

THE SEARCH FOR PATTERNS IN THE BALANCE OF NATURE: ADVANCES AND RETREATS

The Robert H. MacArthur Award Lecture

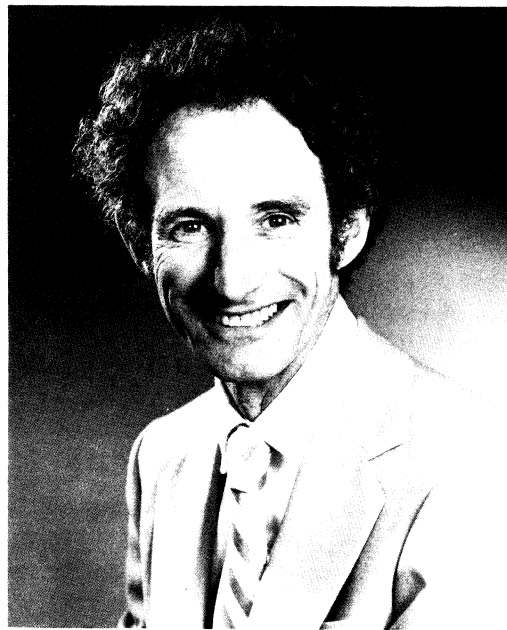
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by

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*I predict there will be erected a two- or three-way classification of organisms and their geometrical and temporal environments, this classification consuming most of the creative energy of ecologists. The future principles of the ecology of coexistence will then be of the form "for organisms of type A, in environments of structure B, such and such relations will hold." This is only a change in emphasis from present ecology. All successful theories, for instance in physics, have initial conditions; with different initial conditions, different things will happen. But I think initial conditions and their classification in ecology will prove to have vastly more effect on outcomes than they do in physics Bird censuses in a habitat in successive years or in similar habitats in one year are usually very similar, while insect censuses (to the extent they can be taken) seem often to differ dramatically from place to place and year to year. Thus, plausibly in our classification, insects, at least of some kinds, will go into a non-equilibrium category and birds into an equilibrium category. But the classification will be more pervasive than these examples suggest; many morphological, behavioral, and genetic parameters will probably be included. There has been a biological tradition of searching for the best organism to solve a problem—like *Drosophila* for chromosome genetics and viruses and bacteria for aspects of molecular genetics. The ecologists should resist this temptation.*

MacArthur (1972; quoted by Colwell 1984)

Understanding the essentials of how species originate was the most important intellectual achievement of the 19th century. It seems to me that the next step—the largely unanswered question for the 20th century

(and maybe the 21st)—is to understand how *many* species there are. The overall question "how many species?" is composed of a mosaic of subsidiary questions: what factors determine the number of species we

expect to find in a given patch, or on a continent, or on the globe? how is the number of species in a given region likely to be affected by particular kinds of natural or human perturbation? how is the total number of species in a region distributed among physical size classes (how many species whose individuals weigh ≈ 1 g versus how many weighing around 1 kg)? and so on. These questions have the same intellectual fascination and importance as questions about the forces binding nuclei or the large-scale structure of the universe. More than this, however, the questions today have a practical urgency for conservation planners and resource managers. This lecture is dedicated to Robert MacArthur not so much because he gave us the right answers, but because he continually reminded us of the right questions.

The lecture is divided into three main parts. The first deals with the dynamical behavior of single populations. Here, recent work shows that simple nonlinearities of the kind that can arise naturally in the regulation of many populations may lead to very complicated dynamics. When compounded with environmental unpredictability and/or heterogeneities in individual behavior or spatial distribution, such nonlinearities can cause problems in analyzing data and in predicting events. The second part briefly surveys some possible effects of competition, mutualism, and predator-prey associations (broadly defined) upon community structure. Lastly, and at greatest length, I discuss work on community-level patterns having to do with food web structure, the relative abundance of species, and the relative numbers of species or of individuals in different physical size classes. This array of topics does not represent a balanced overview, but rather reflects my own interests and enthusiasms.

In all, I think a message does emerge from this survey. On the one hand, I believe there are no grand generalizations, no "inverse square laws" of ecology, no naive dichotomies into density-dependent and density-independent populations or into equilibrium and nonequilibrium communities. On the other hand, I do not despair that there is only a jumbled accumulation of facts, each particular to its own circumstances and all adding up to no more than a Geertzian (1973) "thick description" of specific situations. MacArthur's words, quoted above, express it well: ecology is a science of contingent generalizations, where future trends depend (much more than in the physical sciences) on past history and on the environmental and biological setting.

REGULATION OF SINGLE POPULATIONS

Some natural populations remain relatively constant from year to year, other exhibit periodic oscillations in abundance (often with densities varying 1000-fold or more between peak and trough), while yet others exhibit irregular fluctuations (often associated with the weather). Much of the earlier (and some contemporary) work in this area sought a simple distinction between

populations held steady by density-dependent regulatory effects and populations fluctuating erratically under the influence of density-independent environmental factors. A lot of this work is, in my view, sterile semantics. Recent research on mathematical models for single populations has shown remarkable, and previously unsuspected, complications in the disentangling of density-dependent "signal" from density-independent "noise." The following account of these studies is essentially a summary of a detailed recent review, in which more attention is given to field and laboratory data (May 1986).

Population dynamics in a deterministic and homogeneous world

In population genetics, the Hardy-Weinberg theorem tells us that gene frequencies do not change in the absence of mutation, migration, drift, selection, and various other things. This theorem may seem daft, because such effects are almost invariably present in the natural world. The real use of the theorem is, of course, as a point of departure for evaluating the effects of mutation, selection, etc. In the same sense, it is useful to begin a discussion of the dynamics of single populations by considering a closed, homogeneous world, in which birth and death rates are deterministically dependent only on population density.

