, warblers, and the like. The species are spectacularly similar in behavior and morphology to their ecological analogues on the continents, even though they have very different evolutionary origins. Many such instances of independently derived but strikingly similar adaptations are known from islands and island continents such as Australia and pre-Pleistocene South America. This drawing is taken from Lack's classic work (1947) on the adaptive radiation of Darwin's finches on the Galápagos Islands. (Reproduced by courtesy of Cambridge University Press.)

Table 1. Estimates of the number of papers on various topics published in the *Journal of Animal Ecology* and in *Ecology* from 1965 to 1975, inclusive

Topic	<i>Journal of Animal Ecology</i>	<i>Ecology</i>
Genetics, evolution	8	14
Behavior, physiology, autecology	201	900
Single population dynamics	120	126
Interspecific competition	20	98
Prey-predator (host-parasitoid and some plant-herbivore)	50	60
Other interactions (mutualism, plant-pollinator, host-parasite, etc.)	9	21
Ecosystems and communities	59	310
Miscellaneous (techniques, etc.)	7	136

Lewin 1983). A survey of journals and texts of the period shows large bodies of work dealing with interspecific relations between prey and predators or between hosts and parasitoids (parasitic wasps and flies). Relations between mutualists and between hosts and their viral, bacterial, protozoan, and helminth parasites did receive less attention, although this is now changing. Table 1 provides support for these impressions, roughly cataloguing the number of articles in the *Journal of Animal Ecology* and in *Ecology* that treat competition, prey-predator, and other relations among species, along with other broad categories, in the period from 1965 to 1975, the decade often considered the heyday of studies of competition. (We would also have analyzed and tabulated the useful compilation of abstracts from other ecological journals published by the *Journal of Animal Ecology*, but these lists do not even include "competition" as a category, although they do include "parasitism.") Table 2 gives a rough count of pages dealing with various kinds of interspecific relations in some ecology texts around 1970.

It has even been argued that competitive interactions have received disproportionate attention during

Table 2. Estimates of the number of pages devoted explicitly to various kinds of interspecific relations in some ecological texts around 1970

Text	Competition	Prey-predator (plant-herbivore, host-parasitoid)	Other, including mutualism and parasitism	Total text pages
P. Colinvaux. <i>Introduction to Ecology</i> . Wiley, 1973.	22	46	0	580
J. M. Emlen. <i>Ecology: An Evolutionary Approach</i> . Addison-Wesley, 1973.	22	44	4	458
C. J. Krebs. <i>Ecology</i> . 2nd ed. Harper and Row, 1972.	41	30	1	631
R. H. MacArthur and J. H. Connell. <i>The Biology of Populations</i> . Wiley, 1966.	10	15	0	193
A. MacFadyen. <i>Animal Ecology: Aims and Methods</i> . 2nd ed. Pitman, 1963.	10	10	0	281
R. M. May, ed. <i>Theoretical Ecology</i> . Blackwell, 1976.	36	53	25	281
E. R. Pianka. <i>Evolutionary Ecology</i> . Harper and Row, 1974.	28	27	5	299
R. E. Ricklefs. <i>Ecology</i> . Chiron, 1973.	41	59	9	780
G. C. Varley, G. R. Gradwell, and M. P. Hassell. <i>Insect Population Ecology</i> . Blackwell, 1973.	28	33	1	178

most of the last century because they fit into a worldview congenial to Western capitalist societies. Not only is this argument inconsistent with the actual record of published work, but it also seems strangely illogical; we find it easy to imagine that dedicated capitalists would rather hear about prey-predator relations than about mere competition.

Having denied one generalization about how social contexts may have affected ecological research, we now offer a different but equally contentious speculation. Studies of ecological roles and relationships, whether based on Eltonian metaphors about the structure of village life or on concrete measurements of niche overlap, seem to us traditionally to have drawn more on the idiom of the social sciences than on that of the physical sciences. This is partly in the nature of the subject. The outcome of interactions among plants and animals is intrinsically probabilistic and circumstantial in a way that most macroscopic physics is not. But frustration with inherently imprecise data too often gives rise, in ecology as in the social sciences, to self-conscious "schools" of thought, and to equally self-conscious obsessions with one or another "scientific method." Contrast this with the irreverent attitude toward the philosophy of science more typical of physics, as seen, say, in Feynman's writing (Feynman et al. 1963; Feynman 1985).

