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From Energetics to Ecosystems:

The Dynamics and Structure of Ecological Systems

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From Energetics to Ecosystems:
The Dynamics and Structure of Ecological Systems

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From Energetics to Ecosystems: The Dynamics and Structure of Ecological Systems

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THANK YOU PETER FOR LEADING THE WAY . . .

PETER YODZIS
AT THE ARBORETUM, UNIVERSITY OF GUELPH, CANADA

The water of spring
Has nothing to do
But flow over these rocks.
24.4.77

Designed by Susan Yodzis

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PREFACE

A BRIEF INTRODUCTION: WEDNESDAYS WITH PETER

"If the theory is a true piece of deductive logic—and not just a guess—then theory in advance of data has the power to help us collect and use data efficiently. The reverse of the coin? Data are treacherous when offered in support of explanations free of theory. Do not trust such explanations, no matter how much data seems to support them."

Mike Rosenzweig

Not long ago John Vandermeer visited me at McGill. Knowing the severity of Peter Yodzis' neurological condition—amyotrophic lateral sclerosis (ALS) or the Lou Gehrig's disease—he suggested we organize an academic symposium in Peter's honor at the University of Guelph. In a sense John's suggestion was similar to the story of Mohammed and the mountain. Peter could not go to a conference but we could bring a conference to him. I agreed, in principle, but was paralyzed by such a seemingly monumental organizational task. I did little. Sometime later I serendipitously related this story to Neil Rooney and David Noakes. Both listened carefully, agreed wholeheartedly with John, and soon after, had planned a colloquium and a book that honored Peter and his significant scientific career. I would like to emphasize that although it was my wish to see the realization of this colloquium and book, they were undoubtedly the result of John's inspiration, and David and Neil's resourcefulness. Such was the way the colloquium and book series in Fundamental Ecology started.

It was at this point that David, Neil, and I began to meet every Wednesday with Peter. Although the intended goal of the meetings was to organize the colloquium, the thread of our conversations often strayed. Ever the passionate scientist, Peter also brought to the table a variety of interests, from the Baltimore Orioles to Haiku poetry, although food seemed to top his list. As such, our discussions were seemingly light in appearance. This was not quite true though. These conversations, although light in some aspects, were underlined with the utmost seriousness—Peter's was dying and he was dying rapidly. On several occasions he would let us know this directly and without fear. An extremely modest but confident man, he wanted to use this last vehicle to make some final statements to his scientific colleagues and friends. Even the light topics of our Wednesday meetings, in hindsight, seem to be interlaced with threads of his personal philosophy on life and science. These same philosophical threads also permeated my graduate experience with Peter. This book is both a Festschrift

for Peter and an attempt to bring some of his unwritten scientific views to life. In what follows, I briefly walk through some of the topics that he quietly and modestly recapitulated to me and others, time and time again.

MATHEMATICS AND ECOLOGY

Peter was a fearless man. He was never afraid of standing alone and perhaps, one could argue, sometimes he chose to stand alone. As he frequently put it, "sometimes one must fight the good fight." He never used this phrase to elevate himself, but rather to point out his undying belief that a person ultimately must stand up for what he or she believes. One of those good fights to him was the formal and rigorous use of mathematics and logic in science.

While studying general relativity theory in physics he saw the power of simplifying or abstracting complex systems. He firmly believed that ecology must develop and hone these same analytical and quantitative skills. Not surprisingly, this belief struck fear into the hearts of almost all undergraduate biology students at the University of Guelph. On another level, however, there were the few who truly held him in highest esteem precisely because he demanded so much of them. He was feared, on average, because he made them learn theoretical ecology, which meant that biology students must be at least modestly able to work with some of the basic mathematical tools of algebra, calculus, and dynamical systems. He was fearless because this does not win you any popularity contests. That being said, I have met more than one student who, although being terrified by his course material, spoke volumes of what Peter actually did for them as ecologists or biologists in the long run.

Peter was disturbed by his belief that ecology was frequently misled simply by the lack of clarity in thought. As a graduate student of Peter's, I quickly realized how thorough he was, as every problem he undertook was subjected to an almost infinite number of perspectives. Calculation after calculation was necessary as rigor was of utmost importance to him. I also think Peter believed that slowly immersing oneself in a problem had the interesting tendency to produce delightful insights. This tendency, he felt, was lost in the push to create volumes of papers as opposed to fewer more sound papers. As a result of his firm beliefs, working with Peter was often challenging. He frequently pushed you to explore further, even when you felt certain that your question had been answered. As we came to know more about a particular problem, he would begin to raise the nastiness of the explorative tasks to new heights, as though even greater insights into a problem demanded a nonlinear increase in workload. As challenging as this process was, and is, I find myself doing similar things to my own students now.

Although he held many beliefs firmly, Peter was not resistant to change as a scientist or a person. This, I imagine, was also part of the "good fight." Like everyone, certain things never pushed him to change his views but when something did potentially modify his view of the world he responded, not

surprisingly, by weeks on weeks of rigorous investigation. Such intense bouts were occasionally followed by a change in viewpoint, a very well-informed change of viewpoint indeed. It was likely this ability to change that enabled him to abruptly abandon theoretical physics for theoretical ecology while he was in Bern, Switzerland. Peter, tweaked by an environmental essay written by Barry Commoner in the *New Yorker*, became engrossed by the problems of the environment. He felt that mathematical theory and his rigorous set of tools might be able to play a role in ecological development. He left physics to change the world, and soon found himself working in the lab of an empirical ecologist (Professor Hans Burla) who helped educate Peter on ecological theory at that time.

During this time, he found out that other physicists like Robert May and Don DeAngelis had also switched to ecology and had begun extending the theories of Alfred Lotka, Vito Volterra, and Robert MacArthur. Although the ecological culture seemed poised for change at this time (e.g., Robert MacArthur's competition theories were forefront in ecology), the academic culture of zoology and botany departments seemed to lag behind. In many departments, a league of natural historians had gathered and, although they collectively represented an enormous wealth of biological knowledge, they had little, if any, training in mathematics. The stage was set for departments to be deeply suspicious of these new theoreticians. Peter's story fit this scenario rather cleanly.

I want to emphasize that the University of Guelph showed tremendous vision to even consider Peter for a position. A good friend and colleague of Peter, David Lavigne, related to me the story of Peter's hiring at the University of Guelph. I imagine that many universities have no such stories simply because most departments resisted change. This is evidenced by the fact that Peter was one of a mere handful of theoreticians in Canada for many years. This is not to say that Peter's hiring was completely embraced by all members of the department, however. In David Lavigne's words:

One day, one of my colleagues on the search committee came to my office with a letter of reference received in support of Peter's application. By this time, if I remember correctly, some of us had identified him as the best candidate, but others weren't so sure. Regardless, my colleague handed the letter to me and said, "What do you make of this?" I read the letter and the sentence I particularly remember went something like this:

"Peter Yodzis is the best young theoretical ecologist on the market today . . . if you can get him, grab him immediately, before someone else does."

I remember thinking, "Great letter," and I said so to my colleague.

His reply went something like this: "Well, yes, it is a very positive letter . . . but who is Robert May? Have you ever heard of him?"

This story points out that the hiring of a new breed of ecologist, a mathematical ecologist, was an uphill battle. It took such brave foot soldiers as Peter to pave the way for change in ecology, and an open-minded department to provide him with that opportunity. This is nothing small; ecology has changed dramatically because of the intellectual curiosity of a fearless few.

The merging of different cultures is rarely seamless and, as ecologists know so well, trade-offs exist. Like many mathematical theoreticians, Peter's daily work habits were at variance with the civil service attitudes that prevailed during the early part of his career. He tended to get in after lunch and stay late into the night, his room shining like a beacon across the night campus. When eyebrows were raised about his peculiar schedule, Peter used to say, somewhat tongue-in-cheek, "I'm a theoretical ecologist; I'm always working!"

More to the point, the sudden prominence of mathematics in ecology also threatened to divide ecologists into two solitudes. Such division is common in most scientific disciplines (e.g., see the famous physicist Richard Feynman's remarks on those who know mathematics and those who do not, in his lecture, The Relation of Mathematics to Physics). Mathematical theory may be especially divisive in a developing science where the cultures have had little time to develop an ability to communicate. Encouragingly, when Peter first started teaching a graduate course at the University of Guelph, three or four faculty actually sat in on the lectures, collected the handouts, and did the assignments. This was the beginning of Peter's final "good fight," to demystify theoretical ecology for empiricists and so begin a discourse in a way that accelerated ecological understanding.

OF GEDANKEN EXPERIMENTS AND THEORETICAL ECOLOGY

"In mathematics the art of asking questions is more valuable than solving problems"

Georg Cantor

If there is one thing I remember most about my meetings with Peter, it is his love of the Gedanken or thought experiment, which can be explained as the distillation of a complex problem into a simpler form. Einstein, and physicists in general, may be the most renowned for the Gedanken experiment. Many physical laws result from setting up complex problems in an answerable way (e.g., "given a world with no gravity then . . . "). This simplification, if done well, brings clarity in understanding, new questions, and ultimately new hypotheses that speak to an otherwise murky situation. I think, to Peter, the Gedanken experiment was a thing to be exalted, and it exemplified the things he loved about the power and beauty of theory.

In a simple sense, the Gedanken experiment has two parts: (1) the simplification process itself and (2) the new intuition it brings. The first part—simplification with controlled loss of information—is ultimately the task of every scientist investigating problems in a complex world. I recall Peter telling me that Robert May was a champion of posing problems in a way that made them answerable and yet shed light on a situation. I would argue that if you study both Robert May and Peter Yodzis' work, you will see that a lion's share of their brilliance is in the setting up of the problem. In essence, they created useful mathematical thought experiments. In this light of posing answerable questions,

Peter felt that an underestimated role of theory was actually developing clear new ecological questions. This sounds obvious perhaps but I do not think it resides firmly in most views of how science works. I can even recall an extremely bright colleague of Peter's, during a discussion on this exact topic, suggesting that we already had too many questions in ecology.

To end this, it is important to point out that different questions likely require different formulations and thus different degrees of abstraction. As questions become increasingly more specific one can imagine that the ability to simplify ought to become increasingly more difficult. We may expect interesting contingencies as we heighten our understanding and explore Nature's amazing eye for detail. Along these lines Peter felt that theory must play a role in understanding and predicting these contingencies. Moreover, theory must also play a role as an integrator of disparate research areas.

It is arguable that this synthetic role of theory is underplayed in today's science where excellence seems so focused on "novel" or "new" ideas. The synthetic part of theory has the ability to open up new questions and suggest new experiments. Take, for example, Peter's speculation that bioenergetics may be able to play such a role in understanding ecological dynamics. Despite the fact that an enormous number of mechanisms can be suggested that stabilize or destabilize predator–prey interactions, he felt that viewing this interaction from an energetic perspective simplified the problem, while still retaining the fundamental properties that determined system dynamics (hereafter called the Yodzis Energy Conjecture). Stated more precisely he suggested that increased energy flows tend to decrease stability; while decreasing energy flow in interactions tends to stabilize interactions. A corollary of the Yodzis Energy Conjecture (which could just as easily be phrased in terms of limiting nutrients) is that any mechanism that retards energy flow between a consumer and a resource stabilizes the dynamics. Thus, if one thinks of any mechanism and considers its implications in terms of flow, then one can intuit the dynamic response. It is hard for me to find a counter to this simple line of reasoning. Importantly, such synthesis then allows us to enter more complex situations (e.g., food webs, ecosystems) with increased understanding. Such a synthesis also suggests a rich number of new experiments in more complex systems, wherein structures can be viewed as exciting or inhibiting flow.

Peter was by no means a natural historian of models, but rather he used them to ask specific questions that he hoped would illuminate our understanding of the way the world worked. A recent trend towards seeing theory solely as a model selection exercise troubled him deeply. Clearly the ability to bring data to bear on models is an important new advance in ecology (e.g., see the burgeoning new literature on model selection) but to Peter modeling alone was not theory. He felt that pure theory organized and honed our thoughts. In this way it put together plausible sets of models that spoke to the way the world might work. Along the way theory thus suggested new data to gather and new ways to look at old data. In this sense, modeling and model selection is an extremely important

part of confronting theory with data and so is an important aspect of theory development. This book is a testament to the fact that Peter's message has been heard. In what follows, I briefly discuss the studies contributed to this book, and how they relate to Peter's work and scientific philosophy.

THE BOOK

This book, in a sense, is representative of some of the developments that have unfolded when mathematics and physics met ecology. Consistent with Peter's interest in carefully structuring a problem, we start the book with a section on simplifying and synthesizing Nature's complex relationships. We then move to a section, which explore the mapping between food web structure and function, and end the book with a section on the role of theory in integrating different research areas. All chapters thus speak to the things Peter Yodzis' thought were fundamental in ultimately understanding complex natural systems.

To begin Section I, Mariano Koen-Alonso's chapter explores one of the most critical aspects to food webs, the multispecies functional response that governs the fate of biomass transfer through food webs. The chapter is a very thorough and much needed review of this subject, especially as more complex food web theory is now relying on specific multispecies functional responses. Richard Williams et al. and Dave Raffaelli follow by considering the potential simplifying power of body size in food webs. The chapter of Williams et al. is an excellent review and synthesis of the baroque work of Peter Yodzis' and Stuart Innes 1992 American Naturalist classic. Further, the authors introduce this technique in a framework that is amenable even to the most mathematically timid ecologist. Raffaelli, on the other hand, makes the thought-provoking suggestion that body size, instead of species, may be a very natural way to aggregate food webs. Since body size frequently determines rates and trophic status, it allows a means to simplify by retaining important functional attributes of ecosystems. Finally, in this section, Adrian deBruyn et al. show how an energy-flow-based view of trophic interactions can be used to meaningfully and simply unfold how food web structure ought to mediate trophic control.

Section II moves on to focus on the role food web structure plays in governing population dynamics. Peter Morin reviews experimental studies and the roles of energy and food web structure on complex dynamics. Similarly, but from a field perspective, Kirk Winemiller grapples with how we can effectively reduce Nature's complexity. Winemiller illustrates his ideas with the wonderfully complex relationships he has documented and studied in tropical river food webs. John Vandermeer follows Winemiller by looking at the role complex dynamics may play in mediating diversity in real systems. His theoretical exploration is interestingly used to consider community structure, neutral theory, and the incredulous diversity of tropical forests. Jim Drake et al. then takes a truly fun look at how such complex dynamics as seen by John may be an inherent and vital aspect of all ecological systems. This section ends with a contribution of

Peter Yodzis and Kevin McCann that unfolds some of the dynamic properties of simple food webs. This chapter was largely written by Peter almost 10 years ago after a publication by Joel Cohen in *Nature* on similar properties of discrete population models.

Finally, Section III looks at recent theory that merges separate research areas. Specifically, we consider a number of chapters that look at microevolution, life history, and ecological dynamics. Junling Ma et al., Don DeAngelis et al., and Hal Caswell, all look at how current ideas from ecology and evolution are beginning to develop a rich research area that operates between microevolution and ecology.

These chapters are the contributions of people interested in honoring Peter and his approach and I thank them for their considerable effort and patience in helping us put this book together. Their contributions are just a sample of the progress that has been made in recent decades, thanks largely to the rigor and theory that Peter and his mathematical contemporaries brought to ecology. Those of us who saw Peter at his last conference would readily say that he was a man who cared deeply about the science of ecology. So very close to his death, even having difficulty in speaking, he rose to the occasion and gave a brilliant hour and a half lecture. Upon his finish, he was greeted with a long standing ovation. A moment I think none of us will forget. There is no doubt in anyone's mind that Peter fought the good fight and he died fighting.

The Peter Yodzis Colloquium on Fundamental Ecology is now an annual event. Peter passed away shortly before the second annual colloquium.

Kevin S. McCann

CHAPTER 1

A PROCESS-ORIENTED APPROACH TO THE MULTISPECIES FUNCTIONAL RESPONSE

MARIANO KOEN-ALONSO

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In other words, to be density-dependent, the enemy must respond to changes in the numbers of the host.[1] The nature of this response is commonly twofold. First, there must be a *functional*[2] response to (say) an increase in the host density, because of the increased availability of victims: as host density rises, each enemy will attack more host individuals, or it will attack a fixed number more rapidly. A frequent, but not invariable result of this is an increase in the numbers of the enemy (a *numerical*[2] influence), due to an increased rate of survival or of reproduction, or both…

<div align="right">M.E. Solomon (1949)</div>

1.1   INTRODUCTION

The concept behind the term "functional response" is present in the works of Lotka (1920, 1925) and Volterra (1928). When Solomon (1949) actually used it for the very first time it already explicitly covered most of the features that we associate with it today. Briefly put, these features are:

(a) The functional response describes the changes in predation rate as a function of prey density: "the enemy must respond to changes in the numbers of the host"

(b) It is a per capita rate, or in a more general sense, a consumption rate per unit of predator: "each enemy will attack"

(c) It may be unbounded, but it is likely to have some bounds: "as host density rises, each enemy will attack more host individuals, or it will attack a fixed number more rapidly"

There are other features that are not mentioned in the extracted paragraph, but that also contributes to the development of current functional response theory, being most relevant the effect of multiple resources, and consequently prey selection/switching, and the impact of predator density on the consumption rate[3].

Another important element from Solomon's paragraph is the explicit dynamic context in which the functional response is presented. The goal of the functional response is not just to measure the impact of predation on the prey population, but also its impact on predator dynamics through the numerical response: "a frequent but not invariable result of this is an increase in the numbers of the enemy."

Therefore, the utility of any discussion on functional responses will be enhanced if we first present some basic elements of predator–prey theory. The reason is simple; although we want to develop functional responses that can incorporate different ecological processes, the final goal is, more often than not,

---

[1]Like in many other early works (e.g., Nicholson 1933, Holling 1959a, Watt 1959), predator–prey and parasite–host terminologies were often used interchangeably.

[2]Italicized in the original paper.

[3]These components were soon incorporated in the theory of functional responses. In 1959 Holling (1959b) was talking about "subsidiary components" in the functional response (e.g., the density and quality of alternate foods, and predator characteristics), while Watt (1959) developed a functional response that has considered interference among predators.

to plug them into predator–prey models. Today, this is not only propelled by our scientific curiosity, but also has important applied implications like development of multispecies dynamic models for management of exploited ecosystems (Yodzis 1998, 2001).

Recent and extensive reviews of predator–prey theory (Murdoch et al. 2003, Turchin 2003) have been focused mainly in systems with typical single-species functional responses; among recent reviews on functional responses (Jeschke et al. 2002, Gentleman et al. 2003), only one actually addresses multispecies functional responses, but without attempting to derive them from a general mechanistic framework (Gentleman et al. 2003).

The objective of this chapter is to present a simple process-oriented approach to derive multispecies functional responses. This approach finds its roots in the works of Holling (1959a, b, 1965), Royama (1971), and Yodzis (1989, 1994). In some ways, this chapter is an extension of Yodzis (1994) to the multispecies case.

1.2   SOME OPERATIONAL DEFINITIONS

- The functional response of a given predator with respect to a specific prey i (F_i) is the amount of prey i consumed by a unit of predator per unit of time.
- If the predator feeds on K different prey resources, the total consumption rate of prey per unit of predator and time (G) can be calculated[4] as $G = \sum_{k=1}^{K} F_k$.
- A laissez-faire functional response is the one, which is only a function of prey densities, but in a more general setting the functional response may also depend on predator density.

1.3   ELEMENTS OF PREDATOR–PREY THEORY

Let us consider a simple case with only one prey and one predator, where N_i and P are the prey i and predator densities, respectively. Furthermore, let us define the functional response of the predator with respect to prey i as $F_i = a_i N_i$, a_i being a constant coefficient. Using this functional response, the Lotka–Volterra model (Lotka 1920, 1925, Volterra 1928) describes the dynamic of a predator–prey system as

$$\frac{dN_i}{dt} = r_i N_i - F_i P$$
$$\frac{dP}{dt} = P[e_i F_i - \delta] \tag{1.1}$$

where r_i is the intrinsic per capita growth rate of prey i, δ is the per capita death rate of the predator, and e_i is a conversion factor of prey i into predator. In the predator equation, the factor in brackets is the "numerical response," and

---

[4]To simplify notation, summations over all prey species like this one will be indicated as $G = \sum_{K} F_k$ throughout the text.

describes the per capita growth rate of the predator as a function of prey consumption (i.e., $\frac{dP}{dt}\frac{1}{P} = f(F_i)$).

Although phrased in terms of abundance density (i.e., number of individuals per unit area), this model was initially presented by Lotka (1920) in terms of biomass. He also stated that e_i was logically bounded between 0 and 1, implicitly recognizing the conservation of biomass principle. This simply means that a predator cannot produce more biomass than the actual biomass of prey consumed (i.e., in this case, e_i represents conversion efficiency).

A natural expansion of Eq. (1.1) is the Rosenzweig–MacArthur model (Rosenzweig and MacArthur 1963, Rosenzweig 1969). A general version of this model can be described as

$$
\begin{aligned}
\frac{\mathrm{d}N_i}{\mathrm{d}t} &= r_i N_i \left(1 - \frac{N_i}{K_i}\right) - F_i P \\
\frac{\mathrm{d}P}{\mathrm{d}t} &= P[e_i F_i - \delta]
\end{aligned}
\tag{1.2}
$$

where K_i represents the carrying capacity of the prey, and the remaining parameters have the same meaning as before. The main differences with the Lotka–Volterra model are the logistic (instead of exponential) growth of the prey in absence of predation, and the form of the functional response (Holling's disc equation is customarily assumed for this model, originally described by Rosenzweig and MacArthur [1963] in graphical terms). If we assume biomass densities, it also conforms to the conservation of biomass principle.

The Lotka–Volterra and the Rosenzweig–MacArthur models are very similar. They share many features. However, not all predator–prey models are like these. There is another substantially different way of modeling predator–prey systems.

The Leslie model (Leslie 1948) describes the predator–prey dynamics as

$$
\begin{aligned}
\frac{\mathrm{d}N_i}{\mathrm{d}t} &= r_i N_i \left(1 - \frac{N_i}{K_i}\right) - (a_i N_i)\, P \\
\frac{\mathrm{d}P}{\mathrm{d}t} &= r_P P \left(1 - \frac{P}{\psi_i N_i}\right)
\end{aligned}
\tag{1.3}
$$

where r_i and r_P are the per capita intrinsic growth rates for the prey and predator, respectively, $a_i N_i$ is the functional response (i.e., $F_i = a_i N_i$), K_i is the carrying capacity of the prey, and ψ_i is a conversion coefficient from prey density to predator carrying capacity.

Even though this model links predator dynamics with prey density, it does not explicitly consider the functional response in the predator equation (although nothing prevents writing $\psi_i N_i = e_i(a_i N_i)$ with e_i as an appropriate coefficient). This model was the first one that used a predator–prey ratio in a trophodynamic model, and served as a source of inspiration for the posterior development of the logistic theory of food web dynamics (Berryman et al. 1995). When expressed in terms of biomass, it does not comply with the conservation of biomass principle.

The Lotka–Volterra, Rosenzweig–MacArthur, and Leslie models are three common examples from the many predator–prey models, which have been developed (see reviews in Royama 1971, May 1973, Maynard Smith 1974, Yodzis 1989, Berryman 1992, Murdoch et al. 2003, Turchin 2003). However, all these models can be grouped into two schools of thought, the "Lotka–Volterra" and the "Leslie" streams, named after the models that originated them. These modeling streams embody conceptually different ways of describing predator–prey dynamics (Ginzburg 1998, Berryman 1999).

In terms of the actual biology, predation means mortality for the prey and acquisition of resources for the predator. In the "Leslie stream," the logistic form is assumed for the predator dynamics, and hence, it does not emulate the role of predation for the consumer. For example, even assuming $\psi_i N_i = e_i(a_i N_i)$ in the Leslie model, the functional response becomes a limiting factor for growth, not its source.

In the "Lotka–Volterra stream," the consumption represented by the functional response truly becomes predator growth, actually linking the two biological sides of the predation process. Furthermore, the link between functional response and predator's growth is usually assumed linear (Ginzburg 1998, e.g., the numerical response in Eqs. (1.1) and (1.2)). For multiple prey, the numerical response can be written as:

$$\frac{dP}{dt}\frac{1}{P} = \sum_K e_k F_k - \delta \qquad (1.4)$$

In this expression, e_i are typically modeled as constant coefficients, implicitly assuming that alternative preys are nutritionally substitutable (Tilman 1982). This means that for the predator, consuming an amount E_i of a given prey i is equivalent to consuming cE_j of another prey j, where c is a constant factor.

However, not all prey resources are necessarily equivalent from a predator's perspective (Tilman 1982, O'Neill et al. 1989). For example, plants taking nutrients from the soil. If one nutrient is scarce, this may limit predator growth regardless of the consumption rates of the others. Hence, the numerical response will depend on both the functional responses *and* the nutritional balance of the diet (i.e., actual diet composition). Equation (1.4) implies that the conversion factors e_i must be functions of the consumption rates (i.e., $e_i = f(F_1, \ldots, F_i, \ldots, F_K)$). Usually, assuming substitutable resources and linear numerical responses appear to be a reasonable and useful approximation (Tilman 1982, Ginzburg 1998), but we should remember that this may not always be the case. The way in which the functional response enters into a predator–prey model is certainly not trivial.

The rest of this chapter will focus on the functional response. We will pay attention to the side of the predation process that has a direct impact on the prey. Nevertheless, those characteristics of the prey that may affect the numerical response (e.g., net energetic value and nutrient content) can certainly affect foraging behavior (e.g., prey selection), and hence, also influence the consumption rate.

1.4 TWO BASIC MULTISPECIES FUNCTIONAL RESPONSES

1.4.1 A question of time

The functional response is defined as a per capita consumption per unit of "total" time, but the derivation of the Holling's disc equation, for example, makes reference to "time exposed to prey" or "foraging time" (Holling 1965, Stephens and Krebs 1986). This discrepancy is often avoided by assuming, explicitly or implicitly, that predators are foraging all the time.

However, this assumption does not always hold. Foraging may also mean that the predator itself is also exposed to sources of mortality, and hence, the trade-off between foraging and other activities can be an important component in the regulation of the predation process (Abrams 1982). Therefore, it is necessary to fill the gap between foraging and total time more formally. In this way, even though we may presume that predators forage all the time, we also allow for the possibility of relaxing this assumption (e.g., Abrams 1982, 1984, 1991).

Let us consider that total time (T) can be partitioned into two mutually exclusive components, foraging and other activities, then

$$T = T_F + T_O \tag{1.5}$$

where T_F is foraging time and T_O is the time assigned to other activities. Using Eq. (1.5), we can define the fraction of the time assigned to foraging (or equivalently the probability of foraging) as:

$$f_F = T_F/T \tag{1.6}$$

which allows expressing total time as a function of foraging time. This probability is often assumed equal to one ($f_F = 1$).

1.4.2 The basic multispecies functional response: common searching time

Holling (1959a) stated that his disc equation was a *basic* functional response. The reason for this terminology was twofold. First, he considered only the minimum components required to derive a plausible functional response. Second, all the "subsidiary components" that may have an effect on the functional response (e.g., alternative prey) can be incorporated later into the basic form as needed.

The original derivation of the disc equation considered only one prey (Holling 1959b), but it was later extended to the multispecies case (Murdoch 1973). The rationale presented here is based on Peter Yodzis' version of this derivation.

Let us assume that total foraging time (T_F) can be divided into two mutually exclusive activities, searching for prey (T_S) and handling prey (T_H), then

$$T_F = T_S + T_H \tag{1.7}$$

If the predator feeds on K different prey resources, and assuming that each unit of prey i requires a constant amount of time to handle it (h_i), then Eq. (1.7) can be rewritten as:

$$T_F = T_S + \sum_K h_k E_k \tag{1.8}$$

where E_i is the total amount of prey i consumed by the predator.

Now, if we define a capture rate[5] for prey i as:

$$C_i = \frac{E_i}{T_S} \tag{1.9}$$

this per capita rate represents the capture (and consumption) of prey i per unit of *searching time*, and if we plug-in Eq. (1.9) into Eq. (1.8) we get

$$T_F = T_S \left(1 + \sum_K h_k C_k \right) \tag{1.10}$$

However, we defined the functional response as the consumption rate per unit of total time, this means

$$F_i = \frac{E_i}{T} = \frac{E_i}{T_F / f_F} = f_F \frac{E_i}{T_F} \tag{1.11}$$

therefore, if we replace E_i and T_F in Eq. (1.11) by Eqs. (1.9) and (1.10), we arrive to

$$F_i = f_F \frac{C_i}{1 + \sum_K h_k C_k} \tag{1.12}$$

This is a basic multispecies functional response that incorporates the ultimate constraint imposed by the time needed to kill a unit of prey. If we define $Q_i = \frac{C_i}{1 + \sum_K h_k C_k}$, then Eq. (1.12) can be described in terms of two general factors that fully define this basic functional response, one is the probability of foraging (f_F), the other is the "functional response while foraging" (Q_i) (Abrams 1982). In this basic functional response, Q_i is a function of all capture rates ($Q_i = f(C_1, \ldots, C_i, \ldots, C_K)$), and if we assume $f_F = 1$, the shape of F_i will depend on the specific form of the capture rate.

1.4.3 The basic multispecies functional response: prey-specific foraging time

In Section 1.4.2, the searching time was common for all preys; when searching, the predator is looking for *any* prey. However, if we consider the case where a

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[5]In Yodzis (1994) the capture rate is called "attack rate." This term has commonly been used for the constant coefficient in the Holling's disc equation. To avoid confusions, Peter Yodzis later suggested the alternative term used in this chapter.

predator is after one, and only one, prey species at a time, its total foraging time can be written as

$$T_\text{F} = \sum_K T_{\text{F},k} \tag{1.13}$$

where $T_{\text{F},i}$ is the foraging time allocated by the predator to go after prey i. If we define $X_i = T_{\text{F},i} / \sum_K T_{\text{F},k}$ it follows that $T_{\text{F},i}$ can be calculated as

$$T_{\text{F},i} = X_i T_\text{F} \tag{1.14}$$

where X_i is the fraction of the total foraging time allocated by the predator to prey i (i.e., $\sum_K X_k = 1$).

Within the foraging time allocated to a given prey, we can still distinguish between the two mutually exclusive activities of searching and handling prey. Furthermore, if we again assume a constant handling time per unit of prey i, $T_{\text{F},i}$ can be written as

$$T_{\text{F},i} = T_{\text{S},i} + h_i E_i \tag{1.15}$$

where $T_{\text{S},i}$ is a prey-specific searching time, h_i is the handling time per unit of prey i, and E_i is the total amount of prey i consumed by the predator. In this case, the capture rate is defined by

$$C_i = \frac{E_i}{T_{\text{S},i}} \tag{1.16}$$

because the time invested in searching for *other* prey species is not actual searching time for prey i.

By combining Eqs. (1.15) and (1.16), the total foraging time allocated to a given prey becomes

$$T_{\text{F},i} = T_{\text{S},i}(1 + h_i C_i) \tag{1.17}$$

and considering Eq. (1.14), the total foraging time can be written as

$$T_\text{F} = \frac{T_{\text{F},i}}{X_i} = \frac{T_{\text{S},i}(1 + h_i C_i)}{X_i} \tag{1.18}$$

It follows that if the predator allocates prey-specific foraging times, the resulting basic functional response can be calculated as

$$F_i = \frac{E_i}{T} = f_\text{F}\frac{E_i}{T_\text{F}} = f_\text{F}\frac{E_i}{T_{\text{F},i}/X_i} = f_\text{F}\frac{T_{\text{S},i} C_i}{T_{\text{S},i}(1 + h_i C_i)/X_i} \tag{1.19}$$

which simplifies into

$$F_i = f_\text{F} X_i \frac{C_i}{1 + h_i C_i} \tag{1.20}$$

In this case, the "functional response while foraging" is defined by $Q_i = C_i/(1 + h_i C_i)$, which is only a function of C_i. Assuming $f_\text{F} = 1$, the shape of this basic functional response is given by the functional forms of X_i and C_i.

1.5   GENERALIST AND SPECIALISTS PREDATORS

A generalist predator is usually described as one that feeds on many resources and has a broad diet, while a specialist predator is the one that depends on one or very few resources (Murdoch et al. 2003). However, it is clear that these terms are describing the extremes of a continuum, and even though they may still be useful in practice, setting the boundary between many and few resources (i.e., the border-line that separates specialists from generalists) is not that simple (Gerking 1994).

In theoretical studies, the use of the term specialist is usually constrained to a predator that consumes only one prey (e.g., Fryxell and Lundberg 1994). However, Eqs. (1.12) and (1.20) may provide, at least at a conceptual level, a wider operational definition for specialist and generalist predators. If foraging time is prey-specific (i.e., when searching, the predator is looking for one specific prey), then the predator is a specialist (Eq. (1.20)); if searching time is common to all possible prey, then the predator is a generalist (Eq. (1.12)). How many species are actually included in the diet from the available prey field will determine the scope within each class of predators.

Although both types of basic multispecies functional responses are possible, they are not necessarily equally probable. The generalist form is likely to be the more frequent one. Let us consider the simplest case possible: two identically parameterized preys that are nutritionally substitutable. Just to make things easier assume $f_F = 1$, $C_1 = C_2 = 1$, and $h_1 = h_2 = 1$ (all with appropriate units), and in the context of Eq. (1.4), $e_1 = e_2$.

Under these considerations, the total consumption rate for a generalist predator (Eq. (1.12)) is

$$G = \sum_{k=1}^{2} F_k = \frac{C_1 + C_2}{1 + h_1 C_1 + h_2 C_2} = \frac{2}{3}$$

while the same rate for a specialist predator (Eq. (1.20)) is

$$G = \sum_{k=1}^{2} F_k = \frac{X_1 C_1}{1 + h_1 C_1} + \frac{X_2 C_2}{1 + h_2 C_2} = \frac{1}{2}$$

both with the corresponding identical units. In the specialist case, this result holds for any combination of X_1 and X_2 (remember that $X_1 + X_2 = 1$).

This simple example indicates that under identical conditions, the predator is better off behaving as a generalist than as a specialist. Its total consumption rate will be higher. Therefore, prey-specific foraging times, although theoretically possible, appear in principle an unlikely proposition.

However, this analysis is rather simplistic; a more thorough examination must take into account many other evolutionary and ecological constraints (e.g., predator fitness, the actual numerical response). For example, if different preys cannot be hunted simultaneously (e.g., if different predatory behaviors are needed, or the preys do not share the same habitat) or, pure and simple, if

different preys are not perfectly substitutable, then prey-specific foraging times can be a valid alternative.

1.6 THE INTERNAL STRUCTURE OF THE CAPTURE RATE: A RECIPE FOR BUILDING FUNCTIONAL RESPONSES

The capture rate describes the per capita consumption rate per unit of searching time. This function is not only a handy concept; it is also a rate feasible to be measured in real systems under appropriate circumstances.

Different mathematical expressions for the capture rate can produce a broad range of functional responses (Yodzis 1994). For example, in the generalist predator case (Eq. (1.12)), $C_i = a_i N_i$ (with a_i a positive constant and $f_F = 1$) generates the multispecies version of the disc equation.

Using the "index method" (Royama 1971), a plausible internal structure for the capture rate can be developed. As Royama (1971) pointed out, this way of adding complexity into the model has "the advantage of illustrating some basic properties that the model must have, without going into too minute and unnecessary details."

Let us assume that a generalized capture rate can be represented as

$$C_i = p_i g_i m_i \tag{1.21}$$

where p_i is a selection factor, g_i is a prey-dependent factor, and m_i is a predator-dependent factor.

The prey-dependent factor is only a function of the density of prey i ($g_i = f(N_i)$), and is directly proportional to the capture rate of prey i in the absence of alternative prey and predator interference/facilitation (i.e., $C_i \propto g_i$). This function typically increases with prey density, and constitutes the functional core of the capture rate.

The selection factor can be either a constant ($p_i = c$), or a function of all ($p_i = f(N_1, \ldots, N_i, \ldots, N_K)$) or some ($p_i = f(N_a, \ldots, N_b)$ with $a, b \in [1, K]$) prey densities, and represents the effect of alternative food choices on the capture rate. It is typically interpreted as the probability of preying on a specific prey i, given the available prey field and the predator-specific mechanism for choosing among alternative prey (i.e., $0 \leq p_i \leq 1$).

The predator-dependent factor is only a function of the density of the predator ($m_i = f(P)$), and represents the effect of predator interference or facilitation on the capture rate. In the absence of these effects, this component can be reduced to a constant ($m_i = c$), or be assigned a conventional value of one ($m_i = 1$).

1.7 THE BOUNDS OF THE FUNCTIONAL RESPONSE

The Lotka–Volterra model (Eq. (1.1)) has a linear and unbounded functional response ($F_i = a_i N_i$). As prey density increases, F_i also increases, and in the limit ($N_i \to \infty$) the functional response tends to infinity. This is probably the first

and most frequent criticism to the Lotka–Volterra model (Watt 1959, Holling 1959a, Ivlev 1961).

An unlimited consumption rate is not only a problem from a theoretical perspective (Watt 1959, Holling 1959a, Ivlev 1961); the empirical evidence also demonstrated that actual consumption rates usually show an upper bound, clearly indicating that the Lotka–Volterra functional response was too simple (Watt 1959, Holling 1959a, b, Ivlev 1961, Murdoch 1969, Hassel et al. 1977, Rindorf 2002).

Lotka (1925) seemed to be aware of this caveat. He wrote, just before presenting his predator–prey equations, "for values of N, P, not too large."[6] If we consider the original Holling's disc equation (Eq. (1.12) with only one prey, $C_i = a_i N_i$ and $f_F = 1$),

$$F_i = \frac{a_i N_i}{1 + h_i a_i N_i} \tag{1.22}$$

we see that for very small prey densities (i.e., $h_i a_i N_i \ll 1$), the disc equation can be approximated by $a_i N_i$. A similar result is obtained if we assume extremely small handling times. Therefore, for very small densities and/or handling times, an unbounded equation may be a reasonable approximation to the functional response. Nevertheless, more realistic and general functional responses require some upper limit to the consumption rate.

The derivation of our basic multispecies functional responses followed Holling's rationale, and hence, it is not a surprise that they share their upper bound with the disc equation. If we assume that $C_i \to \infty$ when $N_i \to \infty$[7] and $f_F = 1$, both the generalist (Eq. (1.12)) and specialist (Eq. (1.20)) basic functional responses have multiple asymptotic values, one per prey species. When $N_i \to \infty$ the generalist functional response has an asymptotic consumption given by $1/h_i$, while in the specialist functional response the asymptotic consumption is X_i/h_i. Considering that X_i is a proportion, the maximum possible asymptotic consumption is $1/h_i$ for both basic functional responses.