If the population in question has discrete, nonoverlapping generations (as do many temperate zone insects), we then have a deterministic but nonlinear relation between the population density in generation t , N_t , and that in the next generation, N_{t+1} . One such relation, propounded for fish populations by Ricker (1954) and for insects by Moran (1950), is

$$N_{t+1} = N_t \exp[r(1 - N_t/K)]. \quad (1)$$

Here r is the intrinsic per capita growth rate of the population, and K the carrying capacity, in analogy with the more familiar logistic equation. An even simpler relation is

$$X_{t+1} = aX_t(1 - X_t). \quad (2)$$

Here X_t is a rescaled population density; a is given by $a = 1 + r$; and the right-hand side is taken to be zero if $X_t > 1$. Other such first-order difference equations from biological contexts are catalogued by May and Oster (1976).

As is by now reasonably well known, equations of this general kind can exhibit an astonishing array of dynamical behavior (May 1974, 1976). If the nonlinearity is not too severe ($r < 2$ in Eq. 1, $a < 3$ in Eq. 2), the population settles to a stable point. As the "hump" in the curve relating N_{t+1} to N_t becomes more steep, this stable point gives way to stable cycles in which the population stably alternates between relatively high and relatively low values (repeating itself at first every 2 generations, and then every 4, 8, 16, . . . , 2^n , as the hump steepens). Finally, for very "boom-

and-bustiness" curves ($r > 2.69$. . . for Eq. 1; $a > 3.570$. . . for Eq. 2), these simple and deterministic relations give trajectories that look like the sample function of a random process; although fully deterministic, the relations give apparently "chaotic" dynamics. (The reader not familiar with all this should try iterating Eq. 2 on a hand calculator, starting with any X between 0 and 1: for $1 < a < 3$, the system will rapidly settle to a constant value; for $3 < a < 3.57$. . . , the bifurcating cascade of cycles with periods 2^n will be seen; for 3.57 . . . $< a < 4$, there will be apparent chaos; and for $4 < a$, X will exceed unity and the population will become extinct.)

These properties are generic to essentially all the density-dependent relations that have been propounded as models for populations with discrete, nonoverlapping generations. Although there are many fascinating and delicate mathematical details, particularly in the chaotic regime, the essential message for the population biologist is that simple, natural, and purely deterministic population models may result in a stable point, or in stable cycles, or in chaos, depending on how nonlinear or "boom-and-bustiness" the regulatory mechanism is.

This peculiar behavior is, moreover, not restricted to populations with discrete, nonoverlapping generations. It can also be seen in populations with continuous growth (described by differential equations), provided there are explicit time lags in regulatory effects. Populations with many discrete but overlapping generations (described by coupled first-order difference equations), such as many fish and mammal populations, exhibit an even more complicated range of behavior.

It is ironic to note that the outcome of severe density dependence (corresponding to a high degree of nonlinearity) is likely to be a chaotically fluctuating population trajectory. The extreme of Nicholsonian density dependence may be practically indistinguishable from Andrewartha and Birchian density independence.

Environmental noise

The ideal of a single population subject to density-dependent regulation in a deterministic and homogeneous world is unlikely to be met outside the laboratory. Within the laboratory, however, the above ideas do seem to be borne out by a variety of studies. In particular, Brillinger et al. (1980) have given a detailed interpretation of Nicholson's (1957) classic blow fly experiments as exhibiting chaotic dynamics (with an almost periodic structure), and Murdoch and McCauley (1985) have reviewed a collection of their own and others' experiments on *Daphnia* populations to argue that qualitative changes in dynamical behavior are produced by what amounts to changes in the steepness of the map relating N_{t+1} to N_t . Even in the natural world, where environmental stochasticity, heterogeneity, and interactions with other species are all likely

to be important, Schaffer (1984) and Schaffer and Kot (1985) have shown that the apparently complicated behavior of some populations (e.g., lynx in Canada and measles virus in human populations) may be described heuristically as being generated by relatively simple nonlinear maps.

In general, however, the dynamical behavior of natural populations will be the outcome of some mixture of density-dependent factors (tending to produce stasis, or stable cycles, or chaos) and density-independent factors (tending to produce unpredictable fluctuations). There has been much debate about the relative strength of signal and noise for particular kinds of populations in particular settings. One suggestion, for instance, is that many populations may be undergoing density-dependent regulation at relatively high (and possibly at relatively low) densities, but exhibiting environmentally driven, and therefore purely density-independent, fluctuations over most of the observed range of densities. In such a case, when most of the population data reflect environmental noise, the regulatory signal may be hard to determine. No matter how weak they may be on average, such signals are ultimately crucial; if density-dependent effects were entirely absent, a population whose vital rates were purely density-independent would, in the long run, either increase or decrease without bound. These points are developed further by Chesson and Case (1985) in their comprehensive review of the ways chance, variability, and history can affect population dynamics: "If one wishes to explain a population's mean density, when sampled over time, a study of density dependence at the population extremes will be necessary. Indeed, density dependence and density independent fluctuations will interact to produce this mean density, as commonly observed in stochastic population models (e.g., May 1973)."

One practical application of some of these ideas arises in the harvesting of fish and other natural populations. Most of the population models used in setting fish and whale quotas (e.g., Beverton and Holt 1957, Gulland 1977) are deterministic. But it can easily be that the influence of environmental noise—and therefore the unpredictability of next year's yield—increases as stock are exploited more heavily. If this is the case, it may be better to reduce harvesting levels, opting for yields that are on average slightly lower but significantly more predictable. It is, however, difficult to come to firm conclusions, because nonlinearities in the density-dependent effects can result in predictions being sensitive to exactly how the environmental noise is put into the equations. In other words, the interplay between noise and intrinsic nonlinearities can give surprises. Steele and Henderson (1984), for example, have suggested that anchovies and other fish stocks may show collapse and rebound on a roughly 50-yr time scale, resulting from the interaction between density-dependent effects and the "pink" frequency spectrum of environmental

noise in the sea (where fluctuations exhibit better correlation over short time spans than over long ones, in contrast with "white" noise, which has no correlations on any time scale).