A case in point is the current belief of some ecologists that interactions within or between species can legitimately be studied only by manipulative experiments in the field. Obviously such a study is best, if it can be done. But many important questions simply cannot be pursued in this way, because they would take too much time or space, or because ethical considerations intervene, or even because conventional replicates and controls are difficult to design in circumstances dominated by history and local accident. Situations that are not amenable to manipulative experimental study do arise in the physical sciences. Purely observational or correlative studies pervade astronomy, cosmology, geology, and much of large-scale meteorology and oceanography. So too, in ecology, different questions may require different approaches. This theme is developed at length in Gould's recent article on evolution in these pages (1986).

Studies of roles and relationships may also be seen as closer to the idiom of the social than the physical sciences in their emphasis on detailed understanding of specific interactions—even on Geertzian (1973) "thick description" of particularities—rather than on statistical analysis of general patterns. Both approaches ultimately contribute to understanding how many wedges fit into the barrel, but there are, as it were, many more studies of the texture and morphology of individual wedges and of the way particular wedges fit together than there are of the overall distribution of sizes and shapes of wedges.

In particular, surprisingly little attention has been paid simply to compiling information about the number of individuals as a function of physical size in a given location, or about the total number of species in different physical size classes, or about the way species are apportioned according to the extent of their geographical distribution. How many species are widespread relative to the number that are very localized? We simply do not know. There has been some empirical work on the distribution of relative abundance of species and on relations between area and number of species, but even this has dealt with particular taxonomic groups of species rather than with the relative abundance or total number of species playing particular roles (regardless of taxonomic affinities). Such systematic compilations are no doubt rare in part because the basic information is hard to get. But lack of good ideas to motivate such work is also important. This is in contrast with the rich diversity of ideas about competitive exclusion, niche overlap, prey-predator coevolution, and so on, that has stimulated so much empirical work on relations within and between species.

## Dynamical systems

A different style is to think of plant and animal species as being broadly analogous to electrical circuits or other machines. If the population is subjected to a particular natural or artificial disturbance, how will it react? This approach may be applied to individual populations, to interactions among populations, or to the study of entire communities of plant and animal species.

A basic question that arises under this rubric concerns the regulation of the size of natural populations. As Gilbert White, Darwin, and others observed long ago, all species appear to have the innate capacity to increase from generation to generation. The task is to untangle the environmental and biological factors that hold this intrinsic capacity for population growth in check over the long run. This task is made more difficult by the great variety of dynamical behaviors exhibited by different populations. Some populations remain roughly constant from year to year, others exhibit regular cycles of abundance and scarcity, and still others vary wildly, with outbreaks and crashes that are in some cases plainly correlated with the weather, and in other cases not (Figs. 3-5).

In an attempt to impose order on this kaleidoscope of patterns, one school of thought sees the relatively steady populations as having "density dependent" growth parameters (with rates of birth, death, and migration depending strongly on population density), while the highly varying populations have "density independent" growth parameters (with vital rates buffeted by environmental events, so that they fluctuate in a way that is wholly independent of population density). This dichotomy has its uses, but it can cause problems if taken too literally. For one thing, no population can be driven entirely by density-independent factors all the time. No matter how severely or unpredictably birth, death, and migration rates may be fluctuating around their long-term averages, if there were no density-dependent effects the population would, in the long run,

either increase or decrease without bound (barring a miracle by which average gains and losses canceled exactly). Put another way, it may be that on average 99% of all deaths in a population arise from density-independent causes, and only 1% from factors varying with density. The factors making up the 1% may seem unimportant, and their cause may be correspondingly hard to determine. Yet whether recognized or not, they will usually determine the long-term average population density.