Together with the actual handling time, other factors can influence the maximum consumption rate (e.g., failed attacks, digestion, and satiation/hunger level) (Holling 1959a, 1965, Mills 1982, Abrams 1990, Jeschke et al. 2002, Essington and Hansson 2004). These factors are usually incorporated by broadening the definition of handling time as "time spent out of the search for prey due to the consumption of one unit of prey." In this standard expansion, handling time takes a form as $h_i = h_{h,i} + f_{dp,i} h_{d,i}$ where $h_{h,i}$, and $h_{d,i}$, are the strict handling and digestion times per unit of prey i, respectively, and $f_{dp,i}$ is the fraction of the digestion time per unit of prey i that the predator spends out

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[6]Lotka (1925) actually used N_1 and N_2 to denote prey and predator densities.
[7]With only one exception (see Sect. 1.7.3), this assumption holds for all functional responses in this chapter.

of the search for prey because it is digesting (i.e., this defines the "digestive pause").

This approach apparently suffices for many applications; a large number of applied and theoretical studies assume generic handling times without further examination (e.g., see the recent reviews of Murdoch et al. 2003, and Turchin 2003). Nevertheless, functional responses explicitly considering digestion and searching for prey as parallel processes have also been developed (e.g., Holling 1965, Jeschke et al. 2002).

Even though multispecies functional responses have multiple asymptotic consumption rates, they are often modeled assuming a single saturation level common to all preys (e.g., Evans 1988, Fasham et al. 1990, McCann et al. 1998, Yodzis 1998, Koen-Alonso and Yodzis 2005). This assumption can be justified on purely pragmatic considerations (i.e., less parameters to be estimated), but there is also some biological basis for it. Based on allometric scaling (Lavigne 1982, Peters 1983, Innes et al. 1987, Brown et al. 2004) and bioenergetic reasoning, Yodzis and Innes (1992) indicated that the asymptotic consumption rate ultimately depends on the physiology of the predator. Considering that most predators appear to be digestion-limited (Jeschke et al. 2002), it seems a biologically sound approximation to model multispecies functional responses with a single saturation rate.

Within our framework, this means assuming a common handling time for all prey ($h_i = h$ for all i). If we define the asymptotic consumption rate as $J_{max} = 1/h$, the basic multispecies functional responses become

$$F_i = f_F \frac{J_{max} C_i}{J_{max} + \sum_K C_k} \tag{1.23}$$

in the generalist case, and

$$F_i = f_F X_i \frac{J_{max} C_i}{J_{max} + C_i} \tag{1.24}$$

in the specialist case.

1.8 SIMPLE MODELS: ONLY PREY-DEPENDENT FACTOR IN THE CAPTURE RATE

The classical classification of single-species functional responses is a graphical one, and contains three basic types (Holling 1959b, 1965). Type 1 corresponds to a functional response that increases linearly with prey density until it reaches a ceiling, from where further increases in prey density do not increase the consumption rate (Figure 1.1a). Type 2 is characterized by a hyperbolic shape, where the consumption rate monotonically decelerates with increasing prey density until it reaches the saturation level (Figure 1.1b). Type 3 functional responses show a sigmoidal shape, and hence, consumption rate has an initial accelerating phase at low prey densities and a decelerating phase at high prey densities until it reaches the asymptotic consumption rate (Figure 1.1c).

Although the Holling's types are the best known, these are not the only shapes a simple single-species functional response can take. We already saw that in the Lotka–Volterra model the functional response is linear but without saturation (sometimes dubbed Type 0) (Figure 1.1d). In some instances, when large densities of prey have a negative effect on consumption rate (e.g., toxicity or predator confusion), the functional response can show a peak at intermediate prey densities, and a subsequent decline at higher densities (dubbed Type 4) (Figure 1.1e) (Gentleman et al. 2003). Finally, the consumption of prey may be completely prevented when prey density is below a threshold (e.g., all prey can find refuge from the predator, or prey density is so low that the predator cannot detect it), above which predation is customary described with a Type 2 shape (Figure 1.1f).

These types are defined for single-species functional responses, but they can be expanded to the multispecies case. Following Turchin (2003), I will disregard the explicit assessment of the Type 1 formulation for one simple reason, hard
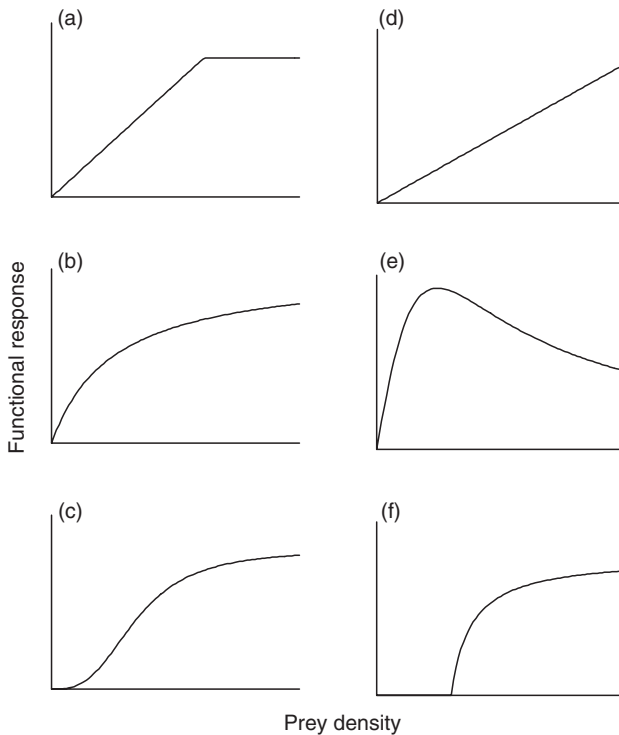

Figure 1.1. Simple single-species functional response models: (a) Type 1, (b) Type 2, (c) Type 3, (d) Type 0, (e) Type 4, and (f) threshold. The traditional Holling classification contains Type 1, Type 2, and Type 3.

corners are not common in natural processes, and hence, Type 2 functional responses should do the same work but better. Type 1 functional responses can be considered an extreme case (or a fully linearized approximation) to a Type 2 functional response. However, we should keep in mind that in some filter-feeding crustaceans, Type 1 appears to be the proper shape (Holling 1965).

In our framework, all the above functional response types can be derived from the basic generalist formulation under the assumption of $f_F = 1$. Furthermore, in all these cases the functional responses will be laissez-faire ($m_i = 1$), and the prey will always be attacked regardless of the prey field ($p_i = 1$). Therefore, the capture rate reduces to $C_i = g_i$. In all these cases, the prey-dependent factors have the following general form: $g_i = a_i' N_i$.

1.8.1 Type 2 functional response

Considering $a_i' = a_i$, where a_i is a positive constant coefficient, the capture rate becomes $C_i = a_i N_i$. As we saw before, this functional response is the multi-species Holling's disc equation:

$$F_i = \frac{a_i N_i}{1 + \sum_K h_k a_k N_k} \qquad (1.25)$$

If we assume a single predator-dependent asymptotic consumption rate $J_{max} = 1/h$, Eq. (1.25) becomes

$$F_i = \frac{J_{max} a_i N_i}{J_{max} + \sum_K a_k N_k} \qquad (1.26)$$

The Type 2 is the most frequent form for modeling the functional response and has served as starting point for many expansions and modifications (Jeschke et al. 2002). It is probably the simplest form, which has an upper bound and a mechanistic derivation.

It is well known that the single-species Holling's disc equation is equivalent to the Michaelis–Menten equation (Caperon 1967, Real 1977). Assuming a single saturation rate, this equivalence also holds for the multispecies case. If we define a half saturation constant as $\kappa = J_{max}/a$, and $a_i = a\rho_i$ where a is a positive coefficient and ρ_i is a dimensionless positive weight factor, then Eq. (1.26) becomes

$$F_i = \frac{J_{max} \rho_i N_i}{\kappa + \sum_K \rho_k N_k} \qquad (1.27)$$

which is the Michaelis–Menten version of the multispecies Holling's disc equation.

Although in practice makes no difference modeling the functional response with Eq. (1.26) or (1.27), the Michaelis–Menten formulation is overparameterized (Gentleman et al. 2003), and there is empirical evidence supporting the theoretical rationale behind Eqs. (1.25) and (1.26) (e.g., Verity 1991).

1.8.2 Type 3 functional response

In this case, a_i' is a function of prey i density ($a_i' = f(N_i)$). We can mention three simple alternative formulations, which produce a sigmoidal shape.

The first one assumes that a_i' is a power function of the density ($a_i' = a_i N_i^{b_i}$ with a_i and b_i positive constant coefficients), and the corresponding capture rate is $C_i = a_i N_i^{b_i+1}$. This generates the following functional response

$$F_i = \frac{a_i N_i^{b_i+1}}{1 + \sum_K h_k a_k N_k^{b_k+1}} \tag{1.28}$$

Most applications of this formulation assume a common predator-dependent b_i (i.e., $b_i = b$ for all prey), customary assumed equal to one (Yodzis 1994, Gentleman et al. 2003, Murdoch et al. 2003, Turchin 2003). This implies that a_i' becomes a linear function of prey density.

If together with a common b_i for all prey, we also assume a single predator-dependent asymptotic consumption rate $J_{\max} = 1/h$, Eq. (1.28) becomes

$$F_i = \frac{J_{\max} a_i N_i^{\theta}}{J_{\max} + \sum_K a_k N_k^{\theta}} \tag{1.29}$$

where $\theta = 1 + b$.

Equations (1.28) and (1.29) are generalized forms because both Type 2 and Type 3 functional responses can be obtained from them depending on parameter values. The multispecies Holling's disc equation is obtained by setting $b_i = 0$ for all prey in Eq (1.28) or $\theta = 1$ in Eq. (1.29).

The second way for deriving a Type 3 functional response assumes that a_i' increases with prey density, but it does it at a continuous decelerating rate until reaching an asymptotic maximum. Unsurprisingly, it is generally modeled as $a_i' = \frac{a_i N_i}{1 + b_i N_i}$, where a_i/b_i is the maximum asymptotic value of a_i'. As far as I know, this formulation was first introduced by Hassell et al. (1977) for the single-species case, and extended by Chesson (1983) to the multispecies one.

The third way for deriving a Type 3 functional response assumes that a_i' is a linear function of prey density as $a_i' = a_i + b_i N_i$, with a_i and b_i constant as coefficients. This approach was developed by Evans (unpublished, cited in Evans and Garçon 1997), and produces a capture rate of the form $C_i = a_i N_i + b_i N^2$. This formulation allows for linear and nonlinear terms in the capture rate, and it was devised assuming the formation of a "search image" by the predator (the nonlinear term). This functional response can produce both Type 2 and Type 3 forms, and collapses to a multispecies Holling's disc equation if $b_i = 0$ for all prey.

The Type 3 functional response was initially referred as the "vertebrate functional response," opposing the Type 1 and Type 2, which were dubbed "invertebrate functional responses" (Holling 1965). This taxonomic distinction

was never intended as a hard classification. It was clear from the beginning that the reasons behind the sigmoidal shape were more tightly linked with the ecological scenario of the predation process, than with the taxonomical identities of predators and prey (Holling 1959b, 1965, Murdoch 1969, 1973, Hassel et al. 1977). Holling (1965) wrote "it is more likely that at least some of the more advanced invertebrates have attack behaviors as complex as those of vertebrates and that, as a result, Type 3 responses can also occur among invertebrates."

Among the proposed mechanisms for explaining Type 3 functional responses were the presence of alternative food sources and prey switching (Holling 1959b, Murdoch 1969), predator learning and the development of search images (Tinbergen 1960, Holling 1965, Murdoch 1973), and the existence of prey refuges (Murdoch 1973).

1.8.3   Type 4 functional response

This form is typically associated with toxicity effects of high prey densities in microbial systems (Gentleman et al. 2003). It is the only formulation where the capture rate does not follow the pattern assumed in Section 1.6 (here, when $N_i \to \infty$ the capture rate $C_i \to 0$, and hence $F_i \to 0$). In this case, a_i' is a decreasing function of prey density, and is customary modeled as $a_i' = 1/a_i + b_i N_i^2$, and hence, $C_i = N_i/a_i + b_i N_i^2$. Considering this capture rate the multispecies functional response becomes:

$$F_i = \frac{N_i}{(a_i + b_i N_i^2)\left(1 + \sum_K \frac{h_k N_k}{(a_k + b_k N_k^2)}\right)} \tag{1.30}$$

which with only one prey collapses to

$$F_i = \frac{N_i}{a_i + h_i N_i + b_i N_i^2} \tag{1.31}$$

which is the standard equation for this functional response in the single-species case (Gentleman et al. 2003).

1.8.4   The threshold functional response

This is the last case of simple functional responses that we will consider here. It simply assumes that there is a threshold prey density below which the predator is unable of feeding. Above that threshold, the functional response takes a Type 2 form.

In this case, a_i' is again a function of prey density and it is defined as

$$a_i' \begin{cases} a_i\left(1 - \dfrac{N_{o,i}}{N_i}\right) & \text{if} \quad N_i > N_{o,i} \\ 0 & \text{otherwise} \end{cases}$$

and hence, the capture rate becomes

$$C_i \begin{cases} a_i(N_i - N_{o,i}) & \text{if} \quad N_i > N_{o,i} \\ 0 & \text{otherwise} \end{cases}$$

where a_i is a positive constant and $N_{o,i}$ is the threshold density for prey i. This capture rate generates the following functional response:

$$F_i = \frac{a_i (N_i - N_{o,i})}{1 + \sum_K h_k a_k (N_k - N_{o,k})} \quad \text{with } a_i (N_i - N_{o,i}) = 0 \text{ if } N_i < N_{o,i} \quad (1.32)$$

If we assume a common predator-dependent asymptotic consumption $J_{\max}$, Eq. (1.32) becomes

$$F_i = \frac{J_{\max} a_i (N_i - N_{o,i})}{J_{\max} + \sum_K a_k (N_k - N_{o,k})} \quad \text{with } a_i (N_i - N_{o,i}) = 0 \text{ if } N_i < N_{o,i} \quad (1.33)$$

One of the simplest theoretical settings which generate this functional response is a perfect prey refuge. The prey remains hidden from the predator until the refuge is full, and after that, the predator feeds upon the exposed and available prey following a Type 2 functional response. This simple argument also provides an intuitive understanding for the reasoning behind the Type 3 as one possible form for implicitly modeling prey refuges; the threshold functional response can be considered an extreme case of S-shaped functional response where the initial accelerating phase equals zero until the inflexion point.

1.9 PREDATOR DEPENDENCE

After the basic dependence on prey density, the influence of predator density on the functional response is a logical next step to add biological realism. This influence is often assumed negative (interference) (Watt 1959, Hassell and Varley 1969, Hassell and Rogers 1972), but positive effects (facilitation) have also been considered (e.g., Royama 1971, Abrams and Ginzburg 2000). Following a time–budget rationale similar to Holling (1959a), Beddington (1975) derived a functional response, which considered both handling time limitations and predator interference. The same functional response was independently proposed by DeAngelis et al. (1975) who did not derive it from basic principles, but performed a thorough analysis of its implications in predator–prey dynamics.

Within our approach, incorporating predator interference or facilitation in the functional response implies that the predator factor in the capture rate is effectively a function of predator density ($m_i = f(P)$). The Beddington–DeAngelis equation, and other forms commonly used to represent predator interference, can be obtained by considering the generalist predator functional

response (Eq. (1.12)). Let us assume that $f_F = 1$, and the factors in the capture rate are $p_i = 1$, $g_i = a_i N_i$ and $m_i = (w_i + P)^{-q_i}$ with a_i, w_i, and q_i positive constants. These considerations define the capture rate as

$$C_i = \frac{a_i N_i}{(w_i + P)^{q_i}} \tag{1.34}$$

which produces the following functional response:

$$F_i = \frac{[a_i N_i/(w_i + P)^{q_i}]}{1 + \sum_K h_k [a_k N_k/(w_k + P)^{q_k}]} \tag{1.35}$$

Now, if m_i is identical for all prey (i.e., $w_i = w$ and $q_i = q$ for all i), this functional response reduces to

$$F_i = \frac{a_i N_i}{(w + P)^q + \sum_K h_k a_k N_k} \tag{1.36}$$

This equation, with $q = 1$ is a multispecies version of the Beddington–DeAngelis equation and with only one prey becomes the original single-species formulation (DeAngelis et al. 1975). If handling time effects are dismissed ($h_i \approx 0$) and $w = 0$, this formulation collapses to the Hassell–Varley equation (Hassell and Varley 1969, Hassell 1971, Beddington 1975).

If we consider the general form (Eq. (1.35)), assuming $q_i = 1$ for all i and neglecting the handling time effect ($h_i \approx 0$), the functional response collapses into

$$F_i = \frac{a_i N_i}{w_i + P} \tag{1.37}$$

which is equivalent to the most commonly used functional response in the Ecopath with Ecosim package (Eq. (1.9) in Walters et al. 1997). This becomes clear if we define $w_i = \frac{a_i}{b_i} + \frac{a_i^*}{b_i}$, where a_i^* and b_i are the appropriate positive constants which satisfies the equation, and write

$$F_i = \frac{a_i N_i}{w_i + P} = \frac{a_i N_i}{\frac{a_i}{b_i} + \frac{a_i^*}{b_i} + P} = \frac{b_i}{b_i} \frac{a_i N_i}{\frac{a_i}{b_i} + \frac{a_i^*}{b_i} + P} = \frac{b_i a_i N_i}{a_i + a_i^* + b_i P} \tag{1.38}$$

where the last expression is the Ecosim form. This functional response was originally derived by considering: (a) there is a foraging arena where prey is exposed to the predator, (b) the movement of prey in and out of the refuge/no predator area is fast enough with respect to predation to be assumed at equilibrium, and (c) there is no handling time limitation for the predator (Walters et al. 1997). Only one of these assumptions is shared with our derivation (no handling time effects). We have already shown other functional responses (Type 3 and threshold), which can also account for prey refuges without

predator interference, and our derivation of Eq. (1.37) did not require the assumption of a refuge but assumed predator interference. Therefore, the same ecological idea can lead to different mathematical formulations, and different ecological ideas can converge to structurally similar mathematical forms.

A quick examination of Eq. (1.34) shows that if $w_i = 0$ and $q_i = 1$, the capture rate becomes a function of the ratio between prey and predator, and so does the corresponding functional response. This kind of dependence is known as ratio-dependence because the functional response is only a function of the relative density of the prey with respect to the predator, the per capita prey density. The alternative concept to ratio-dependence is known as prey-dependence and implies that the functional response is a function of the actual prey density (Abrams 1994). All the functional responses in Section 1.7 are prey-dependent functional responses.

The issue of ratio-dependent versus prey-dependent functional responses was the subject of a very intense debate among ecologists in recent years (e.g., Arditi and Ginzburg 1989, Gutierrez 1992, Abrams 1994, Gleeson 1994). The question under discussion was which of these two types of dependency was more adequate to model predator–prey dynamics. This controversy has been mostly settled by recognizing that: (a) both precise prey-dependence and ratio-dependence are expected to be rare, (b) predator dependence in a more general sense is likely to be common, and (c) precise prey- or ratio-dependent formulations are simplified starting points for modeling real systems (Abrams and Ginzburg 2000). However, differences of opinion still exist regarding which type of dependency represent a more theoretically sound starting point (Abrams and Ginzburg 2000). In the context of this discussion, the generalized predator interference equation presented in this section (Eq. (1.35)) is capable of producing ratio-dependent functional responses, but also provides a flexible framework to explore other possibilities of predator interference (e.g., Beddington–DeAngelis and Ecosim). This reinforces the idea that ratio-dependence is just a strong case of predator interference, although we should realize that $q_i > 1$ will produce even more extreme predator interference effects than ratio-dependence.

The generalized predator-dependent formulation (Eq. (1.35)) emerges from considering one simple form for m_i; other functional forms are certainly possible. Furthermore, the capture rate as stated in Eq. (1.34) only allows for predator interference; although the same structural equation can also be used for describing predator facilitation. We can accomplish this by relaxing one of the assumptions and allowing negative values for q_i.

Setting $q_i = 0$ for all i in Eq. (1.35) (or $q = 0$ in Eq. (1.36)) reduces the functional response to the multispecies disc equation (Eq. (1.25)), and hence, it eliminates the dependence on predator density. This collapse to a Type 2 is a consequence of the initial choice for g_i. Different g_i formulations, like the ones in Section 1.7.2, for example, would make the functional response to collapse into the corresponding laissez-faire Type 3 form.

1.10   PREFERENCE, PREY SWITCHING, AND DIET CHOICE

1.10.1   Preference and prey switching

The idea of prey preference is inherently a multispecies one. Broadly speaking, it implies that given equal densities for all prey, the predator may still consume some of them more often than others (Murdoch 1969, Manly et al. 1972, Murdoch et al. 1975, Chesson 1978, 1983). Although the term "preference" seems to imply an active decision by the predator, we should keep in mind that this is not necessary for prey preference to exist. There are many plausible causes that are unrelated to predator's behavior (e.g., detectability of prey) (Gendron 1987).

   More formally, we can relate the proportion in the diet of a given prey with its proportion in the environment (availability) as follows:

$$\frac{F_i}{\sum_K F_k} = \frac{\phi_i N_i}{\sum_K \phi_k N_k} \tag{1.39}$$

where F_i and N_i are the functional response and density of prey i, respectively, and ϕ_i is the "preference" for prey i. Since ϕ_i is a relative measure, it is customary to normalize it to one ($\sum_K \phi_k = 1$) (Chesson 1978, 1983). If F_i and N_i are know, ϕ_i can be estimated as (Chesson 1978):

$$\phi_i = \frac{F_i/N_i}{\sum_K F_k/N_k} \tag{1.40}$$

Based on Eq. (1.39), we can write the ratio between the proportions of two prey in the diet as:

$$\frac{F_i}{F_j} = \frac{\phi_i N_i}{\phi_j N_j} = \varphi_{ij} \frac{N_i}{N_j} \tag{1.41}$$

where $\varphi_{ij} = \phi_i/\phi_j$ is a measurement of the "pairwise relative preference" of prey i with respect to prey j. It follows from Eq. (1.41) that if the pairwise relative preference is constant; any change in the ratio of the consumption rates is a consequence of a change in the ratio of the prey densities. However, if the pairwise relative preference is variable (i.e., φ_{ij} is a function), then a change in the ratio of the consumption rates is not directly proportional to a change in the ratio of the densities anymore. This phenomenon is what we define as prey switching between the two preys (Murdoch 1969, Murdoch et al. 1975).

   By solving Eq. (1.41) for φ_{ij} we obtain

$$\varphi_{ij} = \frac{F_i}{N_i} \frac{N_j}{F_j} \tag{1.42}$$

which provides a way for detecting prey switching between two preys. If the result of Eq. (1.42) is a constant, there is no prey switching, if it is a function, prey switching will occur.

For example, if we consider a multispecies Type 2 functional response (e.g., Eq. (1.25)), then Eq. (1.42) becomes

$$\varphi_{ij} = \frac{F_i}{N_i}\frac{N_j}{F_j} = \frac{a_i N_i}{N_i\left(1 + \sum_K h_k a_k N_k\right)}\frac{N_j\left(1 + \sum_K h_k a_k N_k\right)}{a_j N_j} = \frac{a_i}{a_j} \tag{1.43}$$

which is clearly a constant. The multispecies Holling's disc equation cannot produce prey switching.

On the other hand, if we consider a multispecies Type 3 like Eq. (1.23), an analogous procedure renders

$$\varphi_{ij} = \frac{F_i}{N_i}\frac{N_j}{F_j} = \frac{a_i N_i^{b_i+1}}{N_i\left(1 + \sum_K h_k a_k N_k^{b_k+1}\right)}\frac{N_j\left(1 + \sum_K h_k a_k N_k^{b_k+1}\right)}{a_j N_j^{b_j+1}} = \frac{a_i N_i^{b_i}}{a_j N_j^{b_j}} \tag{1.44}$$

In this case, the relative preference is a function of both prey densities, and hence, this Type 3 functional response produces prey switching.

Furthermore, if we consider the general predator interference functional response (Eq. (1.35)), the result of Eq. (1.42) is

$$\varphi_{ij} = \frac{F_i}{N_i}\frac{N_j}{F_j} = \frac{a_i(w_j + P)^{q_j}}{a_j(w_i + P)^{q_i}} \tag{1.45}$$

In this case, φ_{ij} is independent of prey density but is still a function of predator density. Therefore, a predator with Eq. (1.35) as functional response will show prey switching, but these changes will be driven by its own density and not the densities of its prey. It is easy to find plausible biological contexts for this observation. Consider the case where predator interference involves stealing the prey that other predator already caught. It is reasonable to think that a predator may go after costly to catch but highly profitable prey if predator density is low, while it may go after less profitable but easy to catch prey when its own density is high, given the higher risk of being robbed.

This result is particularly interesting because it implies that prey switching can be driven by both, prey and predator densities. Although the classical definition involves prey-driven prey switching (Murdoch 1969, Gendron 1987, Abrams and Matsuda 2003), this is just a consequence of the lack of prey switching studies using predator-dependent functional responses. However, the phenomenon described by Eq. (1.45) implies a functional dependency of the pairwise relative preference with density, and hence, it clearly fits in our concept of prey switching, although in this case it is predator-driven prey switching. It follows that we can also have predator- *and* prey-driven prey switching (e.g., replace $g_i = a_i N_i$ in Eq. (1.34) by $g_i = a_i N_i^2$).

If we examine the definitions of prey preference and prey switching, one feature becomes obvious. Both concepts describe the output of the predation process, not how this output is produced. Prey switching has been observed in many cases (Holling 1959b, Murdoch 1969, Manly et al. 1972, Murdoch and Marks 1973, Murdoch et al. 1975, Hassell et al. 1977, Greenwood and Elton 1979, Bergelson 1985, Hughes and Croy 1993), but the mechanisms that generate it are not always the same, and many times they are not even known. One of the hypothetical explanations behind Type 3 functional responses is the ability of predators to switch among prey, and often Type 3 functional responses are used to implicitly model this kind of phenomenon (e.g., Koen-Alonso and Yodzis 2005). This approach ensures that prey switching is allowed while reduces the complexity of the model to be implemented. However, not all prey switching are created equal.

Gentleman et al. (2003) classified laissez-faire multispecies functional responses according to their capacity for producing prey switching. They proposed three classes of functional responses; (a) Class 1, where no switching occurs, (b) Class 2, where passive switching occurs, and (c) Class 3, where active switching occurs. The difference between passive and active switching is based on the ability of predicting switching from knowledge (i.e., parameters) of the single-species functional responses. For example, the Type 3 functional response considered in Eq. (1.44) is a "Class 2" because all the parameters which define φ_{ij} can be estimated from the functional response of each prey in isolation (i.e., a_i and b_i can be estimated with only prey i present, while a_j and b_j can be obtained when only prey j is present).

If switching occurs, but the output of switching cannot be predicted from the single-species functional responses, then an "active selection" by the predator must occur; the parameters in φ_{ij} can only be estimated if both prey are present (Gentleman et al. 2003). This "active selection" essentially involves a diet choice, which depends on the available prey field. Within the approach developed here, this diet choice is represented by the selection factor p_i (see Section 1.5). Therefore, if we consider p_i the difference between Class 2 and Class 3 becomes clearer. When prey switching occurs, Class 2 functional responses are the ones where p_i is constant or only depends on N_i, while in Class 3 functional responses p_i depends on one or more prey densities N_j, with $i \neq j$.

1.10.2 Diet choice and the functional response

The selection factor p_i describes the way in which prey densities affect the predation process through diet choices. The consequences of these choices emerge as preferences and prey switching. Therefore, unlike generalized Type 3 formulations like Eq. (1.28), explicitly modeling p_i allows more detailed studies on how diet choice affects the predation process. The cost of these details is more complex models, which in turn require more and better data to discriminate among potential alternatives.

Many different models have been used to explicitly model diet choice in the functional response (e.g., Fasham et al. 1990, Fryxell and Lundberg 1994, McCann et al. 1998, Strom and Loukos 1998, Post et al. 2000, van Baalen et al. 2001, Abrams and Matsuda 2003, Ma et al. 2003). In general terms we can group them within two families, one where optimal foraging arguments are used to derive the diet choice function, and the other one where diet choice is simply a function of prey densities, without relying on optimal foraging theory.

Within the optimal foraging family, the selection factor p_i is usually derived from the prey algorithm and the zero-one rule (Pulliam 1974, Charnov 1976, Stephens and Krebs 1986). Optimal foraging theory predicts that: (a) prey species will be incorporated in the diet according to the rate of net energy intake they render to the predator, (b) the probability of preying upon a given prey species is either zero or one (i.e., the predator will always or never go after the prey), and (c) the probability of preying upon a given prey is not a function of its own density, but it depends on the densities of the prey species already in the diet (Charnov 1976, Stephens and Krebs 1986).

In the two prey species case, this means that the p_i will be only a function of the most profitable prey, and to smooth the step function implied by the zero-one rule, it is common to model this probability using a sigmoid function (e.g., Fryxell and Lundberg 1994, Strom and Loukos 1998, van Baalen et al. 2001). If we define that $i = 1$ corresponds to the most profitable prey, a commonly used formulation is:

$$p_i \begin{cases} 1 & \text{if} \quad i = 1 \\ \dfrac{N_{o,1}^u}{N_1^u + N_{o,1}^u} & \text{if} \quad i = 2 \end{cases} \qquad (1.46)$$

where $N_{o,1}$ is the threshold density of prey 1 which triggers the consumption on prey 2 (i.e., in a true step function, $p_2 = 0$ if $N_1 > N_{o,1}$, and $p_2 = 1$ if $N_1 < N_{o,1}$), and u is a positive constant which defines the width of the range of N_1 where the transition from $p_2 = 0$ to $p_2 = 1$ takes place.

Using this definition of p_i, considering $g_i = a_i N_i$ with a_i a positive constant, assuming $f_F = 1$ and for the two-prey case, the basic generalist functional response becomes

$$F_i = \frac{p_i a_i N_i}{1 + \sum_{k=1}^{2} h_k p_k a_k N_k} \qquad (1.47)$$

This functional response is commonly used in theoretical studies of diet choice and its impact on predator–prey dynamics (Fryxell and Lundberg 1994, van Baalen et al., 2001, Ma et al. 2003).

Although Eq. (1.46) is a simple representation of p_i within an optimal foraging framework, other options have also been explored to study more complex scenarios (e.g., Strom and Loukos 1998, Abrams 1999, Abrams and Matsuda 2003, Ma et al. 2003). It is noteworthy that Eq. (1.46) only applies to the

two-prey case. As far as I know, a generalized multispecies version of it does not exist. Nevertheless, some formulations implicitly inspired by optimal foraging theory have been proposed (e.g., the "Abundance-Based II" model, Table 4a in Gentleman et al. 2003).

On the other hand, generalized multispecies formulations for p_i which do not rely on optimal foraging arguments are readily available (Chesson 1983, Fasham et al. 1990, McCann et al. 1998, Koen-Alonso and Yodzis 2005). In these models, p_i is typically represented as a weighed proportion of the densities of the prey. Let us define p_i as

$$p_i = \frac{\eta_i N_i^b}{\sum_K \eta_k N_k^b} \tag{1.48}$$

where b is a predator-specific positive constant, and η_i is a dimensionless weight factor subject to the constraint that $\sum_K \eta_k = 1$.

If we assume $f_F = 1$, define p_i according to Eq. (1.48), $g_i = a_i N_i$ with a_i a positive constant, and $m_i = 1$, the obtained capture rate is

$$C_i = p_i a_i N_i = \frac{\eta_i N_i^b}{\sum_K \eta_k N_k^b} a_i N_i \tag{1.49}$$

and if we consider the basic generalist form (Eq. (1.12)), the functional response becomes

$$F_i = \frac{p_i a_i N_i}{1 + \sum_K h_k p_k a_k N_k} = \frac{\eta_i a_i N_i^{b+1}}{\sum_K \eta_k N_k^b + \sum_K h_k \eta_k a_k N_k^{b+1}} \tag{1.50}$$

This formulation was derived by Peter Yodzis, and was called frequency-dependent predation functional response by Koen-Alonso and Yodzis (2005). Let me rename it here as the Yodzis functional response.

The Yodzis functional response is a laissez-faire form, which explicitly allows for prey-driven switching. If $b = 0$ it collapses to the multispecies Holling's disc equation (Eq. (1.25)), but it also collapses to a Type 2 form if only one prey species is present. If we assume a single predator-specific asymptotic consumption rate ($J_{max} = 1/h$ with $h_i = h$ for all i), this functional response becomes

$$F_i = \frac{J_{max} \eta_i a_i N_i^{b+1}}{J_{max} \sum_K \eta_k N_k^b + \sum_K \eta_k a_k N_k^{b+1}} \tag{1.51}$$

which can be written in a Michaelis–Menten form (i.e., $\kappa = J_{max}/a$ and $a_i = a\rho_i$) as

$$F_i = \frac{J_{max} \eta_i \rho_i N_i^{b+1}}{\kappa \sum_K \eta_k N_k^b + \sum_K \eta_k \rho_k N_k^{b+1}} \tag{1.52}$$

Several formulations used in the literature are particular cases of the Yodzis functional response (Fasham et al. 1990, McCann et al. 1998, 2005).

If we take the Michaelis–Menten form (Eq. (1.52)) and consider $b = 0$, the selection factor p_i becomes constant and equal to η_i (i.e., $\sum_K p_k = \sum_K \eta_k = 1$). With only two prey species we can write $p_2 = 1 - p_1$ and express both selection factors as functions of p_1. This formulation has been used to study the effects of omnivory, allochthonous inputs, and interaction strengths on food web stability (McCann and Hastings 1997, Huxel and McCann 1998, McCann et al. 1998).

The Fasham functional response is widely used to model diet choice in biogeochemical models (Fasham et al. 1990, Strom and Loukos 1998, Gentleman et al. 2003). This formulation can also be obtained from the Michaelis–Menten form of the Yodzis functional response by assuming $b = 1$ and $\rho_i = 1$ for all i. Considering the Holling form (Eq. (1.50)), and again assuming $b = 1$, the Yodzis functional response becomes another formulation often used to model explicit diet choice or implicit spatial structure (Eq. 1 in McCann et al. 2005).

Representing p_i as a function of the prey field is not the only way in which diet choice has been explicitly modeled in the functional response. As defined here (Section 1.4.4), a specialist predator is always going after one prey species at a time, and hence, p_i must always be equal to 1. In such case, diet choice should be associated with the assignation of foraging time to each prey. Considering the basic specialist functional response (Eq. (1.20)), this means that the fraction of foraging time assigned to prey i (X_i) becomes a function of the prey field.

Let us assume $f_{\mathrm{F}} = 1$, and define $p_i = 1$, $m_i = 1$, and $g_i = a_i N_i$ with a_i a positive constant. If the specialist predator assigns foraging time proportionally to the abundance of the prey in the environment, the fraction of foraging time assigned to prey i can be written as

$$X_i = \frac{\pi_i N_i}{\sum_K \pi_k N_k} \tag{1.53}$$

where π_i is a dimensionless weight factor subject to the constraint that $\sum_k \pi_i = 1$. Then, the corresponding functional response becomes

$$F_i = \left(\frac{\pi_i N_i}{\sum_K \pi_k N_k} \right) \left(\frac{a_i N_i}{1 + h_i a_i N_i} \right) \tag{1.54}$$

If we assume a common asymptotic consumption rate for all prey (i.e., $J_{\max} = 1/h$ with $h_i = h$ for all i), and allow for prey-specific half saturation densities (i.e., $\kappa_i = J_{\max}/a_i$), this functional response can be written in a Michaelis–Menten form as

$$F_i = \left(\frac{\pi_i N_i}{\sum_K \pi_k N_k} \right) \left(\frac{J_{\max} N_i}{\kappa_i + N_i} \right) \tag{1.55}$$

This formulation has been used by Post et al. (2000) to study the effect of diet choice in linked food chains. Although Post et al. (2000) explicitly stated that X_i "represents the proportion of time the predator spends feeding on each food chain" (we can replace "food chain" by "prey" without distorting the original meaning), they failed to recognize the difference between X_i and p_i (i.e., the difference between a generalist and a specialist predator) when comparing their results with previous works (McCann and Hastings 1997, Huxel and McCann 1998, McCann et al. 1998). Fortunately, this difference has no impact in their conclusions. For the sake of fairness, we should point out that this difference also escaped McCann et al. (2005) who said in their Appendix S2 while referring to a functional response of the form of Eq. (1.50) "There is a modest difference.... Post et al. (2000) curiously ignored the preference (our p_i) in the denominator of the functional response."

   Therefore, the effect of diet choice in the functional response has been modeled using a wide variety of mathematical formulations. Many of these forms can be obtained as special cases within the general framework developed in this chapter. For generalist predators, the explicit representation of diet choice has typically involved modeling the selection factor p_i as a function of prey densities (Fasham et al. 1990, Fryxell and Lundberg 1994, McCann and Hastings 1997, Huxel and McCann 1998, McCann et al. 1998, 2005, van Baalen et al. 2001, Abrams and Matsuda 2003, Ma et al. 2003). In some instances this probability is formulated using optimal foraging theory (e.g., Fryxell and Lundberg 1994, van Baalen 2001, Ma et al. 2003), although many applications do not rely on optimality arguments (e.g., Fasham et al. 1990, McCann and Hastings 1997, Huxel and McCann 1998, McCann et al. 1998, 2005). Among these last ones, the Yodzis functional response appears as a generalized equation from which frequent formulations can be obtained. On the other hand, diet choice in specialist predators has been modeled by making the fraction of foraging time allocated to each prey a function of the prey field (Post et al. 2000).

1.10.3   Food as poison effect: biology or poor modeling?

The development of multispecies functional responses poses questions that could not be foresight from the analysis of single-species formulations. One of these dilemmas is the "food as poison" (FAP) effect[8]. This phenomenon implies that the total consumption rate G decreases when the density of one prey species increases and the others remain constant (or vice versa, G increases when one prey species decreases). Of course, Type 4 functional responses cause a FAP effect, but in multispecies scenarios many other formulations can also generate it. More formally, this effect is present if

[8]The expression "food as poison" to describe this effect was coined by Geoff Evans. Gentleman et al. (2003) refers to it as "suboptimal" foraging. I chose "food as poison" because it has no optimality implications (unnecessary in my opinion), and it sounds great, doesn't it?

$$\frac{\partial G}{\partial N_i} < 0 \tag{1.56}$$

Studying plankton dynamics, Fasham et al. (1990) detected this phenomenon when modeling switching in the zooplankton functional response, and suggested that may be related to the cost of switching. More recently, Gentleman et al. (2003) explored this issue in a set of functional responses, and found that this effect is not always associated with prey switching.

