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Unanswered questions in ecology

Sir Robert May, AC FRS

Chief Scientific Advisor to HM Government, Department of Zoology, University of Oxford, Oxford OX1 3PS, UK

This is very much a personal view of what I think are some of the most important unanswered questions in ecology. That is, these are the questions that I expect will be high on the research agenda over the coming century. The list is organized hierarchically, beginning with questions at the level of individual populations, and progressing through interacting populations to entire communities or ecosystems. I will try to guess both at possible advances in basic knowledge and at potential applications. The only thing that is certain about this view of the future is that much of it will surely turn out to be wrong, and many of the most interesting future developments will be quite unforeseen.

Keywords: ecology; populations; nonlinear dynamics; species; conservation

1. INTRODUCTION

Ecology is a young science. Arguably the first ecological text is Gilbert White's *Natural history of Selborne*, published in 1789. This work goes beyond earlier fascination with descriptive natural history to begin to frame analytical questions about, for instance, what governs the abundance—and vastly different fluctuations in abundance—of swifts and wasps in Selborne. The 19th century saw what I believe to be the most important advance in humanity's intellectual history, with the advent of Darwin's and Wallace's understanding of the basic ideas of evolution by natural selection. But this 19th-century advance in our comprehension of the evolutionary drama was not matched by analytical advances in exploration of the ecological stage on which it is played. In describing the 'struggle for existence' which underlies evolution, Darwin reached, for instance, for metaphors of wedges in a barrel to illuminate a discussion of what we might call 'competition for niche space among species'. But there was, at that time, no attempt—either quantitative or qualitative—to measure the shape and size of the wedges or niches, much less to see if or how they fit together in the barrel. In short, ecological studies lagged behind evolutionary ones in the 19th century.

The British Ecological Society (BES) is the oldest society of its kind, founded in 1913, much later than most other scientific societies. The Ecological Society of America (ESA) followed in 1915. Up to around the middle of the 20th century, the research publications in the journals of both BES and ESA remained predominantly descriptive and classificatory, with much of the focus on plant communities. The pioneering work of animal ecologists, notably C. S. Elton and D. Lack, began to pose some theoretical questions: Why do populations of small boreal mammals so often show marked cycles in abundance? What determines the limits to similarity in beak sizes among co-occurring finches in the Galapagos? At the same time, more purely mathematical studies by V. Volterra, A. J. Lotka, V. A. Kostitsin and others gave hints at the oversimplified beginning of

answers to these questions: predator–prey systems have an inherent propensity to cycle; competing species may coexist, or one may exclude the other (with the winner, in some circumstances, depending on initial abundances). In the third quarter of the century, G. E. Hutchinson, R. H. MacArthur and others speeded up the pace of advance by combining empirical observations with analytical approaches (often explicitly mathematical) to frame clear lines of attack on ecological questions. Influential undergraduate texts began to reflect this progress: Odum's (1953) *Fundamentals of ecology*, with its systems approach, seeing ecosystems almost as factories to be understood in terms of production and energy flows; Begon, Harper & Townsend's (1986) *Ecology: individuals, populations, and communities*, with its presentation of interacting populations of plants and animals as dynamic entities, responding to each other and to environmental changes; Krebs & Davies's (1993) *Introduction to behavioural ecology*, aspiring to connect ecology and evolution by showing how evolutionary forces influence the behaviour of individual organisms in particular environments, opening the possibility of explaining the dynamics of populations and ecosystems in terms of demographic parameters shaped by evolution.

The foregoing historical cartoon is ruthlessly abbreviated and simplified. It brings us to today, at the cusp of the Millennium, when, for all the accelerating advances of recent years, I believe that some of the most important questions of ecological science remain wide open. A selected, and far from exhaustive, list of such unanswered questions follows. For a rather different, but similarly selective, view of the future, see Levin *et al.* (1997).