## *The problem of determining what, if anything, regulates particular natural populations has engaged ecologists continuously over the past century*

We may think of the density-dependent effects as a "signal" that tends to make the population increase from relatively low values or decrease from relatively high ones, while the density-independent effects act to produce "noise" in the population dynamics. Our job is to separate the signal from the noise. For populations that remain relatively constant, or that oscillate in repeated cycles, the signal is fairly easily characterized (even though the causative biological mechanism may remain unknown). But for irregularly fluctuating populations we are likely to have too few observations to have any hope of extracting the signal from the overwhelming noise.

Two further complications have come to ecologists' attention only in the last few years. First, even if there were some purely deterministic equation (all signal, no noise) that reliably predicted future population size, the nonlinearities inherent in even the simplest such density-dependent equation can produce bizarre dynamics (May 1974). Consider, for example, the relation

$$N_{t+1} = aN_t(1 - N_t)$$

Here the population has discrete, nonoverlapping generations, as do many temperate-zone insects.  $N_t$  is the density (normalized to be less than unity) in generation  $t$ , and  $N_{t+1}$  the corresponding density in generation  $t + 1$ ;  $a$  is some chosen constant.

As can be verified by iterating the equation on a hand calculator, if  $1 < a < 3$ , then the population settles to a steady value, as our intuition would suggest. If  $3 < a < 3.570\dots$ , then the population settles into a steady cycle, alternating between high and low values (and repeating every two generations for  $a$  at the low end of the range, or every 4, 8, 16, ...,  $2^n$  generations as  $a$  increases). For  $3.570\dots < a < 4$ , this simple and purely deterministic equation describes an apparently random or "chaotic" population trajectory. (For  $a > 4$ ,  $N$  runs away to minus infinity.) Weird as this spectrum of behavior may be, it is not peculiar to this equation. Rather, it is generic to essentially all difference equations describing a population with a propensity to increase at low values and to decrease at high values. Similar behavior arises if there are many discrete but overlapping generations, or even





Figure 3. The common swift, seen here in flight, is one of many species of birds that tend to have remarkably constant population sizes. Such constancy suggests that their rates of survival and reproduction are related inversely to population density, probably by the availability of limiting resources such as food. In the late eighteenth century Gilbert White found exactly eight pairs of common swifts breeding in the village of Selborne. When Lawton and May (1983) recently returned to Selborne they found twelve pairs in the village, which has changed in many ways during the last two centuries. (Photography courtesy of François Merlet/Bruce Coleman, Inc.)

if population growth is continuous but with time delays in the regulatory mechanisms.

The mathematics of these deterministically chaotic phenomena were first set out by Myrberg (1962) and subsequently rediscovered independently by several people. But they remained a relatively arcane mathematical curiosity until population biologists moved them to center stage in the mid-1970s (Li and Yorke 1975; May 1976; May and Oster 1976). Since then, the subject has grown explosively, with deterministic chaos finding applications in fluid turbulence, circuit theory, structural mechanics, plasma physics, and elsewhere. In retrospect, it seems odd that such chaotic dynamics were not noted earlier, because entomologists and fisheries people studied equations like the one above back in the 1940s and 1950s (e.g., Moran 1950; Ricker 1954). Although these workers did find chaotic and cyclic dynam-

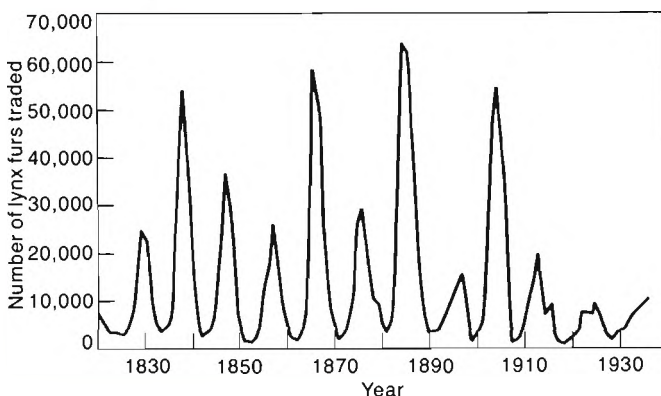


Figure 4. The lynx is the classic example of a species with regularly oscillating numbers, as is demonstrated by this graph showing fluctuations in the number of Canada lynx furs traded by the Hudson's Bay Company between 1821 and 1934. It was formerly believed that lynx were partners in a dynamically unstable association with their main prey, the snowshoe hare. But recent work suggests that the cycle is driven by the interaction between the hare and their food plants (e.g., Keith 1983), with the lynx being carried along more or less passively by changes in the abundance of the hare. (After Elton and Nicholson 1942.)

