STABILITY AND COMPLEXITY IN
MODEL
ECOSYSTEMS

WITH A NEW INTRODUCTION BY THE AUTHOR

ROBERT M.
MAY

STABILITY AND COMPLEXITY IN

Model
Ecosystems

PRINCETON LANDMARKS IN BIOLOGY

The Theory of Island Biogeography
by Robert H. MacArthur and Edward O. Wilson
With a new preface by Edward O. Wilson

Stability and Complexity in Model Ecosystems
by Robert M. May
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Preface

This book surveys a variety of theoretical models, all bearing on aspects of population stability in biological communities of interacting species. Some of the broader themes are the relation between stability and complexity in general multispecies models; the relation between stability in randomly fluctuating environments as opposed to deterministic ones; and the way environmental fluctuations are liable to put a limit to niche overlap, a limit to similarity, among competing species in the real world. Minor themes include the way nonlinearities can produce stable limit cycle oscillations in real ecosystems; the role played by time-delays in feedback mechanisms, and the way that addition of extra trophic levels can stabilize them; the relation between stability within one trophic level and total web stability; and why strong predator-prey links may be more common in nature than strong symbiotic links. The survey is neither impersonal nor encyclopaedic, but rather is an idiosyncratic reflection of my own interests.

This work seeks to gain general ecological insights with the help of general mathematical models. That is to say, the models aim not at realism in detail, but rather at providing mathematical metaphors for broad classes of phenomena. Such models can be useful in suggesting interesting experiments or data collecting enterprises, or just in sharpening discussion. The book is primarily directed at the field and laboratory ecologist, and the text is hopefully accessible to people with minimal mathematical training. (In cases where the mathematical technicalities are likely to be of some general interest to theoretical biologists, they are set out in self-contained appendices.)

Above all, I thank Robert MacArthur, without whose stimulating encouragement the book would not have been written.

Sydney University, 1972   R. M. M.

Preface to the Second Edition

On the occasion of a second edition, any author of a technical book must be visited by the temptation to rework the text, bringing things up to date. I do not enjoy writing, and therefore find this temptation easy to resist.

What I have done, however, is to add a short section labelled Afterthoughts, which is located after the original Appendices (pp. 211ff.). Part of this section contains general remarks, prompted by hindsight, on some of the main themes of the book. There is also an attempt to give, for various specific topics, a terse account of the main developments that have occurred since the book was written.

The list of acknowledgments should be expanded to include Gail Filion and John Hannon of Princeton University Press, whose interest and efficiency saw this book (and others in the series, before and since) through to speedy publication.

Princeton University, March 1974   R. M. M.

Introduction to the Princeton Landmarks in Biology Edition

It is simultaneously a pleasure and an embarrassment to write an introduction to this book's canonization as a *Landmark In Biology* by Princeton University Press. The pleasure needs no explanation. The embarrassment—almost an elegiac embarrassment, to attach an improbable adjective— comes from reading the book again in the light of subsequent advances in the subject, and realizing how inadequate any brief attempt to set it in perspective against the contemporary scene must be.

This observation can be expressed a bit more quantitatively. The reprinting is of the 1974 second edition, produced roughly one year after the book's first appearance in 1973 by the simple expedient of adding 30 pages of self-contained "Afterthoughts" (complete with its own bibliography). The original 1973 edition had 235 pages. This represents growth at a rate of around 10% a year, which would compound to over 3,000 pages by the year 2000.

So this updating introduction is necessarily going to be highly selective.

As set out in the original Preface and Introduction (Chapter 1), the book's broader themes deal with stability and complexity in general multispecies models, with the relation between population stability in realistic, fluctuating environments as distinct from unrealistic, deterministic ones, and with the way environmental fluctuations may limit similarities among competing species. Underlying all this, however, is a basic approach, which was not common in ecology and population biology studies at the time, of

viewing biological populations as dynamical systems, ame-
nable to the analytic approaches long-familiar in the physi-
cal sciences. Although much of the discussion in the book
uses linearization techniques, the basic systems are usually
nonlinear and some of the consequent, explicitly nonlinear
behavior that can arise is emphasized. But there would be
much more in this vein if I were rewriting the book today.

In what follows, I will sketch how I see the current state
of play, and how this earlier book relates to it, under four
interlinked general headings: (1) populations as dynamical
systems; (2) stability, complexity, and diversity; (3) effects
of environmental fluctuations; and (4) limits to similarity
("how many species?").