Spatial and behavioral heterogeneities

Most natural populations see their physical surroundings as a mosaic of patches, among which they are distributed in a nonuniform way. The resulting range of dynamical behavior is much wider than is possible in a homogeneous environment (e.g., Levin 1976). As illustrated in detail for specific insect populations by Hassell (1978) and others, the survival and reproductive success of an individual will often depend on the density of conspecifics in its patch. The net outcome may be that density-dependent differences among subpopulations in patches within any one generation are more important in regulating the insect population than are the more conventionally appreciated effects of differences in overall population density between generations.

Spatial heterogeneity can also make vividly clear the way in which questions about equilibrium or predictability depend on the scale at which they are asked. There appear to be many situations in which events within any one patch are highly variable and wholly unpredictable while overall population densities can be quite stable.

Behavioral differences among the individuals in a population can similarly influence the dynamics. De Jong (1979), Lomnicki (1986), and others have shown how particular kinds of behavioral heterogeneity can influence population dynamics. Such studies point the way to understanding the biology of populations in terms of the behavior of individuals, and thence connecting population-level phenomena to evolution (which acts on individuals).

Once again, the interplay between nonlinear dynamics and spatial or behavioral heterogeneities can do things that defy simple intuition.

As a somewhat topical example, consider a deliberately oversimplified model for the epidemic spread of a sexually transmitted disease in a closed population (approximately the case for AIDS among homosexuals in San Francisco), all of whom are initially susceptible. Suppose the degree of sexual activity varies among the members of the population at risk, such that p_i gives the proportion having on average i sexual partners per unit time ($\sum_i p_i = 1$). Suppose further that the probability for a susceptible individual to acquire infection, per unit time, is proportional to: (1) his average number of sexual partners, i , and (2) the probability that any given partner is infected (which changes as the epidemic progresses). If we treat this behaviorally heterogeneous population as homogeneous, with each individual having a number of sexual partners equal to the appropriate average over the population, the total frac-

tion of the population to be infected by the time the epidemic has run its course, I , is given by the classic Kermack-McKendrick (1927) equation:

$$I = 1 - \exp(-R_0 I). \quad (3)$$

Here R_0 is the basic reproductive rate of the infection, defined as the average number of secondary cases produced by an infected individual in a wholly susceptible population; $R_0 = \kappa\beta c$, with κ the average duration of infectiousness, β the probability that an infected individual will transmit infection to a susceptible partner, and c the appropriately averaged number of partners ($c = \sum_i i^2 p_i / \sum_i i p_i$; see May and Jose 1986). This proportion infected, I , for the homogenized approximation is illustrated as the top curve in Fig. 1, where we see that I rapidly approaches 100% as R_0 increases beyond unity.

On the other hand, the calculation can be done more accurately by first computing the fraction ever infected in the i^{th} class of sexual activity, I_i , and then averaging these fractions I_i to get the overall average $I = \sum_i p_i I_i$.

Under the assumptions spelled out above, I_i is given by

$$I_i = 1 - e^{-i\alpha}. \quad (4)$$

The variable α depends only on R_0 and the distribution function p_i , according to

$$\alpha = R_0 \left[\sum_i i(1 - e^{-i\alpha})p_i \right] / \sum_i i^2 p_i. \quad (5)$$

In Fig. 1, p_i is assumed to obey a gamma distribution, so that I depends only on R_0 and on the coefficient of variation, cv , of the distribution of p_i ($cv = \sigma/m$, where σ^2 is the variance and m the mean of p_i). It will be seen that the fraction ever infected, I , is much less than would be estimated by first averaging and then treating the population as homogeneous, once the heterogeneity in sexual practices becomes significant (i.e., once fluctuations in i exceed the average value of i ; once cv exceeds unity).

These results are obtained and discussed in May and Jose (1986). Similar phenomena for the case of endemic infections in behaviorally heterogeneous populations are discussed by Hethcote and Yorke (1984).

Fig. 1 is representative of a range of other examples that could be given. The nonlinearities in population processes have the consequence that it can be misleading to work with simple averages over environmental stochasticities, or over spatial or behavioral heterogeneities.

Implications for data analysis

The time-honored approach to seeking to understand what regulates a population is essentially to plot the overall average population density at a given stage of the life cycle in one generation against that in the

previous generation, N_{t+1} against N_t . Such “ k -factor analysis,” or similar analyses, can often reveal at which life stage density-dependent factors enter, and with what strength. But if, as indicated in the previous section, much of the density-dependent regulation comes from spatial or behavioral heterogeneity within one generation, depending only weakly on the average population density in that generation, such analyses may be of little use.

M. P. Hassell (1985, and *personal communication*, Hassell and May 1985) has been studying models in which the overall population dynamics is derived from individual foraging or egg-laying behavior in a patchy environment. He then introduces environmental noise into various of the parameters characterizing individual behavior. In this way, Hassell generates pseudo-data (which often look very noisy) from specified mixtures of density-dependent and density-independent effects. Such pseudo-data can then be used to see to what extent standard methods can indeed tease out the underlying mechanisms. Not surprisingly, Hassell finds that environmental stochasticity combined with spatial or behavioral heterogeneity can often make density dependence undetectable by the conventional, inter-generational analyses.

These imaginary worlds are useful, both in showing the complexities that arise when spatial and temporal heterogeneities roil together with intrinsically nonlinear dynamics, and in serving as test-beds for the design of better methods for analyzing real data. Unfortunately, one conclusion is that information about the overall average density of a population in successive generations is sometimes of little use, and that data about the variation in density among patches within a generation are often needed; such data are rarely available.