ics in their numerical studies (carried out on mechanical calculators!), they were looking for steady solutions, and having found them, they went no farther. It is interesting that the simplest possible mathematical model for a host population with discrete generations, regulated by a lethal pathogen that spreads epidemically through each generation before reproduction, has *only* chaotic solutions—no stable points or stable cycles (May 1985). Deterministic chaos might have forced itself on our attention long ago if only someone had thought to look at such a model; Nicholson and Bailey came close in the 1930s, when they studied insects regulated by parasitoids.

The lesson to be drawn from these simple models is that density dependence can give rise to a wide range of dynamical behaviors, from constancy through stable cycles to apparent chaos, even in the complete absence of noise. It is therefore not surprising that many regularly oscillating populations are found in nature. More confusingly, we have the possibility that some irregularly fluctuating populations may be driven by nonlinear signals (corresponding to strong density dependence), and not necessarily by density-independent noise. Thus there is irony in the classical disputes between Nicholson (who believed that density-dependent effects were pervasive, holding most populations relatively steady) and Andrewartha and Birch (who held that density-independent effects were generally the rule, causing most populations to fluctuate markedly), when we observe that strong density dependence will typically produce erratic fluctuations!

A further complication in the extraction of signal from noise in population data arises when the organisms are distributed unevenly in space, as most are, rather than homogeneously. Conventional methods of "k-factor analysis" seek to determine which stages in complex life cycles account for the density-dependent signals, by comparing overall population densities at each life stage with the corresponding densities in the next generation. But if the overall population is distributed nonuniformly over many patches, with different densities in different patches, it can be that much of the density-dependent regulation takes place within patches. Hassell (1985) has shown that in such circumstances the density-dependent signals can be effectively masked by noise if one seeks them by conventional comparisons of overall densities in succeeding generations.

The problem of determining what, if anything, regulates particular natural populations has engaged ecologists continuously over the past century. It now seems clear that all populations are regulated by a

mixture of density-dependent and density-independent effects, in varying proportions. The interesting questions are how life-history parameters evolve under such different circumstances, and what is the consequent balance between nonlinear signal and noise. Against this growing awareness of the technical complexity of the real issues, the polarized debates between "density dependent" and "density independent" schools, with all their schisms and sects, make fascinating reading. The emphasis on refining definitions, rather than looking at data, can be so extreme as to make one believe that there really might be a time warp connecting our century to the thirteenth. Kingsland (1985) has written a fine narrative history covering much of this material, but it may take a psychohistorian to do it full justice.

Simple mathematical models for competition and predator-prey interactions were pioneered by Lotka and Volterra in the 1920s and 1930s (see Lotka 1925). Much earlier, Nägeli (1874) had published the Lotka-Volterra competition equations in the plant literature, but they sank without a trace because they had surfaced in a

community that was resolutely unwilling to see biological questions in mathematical terms. The Lotka-Volterra equations describe an unrealistic world that is deterministic and homogeneous in space and time, but they nonetheless stimulated much ecological research by revealing the essential dynamical features of competitive and predator-prey interactions: the competitive exclusion principle and oscillatory dynamics, respectively.