(1) POPULATIONS AS DYNAMICAL SYSTEMS

In 1973, it seemed a good idea to begin a monograph
aimed at ecologists with an accessible and intuitively ori-
ented (as distinct from ponderously formal) account of
some basic ideas about dynamical systems. Thus Chapter 2
discusses the differences between local and global stability
for nonlinear systems, before exploring linearized approx-
imations and how the eigenvalues of a community matrix
relate to such linearized stability properties. This discus-
sion, for example, explicitly gives the Lyapunov function
for the logistic equation (p. 20; something I have not seen
in an ecology book before or since), thus demonstrating
that in this case a linearized analysis gives the global stabil-
ity properties. For ecological theory in the 1960s, popula-
tion cycles meant the structurally unstable neutral cycles—
frictionless pendulums—of the Lotka-Volterra equations,
with periods set by the population parameters, but with am-
plitudes arbitrarily determined by initial conditions. New to
most ecologists were the nonlinear phenomena of stable
limit cycles, which can arise so naturally by predator-prey

interactions or other time-delayed regulatory mechanisms, and whose periods and amplitudes are both determined by population parameters.

Furthermore, most theoretical ecology of that time was—as fairly universal elsewhere in science, virtually since Newton—cast in terms of continuous systems and differential equations. But for many, and indeed arguably for most, biological populations, growth is a discrete process. The appropriate equations are difference equations, not differential equations. Many insect populations appear as discrete, nonoverlapping generations; the corresponding description is in terms of first-order difference equations. Most other insects, along with most vertebrate populations, are made up of discrete but overlapping age classes (higher-order difference equations), which may sometimes be usefully approximated as continuous (differential equations). Hence the distinction made, and the "compare and contrast" discussion, between continuous and discrete population models in Chapter 2 (e.g. Figures 2.1 and 2.2).

As I look back, 25 years on, this scene-setting chapter looks prehistoric. But it does mark the beginning of a seismic shift. Yet earlier work either explicitly or, more usually, implicitly tended to assume that the "balance of nature" would keep population numbers roughly steady from year to year, except insofar as they were affected by fluctuating environmental events. The recognition that the internal dynamics of nonlinear systems could result in the noise-free "equilibrium" being a roller-coaster limit cycle—autonomously driven by virtue of regulatory effects (food supplies, predators, infectious diseases, nest sites, or whatever) themselves being dependent on population density—put an end to simplistic discussions of nature's balance.

But much more followed in the middle 1970s. More attention to discrete time models (difference equations) for population growth led to the realization that the simplest

nonlinear equations, representing how biological popula-
tions may be regulated by feedback mechanisms, can ex-
hibit a bewildering, almost magical, array of behavior. The
very simplest such equations, of the kind suggested by var-
ious people working on insect and fish populations as de-
scriptions of their systems, can—although purely determin-
istic, with no statistical elements—give rise not only to the
expected constant "equilibrium" solutions, but alternatively
to stable and self-generated cycles of boom and bust, or
even more surprisingly to apparently random fluctuations.

For a population, such as many temperate insects, with
discrete nonoverlapping generations (adults appearing each
year, laying eggs to develop into next year's adults, then
dying), a simple metaphor is $x_{t+1} = rx_t (1 - x_t)$. Here x_t
is the population in year t, scaled so that if x ever gets as
large as 1 it extinguishes itself, and r is its intrinsic growth
rate at low density (when x is close to 0). As most readers of
this book today will know, and as can be verified by iterat-
ing this simple equation on a handheld calculator, if r is
between 1 and 3, this equation describes a population
which settles to a constant equilibrium value, as earlier eco-
logical intuition required. If r is above 3, but below about
3.57, we see self-sustained cycles. For r bigger than 3.57, but
below 4, there is "chaos": apparently random fluctuations,
generated by this trivially simple deterministic equation.
Moreover, not only can trajectories of the above "quadratic
map" and other first-order difference equations look ran-
dom, but also the trajectories are so sensitive to initial con-
ditions that long-term prediction—even though we know
the simple and fully deterministic equations governing the
metaphorical population—is impossible. This latter is the
defining property of deterministic "chaos."