INTERACTING POPULATIONS

Competition

The early work of Lotka and Volterra indicated that species can coexist only if intraspecific competition is more intense than interspecific. In an attempt to provide an operational measure of the limiting similarity among coexisting competitors, May and MacArthur (1972) suggested the requirement that d , the average difference between two species in their use of a differentiating resource (e.g., food size or foraging height) should exceed w , the range of use of the resource found within either species. This rule, $d/w > 1$ (with the inequality interpreted as a rough approximation), had the appeal of representing a kind of microscopic version of the older, macroscopic, Lotka–Volterra result.

The subsequent fate of this idea re-echoes many of the themes just sounded for single populations. For one thing, the result depends on environmental noise being introduced in a particular way. But, as subsequently shown by Turelli (1977), Chesson (1985), and

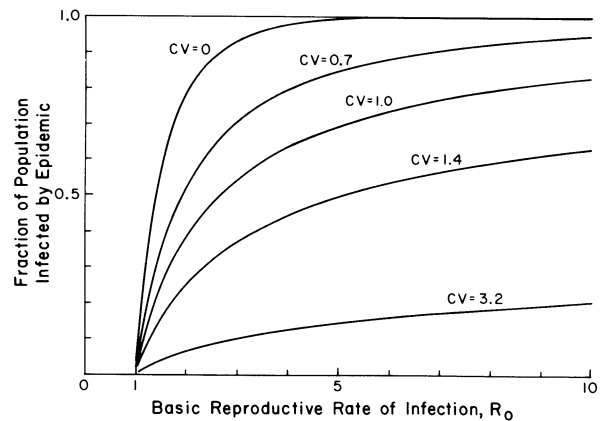


FIG. 1. The total fraction, I , who are infected by an epidemic of a sexually transmitted disease in a closed population is shown as a function of the basic reproductive rate, R_0 , of the infection (if $R_0 < 1$, the epidemic cannot spread and $I = 0$). The top curve corresponds to a homogeneous population (with coefficient of variation $cv = 0$) in which all individuals have, on average, the same epidemiological properties. The lower curves plot I against R_0 for increasing amounts of heterogeneity in sexual habits, and therefore in transmission of infection, within the population; specifically, the curves correspond to the distribution of numbers of sexual partners per unit time having $cv = 0.7, 1.0, 1.4,$ and 3.2 , respectively. For further discussion, see Regulation of Single Populations: Spatial and Behavioral Heterogeneities. (From May and Jose 1986.)

others, environmental stochasticity can influence competitive coexistence in many different ways, depending on how the noise affects the population parameters and on how various components of the noise are correlated one with another. The result is a kaleidoscope of possibilities, with some kinds of environmental stochasticity making coexistence harder and other kinds making it easier (for instance, by guaranteeing that no one species competitively dominates for too long). Chesson's (1985) recent review makes a start toward codifying this range of possibilities.

For another thing, spatial heterogeneity can promote coexistence. It has long been appreciated, for example, that superior vagility can enable an inferior competitor to persist in an environment of ephemeral patches (Hutchinson 1951, Horn and MacArthur 1972). More recently, it has been recognized that inferior competitors can persist in patchy and ephemeral environments, without any compensating superiority in colonizing ability, provided only that individuals of competitively dominant species tend to be clumped, rather than randomly distributed, among patches (Atkinson and Shorrocks 1981, Hanski 1983, Ives and May 1985). I think this latter mechanism may be a powerful promoter of species diversity among insects.

Prey–Predator systems

In the 1920's and 1930's, Lotka, Volterra, and others studied differential equations as largely abstract models

for interactions between prey and predator populations with continuously overlapping generations. Around the same time, Nicholson and Bailey developed difference-equation models for describing the interactions between insect hosts and their hymenopteran or dipteran parasitoids, with both populations having discrete, nonoverlapping generations. Models of the Lotka–Volterra kind have undergone much further development, with their nonlinear limit cycles (and, in some extensions, chaotic dynamics) now well understood, but they continue to bear a rather metaphorical relation to real prey–predator associations. In contrast, work on host–parasitoid and other arthropod prey–predator associations seems to me to have gone forward in a coordinated way, combining field and laboratory experiments with mathematical models; components of the overall interaction (searching behavior, handling time, and so on) have been dissected out and studied in detail. In part, this may be because the relatively small size and short life-span of invertebrates tends to make them more amenable to such an analytic program of experimental research than is the case for most vertebrates. What works for *Cyzenis* and the winter moth is simply infeasible for lions and zebras.

Although receiving scant attention from either empiricists or theoreticians until recently, the interactions between viral, bacterial, protozoan, and helminth parasites and their hosts illustrate many of the basic dynamical and evolutionary properties of prey–predator associations, often in unusually clear ways (Anderson and May 1978, 1979, 1981, Price 1980, Toft 1986). The propensity for prey–predator associations to exhibit oscillations, with a period approximately equal to the geometric mean of prey and predator characteristic time scales, is nowhere illustrated so quantitatively as in the well-documented interepidemic cycles of measles, whooping cough, and other childhood diseases in developed countries. Theory suggests this period is $T = 2\pi(A\tau)^{1/2}$, where A is the average age at infection (prey life-span) and τ the average duration of infection (predator life-span), and this model agrees well with the public health data; for further details, see May (1985). Other confrontations between this special case of prey–predator theory and practical applications are reviewed by Anderson and May (1985). More broadly, I think diseases and parasites affect the numerical abundance and geographical distribution of many plant and animal species, and that a better understanding of the role of disease is particularly important in conservation biology.

Mutualism

For long an “orphan interaction,” mutualism is coming into its own as more work is done on tropical ecosystems and as the effectively mutualistic consequences of many indirect interactions are better appreciated (Addicott 1986, Wilson 1986). Reviewing her own and other experimental studies of ant–aphid/

membracid associations, Bristow (1984) has argued that, even in the temperate zone, direct mutualisms may make a larger contribution to community or guild structure than is commonly thought; although usually facultative rather than obligate (in contrast with many tropical mutualisms), temperate zone mutualisms can attain a high degree of fine-tuning with almost no loss in flexibility in response to environmental vagaries, by the species involved relying on simple behavioral cues and behavioral mechanisms.