From this beginning grew a continuing tradition of studies on the dynamics of host-parasitoid and arthropod prey-predator systems, in which carefully designed field and laboratory experiments are combined with theoretical models to elucidate how individual biological components of the interactions between and within species affect the persistence and abundance of both populations (Hassell 1978). Such interdigitation between theory and experiments in field and laboratory has been helped by the relative simplicity of the predatory behavior and the interlocked life cycles, as well as by the spatial and temporal scales of the studies, which are consistent with the time scales of research grants and



Figure 5. This swarm of desert locusts photographed in Ethiopia in 1968 represents a pattern of population regulation in which there are dramatic and highly irregular changes of abundance. Such chaotic fluctuations may be driven by random environmental contingencies, as they almost certainly are here. But recent theoretical work shows that the full spectrum of dynamical behavior, including chaotic fluctuations, can arise from purely deterministic causes if the population has a high capacity for growth and simultaneously experiences strongly density-dependent mortality or fecundity. (Photograph courtesy of G. Tortoli/FAO.)



tenure decisions. Studies of competition and predation among vertebrates (disproportionately birds), on the other hand, typically deal with longer-lived, wider-ranging, and generally more complicated organisms, which makes detailed correspondence between mathematical models and real mechanisms difficult to achieve. This may be why studies of competition and prey-predator relations in vertebrates have been more often in the "roles and relationships" mode, while invertebrate host-parasitoid (and more recently, host-pathogen) studies have been approached more often from the "dynamical systems" point of view.

Entire communities may likewise be conceived as reactive dynamical entities, in various ways. The food web may be seen as a conduit for the flow of energy or of specific nutrients. The matrix of connections among species may itself be viewed as a dynamical construct. Adopting any of these viewpoints, we can ask questions about the dynamical response of the structure with respect to specific kinds of perturbations. A big problem is that variables must be aggregated, and many details left out, if the dynamical behavior of the system is to be understood. This process remains more an art than a science, which is part of the reason why so few firm answers can be given to questions about the effects on particular ecosystems of, say, acid rain, or excess CO<sub>2</sub>, or heavy fishing.

## Motives and strategies

An area of ecological research currently seeing much excitement and expansion is that concerned with the way in which natural selection influences the social behavior of animals. Most studies in evolutionary ecology over the past century have focused on those factors directly affecting the chance that an individual will survive to reproduce: strength, speed, camouflage, a well-advertised nasty taste or a misleading mimicry of someone else's advertisement, and so on. Although there can be overall advantages to living in groups (for instance, greater foraging efficiency or protection against predators), many features of social behavior have, until recently, seemed difficult to explain with a theory that is based on individual, not group, advantage. The problem is epitomized in Darwin's observation that the existence among social insects of worker castes that are sterile, leaving no offspring, seems flatly opposed to any notion of evolution by natural selection based on reproductive success. In the *Origin* he calls this the "one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory" (p. 236). With typical insight, he goes on to give intuitive reasons why natural selection might sometimes operate at the level of family groups rather than individuals.

More than 100 years elapsed before Hamilton (1964) showed how the synthesis of Mendelian genetics with the Darwinian theory of natural selection allowed a more analytic discussion of the evolution of "altruistic" traits (defined as those which harm the individuals who manifest them, while benefiting other individuals). Within a given family structure, the average genetic relationship between any two individuals can be calculated. For example, in a diploid species, with no inbreed-

ing, full siblings have on average 1/2 of their genes identical by common descent. More generally, we can define the "coefficient of relationship,"  $r$ , between two individual A and B as the conditional probability that B has a particular gene, given that A has it. (We can also define  $r$  as a genotypic correlation or regression coefficient.) In diploid species,  $r$  is 1/2 for parent and offspring as well as for siblings, 1/4 for uncle and nephew or grandparent and grandchild, 1/8 for first cousins, and so on.

## *Behavioral ecology is showing us in a quantitative way how evolution molds social behavior among nonhuman animals*

An apparently altruistic act will in fact benefit the genes involved if the reproductive success (Darwinian fitness) lost by the altruist in being altruistic is more than offset by the sum of its relatives' consequent gains in reproductive success, after these gains have been discounted by the relevant coefficients of relationship,  $r$ . Hamilton introduced the term "inclusive fitness" to characterize the net selective value (to an individual) of having a given structure or behavior; it is the sum of the individual's effects on its own fitness plus its effects on the fitnesses of related individuals, discounted by the relevant  $r$  values. Natural selection tends to maximize an individual's inclusive fitness (rather than its simple Darwinian fitness) in those social situations where the two kinds of fitness are not identical.