Using our basic functional responses, it is possible to explore why, and in which context, FAP effects can be expected. Let us start with the basic generalist formulation, assuming $f_F = 1$, and a generic capture rate $C_i = p_i g_i m_i$. In this case, the total consumption rate becomes

$$G = \sum_K F_k = \frac{\sum\limits_K p_k g_k m_k}{1 + \sum\limits_K h_k p_k g_k m_k} \tag{1.57}$$

and hence, the partial derivative of G with respect to the density of any given prey i is

$$\frac{\partial G}{\partial N_i} = \frac{\left(\frac{\partial g_i}{\partial N_i} p_i m_i + \sum\limits_K \frac{\partial p_k}{\partial N_i} g_k m_k\right)\left(1 + \sum\limits_K h_k p_k g_k m_k\right)}{\left(1 + \sum\limits_K h_k p_k g_k m_k\right)^2} - $$
$$ - \frac{\left(\sum\limits_K p_k g_k m_k\right)\left(\frac{\partial g_i}{\partial N_i} h_i p_i m_i + \sum\limits_K \frac{\partial p_k}{\partial N_i} h_k g_k m_k\right)}{\left(1 + \sum\limits_K h_k p_k g_k m_k\right)^2} \tag{1.58}$$

Although Eq. (1.58) looks daunting, a careful examination will provide us with some insights on the sources of FAP effects. Since the denominator is always positive, the negative sign, which indicates a FAP effect must come from the numerator. Now, to simplify the analysis, we can consider two scenarios.

First, let us assume that the selection factor is constant, and hence, $\partial p_j / \partial N_i = 0$ for all $j = 1, \ldots, i, \ldots, K$. Under this assumption, Eq. (1.58) collapses to

$$\frac{\partial G}{\partial N_i} = \frac{\frac{\partial g_i}{\partial N_i} p_i m_i \left[1 + \sum\limits_K p_k g_k m_k (h_k - h_i)\right]}{\left(1 + \sum\limits_K h_k p_k g_k m_k\right)^2} \tag{1.59}$$

Given that all known factors in the numerator (h_i, p_i, g_i, and m_i) are positive, and $\partial g_i / \partial N_i$ is always positive (the only exception is the Type 4 functional response), the only way of getting $\partial G / \partial N_i < 0$ in Eq. (1.59) is through the factor

($h_k - h_i$). Therefore, a FAP effect will occur only if the handling time for prey i is large enough to make negative the factor in brackets in the numerator. This will occur when a prey, which requires a large handling time increases its density. The predator will tend to consume it more often, which implies using significantly more time handling prey, and hence, G will decrease. This is a case of handling time driven FAP effect (Gentleman et al. 2003).

For the second scenario, let us assume that $h_i = h$ for all prey. In this case, Eq. (1.58) becomes

$$\frac{\partial G}{\partial N_i} = \frac{\frac{\partial g_i}{\partial N_i} p_i m_i + \sum_K \frac{\partial p_k}{\partial N_i} g_k m_k}{\left(1 + \sum_K h \, p_k g_k m_k\right)^2} \tag{1.60}$$

Again, with the only exception of Type 4 functional responses, a $\partial G/\partial N_i < 0$ implies that $\partial p_j/\partial N_i < 0$ for at least enough prey species to make negative the summation in the numerator. For example, if we consider p_i as defined by Eq. (1.48), then $\partial p_j/\partial N_i < 0$ for all $j \neq i$. It follows from here that, if together with a common handling time (i.e., a predator-specific asymptotic consumption rate), we also assume constant selection factors, then FAP effects cannot occur.

Therefore, for generalist predators, FAP effects have two clear causes. One is the differences in handling time between prey species, the other is the dependence of the selection factor on the prey field. Of course, both causes can occur at the same time.

Now, can FAP effects occur in specialist predators? If we repeat the analysis using the basic specialist functional response, and remember that in this case $p_i = 1$ for all i, then $\partial G/\partial N_i$ becomes

$$\frac{\partial G}{\partial N_i} = X_i \left[\frac{\frac{\partial g_i}{\partial N_i} m_i}{(1 + h_i g_i m_i)^2} \right] + \sum_K \frac{\partial X_i}{\partial N_i} \left[\frac{g_k m_k}{1 + h_k g_k m_k} \right] \tag{1.61}$$

This result indicates that, in an analogous manner to the generalist equation, FAP effects are possible if enough $\partial X_i/\partial N_i$ are negative. However, unlike the generalist case, differences in handling time cannot produce FAP effects. The reason for this is simple; the specialist predator allocates fractions of its total foraging time to each prey. This is also the reason why the dependency of X_i on the prey field is the only way to cause a FAP effect in this type of predator.

Although we have identified the origins of FAP in multispecies functional responses, one question remains: is this phenomenon biologically sound or it is a pathological problem of our mathematical description of the predation process?

If FAP effects are pathological to our way of modeling predation, then virtually all explicit representation of diet choice in functional responses are questionable. This is interesting for several reasons. First, it casts doubts on most studies on diet choice in functional responses. Second, we know that diet

switching occurs (Holling 1959b, Murdoch 1969, Manly et al. 1972, Murdoch and Marks 1973, Murdoch et al. 1975, Hassell et al. 1977, Greenwood and Elton 1979, Bergelson 1985, Hughes and Croy 1993), but we are faced with the paradox that implicit representations of this phenomenon cannot produce FAP, while explicit representations (supposedly more mechanistic, and hence, biologically sound) typically generate it.

Gentleman et al. (2003) strongly advised against the use of functional responses, which produce FAP. Based on optimal foraging ideas, they argue that natural selection would tend to minimize this kind of phenomena, although they also recognize that there are biological arguments that can explain it. Among these are the energetic cost of switching (Fasham et al. 1990), or that fitness may be unaffected by foraging yield (Holt 1983).

In some cases, FAP effects appear at intermediate densities of prey, in others, this phenomenon occurs when the density of the prey is relatively low, while in other instances it shows at both high and low densities (Gentleman et al. 2003). In my opinion, the ecological soundness of these FAP effects is not the same. If FAP is acceptable under the hypothesis that it represents the cost of switching, then I would expect FAP at low densities (e.g., the Yodzis and Fasham functional responses). However, if the explanation for FAP is the lack of a strict relationship between fitness and foraging, I would tend to expect FAP to occur at high densities of prey, or at least above some threshold. Therefore, situations where FAP occurs at low and/or high prey densities may be biologically acceptable. However, the occurrence of FAP effects at intermediate densities does not have any clear biological support.

Although this dilemma cannot be solved here, we need to remember that the functional response model must be selected after a thorough examination of its assumptions, implications, its match with our working hypotheses, and the quantity and quality of the data that we have available to test them. Today, there is a large set of tools that can be used to evaluate if a given formulation is a good description of the data, including classic likelihood ratio tests (e.g., Hilborn and Mangel 1997), information theoretic approaches (Burnham and Anderson 2002), and bayesian statistics (Gelman et al. 2000). Therefore, more important than if the selected functional response produces FAP effects or not, it is the fact that we have selected that formulation for specific reasons.

1.11   MIMICKING SPACE

Adequately incorporating the role of space and spatial scales in population and community dynamics is one of the major challenges in ecology (e.g., MacArthur and Pianka 1966, MacArthur and Wilson 1967, Holt 1996, Tilman and Kareiva 1997, Hanski 1999, Thomas and Kunin 1999, Ritchie and Olff 1999, McCann et al. 2005). In the context of functional responses, we have already mentioned some cases where spatial elements are implicitly represented in the structure of

the equations. For example, threshold and Type 3 functional responses can represent the presence of prey refuges.

Using spatially explicit predator–prey dynamic models (i.e., explicitly modeling patches and movement among them) together with aggregation methods, Poggiale (1998) derived the Type 2 and the Beddington–DeAngelis functional responses, showing that these equations can implicitly represent spatial scenarios. In a similar fashion, McCann et al. (2005) found that a functional response like Eq. (1.50) also implicitly represents cases where the foraging scale of the predator is similar to the habitat scale of the prey. In this case, the selection factor in the functional response becomes a selection factor of the foraging patch.

Within the framework developed here, the representation of spatial structure can be approached in a very simple way. The basic specialist functional response (Eq. (1.20)) assumes that the predator is after one, and only one, prey species at the time. Although it may be reasonable in some cases, we already saw that this assumption looks unlikely for most predators. However, this mutually exclusive assignation of foraging time becomes absolutely believable for representing foraging patches; a predator cannot forage in two places at once. Therefore, we can use the specialist equation to explore how spatial structure can be explicitly incorporated in the functional response.

Let us rewrite the basic specialist functional response (Section 1.4.3) as $F_{i,z} = f_F X_z Q_{i,z}$ This equation represents the functional response of prey i within a patch z, where X_z is the fraction of the foraging time assigned by the predator to the foraging patch z, and $Q_{i,z}$ becomes the "functional response while foraging *within the patch*." In this spatial context nothing prevents assuming that the predator behaves as a generalist within a patch. Therefore, we can consider the Q_i function defined in the basic generalist equation (Section 1.4.2) and write

$$F_{i,z} = f_F X_z \frac{C_{i,z}}{1 + \sum_{K(z)} h_k C_{k,z}} \tag{1.62}$$

which is the functional response for prey i in the patch z, $C_{i,z}$ is the capture rate for prey i in patch z, and the summation in the denominator is over all prey within that patch. Based on this equation, and considering a total number of patches z, a basic spatial multispecies functional response can be written as

$$F_i = f_F \sum_z \frac{X_z C_{i,z}}{1 + \sum_{K(z)} h_k C_{k,z}} \tag{1.63}$$

As we did before, we can assume different internal structures for $C_{i,z}$ and build different spatial functional responses. Although the factors in $C_{i,z}$ will be functions of the within-patch densities, parameterizations of $g_{i,z}$ and $m_{i,z}$ for the same prey are likely to be common, while $p_{i,z}$ can be expected to vary due to differences in prey field composition among patches. The spatial concept behind this functional response (Eq. (1.63)) is no other than the coarse and fine-grained environment sensu MacArthur and Pianka (1966), where predators perceive a

homogenous environment within a patch, but perceive patches as distinct and separate habitats.

1.12 CONCLUDING REMARKS

Modeling multispecies systems is a complex task, and developing models, which can also be used for making management decisions is even more complicated. Nevertheless, successful conservation and sustainable use of ecological systems require a level of integration that makes unavoidable the development of operational food web models (Yodzis 1996, 1998, 2001, Fulton et al. 2003).

In these models, the functional response has a particularly important role. Its mathematical form has strong effects on the overall dynamics (e.g., Murdoch et al. 2003, Turchin 2003, McCann et al. 1998, 2005), the stability of the system (e.g., May 1973, Oaten and Murdoch 1975, Armstrong 1976, McCann 2000, Gross et al. 2004), and represents our best understanding of the predation process (e.g., Yodzis 1994, Koen-Alonso and Yodzis 2005). Unfortunately, real systems are complex, and we typically lack of enough information to choose any particular formulation with certainty (e.g., Fulton et al. 2003, Mackinson et al. 2003). For this reason, it is extremely important that we explore more than one option; a single model structure cannot provide robust answers (Koen-Alonso and Yodzis 2005).

To make things worse, different ecological hypotheses can converge into similar mathematical descriptions. Therefore, the adequacy of a given formulation for describing empirical observations cannot be taken as support for the ecological rationale that produced the equation, unless the assumptions involved in such rationale can also be independently validated.

However, we have a powerful tool to face this daunting prospect: critical thinking. The aim of this chapter is to provide enough elements to make profitable its exercise. The framework developed here is process-oriented, focuses on plausible mechanisms, and provides the building blocks for constructing biologically sound multispecies functional responses. The concept is simple, instead of picking a functional response from the shelf, build your own. Let the biology of what you are trying to model guide you, and start simple. There is always time to add complexity, but we need to know the consequences of the simplest ideas first. This creates a baseline for comparisons. As Evans (1988) said "The world is too complicated to understand all at once, and we make progress by discovering which complications to ignore."

Although the final product is admittedly incomplete, this is a small attempt of putting together a simple, but still comprehensive, theory of multispecies functional responses. Seeking for a self-consistent theory is always intrinsically important, but as Peter Yodzis (1989) wrote "there is another, more subtle and marvelous, function of theory. A theory has a sort of life of its own, a course of development that flows from its inner logic. And in course of this

process the theory will often *generate new hypotheses*, which, often enough, can be tested in the field or lab."

1.13   ACKNOWLEDGMENTS

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CHAPTER 2

HOMAGE TO YODZIS AND INNES 1992: SCALING UP FEEDING-BASED POPULATION DYNAMICS TO COMPLEX ECOLOGICAL NETWORKS

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2.1 INTRODUCTION

Scientists have long strived to simplify and abstract nature into fundamental categories and statements that could yield understanding of, and predictive insight into, the phenomena they study. Only a few of such abstractions survive the test of time and continue to yield both broad and deep scientific insights. Here, we explore an ecological abstraction that many ecologists including ourselves have found very useful and especially insightful. While it is only one of many abstractions of population growth in nature, we focus on it here because it appears likely to survive the difficult and important transition from modeling a few trophically interacting species to modeling the large complex networks more like those we see in nature. To survive this mission, we desire maximum correspondence with nature and empirical tractability combined with minimal complexity. That is, we want abstractions based on the fewest but most useful and easily measured parameters in order to minimize the costs of complexity while trying to model it.

This abstraction is the bioenergetic approach of Yodzis and Innes (1992) that provided an important foundation for many further advances by Peter Yodzis and other colleagues, especially his former student Kevin McCann (McCann and Yodzis 1994, 1995, McCann and Hastings 1997, McCann et al. 1998) plus further developments by many others (e.g., Fussman et al. 2000, Post et al. 2000, Callaway and Hastings 2002, Brose et al. 2003, Williams and Martinez 2004, Bascompte et al. 2005, Shurin and Seabloom 2005). At its core, the advance of Yodzis and Innes (1992) was to distinguish two fundamental aspects of organisms as central to the modeling of their feeding interactions and population dynamics: body size and metabolic type. The relevance of body size to "metabolism" or the energetic maintenance cost of staying alive has recently become a spectacularly successful and currently highly active research program (Whitfield 2004). Much earlier, Yodzis and Innes (1992) realized that the combination between the biological importance and empirical ease of measuring body size made it an ideal variable to incorporate into population dynamics. The other distinction, that of metabolic type, recognizes that all bodies are not the same and that, in particular, fundamental distinctions among plants, invertebrates and endotherm, and ecotherm vertebrates needed to be made in order for body size to reasonably predict both the metabolic and maximum assimilation rates of organisms. Once such distinctions were made, each group of organisms could be simply modeled as an undifferentiated stock of biomass that grows and shrinks depending on losses to predation and metabolic costs and gains from animal feeding activities and plant net primary production.

Though important and productive, the Yodzis and Innes approach is highly abstract and rather difficult to comprehend in an intuitive manner. For example, in the more useful nondimensional form of the model, several parameters, such as maximum assimilation rates, are numbers "per," or relative to, metabolic rate. Having struggled to embrace, employ, and expand the Yodzis

and Innes approach, we have discovered important clarifications and characterizations of their approach. This chapter redescribes their approach and how it can be more rigorously applied to networks with many more species and also to more mechanistic treatment of basal species such as plants that consume abiotic resources in order to grow.

2.2 HISTORY OF CONTINUOUS TIME PREDATOR-PREY POPULATION DYNAMIC MODELS

Historically, predator-prey population dynamics have been modeled with continuous time models that describe infinitesimally small changes of species i over time in population numbers or biomasses, B_i, by differential equations for dB_i/dt. The prey population biomass, B_i, has an intrinsic growth, G_i, and loses biomass to consumption by the predator population. The predator population of species j, B_j, gains biomass by consumption and loses biomass due to respiration and death. This yields the following set of differential equations:

$$\frac{dB_i}{dt} = B_i G_i(B_i) - B_j F_{ji}(B_i) \tag{2.1}$$

$$\frac{dB_j}{dt} = -B_j T_j + B_j e_{ji} F_{ji}(B_i) \tag{2.2}$$

where F_{ji} is the functional response that quantifies the dependence of per capita of species j (unit B_j) consumption on the density of prey species i. The product of predator density, B_j, with per capita consumption, F_{ji}, yields the total consumption. T_j is the sum of the metabolic and death rates of predator j and e_{ji} is the efficiency of predator j at converting the biomass of prey i that predator j kills or otherwise removes from prey i into predator j's biomass. Early attempts used linear interaction terms to describe the increase in per capita consumption with prey density:

$$F_{ji} = a_{ji} B_i \tag{2.3}$$

This "Lotka-Volterra" functional response assumes that the per capita consumption does not saturate at high prey densities, which causes an infinite linear increase of consumption with prey density. In response to this ecologically unrealistic assumption, many empirical and theoretical studies described multiple forms of functional responses (Holling 1959, Real 1977, Murdoch and Oaten 1975, Beddington 1975, DeAngelis et al. 1975, Arditi and Akcakaya 1990). All these studies described nonlinear functional responses with consumption saturation at high prey densities (see examples below). These functional responses can be prey-dependent (i.e., depend on the density of the prey), predator-dependent (i.e., depend on the density of the predator), or ratio-dependent (i.e., depend on the ratio of the predator to the prey). Implementations of these nonlinear functional responses in population-dynamic models of the form (Eqs. (2.1, 2.2)) are known as McArthur-Rosenzweig models

(Rosenzweig and MacArthur 1963). These models improve the Lotka-Volterra model by using more realistic nonlinear functional responses, but just as in Lotka-Volterra models, the parameters describing the species' metabolic rates, their maximum consumption (the saturation level of the functional response), intrinsic production-biomass ratios of the prey population, and biomass conversion efficiencies are parameters that are estimated independently and are unrelated to species' traits.

   In their seminal work, Yodzis and Innes (1992) used allometric relationships to relate production, metabolic, and maximum consumption rates to the species' body masses and their metabolic categories. This approach yields a model that is intermediate in its level of detail, more constrained by known biological properties of the system than some of the highly abstract models (e.g., Lotka-Volterra and Rosenzweig-McArthur) that are studied, but less constrained than a model tailored to a specific system. The use of allometric scaling introduced empirical realism and parameter interdependence into the models, which substantially reduced the space of possible parameter combinations. Awareness of this interdependence helped show that parameter combinations of species' metabolic rates and maximum consumption rates that were previously thought possible were shown to be impossible (e.g., compare McCann and Yodzis 1995 with Hastings and Powell 1991).

2.3 MULTISPECIES VERSION OF THE BIOENERGETIC MODEL OF YODZIS AND INNES (1992)

The bioenergetic model of Yodzis and Innes (1992) is of the interaction between one consumer and one resource. Here, we extend their formulation to multi-species systems that may have multiple primary producers. For species that are primary producers, their population's rate of change of biomass over time is given by

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = B_i G_i(\vec{B}) - \sum_{j=\text{predators}} B_j F_{ji}(\vec{B})/f_{eji}. \tag{2.4}$$

For species that are consumers, the rate of change of the biomass of its population is given by

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = -B_i T_i + B_i \sum_{j=\text{prey}} e_{ij} F_{ij}(\vec{B}) - \sum_{j=\text{predators}} B_j F_{ji}(\vec{B})/f_{eji} \tag{2.5}$$

In these equations, B_i is the biomass of population i, G_i is the mass-specific net growth rate of primary producer population i and is potentially a function of the biomasses of any or even all of the populations in the system, T_i is the mass-specific respiration rate, F_{ij} is the rate of consumption of population j by population i (i.e., the rate population j loses biomass due to consumption activities of i such as herbivory, predation, infection), e_{ij} is an assimilation

efficiency equal to the fraction of the biomass of species j lost due to consumption by species i that is actually metabolized, and f_{eij} is ingestion efficiency equal to the fraction of biomass lost from resource j that is actually ingested by consumer i (e.g., some carnivores do not consume the whole of a kill nor do parasitoids consume all of a host). Assimilation efficiency is separated from ingestion efficiency because the former can theoretically be allometrically scaled while the latter is less systematic and contingent on natural history of consumption such as that between a nematode that causes a disease that kills a host and a different nematode that parasitizes a host without killing it. The former nematode has a much lower f_{eij} than the latter.

Equation 2.4 states that the rate of change of the primary producer's biomass is made up of two components. The first term is the gain in biomass from the species' intrinsic net growth that includes biomass gain from primary production and biomass loss from metabolism. The second term is the loss of biomass from consumption by each predator of the species. Similarly, the rate of change of a consumer's biomass (Eq. (2.5)) is made up of three parts. The first term is the loss in biomass from the consumer metabolizing energy for respiration. The second term is the gain in biomass from consuming various resource species. The third term is the loss of biomass from consumption by each predator or other consumer (herbivore, parasites, etc.) of the species.

The rate of ingestion of resource j by consumer i is given by a multispecies functional response which saturates at some maximum ingestion rate. It is convenient to assume that the functional response has the form

$$F_{ij}(\vec{B}) = J_{ij}\widehat{F}_{ij}(\vec{B}) \tag{2.6}$$

where J_{ij} is the maximum ingestion rate of prey item j by consumer i and $\widehat{F}_{ij}(\vec{B})$, the normalized functional response, is a function that ranges between zero and one and is potentially a function of the biomasses of all species in the system.

The mass-specific growth rate is assumed to be of the form

$$G_i(\vec{B}) = r_i\widehat{G}_i(\vec{B}) \tag{2.7}$$

where r_i is the maximum mass-specific growth rate and $\widehat{G}_i(\vec{B})$, the normalized growth rate, is a function whose maximum value is equal to one and is potentially a function of the biomasses of all species in the system.

Using these expressions for the functional response and growth rate, the two equations for the rate of change of biomass (Eqs. (2.4, 2.5)) can be written as

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = r_iB_i\widehat{G}_i(\vec{B}) - \sum_{j=\text{predators}} B_jJ_{ji}\widehat{F}_{ji}(\vec{B})/f_{eji} \tag{2.8}$$

for primary producers; and

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = -B_iT_i + B_i\sum_{j=\text{prey}} e_{ij}J_{ij}\widehat{F}_{ij}(\vec{B}) - \sum_{j=\text{predators}} B_jJ_{ji}\widehat{F}_{ji}(\vec{B})/f_{eji} \tag{2.9}$$

for consumer species.

Yodzis and Innes (1992) introduced allometric scaling relationships for the physiological rates for the model described in Eqs. (2.8) and (2.9). These rates are the intrinsic growth rate of the resources, the respiration rate of consumers, and the maximum consumption rate of a resource by a consumer. To simplify the model, all rates are assumed to scale as $M_i^{0.75}$, where M_i is the body mass of species i. Yodzis and Innes (1992) simply described M_i as "adult body masses for the populations." No reference is made as to whether this is the mean, median, or more sophisticated estimate of the body mass that accurately characterizes a population with variable body sizes within this model. Further progress on this fundamental question has occurred only recently (Savage 2004, Economo et al. 2005). In any case, all rates are normalized to the chosen species' body mass. These mass-specific rates scale with $M_i^{-0.25}$ $(=M_i^{0.75}/M_i)$.

The mass-specific respiration rate, T_i, is given by

$$T_i = a_{Ti}M_i^{-0.25} \tag{2.10}$$

The mass-specific maximum assimilation rate, $e_{ij}J_{ij}$, is given by

$$e_{ij}J_{ij} = f_{Jij}a_{Ji}M_i^{-0.25} \tag{2.11}$$

The mass-specific maximum growth rate of a producer species is given by

$$r_i = f_{ri}a_{ri}M_i^{-0.25} \tag{2.12}$$

The constants a_T, a_r, and a_J, all with units of (mass$^{0.25}$time^{-1}) have been determined from empirical data. Throughout the model, biomass is used as a surrogate for energy, so rates of energy respiration are converted to rates of biomass loss due to respiration and variations in energy content per unit biomass in different organisms within a metabolic type are ignored. However, these constants do vary between metabolic groups of organisms including plants, invertebrates, and ectotherm and endotherm vertebrates but still remain the same for species within the same metabolic group despite dramatic variation in mean body mass (Yodzis and Innes 1992, Ernest et al. 2003, Brown et al. 2004). These values are not universal for the whole system when the system is made up of species with different metabolic types. The constants f_{Jij} and f_{ri} are fractional quantities whose value may be specified for each specific population or feeding interaction in a particular ecological context.

One of the least intuitive aspects of this model concerns the model's timescale. Yodzis and Innes (1992) normalize time to the growth rate of the single primary producer in their model. Here, time is normalized to the growth rate of a chosen primary producer k (Eq. (2.12)) by introducing a new nondimensional time variable t':

$$t = \frac{t'}{r_k} = \frac{t'}{f_{rk}a_{rk}M_k^{-0.25}} \tag{2.13}$$

This means that a unit of time is defined as the inverse of the growth rate of primary producer k. This time varies greatly, for example, between

phytoplankton and redwood species. Once species k is chosen and time is scaled accordingly, several constants are defined as follows:

$$r_i = \frac{f_{ri}a_{ri}}{f_{rk}a_{rk}} \left(\frac{M_k}{M_i}\right)^{0.25} \tag{2.14}$$

$$x_i = \frac{a_{Ti}}{f_{rk}a_{rk}} \left(\frac{M_k}{M_i}\right)^{0.25} \tag{2.15}$$

$$y_{ij} = \frac{f_{Jij}a_{Ji}}{a_{Ti}} \tag{2.16}$$

The first parameter r_i is the relative mass-specific growth rate of producer species i normalized with the growth rate of the chosen producer species k. Similarly, x_i is the mass-specific metabolic rate of species i relative to the chosen timescale of the system. Finally, the nondimensional constant y_{ij} is the maximum ingestion rate (biomass per unit time) of prey species j by predator species i relative to the metabolic rate of species i (biomass per unit time).

This allows the governing Eqs. (2.8, 2.9) to be written as

$$\frac{dB_i}{dt'} = r_i B_i \hat{G}_i(B) - \sum_{j=\text{predators}} x_j y_{ji} B_j \hat{F}_{ji}(B)/f_{eji}e_{ji} \tag{2.17}$$

for primary producers; and

$$\frac{dB_i}{dt'} = -x_i B_i + x_i B_i \sum_{j=\text{prey}} y_{ij} \hat{F}_{ij}(B) - \sum_{j=\text{predators}} x_j y_{ji} B_j \hat{F}_{ji}(B)/f_{eji}e_{ji} \tag{2.18}$$

for consumer species.

Overall, the formulation of this population dynamic model by Yodzis and Innes (1992) is based on three steps: (1) the parameters of the simple but highly abstract population dynamic model (Eqs. (2.8, 2.9)) are reformulated as mass-specific parameters (2.10–2.12). This allows seeding the model based on regressions that yield key parameters as a function of species' body mass; (2) time is nondimensionalized using the inverse of the maximum growth rate of producer k (2.13), so the model's time scale is expressed relative to the growth rate of that producer; (3) the mass-specific growth and metabolic rates of the model are normalized by the time scale (Eqs. (2.14, 2.15)), while the maximum ingestion rate is normalized by the metabolic rate (Eq. (2.16)). These three steps yield a population dynamic model with mass-specific parameters using a time-scale based on the growth rate of a chosen primary producer (Eqs. (2.17, 2.18)).

2.3.1 Parameter values

Key parameters include three very general constants; a_i for each metabolic category of the species, three fractions f_i with values between zero and one that depend on the specific ecological circumstances of the system being

modeled, and the efficiency e_{ij} that simply depends on whether the resource is a plant or animal. The values given in Yodzis and Innes are collected below.

	Endotherm	Vertebrate ectotherm	Invertebrate	Phytoplankton
$a_T(\text{kg}^{0.25}\text{year}^{-1})$	54.9	2.3	0.5	
$a_J(\text{kg}^{0.25}\text{year}^{-1})$	89.2	8.9	9.7	
$a_r(\text{kg}^{0.25}\text{year}^{-1})$	34.3	6.6	9.2	0.4

	Plant resource	Animal resource
e_{ij}	0.45	0.85
f_r		Of the order 0.1
f_J		1.0 (endotherms), 0.2 (ectotherms), 0.3 (invertebrates)
f_e		1 for grazers and parasites; < 1 for some carnivores

To fully specify the model, the normalized growth function and functional response need to be defined.

2.4   GROWTH RATE MODELS

The simplest resource growth model is unconstrained exponential growth, in which case $\hat{G}_i(B) = 1$. The more advanced and commonly used logistic growth model which decreases the growth of a species as it reaches and exceeds its carrying capacity is given by

$$\hat{G}_i(B) = 1 - B_i/K_i \qquad (2.19)$$

where K_i is the system's carrying capacity for producer species i. These two growth models are specific in two ways: (i) they describe net-growth that includes gross primary production as well as metabolism, and (ii) they do not account for effects of shared-resource consumption such as competition amongst primary producers in a multispecies community. To address (ii) in a community with multiple primary producer species (Brose et al. 2005), growth can be modeled as a function of the consumption of l limiting physical resources R_l (Tilman et al. 1997, Huisman and Weissing 1999):

$$\hat{G}_i(B, R) = \text{MIN}\left(\frac{R_1}{K_{1i} + R_1}, \ldots, \frac{R_l}{K_{li} + R_l}\right) \qquad (2.20)$$

K_{li} is the half saturation constant for resource l, and MIN is the minimum operator specifying that the least available resource relative to its half saturation constant limits growth of the producer. These half saturation constants indicate the nutrient concentration at which the consumer attains half its maximum rate of nutrient consumption. The variation of resource l's density with time is given

by a two-term equation where the first calculates abiotic effects on resources concentration and the second term calculates effects of biotic consumption:

$$\frac{\mathrm{d}R_l}{\mathrm{d}t} = D(S_l - R_l) - \sum_{i=\text{producers}} (c_{li}\hat{G}_i(R)B_i) \qquad (2.21)$$

where c_{li} is the fraction of resource l in the biomass of producer species i. The resource dynamics depend on a turnover rate D that is one divided by the mean residence time of the nutrient in its abiotic matrix (e.g., water, soil). Resource l is added to the matrix with a supply concentration of S_l, and its removal depends on the current resource content of the system, R_l. This Monod model of growth is well-established in plant ecology and the producer species compete by utilizing shared physical resources (Miller et al. 2005). The competition hierarchy is based on the half saturation constants, where lower K_{li} indicate "utilization efficiencies" or higher consumption rates at nonsaturating resource concentrations for primary producer species i consuming the physical resource l.

2.5 FUNCTIONAL RESPONSES

We discuss here multispecies versions of a few of the many models of functional response that have been studied. It is well known that the stability of small systems is quite sensitive to the choice of the functional response (e.g., DeAngelis et al. 1975, Murdoch and Oaten 1975, Yodzis and Innes 1992), and preliminary work shows that large systems are similarly sensitive (Williams and Martinez 2004). For more complete reviews of this very important and difficult topic, see Gentleman et al. (2003) and Jeschke et al. (2002).

2.5.1 Type II multispecies functional responses

Holling (1959) described the changing feeding rate of a predator in response to variations in prey density. In his type II functional response model, the predator divides its time between searching for prey, during which prey is captured at some fixed rate, and processing captured prey, during which time no searching takes place. If a is the rate of capture rate (units 1/time), b is the handling time (units: time/prey), and D is the prey density (number of individuals), then the rate of consumption of the predator, F, is the maximum amount potentially captured divided a term that decreases this rate as handling time increases above zero:

$$F = \frac{aD}{1 + abD} \qquad (2.22)$$

Murdoch (1973) generalized Holling's (1959) type II functional response to predators with multiple prey by lowering the maximum possible amount

captured of a single species by a term in the denominator that sums the time needed to handle all prey species captured:

$$F_{ij} = \frac{a_{ij}D_j}{1 + \sum_k a_{ik}b_{ik}D_k} \tag{2.23}$$

Here F_{ij} is the rate at which species j is consumed by the predator i, D_j is the density of species j, a_{ij} is rate at which the predator i attacks species j and b_{ij} is the time it takes predator i to handle prey item j.

Defining $c_{ij} = 1/b_{ij}$ as the maximum rate at which predator i can consume prey j in the absence of other prey and $D_{0ij} = 1/a_{ij}b_{ij}$ as the half-saturation density of predator i on prey j in the absence of other prey, this can be rewritten as

$$F_{ij} = \frac{c_{ij}D_j/D_{0ij}}{1 + \sum_k D_k/D_{0ik}} \tag{2.24}$$

2.5.2 Non-type II multispecies functional responses

If the attack rate is a function of the density of the prey, then the model of predation can relax predation pressure on rare prey more than the type II model. This can give rise to a sigmoidal, or type III functional response (Holling 1959). Predator interference can also modify the attack rate. In this case the attack rate decreases with increasing prey density (Beddington 1975, DeAngelis et al. 1975) compared to the rate given by the type II model. In general, rather than being constant, the attack rate a in (2.22) or a_{ij} in (2.23) is made a function of the predator and prey densities $\hat{a}_{ij}(D_i, D_j)$, but otherwise the functional response given in (2.22) or (2.23) is unchanged.

2.5.3 Type III

Real (1977) introduced a generalized type III functional response by defining $\hat{a}_{ij} = a_{ij}D_j^q$. When $q = 0$ in the equation below, (Eq. (2.25)) reduces to the attack rate used in the standard type II response (Eq. (2.22)). Using the half-saturation density of the prey as a natural scale for a feeding interaction suggests using an attack rate of the form $\hat{a}_{ij} = a_{ij}(D_j/D_{0ij})^q$. The functional response is then

$$F_{ij} = \frac{c_{ij}(D_j/D_{0ij})^{1+q}}{1 + \sum_k (D_k/D_{0ik})^{1+q}} \tag{2.25}$$

2.5.4 Predator interference

Beddington (1975) and DeAngelis et al. (1975) independently proposed a functional response in which predators spend some of their foraging time interacting with members of their own species, which reduces the rate at which predators

capture prey. Assuming that this effect is the same for all prey species and that $a_{ij,\text{Interference}} = a_{ij,\text{NoInterference}}/(1 + d_i N_i)$ where d_i is a positive constant that describes the amount of interference and N_i is the number of individuals of predaceous species i, the resulting functional response is

$$F_{ij} = \frac{c_{ij}(D_j/D_{0ij})^{1+q}}{1 + d_i D_i + \sum_k (D_k/D_{0ik})^{1+q}}. \tag{2.26}$$

The preceding functional responses are for the rate at which a predator consumes individual prey items. By redefining the various parameters as per unit biomass rather than per individual, the functional response (Eq. (2.26)) can be rewritten in the form used in Eq. (2.6):

$$F_{ij} = J_{ij}\widehat{F}_{ij}(\vec{B}) = J_{ij}\frac{(B_j/B_{0ij})^{1+q}}{1 + d_i B_i + \sum_k (B_k/B_{0ik})^{1+q}} \tag{2.27}$$

Here B_i is the biomass of species i, B_{0ij} is the half-saturation biomass of predator i consuming prey j, and J_{ij} is the maximum rate at which predator i can consume prey j (biomass per unit time).

It is informative to look at the role of the various parameters in this functional response in determining prey preference. Following the analysis of Chesson (1983) and Gentleman et al. (2003), and using the notation introduced above for biomass-based functional response (Eq. (2.27)), a predator's relative preference of one resource over another is defined as

$$p_{ijk} = \frac{F_{ij}/B_j}{F_{ik}/B_k} = \frac{J_{ij}B_j^q/B_{0ij}^{1+q}}{J_{ik}B_k^q/B_{0ik}^{1+q}},$$

where the predator is species i and the two prey species are j and k. The term "switching" is used to describe situations in which the preference changes with changes in the relative resource density B_j/B_k. In the terminology of Gentleman et al. (2003), when $q = 0$ the response is class 1 and has no switching, and when $q \neq 0$, the response is class 2 and has passive switching.

For the type II response ($q = 0$), the preference is

$$p_{ijk} = \frac{J_{ij}/B_{0ij}}{J_{ik}/B_{0ik}}$$

This shows that a resource species is preferred either because its consumer species has a greater maximum rate of intake of the resource species or the consumer has a smaller half-saturation density for the resource. When the passive switching of a type III response is added, a resource will also be preferred when it has a higher relative density.

Table 2.1. Mathematical expression and their descriptions

Expression	Description
dB_i/dt	Change in population density of species i with time t
B_i	Population density of species i
G_i	Mass-specific net growth of species i
T_i	Mass-specific respiration (metabolic growth rate)$^{-1}$ of species i
r_i	Maximum mass-specific growth rate of species i
F_{ij}	Functional response = the fraction of the maximum consumption rate of the population of species i by the population of species j (i.e., per capita consumption of j by i)
e_{ij}	Assimilation efficiency = fraction of the biomass of species j lost due to feeding by species i that is metabolized by species i
f_{eij}	Ingestion efficiency = fraction of biomass of species j lost due to feeding by species i that is ingested by species i
a_{ji}	Attack rate of j on i
(B^V)	Biomass loss from metabolism
J_{ij}	The population of species i's maximum rate of ingesting the population of species j
G_i	Normalized growth rate of species i
M_i	Adult body mass among the population of species i
a_{Ti}	Mass to respiration conversion constant for species i
a_{Ji}	Mass to assimilation conversion constant for species i
$a_r,$	Mass to growth conversion constant for species i
f_J, f_r	Fractional constants
x_i	Constant mass-specific metabolic rate of species i relative to the maximum growth rate of a chose producer species
y_{ij}	Maximum ingestion rate of resources species j by consumer species i relative to metabolic rate of species i
r_i	Relative mass-specific growth rate of producer species i
K_i	System's carrying capacity for resource I
R_l	Limiting physical resources
l	A particular resource
c_{li}	Fraction of resource l that comprises the biomass of producer species i
D	(Eq. (2.21)) turnover rate of resources
D	(Eq. (2.22)) prey density
d	Positive constant describing amount of interference (Eq. (2.26))
B_{0ij}	Half-saturation biomass of predator I consuming prey j
q	Control parameter within functional response equations

2.6   CONCLUSION

With this modeling framework that extends Yodzis and Innes (1992) nonlinear approach to many species systems and functional responses, a new frontier of more empirically-based theoretical explorations of the structure and dynamics of complex networks is opened to researchers. Early explorations have shown, for example, that 50-species networks that allow most species to persist have food-web structure more like the empirically corroborated "niche model" than the ecologically unrealistic "cascade" and "random" models (Martinez et al. 2006). Such explorations have also shown how small variations in functional

responses have dramatic effects on the stability and persistence of species within the simulated networks (Williams and Martinez 2004). Body-size ratios have also been shown to have similarly dramatic effects which help explain a recently discovered systematic difference between the body-size ratios of endotherm and ectotherm vertebrate predators (Brose et al. in review). Furthermore, this framework has been applied to the analysis of keystone effects which found that increased nutrient supply can systematically increase the strength of interactions measured by simulating the removal of keystone species from complex ecological networks (Brose et al. 2005). This of course points the way towards more compelling theoretical investigations of applied issues such as the effects of biodiversity loss and species invasions (Gibbs 2003) but such applications are not without significant problems (Paine 2004, Martinez and Dunne 2004).