COMMUNITY-LEVEL PATTERNS

In the 1950's and 1960's some tentative generalizations about community structure were propounded. One such generalization held that complex ecosystems are more stable. Many well-meaning environmentalists embraced this “law” as providing a “scientific” justification for preserving complexity and diversity (because it fosters stability, self-evidently A Good Thing). Another generalization suggested that roughly 10% of the energy at one trophic level makes its way into the next. These generalizations are still found in introductory biology texts, and as the “right” answers to tests given to students, at least in practice SAT and GRE books.

Further investigation and thought has shown the truth to be more complicated and various than suggested by the 10% law, or “complexity implies stability,” or other such rules. What now seems under way is a second generation of attempts at codification, seeking to find patterns, while acknowledging that the patterns are likely to differ among groups of organisms and among environments (homeotherms versus poikilotherms, benthic systems versus pelagic ones, and so on). A very selective review of some of these attempts now follows.

Structure of food webs

The appealing generalization that complex ecosystems are more stable was propounded by Elton (1958), and quickly gained currency. Complexity was measured roughly by the number of species, S , or by the richness of the web of interactions among them, while stability was even more roughly defined in terms of ability to recover from disturbance, or of levels of fluctuation of constituent populations (Elton 1958, May 1973).

Among the arguments assembled in support of this idea by Elton was the observation that simple mathematical models for prey–predator systems (e.g., Lotka–Volterra, Nicholson–Bailey) tend to exhibit undamped or even diverging oscillations. Beginning with the observation that the corresponding mathematical models for n prey and n predators are characteristically even less stable, a variety of empirical and theoretical arguments have suggested that there is no simple relationship between stability and complexity (both words having the rough meanings given above; see May 1973, Goodman 1975, Pimm 1982). In particular, Wolda's

(1978) studies indicate no substantial differences in the range of fluctuations shown by tropical versus temperate insect populations. Insofar as any mathematical generalization exists, it is that randomly constructed ecosystems are likely to become less stable—more prone to fluctuation and less able to recover from disturbance—as they become more complex (May 1973).

If, indeed, complex ecosystems tend to be dynamically fragile, we may expect to find them in relatively predictable environments. There is some quantitative evidence to this effect (Cohen et al. 1985, as discussed below). More generally, however, it must be recognized that real ecosystems are not randomly assembled, but rather are the winnowed product of natural selection acting on their constituent individuals. This prompts a search for those structural features that may confer resilience on particular food webs. Over the past 10 yr or so, this search has been pursued using mathematical models to explore what structures we might expect, and empirical analysis of real food webs to determine what structures are found.

Briand (1983, and *personal communication*) has compiled a particularly valuable catalogue of food webs whose structure has been elucidated. This collection now runs to 62 food webs, including 13 from a list by Cohen (1978) that stimulated earlier interest. Briand's 62-web collection breaks down into 19 from relatively constant environments versus 43 from fluctuating environments; 14 communities are tropical, 38 are temperate, and 10 are from high latitudes; 32 are from aquatic environments, 9 are terrestrial, and 21 are from the land-sea interface. The compilation of such catalogues is, of course, beset with many difficulties: one wants the "community" web, not a subset of species traced up from one resource or down from one top predator; one must decide, arbitrarily, which links are regarded as too weak or too unusual to list; different researchers may have followed different procedures and had different biases in tabulating individual webs; species are sometimes identified individually and sometimes lumped; and so on (see Briand 1983, May 1983). Such difficulties are easier to identify than to solve.

One early theoretical suggestion, based on food web stability, was that the number of species, S , should be inversely correlated with the connectance of the web, C ; C is defined as the ratio between the actual number of links in the web and the maximum number that are topologically possible (May 1972). As discussed by Rejmanek and Stry (1979), Yodzis (1980), Pimm (1982), and others, the product SC is indeed roughly constant, at around 3–5, for all webs. This fact, however, does not validate the particular dynamical argument that first suggested the relation. The observed relation follows more generally if all species, on average, interact directly with only a handful, $n \approx 3-5$, of other species; then, for large S , $C \approx nS/S^2$ and $SC \approx n$. More precisely, Cohen and Newman (1985; see also Briand and

Cohen 1984) have shown that Briand's 62 food webs possess the property they call "link-species scaling invariance": the ratio of the number of links, ℓ , to S is roughly constant, with $\ell/S = 1.86$ (where S ranges from 3 to 33 among the 62 webs). The average number of species with which a given species interacts directly, n , is related to ℓ simply by $n = 2\ell/S$, whence $n \approx 3.7$ for these 62 webs. But why species should, on average, interact so consistently with 3–5 others remains unexplained.

Cohen et al. (1985) have further shown that the ratio of ℓ to S , and thus the product SC , is systematically higher for the 19 webs in constant environments ($\ell/S = 2.31$; $n = 4.6$) than for the 43 webs in fluctuating environments ($\ell/S = 1.62$; $n = 3.2$). That is to say, for a given species richness, connectance is significantly higher in constant than in fluctuating environments. This accords with the tentative theoretical suggestion that complex ecosystems tend to occur in predictable habitats.

Briand (1983) has also used his 62-web collection to investigate other differences among different environments. An intriguing finding is that food webs in two-dimensional environments (benthic; intertidal) tend to be wider and shorter—relatively more species of herbivores and fewer trophic levels—than those in three-dimensional environments (pelagic; three-dimensional terrestrial), where webs are relatively thin and long.