Hamilton used this concept of inclusive fitness to attack the problem that had so deeply troubled Darwin, namely, the evolution of extreme reproductive altruism among the social Hymenoptera (ants, bees, and wasps), where sterile female workers spend their lives raising the male and female offspring of their mother, the queen. Hymenoptera are haplodiploid; males develop from unfertilized eggs and are thus genetically haploid, while females develop from fertilized eggs and are diploid. Because a male has only one set of chromosomes, his daughters are genetically identical for the half of their genome received from their father, but they are genetically variable in the usual way for the half of their genome received from their mother. As a consequence of this peculiar system of inheritance, full sisters are more closely related to each other ( $r = 3/4$ ) than they are to their own children ( $r = 1/2$ ) or to their brothers ( $r = 1/4$ ), while males are more closely related to their daughters ( $r = 1$ ) than they are to their siblings ( $r = 1/2$ ).

It follows that the daughters of a queen, when faced with the choice of rearing their own daughters or staying at home to rear younger sisters, might often do better, in an evolutionary sense, by staying at home to work for their mother. By rearing sisters, a female can send more of her genes to the next generation than she can by rearing the same number of daughters. This special feature of haplodiploidy may therefore help to explain why sterile workers have evolved independently at least

13 times among the Hymenoptera, but only once (in the termites) elsewhere in the class Insecta, even though the Hymenoptera comprise only 6% of all insect species. A telling point is that this altruism is sex-limited: only females are workers, and all males are reproductive.

Trivers and Hare (1976) extended this analysis to make some quantitative predictions. If all the eggs of a haplodiploid queen are sired by the same male, and if the colony's sex ratio is controlled by the *workers*, then the ratio of investment in reproductive offspring of the two sexes (virgin queens and males) will be 3:1 over the population as a whole. (This ratio is a reflection of the fact that a worker is three times more closely related to her reproductive sisters than to her brothers; it follows that working on sisters yields a larger net genetic return than does working on brothers, whenever the population-wide ratio of investment is less female-biased than 3:1.) But if the *queen* controls the ratio of investment then it should be 1:1 over the population as a whole, because a queen is equally related to her offspring of each sex.

Trivers and Hare were able to estimate ratios of investment for 21 species of ants that appear to meet the assumptions of this model. The data show considerable scatter, but on average the 21 species are remarkably close to the 3:1 ratio predicted if the workers have control. In slave-making species the queen's brood is reared not by her daughters but by slaves, which are stolen from other species and which therefore have no genetic relationship to the brood. In such species the queen might plausibly gain control, and the two slave-making species studied by Trivers and Hare do indeed show investment ratios closer to 1:1 than to 3:1. (For a recent review of the arguments and evidence, see Nonacs 1986.)

More generally, inclusive fitness and related concepts are being applied to analyze the evolution of group size, mating systems, patterns of parental investment in offspring (including, in particular, the sex ratio), and a variety of other such factors governing the structure of animal societies (for reviews see Wilson 1975; Krebs and Davies 1981; Trivers 1985). Such analysis is often facilitated by thinking of the animal as playing a "game" against other members of its species, and asking what "strategy" would maximize its inclusive fitness, subject to the environmental and physiological constraints facing it (see Maynard Smith 1982). Such an unbeatable or "evolutionarily stable" strategy (ESS) can be far from obvious. The ESS is often a mixture of two or more "pure" strategies, and this mixture may have well-determined, constant proportions, or it may vary cyclically or even chaotically in time.

Many of these ideas about mating strategies and other aspects of group life can best be tested by comparing geographically distinct subpopulations, or closely related species, or even genera, looking at the way similarities and differences in social organization correlate with similarities and differences in the ecological setting. Such studies refute the criticism that evolutionary theory is merely a collection of *Just So Stories*, in which particular aspects of morphology or behavior are argued to be "optimally designed" to fulfill purposes which are tautologically inferred from the features in question. For example, Harcourt and his colleagues

(1981) showed that primate species with different kinds of mating systems exhibit significantly different statistical relationships between average body weight and testis weight; species with monogamous or polygynous single-male groups tend to have smaller testes for their body sizes than do species with promiscuous multiple-male groups. This qualitative difference is predicted by a simple evolutionary argument. We could easily test both the argument and the empirical relationships by predicting the mating system of a new primate species, knowing only its average body and testis weights.