2. WHAT DETERMINES POPULATION DENSITY?

All biological populations fluctuate in abundance over time. The degree of fluctuation varies greatly among populations, affected both by external environmental or other factors whose effects are independent of population density, and by factors whose impact does depend on population density. The long-term average about which

any given population fluctuates (either a little, like Gilbert White's swifts, or a lot, like his wasps) will ultimately be set by the density-dependent factors. In the absence of such nonlinear regulatory mechanisms, a population will either pursue a fluctuating trajectory to extinction, or balloon toward infinity. Perhaps the most striking illustration of ecology's comparative lack of an analytical tradition—thinking of populations as dynamical systems—is the long-running, verbal debate, reminiscent of medieval scholasticism, about the relative roles of density-dependent and density-independent mechanisms in setting population sizes (for an excellent review, see Sinclair 1989).

This being said, the task of elucidating the density-dependent and independent regulatory mechanisms for specific populations continues to prove very difficult. Gilbert White observed that there were eight breeding pairs of swifts in Selborne, year after year. Given their capacity to double their population each year by producing typically two offspring, he asked what governed their steady abundance. When I ask my ornithologist friends, I get a range of guesses, but no agreed answer. Maybe nesting sites. But in White's day, the swifts nested in the church tower or in the thatched roofs of cottages, whereas for today's steady population of roughly 12 pairs (which, to ecological accuracy, is equal to eight, representing 200 years of constancy!) the church tower is sealed against squirrels and thatching is essentially gone. Maybe food supplies. But, although field patterns have changed little, it strains credulity to suggest that the abundance of swifts' insect food has remained constant under great changes in farming practice. In short, there is no predictive understanding of why the population density of swifts in Selborne is what it is, and has been for over 200 years.

On the one hand, I could give a huge list of density-dependent factors that are involved in setting the long-term abundance of plant and animal populations. I could, however, multiply endlessly the Selborne story, giving example upon example of well-studied populations where we have no confident understanding as to what ultimately sets their abundance. On the other hand, for practical problems—fisheries management, whaling quotas, harvesting terrestrial animals, predicting outbursts of insect pests—we do have effective methods for short-term prediction. They are mainly phenomenological, based to varying degrees of sophistication on projecting trends. In this sense, I could make a fairly confident projection that the swift population of Selborne will be 12 pairs in ten years' time. But lacking fundamental ecological understanding of the underlying regulatory mechanisms, we can only guess at the long-term changes in the same populations that will be caused by various kinds of environmental and other changes. What level of harvesting will cause fisheries to collapse? What, quantitatively, will be the effects on particular bird populations of further changes in agricultural practice? Phenomenology has its uses, but until we really understand why there were and are about ten pairs of swifts in Selborne, rather than one or 100, we cannot claim to predict the effects on them of present and future changes in climate, landscape or whatever. To put it another way, I think ecologists have their analogue of the chemists' heuristic periodic table, which is adequate for

many practical purposes, but we lack the analogue of the underpinning atomic chemistry.

I hope that the 21st century will see advances in fundamental understanding of the average magnitude, and differing degrees of fluctuation, in plant and animal populations. The difficulty has been that most density-dependent regulatory effects acting on a population—food supplies, predators, disease, competing species and so on—are themselves affected by the populations they are interacting with. The nonlinearities inherent in such dynamical systems make it essentially impossible to 'take the system apart', studying it piece by piece in a controlled and comparative way, in the manner that has been so effective for the linear problems that dominate so much of classical physics. But I think recent advances in understanding nonlinear dynamical systems give cause for optimism.

Having described at length what I see as one of the main problems of 20th-century ecology, I shall now give a telegraphic sketch of some of the developments that I think hold hope.

The simplest, purely deterministic, models of density-dependent population change were shown in the 1970s to be capable of amazingly complicated dynamics, ranging from stable points, through stable cycles, to apparently random or 'chaotic' fluctuations (May 1974, 1976). These simplest models were first-order difference equations (such as $N_{t+1} = N_t[1 - aN_t]$), originally propounded as crude first approximations to the dynamics of particular insect and fish populations. This ecological work was one of the two strands that brought 'chaos' centre stage, the other being Lorentz's work on three-dimensional continuous systems in meteorology (Gleick 1987). The earlier, and to my mind silly, debates between proponents of density-independent versus density-dependent regulation had implicitly assumed that strong density independence led to erratic fluctuations and density dependence to population constancy. The advent of 'deterministic chaos' stood all this on its head, with strong density dependence causing population fluctuations as erratic, and—as a result of sensitivity to initial conditions—as unpredictable as anything density-independent external noise could produce. In this light, the agenda for understanding the dynamical behaviour of populations becomes one of unravelling density-dependent 'signals' from density-independent 'noise', in complex nonlinear systems where even a purely deterministic signal may be apparently random, and long-term-unpredictable, chaos.