Another interesting pattern found by Cohen and Newman (1985) and Briand and Cohen (1984) is that the proportions of basal species, intermediate species, and top predator species are roughly invariant, in the ratios 0.19:0.53:0.29, in Briand's 62 webs. There is also a "link scaling law": the proportion of trophic links in the four categories basal species—intermediate species, basal-top, intermediate—intermediate, and intermediate-top are also approximately invariant, in the ratios 0.27:0.08:0.30:0.35, for the 62 webs. Cohen and Newman (1985) show that these two quantitative patterns can be derived, to a good approximation, from the (unexplained) link-species scaling invariance pattern, if we assumed the species are ordered in a cascade or hierarchy such that a given species can prey on only those species below it and can be preyed on by only those species above it in the hierarchy.

In Briand's 62 webs, the average length of the food chains (the average number of links—eaten to eater—connecting top predators to basal resources) ranges from 5.9 to 1.9, with a mean of 2.9. That is, food chain lengths are relatively constant and relatively short. The conventional explanation used to be that inevitable inefficiencies in energy transfer from one level to the next precluded the possibility of long chains in which predator was piled upon predator. This explanation would suggest that food chains should be longer in highly productive environments (with a larger energy base) and in communities of cold- rather than warm-blooded species (because the efficiency of energy trans-

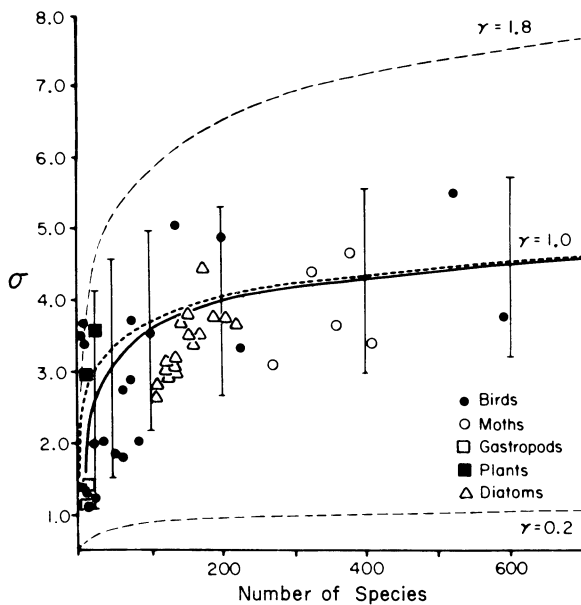


FIG. 2. A plot of S , the number of species, vs. σ , the standard deviation of the logarithms of the relative abundances, for various communities of birds, moths, gastropods, plants, and diatoms. The dashed line labeled $\gamma = 1$ shows the relation between S and σ for Preston's (1962) "canonical" lognormal distribution; the other dashed lines labeled $\gamma = 0.2$ and $\gamma = 1.8$ are the bounds to the range of S - σ relations that might be expected from general mathematical properties of the lognormal distribution, for large S and reasonable ranges of values for the total number of individuals, N . The solid line is the mean relation predicted by Sugihara's (1980) model of sequential niche breakage, and the error bars represent \pm two standard deviations about this mean. (After Sugihara 1980.)

fer between trophic levels is significantly higher for ectotherms than for endotherms). Neither tendency holds. Recent work has explored a variety of other possibilities, including that food chain lengths may be controlled mainly by dynamical considerations, with long chains leading to excessive levels of population fluctuation (Pimm and Lawton 1978). As I see it, this question remains wide open.

Relative abundances of species

Questions about commonness and rarity of species are of fundamental interest, and have important applications in conservation biology and elsewhere. Indeed, the phrase "patterns in the balance of nature" in my title is borrowed from a book by Williams (1964) dealing with the relative abundances of species. Following MacArthur's (1960) pioneering work, much has been done both in elucidating the variety of patterns of species relative abundance (SRA) found in nature, and in trying to understand the mechanisms underlying these patterns.

In early successional communities, and in environments disturbed by toxins or "enriched" by pollution, steeply graded distributions of relative abundance are

commonly seen, with a handful of dominant species accounting for most of the individuals present. Conversely, in relatively undisturbed "climax" communities consisting of many species, relatively even distributions of relative abundance are typical; very often, such SRAs are distributed according to a "canonical lognormal" distribution, as illustrated in Fig. 2. Such trends in SRA show up in studies of old field succession. The effects of pollution or other systematic disturbances (as in the Rothamsted grass plots; Tilman 1982) reveal the same trends, except that time effectively runs backward, so that the trend is from evenness to dominance. This range of topics is reviewed elsewhere (May 1981), and I now focus only on the canonical lognormal distribution.

It is not surprising that the relative abundances within a fairly large group of species will be distributed lognormally. The relative abundances are likely to be governed by the interplay of many more-or-less independent factors. It is in the nature of the equations of population dynamics that these several factors should compound multiplicatively, and the statistical Central Limit Theorem applied to such a product of factors implies a lognormal distribution. That is, the lognormal distribution arises from products of random variables, and factors that influence large heterogeneous assemblies of species indeed tend to do so in this fashion. This general observation, however, tells us nothing about the relationship between σ (the standard deviation of the logarithms of the relative abundances) and S (the total number of species present). The puzzling fact is that very many assemblies have SRAs that obey the canonical lognormal distribution, that is, that have the unique relationship between σ and S illustrated by the curve labeled $\gamma = 1$ in Fig. 2, although this curve represents just one of an infinite family of possible lognormal distributions. Preston (1962) first noted this remarkable fact, and indeed canonized it.

May (1975) conjectured that the canonical property may be merely an approximate mathematical property of all lognormal distributions for large S . The parameter γ can be estimated if S and the total number of individuals, N , are both known. By making plausible assumptions about the likely range of N/S , I concluded that γ was unlikely to be less than ≈ 0.2 or greater than ≈ 1.8 . I thought this range of γ -values could encompass the data in a reasonable way.