Simple evolutionary theory has also been used to derive a quantitative explanation of sex change in sequentially hermaphroditic animals. If some individuals that begin life as males later become females, the species is said to exhibit protandry; the reverse sequence from female to male is called protogyny. Sequential hermaphroditism is widespread among marine invertebrates and fishes, where growth typically continues throughout life and reproductive success tends to be strongly related to size in ways that differ for males and females. Game theory suggests that the ESS will often be a mixed strategy, with a proportion  $P$  of individuals remaining female (or male) throughout life, while the remaining proportion  $1 - P$  exhibit protandry (or protogyny) (Charnov 1982). The proportion  $P$  depends on the reproductive success of a female (or male) hermaphrodite relative to that of a female (or male) whose sex remains constant. Data for protandrous shrimp and protogynous coral-reef fish are in good agreement with the theory, as shown in Figure 6.

Strong passions have been aroused by the suggestion that our own species may exhibit behavioral tendencies that evolved under the influence of selective forces similar in kind to those that behavioral ecologists study

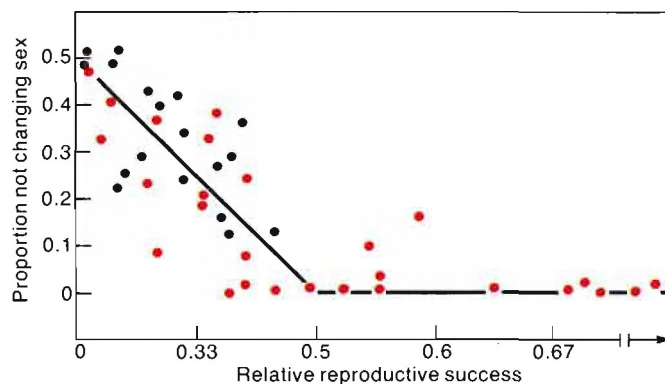


Figure 6. Studies of sequentially hermaphroditic species have confirmed the theoretical expectation that the frequency of sex change should be quantitatively related to the relative reproductive success of individuals who do and do not change sex. In protandrous species, individuals who begin life as males later become female, but individuals who begin as females never change. In protogyny it is females who later become male, while males never change. Theory predicts that the proportion of lifelong females (or lifelong males) will decline to zero as the reproductive success of female (or male) hermaphrodites approaches one half that of lifelong females (or lifelong males). Data for protandrous shrimp (colored dots) and protogynous fish (gray dots) closely follow the theoretical expectation indicated by the black line. (After Charnov 1982.)

in other species. Some of this passion is directed against particular claims and speculations, but much of it is directed against the whole idea that patterns of human social behavior might even dimly reflect the ecological context in which our species evolved. Many social scientists (and some biologists) seem to believe that human culture is a transcendent thing that sets us apart from the rest of the living world. Perhaps they are right. But the debate that began with the publication of Wilson's *Sociobiology* (1975) has done little to illuminate the question because it has been fueled, to an extent not widely appreciated, by the simple misunderstanding of terms and concepts.

For example, the teleological language of aims and motives is used in behavioral ecology as a convenient shorthand for more cumbersome operational statements. No one has seriously suggested that animals have conscious "strategies," but rather that natural selection acting on genotypic variation within populations will tend to produce the outcome that maximizes inclusive fitness, under the given conditions and other constraints. The result is *as if* each individual were "trying" to be as reproductively successful as possible. In calling this kind of outcome an evolutionarily stable strategy, one is making a claim about the dynamics of natural selection. The claim does not in any way imply that the creatures involved are willfully plotting and scheming, much less doing sums.