New techniques for thus distinguishing the apparent randomness of chaotic signals from the 'real randomness' of density-independent noise are being developed (e.g. Sugihara & May 1990; Hastings *et al.* 1993), with applications ranging well beyond ecology.

The most clear-cut illustration of the complexities inherent in nonlinear population dynamics have been demonstrated in the laboratory. In a series of beautiful experiments, Constantino *et al.* (1995) have shown how, essentially by changing development rates, laboratory populations of *Drosophila* in constant environments can move, in a way that is predictable, from steady cycles to chaotic fluctuations. Some other, less definitive, examples are reviewed by Murdoch & McCaughley (1985).

Field studies are obviously much trickier, owing partly to environmental noise and partly to nonlinear interactions with other populations. But these are the problems we need to deal with. Using the methods mentioned above to distinguish chaos (density-dependent signals) from noise (density-independent effects), Stenseth (1995) has, I think, gone a long way towards resolving the long-standing question of what causes the celebrated cycles (with roughly 11-year period) seen over the past 150 or so years in lynx and snowshoe hares in Canada. He finds the hare dynamics to show the signature of almost-periodic chaos, with two interactive variables in the dynamical system. The methods used in decoding such time-series do not tell you what these 'active variables' are; they only tell you the dimensionality of the system. For the lynx, in contrast, the time-series has the signature of almost-periodic chaos with one interactive variable. We could conjecture that the lynx dynamics are driven by its interaction with hares, whereas hare dynamics involve both lynx and food supply. But whatever the biological factors actually are, the dimensionality of the system can be fairly confidently ascribed. Interestingly, this dimensionality agrees with earlier suggestions, based on ecological arguments (May 1973).

Dixon *et al.* (1999) have similarly applied these new techniques to give predictive insights into recruitment of certain tropical fish populations. Again, the time-series analysis illuminates the dimensionality of the system, and provides a novel route to projections, without identifying the specific biological variables. Yet further examples of preliminary application of these techniques to data on erratic, roughly two-year, cycles in measles incidence, and to the abundance of diatoms around San Diego, are given by Sugihara & May (1990). Further work on the measles data, which has become a test-bed for the development of these new nonlinear techniques for short-term forecasting as a signature of deterministic chaos, is surveyed by Levin *et al.* (1997).

The big problem with all such analysis of time-series data, seeking to identify the dimensionality of nonlinear signals versus noise, is that they need long runs of data (long compared with the time interval on which significant changes can occur in the population size). Such long series are rare in ecology. These problems being acknowledged, I nevertheless think that the growing recognition of the difficulties in disentangling deterministic signals from external noise in nonlinear ecological systems is at last clearing the ground for a more mature approach to the fundamental problem of ecology, namely what determines the density of populations. For a recent overview, see Zimmer (1999) in the special issue of *Science* devoted to 'complexity'.

3. SPATIAL STRUCTURE OF POPULATIONS

So far, I have focused on the overall size or density of populations and, by implication, how they change over time. Spatial aspects of population dynamics are also important, and are receiving increasing attention.

As more has been learned over the past few decades, both empirically and theoretically, about the dynamics of interacting populations, we have come to realize that spatial structure can be crucial for the long-term persis-

tence of predator-prey associations, for certain kinds of competing populations, and elsewhere. With the diminishing size and increasing fragmentation of the habitats of many species, these questions have ever-increasing practical significance.

Much of the work on spatial aspects of population dynamics is further complicated by the recognition that simple nonlinearities in population interactions, coupled with movement on some spatial mosaic of patches, can give rise to complex cyclic or chaotic spatial patterns. For instance, a good deal of theoretical and empirical evidence suggests that the persistence of host-parasitoid systems depends on the details of non-uniform distributions of hosts and parasitoids among patches (leaves, plants, etc.). These distributions can be generated by inhomogeneities in the environmental substrate. But, alternatively, they can be self-organized by simple movement patterns—specified fractions of hosts, and of parasitoids, moving to adjacent patches each generation—coupled with the nonlinear dynamics of host-parasitoid interactions. Such patterns can be swirling spirals, apparently random or chaotic distributions which change kaleidoscopically from generation to generation, or even apparently static distributions of 'good' and 'bad' host patches, all self-assembled by the nonlinear spatio-temporal dynamics within a habitat that is itself homogeneous and unchanging (Hassell *et al.* 1991, 1994). Maron & Harrison (1997) have reported a possible example of such a host-parasitoid system in California. Broadly related phenomena of self-organized travelling waves have been suggested for voles by Ranta & Kaitala (1997).