Addressing these and many other challenges of modeling and managing ecosystems will involve a great deal of work to understand the sensitivity of simple and complex models to their many parameters described here. These parameters are needed to base models firmly on ecological observations while attempting to predict ecosystem behavior. Others have found that even more parameters are needed to successfully apply Yodzis and Innes' approach to even simple 2-species systems in chemostats (Shertzer et al. 2002). This means that more work is needed beyond understanding and empirically-basing model parameters before application of such models to specific complex ecological systems. For example, beyond the evolution parameters incorporated by Shertzer et al. (2002), better models of multispecies functional responses are needed (Gentleman et al. 2003). The specific functional response or responses used in the model and the values of the various parameters these responses introduce should be based on empirical knowledge of the system of interest. In addition, the approach presented here could also easily be extended to include the effects of temperature variation on system stability using the methods developed in Vasseur and McCann (2005). While conducting such work is clearly a hugely difficult and important challenge, we thank Peter Yodzis and his coworkers for making spectacularly important contributions to addressing the challenge and providing some of the most creative and rigorous foundations for current and future research on complex ecosystems.

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CHAPTER 3

FOOD WEBS, BODY SIZE AND THE CURSE OF THE LATIN BINOMIAL

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3.1   INTRODUCTION

The interrelatedness and interdependency of organisms in natural systems must have been part of the model framework with which early humans made sense of their environment and their place within it, and which persists today in all cultures in its various forms. Ecologists have formalised these relationships and dependencies, in diagrammatic and mathematical forms, as systems of trophic networks or food webs, and, taking a wider view, as ecosystems. In the present context of food webs, the details of the arrangement of the organisms in time and space and the flow of materials between them, have demanded a great deal of attention from researchers, both empiricists and theorists, and will continue to do so. Historically, food web research has necessitated a reductionist approach in order to cope with the complexity apparent in real interacting systems; trophic data have usually been collected at a high resolution, often at the level of the individual species (Table 3.1).

The scheme devised and promoted by Linnaeus for classifying similar individual animals and plants into genera and then species, the Latin binomial

Table 3.1. The various ways in which elements and linkages may be represented in food webs

Elements

Functional groupings: e.g., primary producers, herbivores, parasites, meso-predators, piscivores, suspension feeders.

Coarse taxonomic groups: e.g., plants, zooplankton, seabirds.

More refined taxonomic groups: e.g., mustellids, nano-flagellates, nematodes, wasps.

Species: e.g., *Nereis diversicolor, Cervus elephas, Quercus robur.*

Life forms of individual species: e.g., larva, 3rd instar, adult, juvenile, female, male, egg, gamete.

Size: *categorical*, e.g., small, medium, large, or *continuous measures*, e.g., mm, g, ml, of body size.

Linkages

Binary linkages 1: between elements based on an expectation of whom is capable of eating whom derived from expert knowledge or literature.

Binary linkages 2: between elements, based on empirical observation, gut contents analysis, and chemical tracers, such as lipids and isotopes.

Quantified linkages 1: measured as the flow of material (energy or a specific element such as C or N) from a resource to a consumer element.

Quantified linkages 2: measured as interaction strength, usually the per capita effect of the consumer on the resource.

Quantified linkages 3: where the functional strength of a linkage is measured as the community-wide impact of breaking the link between consumer and a resource.

Note: In its simplest form, a food web is a network of information about who eats whom. For empirical webs (and for many model webs) the information encoded in the elements varies tremendously according to the degree of resolution, whilst the linkages between elements varies from simple observed or hypothesised binary to chemical flows to keystone effects

system, has provided natural sciences with one of its most important tools. Our understanding of the natural world today is largely coloured by our day-to-day use of the Latin binomial, and food web ecology is no exception. Apart from the early studies by Elton (1927) and others, and the ecosystem ecology school, food web ecologists have tended to cling on to the sanctity of the species for their various approaches. Here, I review those species-centric approaches for exploring the structure and dynamics of food webs and discuss several approaches that explicitly recognise the importance of body size as a species trait, as well as the perspectives which do not recognise species at all, only body size. Finally, I question whether our adherence to Latin binomials for the empirical analyses of food webs makes sense in terms of the way in which natural systems appear to operate, and whether the species-centred approach has in fact been a limiting constraint for understanding the dynamics and structure of food webs.

3.2   REDUCTIONIST APPROACHES TO FOOD WEBS

One of the major challenges faced by empiricists is how best to describe real food webs so that they can be viewed and analysed sensibly, and any regularities in their structure and dynamics identified. Picture representations of the trophic linkages between species (food web diagrams), are pleasing to the eye and are

useful for conveying the impressive complexity, apparent interrelatedness, and interdependency of ecological systems to stakeholders, policy makers, and managers, but are of limited value for analytical purposes. This is especially the case for large food webs where the taxa are resolved to species level. There have been various attempts over the last 80 years to reduce this complexity by grouping elements and/or linkages within the web to provide new representations, which make interweb comparisons more tractable. Such comparisons may reveal features or patterns, which are common to different webs, implying certain constraints on web architecture, which may in turn hint at underlying processes.

Elton (1927), Lindeman (1942), and others working in this area more than 50 years ago were amongst the first to successfully reduce web complexity and reveal important underlying structure and dynamics. For instance, they recorded regularities in the proportions of biomass in different functional groupings of organisms, primary producers and succeeding tiers of consumers, which generate the so-called pyramid of biomass. The relatively high species richness within each food web could be reduced to a very small number, typically three or four data points (trophic levels), allowing researchers to derive concepts such as the ecological efficiency of energy transfer between different trophic levels. These concepts in turn provided the framework for much of the thinking in the 1960s and 1970s behind an extremely important (but now sadly overlooked) initiative, the International Biological Programme, IBP (McIntosh 1985), whose legacy includes the "how-to-measure" IBP manuals that most ecologists use today in one form or another, and the many energetics as well as binary food webs that are the stock in trade of food web theorists (e.g., Cohen et al. 1990). In addition to the foundations laid for future work at the ecosystem level through the IBP, one of the most important contributions made by Elton and others to food web research was to be prepared to relinquish the complexity of food web diagrams and hence to abandon the species as the fundamental unit for these particular analysis, although Elton always remained a strong advocate of population biology for understanding community dynamics (Warren 2005).

The 1970s and 1980s saw a drift away of mainstream ecologists from the energy-based approaches, which had characterised the IBP, towards experimental approaches for assessing species interactions in food webs (Raffaelli 2000, 2005), exemplified by intertidal ecologists such as Bob Paine, Bruce Menge, Tony Underwood, Steve Hawkins, and many others (see Raffaelli and Hawkins 1996, Raffaelli and Moller 2000 for a comprehensive bibliography). These and other researchers were able to demonstrate the persuasive power of small-scale replicated manipulative field experiments for rigorous hypothesis testing and many of the paradigms in mainstream ecology derive from that period. At the same time, the research community concerned with energy flow approaches was making important developments in the area of trophodynamic systems (e.g., Christensen and Pauly 1992, Ulanowicz 1996, Jorgensen 1998). The fruit of the

food web experimentalists has been the reduction of the complexity of real food webs to a subset of those taxa and trophic linkages, which are regarded as functionally important (sensu Paine 1980) for organising the community. However, it should be noted that this reductionist approach still views the species as the fundamental datum.

In more recent years, there has been a return towards detecting recurrent patterns across different food webs through comparison of web descriptive statistics (e.g., Cohen et al. 1990). The approach differs from that of earlier researchers like Elton (1927), in that it retains the complexity of the food web diagram where each node is represented by a taxon (in most instance this will be a species) and the linkages are binary (either present or not). A tantalising variety of such statistics can be derived, including web size, linkage density, connectance, proportions of different kinds of species, and food chain lengths. The outcomes from these analyses have proved intriguing and have yielded insights, often appearing to confirm predictions of earlier theory, but the overall approach was not universally well-received in its early days. This is mainly because of the variable quality of the food web diagrams, the majority of which were never intended by their original authors for such analyses (e.g., Hall and Raffaelli 1991, 1993, 1997).

One response to the need to standardise on elements in food webs has been the documentation of larger webs where the majority of elements have been resolved to species level. In some cases (e.g., Woodward et al. 2005) this is the outcome of considerable field effort to document actual linkages, and in other studies, lists for particular areas are made or obtained and then the linkages between them estimated by a combination of direct observation, the literature or expert knowledge. The latter two approaches are almost guaranteed to overestimate diet breadth, and hence connectance, since literature and expert knowledge are usually based on regional scale knowledge, whereas the linkages in the local-scale web will be a reduced sub-set of the possible linkages (Hall and Raffaelli 1997) and care needs to be taken with such analyses. Better documented and more evenly resolved food webs are now available and the analyses carried out on these are much less open to criticism (e.g., Solé and Montoya 2001, Dunne et al. 2002). Nevertheless, the basic datum for such analyses remains the species (and the linkages between them).

3.3   APPROACHES WHICH ACKNOWLEDGE BODY SIZE

The statistics and patterns derived from species-orientated food web analyses are important, not least because they can be used to validate or parameterise static or dynamic models, one of the most elegant and influential of which is the Cascade model (Cohen et al. 1990). Not only is the latter partly parameterised by one such pattern, the links per species; it is also able to predict a range of other food web patterns (Cohen et al. 1990). The cascade model takes its name from the hierarchical nature of the trophic interactions within the

food web: species are only allowed to eat a restricted selection of other species. The basis for this constrained trophic rule may be related to species attributes, such as body size (e.g., Elton 1927, Warren and Lawton 1987), and this has been elegantly explored further by Warren (1996) and by Williams and Martinez (2000). However, the basic element in the food web remains the Latin binomial.

The reluctance of many food web ecologists to let go of the species as the fundamental datum is surprising given the evidence that traits such as body size may be more important than species identity in determining trophic interactions and driving community dynamics. For instance, Elton (1927) recognised that there was a pattern in the relative body sizes of predators (larger) and prey (smaller), whilst Ryther's (1969) pioneering analysis of food web structure and fisheries yields in different parts of the ocean is predicated on body-size ratios of predators and prey, irrespective of taxonomy. He argued that the length of food chains is a function of the body size of the primary producer and the number of steps (more in open oceans where the primary producers are tiny, and fewer in upwelling areas, where the primary producers are large) required to package progressively larger parcels of energy into prey that could be taken by the largest predatory fish caught by humans. Using simple size-based rules, Ryther (1969) derived estimates of global fish biomass and sustainable yield, which were impressively close to contemporary independent estimates. Size-based patterns for predator-prey interactions are now well documented (e.g., Cohen et al. 1993) and the likely effects of changes in body size have been explored (e.g., Yodzis and Innes 1992, Jennings et al. 2001).

Finally, there is now compelling evidence for a link between the body sizes of consumers and their resources and the dynamics and structure of food webs. Predator-prey body-size ratios have been shown to affect the magnitude of interaction coefficients, and hence system resilience, in simple linear food chain Lotka-Volterra models (Jonsson and Ebenman 1998). Using an empirical approach to quantify per capita effects in experimental arenas of different-sized predators and prey, Emmerson and Raffaelli (2004) derived a general and simple relationship between predator-prey body size ratio and interaction strength. Construction of Lokta-Volterra models of real food webs for which body sizes and abundances are well documented, such as the Ythan Estuary and Broadstone Stream, have allowed a range of insights into the dynamic consequences of process such as extinctions and invasions in complex systems (Emmerson et al. 2005). The linkages between body size, abundance, and food web structure have also been highlighted by recent work by Joel Cohen and colleagues (Cohen et al. 2003, Reuman and Cohen 2004, Cohen and Carpenter 2005), to reveal a trivariate relationship (Figure 3.1) for Tuesday Lake, and possibly Broadstone Stream (Woodward et al. 2005). How general these patterns are across other real, well-documented food webs remains to be established, but the approach shows good potential for incorporating body size considerations in food web theory.
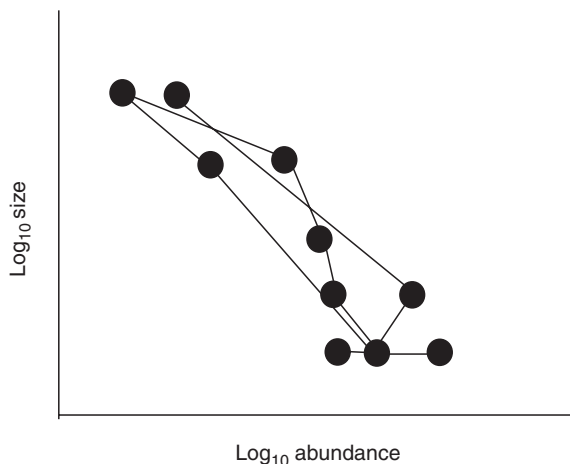
Figure 3.1. The trivariate (body size, abundance, trophic links) representation of a food web (Ythan estuary from Figure 3.3). (After Cohen et al. [2003].)

3.4   BODY-SIZE DISTRIBUTIONS AND TROPHODYNAMICS

Given the importance of body size for trophodynamics, it is worthwhile to ask whether there are regularities in body size distributions in nature that could in turn be related to regularities in trophodynamics. There is now a considerable literature on such distributions, much of it dealing with macro ecological patterns (Brown 1995, Damuth, 1987, Peters 1983, Lawton 1990, Cotgrave 1993, Blackburn and Gaston 1999, Gaston and Blackburn 2000). One of the most elegant and thought-provoking analysis in the food web context is Holling's (1992) thesis concerning the existence of ecosystem discontinuities in time and space. Essentially, Holling (1992) argues that dominant ecological structures in ecosystems entrain ecological processes so that the latter become associated at particular scales, with both process and pattern taking on a "lumpy" appearance. Furthermore, this lumpiness is reflected in multimodal body size distributions of taxa, the troughs between modes representing textural discontinuities in the ecosystem. Holling's thesis poses at least two questions: what evidence is there that body size distributions are multimodal? And, if so, how might the modality be related to regularities in trophodynamics?

Holling (1992) has addressed the first question extensively. Multimodal distributions were found for individual taxa (North American birds and mammals) but analysis of marine taxa-independent body size-distributions, which embrace much of the food web, also show multimodality. For marine benthic systems (Schwinghamer 1981, Warwick 1984, Raffaelli et al 2000), the locations of troughs between the modes seem to relate to habitat discontinuities within the
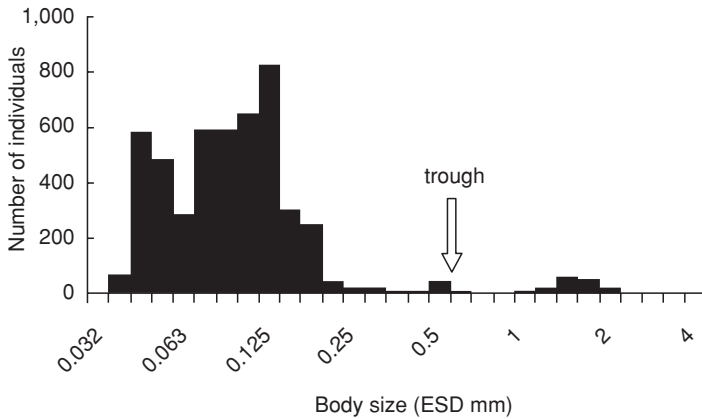
Figure 3.2. The body size spectrum of organisms ranging from 32 microns to 4mm equivalent spherical diameter (ESD) from the Ythan estuary, Scotland (data from Raffaelli et al. [2000]). The location of the trough separates meiofauna from macrofauna and is thought to represent a scale shift from interstitial to burrowing lifestyles.

sediment, at least in some studies (Figure 3.2). Open water systems also show multimodality in body-size distributions but the positions of modes and troughs are not as conservative as those for benthic systems and changes with the seasonal dynamics of the water body as well as with location (e.g., Sheldon and Parsons 1967, Sheldon et al. 1972, Sprules and Munawar 1986, Kerr and Dickie 2001), perhaps reflecting the lack of structural architecture in those systems (Holling 1992). The trophic consequences of multimodality for benthic systems remains to be explored, but there is considerable evidence that for open water systems these size spectra are related to trophodynamics: as in Ryther's (1969) analysis, smaller particles are ingested by larger particles, irrespective of taxonomy.

3.5 BODY SIZE AS A FIXED TRAIT OR A CONTINUOUS FUNCTION?

In the vast majority of the body-size approaches described above, body size is taken as a fixed trait of a species, usually adult body size (maximum or mean). However, as smaller particles grow into larger particles and they change their position within the size spectrum to feed on and be fed upon by different sized particles. This was clearly recognised by Hardy (1924) in his depiction of the food web in which the herring (*Clupea harengus*) is embedded. Young herring only a few millimetres in length consume phytoplankton, larger herring 20–30 mm in length take copepods, whilst adults several tens of centimetres in length take sand eels and larger zooplankton such as amphipods and sea snails. Many animal taxa show similar shifts in diet with growth (Woodward et al. 2005). One way to cope with this is to regard the different life stages as pseudospecies, functionally different organisms, but this is only appropriate where there is a

clear step-like shift from one diet to another. For instance, Hall and Raffaelli (1991) considered O-group flounder (*Platichthys flesus*) and ducklings of the Eider (*Somateria mollissima*), as separate elements in their analysis of the Ythan estuary food web. Juveniles of flounder and Eider, which forage in quite a different manner to larger adult individuals, have a different diet and different consumers. Insects with complete metamorphosis provide another example.

Failure to acknowledge such shifts in individual species can have important consequences for our understanding of food web dynamics, even more so if the species concerned are dynamically important, such as keystones, at some time in their life-history (Woodward et al. 2005). For instance, de Roos and Persson (2002), Persson and de Roos (2005) and de Roos et al. (2003) have shown that changes in the population size structure of piscivorous fish may be responsible for regime shifts in lake food webs, depending on the dominance of age (size) cohorts in the population. Woodward et al. (2005) also argue that cannibalism is often prevalent when large and small instar larvae in streams overlap in time and space (intercohort predation) predation, although the dynamics
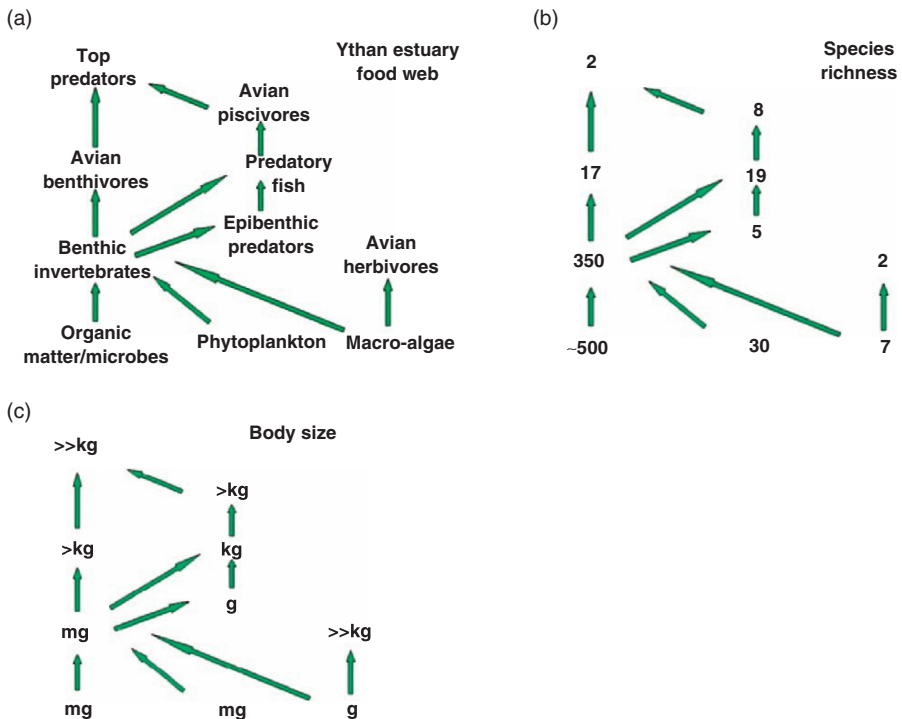
Figure 3.3. A generalised representation of the Ythan estuary food web (after Hall and Raffaelli 1991) showing (a) functional elements, (b) the number of species within each element, and (c) the body weights of taxa within those elements.

consequences of such interactions for food web stability are poorly understood at present, unlike the consequences of intraguild predation (Holt and Polis 1997, Persson 1999).

The distributions of body sizes in food webs also have consequences for extinction patterns in these systems (e.g., Petchey et al. 2004, Solan et al. 2004, Raffaelli 2004). Because larger body-size taxa tend to occur towards higher trophic levels, and species richness is generally higher at lower trophic levels (Figure 3.3), different biodiversity loss scenarios will affect trophic levels in very different ways. Scenarios based on habitat fragmentation will tend to affect larger body-sized taxa disproportionately, whilst smaller body-size taxa are more vulnerable to disturbances such as contamination. Conversely, the higher biodiversity at lower trophic levels implies that there may be more "functional insurance" amongst such species, in contrast to that at higher trophic levels, with implications for trophic cascades and other major changes in system dynamics following the loss of one or a few top species.

3.6   CONCLUSIONS

In summary, the Latin binomial of most species, such as the herring *C. harengus*, does not exist as a trophic entity, but as a particle continuously changing in size, interacting with other such particles which we also conveniently label with Latin binomials, which have no trophic reality for the herring. In this sense, the Latin binomial is little more than a crude model we use to organise the world around us but which captures little of the complexity of the continually changing trophic networks that develop and dissolve as individuals in the food web change in body size (or in other traits). In this respect it should be noted that body size is only one of a number of traits that can determine consumer-resource interactions. There is an extensive literature showing how phytophagous insect–plant interactions are determined, at least in part, by plant biochemistry and the mechanisms available to the insect for dealing with secondary compounds or physical defences. Similarly, the stoichiometry of basic chemical elements at different levels in a food chain can have profound effects on who eats whom and how much (Sterner 1995, Woodward et al. 2005, and references therein). The arguments presented here probably apply as much to these kinds of traits as to body size.

I have argued that representing the elements in empirical food webs as static and immutable taxa fails to acknowledge the true basis for trophic interactions and their dynamic nature. In nature, consumers do not recognise Latin binomials, only those items which can or cannot be eaten. Even the majority of those explorations of large food webs, which acknowledge the importance of body size still tend to view size as a fixed trait rather than a continuously changing variable. Until we find a way to move beyond the preoccupation of food web ecologists with the Latin binomial, developments in food web theory are likely to be extremely slow.

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CHAPTER 4

AN ENERGETIC FRAMEWORK FOR TROPHIC CONTROL

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4.1   ABSTRACT

Empirical and theoretical work has identified a bewildering array of ecological phenomena that can mediate the relative importance of top-down and bottom-up control in food webs. Here, we show that one essential similarity of these various phenomena is in how they alter patterns of energy flow among species. We use a simple model, examined from the perspective of energetic efficiencies, to develop the following synthesis: (1) unimpeded vertical energy flow permits strong top-down control; (2) various phenomena weaken or truncate top-down control by imposing "bottlenecks" to vertical energy flow, either by impeding transfer *between* trophic levels, or by reducing the efficiency with which energy is passed *through* a trophic level; and (3) alternative energy pathways can circumvent a bottleneck and reestablish strong top-down control. Our analysis leads to a number of general predictions for patterns of trophic control within and among food webs.

4.2   INTRODUCTION

Peter Yodzis felt strongly that theory must play a major role in simplifying complex ecological problems. Along these lines, Peter felt that a powerful role of theory was its ability to synthesize a suite of results within a common and easily interpretable framework. It is a special thing when a theory can take a complex set of results and unite these results coherently. Perhaps not surprisingly, Peter Yodzis felt that energetics may sometimes form such a common thread (conversations with KM). This chapter seeks to unite the different results of trophic control (i.e., top-down and bottom-up control) by understanding how structure (food webs, nutrient limitation etc.) influences energy transfer and how this in turn determines the type and extent of trophic control.

Energy flow through populations and trophic levels is a fundamental and unifying principle in ecosystem science (Lotka 1925, Lindeman 1942, Odum 1968, Yodzis and Innis 1992). However, energetics-based modeling of food web dynamics has been criticized. Some authors have cited a lack of correlation between the magnitude of energy flows and dynamic features such as trophic control or stability (Paine 1980, Dayton 1985, Menge and Sutherland 1987, Polis 1994). Others have argued conceptually that the magnitude of some important interactions exceeds the magnitude of their energy transfer (Polis and Strong 1996). Even when a role of energetics in food web dynamics is recognized, there is disagreement as to the exact nature of this relationship (Hairston and Hairston 1993, Moore et al. 1993a, de Ruiter et al. 1995, 1998, Teng and McCann 2004, deBruyn et al. 2004). Indeed, the reciprocal relationship between energy flow and food web dynamics appears to be just as complex

as other aspects of food web ecology. The analysis we present in this chapter provides one useful framework for exploring the relationship between energy flow and food web dynamics. The efficiency with which energy is passed through a food web is a key element of this framework. We show that a food web with efficient vertical energy transfer is characterized by strong top-down control, and consequently exhibits cascade dynamics. Characteristics of food webs that enhance recipient control (Polis and Strong 1996) also enhance efficient vertical energy transfer. Furthermore, we show that energy flow and energetic efficiencies respond in predictable ways to various widely studied ecological phenomena known to affect trophic control. The effects of these phenomena on energy flow and trophic control tend to fall into two categories, which we refer to as bottlenecks due to *impeded transfer* and *inefficient conversion*. The type of bottleneck present and the location of the bottleneck within the food web will determine where top-down control arises. We end by discussing the results in a more general context and suggesting avenues for future research.

4.3   THE MODEL

In this analysis, we consider a model of four interacting species (McCann et al. 1998):

$$\frac{\mathrm{d}R}{\mathrm{d}t} = rR\left(1 - \frac{R}{K}\right) - R\left[\frac{\mathrm{d}_1 a_{C_1} C_1}{R + R_0} + \frac{a_{C_2} C_2}{R + R_0}\right]$$

$$\frac{\mathrm{d}C_1}{\mathrm{d}t} = C_1\left[\frac{\mathrm{d}_1 a_{C_1} e_R R}{R + R_0} + \frac{(1 - \mathrm{d}_1) a_{C_1} e_{C_2} C_2}{C_2 + C_0} - \frac{\mathrm{d}_2 a_P P}{C_1 + C_0} + x_{C_1}\right]$$

$$\frac{\mathrm{d}C_2}{\mathrm{d}t} = C_2\left[\frac{a_{C_2} e_R R}{R + R_0} - \frac{(1 - \mathrm{d}_1) a_{C_1} C_1}{C_2 + C_0} - \frac{(1 - \mathrm{d}_2) a_P P}{C_2 + C_0} + x_{C_2}\right] \tag{4.1}$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = P\left[\frac{\mathrm{d}_2 a_P e_{C_1} C_1}{C_1 + C_0} + \frac{(1 - \mathrm{d}_2) a_P e_{C_2} C_2}{C_2 + C_0} + x_P\right]$$

$$\mathrm{d}_1 = \frac{\Omega_{C_1 R} R}{\Omega_{C_1 R} R + (1 - \Omega_{C_1 R}) C_2} \text{ and } \mathrm{d}_2 = \frac{\Omega_{P C_1} C_1}{\Omega_{P C_1} C_1 + (1 - \Omega_{P C_1}) C_2}$$

where R is the density of resource biomass, C_1 and C_2 of intermediate consumers' biomass, and P of top predator biomass. The parameters correspond to a bioenergetic interpretation of the Rosenzweig–MacArthur model proposed by Yodzis and Innis (1992) where r is the intrinsic rate of increase of the resource, K is the resource carrying capacity, R_0 and C_0 are half saturation densities, x_i is the mass-specific energetic losses from species i (metabolic expenditures, mortality not attributable to the feeding interactions described in this model), a_i is the specific ingestion rate of species i, e_i is the assimilated proportion of energy ingested from species i, and Ω_{ij} is a fraction indicating the preference of species i for consuming resource species j (Chesson 1983).

4.4   ENERGY FLOW AND CONTROL IN FOOD WEBS

In this section we explore three types of food webs. First, we review the classical top-down view of food webs that arises when communities have a smooth, sequential transfer of energy up the trophic hierarchy (Figure 4.1a). Second, we explore cases in which we consider the flow of energy up the trophic hierarchy to be attenuated, either by inefficient conversion (i.e., energy is dissipated within a trophic level) or by impeded transfer (i.e., some pathways are not connected, or are only weakly connected, to higher trophic levels) (Figure 4.1b). Third, we examine cases in which energy can circumvent such blockages by traveling along alternative pathways (Figure 4.1c).

We make use of the ecosystem efficiency metrics proposed by Lindeman (1942) and Odum (1957) to describe the patterns of energy flow under the various configurations of our model food web. To reflect the transfer of energy among trophic levels, we calculate the *utilization efficiency* (sensu Odum 1957) of top predators, $E_{U,P}$, which is simply the ratio of ingestion by P (I_P) to production by all members of trophic level C (G_C):

$$E_{U,P} = I_P/G_C \tag{4.2}$$
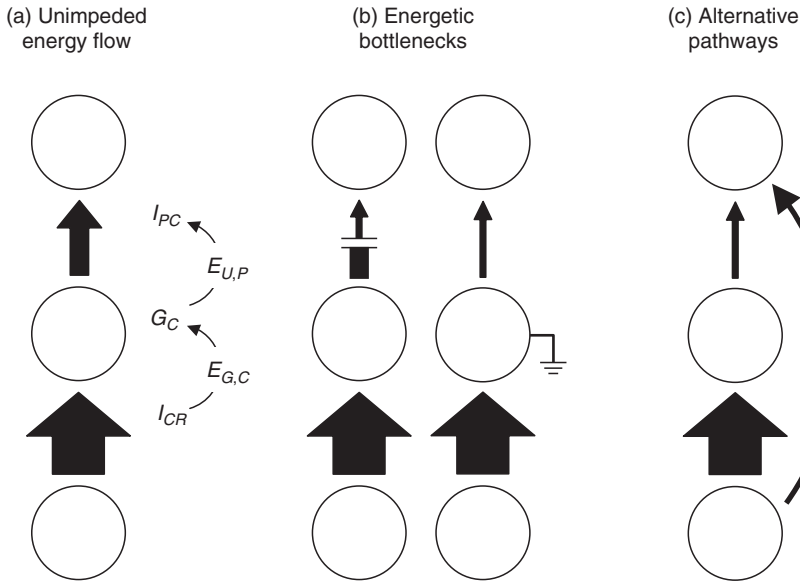
Figure 4.1. Three generalized patterns of energy flow: (a) energy flows vertically with relatively high efficiency in the conversion of ingested resources into production of intermediate consumers (ecological growth efficiency, $E_{G,C}$) and in the utilization of intermediate consumer production by top predators (utilization efficiency, $E_{U,P}$); (b) vertical energy flow is attenuated when one or both of these efficiencies are reduced; (c) vertical energy flow is reestablished along an alternative pathway. Top-down control is strong in (a), weakened in (b), and restored in (c).

where production G is the sum of all consumption by a species' predators plus all unconsumed production. We assume that unconsumed production represents a constant fraction, arbitrarily set at 10% of mass-specific energy losses (x_i).

To capture how efficiently energy is moved through a trophic level, we calculate the *ecological growth efficiency* of intermediate consumers, $E_{G,C}$. Here we distinguish between two forms of E_G. True (or gross) E_G is the real efficiency with which C_1 and C_2 convert ingested prey into biomass.

$$E_{G,C_1} = G_{C_1}/(I_{C_1R} + I_{C_1C_2}) \qquad (4.3)$$

$$E_{G,C_2} = G_{C_2}/I_{C_2R} \qquad (4.4)$$

Apparent (or net) E_G, on the other hand, reflects how efficiently trophic level C as a whole converts ingested R into biomass, which is in turn available for consumption by P. This is the efficiency of the C trophic level as perceived by a top predator. In some cases (e.g., with intraguild predation of C_1 on C_2) not all prey will be R and not all produced C will be apparent to P. Apparent E_G in this case will differ from true E_G:

$$E_{G\Sigma C} = (G_{C_1} + G_{C_2})/(I_{C_1R} + I_{C_2R}) \qquad (4.5)$$

4.4.1 Top-down control and vertical energy flow

We start by assuming that the pathways of energy flowing through a food web move strictly upward through the trophic hierarchy (i.e., no lateral pathways) and that all pathways start from the basal resource and finish at the top predator (i.e., no disconnected pathways). Further, we assume that intraspecific interference occurs only at the basal resource trophic level, and we assume no relative food shortage for any consumer, sensu Polis and Strong (1996). Thus, we assume a very simple biological world in which energy flows vertically through food webs relatively unimpeded except for natural losses due to the inability of consumers to perfectly convert resource biomass into consumer biomass (i.e., losses to metabolism, excretion, etc.). Intraspecific interference in the basal resource simply assumes that in the absence of predation, the basal resource reaches some maximum density permitted in the environment (i.e., the carrying capacity, K, of system (4.1)). An example of such a food web model is system (4.1) without intraguild predation (i.e., the intermediate consumers do not feed on each other) and with a generalist top predator (i.e., no disconnected pathways). This model is consistent with top-down ecological theory in that it assumes omnivory is rare (Pimm and Lawton 1978), that intraspecific interference occurs only at the basal resource trophic level (Oksanen et al. 1981, section 4.2.4 in Pimm 1982, Carpenter et al. 1985), and that food webs are composed largely of edible resources. The food web is vertically modular in that each species can be easily lumped into a trophic level (i.e., C_1 and C_2 could be

modeled as a single intermediate consumer, C, and still give the same qualitative results for trophic control).

This set of assumptions leads to a top-down food chain view of the world, and as found in previous theory (Hairston et al. 1960, Oksanen et al. 1981, Carpenter et al. 1985, Moore et al. 1993b, 2003), implies that food webs that can provide ample energy to the top predator are controlled by predation. Increases in productivity (the basal flux of energy) go to the top trophic level and every second trophic level below. Figure 4.2 depicts a trophic cascade for system (4.1) across a range in carrying capacity K. Increased environmental productivity leads to an increase in the top trophospecies P, which then regulates the intermediate consumer trophospecies (C_1 and C_2, which both essentially remain at a constant density), which in turn releases the basal resource, R, from the regulatory influence of the intermediate consumers so that R increases. The trophic cascade can be extended to show that increases in productivity
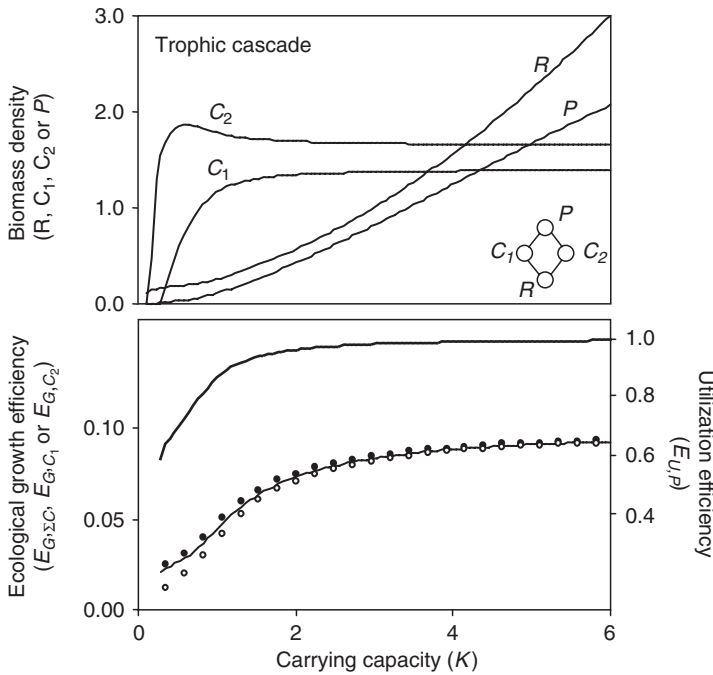
Figure 4.2. Model results showing trophic cascade dynamics in a food web with unimpeded vertical energy flow. *Top panel*: Equilibrium biomass densities of top predator (P), intermediate consumers (C_1 and C_2) and basal resource (R) across a gradient of carrying capacity (food web structure as depicted; C_1 and C_2 shown x5). *Bottom panel*: Ecosystem metrics reflecting efficiency of energy transfer through trophic level C ($E_{G,\Sigma C}$, refers to the lower line) and between trophic levels C and P ($E_{U,P}$, refers to the upper line and $E_{G,C}$, to the lower line). Parameters: $r = 0.5$; $a_{C1} = 3.5$; $a_{C2} = 3$; $a_P = 0.9$; $e_R = 0.1$; $e_{C1} = e_{C2} = 0.15$; $R_0 = 5$; $C_0 = 8$; $x_R = -0.001$; $x_{C1} = x_{C2} = -0.01$; $x_P = -0.005$; $\Omega_C = 1.0$; $\Omega_P = 0.5$.

are expected to increase the top trophic level and every second trophic level below, regardless of the length of the food chain (Oksanen et al. 1981).

Lindeman's ecosystem metrics provide a complementary perspective on this phenomenon. At low K, the system cannot support an effective population of P and both utilization and ecological growth efficiencies are consequently relatively low. $E_{U,P}$ is low because P is unable to consume all the production of ΣC. $E_{G,\Sigma C}$ is low because C is only weakly grazed by P, and therefore represents a relatively large population with slow turnover in which a substantial fraction of lost energy is metabolic expenditure (x). A relatively large, weakly grazed (bottom-up controlled) resource population also produces a relatively large amount of detritus, as many members die before they are eaten (Cyr and Pace 1993). As K increases and P establishes top-down control, $E_{U,P}$ increases rapidly and stabilizes at a value near unity. High $E_{U,P}$ reflects an unimpeded and efficient vertical flow of energy from C to P, and consequently strong top-down control (Hairston and Hairston 1993, Ruesink et al. 2002). The ecological growth efficiencies $E_{G,\Sigma C}$, $E_{G,C1}$, and $E_{G,C2}$ follow a similar pattern, increasing at low K and leveling off at a value determined by the assimilation efficiencies (e) and net production efficiencies (determined by x) of C_1 and C_2. Both intermediate consumers are converting ingested prey into consumer biomass with realistic efficiency, and all of this production is apparent to the top predator.