A remarkable but sadly indicative example of the way these ideas are sometimes misunderstood can be found in a polemical tract by the anthropologist Sahlins (1976). Sahlins explains that inclusive fitness is not likely to be a factor even in nonhuman animal societies because, even assuming that animals can accurately recognize kin of varying degrees, they plainly cannot perform the necessary calculations involving  $r$ , lacking as they do the ability to handle fractions: "Fractions are of very rare occurrence in the world's languages, appearing in Indo-European and in the archaic civilizations of the Near and Far East, but they are generally lacking among the so-called primitive peoples. . . . I refrain from comment on the even greater problem of how animals are supposed to figure out . . . that  $r$  (ego, first cousins) =  $1/8$ . The failure of sociobiologists to address this problem introduces a considerable mysticism in their theory" (p. 45). Two cultures, indeed!

In short, the burgeoning field of behavioral ecology is showing us in a quantitative way how evolution molds social behavior among nonhuman animals, and also, if more tentatively at present, among plants. Whether the ideas will one day significantly illuminate human social behavior is still an open question.

## A view to the future

One inducement to write this article was the promise that we could end by indulging our opinions about future directions. Some predictions are fairly safe and unexciting. Work in relatively neglected areas such as the ecology of mutualistic, host-pathogen, and host-parasite interactions is likely to increase. As in the past, the majority of published studies will probably continue to deal with the behavior, physiology, distribution, and

other aspects of the autecology of individual species. Such studies are the bricks out of which our house is built, and they remain the basis for well-designed efforts in conservation and resource management.

Research on tropical ecology will surely continue to grow, in response both to the scientific importance of the subject and to the needs of conservation biology. But whether it will grow fast enough is still not clear. Many people (e.g., Raven et al. 1980; Wilson 1984, 1985) have argued that tropical ecology is badly underfunded; we find the arguments persuasive. The tropics are the richest, most complex ecosystems on the planet. They are also the most poorly known and the most seriously threatened (see Fig. 1). These are reasons enough, in our

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*Research on tropical ecology will surely continue to grow. . . . But whether it will grow fast enough is still not clear*

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view, to double and redouble our efforts in tropical biology. But in addition, the tropics are certain to hold thousands of yet undiscovered species of potentially significant economic value as sources of food, timber, pharmaceuticals, insecticides, and the like. We clearly have much to gain from learning more about tropical species and communities as quickly as possible. Or to put it the other way around, we probably have more than we can imagine to lose, for ourselves and for posterity, if we fail to do so.

Likewise, it is not clear whether taxonomy, particularly invertebrate taxonomy, will continue to suffer the neglect it has experienced for the last several decades. Given the obvious excitement that currently prevails on the frontiers of ecology and evolution, it is perhaps not surprising that universities are often reluctant to support the quiet, "old-fashioned" enterprise of systematically describing and classifying nature's riches. But our ultimate understanding and our success in management depend absolutely on our knowing what is there! It is incredible and scandalous that in 1986 there can be argument as to whether the global total is closer to 5 million or to 50 million species, with fewer than 2 million species currently classified (see Erwin 1983; Wilson 1985). Most of the unknown species are in the tropics, of course, but by no means all of them.

At the level of general mechanisms, we expect to see growth at the interface between behavioral ecology and population dynamics. Behavioral ecologists are typically concerned to understand how natural selection shapes individual behavior and social organization. They rarely ask about the consequences for overall population dynamics. From the other side, population biologists seldom ask how demographic parameters (e.g., density-dependent birth, death, and migration rates) derive from the underlying behavior of individuals. We see signs suggesting that these connections will increasingly be studied. For example, the current record for attendance at symposiums sponsored by the British Ecological Soci-



ety was set in 1984, when the subject was "Behavior and Dynamics." (The proceedings have been published in a volume edited by Sibly and Smith, 1985.) There certainly is need for behavioral ecologists to work up toward the population consequences of behavior, and for population biologists to work down toward the individual behavior that determines population parameters. Only in this way can the population and community properties that have fascinated ecologists for over a century at last be linked, via the behavior of individuals, to the evolutionary pressures that have shaped them.

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