More generally, many populations persist by virtue of a shifting pattern of local extinctions and recolonizations within a spatial mosaic of patches. The dynamics of such 'metapopulations', as illustrated by specific field studies, are surveyed by Hanski (1999). This work has great relevance to the persistence of many such metapopulations, engaged in competitive, predator-prey or mutualistic interactions, as habitat losses cause the total number of patches to decline (Nee *et al.* 1997). Nonlinearities produce threshold phenomena, often of a counterintuitive kind, beyond which species are doomed to extinction. Tilman *et al.* (1994) used the phrase 'extinction debt' to refer to such metapopulation species, where habitat loss has already shifted the spatial dynamics to a point where eventual extinction is inevitable, as local extinctions outrun recolonizations, even though the final tombstone may lie far in the future.

The above only hints at some of the questions for the next century's agenda, as spatial aspects of the dynamics and persistence of populations of plants and animals are more fully explored (Levin 1994; Levin & Pacala 1997). Among these agenda items, I would highlight two. First, a better understanding of the way a population's spatial structure can affect the response to external perturbation, especially the persistence of transients (Hastings & Higgins 1994). Second, the development of methods—akin to those for distinguishing low-dimensional chaos from 'real randomness' in time-series—for discriminating spatial structure due to environmental heterogeneity from that which is self-organized by spatio-temporal nonlinearities within a homogeneous environment.

4. SCALE OF ECOLOGICAL STUDIES IN SPACE AND TIME

Weatherhead (1986) surveyed 308 empirical studies and found their mean duration to be 2.5 years. Tilman (1989) examined 749 studies published in *Ecology* from 1979 to 1989, and found only 13 (1.7%) were field studies of more than five years' duration; out of a total of 180 manipulative experiments in the field or laboratory, 31 (7%) lasted more than five years, whereas 72 (40%) lasted less than one year.

Turning to the spatial dimensions of ecological research, Kareiva & Anderson (1989) surveyed the 97 manipulative field experiments published in *Ecology* between 1980 and 1986, and found 43 (44%) to have a characteristic physical scale of less than 1 m; only 24 (25%) had a characteristic dimension in excess of 10 m.

All this is both understandable and unfortunate. Understandable in that the time-scale fits with PhD and typical research grant durations, while the small spatial scale favours the control, replication and precision, which is always the ideal, but which can be more difficult in large-scale field studies. Unfortunate in that many of the most intellectually challenging and practically important problems of contemporary ecological science are on much longer time-scales and much larger spatial scales (Edwards *et al.* 1994).

Underlining these observations is the fact that many important aspects of the structure and persistence of populations, communities and ecosystems may be disproportionately influenced by relatively rare events. And yet another outcome of recent work on nonlinear dynamical systems is the finding that 'Complex systems form structures [which] vary widely in size and duration. Their probability distributions are rarely normal, so that exceptional events are not that rare' (Goldenfeld & Kadanoff (1999), whose more detailed discussion should be read). There are echoes of this in the recent work of Harte *et al.* (1999), discussed below.

Recognizing these problems, the National Science Foundation in the USA, and Natural Environment Research Council in the UK, have established special programmes to support long-term ecological research. The problem of research on large spatial scales can be more difficult, partly for the expense and coordination it can entail, but even more for its seeming lack of rigour and precision, compared with 'bottle experiments' in the laboratory. I think we need to pay pre-emptive attention to Tukey's (1962) advice that 'far better an approximate solution to the *right* question than ... an exact answer to the *wrong* question, which can always be made precise'.