This view of food chain control has the virtue of being very simple and yet still finding a large amount of empirical support (e.g., Dayton 1985, Carpenter et al. 1985, Power 1990). Nevertheless, it is also obvious that it does not apply to many ecological systems (e.g., McQueen et al. 1986, Brett and Goldman 1996). We now show some cases in which this simple view is inadequate. Our investigations remain embedded in energetic reasoning but consider cases in which energy flow does not follow the strict unimpeded vertical ascent that is at the base of the trophic cascade view presented here.

4.4.2 Bottom-up control: impeding the vertical flow of energy

In this section, we explore the consequences of impeded transfer pathways and inefficient conversion steps in food webs. Both phenomena attenuate the vertical flow of energy from the resource to the top predator relative to the case presented above. Below, we show with examples how these energetic bottlenecks can predictably mediate trophic control within a food web.

4.4.2.1 *Example 1: Impeding transfer via disconnected pathways*

One obvious energetic bottleneck occurs when a system has trophospecies that specialize on a subset of resources in the lower trophic level (and hence do not consume all resource species in the modular component of the food web under consideration). Similar specialization may arise if the lower trophic level is comprised of coexisting resources, some of which are inedible (i.e., low or zero

values of a_{ij}). Both mechanisms impede the vertical transfer of energy in a food web.

System (4.1) can model such a situation if we allow the top predator P to feed exclusively on the intermediate consumer species C_1. Increases in productivity that flow from the resource R to consumer C_2 reach a bottleneck, and are inaccessible to the top trophic level P. All increases in productivity result in increases in C_2, with no change in density of any other member of the food web module (Figure 4.3). In essence, C_2 is the better competitor in the intermediate consumer trophic level, due to the preferential feeding of P on C_1. The intermediate consumer trophic level (specifically, C_2) controls increases in productivity because of an energetic bottleneck in the pathway to higher levels ($C_2 - P$).

The situation becomes more interesting if we relax the assumption of inedibility or predator specialization by allowing P to consume C_2 but still strongly prefer C_1 ($\Omega_{PC1} = 0.9$). The results in such a case are largely the same as in the previous example since the flow of energy is still effectively disconnected from the top predator; most of the energy goes to increasing C_2 (Figure 4.4). However, the weak $P - C_2$ connection allows P to increase modestly, which
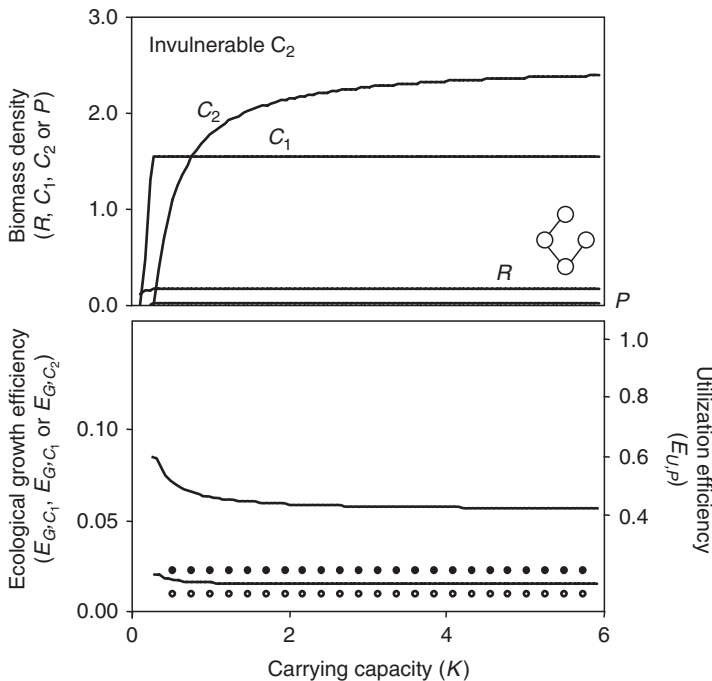
Figure 4.3. Model results showing the effect of a bottleneck (impeded energy transfer) in a food web with an invulnerable intermediate consumer. *Top panel*: Equilibrium biomass densities as in Figure 4.1. *Bottom panel*: Ecosystem metrics as in Figure 4.1. Parameters as in Figure 4.1 except: $\Omega_P = 1.0$.
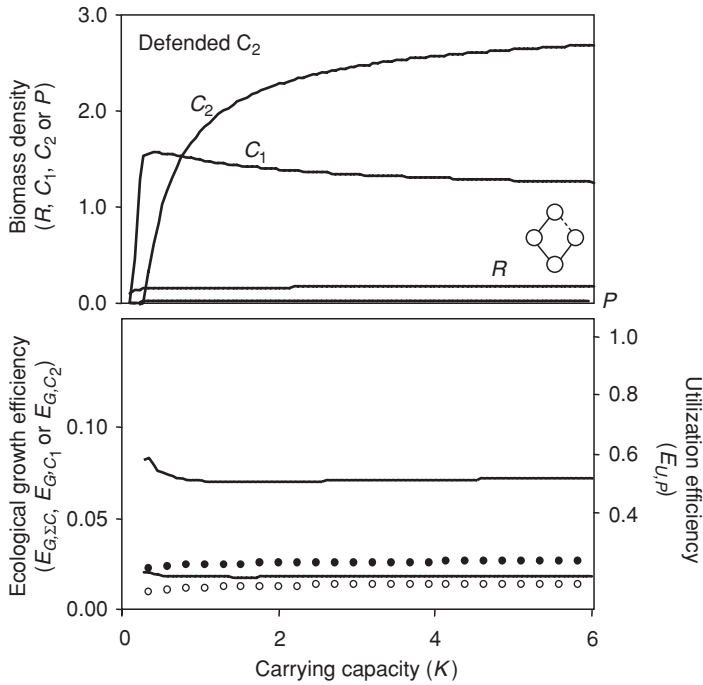
Figure 4.4. Model results showing the effect of a bottleneck (impeded energy transfer) in a food web with a defended intermediate consumer. *Top panel*: Equilibrium biomass densities as in Figure 4.1. *Bottom panel*: Ecosystem metrics as in Figure 4.1. Parameters as in Figure 4.1 with the following exceptions: $\Omega_P = 0.9$.

decreases C_1, which, in turn, allows R to increase slightly. Lindeman's ecosystem metrics show more dramatically how this change to food web structure affects vertical energy flow. $E_{U,P}$ is about half of that in the trophic cascade scenario (Figure 4.2) because P cannot access much of the production of ΣC. $E_{G,\Sigma C}$ is about an order of magnitude lower than in the trophic cascade scenario, reflecting large intermediate consumer populations with slow turnover, symptomatic of bottom-up control. $E_{G,C_1} > E_{G,C_2}$ because C_1 experiences more grazing by P. All three trophic levels increase, but again the largest increase is immediately below the C–P energetic bottleneck. Top-down control is weakened along the pathway that imposes this bottleneck and this is reflected in lower energetic efficiencies.

4.4.2.2 Example 2: Impeding transfer via consumer interference

A second form of bottleneck occurs when the trophospecies comprising a trophic level experience intraspecific (a species interferes with itself) or intratrophic (species at the same trophic level interfere with each other) interference that reduces attack rate. Interference that arises in consumption and influences

attack rates materializes in mathematical models within the functional response. This has been included in a general form by Hassel and Varley (1969) such that attack rates (a) are a function of both resource (R) and consumer (C) density:

$$a_{CR} = Q\frac{R^n}{C^m} \tag{4.6}$$

A specific example of this in which $m = n$ is the ratio-dependent formulation of Arditi and Ginzburg (1989). Both formulations imply that at high consumer densities the per capita rate of energy flow from a resource to its consumer becomes more impeded due to interference. The well-known theoretical result of consumer interference is that increases in productivity are shared as increases in both resource and consumer densities (Getz 1984, Arditi and Ginzburg 1989). Again, top-down control is weakened along the pathway that imposes an energetic bottleneck. The more strongly this bottleneck attenuates the flow of energy to the consumer (reducing $E_{U,\,P}$), the more of that energy remains to produce increases in density directly below the bottleneck (reducing $E_{G,\,\Sigma C}$).

4.4.2.3 Example 3: Inefficient conversion due to lateral energy flow

An energetic bottleneck can also arise when a trophic level is comprised of omnivorous species that feed within their own trophic level (i.e., intraguild or intratrophic predation). The food web now has a lateral flow in addition to the vertical flow assumed in the linear food chain case. To understand how this influences control, we examine the following extreme cases in system (4.1): (a) intraguild predation is strong (C_1 prefers C_2), and; (b) intraguild predation is weak (C_1 prefers R). Both have repercussions relative to the trophic cascade view.

Figure 4.5 depicts the case in which the C_1 consumer feeds preferentially within its own trophic level. Under this scenario, intraguild predation can create two phases of control across the productivity gradient. At low productivity, we see bottom-up control: the resource trophic level is little influenced by intermediate consumers and basal productivity increases go almost strictly to the resource R, with a little going to C_2 and P. During this phase, energy moves up to P largely through the $R-C_2-P$ and the $R-C_2-C_1-P$ pathways. Following trophic cascade theory, the first path leads to increases in R and P, and the second to increases in P and C_2. $E_{U,P}$ is slightly lower than in the trophic cascade model (Figure 4.2), reflecting a weakening of P's top-down control on the intermediate consumer trophic level as a whole. A more dramatic effect is seen in the net growth efficiency of ΣC because much of the production of C_2 is consumed by C_1, and therefore unavailable to P. $E_{G,\Sigma C}$ is consequently lower than in the trophic cascade model and declines further with increasing K as C_2 escapes from top-down control by C_1. The ecological growth efficiency of C_2 alone is relatively high, however, reflecting top-down pressure from both C_1 and P and consequently high turnover of C_2.
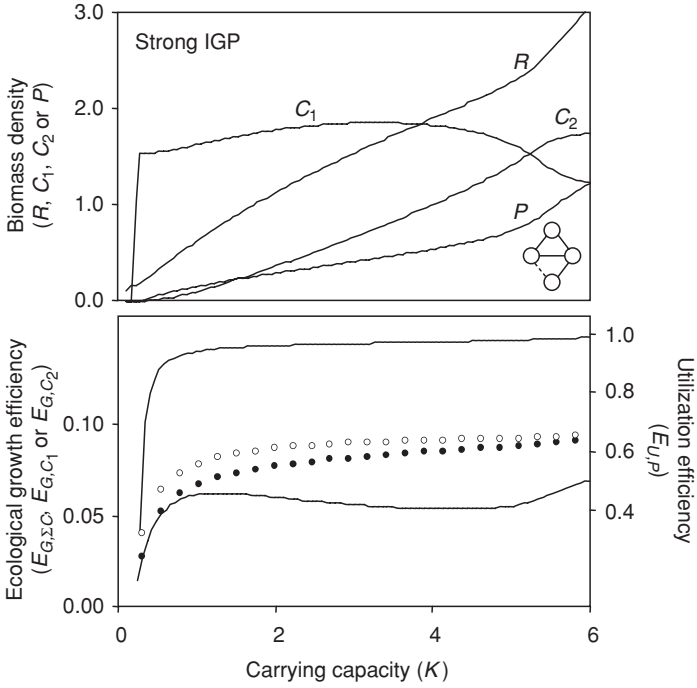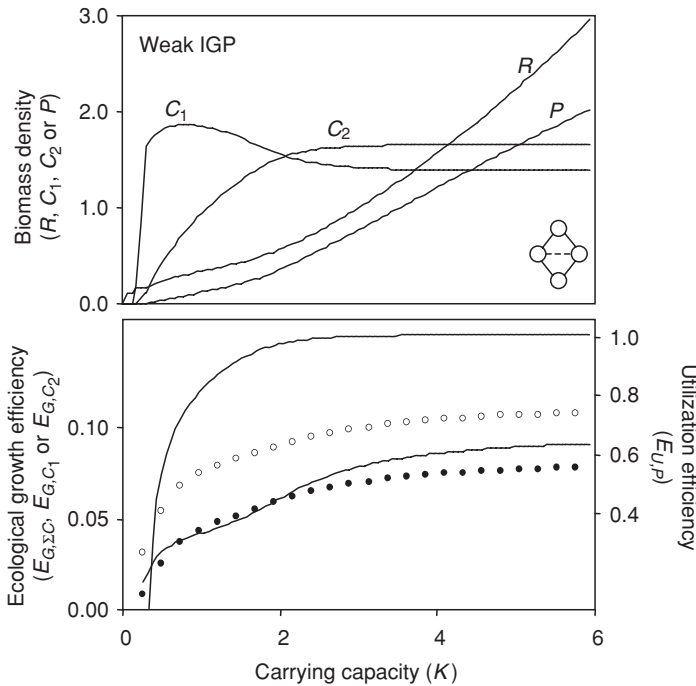
Figure 4.5. Model results showing the effect of a bottleneck (inefficient energy conversion) in a food web with strong intraguild predation. *Top panel*: Equilibrium biomass densities as in Figure 4.1. *Bottom panel*: Ecosystem metrics as in Figure 4.1. Parameters as in Figure 4.1 except: $a_{C1} = 3$; $a_{C2} = 3.5$; $\Omega_{C1} = 0.1$.

As R reaches higher densities the $R-C_1$ pathway becomes more important regardless of C_1's preference for C_2. Soon, the C_1-C_2 pathway is marginalized and the $R-C_2-P$ food chain and the $R-C_1-P$ food chain are responsible for relatively unimpeded vertical energy flow. Hence, we see reassertion of top-down control in very productive environments. High productivity enables enough energy to bypass a lateral flow bottleneck to produce a classic trophic cascade and $E_{U,P}$ and $E_{G,\Sigma C}$ start to return to the values seen in the trophic cascade model.

Figure 4.6 depicts the case of weak intraguild predation. Here, like the high-productivity phase of the case above, we see something analogous to a weak trophic cascade. Most increases in productivity go to R, not P. So, even a weak lateral flow due to predation within a trophic level can reduce the strength of the trophic cascade.

4.4.2.4 Example 4: Inefficient conversion due to density-dependent attrition

Negative interactions that do not influence attack rates (Example 2) and do not involve intraguild predation (Example 3) are most simply and frequently

Figure 4.6. Model results showing the effect of a bottleneck (inefficient energy conversion) in a food web with weak intraguild predation. *Top panel*: Equilibrium biomass densities as in Figure 4.1. *Bottom panel*: Ecosystem metrics as in Figure 4.1. Parameters as in Figure 4.1 except: $a_{C1} = 3$; $a_{C2} = 3.5$; $\Omega_{C1} = 0.9$.

modeled as density-dependent losses in biomass (McCann et al. 1998). This describes phenomena that tend to dissipate the energy obtained by a trophic level before that energy can be passed up to higher trophic levels. The physiological expense of parasites and pathogens is a good example of this: while the amount of energy ingested by a disease organism may be negligible, the total energy lost to the host (e.g., immunoresponse, avoidance behavior, impaired digestion) is much larger (Polis and Strong 1996). Energy expenditure may also be increased by factors intrinsic to the trophospecies (e.g., competition for territory), or by trait-mediated interactions with other trophospecies. There are many examples of trait-mediated interactions in the literature on optimal foraging (Abrams 1993b, Abrams et al. 1996).

For a single species C, density-dependent attrition may be modeled with a $-C^2$ term. For two species (say, C_1 and C_2) this may be modeled similarly as $-C_1C_2$ (McCann et al. 1998). The result of this type of differentiation are well known and are not distant from Example 2. Increases in productivity are shared by both consumer and resource. At low densities of consumer the results are biased towards larger increases in the consumer (top-down) while at high

densities of the consumer results are biased towards larger increases in resource (bottom-up).

4.4.2.5 *Example 5: Inefficient conversion due to nutrient limitation*

An important criticism of most energetic representations of food webs concerns the role of inorganic nutrients: nutrients are not energy, and are poorly represented as another trophic level below plants (Polis and Strong 1996). The ultimate source of energy in most food webs is the sun; the key role of nutrients is in governing the rate at which the sun's energy is fixed into producer biomass. Nutrient concentrations and stoichiometry and are thus better represented in system (4.1) as parameters influencing K and r, rather than as state variables.

Nutrient limitation can also be a source of energetic bottlenecks in consumer trophic levels. In a simplified sense, energy assimilation or conversion by consumers may be limited by low resource quality (Sterner and Hessen 1994). Consumer attack rates are not directly affected, but consumers are constrained in their ability to convert ingested food into their own biomass. This is analogous to Example 4 above, in that only a fraction of the energy removed from R is available to C.

The range of responses to increasing productivity, then, depends on how the limiting nutrient increases with increasing productivity (e.g., DeAngelis 1992). If a consumer requires a single limiting nutrient that does not increase with K, no additional resource production can be transformed into consumer biomass, and increases in productivity will produce increases only in R. A more likely situation involves multiple limiting nutrients that increase with K in some complex way; in this case, increases in productivity are shared by the consumer and resource (Moe et al. 2005).

4.4.3 Re-establishing top-down control: Alternative pathways for the vertical flow of energy

The previous section was primarily concerned with how energetic bottlenecks arise due to interactions among trophospecies, and how different food web structures can thus be expected to weaken top-down control. Other phenomena can influence the balance of top-down and bottom-up control in food webs. In some cases, this is because energy is transferred along pathways not represented in system (4.1), and can effectively circumvent energetic bottlenecks in those pathways. We now turn to three previously investigated cases as examples.

4.4.3.1 *Example 6: Omnivory*

In most real food webs, energy is not so simply coupled between successive consumer trophic levels as implied in system (4.1). For example, many consumers feed at more than one trophic level, obtaining energy along pathways not represented in this system. In an energetic context, these pathways have

two main implications. First, omnivorous feeding links increase the energy potentially available to the omnivorous consumer. Second, these feeding links provide pathways for energy flow that circumvent the traditionally recognized sequence of energy transfers, extending the regulatory influence of a trophic level beyond those immediately adjacent.

The energy potentially available to an omnivorous consumer increases by about a factor of 10 for every trophic level "skipped," although the actual benefit may be much smaller. In system (4.1), for example, the productivity of R is about ten times that of C, so P can double its resource base by replacing 10% of its diet with R. There may be great advantages to predators feeding at the higher trophic level, however: when top predators are forced to feed at lower trophic levels, prey may be less energy dense (e.g., plants or small invertebrates with a higher proportion of exoskeleton) and are often smaller, so each feeding bout provides a smaller energetic return. In size-structured food webs, feeding itself can become energetically unfavorable when prey are too small, and predators can become stunted (e.g., fish in lakes with limited prey selection; Trudel et al. 2001, Sherwood et al. 2002). If higher trophic level prey are of relatively high quality and freely available, the purely energetic benefit of omnivory is dubious. Stated more generally, animals are usually well adapted to feeding on only a subset of all possible prey species. Nonstandard prey can be an important source of essential nutrients (e.g., Matsumura et al. 2004), but the net energetic benefit and the potential for trophic control may often be small.

The converse of R's energetic importance to P is the potential for top-down control of R by P. This can be important if the attack rate of P on R is comparable to that of C on R (i.e., a_{PR} is not $<< a_{CR}$), but a_{PR} will approach a_{CR} only if P has a substantial source of energy in addition to that obtained from C. In the absence of such a subsidy to P, the productivity of P is constrained to be much less than (about one tenth) that of C, and attack rates will be similarly smaller. The resource, R, may itself provide this subsidy, but only if the energetic return to P from feeding on R approaches that from feeding on C. As discussed above, this is unlikely to be the case in any size-structured food web. Another form of subsidy to P (e.g., allochthonous inputs) could augment the density of P and increase its ability to exert top-down control on R (Polis and Strong 1996, Polis et al. 1997).

A more important effect of omnivory, at least in the present context, is as an alternative pathway for energy flow. We can imagine this in system (4.1) if we permit P to feed on C_1, C_2, and R. A bottleneck that reduces the flow of energy from C to P (e.g., defended or inefficient C) will weaken top-down control. The energetic benefit of feeding strictly on C_1 and C_2 is reduced, and P may gain some net benefit from including R in its diet. Omnivory can thus augment densities of P and reestablish top-down control. This sort of alternative pathway will not alleviate a bottleneck due to saturated P or low-quality R.

4.4.3.2 Example 7: Stage structure and life history omnivory

Another form of omnivory involves ontogenetic shifts in resource or habitat use, such that as a consumer individual matures from juvenile to adult the consumer species changes what it feeds on (Werner and Gillam 1984, Mittelbach et al. 1988). A single taxonomic species may thus inhabit two (or more) trophospecies in different parts of its life cycle. We can imagine an example of this in system (4.1) if we consider C_1 to be the juvenile form of P. As individuals in C_1 mature, they move their stored energy (as biomass) to P. This process represents a nontrophic flow of energy that can circumvent a bottleneck between C and P. This flow is also potentially more efficient than a strictly trophic transfer of energy. All of the successfully maturing C_1 biomass is added to P, without the losses associated with imperfect conversion of assimilated prey.

Mittelbach et al. (1988) have shown that this form of differentiation can lead to different trophic control depending on which stage of the consumer is most limited. For example, if the juvenile stage is limited (say, C_1 is subject to an energetic bottleneck like nutrient limitation) and increasing productivity increases recruitment (begins to remove the bottleneck) then these increases in productivity are efficiently transferred to the adult stage (P) and the system experiences stronger top-down control. However, if the adult stage is limited, increasing productivity that favors juveniles does not eliminate the bottleneck and the system is best described by bottom-up control. McCann and Yodzis (1998) have shown this using a stage-structured fish model in which juveniles and adults feed on different resource bases.

In general, stage-structured omnivory provides an efficient, alternative pathway to energy flow between consumer trophospecies. If energy is already flowing smoothly between these trophospecies, this alternative linkage will simply increase transfer efficiency, resulting in a higher biomass of P per unit C produced. If there is some impediment to the efficient conversion of ingested C into P (e.g., inefficient feeding in P), this alternative pathway will tend to alleviate that impediment and strengthen top-down control. Similarly, if trophic energy transfer between these trophospecies is impeded (e.g., saturated P), this alternative pathway will reestablish a smooth flow of energy and strengthen top-down control.

4.4.3.3 Example 8: Allochthonous inputs

Sources of energy external to the food web under study are another way to circumvent an energetic bottleneck. If this energy is in the form of a basal resource (R_2) available to all primary consumers, or additional prey (C_3) available to all predators, the result is the well-known "apparent trophic cascade" (Polis and Strong 1996, Polis et al. 1997, Moore et al. 2004). In the absence of energetic bottlenecks, this allochthonous energy flux travels to the top of the food web and supports the typical pattern of alternating increases

associated with the trophic cascade. Trophic levels below the top predator may be suppressed to densities below what they would be in the absence of the allochthonous input, because this additional energy supports more top predators than would otherwise be possible.

How allochthonous inputs interact with the energetic bottlenecks described above depends entirely on where in the food web the input is received, relative to the location of the bottleneck. An allochthonous input available to an inedible prey trophospecies (C_2 in Example 1) would benefit only that trophospecies. Figure 4.7 shows the result of an allochthonous input above a bottleneck: a defended prey trophospecies (C_2) prevents R and P from responding to increasing K (Figure 4.4), but a small subsidy to P reestablishes top-down control and permits a trophic cascade (Figure 4.7). Efficiencies of energy transfer and conversion are restored to the high values observed in the trophic cascade model.
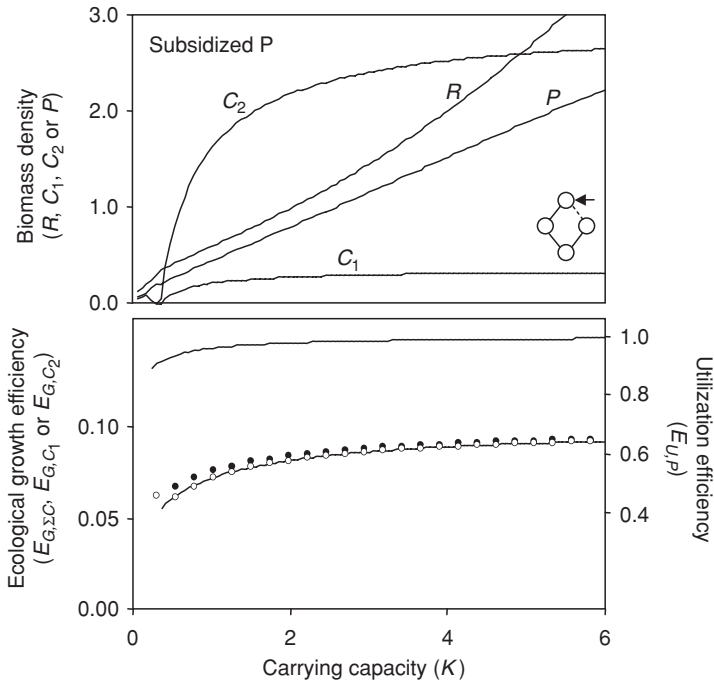
Figure 4.7. Model results showing how an allochthonous subsidy to P can circumvent a bottleneck (impeded energy transfer) in a food web with a defended intermediate consumer. *Top panel*: Equilibrium biomass densities as in Figure 4.1. *Bottom panel*: Ecosystem metrics as in Figure 4.1. Parameters as in Figure 4.1 except: $\Omega_P = 0.9$; subsidy to $P = 0.001$.

4.5 DISCUSSION

There is a long-standing debate over what controls trophic level biomass within natural ecological communities. Some have argued that food webs are generally controlled by predation (Hairston et al. 1960, Oksanen et al. 1981, Carpenter et al. 1985), while others have argued that food webs are generally controlled by resources (Elton 1927, Lindemann 1942, White 1978). The emerging consensus is that communities are co-limited by both predators and resources (Getz 1984, Arditi and Ginzburg 1989, McQueen et al. 1989, Leibold 1989, Strong 1992). One of the major problems facing ecologists is to detail under what conditions should the relative influence of different forms of control change in a natural community (Hunter and Price 1992). Although a number of interesting review papers have been produced on this topic (e.g., Strong 1992, Polis and Strong 1996, Berlow et al. 2004), attempts at a theoretical synthesis are still rare (e.g., Abrams 1993a, Borer et al. 2005). We believe that energetic reasoning provides a useful framework within which to develop such a synthesis.

Not surprisingly, our analysis shows that phenomena that impede the transfer of energy between trophic levels weaken or truncate top-down control between these levels (Kemp et al. 2001, Ruesink et al. 2002, deBruyn et al. 2004). In the simple food web examined here, this produces an increase in the trophic level below the bottleneck and a trophic cascade below that. Specialist predators and defended prey are widespread phenomena that can produce this type of bottleneck (Chase 1999, Vos et al. 2004). Vertical transfer of energy can also be impeded if predators become saturated (Kemp et al. 2001) or otherwise prevented from consuming all available prey production (e.g., by interference from other species at the same or other trophic levels), or if prey are spatially or seasonally unavailable to predators (Ruesink et al. 2002, deBruyn et al. 2004).

Phenomena that inhibit the efficient conversion of energy within a trophic level weaken top-down control by attenuating the energy available to the next higher trophic level. This type of bottleneck will most often lead to increases in productivity being shared by all trophic levels. Negative interactions among members of a trophic level that lead to higher energy expenditures, and thus leave less energy for production, can include territorial displays, interference competition for prey, or any other kind of agonistic interaction. Many strong nonfeeding interactions also fall into this category, including parasite and pathogen effects on consumer physiology.

Finally, phenomena that act to circumvent the bottlenecks described above can reestablish the vertical flow of energy and permit strong top-down control. If a species above a bottleneck obtains an energy subsidy (e.g., via omnivory or allochthonous inputs), the limitation imposed by the bottleneck may be partially or completely obviated.

Our analysis leads to a number of general predictions for patterns of trophic control within and among food webs:

1. Food webs with unimpeded vertical flow of energy ought to be dominated by predation. The characteristics of such webs include generalist predators, undefended prey, no strong density dependence in any consumers and no substantial omnivory. Specialist predators, or those faced with well-defended prey, ought to have weak control over the next lower trophic level. In the absence of other bottlenecks, trophic control will be strong below this link. Webs with intraguild predation can experience a range of trophic control depending on environmental productivity. In low-productivity environments, such webs ought to be bottom-up controlled, whereas high-productivity environments should support strong top-down control.

2. Nontrophic (or not purely trophic) interactions can also cause bottlenecks: parasites and pathogens increase expenditures and losses of energy, mainly because of how they change the energy budgets of host populations, rather than for the energy they themselves assimilate. Species that have heavy parasite or pathogen loads will transfer energy inefficiently to their predators, and should not experience strong top-down control.

3. Pathways that tend to subsidize top predators (especially allochthonous inputs to P) should permit top-down control even in the presence of the bottlenecks described above.

These general predictions could be tested by a series of experiments to map out the types of food webs, and the locations within these webs, where we tend to find strong top-down control.

The benefits of modeling within an energetic framework are considerable (Yodzis and Innis 1992, Berlow et al. 2004). Energy provides a common currency with which to link different levels of biological organization, making it possible to quantitatively integrate information from studies in physiology, population, community, and ecosystem ecology. Energetic parameters have been well studied and often quantified, and can thus be used to put realistic limits on possible interaction strengths. As well, energy flows are concrete phenomena, and may be more accessible to nonmathematical ecologists than more abstract representations of interaction strength. We suggest that future work will benefit from a consideration of the energetic consequences of all forms of interspecific interactions.

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CHAPTER 5

EXPERIMENTAL STUDIES OF FOOD WEBS: CAUSES AND CONSEQUENCES OF TROPHIC INTERACTIONS

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5.1 ABSTRACT

This chapter reviews some of what we have learned from experimental studies of food webs conducted in an assortment of natural and constructed systems. The main themes are the roles of energy and other factors in determining food chain properties, the consequences of omnivory for the dynamics of omnivores and their prey, and the impacts of food web complexity on population and community dynamics. Throughout, I emphasize the important interplay between the roles of theory and experiment in advancing our knowledge of community ecology. I also describe other key phenomena that remain poorly integrated in food web theory and that also require much additional experimental work. These areas include the development of inclusive frameworks for ecological networks that incorporate nontrophic interactions, such as some mutualisms, and the incorporation of evolutionary dynamics in the consideration of food web architecture.

5.2 INTRODUCTION

It seems particularly fitting to reflect here on a few of the many important ideas that Peter Yodzis developed about the structure and functioning of the complex ecological networks that we call food webs. Yodzis' *Introduction to Theoretical Ecology* (1989) provided a comprehensive summary of many of the still unanswered (or partially answered) questions about food web organization at a time when ecologists had a renewed interest in using experiments and observations to explore the properties of ecological networks. The food web literature has proliferated to the point where a single book chapter cannot even begin do it justice, and readers should consult the recent book by de Ruiter et al. (2005) for a comprehensive survey of recent advances. Consequently, this chapter focuses on a select subset of food web questions that interest me, drawing on problems that my students and I have worked on, as well as on related studies conducted by others in other systems.

5.3 ENERGY AND OTHER FACTORS AFFECTING THE LENGTH OF FOOD CHAINS

Yodzis (1989) pointed out that what once seemed like a well accepted and intuitively satisfying explanation for the apparently short length of food chains, the inefficiency of energy transfer between trophic levels, fell into disfavor in the fourth quarter of the twentieth century. The problem was twofold. First, simple models of food chains suggested an alternative cause, specifically the reduced dynamic stability and slow recovery from perturbations that seemed to characterize longer model chains (Pimm and Lawton 1977, 1978). It was subsequently suggested that this prediction was an artifact generated by confounding the frequency of stabilizing density-dependent population regulation with the length of model food chains (Sterner et al. 1997), but not before a number of experimental studies had already been done to test the predictions of the theory. Second, although inefficiency of energy transfer would predict the existence of longer food chains in more productive environments, there was little empirical support for this pattern. If anything, some of the longer food chains and more complex food webs seemed to occur in less productive situations, rather than in the most productive environments (Pimm and Lawton 1977, Pimm 1982). This apparent inconsistency must be tempered by the realization that there were very few detailed descriptions of any food chains or webs at the time (see Cohen 1978). The relatively small number of highly resolved food webs that have since accumulated (e.g., see Winemiller 1990, Martinez 1991, Dunne et al. 2002) suggest that the empirical data used to motivate these theoretical studies were imperfect at best. Nonetheless, if food chains really were shorter than one might predict from gross patterns of energy availability, an explanation was required.

Empirical studies designed to evaluate the roles of energy limitation or population dynamics in limiting food chain length take two forms. One kind

of study examined the consequences of increasing or decreasing the availability of energy for food web development, while monitoring the structure of simple food chains consisting of rapidly growing organisms. If more energy allowed longer food chains to develop and persist, it would seem plausible for ecological energetics to play some role in controlling food chain length. Such studies have a few key requirements. First, the organisms must reproduce sufficiently rapidly that responses to alterations in energy availability would be readily apparent over the short time scales that characterize most ecological experiments. Second, alterations of energy availability would have to be sufficiently large to ensure that a change at the bottom of the food chain would propagate up the chain and alter the number of trophic levels that manage to persist. The basic theory underlying this idea has been developed by Fretwell (1977) and Oksanen et al. (1981, see Figure 5.1). Given the common rule of thumb that efficiency of energy transfer between trophic levels is about 10%, energy availability would have to be manipulated by over an order of magnitude (e.g., at least tenfold) if one reasonably expected to see the addition or loss of a top trophic level. Third, it is essential to be able to clearly place the organisms involved on particular trophic levels—this means that relatively linear food chains without substantial omnivory are required. A remarkably small number of experiments satisfy all of these requirements, but they do suggest that energy can play an important role in determining food chain length.

Jenkins et al. (1992) tested the effects of variation in productivity on the relatively simple food webs that develop in water-filled tree holes in tropical Australia. The longest food chains in naturally occurring tree holes were re-solved to four trophic levels, (1) detritus, primarily leaf litter that falls into the tree holes and forms the basal trophic level and main source of energy that supports the food chain, (2) larval mosquitoes and chironomid midges, (3) larvae of a predatory midge, *Anatopynia*, and (4) predatory tadpoles of the frog *Lechriodus fletcheri*. Jenkins et al. exploited the convenient fact that typical tree hole food webs will develop in small water-filled plastic containers placed near the trees. Jenkins et al. (1992) examined patterns of food web development over a range of experimentally manipulated levels of productivity that varied over 2 orders of magnitude, including levels of detritus input that were natural, $0.1 \times$ natural, and $0.01 \times$ natural, in other words, a reduction in productivity that should result in the loss of at least one trophic level from the top of the food chain. Food chain development was followed for 48 weeks, long enough so that even relatively long-lived top predators would have sufficient time to respond to energy reductions. Decreasing productivity reduced the number of coexisting species, the number of trophic links, and maximum food chain length. There seemed to be clear evidence that energy played a role in limiting food chain length in this system.

Kaunzinger and Morin (1998) used a simple microbial system to test for effects of productivity on food chain length. In the longest three-level food chains the basal level was the bacterium *Serratia marcescens*, which was consumed by

the ciliated protist *Colpdium striatum*, which was in turn consumed by the top predator, the ciliate *Didinium nasutum*. As constructed, the system is without any omnivorous species, so the trophic position of each species is known without error. The species all have generation times from a minimum of about 30 minutes for *Serratia*, to about 6 hours for *Didinium*, so population-level responses to productivity are rapid. Productivity was manipulated by varying
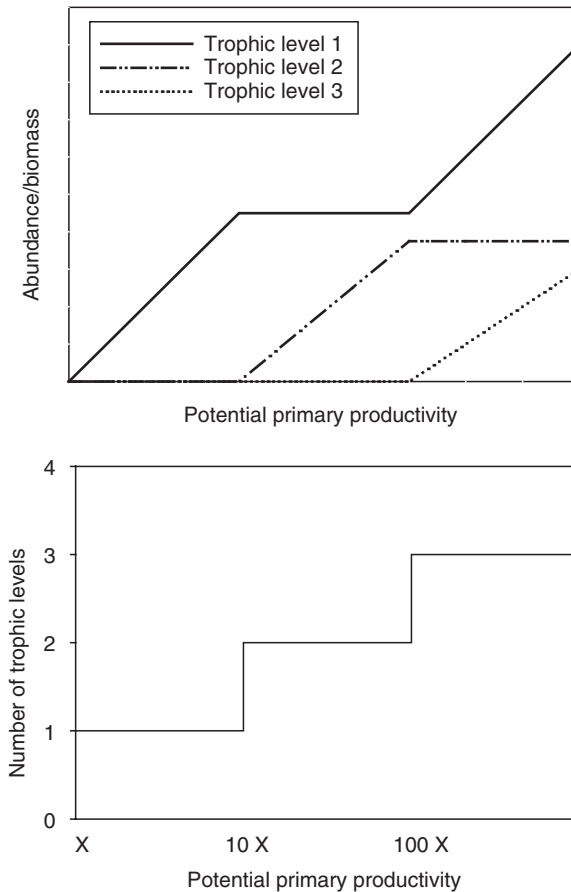

Figure 5.1. Potential effects of energy (productivity) on the abundance of organisms on different trophic levels with consequent effects on food chain length. Ideas here follow generally from Fretwell (1977) and Oksanen et al. (1981). In the *bottom panel*, X refers to the mimimal level of productivity required to support a positive population density in the basal trophic level, level 1. Assuming a 10% efficiency of energy transfer between trophic levels and similar energetic requirements across trophic levels, a second trophic level is added with an order of magnitude increase in productivity (10 X), and a third trophic level is added when productivity increases by two orders of magnitude (100 X). Different efficiencies of energy transfer, or minimal amounts of energy required to maintain a viable population in each trophic level, would produce different patterns of transitions.

the concentration of nutrients in the medium that are consumed by the bacteria. Three-level food chains, those containing the top predator *Didinium*, only persisted at higher levels of productivity (Figure 5.2). At lower levels of productivity the top trophic level failed to persist. This pattern also provides clear support for the role of energy transfer in limiting the length of relatively simple linear food chains. Patterns of change in the abundance of species on each trophic level are also consistent with simple prey-dependent models of predator–prey interactions (e.g., Leibold 1996), but are not consistent with ratio-dependent models (e.g., Abrams and Ginzburg 2000).