These observations, motivated by purely ecological ques-
tions, were one of the two strands of thought that brought
chaos center stage across the sciences (May, 1974, 1976;

Gleick, 1987). The other strand was Lorenz's (1963) mete-orological metaphor, based on a more complicated set of three deterministic differential equations. In problems in-volving continuous change, described by differential equa-tions, we need at least 3 dimensions before the chaotic complications of "strange attractors" can arise (in 2 dimen-sions, chaotic orbits would imply trajectories crossing each other, which is a no-no). Many interesting ecological phe-nomena have since arisen in relatively simple, but neverthe-less 3-dimensional or higher, ecological situations with con-tinuous time. But none of these interesting applications has the striking simplicity of the 1-dimensional difference equa-tions which were so influential in the emergence of chaos.

The broad implications of cyclic and, even more, of cha-otic dynamics for ecology are widespread. The earlier, and I think silly, debates between proponents of density-inde-pendent versus density-dependent regulation had implicitly assumed that strong density independence led to erratic fluctuations, and density dependence to population con-stancy. The advent of "deterministic chaos" stood all this on its head. Strong density-dependence can cause population fluctuations as erratic, and—as a result of sensitivity to initial conditions—as unpredictable as anything density-independent external noise could produce. This redefines the agenda for understanding the dynamical behavior of populations, to one of unraveling density-dependent "sig-nals" from density-independent "noise," in nonlinear sys-tems where even a purely deterministic signal may be ap-parently random, and long-term-unpredictable, chaos.

Such a redefined agenda brings us to the flip side of the chaos coin. We now have to look at apparently random time-series of data, be they from the stock market or currency exchanges or in ecology, and ask are we seeing "random walks down Wall Street" or deterministic chaos or, often more likely, some mixture of the two. 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 and May, 1990; Hastings et al., 1993), with applications ranging well beyond ecology.

The most clear-cut illustrations of the complexities inherent in nonlinear population dynamics have been demonstrated in the laboratory. For instance, Constantino et al. (1995) have shown how, essentially by changing development rates, laboratory populations of *Drosophila* in constant environments can move, in a predictable way, from steady cycles to chaotic fluctuations. Some other early examples are reviewed by Murdoch and McCaughley (1985).

Field studies are obviously much trickier, because they will always involve disentangling the effects of environmental noise from those of nonlinear interactions with other populations. These are, however, the problems we really need to deal with. Using the methods mentioned above to distinguish chaos (density-dependent signals) from noise (density-independent effects), Stenseth (1995) has gone a long way toward 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 (see p. 92 in Chapter 4). Stenseth 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 by these new techniques. I find it pleasing

that Stenseth's findings agree with my much earlier sugges-
tions, based on ecological arguments, set out in this book
(see pp. 102–107).

Dixon et al. (1999) have similarly applied these new tech-
niques to give predictive insights into recruitment of cer-
tain 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 the preliminary
application of these techniques to data on erratic, roughly
2-year, cycles in measles incidence, and to the abundance
of diatoms around San Diego, are given by Sugihara and
May (1990). Further work on the measles data, which has
become a test-bed for the development of these new non-
linear techniques for short-term forecasting as a signature
of deterministic chaos, is surveyed by Levin et al. (1997).

The big problem in all such analyses of time-series data is
that they need long runs of data (long compared with the
time interval during 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 disentan-
gling 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).

Essentially all the discussion in my 1973 book ignored
the effects of spatial heterogeneity. Although usual in those
far-off days, such omission is egregious. The subsequent
three decades have seen a great deal of work on the many
different ways in which spatial considerations can be eco-
logically important. Among these are questions of spatial
chaos. In particular, one currently unsolved problem is the
development of methods—akin to those for distinguishing

low-dimensional chaos from "real randomness" in time-series—for discriminating spatial structure caused by environmental heterogeneity from that which is self-organized by spatiotemporal nonlinearities within a homogeneous environment. For theoretical and experimental discussion of some of these issues, see Levin and Pacala (1997), Hanski (1999), Maron and Harrison (1997), Ranta and Kaitala (1997), Nee et al. (1997), Hastings and Higgins (1994), and Hassell (2000).