The data put together by Sugihara (1980) in Fig. 2 make it clear, however, that real SRAs obey the canonical relation more closely than can be explained by these mathematical generalities alone. Sugihara has also suggested a biological mechanism that will produce the observed patterns. He imagines the multidimensional "niche space" of the community as being a hypervolume broken up sequentially by the component species, such that each of the S fragments denotes the relative abundance of a species. This is both biologically and mathematically very different from MacArthur's mod-

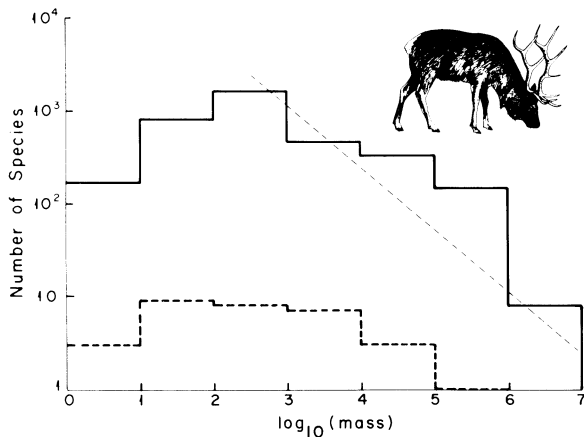


FIG. 3. The numbers of species (S) of all terrestrial mammals (solid histogram) and of British mammals (dashed histogram), excluding bats, are shown distributed according to mass categories (mass expressed in grams). Note the doubly logarithmic scale. The thin dashed line illustrates the shape of the relation $S \sim L^{-2}$, where L is characteristic length. (After May 1978.)

el in which a “stick” is broken simultaneously into S pieces. The sequential breakage pattern (with any fragment being equally likely to be chosen for the next breakage, regardless of size) seems more in accord with evolutionary processes, and the patterns of relative abundance thus generated are unlike those of the “broken stick” model. The solid line in Fig. 2 shows the mean relation between S and γ predicted by Sugihara’s model, and the error bars show the range of \pm two standard deviations about the mean. The model’s fit to the observed distribution patterns does not prove it is necessarily correct; it is possible that other biological assumptions could produce similar distributions of SRA.

Number of individuals versus physical size

There are a variety of other patterns in the distribution and abundance of organisms that have received little attention. For example, in a given region, what is the relation between numbers of individuals and their physical size (mass or characteristic length)? How is the number of individual animals in the 0.1–1 cm size class related to the number in the 1–10 cm class?

Morse et al. (1985) have compiled some facts bearing on this question for insect populations, and have also advanced a qualitative explanation for these facts. They begin with the assumption that roughly equal amounts of energy flow through each size category; although very unlikely to be true in general, this assumption is supported by some evidence from organisms ranging widely in size (Odum 1953). Given this assumption, along with the usual manner in which metabolic costs become relatively larger at smaller sizes, the total number of individuals, N , in the size class with characteristic mass M and length L may be expected to scale as $N \sim M^{-0.75} \sim L^{-2.25}$ (e.g., Peters 1983:329). That is,

for a 10-fold decrease in characteristic length we would, on this basis, expect a roughly 180-fold increase in the total number of individuals ($10^{2.25} \approx 180$).

As seen through the eyes of individual organisms, however, the structure of the habitat—and hence the number of possible ways of making a living—is unlikely to scale linearly with L . Morse et al. pursue this complication by using ideas about the fractal geometry of nature (Mandelbrot 1977, Loehle 1983). Consider, by way of illustration, the length of the coastline of Britain. If we measure it on a 1-km scale we get one answer. Measuring on a 10-m scale, we would get another, larger answer. A yet larger answer would be obtained on a 1-cm scale, and so on. The coastline of Britain is thus not simply one-dimensional, but has a “fractal dimension,” D , such that the perceived length depends on the step-length of measurement, λ , as λ^{1-D} . If $D = 1.5$, for example, a 10-fold reduction in the measurement scale (from, say, 1 m to 10 cm) will result in the apparent length increasing by a factor of $10^{0.5} \approx 3$. Morse et al. applied these notions to measure the profiles of various kinds of vegetation at different scales, concluding that D of such habitats ranged from ≈ 1.3 to ≈ 1.8 , with an average ≈ 1.5 . That is, for herbivorous insects that exploit their surroundings in an essentially one-dimensional way (using the edges of leaves, or the like), a 10-fold decrease in physical size produces a roughly 3-fold increase in the apparently available habitat; for creatures exploiting their environment in an essentially two-dimensional way (using surfaces rather than edges), the effect must be squared, so that a 10-fold decrease in physical size produces an effectively 10-fold increase in apparent habitat. These two factors (the one-dimensional factor 3 and the two-dimensional factor 10) are likely to bound the range of possibilities found in actual assemblies of insects.

Combining these fractal aspects of habitat percep-

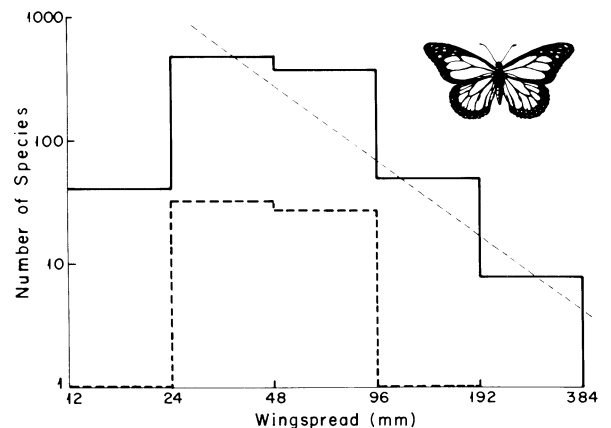


FIG. 4. The numbers of species (S) of butterflies in the Australian geographical realm (solid histogram) and in Britain (dashed histogram) are shown classified according to size (wingspread). The thin dashed line corresponds to the relation $S \sim L^{-2}$, as in Fig. 3. (After May 1978.)