Evidence for comparable patterns in natural systems remains elusive, in part perhaps because of the technical difficulties in unambiguously assigning species to trophic levels or measuring productivity. For example, Post et al. (2000) failed to find a relationship between food chain length and productivity in a survey of natural lakes, but did find that larger lakes tended to support longer food chains, a pattern that appeared to be independent of differences in productivity among lakes. Their finding is superficially similar to the idea that larger predators located higher in the food chain should require larger home ranges to collect the necessary amount of energy to persist (Slobodkin 1960). The pattern reported by Post et al. (2000) relies on the indirect measurement of the trophic
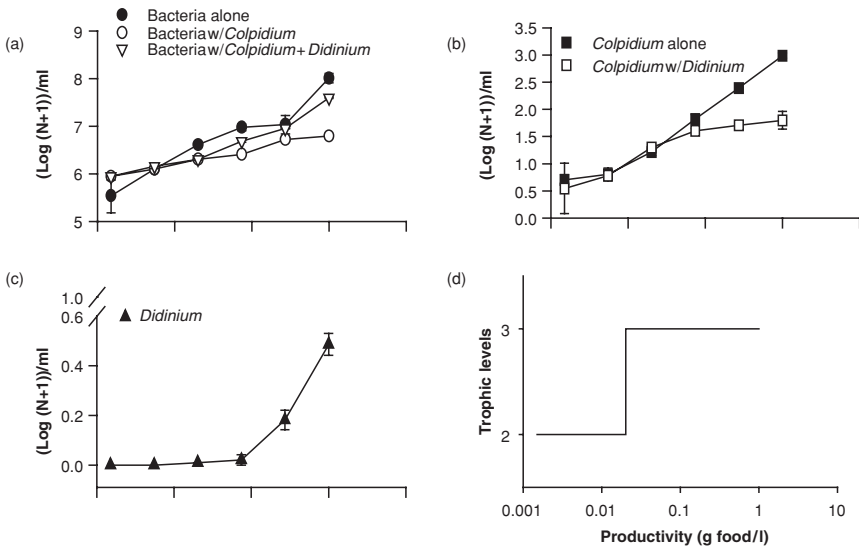
Figure 5.2. Effects of experimental manipulations of productivity (concentration of nutrient medium) on simple linear microbial food chains (Kaunzinger and Morin 1998). Patterns of abundance of organisms on different trophic levels are largely consistent with the predictions of simple models for (a) the basal level (bacteria), (b) trophic level 2, *Colpidium*, and (c) trophic level 3, the top predator *Didinium*. (d) Food chain length displays an integer increase from two to three as productivity increases beyond the two lowest levels of productivity.

position of top predators, rather than on knowledge of the entire food chain. They used stable isotope ratios to infer the maximum trophic level of various fish species in their sample of lakes. Using this approach they found that the same species of top predator, in this case the lake trout, occupied trophic position 4 in smaller lakes and trophic position 5 in larger ones. This could happen if a new intermediate trophic level was inserted into the food chain in larger lakes, but direct evidence for this insertion, or a mechanistic explanation for why it should happen as a function of lake size, is wanting. Post et al. (2000) and Post (2002) have suggested that the dependence of food chain length on energy inputs shown by Jenkins et al. (1992) and Kaunzinger and Morin (1998) may be a feature of relatively unproductive systems, although that conjecture remains untested.

The other approach used to evaluate links between population dynamics and food chain length involves comparisons of the dynamics of species that occur in webs of differing length. This approach is subject to the first two requirements listed above for studies of energy limitation and food chain length. Population dynamics must be sufficiently rapid so that differences can be observed, and species should be readily assignable to known trophic levels to ensure that differences in food chain length occur. Again, there are relatively few studies that fit the bill. These rely on using a statistical signature of population dynamics that would be consistent with the decreasing stability of populations in food chains of increasing length. That signature is an increase in the temporal variation in population size, measured either as the standard deviation of the logarithm of population size over time, or the coefficient of variation of population size over time (see Morin and McGrady-Steed 2004, Cottingham et al. 2001). If the models are correct, population dynamics should be more variable in longer chains, and that increased variation should lead to higher values of temporal variability for the same species embedded in longer food chains. Lawler and Morin (1993) found that the population dynamics of protists in relatively simple laboratory food chains become more variable with modest increases in food chain length. Comparisons of the temporal variability of populations of the same bacterivorous protists in short food chains where the bacterivores were the top predators, and in food chains that are just one trophic level longer where the bacterivores are intermediate species preyed on by another predatory protist point to increased temporal variation in abundance in the majority of longer food chains. Increased temporal variation in abundance would be consistent with longer return times in longer food chains, as suggested by Pimm and Lawton (1977).

There is also reason to suspect that energy and population dynamics can interact in ways not directly considered by Pimm and Lawton (1977), as described in earlier models by Rosenzweig (1971) in the context of the "paradox of enrichment." Rosenzweig found that a number of different predator–prey models became increasing unstable as systems were made more productive—a consequence of increasing rates of increase or carrying capacities in the

models. In this scenario, adding energy to a simple food chain might destabilize the system, and create a shortening of the chain. Of course it is possible that the addition of another trophic level to an energetically enhanced chain could offset the destabilizing effects of enrichment, though the findings of Pimm and Lawton (1977) might argue against this. However, addition of weakly interacting species to the food web has been suggested to confer increased stability on unstable systems (McCann et al. 1998), so some kinds of increased trophic complex may help to offset the predicted destabilizing effects of enrichment.

There is surprisingly little empirical support for the kinds of dynamical responses predicted by the paradox of enrichment. Experimental manipulations of productivity in relatively simple aquatic food webs have suggested clear destabilizing effects of enrichment on population dynamics (McCauley et al. 1999), although such responses fail to appear in more complex aquatic food webs, particularly where competition between edible and inedible algae decouples effects of enrichment from consumers higher in the food chain (McCauley and Murdoch 1990). Analogous findings come from laboratory studies of simple microbial food chains that become more stable as the availability of food is reduced (Luckinbill 1974). It is possible that the models that predict destabilization as productivity increases are too simple to capture the dynamics of complex natural systems.

True to form, Yodzis (1989) suggested another possible response of food webs to enrichment, the idea that increased availability of energy might allow food webs to become broader rather than longer, specifically by allowing more parallel food chains to persist in more productive environments. To my knowledge, this hypothesis has not been explored either by examination of empirical food web patterns, or by modeling. It remains an interesting idea.

5.4   FOOD WEB COMPLEXITY AND STABILITY

Other ideas related to the stability and complexity of food webs have also received some attention from experimental ecologists. The tension between qualitative assertions that more complex systems seem more stable (Elton 1958) and quantitative modeling suggesting the opposite (May 1972) reflects some confusion about whether stability refers to the dynamics of the entire system or the component populations. As King and Pimm (1983) pointed out, increasing complexity can increase the stability of the aggregate properties of the entire food web, while decreasing the stability of some of the component populations. Evidence consistent with this aggregation-contingent set of predictions comes from a variety of sources, including terrestrial plants (Tilman 1996) and microbes (Naeem and Li 1997, McGrady-Steed et al. 1997). In some analyses, there is no clear relationship between the complexity of the system and the stability of component populations (McGrady-Steed and Morin 2000).

   Few studies have directly examined whether systems of increasing complex-
ity are more likely to be unstable in the sense that some populations in those
systems are more likely to go extinct as systems become more complex.
Lawler (1993) provided one direct test of this idea, and the patterns that
she found are in fact consistent with the theory developed by May (1972).
When four different stable predator–prey species pairs (2-species systems) are
combined to form 4-species systems, these more complex systems tend to
show increased frequencies of species extinction. When all four stable species
pairs are combined to form an 8-species system, extinction rates increase
further (Figure 5.3). In other situations, increasing the complexity of a single
trophic level, the prey, seems to increase the stability of a single species on a
higher trophic level (Petchey 2000). Obviously, much more work needs to be
done to determine whether there is a consistent effect of complexity on the
stability of entire systems or their component populations. Again, theory
suggests that the effects of increased complexity may depend importantly on
the way that species interact. In particular, weakly interacting species may
tend to stabilize interactions between strongly interacting species (McCann
et al. 1998).
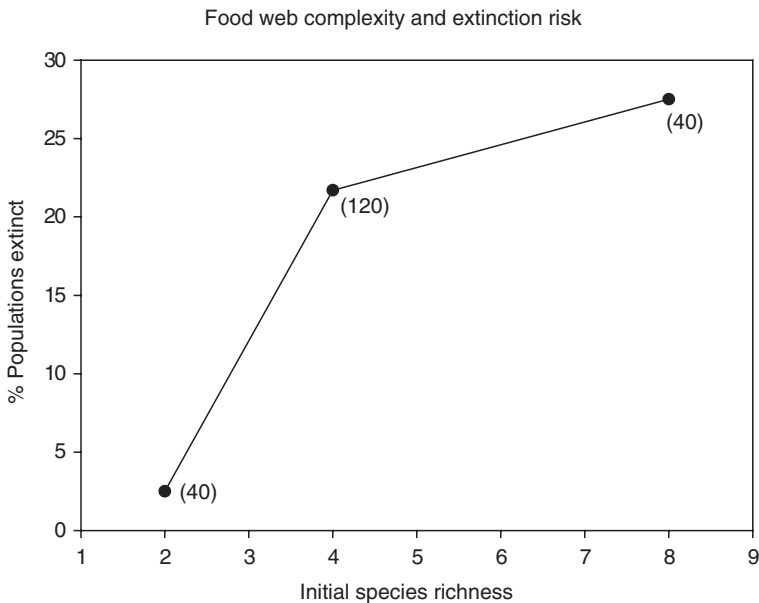
Figure 5.3. Effects of food web complexity on the fraction of populations going extinct within
experimental food webs. Numbers in parentheses refer to the total number of predator and prey
populations at each level of complexity on which extinction frequencies are based. Data from Lawler
(1993).

5.5   OMNIVORY AND ITS CONSEQUENCES

Another generalization based on the early models of Pimm and Lawton (1977, 1978) was that omnivory, defined as feeding on more than one trophic level, seemed to destabilize the majority of model food chains. This prompted considerable debate about the commonness or rarity of omnivory in natural systems (Pimm 1982, Polis 1991), a debate to which Yodzis (1984) contributed. As in the case for the factors that influence the length of food chains, there has been rather little direct experimental study of the population dynamics of omnivores, and much of what has been done has focused on species that are intraguild predators (sensu Polis et al. 1989). These few studies, mostly of microbes (Lawler and Morin 1993, Morin and Lawler 1996, Morin 1999, Diehl and Feissel 2000, 2001, Price and Morin 2004), but also of arthropods (Borer et al. 2003), are broadly consistent with the prediction that the identity of dominant species in an intraguild predation community module will shift with changes in the productivity of the system. Some features of these systems are also consistent with predictions of reduced *system* stability (some species go extinct), although the omnivores themselves often display highly stable dynamics by virtue of their ability to switch to other resources in the event that one of their prey species is lost. More recent theoretical work (McCann and Hastings 1997) has shown that while web model with omnivory are often unstable in the strictly mathematical, in that they do not settle down to a point equilibrium after perturbation, omnivory can reduce chaotic dynamics and move cyclic population dynamics away from very low values that may promote extinctions.

   The other interesting consequence of omnivorous intraguild predation interactions is that they can produce priority effects that shift the identity of dominant species in ways that depend on system productivity and the sequence of species entry into the system (Holt and Polis 1997, Morin 1999, Borer et al. 2003, Price and Morin 2004). The role of such historical contingencies in generating variation among natural communities seems potentially great, but such interactions remain little explored by field experiments.

5.6   PATTERNS OF ASSEMBLY, INVASION, AND SPECIES RESPONSES TO PERTURBATIONS IN FOOD WEBS

There are a number of other features of food web organization that are gradually yielding to experimental study, although in many cases the theoretical framework for these phenomena remains incompletely developed. An issue related to the stability of systems of varying complexity discussed above is how such complex systems will respond to externally driven perturbations, such as directional environmental changes caused by temperature (global warming) or nutrient loading (eutrophication). Some effects of enrichment have already been described in the context of the determinants of food chain

length. Responses to directional change in temperature appear to be complicated by trophic interactions that make simple predictions based on the physiological envelope approach unrealistic (Davis et al. 1998, Petchey et al. 1999, Jiang and Morin 2004a). One pattern that emerges from these studies is that food web changes in response to increased temperature are complex, and they are not simply predictable from knowledge of the physiological limits of individual species. Another pattern is that species loss is nonrandom across trophic levels, with species located higher in the food web being at greater risk of extinction (Pounds et al. 1999, Petchey et al. 1999). The reasons for this may not be as simple as the usual correlates of high trophic status, such as larger body size and smaller population size, which are sometimes associated with increased extinction risk via demographic processes.

The ways that food webs gain species, either via invasion or other assembly processes, can also have persistent effects on food web properties. One common pattern that has emerged from observations of natural systems at larger spatial scales is that the number of native and nonnative (invasive) species seems to be positively correlated (Stohlgren et al. 1999, Levine 2000). The tempting conclusion that is sometimes drawn from these observations is that more diverse systems appear to be more frequently invaded than less diverse systems. The problem inherent in making such conclusions is that diversity may simply be correlated with some other factor that drives both the diversity of native and invasive species. Jiang and Morin (2004b) showed how this can happen in relatively simple laboratory systems assembled from a common pool of aquatic microorganisms over a gradient of productivity. As productivity increased, so did the diversity of the local communities that became established. In turn, when these communities were subjected to invasions by two species that were not part of the initial pool of community members, both invaders appeared to perform best in the most diverse (and productive) communities. However after statistically controlling for the correlation between species richness and productivity via partial correlation analysis, it became clear that productivity (and not species richness) was the driving factor that determined the success of these model invaders.

We still know relatively little about the role of historical contingencies in determining the properties of food webs. Recent work by Fukami and Morin (2003) shows that productivity–diversity patterns in relatively simple laboratory food webs can be strongly influenced by the order of species assembly from the same common pool of potential community members. Other ideas invoked to explain the range of productivity–diversity patterns include effects of local and regional processes (Chase and Leibold 2002), interactions between disturbance and competition (Kassen et al. 2000, Buckling et al. 2000), and interactions between consumers, competing prey, and productivity (Leibold et al. 1997, Jiang and Morin 2005). Since a number of different processes can apparently produce very similar patterns, experiments that target the process are essential to sort among competing hypotheses.

5.7 SOME IMPORTANT UNRESOLVED ISSUES, MUTUALISTS AND OTHER NONTROPHIC INTERACTIONS, AND PARASITES

Although there has been a recent renaissance in the theoretical and experimental study of food webs, it is clear that we still have much to learn about how these extraordinarily complex ecological networks assemble and operate. Most of our studies of well-characterized laboratory systems are of systems that are necessarily much less complex than their natural counterparts, but which are often of comparable complexity to the simplest models. We need to explore how increasing complexity might change the properties of natural systems and the theoretical constructs that we use to model them. Food webs also tend to ignore nontrophic interactions like mutualisms, which may confer substantial stability on complex ecological networks (Bruno et al. 2003). Some intriguing preliminary explorations of interactions among species involved in mutualisms point to some fundamental differences in the organization of these interactions, which could in turn have profound implications for the larger ecological networks in which they are embedded (Jordano et al. 2003). Similarly, the inclusion of parasite–host interactions into food webs changes many conclusions that have been made about classic patterns in food web metrics (Huxham et al. 1995, Lafferty and Kuris 2002, Memmott et al. 2000). While we still know relatively little about the role of various processes in driving food web patterns, as Yodzis (1989) so correctly pointed out, "We have made great progress in our understanding of what the issues are." Further progress will require clever experiments in natural and constructed systems, together with increasingly detailed descriptions of natural systems, to sort out where and when various processes contribute in important ways to food web patterns.

5.8 ACKNOWLEDGMENTS

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CHAPTER 6

INTERPLAY BETWEEN SCALE, RESOLUTION, LIFE HISTORY AND FOOD WEB PROPERTIES

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6.1   ABSTRACT

Perhaps the greatest challenge for ecologists is to predict population dynamics and ecological interactions of species-rich systems. In studying food webs of species-rich systems, ecologists necessarily sacrifice much resolution and complexity of the real world. Moreover, species life history strategies interact with environmental variation at multiple scales in space and time to yield variable degrees of density-independent population regulation. Is the quest for predictive food web models too daunting of a challenge? Peter Yodzis clearly recognized and articulated the principal obstacles and parameters of the problem. The indeterminacy of ecological dynamics in species-rich food webs is apparent,

even when species interactions are projected using relatively simple functions. Peter shed much light on the manner in which life history strategies, scale, and resolution in food webs influence population dynamics. Can the taxonomic and ecological diversity of nature be defined in units that permit prediction of population dynamics? This chapter reviews these issues, and briefly describes recent empirical field research in a tropical river designed to reveal food web structure and dynamics based on web modules. Evidence from recent field experiments suggests that, at appropriate scales of resolution, we may be able predict dynamics of some of the major elements of the system. To bridge the gap between food web theory and empirical research, several theoretical and, as importantly, practical issues will require greater attention than they have received in the past.

6.2   INTRODUCTION

The food web provides perhaps the most versatile model for dealing with ecological structures, dynamics, and functions at the community and ecosystem levels. Two fundamental challenges in food web research were clearly articulated by Peter Yodzis: the implications of how we model interaction strength for predicting dynamics in large complex systems, and the effects of scale and resolution on food web patterns and dynamics. According to Yodzis (1988) "the long-term outcomes of press perturbations [i.e., experiments that depress one or more populations to monitor responses by others] are highly indeterminant, in terms of both whether species densities increase or decrease and of which interactions have the largest effects." In a press perturbation experiment, the effect of species i on species j is given by $dN_{ei}/dI_j = -(A - I)_{ij}$, where N_{ej} is the equilibrium density of species i, I_j is the rate of addition of species j, and A is the community matrix. Yodzis further maintained that "predicting those long-term effects not only requires data on the strengths of many interactions in the system, it requires very accurate data on many interaction strengths. This is a daunting prospect indeed." The empirical estimation of variation in interaction strength assumes even greater importance when we consider an additional conclusion from Yodzis's research: "There seems to be some indication, in the case of topological indeterminancy [i.e., inability to predict which species interactions will be present], that the indeterminancy is less severe in food webs that are more finely differentiated in the identification of trophospecies. . . . topological indeterminancy might be in part an artifact of aggregated models" (Yodzis 1988). One way that Yodzis addressed this dilemma was to simulate food web dynamics based on bioenergetics and allometric relationships (Yodzis and Innes 1992). Results from press perturbations simulations were examined as probability distributions of response variables that are skewed relative to expectations-based interactions between a single predator and prey (Yodzis 1998, 2000).

In addition to focusing on equilibrium solutions, the community matrix modeling approach assumes that every species can potentially influence every

other species in the system via the network of interactions, both direct and indirect. This leads us to a very fundamental question: How are food webs structured? The answer is not derived only from the measurement of nature, but also depends on conceptualization of the model. Winemiller and Layman (2005) recently described four alternative concepts of food web structure. Their *spiderweb* model views the network of species trophic interactions as a complex network in which every species influences every other species via direct or indirect pathways. This view of food web dynamics is consistent with community matrix and network models that reveal the relative influence of indirect interactions. Effects from press perturbations might be expected to propagate through the network in a sort of quasiradial fashion in which the magnitude of change is a function of proximity to the source perturbation. Some have questioned the spiderweb model of food webs on the basis that many, or perhaps most, species appear to be influenced by only a few species (Berryman 1993).

Their second model, the *Christmas tree*, views communities as having structural species that are essential in governing production dynamics, environmental conditions, etc., and that also support interstitial species. The latter may constitute a large fraction of species richness, but with relatively little effect on structural species or ecosystem dynamics. Their *onion* model views species' potential to affect other species and the ecosystem as a nested hierarchy in which a group of core species have strong effects on peripheral species. The peripheral species in the most distal layers of the onion would be strongly influenced by, but have the weakest affects on, species populations within interior layers. Their *Internet* model of food webs stresses the importance of network architecture in determining the relative influence of species (nodes) on other species. Species directly connected to highly connected nodes (hubs) have greater potential to influence large numbers of species than those lying at the ends of long chains containing single links. The answer to the question of how food webs are structured will be determined from empirical research.

This chapter briefly reviews some of the fundamental challenges to the empirical study of food webs. Some of these challenges are logistical and, though potentially surmountable, will likely will be met only in studies of relatively small, low-diversity systems and perhaps in a very few systems for which major long-term funding permits detailed investigations of major ecosystem components. The more serious limitations are related to theoretical questions, such as how to define interaction operationally, or how to integrate life history variation or indirect interactions into models of food web dynamics. These kinds of challenges will be more difficult to address. This chapter also summarizes 10 years of research by the author and colleagues on the food web of the Cinaruco River in Venezuela. Highlighted are the many challenges of research on a species-rich system with strong abiotic temporal dynamics and high spatial heterogeneity. Although we are just beginning to understand the structure and dynamics of this tropical ecosystem, the study of web modules (subsets of co-occurring species and resources that interact and influence one

another) has enabled us to predict some patterns and dynamics of important food web elements.

6.3 EMPIRICAL FOOD WEB RESEARCH

Although the comparative study of food webs has generated tremendous interest among both theoreticians and empiricists, progress has been hindered by the quantity and quality of empirical data. To date, most results from comparative food web research have been confounded by biases in the fundamental units of comparison (Paine 1988, Winemiller 1990, Polis 1991). These biases are derived from issues of scale, especially differences in (1) definitions of food web boundaries, (2) definitions of species and feeding links, (3) methods of estimating consumption or species interaction, and (4) the manner in which food web data are reported in the literature. Most food web patterns, such as constant connectance (Martinez 1992), seem to result from the different criteria and methodologies used by field investigators and data compilers rather than from ecological processes.

Sources of bias in food web analysis have been discussed in the literature, yet many of these critical points have been downplayed repeatedly, and when identified, their potential effects on food web trends have been assumed to be negligible (Sugihara et al. 1989, Cohen et al. 1990, Pimm et al. 1991, Williams and Martinez 2000, 2004). Comparative studies that have employed internally consistent methodologies have emphasized the serious limitations of datasets compiled from the literature and have yielded little or no corroboration of earlier "food web laws" (see also Hildrew et al. 1985, Winemiller 1989, 1990, Warren 1990, Martinez 1991, Polis 1991, Schoenly and Cohen 1991, Reagan and Waide 1996). The most essential elements of empirical food web research are highly sensitive to scale.

6.4 EVERY FOOD WEB IS A SUBWEB

Large variation in structural complexity is obvious among sets of community webs gathered from the ecological literature for comparative study (Cohen 1978, 1989, Pimm 1982, Briand 1983, Cohen and Newman 1985, Cohen et al. 1990, Williams and Martinez 2000). In most of the comparative food web literature, the fundamental unit for comparisons, the community, is a collection of taxa grouped together by arbitrary spatial and temporal criteria. Arbitrary variation among these units introduces bias into comparisons. Some community food webs simplify the complex network of feeding interactions within species-rich communities by reporting only those interactions perceived as being strong or important. Others have described feeding relationships in greater detail for a subset of species within a larger community. Polis (1991) described the challenges associated with compilation of a food web for the Coachella Valley, California. He identified a strong trade-off between taxonomic completeness and precision

in estimating the presence or absence of species interactions. He estimated that complete accounting of all species within major taxa (plants, animals, parasites, and microorganisms) would total 10^3–10^5 in most cases.

Most reported food webs focus on a particular taxonomic group of special interest to the field investigator. For example, Martinez (1991) defined the Little Rock Lake community as all "organisms that spend virtually all the specified life stage at or below the lake's surface." His food web contained 6 fish species (4 species were divided into 2 life stages), 110 invertebrates, and 60 algae. The Little Rock Lake food web contains high taxonomic resolution (mostly to the level of species or genus), however this incurs a strong trade-off with the accuracy and precision of feeding interactions estimated from field studies or inferred from literature sources (based on studies at other locations) and expert opinions.

Despite the difficulties inherent in defining the boundaries of natural communities, large food webs can be divided into subwebs by objective criteria. A food web comprised of a single consumer species and all of its prey is a subweb within a larger interactive trophic network. Following Cohen (1978), a "sink subweb" consists of all the prey taken by a predator plus all prey consumed by the prey of this designated top predator, and so on. Alternatively "source subwebs," include a set of one or more basal species (usually, but not necessarily, plants), their consumers, and predators of their consumers (Cohen 1978). "Basal species" are those having predators but no prey, "top species" have prey but no predators, and "intermediate species" have at least one prey and one predator (Cohen and Briand 1984). Polis (1991) gave compelling arguments that top species that are entirely without enemies (i.e., predators, parasitoids, and parasites) do not exist in nature.

Since any community food web is actually a subweb within a larger open system (linked and nested within the biosphere), sink and source subwebs of various kinds might provide less biased units for comparisons. Because sink webs are subsets of larger, subjectively defined community webs, food web statistics might be expected to differ in comparisons between the two. Indeed, a number of quantitative measures varied greatly between community and sink webs in tropical aquatic webs (Winemiller 1989, 1990). The top predator in these sink webs was defined as the consumer with the highest trophic position within a community trophic continuum calculated from the bottom-up using volumetric dietary data. Yet in contrast to Cohen and Briand's definition, top predators in these webs were sometimes consumed by species at lower trophic levels. Future empirical studies will need to do a better job of defining and standardizing food web boundaries, probably as subwebs defined by various objective criteria.

6.5 TROPHOSPECIES AND OTHER KINDS OF NODES

One could argue that all comparative food web analyses are confounded by large differences in levels and criteria for taxonomic aggregation (Paine 1988, Lawton 1989, Winemiller 1990, Polis 1991, Martinez 1994, Solow and Beet

1998, Yodzis and Winemiller 1999). Food web nodes are usually comprised of lumped species populations referred to as "trophospecies" (Yodzis 1988) or simply as "species" (Cohen 1978, Pimm 1980, 1982, Briand 1983, Auerbach 1984, Sugihara 1984, Cohen and Newman 1985). According to Pimm et al. (1991), trophospecies are sets of organisms with identical prey species and identical predators. If trophospecies share precisely the same set of predator and prey, it is highly unlikely that any biological species could be grouped in this manner.

Pimm (1982) observed that all published food webs appeared to involve some degree of lumping into functional trophospecies, particularly at lower trophic levels where plants and invertebrates predominate. He felt that most ecologists exhibit antipathy for plant and invertebrate taxonomy. More likely, the causal factors for this pattern are lack of taxonomic expertise for the species-rich invertebrates, logistical limitations, and a focus on questions regarding taxa at higher trophic levels. Most field investigators appear to have aggregated species by taxonomic rather than functional criteria when creating food web diagrams. Given that some taxonomic lumping must occur in all large food webs, a primary concern is that large variation in the degree of lumping among widely divergent studies may invalidate empirical food web comparisons. While this problem has been recognized previously (Glasser 1983, Paine 1983, 1988, Winemiller 1990, Polis 1991, Cohen et al. 1993), many investigators have opted to proceed with their analysis with an apology that no other information is currently available, often followed by a plea for more precise information (Pimm 1982, Schoener 1989, Cohen et al. 1990, Pimm et al. 1991, Williams and Martinez 2000).

The pitfalls associated with comparisons of food webs from studies with different goals are illustrated by comparing species that occur both in Zaret and Paine's (1973) Lake Gatún, Panama web and Winemiller's (1990) Costa Rican stream webs. Zaret and Paine published their food web as "a generalized view of the trophic structure of Lake Gatún, based on information from stomach analyses and direct observations." *Cichlasoma maculicauda* in the Lake Gatún food web had a single food resource, filamentous green algae. Based on stomach contents analysis, *C. maculicauda* in Caño Agua Fría Viejo, Costa Rica fed on more than 30 general prey categories in varying proportions that depended on season (32 items—wet season, 33 items—dry season, N stomachs examined = 155). Filamentous algae represented only 1 of 43 aggregate prey categories discovered in stomachs of *C. maculicauda* from Costa Rica. A similar contrast is seen in the diet of the piscivorous eleotrid *Gobiomorus dormitor*. Zaret and Paine listed a single fish species as the prey of *Gobiomorus*, whereas stomach contents data from Costa Rica (168 stomachs) yielded a conservative estimate of 12 prey categories. These large disparities are less influenced by environmental differences than methodological inconsistencies. The Panama study used a greater degree of prey lumping and intentionally omitted many prey items from the food web diagram, because those items were

deemed unimportant for the primary objective of the report, documentation of the response of the lake community to an exotic predatory fish.

Sugihara et al. (1989) recognized the lack of uniformity in the level of species aggregation among 113 food webs compiled for comparative analysis (Cohen 1989). Using an algorithm that collapsed species into aggregate trophospecies, they found that four of five food web properties were sensitive to aggregation beyond the level of trophically equivalent species (species having identical predators and prey). All five measures were robust against grouping of "trophic equivalents," and one measure (rigid circuitry) was robust even when lumping species beyond the level of trophic equivalents. Rigid circuitry is a property derived from graph theory that reflects guild structure in simple food web diagrams. It is not surprising that functional constraints on feeding or habitat utilization that produce guild structure yield similar community patterns when the most similar species are grouped into trophospecies. Sugihara et al. (1989) offered an overall assessment that food web regularities "may be legitimate despite understandable worries about the nonuniformity of trophic resolution in the data." Their optimism would only be warranted if one could demonstrate that widespread grouping of species into trophospecies in published food webs involves trophic equivalents in all instances. More often than not, species near the bottom of food webs have been aggregated on purely taxonomic grounds (e.g., beetles, ants, algae), because detailed feeding data are unavailable. In addition, the reported food web regularities (Briand and Cohen 1984, Cohen and Briand 1984, Cohen et al. 1990, Pimm et al. 1991) that involve scale invariance (value constancy with changing species richness) are actually more random (slope = 0 in association with low correlation among scattered points) than regular (slope = 0 for points lying on a straight line; Winemiller 1990).

Martinez (1991, 1993) examined the sensitivity of food web patterns to changes in resolution of nodes following hierarchical aggregation based on species' trophic similarities (Jaccard index) and the minimum-, maximum- and average-linkage clustering methods. His Little Rock Lake food web contained 182 species identified mostly to genus and species (Martinez 1991). The first aggregation grouped trophic equivalents (primarily algae species at the base of the food web) and reduced the number of nodes to 93; thereafter clustering reduced the number of nodes until a low of 9 functional groups was obtained. In each case, the influence of node aggregation on web metrics was major. Number of links per species, distribution of chain lengths, distribution of species trophic levels, the proportion of top species, and the proportion of links to top species were highly sensitive to aggregation. Connectance, the ratio of predators to prey, proportions of intermediate and basal species, and the proportion of links between intermediate and basal species also varied with node aggregation but were somewhat less sensitive. Martinez (1991) concluded that most of the early food webs from which "food web laws" were derived are equivalent to the highly aggregated versions of the Little Rock Lake food web.

Yodzis and Winemiller (1999) examined the performance of alternative methods for aggregating species into trophospecies. Using Winemiller's (1990) Caño Maraca, Venezuela, food web, they used an additive versus a multiplicative method to combine each species dual role as a resource and consumer. Similarity in feeding links was based on topological (presence/absence) and flow (volumetric) linkage patterns. For a given measure of similarity, 6 alternative algorithms were employed to derive 24 trophic hierarchies (dendrograms). In general, there was little correspondence between species overlap in resource use and the extent to which predators were shared. The additive method of combining species' resource and consumer roles performed better, and weak links had a large influence. Maximum and average clustering algorithms performed best, but it was unclear how to select a similarity criterion for assignment of trophospecies. Objective methods and criteria for creating trophospecies remain elusive (see also Solow and Beet 1998). Until this issue can be better resolved, empirical food web research is seriously hindered. Because differences in the level of taxonomic identification among trophic units influences food web properties, comparative studies require unambiguous criteria for defining trophic units and estimating predator–prey links.

6.6   VARIATION IN THE MAGNITUDE OF TROPHIC INTERACTIONS

MacArthur (1972) and Paine (1980) emphasized the fact that species interactions within trophic networks are extremely variable in magnitude and duration. Strong predator–prey interactions are likely to have greater influence on the local distribution and abundance of organisms than weak or spurious interactions (Paine 1980, 1983). However, the presence of many weak interactions may stabilize community dynamics (Yodzis 1981, McCann et al. 1998). Very few empirical food web studies have examined temporal variation in the strength and duration of predator–prey interactions (e.g., Winemiller 1990, Tavares-Cromar and Williams 1996). Most comparative studies have dichotomized consumption into a matrix of binary presence/absence elements (web topology). Discussions of the methods for estimating links and the level of confidence in the empirical datasets are rare in the literature.

Winemiller (1990) estimated volumetric consumption from stomach contents and calculated food web statistics at several threshold intervals for trophic links. A series of threshold intervals was used to successively exclude "weak" links defined by fractional volumetric consumption during various seasons of the year. Data were then log-transformed and link threshold was then treated as a covariate in comparisons of characteristics of different aquatic food webs. Although this method requires large amounts of dietary data, greater numbers of comparisons are possible among webs defined according to levels of weak link exclusion. Moreover, the shapes of the curves derived from plotting food web statistics versus link threshold reveal additional features of food web structure. For a given web, linkage density must decline as the link threshold

increases, yet a large negative slope in the bivariate relationship reflects a food web dominated by many links of small magnitude. Other measures, like the average number of predators per prey node, need not decline at higher link thresholds, although this trend was predominant in tropical aquatic food webs.

Frequency of prey consumption is another measure of the magnitude of predator–prey interactions. Goldwasser and Roughgarden (1993) estimated the frequency of consumption for 44 terrestrial species in the cumulative food web of the Caribbean island of St. Martin. Diet data for lizards and birds were based on stomach contents reported in literature. Nematode parasites of lizards were revealed from dissections, and invertebrate diets were based on relative abundances of different taxa (most were aggregated into orders) in their environment. Estimates of frequency of consumption were reported as the number eaten per day (these units were directly estimated in one bird study). In order to scale highly disparate data into the same units of consumption frequency, "more-or-less arbitrary decisions" were required. For example, cannibalism and feeding loops were excluded based on Cohen's (1978) finding that they are rare in the early food web diagrams. Arthropod diets were based on entomology texts, and frequencies of prey consumption (number/day) were weighted by the relative abundances of prey and multiplied by either 10 or 100 to account for the higher densities of these small species at lower trophic strata. Virtually all web characteristics deviated from expected values based on patterns in the EcoWeb dataset (Cohen 1989) and predictions of the cascade model of food web structure (Cohen and Newman 1985). Because the authors did not expect all of their estimates of feeding frequencies to reflect true consumption, they made no attempt to examine food web properties at different link thresholds based on variation in feeding frequencies. Despite highly arbitrary nature of the St. Martin food web, this attempt to estimate link strengths clearly highlights the challenges that arise in estimating food web structure by taking into account variation in the strength of pairwise interactions (see Bersier et al. 2002, Berlow et al. 1999, 2004). Predator–prey interactions are highly variable, both in time and space, and this variation must be estimated and incorporated into descriptive and comparative food web research.

6.7 ESTIMATION OF TROPHIC LINKS IS ALWAYS IMPERFECT

The empirical food web literature has been surprisingly uncritical toward estimates for trophic links. Caddy and Sharp (1986) reviewed the following techniques for estimating marine and aquatic trophic relationships: (1) direct observation, (2) experimental studies, (3) examination of morphological adaptations, and (4) stomach contents analysis. These methods also apply to terrestrial food webs. Stable isotope ratios in tissues also can be used to achieve crude estimates of trophic relationships (Lajtha and Michener 1994). In addition to ratios of naturally occurring isotopes, radioactive isotopes (H^3, P^{32}) have been introduced into ecosystem components to quantify feeding rates (Odum and

Kuenzler 1963). Data from short-term observations can be used with individual-based simulation models (DeAngelis and Gross 1992) or aggregate food web models (Christensen and Pauly 1992) to estimate feeding dynamics over a longer time periods and across variable environmental conditions.

Indirect methods of feeding estimation (including radiotracers, isotopic ratios, and field experimentation) carry their own limitations. Teams of taxonomic specialists might reduce the margin of error in producing estimates of predation rates in natural systems. A complete description of a large food web would likely require a huge staff and budget. Given that ecologists are not likely to see this level of funding in the foreseeable future, we are faced with the unfortunate reality that progress must be made with imperfect knowledge of the true ecological relationships. Ecologists must proceed nonetheless, provided that they acknowledge methodological limitations and establish objective criteria for quantitative analyses.

Cohen and Newman (1985) attempted to account for observer bias in empirical food web structure using a model of imperfect observation. Their model assumed that the probability of correctly recording a feeding link between two species involved in a predator–prey interaction is inversely related to the size of the food web. As webs accrue more species, the fraction of real predator–prey interactions reported declines according to the function $P(C_1S_T)$, where C_1 is web connectance, and S_T is the number of trophospecies. Based on comparisons of empirical webs, C_1 was assumed to be approximately 2. By running simulations that combined the observer bias model with a model of food web dynamics at the edge of linear local stability, Cohen and Newman estimated that just 10% or fewer of the actual dynamic interactions among species are recorded for communities containing 50 or more species. The authors pointed out that both models are based on many untested assumptions, yet they "would not be surprised if the qualitative behavior derived from the collection of assumptions corresponds well with what would be predicted from vastly more realistic models." The risk in this approach is that patterns can sometimes mask the processes that created them, even when we possess complete knowledge of the system (Neill and Gallaway 1989).

Taxonomic resolution incurs a negative trade-off with resolution of feeding interactions in food webs. Hildrew et al. (1985) used stomach contents analysis to estimate invertebrate feeding interactions in a small acidic stream. Because some chironomid larvae (Diptera) were known to regurgitate stomach contents during preservation, no attempt was made to quantify feeding rates. Their topological food web contained only 24 species but 96 feeding links. Martinez (1991) claimed to have "directly documented" trophic interactions in the Little Rock Lake community by interviewing ecologists involved in studies of various higher taxa and by reviewing literature. The Little Rock Lake food web is a composite topological web that combines diverse sources of information without regard for temporal or spatial variation and contains no estimates of interaction strengths. Whereas the focus of Martinez's analysis, the level of

taxonomic resolution, was shown to have large effects on several food web properties, feeding links were crudely estimated. The average number of links per species was 11 in an aggregated food web containing 93 "trophospecies." In the fully resolved Little Rock Lake food web, largemouth bass fed on 95 taxa (including all of the fish and zooplankton species in the lake, 2 of 18 benthic microcrustaceans, 46 of 52 aquatic insects, a worm, a leech, a triclad, and one amphipod). Strangely, bass ate only one of the four species of dragonfly nymphs, yet they consumed the full complement of other aquatic insects. Other predators were more specialized. Triclads ate only harpacticoid copepods. The amphipod *Crangonyx gracilis* specialized on filamentous algae (notably, it consumed the entire assemblage of 25 filamentous algae genera). Given large uncertainties associated with estimation of trophic links, the question of taxonomic scale seems almost moot.