One thing is clear. Although "chaos" is not treated in the 1973 book, it burst onto the wider scene very soon afterward, largely as a result of the spirit of that era in ecology, from work on 1-dimensional difference equations or "maps" (Li and Yorke, 1975; May, 1974, 1976; May and Oster, 1976). This was not, as often misunderstood, ecologists applying current ideas about chaos. It was ecologists independently finding chaos, and finding it in discrete-time 1-dimensional difference equation systems which were simpler and more easily understood than the 3-dimensional continuous-time systems of differential equations which represented the second, distinct strand in the emergence of general recognition of the phenomenon. The recognition that simple and fully deterministic rules or equations can generate dynamical patterns which are effectively indistinguishable from random noise has very deep implications for science. It effectively marks the end of the Newtonian dream that knowing the rules will enable prediction; predicting local weather beyond about 10–20 days is not just a problem of computational power, but of the inherent unpredictability of chaotic dynamical systems.

(2) STABILITY, COMPLEXITY, AND DIVERSITY

Again, it is hard to look back from the turn of the millennium and grasp the mind-set of 1973. Perhaps the best way

to drive this message home is to observe that the word "diversity" did not appear in this book's index in 1973.

Then, as set out in Chapter 3, there was a widespread impression that more species in a community or food web, and more interspecies interactions or links among them, would confer greater dynamical stability (in the form of being better able to survive disturbance without losing species, or simply having lower levels of fluctuation in individual populations). Pages 37–40 and 172–173 give a sense of yesterday's debate about "stability and complexity," and I think today's reader might find it a bit surprising. The debate, and the terms in which it was conducted, are certainly quite different from much of today's debates about "the consequences of diversity," which, however, often unintentionally misrepresent the earlier debates as having been about just the same things as today.

Today, most discussion of the "diversity-stability hypothesis" is conducted under the rubric of field or laboratory experiments, showing that in a particular place or environment, plots with greater diversity maintain greater primary productivity following disturbance. These are interesting questions, but they are substantially different from those engaged under this general heading 30 years ago, and I think it is a bit confusing to suggest otherwise, as often is done.

Neither *then* nor *today* does the stability/complexity/diversity debate give much attention to why there are more species in some places than in others. Thus most of the above-mentioned experiments artificially increase or decrease species numbers, to explore how this affects primary production under disturbance, without asking why some natural systems are very productive with few species, whilst others are very species-rich. Ultimately, however, these latter may be the questions of greatest relevance to conservation biology and to continued delivery of "ecosystem services" (Daily, 1997).

Looking at Chapters 3 and 7, one way to capture the flavor of the 1973 debate is to note (pp. 40 and 173) that one of Elton's arguments for complexity-promotes-stability was that simple mathematical models of one-predator-one-prey systems do not possess a stable equilibrium point. As I observed then, this is only half of an argument, and the other half—stability properties of corresponding n-predator-n-prey models—stood Elton's argument on its head. Chapter 3 draws together several different lines of attack, to show clearly that the stability of an ecosystem (ability to withstand disturbance without losing species) is not automatically enhanced by complexity (more species, or more connections). Indeed, as a generality, quite the contrary. This result for arbitrarily general model ecosystems, however, says little about real ones. In this sense, I think the main impact of the book in the early 1970s was to clear the undergrowth, and refocus the agenda of that time to asking what are the special kinds of food web structure, or patterns of interrelationship among species, which reconcile increasing species richness with ability to persist under disturbance.

It should be emphasized that the study of model ecosystems never was more than a corner of a larger canvas, painted by field and laboratory experimenters. Nevertheless, the theme of relationship between the network structure of food webs and their ability to handle perturbation is central in ecology, as in many other subjects. Some of the inspiration for Chapter 3 came from the work of Gardner and Ashby (1970), which suggests that large complex systems, with component elements or nodes connected at random, may be expected to be stable up to some critical level of connectance, and suddenly collapse beyond that (pp. 62–67). The reorientation of this question to what kinds of connectance patterns are likely to be most resistant to specific kinds of disturbance is of continuing relevance in ecol-

ogy, as elsewhere. For example, recent work by Albert et al. (2000) on the relation between the structure of networks and their vulnerability to disturbance shows that, for networks with high coefficient of variation (standard deviation/mean) in the distribution of connections among nodes, as is the case for the Internet and World Wide Web, the system is robust to random removal of links, but very highly vulnerable to attacks deliberately targeted at the most highly connected nodes.

Today's research involves experiments, in the field (often on a large scale) and in the laboratory (often purpose-built), along with new theory. The work can be viewed under three broad headings, which are interlinked but also susceptible to being confused one with another. One category embraces questions about the effects of disturbance upon productivity, often primary productivity of plants, of a community or ecosystem. A second asks about corresponding levels of fluctuation in the constituent populations; this can shade into asking about whether populations persist under disturbance. A third set of questions, perhaps less commonly asked, concerns why some natural communities have lots of species, and some few.