5. STABILITY AND COMPLEXITY IN ECOLOGICAL COMMUNITIES

The appealing generalization that complex ecosystems are more stable was first set out by Elton (1958), and quickly gained currency. Complexity was roughly defined by the number of species, S , or by the richness of the web of connections among them ('connectance', C , is the number of observed links in the food web, as a ratio to the total number topologically possible). Stability was even more roughly defined, for example as ability to

recover from disturbance ('recovery time', T_R , measured as the reciprocal of the dominant eigenvalue of an interaction matrix), or the average level of fluctuation of constituent populations. Closer examination in the 1970s, however, suggested that model ecosystems constructed as a random assembly of interacting species are more likely to become less stable—more prone to fluctuation and less able to recover from disturbance—as they become more complex (May 1973).

But real ecosystems are not randomly constructed. They are, rather, the winnowed survivors of evolutionary processes acting on their constituent individuals. Insofar as there is any generality, it is that complex ecosystems tend to be more dynamically fragile, with individual populations characterized by higher levels of fluctuation (the system's internal modes of vibration more weakly damped) than simpler ones. This has refocused the agenda towards a better understanding of the structure—and functioning—of real ecosystems, along with a search for those special kinds of interaction structures that tend to favour persistence, that is ability to cope with disturbance (Pimm *et al.* 1991). As the programme of research continues to unfold, it defies any easy generalization. Sometimes—both in models and in the real world—the loss or removal of an individual species can cause great changes in the ecosystem, with cascades of subsequent loss. Such 'keystone' species, however, appear to be relatively rare; species with weaker effects, resulting for example from lower abundance, can nevertheless have varied and important influences on the overall dynamics of the assembly (Paine 1992; Berlow 1999).

In particular, suppose we focus on a single trophic level, with N species competing along some resource spectrum (e.g. each species has some 'utilization function' characterizing its preferred sizes of food items, along some overall size distribution for this food resource). Simple models suggest that, as more and more species are packed in, on the one hand the resource is more fully used and perturbations to the size of the total population of competing species are more swiftly damped. On the other hand, fluctuations in the abundance of individual populations get larger as N increases, in such a way as to suggest, in practice, some limit to the number of co-existing competitors (May 1973).

More recently, Tilman (1999) has drawn together these and other theoretical arguments, with a series of well-designed field experiments on plant communities, to support the broad conclusion that 'increases in diversity cause community stability to increase, but population stability to decrease', as suggested by May's (1973) earlier and cruder model ecosystems. These and other experiments (e.g. Naeem *et al.* 1994) also show that 'greater plant diversity leads to greater primary productivity'. It is worth noting, in passing, that both Tilman's work and that reported by Naeem *et al.* are supported by grants for long-term ecological research, in the USA and UK, respectively.

In short, today's conventional wisdom about the stability–complexity relationship is vastly more textured than the 'complexity begets stability' of the 1960s. But very little of the newer work takes up the question of why some ecosystems have many more species than others. My own picture, painted with the coarsest of brushes, is that

most ecosystems are in tension between evolutionary forces (which tend to add species, efficiently to exploit or subdivide every available niche) and dynamical considerations (increasing species numbers in general makes for greater dynamical fragility—higher levels of fluctuation—in individual populations). Suppose there is some average level of population fluctuation for individual populations, such that the rate at which species are lost is very roughly balanced by new species being added. Then, if the environment is relatively steady and predictable, the trade-off between these opposing tendencies—evolution favouring increasing species number, individual dynamics favouring fewer—can be set at a relatively high number of species. Conversely, in highly unpredictable and environmentally buffeted environments, the premium will be on dynamic robustness of populations, and the opposing tendencies will tend to reach a set point with relatively fewer species. Note that a basic assumption here is that the overall average level of fluctuations shown by populations in highly diverse communities (in relatively steady environments) will be much the same as in less diverse communities (in relatively unsteady environments); such evidence as has been assembled seems to support this. Also note that these ideas suggest that a community's biodiversity is correlated with the predictability of its environment, and not with its overall productivity. This, too, seems roughly consistent with broad observations: tropical rainforests, coral reefs and some old deep lakes, such as Baikal, are all relatively steady environments with high biodiversity, but the first two are highly productive and Baikal is not; conversely, the unpredictable and unsteady environments of estuaries, salt marshes and Arctic tundra are all characterized by low diversity, although again the first two are highly productive and the third is not.