Havens (1992) analyzed features of "nonaggregated natural webs sampled consistently and constructed from identical linkage criteria." Data for his 50 food webs of small lakes and ponds were derived from cumulative lists of species from sampling performed by the Adirondack Biota Project. Feeding links were assigned based on diet information in Martinez (1991), Scott and Crossman's (1973) *Freshwater Fishes of Canada*, Sprules and Bowerman (1988), and two other literature sources for invertebrates. Because little detailed information on fish diets appears in Scott and Crossman's book, one can only assume that Martinez's assumptions regarding food web interactions were replicated in Havens' webs. Similarly, Sprules and Bowerman (1988) obtained knowledge of feeding links between invertebrates and their prey "from the extensive literature available and from the collective experience of people in our laboratory." Whenever literature reports provide the basis for the estimation of feeding links, no spatial or temporal variation in predator–prey interactions is possible. Most comparative food web studies have been derived mainly from faunal surveys and therefore could not estimate variation in feeding interactions.

Accurate estimates of feeding behavior by all species of even a small community obviously pose a daunting task. Practical problems of prey identification were discussed by Paine (1988), Winemiller (1990), and Polis (1991). Ultimately, some imprecision and inaccuracy will be associated with the identification of food web links and the estimation of their magnitudes. Species with broad diets require larger samples for quantitative diet estimation than relatively specialized feeders. As in any form of measurement, reported estimates for the strength of predator–prey interactions are imperfect. Most biological parameters are reported in the scientific literature using measures of central tendency with associated error statistics. Unfortunately, this convention is seldom possible for food web units. In the case of diet estimation through stomach contents analysis, individual consumers usually contribute only one estimate of their feeding behavior (i.e., they are usually euthanized). Given the fact that food web data are exceedingly difficult to gather and impossible to replicate, investigators must provide an assessment of the reliability of their observations or

measurements. A lucid account of methodology and sample sizes would provide a modest beginning. In this manner the suitability of data for meta-analysis could be evaluated.

6.8 SPATIAL AND TEMPORAL VARIABILITY

A large body of literature indicates that most ecological communities do not occur in highly stable environments, and some (perhaps most) only rarely or intermittently experience strong density-dependence or exhibit equilibrium population dynamics (Wiens 1984, Schoener 1982, Strong 1986, Menge and Sutherland 1987, Dunson and Travis 1991). Furthermore, few predators appear to forage on prey in constant ratios over time during their entire life cycle. Aquatic organisms, in particular, reveal much ontogenetic, size-dependent predation (Brooks and Dodson 1965, Werner and Gilliam 1984). In addition, diet composition frequently shifts in response to seasonal changes in the availability of preferred food resources. For example in the Venezuelan llanos, loricariid catfishes consume aquatic primary production mostly in the form of living algae during the wet season and in the form of dead macrophyte tissues (detritus) during the dry season (Table 6.1). This sort of seasonal variation in fish diets is more the norm than the exception (Werner and Gilliam 1984), even at less seasonal locations in the tropics (McKaye and Marsh 1983). Seasonal changes in fish species richness and abundance in the pelage zone of the Sea of Cortez was assumed to yield a more complex food web with longer chains during the summer (Klimley et al. 2005).

The behavior of individual organisms and temporal dynamics of populations within food webs can be interpreted in terms of the seasonal influence of specific environmental components, both abiotic and biotic. Large seasonal differences are observed in several properties of tropical aquatic food webs (Winemiller 1990, 1996). In the Venezuelan llanos, dry season contraction of aquatic habitats increases fish densities and results in more frequent predator–prey encounters. Thus the mean number of prey per predator node increases during the period of gradual drying (transition season) when prey densities are high. The number of prey consumed per predator node declines during the peak dry season when small species vulnerable to piscivores are reduced by predation mortality, then decreases further as fishes and other organisms are dispersed in expanded aquatic habitat during the wet season. The mean number of predators per node is about the same during the wet and transition seasons, because even though fish densities are very low in the expanded wet season environment, more different kinds of fishes are present in the local ecosystem due to immigration into the productive wetland. This example illustrates why certain food web parameters cannot be interpreted without knowledge of the physicochemical and production dynamics the system.

Food web properties vary in space and time under the influence of multiple factors associated with internal dynamics as well as external environmental

Table 6.1. Seasonal composition of diets of two catfishes in the Venezuelan llanos

	Food category	Wet	Dry
	Fine detritus (2)	0.354	<u>0.817</u>
	Vegetative detritus (1)	<u>0.250</u>	0.104
	Diatoms, desmids (2)	<u>0.270</u>	0.027
Pterygoplichthys	Filamentous algae (1)	0.034	0.022
multiradiatus	Spores (2)	0.013	0.006
(Loricariidae)	Protozoa, difflugiids (2)	<u>0.027</u>	0.006
	Copepods (1)	<u>0.007</u>	–
	Chitin fragments (1)	0.023	0.015
	Sample N	20	20
	Detritus (2)	0.004	0.009
	Seeds (1)	0.001	0.005
	Snails (1)	<u>0.119</u>	0.007
	Mussels (1)	0.012	–
	Copepods	–	0.021
	Cladocerans (1)	<u>0.049</u>	0.005
	Eubranchipods (1)	<u>0.070</u>	–
Pimelodella sp.	Ostracods (1)	0.005	–
(Pimelodidae)	Prawns (1)	<u>0.124</u>	0.004
	Ephemeroptera (1)	<u>0.096</u>	0.007
	Aquatic Coleoptera (2)	0.018	<u>0.247</u>
	Aquatic Diptera (3)	<u>0.318</u>	0.132
	Other aquatic insects (2)	0.082	0.144
	Scales (2)	0.077	0.054
	Fish eggs (1)	0.001	<u>0.243</u>
	Fish (1)	–	<u>0.088</u>
	Sample N	62	62

Note: Dominant diet items for each season are underlined. The number of operational taxonomic units used in related food web analyses appears in parentheses after each diet category

factors. Precise, accurate, and reliable estimates of empirical food webs would open up exciting new avenues of comparative research. For example, Briand (1983), Cohen and Briand (1984), and Briand and Cohen (1987) classified 62 food webs as being associated with either fluctuating or constant habitats. Aside from the questionable classification scheme used in producing Briand's environmental categories, large variation in the units of comparison, methodologies, time intervals of study, and sample sizes among studies rendered this comparison essentially meaningless. This important topic could be approached with greater rigor by comparing a smaller number of systems based on more standard methods. If food webs are to provide greater insights into the relative roles of abiotic versus biotic factors and density-dependent versus density-independent influences on community properties, then variation in the strength of species interactions must be estimated quantitatively.

Spatial scales and boundaries profoundly influence ecosystem processes and the stability of food web elements (Holt 2002). Spatially structured population models have very different dynamics than unstructured models. In some cases, metapopulations of consumers may have variable and complex responses to variation in resource levels at the patch scale. At the landscape scale, movement of material and organisms between major habitat boundaries can profoundly influence food web dynamics (Polis et al. 1997). Holt (2002) developed theoretical models in which immigration could either stabilize or destabilize local population dynamics. In a three-level food web, top predators with larger ranges than their prey moderated unstable interactions between the second-level consumers and basal resources. Thus, food web dynamics are highly sensitive to spatial dynamics via multiple mechanisms, and these dynamics influence patterns observed in comparative studies. For example, food chain length in lakes has been shown to correlate with lake size more than primary productivity (Post et al. 2000). It is now difficult to imagine how food web ecology could be separated from spatial ecology in any but the most trivial manner.

6.9 VARIANCE IN SPECIES ABUNDANCES AFFECT FOOD WEB PROPERTIES

Just as the magnitude of trophic interactions can vary with time and space, population densities and structures frequently vary over space and time. Schoenly and Cohen (1991) noted that, in addition to temporal variation in diets, seasonal changes in the residence time of species in the community cause temporal variation in food web structure. Likewise, Winemiller (1990) discussed the influence of seasonal hydrology, variation in production sources, reproduction, and local fish migrations on the properties of aquatic food webs in the tropics.

What are some potential implications of variance in population densities for food web structure and function? Consider a species with a broad diet. If the species is extremely rare, its overall effect on the system may be trivial. Conversely, a functionally significant prey species might be rare if it is kept in check by strong interactions with predators (Paine 1980). Whether or not the rare species is involved in significant food web interactions may depend on whether the perspective is by predators from above, or by prey from below (Polis 1991). Furthermore, a superabundant species exhibiting numerous weak interactions could be important in food web dynamics. There appears to be no means for determining a priori which rare species should be excluded from the analysis. The current practice in comparative studies is to either omit rare species or to give them equal status with common species, neither of which seems very satisfactory.

Power (1990) discussed the implications of variable population densities on food web properties. The ecological significance of an observed trophic link is determined by the functional and numerical predation responses. Therefore, the structure of static topological food webs depends upon densities of predators and prey, which in turn are derived from rates of biomass accumulation,

population growth rates, and predation rates during preceding time intervals. Models of ratio-dependent predation (where the functional response depends on the ratio of predator to prey rather than prey density) can yield dynamics quite different from simulations based on the familiar Holling (1966) predation model (Artidi and Ginzburg 1989). Berryman (1992) observed that the behavior of Lotka-Volterra predation models, with either logistic modifications to predator and prey or with ratio-dependent functional responses, have greater biological realism than models with classical functional responses. By omitting species densities, static topological food webs have little or no relationship with their own dynamics. To achieve even modest coupling between web structure and dynamics requires data for community composition, species interactions, web architecture, and population densities (de Ruiter et al. 1995, Morin and Lawler 1995, Berlow et al. 2004).

6.10 INFLUENCE OF ABIOTIC AND BIOTIC ENVIRONMENTAL FACTORS

In much of the food web literature, the formulation of intriguing problems and clever analytical approaches seem to have taken precedence over environmental biology as well as concerns for how data are acquired and analyzed (see also discussions by Paine 1988, Lawton 1989, Winemiller 1990, Polis 1991). Once the empirical data and analytical methods manage to narrow the gap with theory, we may gain important new insights into some old, but fundamental problems. Much of food web theory implies an equilibrium or density-dependent world, however ecologists understand very well that ecological systems are influenced simultaneously by a host of density-independent and density-dependent factors that vary over time and space.

Table 6.2 lists some of the major factors known to influence population dynamics. Only two of the seven factors (predation/parasitism and food availability) are explicitly represented in food webs. In any large food web, some feeding relationships will have disproportionate and major impacts on the community. Consider, e.g., the major role that African elephants play as architects of savanna ecosystems. In contrast, consider the food chain of leaf-cutter ants (*Atta* sp.)—fungi—vegetation (3 nodes, 2 links). Fungi are a crucial food web element in terms of the physiological ecology of leaf-cutter ants. By itself, *Atta* cannot extract nutrition from plants in a manner that meets their physiological requirements, and are therefore dependent upon their association with fungi. If leaf-cutters were to suddenly evolve their own biochemical capacity to digest and assimilate plants directly, what kind of ramifications would the elimination of the fungus (1 node, 1 link) have at the level of the overall food web? According to the energetic view of food webs, there would be a major effect. In terms of the network of population interactions, it might be very insignificant.

Whether or not they choose to deal with it directly, most ecologists are keenly aware of the role that historical biogeography plays in setting the stage for

Table 6.2. Factors that influence local population densities

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1. Abiotic (climatic) density-independent influences
*2. Predation, parasitism
*3. Nutrients, food availability
4. Available space and physical habitat
5. Mutualism (e.g., pollinators, seed dispersers)
6. Commensalism (e.g., enhancement of physical habitats, enhanced foraging success, enhanced predator deterrence)
7. Intrinsic genetic factors (e.g., inbreeding depression, sex ratio, mating systems, life history strategy)
8. Emigration and immigration from other habitats or regions (e.g., spatial subsidies)

Note: Asterisks denote factors that are explicit in food web models

contemporary ecological interactions. Yet few methodologies have been developed for identifying or adjusting for the influence of historical constraints on community features (Endler 1982, Ricklefs 1987). The influence of historical factors (invasions, local extinctions, and succession) on food web features has been investigated from both theoretical and experimental standpoints (Yodzis 1984, Post and Pimm 1983, Drake 1990, 1991, Fukami and Morin 2003), but only superficially from a comparative standpoint (Beaver 1983, Kitching 1987, Winemiller 1990). Priority effects in contemporary biological interactions can greatly influence community dynamics and structure (Drake 1991, Fukami and Morin 2003). The food web structure and dynamics of some, perhaps even most, ecosystems would be impossible to interpret or predict without fundamental understanding of abiotic drivers, such as coastal upwelling or advective currents that deliver resources and new population recruits (Menge et al. 2003).

6.11   LIFE HISTORY STRATEGIES INFLUENCE POPULATION DYNAMICS

The influence of alternative life history strategies on food web structure and function has scarcely been addressed (Polis et al. 1996, Scharler et al. 2005). For example, the relative impact of a strong feeding link on an opportunistic (r-selected) prey population is certainly less than the same level of interaction with a relatively K-selected prey with a low intrinsic rate of natural increase. Species life histories vary in their demographic responses to seasonal environmental variation as well as manifestation of the storage effect (Chesson and Huntley 1989). According to Chesson (2000), the storage effect promotes species coexistence via three mechanisms: buffered population dynamics (e.g., long-lived life stages that can endure periods of unfavorable environmental conditions), interspecific differences in response to environmental variation (see also Tilman 1982), or covariance between environmental conditions and competition (i.e., as environmental conditions improve for a species, its demand for resources increases which eventually results in greater competition).

Stochastic environmental disturbances can actually favor populations with buffered population dynamics and high recruitment variation (Higgins et al. 2000).

Terrestrial and aquatic food webs seem to differ in at least one fundamental aspect associated with life history strategies. Terrestrial food webs contain many long-lived (environmentally buffered) plants (especially trees and shrubs) that are grazed by animals with considerably shorter life spans. Many of these herbivores, both vertebrates and invertebrates, are in turn consumed by carnivores that may or may not have longer life spans and greater environmental buffering (e.g., vertebrate carnivores versus parasitoids). In aquatic food webs, the most important primary producers consumed by herbivores are short-lived algae with high population turnover rates. The predominant consumers of algae are small invertebrates (microcustacea and immature stages of insects), which in turn are consumed by larger vertebrates. This trend of increasing body size with trophic level has long been noted (Elton 1927) and sometimes used as a basis for explaining food web structure (Cohen and Newman 1985, Warren and Lawton 1987). Analysis of a version of the Ythan estuary web (Hall and Raffaelli 1991) that included parasites demonstrated very weak body size—trophic position relationships, which suggested body size relationships may be poor predictors of interaction strength for dynamic models (Leaper and Huxham 2002).

Life history strategies have been incorporated into a variety of dynamic modeling approaches, but, aside from using body size, how can this critical source of variation affecting population and community dynamics be captured by an empirical description of food webs? The manner that species with different life history traits respond to different aspects and spatiotemporal scales of environmental variation will differ in ways that are difficult to build into dynamic food web models. Winemiller (1996) categorized species in river food webs according to a triangular life history gradient with three endpoint strategies. This triangular gradient seems to describe patterns of variation among basic life history traits of fishes reasonably well, and also can be derived from fundamental demographic relationships (Winemilller and Rose 1992, Winemiller 2005). The problem with this application to empirical food webs is that species lying on a continuous gradient are forced into discrete categories. Nonetheless, it represents one empirical means of integrating variation in life history strategies with food web structure. The effects of population structure (McCann et al. 1998) and life history strategies on food web structure and dynamics surely will be a fruitful area for inquiry.

6.12 DEALING WITH COMPLEXITY AND VARIABILITY: FOOD WEB RESEARCH ON A TROPICAL RIVER

The remainder of this chapter examines these issues from the perspective of empirical field research in a tropical river. The Cinaruco River, Venezuela, is a dynamic and spatially heterogenous ecosystem that supports extremely high

species richness and ecological diversity. The river contains more than 280 fish species with trophic niches ranging from detritivores to herbivores, invertivores, and piscivores spanning a wide range of body sizes and life history strategies. Can this high diversity and complexity be examined in units that permit prediction of ecological dynamics? It probably is not reasonable to seek a set of universal, standardized methods for empirical research on every element of the food web from bacteria to river dolphins (*Inia geoffrensis*). To some extent, protocols must be devised and adapted in response to the characteristics of the system. My colleagues and I are attempting to understand the structure and dynamics of the Cinaruco food web by dealing with components on scales of time, space, and taxonomy that are defined by rather obvious spatiotemporal boundaries as well as practical constraints. We organize the food web into modules defined on the basis of habitat features and associated biota (habitat modules) and sink or source webs (trophic modules) that may or may not be associated with a single habitat module (Figure 6.1). Trophic modules that are sink webs defined by large mobile predators will unite habitat modules in the manner described by Holt's (1996) spatial food web model. Holt's model, which builds on ideas from the island biogeography theory, describes well the spatial patterning of littoral-zone species assemblages that are mixtures of relatively sedentary species with strong habitat affinities and relatively mobile species that
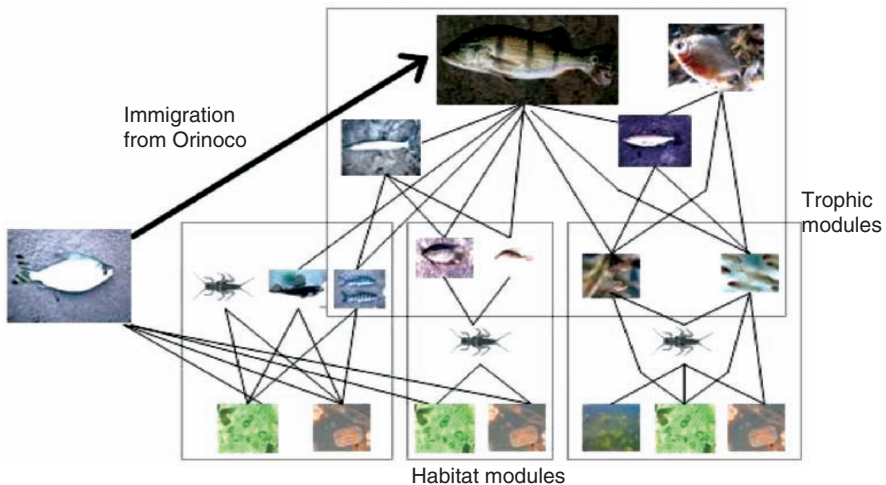
Figure 6.1. Schematic diagram of the Cinaruco River food web modules (e.g., rocky shoals, woody debris, sandbank), trophic modules (sink subwebs at top, and source subwebs at bottom), and a food web spatial subsidy in the form of a migratory benthivorous fish (*S. kneri*) consumed by predatory *Cichla temensis*.

move frequently among habitats (see Jepsen et al. 1997, Hoeinghaus et al. 2003, Arrington and Winemiller 2005, 2006. Arrington et al. 2005, Layman et al. 2005a).

We have adopted three approaches to reveal the structure and dynamics of food web modules. First, we estimate species distribution and abundance patterns over time (hydrologic seasons in this lowland river) and space (habitats), and then quantify diets via stomach contents analysis (Layman et al. 2005a, b). Stomach contents analysis allows identification of prey taxa with relatively high resolution, but requires large samples, especially for consumers with broad diets. Because these efforts are time and labor intensive, we are also examining aspects of the food web using stable isotopes of carbon (useful for estimating certain terrestrial and aquatic primary production sources) and nitrogen (useful for estimating trophic positions of consumers). Stable isotope research provides an estimate of the overall structure of the river food web (see Jepsen and Winemiller 2002) and the relative importance of autochthonous and allochthonous food resources supporting omnivores and carnivores (Layman et al. 2005a, b). For example, species of herbivorous characid fishes show significant interspecific variation in carbon and nitrogen stable isotope signatures that reflects partitioning of aquatic and terrestrial food resources, such as plankton, insects, fruits, seeds, and leaves (Figure 6.2). Stable isotope data also have assisted in revealing the importance of a spatial food web subsidy in the form of benthivorous fish that migrate seasonally between the highly productive Orinoco River and the unproductive Cinaruco River (Winemiller and Jepsen 2004). The basis for the latter estimates is small but consistent differences in the carbon isotopic signatures of biota living in acidic "black waters" of the Cinaruco River compared with biota from the neutral "white waters" of the Orinoco.

The third approach is field experimentation in which various species or functional groups are excluded or confined to areas of habitat in order to discover their effects on other food web elements. When large piscivores were excluded from large areas of sand bank, there were significant increases in the abundance and diversity of fishes in the range of prey sizes consumed by these predators (as determined from stomach contents analysis), but no responses were observed within the assemblage of smaller fishes (see Layman and Winemiller 2004). Similar results were obtained when assemblages of entire lagoons were manipulated by commercial net fishers (Layman et al. 2005a). Like the mesh on our fish exclosures, the mesh of commercial seine nets remove the largest fishes while allowing smaller fishes to pass unharmed. The consistent results from these manipulations conducted in two different habitats at two different spatial scales ($500 \, m^2$ on river channel shorelines versus several thousand m^2 in lagoons) give us confidence that field manipulations scale up to entire habitat patches on the landscape. Removal of large piscivores and detritivorous fishes that are their principal prey results in longer, and presumably less energetically efficient, food chains that start with algae and lead to aquatic invertebrates, small invertivorous fishes and small piscivores (Layman et al. 2005a).
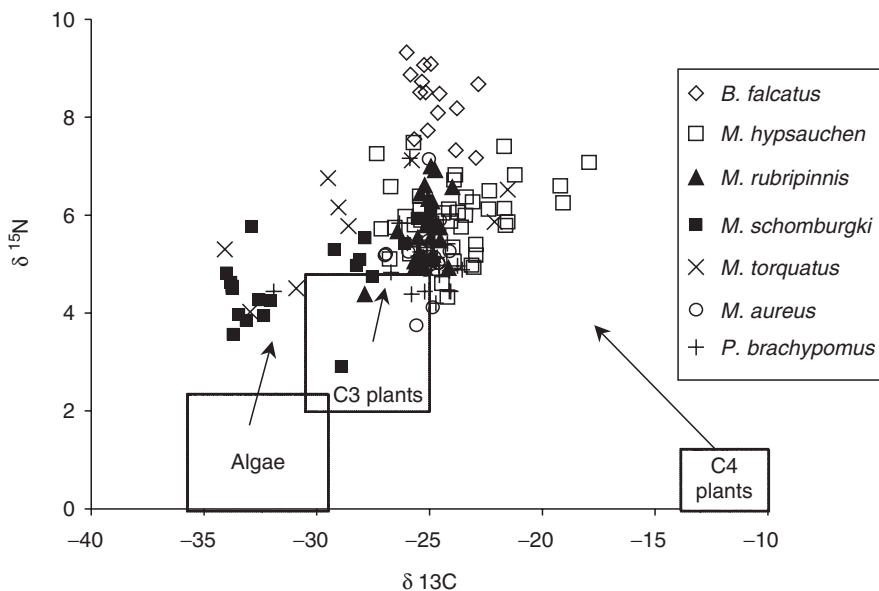
Figure 6.2. Plot of stable isotopic signatures of carbon and nitrogen for herbivorous characid fishes of the Cinaruco River in relation to the range of variation in carbon and nitrogen signatures for three basal sources. Carbon ratios of consumers are a proportional assimilation of sources, whereas nitrogen ratios are fractionated (2–3%) with each successive trophic level. The plot reveals high overlap in trophic niches among some species (e.g., *Metynnis hypsauchen*, *M. rubripinnis*, and *Myleus aureus*), and a high degree of resource partitioning between certain species pairs (e.g., *Brycon falcatus—M. schomburgki*, *B. falcatus—M. torquatus*, *M. hypsauchen—Piaractus brachypomus*).

We conducted fish exclusion and enclosure experiments to examine the role of benthivorous fish on sediments of the littoral zone module in channel and lagoon habitats. Selective exclusion of large or small fishes revealed strong fish effects on organic sediments and chlorophyll during the low water season, but not during the rising water period (Winemiller et al. 2005). The species that reduces most of the organic material from the surface of sediments is the migratory fish, *Semaprochilodus kneri*, which is abundant in the river during the low water period, but absent during the flood period when it spawns and feeds in the Orinoco River. Ongoing studies are examining effects of these fish manipulations on sediment particle size, rates of nutrient regeneration in sediments, and meiofauna community structure.

At the same time we are investigating food web modules, we also are investigating spatial and temporal variation in abiotic environmental factors and primary production (Cotner et al. 2005, Montoya et al. 2005, Roelke et al. 2005) and biota–habitat relationships (Arrington and Winemiller 2005, 2006, Willis et al. 2005). These studies have revealed a strong and pervasive influence of the annual hydrological regime on water chemistry, dissolved nutrient

concentrations, phytoplankton, and densities of aquatic organisms. Significant spatial variation in limnological and faunal attributes is observed both within and between major habitat types, particularly during the low water period when the landscape becomes more strongly differentiated, and nutrients, phytoplankton, and organisms are more concentrated in the reduced volume of aquatic habitat.

We have only scratched the surface in understanding the spatial and temporal variation in the structure of the Cinaruco River food web. New and sometimes surprising findings from descriptive research and experimental manipulations of food web modules are increasing our ability to predict changes in response to seasonal hydrology as well as human impacts. A reliable and detailed description of the taxonomically complete Cinaruco food web may not be a realistic expectation. Nonetheless, as our understanding of modules increases, we hope to expand geographic scales by joining the pieces together in a great interactive network that spans a variety of habitat types. We agree with Reagan and Waide (1996), that complex, species-rich food webs can only be understood through sustained efforts of long-term field research involving multiple, interacting components and processes.

6.13   ACKNOWLEDGMENTS

6.14   LITERATURE CITED

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CHAPTER 7

HETEROCLINIC CYCLES IN THE RAIN FOREST: INSIGHTS FROM COMPLEX DYNAMICS

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7.1   ABSTRACT

One of the persistent paradoxes of ecology has been the existence of megadiverse ecosystems such as tropical rain forests and coral reefs. A long tradition of applying ecological theory to this problem has not been completely satisfactory to most practitioners. Recent advances in the theory of population interactions involving nonlinear complications may shed light on this classic question. Using data from a 15-year study of post-hurricane succession in a forest in eastern Nicaragua, data are presented consistent with the hypothesis that alternative basins exist in the dynamics of this particular rain forest, suggesting that some form of complicated nonlinear dynamics might be partially responsible for the maintenance of species diversity. In particular, the existence of unstable heteroclinic cycles driven by the enemies hypothesis could, in theory, allow for the

coexistence of many species that, in the context of classical theory, should competitively exclude one another.

7.2   THE IDEA OF COMMUNITY STRUCTURE IN HISTORY

Darwin and Wallace traveled the world and marveled at its rich patterns of biodiversity, independently arriving at an elegant solution to the general problem of where it all came from. However, another problem they recognized has proven to be far more recalcitrant. Although evolution through natural selection explains the origin of biodiversity as elegantly as gravity explains the motion of the planets, the ecological dynamics of that biodiversity remains as elusive as dark energy. Darwin's use of detailed natural history observations to elaborate the nature of the "force of selection," as he called it, could be considered as the first modern attempt at elaborating the ecological dynamics that determined whether a particular spot on earth contains one or 100 species. The giants on whose shoulders we sit have pondered this question ever since. Probably, every generation of ecologists feels that, perched on those shoulders, the nature of our metaphorical dark energy is very close to being illuminated. The current generation is no different, to be sure.

The formulation of frameworks that might help make sense of this fundamental problem that has long been a major activity in the field of ecology. Of the more mathematical representations, the framework of Yodzis (1978) can be viewed as summarizing much of the earlier literature, at least in a very general way. Yodzis focused on "competitive" communities and broadly categorized them into two general types—those characterized by a relatively large degree of interspecific competition and those characterized by a small degree of the same. Since the first type, large competition coefficients, would mean that the species that arrived in an area first would dominate the area, and he termed this type as "founder-controlled communities," to be contrasted to the second type, small competition coefficients, in which the species that had the largest competitive advantage would likely dominate, which he termed "dominance-controlled communities." Taking the classical Lotka–Volterra competition equations as a starting point, founder-controlled communities are those in which the competition coefficients are all >1.0, and dominance-controlled communities as those in which the competition coefficients are all <1.0.

Yodzis' framework is certainly useful in categorizing theoretical models of competitive communities. It may also be useful in viewing the intellectual history of the subject. As the descriptive natural historical approach to ecology gave way to a more quantitative approach with the elaborations of Lotka and Volterra in the 1920s, followed by the influential experiments by Gause a decade later, competition became a focus. A milestone, in several ways, was the special meeting of the British Ecological Society in 1944 in which some of the world's most famous ecologists discussed the proposition that Gause's principle of competitive exclusion be taken as the foundation of community ecology

(Anonymous 1944). The implicit conclusion of that meeting was that yes, such an adoption would be a good thing, elevating the competitive exclusion principle to a foundational standard, implicitly on par with natural selection. Such a conclusion was not unanimous, with insect ecologist Diver cautioning that nature's complexity mitigated against the universal operation of such a simple principle and the ever insightful Haldane wondering about the effects of parasites that attack more than a single species (Anonymous 1944). We shall return to Haldane's insights later. This historical meeting to some extent set the stage for ecologists to think more in terms of dominance-controlled communities.

If that meeting of the British Ecological Society was a culmination of the first century of post-Darwin thought on ecology, a couple of insights of Hutchinson would prove to usher in the next half century. One was in the deceptively titled "Concluding Remarks" (1957) and the other was the "Paradox of the Plankton" (1961). "Concluding Remarks," the last chapter in the *Cold Spring Harbor's 1957 Symposium on Quantitative Biology*, formulated the venerable idea of the ecological niche as a formal hypervolume and, more importantly, coupled the idea of niche overlap with the idea of competition. The importance of this work can hardly be overemphasized. Indeed, as noted by Lewontin (2000), the idea of the niche coupled with Darwinian adaptation, provides an incredibly powerful general theory of biodiversity—organisms adapt to fit into niches. While such a framework is largely incorrect (Lewontin 2000, Olding-Smee et al. 2003), the idea of niche hypervolume and the overlap between the niches of two species being related to the interspecific competition between the two, remains an important theoretical grounding for at least one school of thought in community ecology.

But it is the other Hutchinson paper, the paradox of the plankton that is most important for the present discussion. It would appear that organisms that do nothing more than float passively in a liquid medium and photosynthesize (i.e., phytoplankton) are all in the same niche, which means that they are likely, according to the basic idea of Gause's principle, to exclude one another until all but one species remains in the community. They seem to be a classic example of a founder-controlled community. The fact that hundreds of species of plankton all coexist in the same medium is thus paradoxical.

The final chapter in this brief historical review was written by MacArthur (1960) when he recognized that there seem to be two classes of communities. On the one hand, there are those composed of populations that are effectively density independent, more or less following the pattern thought to be so common by the Australian school led by Andrewartha and Birch (1954). MacArthur noted that these communities are effectively populated with fugitive-like or opportunistic species, growing exponentially for some period of time before a density-independent force drove them to lower densities from where they once again grew exponentially. He noted that such a pattern would likely result in a lognormal distribution, as had, by that time, been noted for many species of organisms (Preston 1948, Patrick 1954). These are the

communities that would, after some additional modifications of the theory, correspond to Hutchinson's paradox of the plankton. Furthermore, as explained below, they correspond in principle to Yodzis' founder-controlled communities.

On the other hand, MacArthur recognized communities in which individual species fit into specific niches, more or less corresponding to the sort of structure that Hairston et al. (1960) imagined when they emphasized the importance of density dependence in maintaining community structure, and certainly what MacArthur and Levins (1968) had in mind when they introduced the idea of species packing. The enormous literature examining the details of food web structure and direct and indirect interactions can be thought of as the offspring of this view (e.g., Spiller and Schoener 1988, 1990, Werner 1991, Werner and Anholt 1996, Polis and Holt 1992, Yodzis 2000). In this chapter it is only important to note that MacArthur recognized this sort of community as a type, the type in which niches were in fact important.

MacArthur's original distinction was based on the idea of density independence which is, formally, quite distinct from what Yodzis' classification implied. However, the spirit of MacArthur's classificatory scheme was that the density-independent pattern could account for the ultimate coexistence of species even though their interactions with one another would imply exclusion over the long term. If all niches were separate, from the point of view of biodiversity, it would not matter whether density independence or density dependence were predominant, all species would be maintained in the system. It is only when niches are equal or, even more problematical, when species were especially antagonistic towards one another such that interspecific effects were greater than intraspecific ones, that density independence is especially important. Indeed, the intermediate disturbance hypothesis, simultaneously invented by Connell (1978) and Huston (1979), implicitly assumes density-independent dynamics in a founder-controlled community, periodically interrupted by some disturbance.

There is a certain utility in adopting Yodzis' classificatory scheme. Founder-controlled versus dominance-controlled can be thought of as defining a continuum, with MacArthur's categories positioned at either end. Virtually the same concepts were recognized in Connell's (1978) nonequilibrium versus equilibrium communities, or Wills et al. (1997) in their non-niche versus niche communities. However, rather than thinking of alternative structures, Yodzis' classification allows us to think of any particular community as occupying some position along this continuum, probably an important advance over debates about which of the community types actually represent the natural world (e.g., Hairston et al. 1960, Slobodkin et al. 1967, Ehrlich and Birch 1967, Murdoch 1966).

Despite the intellectually satisfying effect of acknowledging a diversity of community types and the likelihood of a world populated by many of those types along the Yodzis gradient, most of the basic questions asked about any of them remain unresolved. In particular, the fundamental question posed by

Hutchinson about founder-controlled communities remains significant, and in my view, unresolved. As argued in Section 7.3, many tropical ecologists have come to think of tropical rain forests as mainly founder-controlled, with the paradox of Hutchinson looming overhead.

7.3 COMMUNITY STRUCTURE AND TROPICAL RAIN FORESTS

There have been numerous schemas to explain the coexistence of large numbers of tree species in tropical forests. Connell (1978) suggested that most theories could be categorized in a dichotomous fashion, equilibrium-based theories, and nonequilibrium-based theories, a position reiterated more recently (Zagt and Werger 1998), and more or less corresponding to the two ends of the Yodzis continuum (equilibrium-based = dominance-controlled; nonequilibrium-based = founder-controlled). Dominance-controlled communities, which involve niche differences among species, include gap partitioning models (e.g., Orians 1982, Brokaw 1985, Denslow 1987) and models of compensatory mortality (Janzen 1970, Connell 1971, Wills 1996). Although these ideas are clear only when species are divided into pioneers and nonpioneers (or perhaps pioneers, intermediates, and primary forest species), proponents of niche-based theory would argue that the division into pioneers and nonpioneers is only an initial rough cut and that finer divisions are not only possible, but also explain much of species coexistence, even if they are difficult to convincingly demonstrate in nature.

Founder-controlled community models emphasize chance and historical effects (Hubbell and Foster 1986, Chessen and Werner 1981), and, most recently, incorporate the concept of recruitment limitation and space (Hurtt and Pacala 1995, Hubbell et al. 1999, Durrett and Levin 1994). These ideas certainly seem obvious with the pioneer/nonpioneer categorization. However, most proponents of founder-control theory would argue that it is within, not among, such guilds that neutrality applies, and since there are only a few guilds, some form of neutrality or founder control is likely to be a major force.

For example, by combining the two extremes of the Yodzis continuum, it has been suggested that founder control operates mainly at the level of recruitment of new individuals into the community, while factors of dominance control, such as competitive exclusion, operate mainly as individuals sort themselves out within treefall gaps (Zagt and Werger 1998). Chance processes are largely associated with founder-controlled communities while predictable processes are largely associated with dominance-controlled communities, in this context. Thus, the interpretation of Zagt and Werger (1998) suggests that both founder control and dominance control may be at play, but operative at different stages of forest succession.

Most recently (Wills 1996, Howe and Miriti 2000) it has been suggested that a dynamic pattern of natural enemy attack could explain the hyperdiverse nature of tropical rain forests, thus incorporating elements of both a nonequilibrium and equilibrium approach. If all species in the forest are subjected to natural

enemies in the form of herbivores, seed predators, or diseases, the so-called Janzen/Connell hypothesis (Janzen 1970, Connell 1971) could apply at a large scale, preventing competitive exclusion at a large scale, even while permitting its classical operation at a small scale. That is, locally abundant species would be especially vulnerable to natural enemies simply because of their locally high population density (in epidemiological terms, as a local population increases in size, it eventually exceeds the critical value that makes $R_o > 1$). Over the long run, a given unit area (the size occupied by the canopy of a large individual adult tree) would be occupied by a succession of species, not quite randomly chosen from the species pool. If an individual of species A is in a location marked by an excessive abundance of conspecifics, the probability of one of its seedlings taking over that spot in the canopy is lowered due to the higher probability of being attacked by a natural enemy, a result of its presence in a locally dense concentration of its conspecifics. Although it may not be obvious intuitively, there are consequences of the natural enemies' specialization patterns that make this viewpoint especially interesting, namely the possibility of heteroclinic cycles associated with intermediate levels of polyphagy (Vandermeer and Pascual 2006, Vandermeer et al. 2006), as described in detail below.

7.4   ALTERNATIVE BASINS IN EARLY RAIN FOREST SUCCESSION

In classic competition theory (e.g., Vandermeer and Goldberg 2003), if the intensity of competition is too high, exclusion will occur, in which one of two species will drive the other to extinction. If the competitive effect is sufficiently symmetrical, the system will be bistable, in that either of the two species can dominate, and the factor determining which will dominate is the founding density of each of the species (consequently the label "founder-controlled"). A saddle point separates two basins of attraction, and if experiments are performed in which the initial densities are varied, the expectation is that sometimes the starting point falls in one basin and one species dominates, other times the starting point falls in the other basin and the other species dominates, as was shown in the classic experiments of Park (1962). This basic idea applies to a multispecies community as well, if the competition coefficients are relatively large, which is to say, if the community is founder-controlled. Much that is debated about the structure of tropical rain forest communities revolves around the question of whether the community is founder-controlled or dominance-controlled, usually summarized as nonequilibrium versus equilibrium, as discussed above. If, as some expect, it turns out that the tree community of a tropical rain forest is an example of a founder-controlled community, we expect, theoretically, that there will be multiple basins of attraction, just as in the case of the bistable Lotka–Volterra competition equations, except that we expect a minimum of the same number of basins as there are species in the community.