An excellent review of this first set of "productivity-stability" issues is by Tilman (1999). A subsection of this synoptic review deals with *Tests of the diversity-stability hypothesis*. Essentially all these are carefully controlled experimental studies in which, in one place, plots were manipulated to produce different degrees of diversity, and then subjected (either naturally or artificially) to environmental change. For example, Tilman (1996, 1999) reports the effects of "11 years of year-to-year variation in climate on the stability of total community biomass in 207 Minnesota grassland plots in which plant diversity had been modified by various rates of nitrogen addition. . . . [finding] a highly significant stabilising effect of plant diversity on the total

community plant biomass of these plots." Other studies, including the controlled-environment Ecotron at Imperial College's field station (Naeem et al., 1994) and a large collaborative project on plant diversity and productivity in grasslands at 8 sites across Europe (Hector et al., 1999), also found greater biomass in plots with more species. This is interesting work, but its relation to ecological stability in the sense used by Elton and Hutchinson, and elaborated in this book is, at best, indirect. Indeed, argument rages over the significance of much of this body of experimental work (Kaiser, 2000). For one thing, if you have more species, you are more likely to have those which are most productive in a given environment, or alternatively which are likely to flourish under a specific environmental fluctuation or challenge; this is an oversimplified version of what Tilman et al. (1997) and, independently, Huston (1997) have called the "sampling effect."

The controversy about whether these manipulative, and arguably rather artificial, experiments prove that natural diversity promotes ecosystem stability, or whether they simply show that if you put together a bigger selection of species, you are more likely to get a subset that are the best mix, has generated some rancor. This was brought to a head by a recent Ecological Society of America (ESA) report, arguing from these experiments that "the prudent strategy [is to preserve] biodiversity in order to safeguard ecosystem processes vital to society." I completely share Tilman's view, as reported by Kaiser (2000): "we have a case where everybody is partly right, and some people are vehemently partly right."

The second set of questions deal with the fluctuations and persistence of individual species within ecosystems. This is the basic focus in Chapter 3, titled "Stability versus Complexity in Multispecies Models," and also in Chapter 6 which restricts attention to competitive interactions within

a single trophic level. In both chapters, the essential conclusion is clear: all other things being equal (which, of course, they often are not in practice), more species and more links among them will make for greater levels of fluctuation in individual species.

The diversity-productivity studies, as just summarized, rarely measure or discuss fluctuations in individual species. Tilman (1999) is a notable exception. He finds, in his review of grassland plots, that "populations were destabilised by increases in diversity." In the single trophic level studies of Chapter 6, we see that the eigenvalues characterizing the internal modes of the system become smaller as the number of species, S (which determines the number of nodes), increases; this means the times taken to recover from disturbance tend to lengthen, making for higher levels of fluctuation in individual species. But, as seen in eq (A.32) and emphasized in the Afterthoughts on page 231, the maximum eigenvalue, which characterizes the stability of the system as a whole, increases (linearly) with S; that is, the total population tends to fluctuate less as S increases. The lack of emphasis of this point in the original 1973 edition is unfortunate, although understandable given the somewhat different questions in vogue at that time. By 1974, I had appreciated the importance of this point more clearly, and if I had been prescient I would have made a bigger thing of it.

The early 1970s and the late 1990s come together nicely in Tilman's (1999) wide-ranging review, based on his MacArthur Lecture: "In total, theory, experiment, and observation agree: diversity stabilises community and ecosystem processes . . . but simultaneously destabilises the dynamics of individual species."

The third set of questions listed above concerns, ultimately, the causes of biological diversity. My own view, set out in Chapter 7 and in the Afterthoughts (see especially

Figure X on page 215, and the accompanying discussion), remains 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 new species are lost is very roughly balanced by new species being added. If the environment is relatively steady and predictable, the trade-off between these opposing tendencies—evolution favoring increasing species number, individual dynamics favoring 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 fluctuation 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.

All three categories of questions are relevant to the larger understanding of the causes and consequences of biological diversity. But the third—and, these days, relatively unfashionable—category of question is, I think, at least as important as the first. To the contrary of the controversial ESA statement alluded to above (Kaiser, 2000), it could be that deeper knowledge of the rules governing ecosystem

assembly could enable "ecosystem services" to be delivered in a world which was grievously biologically impoverished. The possibility that the world of the cult movie "Bladerunner" may be sustainable cannot be ruled out just because I—and probably you—would not wish to live in it.