In summary, we need a better understanding of the structure and functioning of ecosystems. The need is heightened by humanity's accelerating impact on global biodiversity. The current lack of consensus about the kinds of issue touched on above is brought home vividly in a recent survey of 'Expert estimates about effects of biodiversity on ecosystem processes and services' (Schlapfer *et al.* 1999). The most notable thing about this survey is the wide variety of opinions expressed on virtually every topic among the 39 'leading ecologists' who responded to the survey (and who knows what the 46 who did not respond thought).

6. FOOD WEB PATTERNS

Another way to approach food webs is to ask questions about their topological structure. How many links, on average, connect top predators to basal resources? How many species, on average, does a given species interact directly with? And how does this depend on the total number of species, S , in the web?

The Tycho Brahe phase of this activity consists of compiling a catalogue of all food webs whose structure has been determined. The current count runs to well over 100 such webs, from land, sea and freshwater (e.g. Cohen *et al.* 1990). The list is beset with problems, which are easier to state than fix. In particular, there is a problem with some species being carefully listed and their links

elucidated, while other ('less sexy') organisms are lumped ('small spiders') and weaker links omitted.

Be this as it may, the next, Keplerian, phase is to seek patterns in these webs (Cohen 1989, 1994; Cohen *et al.* 1990; Pimm 1982; Sugihara *et al.* 1989). One interesting, though controversial, suggestion is of 'link-species scaling invariance' (LSSI). LSSI—the ratio of the total number of observed links, L , to total species numbers, S —is roughly constant, at around two. That is, the average number of species with which a given species interacts, $n = 2L/S$, is around four, independent of S . Subsequent debate suggests this observation may be partly a consequence of the tendency to aggregate species being itself S dependent, so that L/S actually depends, albeit weakly, on S (e.g. Pimm *et al.* 1991). Earlier work on the stability of model ecosystems had suggested that the product of S and connectance, C , might be expected to be roughly constant (May 1973). But, for large S , connectance is related to L by $C = 2L/S^2 = n/S$, whence the empirical LSSI rule gives us that SC is roughly constant, as theoretically predicted. Heady stuff, verging on the Newtonian. More sober reflection, however, reminds us both of the fragility of this theoretical argument (May 1973) and of the shaky empirical basis of the LSSI rule, and also notes that it would be nice to understand why n is as small as four (if indeed it truly is).

Another important empirical finding to emerge from the food web catalogues is that the average length of food chains, connecting top predators to primary producers (plants), is typically short, usually ranging from two to, at most, six links, and on average being roughly three links long. Why are food chain lengths so 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 transfer between trophic levels is significantly higher for ectotherms than for endotherms). Neither tendency is observed. 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. As I see it, this is a central question for ecological science. It remains wide open.

7. RELATIVE ABUNDANCE OF SPECIES

Questions of commonness and rarity underlie much of contemporary conservation biology (Gaston 1994; Rabinowitz *et al.* 1986). A necessary, if not sufficient, condition for answering such questions is to understand the factors governing the relative of abundance of species, SRA.

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 particular member of the family of lognormal distributions, the ‘canonical lognormal’ (Preston 1962; May 1975).

I think it unsurprising 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 the several factors should compound multiplicatively, and the statistical Central Limit Theorem applied to such a product of factors implies a lognormal distribution. The puzzling fact, canonized by F. W. Preston, is that very many species’ assemblies have SRAs that cluster around one particular member of the infinite family of lognormal distributions, characterized by a ‘canonical’ relationship between σ (the standard deviation of the logarithms of the relative abundances) and S (the total number of species present). So here is another empirical observation that calls for basic explanation. My own rather unsatisfactory suggestion (May 1975) is that the canonical property is merely an approximate mathematical property of lognormal distributions with S large and total numbers of individuals, N , much larger than S (any relationship between N and S maps into a relationship between σ and S).

Sugihara (1980), however, has suggested that the ‘canonical’ property is more precise than can be explained by my arm waving. He offers instead 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 model 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 earlier ‘broken stick’ model. Sugihara’s simulations predict a distribution of SRA that is very close to the canonical lognormal once $S > 20$ or so, and which fits a large range of data on communities of birds, moths, plants and diatoms.