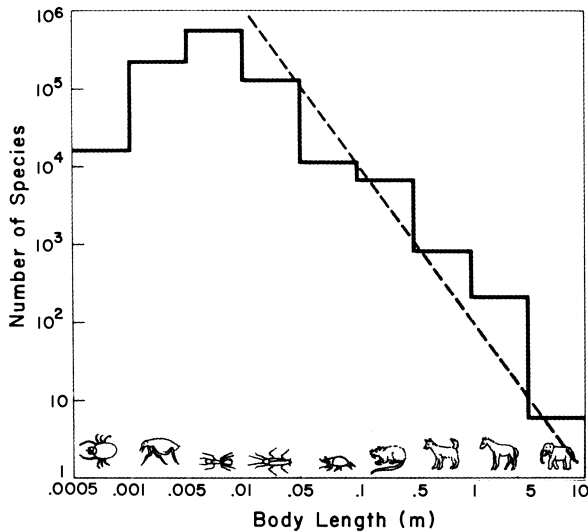


FIG. 5. A crude estimate of the distribution of all terrestrial animals categorized according to characteristic length L . The dashed line indicates the relation $S \sim L^{-2}$, as in Fig. 3 (S = number of species). (After May 1978.)

tion with the metabolic considerations discussed above, Morse et al. (1985) conclude that a 10-fold decrease in characteristic length, L , is likely to produce an increase in N that lies between 500 and 2000 (that is, roughly between 3 and 10 times 180). This very rough expectation is borne out surprisingly well by data for the number of individual arthropods of different body lengths found on vegetation in places ranging from primary forests, primary riparian vegetation, and secondary vegetation in the New World tropics, to temperate habitats, for example birch trees on Skipwith Common in North Yorkshire.

Number of species versus physical size

Other patterns are to be sought in the number of species in different categories of physical size, within a given region.

I have elsewhere reviewed the meager amount of available information that bears on this question (May 1978). Fig. 3 shows the way in which all 3000 or so mammalian species, excluding bats and marine mammals, are apportioned among mass classes (Van Valen 1973). A corresponding treatment, but restricted to the mammal species of Britain, again excluding bats and marine mammals, is also shown in Fig. 3 (May 1978). Britain's mammals appear to obey the global pattern of species versus size, appropriately scaled down. Fig. 4 shows the corresponding species-size relation for butterflies in the Australian geographical realm, and in Britain. Again, the British assembly appears to exhibit roughly the same species-size pattern as the Australasian assembly, scaled down by virtue of the smaller total number of species. Similar figures for other groups are given by May (1978).

Fig. 5 gives a crude estimate of the way in which the

global totality of terrestrial animal species, from mites to elephants, are distributed according to characteristic length. As discussed fully in the original presentation (May 1978), the data in Fig. 5 are the result of a multitude of rough and uncertain estimates. The most serious problem is our current uncertainty, by a factor 10 or more, of the total number of species on the globe. This uncertainty centers on insects and other small creatures, and could well raise the totals in the categories below 1 cm in Fig. 5 by almost an order of magnitude.

Figs. 3–5 and similar treatments represent rough assessments of the facts. Very few ideas have been advanced in explanation of these facts about species-size distributions. Interestingly, one of the few theoretical ventures into this arena is the only paper written jointly by Hutchinson and MacArthur (1959), in which they advance arguments for expecting an L^{-2} relation between the number of species and the characteristic length of constituent individuals, L . This conjectured L^{-2} , or $M^{-2/3}$, relationship is illustrated by the dashed lines in Figs. 3–5. The argument of Hutchinson and MacArthur is essentially that, for terrestrial organisms, the world is seen as two-dimensional, and therefore the possibility of finding new roles (and thence new species) scales as L^{-2} . Whatever the intrinsic merits of this suggestion, the work of Morse et al. (1985) indicates that: (1) for insects, at least, the environment is perceived as somewhere along the continuum from one-dimensional to two-dimensional and (2) the perceived environment scales with a fractal dimension $D > 1$. Thus Hutchinson and MacArthur's argument should possibly translate to an expected scaling of S with L bounded by $S \sim L^{-D}$ and $S \sim L^{-2D}$. With Morse et al.'s (1985) value of $D \approx 1.5$, this argument would replace the dashed L^{-2} lines in Figs. 3–5 with lines lying between $L^{-1.5}$ and L^{-3} .

All this is, however, extremely conjectural. What we really need are both more empirical data about actual species-size relations in species assemblies in a range of geographical areas, and new ideas about possible mechanisms.

CONCLUSIONS

This lecture has tended to approach its subject from the slant of a physicist rather than a naturalist. Although much of the material has been summarized very briefly, the emphasis has been on analytic comparisons within compilations of data, and on the use of deliberately simplified models to help illuminate the mechanisms that may underlie the data. As typified by the discussion of food web structure, there is interest not only in broad trends but also in the residual variance about the trends (and in the way such variance may correlate with particular environmental or biological circumstances). As stated in MacArthur's words at the outset, we seek to find at best contingent generalities.

Such a theoretically oriented approach is, of course, only one among many alternatives, each with its special strengths and weaknesses. Painstaking observations and manipulative experimental studies of the autecology of individual species are essential for rational management or conservation in many practical situations. This being acknowledged, it remains true that information of the general kind shown in Fig. 5 is basic to an ultimate understanding of the world we have inherited. In an age where we are exploring the origins and boundaries of the universe, and where most readers could give an accurate estimate of the number of atoms contained in this issue of *Ecology* (thus quantifying the virtually unimaginable), it is appalling that we do not know to within an order of magnitude how many species of plants and animals we share the globe with. Fewer than two million are currently classified, and estimates of the total number range from 5 to 50 million (Erwin 1983, Wilson 1985). Even less can we explain from first principles why this number is of the general order of 10^7 , rather than 10^4 or 10^{10} . Such ignorance surely reflects the vagaries of intellectual fashion, and the politics of funding, rather than any dispassionate assessment of the fundamental importance of the questions.

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