(3) EFFECTS OF ENVIRONMENTAL FLUCTUATIONS

When *Model Ecosystems* was written, theoretical population biology consisted mainly of deterministic differential equations. In addition to its discussion of discrete-time difference equations, the scene-setting Chapter 2 discusses the way different kinds of stochasticity can affect a population's dynamical properties.

In particular, the chapter introduced the terms *Demographic Stochasticity* and *Environmental Stochasticity*, and discussed the distinction between them. Today, the terms are common currency, and few would win a trivia prize for identifying their origin. When environmental stochasticity is introduced in a simple way, Figure 2.4 illustrates the rough, qualitative differences in stability properties that arise, compared with corresponding deterministic systems, Figure 2.2.

The effects of environmental stochasticity are further explored in Chapter 5. For white noise in systems of differential equations, the distinctions between the Ito and Stratonovich calculi (which depend upon whether, in the underlying limit process, the noise correlation time or the dynamical time interval went to zero first) are set out telegraphically on page 204 and more fully, with emphasis on the gist rather than the formalism, on page 230. A minor industry has subsequently developed around these arcana. Chapter 5 applies this discussion of stochastic differential equations to a qualitative discussion of criteria for popula-

tion persistence, or of fluctuation to extinction, in such randomly varying environments.

Subsequent work, which I will not review fully here, has rightly recognized that the ecological effects of environmental stochasticity can depend greatly on the detailed properties of the noise. The "color" of the noise—whether it has no temporal correlations ("white"), or whether it is relatively more highly correlated over short ("red") or alternatively long ("blue") time intervals—can significantly affect the outcome. So, too, can questions of whether the noise enters additively or multiplicatively (as in eq (5.10) and (5.11)), and if the latter, into exactly which term. For a review of some of these issues, in nonlinear contexts which include chaos, see Tong (1995).

Some of this work has found applications, which I think are particularly interesting, in fisheries management. The older, and essentially deterministic, ideas about "maximum sustainable yield," MSY, have given way to management approaches which recognize that such MSY criteria may result in greatly enhanced population fluctuations, which have obvious adverse consequences. The management rules subsequently employed by the International Whaling Commission, and currently used by North Sea fisheries and others, explicitly recognize these kinds of effects (see e.g. Beddington et al., 1984). The subsequent collapse of so many fisheries sadly represents disjunction between sound advice and its implementation.

There are also implications for basic ecological theory. Some very early researchers (e.g. Andrewartha and Birch, 1954) seem to have thought that pure, density-independent noise could explain how populations behave over time. Such beliefs fail to appreciate that, in the absence of any density-dependent effects whatsoever, a population—however much it may fluctuate up and down, driven by environmental vagaries—will on average either decrease to ex-

tinction or expand indefinitely (unless, by a miracle, birth and death rates exactly cancel, in which case extinction times can be very long). There has, however, been much interest over the past three decades in elucidating the role of population fluctuations (caused mainly by environmental, but occasionally demographic, stochasticity) in competitive coexistence and exclusion, in time scales to extinction following habitat modification or other perturbations, in community composition and patterns of relative abundance (particularly in very species rich places), and in much else. One occasionally acrimonious strand of this area of activity is, in effect, attempts to revisit the old Andrewartha-Birch/Nicholson-Bailey debates about the extent to which populations are regulated by density-dependent versus density-independent factors (one paper labels it "new wine in old bottles"; I think it is undrinkable wine, relabeled for marketing purposes). Clearly, both kinds of factors matter, in different proportions for different cases. For an admirably incisive review, see Sinclair (1989).

(4) LIMITS TO SIMILARITY

Under the first three headings, I have been able to sketch major advances in our understanding, often resulting in the 1973 book being of little but historic interest. The fourth heading, asking about how similar can competing species be yet coexist, was a hot topic of the 1960s and early 1970s. The idea set out in Chapter 6, that population fluctuations caused by environmental variability might tend to extinguish some competitors that were too similar in their use of resources of one kind or another (even though the populations could indefinitely co-occur in a purely deterministic world), seemed at that time to offer insights. The consequent broad suggestion that the limits to niche overlap may be set roughly by average differences between

populations (d) being not much less than average differences within either population (w) in respect to resource use, held a promise of bringing some much-needed detail and specificity to the "how many species" questions under heading (2) above.