A different approach to generating distributions of SRA has recently been proposed, as one particular application of more general ideas based on patterns being self-similar on different scales; these ideas, in turn, come from research on chaos and fractals. Here self-similarity is taken to mean that patterns do not vary with spatial scale. Suppose we halve an area A , then the fraction of the original species now found in the halved area is independent of A . This assumption generates SRA distributions that are similar to lognormal ones around their peaks, but with fatter tails to the rare end (Harte *et al.* 1999). That is, compared with Sugihara’s or lognormal distributions, such SRAs predict higher proportions of rare species. The shape of Harte *et al.*’s curves gives somewhat better fits to most observed SRAs than does the canonical lognormal, with Sugihara’s curves roughly intermediate (the ‘fat rare tail’ had previously been

noted). I have some reservations about this stimulating new work. For one thing, I prefer a view of the world as many random factors (possibly different in separate halves of an island) to the assumption of simple self-similarity (with its implicit assumption of a kind of homogeneity). More important, Harte *et al.* offer no attempt at explaining the ‘canonical’ aspect of the particular members of their family of curves which fit the data.

I have dwelt on these questions, because they touch on much larger issues, mentioned above (Goldenfeld & Kadanoff 1999). There is growing awareness that, in situations where nonlinear dynamics underlie the observed phenomena, standard assumptions about Gaussian distributions may be inappropriate. One important consequence is that ‘rare events’, or rare species, may occur more often than Gaussian intuition suggests (McClintock 1999).

8. RELATIONSHIPS BETWEEN SPECIES NUMBERS, SIZES, RANGES, ETC.

The term macroecology (e.g. Brown 1995) has been coined to stand for a growing interest in a variety of inter-linked relationships between distributions of SRA (as just discussed), geographical ranges, physical sizes and so on. Each such relationship is a piece in the jigsaw we must fit together before we can make predictive statements about the consequences of biodiversity loss. I shall not attempt a catalogue of current questions, but will highlight just two.

First, there is a rough empirical rule about the relationship between the areas of real or virtual islands and the numbers of species on them. Whether counting birds, butterflies, plants or copepods in ponds, a tenfold smaller area contains roughly half the species. This can be expressed as an approximate power law, $S \sim cA^z$, where c is some constant and $z \sim 1/4$ (Preston 1962; MacArthur & Wilson 1967). Although there are exceptions, particularly for continental comparisons among areas, this empirical rule is fairly robust. Remarkably, it can even claim a theoretical underpinning: for large S , the canonical lognormal distribution of SRA gives us $S \sim kN^{1/4}$, with k some constant. If, further, we assume the total number of individuals, N , is linearly proportional to area, A , then—abracadabra—we have the observed species–area relationship, with the observed $z \sim 1/4$. This gives added motivation to a better understanding of why we see the canonical lognormal. Harte *et al.*’s (1999) alternative approach also yields a species–area power law, but the parameter z remains purely arbitrary.

The species–area relationship is widely used in rough assessments of likely future rates of species extinction. Although not strictly a valid application of the above relationship (which, both empirically and theoretically, applies to island assemblies roughly at equilibrium), we can equate observed rates of tropical deforestation (1–2% each year) to loss of habitat area, and thence assess the annual proportion of species committed to extinction (0.25–0.5%, which translates to expected species’ lifetimes, at that rate, of a few hundred years, compared with average background lifetimes seen in the fossil record of a few million years). So, a more secure understanding of such relationships has great practical importance.

Second, we know little about distributions of geographical ranges, either within groups of species or

among them. There are again suggestions that the distributions are often lognormal, although again with a 'fat tail' to the small range end (see Gaston (1996) for a good review). Even more interesting, I think, are questions as to differences in average range size among different groups. In particular, there is a suggestion that comparatively big animals and, conversely, micro-organisms tend to have large geographical ranges, with smaller animals typically having smaller ranges. Among other things, this raises the question whether the global number of species of organisms less than 1 mm long will be vast (as suggested by the rough rule that each tenfold reduction in length increases the number of species of animals one hundredfold, at least down to around 1 mm; May 1978), or whether micro-organism species are very widely dispersed, making them ubiquitous and consequently having moderate global richness of species (a view convincingly argued, with supporting data from chryso-monad flagellates, by Finlay & Clarke (1999)). Clearly, these are central questions both for evolutionary ecologists and for conservation practitioners.