Notice that this work was always painted with a broad brush. The limits to similarity were never faintly like a crisp inequality, d > w. For one thing, the environmental variability (characterized by some value σ^2) necessarily was a factor; in the deterministic limit $\sigma^2 \to 0$, the models of Chapter 6 give no limits. But Chapter 6 always makes plain that any such models were sensitive to detail: the environmental variability enters only logarithmically (via $\ln\sigma^2$) in the basic one-trophic-level, one-resource models of Chapter 6 (see p. 152); it enters alternatively as $(c\sigma^2)^{1/2}$, where c is some constant, in eq (6.33); and, in general, the suggested criterion is only a qualitative one. Some subsequent studies, pointing out small quantitative (factors of order 2) differences between the rough analytic expressions in Chapter 6 and detailed numerical simulations, are a bit silly.

Alas, there are other and more serious problems with Chapter 6. My criteria that set limits to similarity on the basis of stability conditions for damping times to be fast enough (eigenvalues to be far enough to the left of the imaginary axis; see Figure 5.2) turn out to be quite sensitive to exactly how and where the environmental noise is put into the population equations. Different kinds of colored noise, and/or noise which enters in ways different from that in Chapters 5 and 6, can lead to different conclusions (in that some such models can put no limits to similarity, beyond those found in the deterministic limit). This tended to usher this work off the stage.

Even more important, perhaps, were reappraisals of the data which had motivated much of this work in the first place. Some of the patterns and assembly rules suggested as

being seen in ecological communities were, admittedly, in need of rigorous validation against appropriate null models. The consequence is that some of the "Comparison with Real Ecosystems" in Chapter 6 (pp. 165–170) now appears naive. I think this wave of methodological rigor was basically a good thing. But, like many good things, it got a bit out of hand.

In particular, I am embarrassed by the enthusiasm of my embracing the d/w ~ 1 criterion (itself, in retrospect, very shaky) to explain Hutchinson's (1959) observation—itself based on earlier work by Dyar and others—that in many groups of animals, "character displacement among sympatric species leads to sequences in which each species is roughly twice as massive as the next," or length ratios of around 1.3 (p. 167; this observation is itself often even shakier). However, some of the criticism of this and other work, seeking to test the validity of such putative patterns against null models, ended up on the wilder shores of silliness. Comparison with null models is admirable, but there are often serious problems in the far-from-trivial task of constructing an appropriate such null. My favorite foolishness was the dismissal of a possible factor-2 size sequence within a particular sympatric family of Hawaiian birds by constructing a null model that pooled *all* Hawaiian birds, from ducks to hummingbirds. Needless to add, this null model dismissed the earlier findings. A highlight of those heady days was Feinsinger et al.'s (1981) brilliant parody which analyzed Bach fugues against a null model (constructed, as was fairly usual, essentially by reshuffling the notes), and scornfully dismissed all earlier conclusions that these fugues were other than random sequences of notes. For an overview of these debates, see Strong et al. (1984) or Harvey et al. (1983).

An unintended result of this toing and froing was a sense, in the 1980s, that studies of limits to similarity were a

bit of a mess. More fertile fields beckoned, and this area has lain relatively fallow. I continue to believe this is a most important area of ecological research, from both fundamental and applied points of view; it needs new and constructive ideas. Current work directed toward understanding the composition and species richness of communities in specific places is largely macroscopic and phenomenological—species-area relations and the like. Questions of limits to niche overlap, among particular species in particular environments, call out for revisiting.

CODA

For the past five years, I have been away from research (for all but one day a week, spent in the Zoology Department at Oxford University) in the very different world inhabited by the Chief Scientific Adviser to the UK Government. My experiences there, especially in relation to concerns about climate change, the potential beneficial and adverse effects upon the environment of new kinds of crops, emerging diseases and antibiotic resistance, and much else, leave me with a strong belief that the kind of fundamental ecological questions raised in this book are even more important now than they were in 1973.

We have made much progress in some areas, little in others. Many central problems remain. Meanwhile, extinction rates among better documented groups currently run about one-thousandfold faster than the average background rates seen in the fossil record, and are set for further acceleration over the coming century (Lawton and May, 1995). We do not even know, to within a factor of 10, how many distinct eukaryotic species we share today's world with. Much to do, much motivation to do it.

Cabinet Office, Whitehall, September 2000   R.M.M.