9. BIOGEOCHEMICAL CYCLES AND BALANCES

Another huge set of problems that await solution in the 21st century is a better understanding of how ecological, physical and chemical processes work together to govern the flows of biologically active molecules such as CO₂, N, P and so on. As one leading example, our lack of detailed understanding of the changing balance of CO₂ on land, in the atmosphere and in the sea undercuts predictions about the effects of climate change, and could impede clear implementation of the Kyoto proposals for reductions of emissions. This terse paragraph serves to flag up these questions, whose solution is made additionally difficult by their global scale and consequent need for international collaboration.

10. CONSERVATION PROBLEMS AND PRIORITIES

Sadly, I see the primary motivation for the research agenda indicated above as underpinning efforts to save what we can from the sixth great wave of mass extinction which currently threatens.

Some of these practical tasks do not need ecological understanding. For one thing, we need synoptic and co-ordinated catalogues of those species that have been named and recorded. Once synonyms are resolved—a task that goes slowly without such a database—the current total of distinct, named species of eukaryotes may be around 1.5 million (May 1999). The proposed Global Biodiversity Informatics Facility may speed this process.

For another thing, we need to speed up the rate of identifying new species. Currently, we add about 13 000 species each year, which when discounted for current rates of resolving synonymies reduces to around 10 000 (Hammond 1995). Plausible estimates of the true number of eukaryotic species alive on earth today lie in the range 5–15 million, although numbers as high as 100 million or as low as three million cannot be excluded (May 1999). My best guess is around seven million. So, at current rates, it would take around 500 years to complete the catalogue. Over the coming century, I expect to see this

process accelerated by revolutionary technological changes, as species are identified and classified on the basis of molecular sequence information. But the expert craft of collecting in the field will be the rate-limiting step, determined by how much effort we devote to recognizing the importance of this task.

With better collections and databases, we will gain a better grasp on the facts about extinction rates. Understanding the causes will often be harder. Ecological understanding begins to come to centre stage as we move up the chain, from documenting rates of extinction, to understanding causes and thence to efforts at rescue. Today, I have the impression that extinction rates vary a lot among different groups on land and in the sea, but that our grasp on the facts is shaky, and our basic understanding of causes even shakier (Diamond 1989; Lawton & May 1995; Roberts & Hawkins 1999).

The 21st century will, I believe, see us having to make difficult choices about where we try to act and what we try to save. These need, in part, to be guided by a 'calculus of biodiversity', asking which choices will maximize not simply the numbers of species, but rather the amount of 'independent evolutionary history' we save for future generations (Vane-Wright *et al.* 1991; Prendegast *et al.* 1993; Nee & May 1997). And all such work must take thoughtful account of the important economic, social and political realities that will increasingly constrain such conservation choices (Millner-Gulland & Mace 1998; Dobson 1998).

Central to this amalgam of ecological, social, political and economic science, as I see it, is field research which asks, for example, how many species of tree must remain in a sustainably exploited forest if the primates are to persist in it. Some see the future challenges of conservation biology as effective preservation of pristine enclaves, surrounded by destruction. Others see the challenges as preserving what is possible in areas exploited, as sustainably as best efforts allow, by humans. I think we need both, and both are difficult. But the latter, 'dual use', areas pose the most severe challenges for ecologists and for social scientists (Terborgh 1999; Soulé & Terborgh 1999).

11. CODA

Some of the questions delineated above have been quite particular, reflecting my own interests. But there is a recurring theme, which deserves emphasis. It is that the nonlinearities inherent in ecological interactions can produce very complex systems even from very simple underlying rules. Conversely, communities and ecosystems can obey simple rules even in complex situations.

The changing world view that is emerging from contemporary work on nonlinear dynamical systems has been eloquently stated for physicists by Goldenfeld & Kadanoff (1999, p. 89): 'Up to now, physicists looked for fundamental laws true for all times and all places. But each complex system is different; apparently there are no general laws for complexity. Instead, one must reach for "lessons" that might, with insight and understanding, be learned in one system and applied in another. Maybe physics studies will become more like human experience'. I would add Amen, in spades, for ecology.

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