A dynamic feature of the bistable situation is that the Euclidian distance (in the space of population densities) between trajectories emanating from distinct

starting points will generally increase over time in the bistable (nonequilibrium) case. Consider, for example, two experiments, one initiated in the basin for which species A will eventually dominate, and one initiated in the basin for which species B will eventually dominate. Even though the initiation points are in distinct basins, they could be very close together (as two drops of water dropped almost exactly on the continental divide, one of which is a millimeter to the west the other a millimeter to the east). Yet as they approach their equilibrium state, the distance between them inevitably increases. In contrast, if the underlying competitive system is one of coexistence of the two competitors, there is a single basin of attraction and any two initiation points will approach the same equilibrium point, and thus the Euclidian distance between them will decrease.

To visualize the pattern expected under either an equilibrium or nonequilibrium situation, standard Lotka–Volterra competition equations were set up with ten equal species, first with standard competition coefficients set at 1.1 (which insures that all but a single species will become extinct, and that the winner will be a consequence of the initial population densities), second with those coefficients set at 0.9 (which insures that all species will be maintained in an equilibrium state). Figure 7.1a displays sample calculations for the multidimensional Euclidean distance between separate runs (representing alternative starting points in the ten-dimensional system). As expected, when the competition coefficients are set at 0.9, all initiation points result in an ultimate decline in the Euclidian distance, since all trajectories are approaching the same equilibrium point. Also, as expected, when the competition coefficients are equal to 1.1, the Euclidian distance tends to increase. However, in the latter case, there is also the possibility of a decrease, when the initiation points for two trajectories happen to fall in the same basin of attraction, two of the distance patterns with competition 1.1 in Figure 7.1a decrease with increasing time.

Calculating the rate at which the Euclidean distance changes between two trajectories is a standard method in stability analysis, and its application is routine in systems of differential equations. But similar computations from data in the natural world are rare. What are required is two or more replicated time series where the systems have begun at similar points such that their convergence or divergence can be observed. Ecological succession comes to mind as an obvious case in which such behavior could be observed. In tropical rain forest situations, natural succession occurs after natural perturbations that would be caused by storms or even simple tree falls, but rarely in a nicely replicated form.

The study of succession in light gaps caused by tree falls has long been a common feature of forest ecology (e.g., Bauer 1964, Denslow 1987, Sipe and Bazzaz 1995), most often associated with the potential for light gaps to act as a disturbance which drives either the equilibrium or nonequilibrium interpretation of species diversity. At a larger scale, periodic storms act to increase the extent and rate of tree falls, sometimes on a massive scale (Canham and Loucks
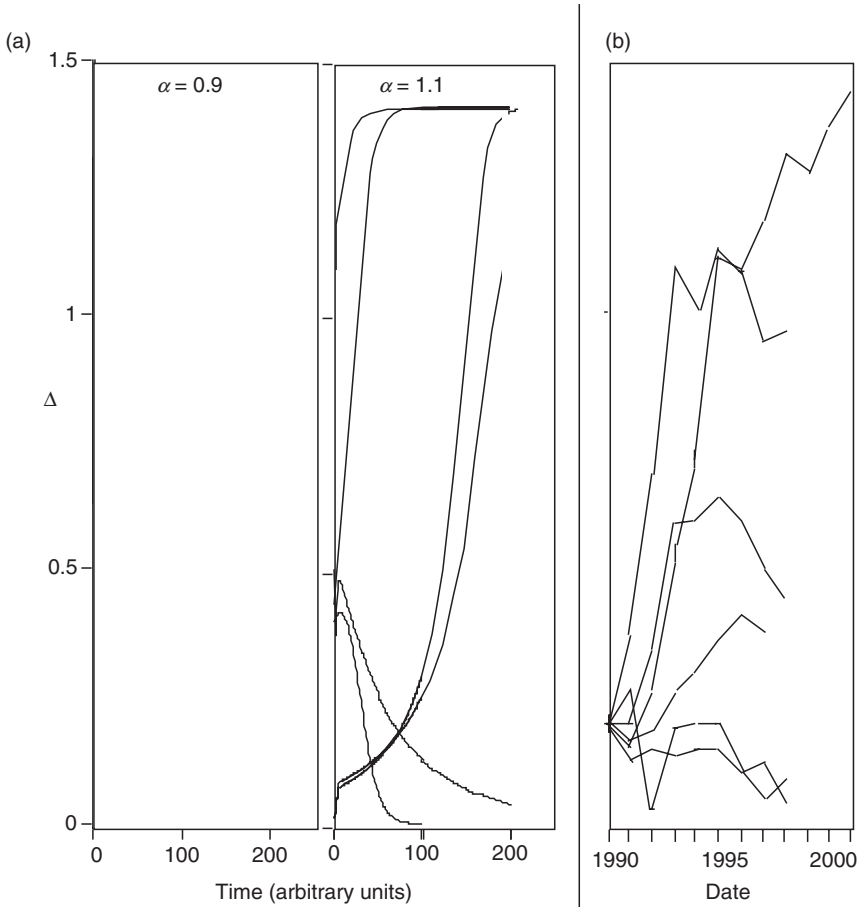
Figure 7.1. Euclidean distance in the space of population densities between alternative trajectories over time. (a) Theoretical expectations shown for six comparisons of either dominance-controlled communities ($\alpha = 0.9$) or founder-controlled communities ($\alpha = 1.1$). (b) Actual euclidean distances for six comparisons of post-hurricane rain forest plots in Nicaragua. (After Vandermeer et al. 2004.)

1984, Boucher 1990, Brokaw and Walker 1991). Damage from a large and strong storm represents an exceptionally large light gap and is thus one end of a scale that begins with a single treefall. More importantly, such an event provides us with an unusual natural experiment. With a storm as large as Hurricane Joan in Nicaragua in 1988 (Yih et al. 1991, Vandermeer et al. 1990), the forest was physically destroyed, yet, because of the recuperative abilities of almost all the tree species, a great deal of resprouting occurred just after the damage, effectively initiating a massive experiment in competition, where all species (~200 in our study) were initiated at the same time point and

we were able to follow them for the next 10 years (Vandermeer et al. 2001, 2004). Separate plots were established, near enough to one another to be independent regarding short-term competitive interactions, but far enough from one another to be thought of as independent samples of the same community. Thus, this data set offers the possibility of asking whether the initial stages of competition follow the expectations of an equilibrium or nonequilibrium situation.

One signal that would help distinguish between these two possibilities (equilibrium/dominance-controlled versus nonequilibrium/founder-controlled) would be the observation of independent trajectories diverging (the drops of water falling on opposite sides of the basin divide). Since the study is in an area that is quite homogenous with respect to topography and soil type, and the hurricane was similarly devastating throughout the region, it is quite reasonable to assume that any difference between two plots is a consequence of either initial conditions or subsequent distinct successional pathways, and not of microsite differences. Because of the arrangement of the study sites (Vandermeer et al. 2001, 2004) there were six possible comparisons in the search for increasing multidimensional distance, the signal for a founder-controlled (nonequilibrium) community and multiple basins.

The results of this study are illustrated in Figure 7.1b (to be compared to Figure 7.1a as a theoretical base, the details of which can be found in Vandermeer et al. 2004). There is a clear pattern in which only two trajectories are clearly declining, while the other four are increasing. We conclude, at least tentatively, that for this particular situation, there seems to be a pattern consistent with a founder-controlled community. It is certainly the case that if these plots were followed for 50 or 100 years, the presently observed pattern could turn out to be one of the initial increases, followed by a decrease, and ultimately consistent with the dominance-controlled community. However, as far as the plots have been followed so far, the pattern seems to be one of increasing Euclidian distance between plots, for some of the comparisons.

Some basic natural history observations at these two sites also support the idea of a founder-controlled pattern. For example, at one of the sites one of the plots had an unusual abundance of one species (*Qualea parensis*) which survived the hurricane, even though experiencing a great deal of damage to each individual tree. One of the other plots at that site had experienced, seemingly because of a chance location of several seed trees nearby, an unusually high density of seedlings and saplings of another species (*Vochysia ferruginea*) in the understory before the hurricane and thus, even though all adults were killed by the hurricane, that plot experienced an unusual abundance of this species. So, one of the plots began growing with an unusual abundance of one species and the other with an unusual abundance of a different species, even though the two plots are only about 400 meters apart. The Euclidian distance between them thus increases as more of the *Vochysias* are recruited at one plot but not the other. In another example, one plot has an unusual abundance of *Hyeronima alchorniodes* and *Dendropanax arborea*, while a nearby plot has few of these two

species but an unusual abundance of *Pourouma bicolor*). This predominance has been increasing in the last 10 years, meaning that the two plots continue to increase their Euclidian distance. As mentioned previously, it could be that *Hyeronima* or *Vochysia* or, for that matter, some other species or group of species will eventually come to dominate both sites and what we are now seeing is nothing more than transient behavior. But, thus far, the data certainly seem remarkably consistent with a founder-controlled interpretation of the community structure of this forest.

7.5   HETEROCLINIC CYCLES IN A FOUNDER-CONTROLLED COMMUNITY

The classic bistable case that results from the Lotka–Volterra equations can become more complicated when multiple species are involved (a remarkable theorem for four or more competing species has, unfortunately, been mostly ignored by ecologists [Smale 1976]). For example, May and Leonard (1975) provided an example in which each of three competing species approaches extinction in an oscillatory fashion. In the particular system they studied, the three species were related to one another in the typical rock, scissors, paper game, in which species A beats species B beats species C beats species A. The result is that species A begins dominating the system, thus reducing species B, which then releases C which increases only to put pressure on A which declines, thus reducing pressure on B which in turn begins to increase and put pressure on C, in a never ending cycle. For a particular parameter set one can calculate that an internal equilibrium point exists (i.e., $A > 0$, $B > 0$, and $C > 0$), but near that point the rock, scissors, paper cycle operates to form expanding oscillations that come closer to the "edges" of the space (i.e., where one or more of the species has a zero population density).

Thus, there is an internal equilibrium point for which all three population densities are greater than zero, but it is an unstable point (also oscillatory), with three saddle points, corresponding to the carrying capacities of each of the species along with the extinction of the other two (Figure 7.2). Thus, the three equilibrium points are $P_1 = (K, 0, 0)$, $P_2 = (0, K, 0)$, and $P_3 = (0, 0, K)$. The system oscillates such that it successively approaches each of the three points, P_1 to P_2 to P_3 to P_1. However, at each cycle the system becomes closer to each of the actual points ($A = P_1$, $B = P_3$, and $C = P_2$), never actually reaching them (except in the limit). This is a classic heteroclinic cycle (Hofbauer and Sigmund 1989, 1998), in which the output from one saddle cycle is connected to the input of another saddle cycle.

It is important to realize that a heteroclinic cycle can be either stable or unstable, just as any other limit cycle. If it is stable, the system gradually approaches the saddle points involved, but if it is unstable, similar to an unstable limit cycle, the system oscillates away from it. The meaning of this basic structure with regard to rain forest communities will be discussed presently.

A

P₁ ○ ----- Saddle point,
A = carrying capacity,
B = C = 0

With C near zero, A
can increase at the
expense of B

With B near zero, C
can increase at the
expense of A

Saddle point,
B = carrying capacity,
C = A = 0

P₃   B

With A near zero, B
can increase at the
expense of C

P₂ ○

C   Saddle point,
C = carrying capacity,
B = A = 0
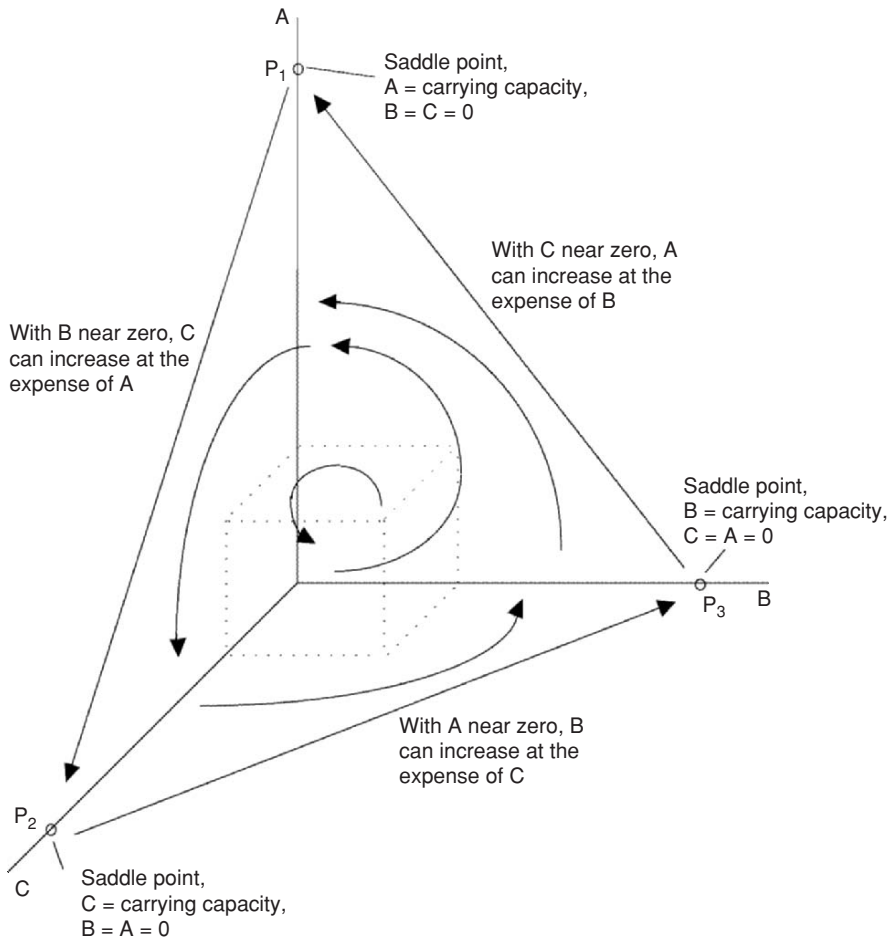
Figure 7.2. Diagrammatic representation of the heteroclinic cycle resulting from the rock–scissors–paper arrangement of competitors studied by May and Leonard (1975).

Recently there has been growing interest in the idea that natural enemies (seed predators, herbivores, and diseases) play an important role in the dynamics of rain forest communities (Wills 1996). The original ideas of Janzen (1970) and Connell (1971) have been resurrected in slightly modified and greatly generalized form to help account for the large number of species in the rain forest. The idea is deceptively simple. As a species becomes locally abundant, perhaps because it had gained an initial advantage over potential competitors, its local high population concentration makes it a target for natural enemies. Its brief competitive advantage is thus eliminated by its natural enemies, and some other species takes its place and becomes, at least temporarily, competitively dominant.

This qualitative idea can be framed in such a way that it appears remarkably similar to the heteroclinic cycles of May and Leonard, as illustrated in Figure 7.3. Rather than a strict rock, scissors, paper game, a multispecies version can be imagined in which species 1 gains a temporary advantage over all others, but by virtue of the hypothesized dynamics, it is doomed because very dominance exposes it to attack by natural enemies. It is intuitively obvious how such an arrangement could result in a heteroclinic cycle, as illustrated in Figure 7.3.

However, there is an important complication involved. When natural enemies are involved, there is an inherent cycle (due to the predator/prey arrangement).
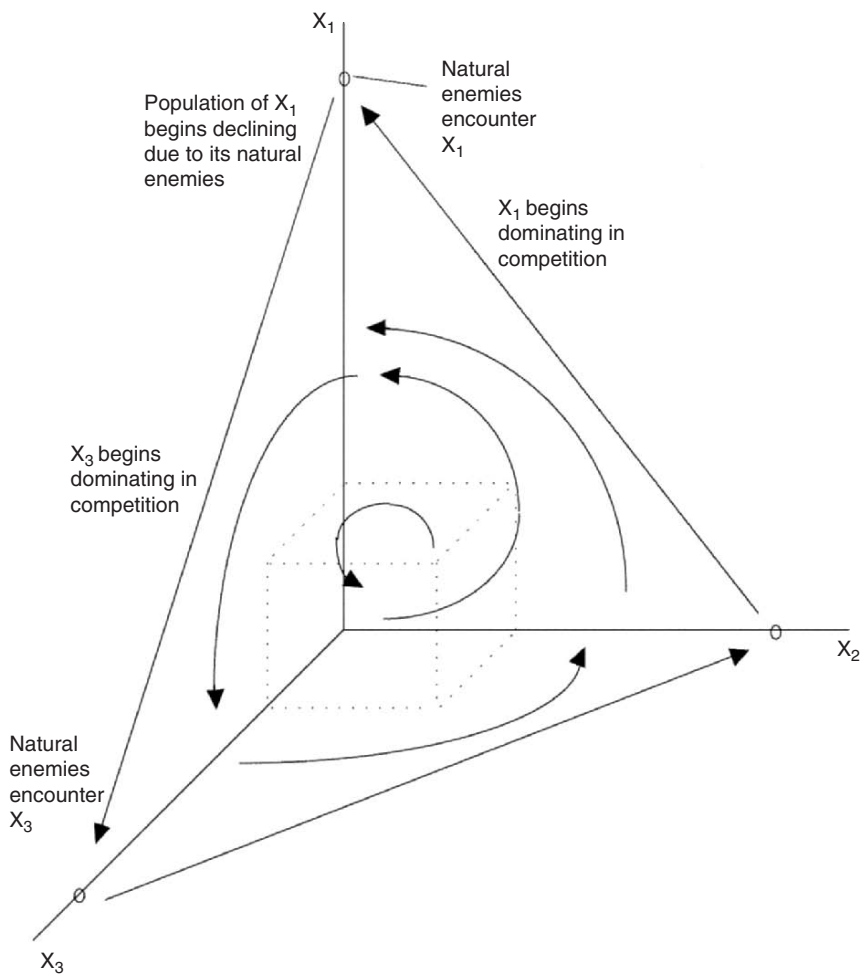
Figure 7.3. Diagrammatic representation of the heteroclinic cycle resulting from the operation of the enemies hypothesis on a founder-controlled community (compared to Figure 7.2).
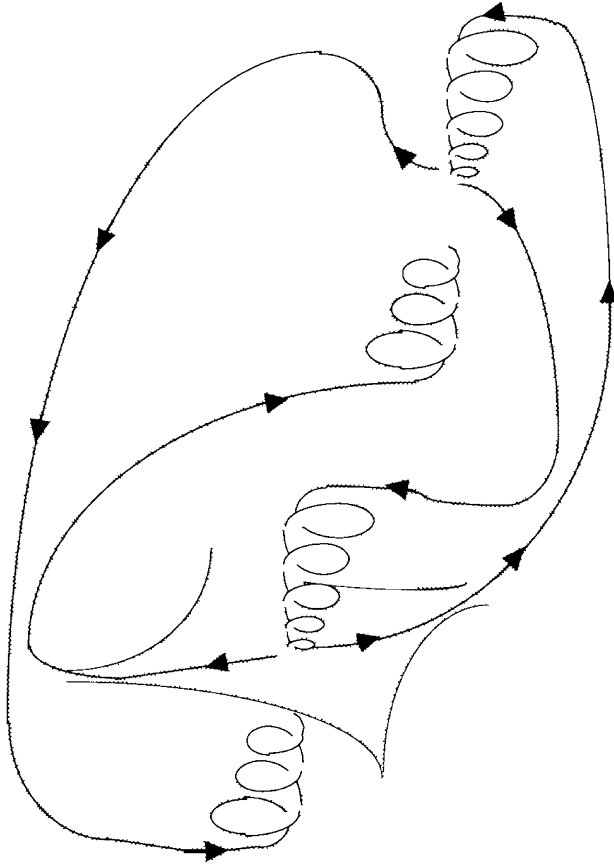
Figure 7.4. Illustration of a heteroclinic cycle in which the saddle points are oscillatory.

A heteroclinic cycle, as noted above, occurs when the outflow from one saddle point is directly connected to the inflow of another saddle point, and vice versa. If the saddle point happens to be an oscillatory one, the underlying dynamics appear more complicated, but they are in principle no different than the simple cycle illustrated in Figures 7.2 and 7.3. The basic form is illustrated in Figure 7.4.

7.6   THE ENEMIES HYPOTHESIS

Species that appear to be ecologically equivalent should not coexist, an idea with a long history, as reviewed at the beginning of this chapter. Indeed, this is the basic problem in founder-controlled communities, where competition coefficients are greater than unity (the situation of neutrality, with competition

coefficients exactly equal to 1.0 is expected to result in the same long-term consequence as a founder-controlled community through random drift—consequently it is reasonable to treat a neutral community as if it were founder-controlled, as is done, implicitly, throughout this chapter). Among the proposed mechanisms to avoid the seeming necessity of competitive exclusion, predation has long been thought to be a leading candidate, beginning with Darwin's famous mowing experiments. This hypothesis takes many forms, from observations of Darwin (1998, also see Van Valen 1974), to an explicit statement by Hutchinson (1948), to the classic experiments that established the central idea of the keystone predator (Paine1974), to experiments with herbivores in grasslands (Harper 1969, Ryerson and Parmenter 2001, Bakker and Olff 2003), to the Janzen/Connell hypothesis (Janzen 1970, Connell 1971) to more recent work with more complicated food webs (Spiller and Schoener 1990) and the implied top-down effect of predators on a lower trophic level (e.g., Schmitz 2003).

More mathematically based theory has also weighed in on the issue. Slobodkin (1961) demonstrated graphically how adding predators could transform competitive outcomes and many subsequent authors elaborated on his basic theoretical scheme (Parrish and Saila 1970, Hsu 1981, Hutson and Vickers 1983, Kirlinger1986, Yodzis 1995, de Roos et al. 1991,1998, Vandermeer et al. 2002). These various theoretical formulations perhaps reached their final conclusion with the work of Schreiber (1997, 1998), demonstrating in a general mathematical form that first, a completely generalist predator could never sustain in perpetuity more than a single competitor species in a founder-controlled community, and second, a minimum of n specialist predators are necessary to sustain n competitors in a founder-controlled community. Schneider's results are general and seemingly close the book on the problem.

However, a new theoretical question seems to emerge from this solution. As a corollary to the fact that a minimum of n specialists are necessary to maintain n competitors, it is also true that if there are less than n predators, the number of competitors will be reduced to one. That is, a founder-controlled community will completely collapse if the number of specialist predators is $n - 1$ or less. In other words, a founder-controlled community maintained in a high diversity state by a single specialist predator acting on each of the species in the community is "structurally unstable" in that if a random event of some sort results in the extinction of any one of the predators, the system collapses entirely. More troublesome is the fact that if a high diversity founder-controlled community has just one of the competitors being controlled by a single predator, that too will be structurally unstable (if that predator should suffer a random extinction, the competitor will drive all the other competitors in the system to zero and the entire system will collapse) (Vandermeer et al. 2006, Vandermeer and Lin 2005).

Thus, it would appear that predators could effectively deter the ultimate collapse of a founder-controlled community. It is, not surprisingly, possible to avoid this conundrum with more complicated formulations. For example,

structured models, either in the sense of age structure or spatial structure (de Roos et al. 1991, 1998, Pascual et al. 2001), or nonlinear behavioral modification such as predator-switching behavior, or stochastic forces (Levins 1979), can indeed permit the species in founder-controlled communities to coexist in perpetuity. However, the question remains whether there is any reasonable formulation short of these complications that will permit the perpetual coexistence of the species in a founder-controlled community. There are two: intermediate polyphagy and multiple unique predators, the second provokes new conceptual difficulties, and leads to a conjecture concerning the "necessity of complexity" as discussed in Section 7.8.

Intermediate polyphagy is explored in detail in other work (Vandermeer 2004, Vandermeer and Pascual 2006, Vandermeer et al. 2006). Here, a simple example illustrates the general point. Suppose a system of ordinary differential equations describes a founder-controlled community of competitors with predators that specialize on a particular prey item (where the prey are in competition with one another), it also eat other prey items at some rate. The following system is an extension of MacArthur's basic consumer/resource system:

$$\dot{P}_i = a[(X_i + c \sum_{j \neq i} X_j)\theta_i - m]P_i \tag{7.1a}$$

$$\dot{X}_i = X_i\left[1 - (X_i - \alpha \sum_{j \neq i} X_j) - a(P_i\theta_i + c \sum P_j\theta_j)\right] \tag{7.1b}$$

$$\theta_i = \frac{1}{1 + b(X_i + c \sum_{j \neq i} X_j)} \tag{7.2}$$

where α is the competition coefficient, a is the predation coefficient, b is the functional response coefficient, and c represents the degree of polyphagy. For the purpose at hand the competition coefficient is set equal to 1.1, thus insuring that, in the absence of predators, all but one of the competitors will be driven to extinction. Furthermore, any population with a density below 10^{-8} is taken to be extinct. Considering a system of four competitors, and four predators, we choose parameters such that neither a set of perfectly specialist nor a set of perfectly generalist predators will provide any respite from the inexorable tendency of one of the competitors to be driven to extinction, and calculate the number of surviving competitor species after 10,000 iterations.

Running this model seven times with random initiation points for all eight species, the average number of competitor species surviving as a function of the degree of polyphagy is shown in Figure 7.5. The pattern is perhaps a bit complicated, but the overall qualitative result is clear and can be repeated for much larger systems (Vandermeer and Pascual 2006). Intermediate levels of polyphagy reduce the likelihood of competitive exclusion. In particular, for this model situation, degrees of polyphagy between about 10 and 30% are capable of
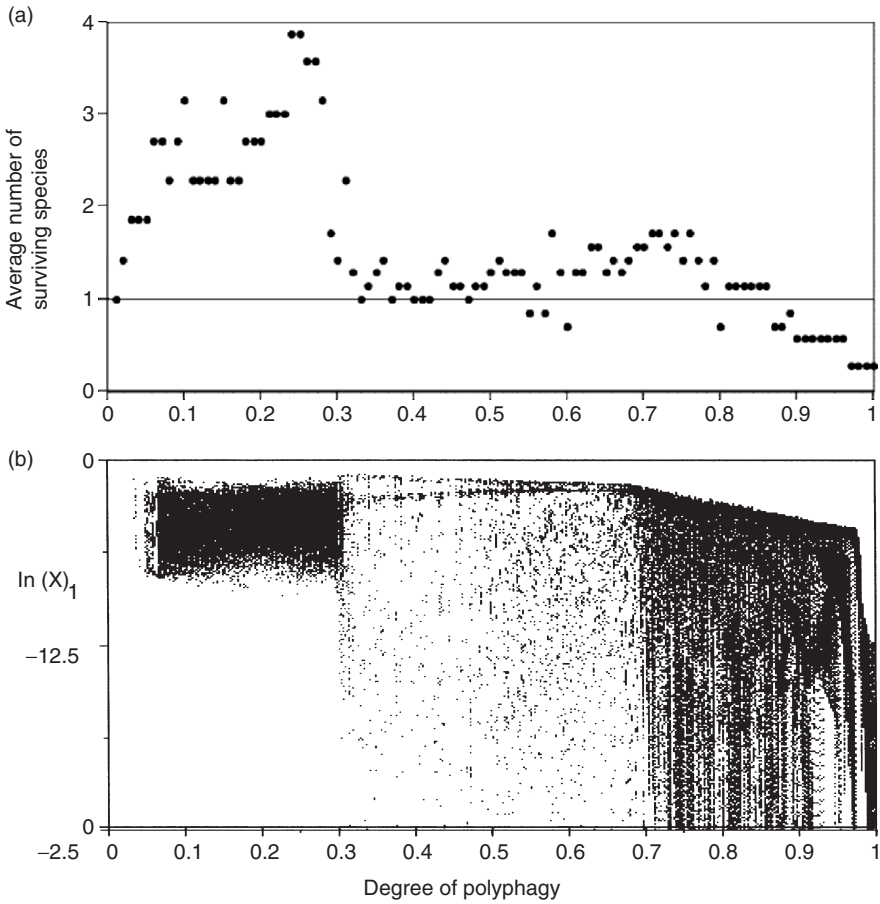
Figure 7.5. (a) Average number of species surviving after 6,000 iterations as a function of the degree of polyphagy in the system (average of seven independent simulations with random starting points), based on Eq. (7.1). Parameter values are $a = 10$, $a = 1.1$, $m = 1$, and $b = 2$. (b) Local minima for the same range of "degree of polyphagy" for the logarithm of the variable X_1.

preserving most, sometimes all, of the competing species. To a great degree the precise result depends on the starting conditions. For example, with polyphagy at 0.27, all four competitor species are maintained in the system for almost all initiation points. However, it is possible to find initiation points for which one or more of the species goes extinct (this usually happens in the transient phase at the beginning of a run). Furthermore, there are other situations in which the entire system collapses (i.e., all four species are lost) mainly because of erratic oscillations in the transient phase, for example, when polyphagy is above 90%. Furthermore, the general result is somewhat complicated if the assumption of pure symmetry is relaxed. These and other complications are explored in detail

elsewhere (Vandermeer and Pascual 2006, Vandermeer et al. 2005). Here, I only wish to note the qualitative result that an intermediate level of polyphagy solves the problem of competitive exclusion in a predator-controlled founder-controlled community, as articulated above. As detailed by Schreiber (1997, 1998), on the one hand, a completely generalist predator is unable to deter the exclusion process in a founder-controlled community, yet, on the other hand, controlling such a community with exactly the same number of specialists as there are competitors would be structurally unstable, thus allowing us to conclude that completely specialist predators also are unable to deter the exclusion process (at least not in the long run). Allowing for intermediate levels of polyphagy is one way of resolving this problem.

This result suggests a somewhat modified goal for field research. Since the original formulation of the enemies hypothesis for rain forests (e.g., Janzen 1970, Connell 1971), there has been a large number of studies focusing on the issue, in terms of seed predation (Boucher 1981, Janzen 1971), herbivores (Sullivan 2003, Barone 2000), and diseases (Gilbert 2002, Gilbert et al. 1994). The majority of these studies have assumed that the natural enemies under study were specialists. That may be true, but it would seem that a new question should be considered, that of the breadth of the niche of the natural enemies. Does the bruchid beetle that attacks the palm seeds in Costa Rica (Wilson and Janzen 1972) also attack other plant species? Seemingly not, but there has never been a complete search for other species that this species of bruchid will attack. Haldane's apparent observation that shared natural enemies could have important consequences for competitive exclusion takes on new significance in light of these theoretical patterns.

7.7 HETEROCLINIC CYCLES AND THE ENEMIES HYPOTHESIS

The pattern illustrated in Figure 7.5a derives from some simple mathematical structures, in particular, from chaos and heteroclinic cycles. First, as noted in recent work (Huisman and Weising 1999, 2001a, 2001b, Passarge and Huisman 2002), coexistence of competitors in a chaotic pattern is likely when nonlinearities are involved. Indeed, for the most part, the dynamical behavior of the system at high species diversity (i.e., within the 10–20% window of polyphagy in Figure 7.5) is chaotic, as illustrated in Figure 7.6a.

An additional dynamic feature is necessary to understand, at least qualitatively, the pattern shown in Figure 7.5a. At relatively high values of polyphagy (above about 30% for the parameter settings that result in Figure 7.5), the system generates a complicated heteroclinic cycle. The way the heteroclinic cycle creates the pattern of Figure 7.5a can be seen in Figure 7.5b, where the local minima of the log of the variable X_1 is plotted for the range of values of degree of polyphagy (parameter c in Eq. (7.1)). For values between about 0.05 and 0.3, the minima are small, but do not always transcend the critical value of 10^{-8} to be judged extinct. At a critical value of about 0.3, the heteroclinic cycle becomes visible, which

(a)

(b)
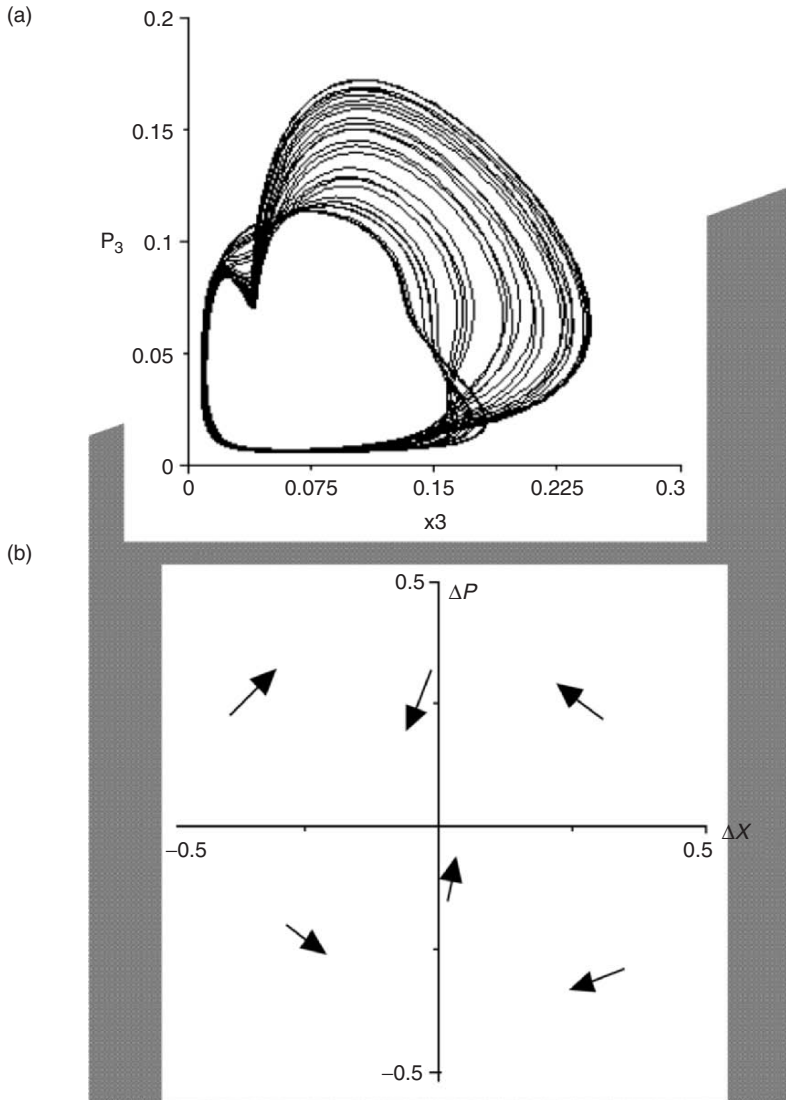
Figure 7.6. Heteroclinic cycles in the four-dimensional system. (a) The space of predator (*P*) versus competitor (*X*). (b) The delta space (the difference between the densities of the two predators versus the difference between the densities of the two competitors), where the four unstable oscillatory situations are clear.

means the variable cycles ever closer to zero (and its logarithm cycles ever closer to minus infinity). Thus, there is a critical point at which the system is likely to have its diversity dramatically reduced, due to the generation of a heteroclinic cycle, the point that can be seen in Figure 7.5a at about 0.3.

A remnant of that cycle can be visualized in a reduced dimensionality of system (7.1). Setting $P_3 = P_4 = X_3 = X_4 = 0$, the system is reduced to the two-competitor two-predator model. For certain parameter settings the system can be forced into a mode of four alternative repellers, each of which is an oscillatory saddle system (oscillations approach a point, but deviate from that point when near it, such that there are effectively repeated oscillatory flybys). Under such circumstances the four-dimensional system can be viewed in two dimensions by defining the following variables:

$$\Delta X = X_1 - X_2$$
$$\Delta P = P_1 - P_2$$

and studying the system in ΔX and ΔP space (referred to here as delta space). In Figure 7.6b a remnant of a heteroclinic cycle based on four oscillatory saddles is illustrated in this delta space.

The reversal of stability of a heteroclinic cycle can explain the results obtained for intermediate polyphagy, as shown diagrammatically in Figure 7.7. In Figure 7.7a, there is a chaotic region bounded by an unstable heteroclinic cycle that pushes trajectories away from the edges toward the center, and an unstable oscillatory point that pushes trajectories away from the center. The resulting chaotic region eventually transcends the extinction limit of the prey species. Figure 7.7b shows an intermediate level of polyphagy in which the chaotic zone has become narrower, such that the extinction limit is no longer violated. Finally, at higher levels of polyphagy the heteroclinic cycle reverses its instability and attracts all trajectories toward the edges, eventually transcending the extinction limit for the prey.

7.8 THE NECESSITY OF COMPLEXITY IN FOUNDER-CONTROLLED COMMUNITIES

Finally we return to a point made earlier. Since it has been rigorously shown that a minimum of n specialist predators are required to stabilize a founder-controlled community of n competitors, it is evident that, even though n such predators could provide that control, such an arrangement would be structurally unstable, since the chance extinction of a single predator would cause the collapse of the entire system. As argued above, one way around this problem is with intermediate levels of polyphagy. However, another way is to have multiple predators controlling each competitor. For example, if there are three competitors in a founder-controlled community and each has a single specialized predator controlling it, if the chance of random extinction of a predator in Δt time is p, the probability of system collapse is p. However, if each competitor has two predators associated with it, the probability of system collapse is $p(1/6)(1/5)$ (the probability that both predators of a given species will become extinct in Δt. Naturally with even more specialist predators associated with each prey species, the probability of system collapse due to a random
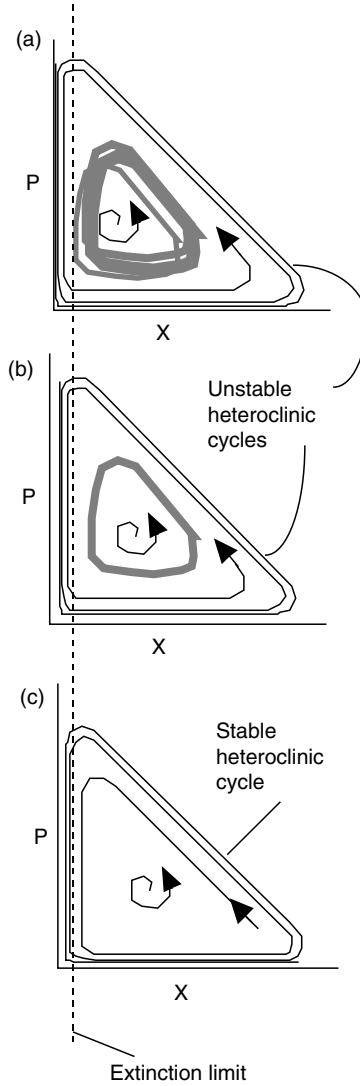
Figure 7.7. Diagrammatic representation of the basic bifurcation between stable and unstable heteroclinic cycle, illustrating the chaotic dynamics (shaded area) that may result from an unstable heteroclinic cycle.

predator extinction becomes very small. Thus, structural stability of a founder-controlled community of competitors can be insured by multiple specialist predators associated with each competitor.

The theoretical problem with this solution derives from the same competitive exclusion principle. The multiple predators must coexist on a single resource.

While this requirement is in violation of classic ideas of competitive exclusion, such a violation is avoided either by the inclusion of critical nonlinearities in the model formation (Armstrong and McGehee 1980) and/or stochasticity (Levins 1979). Either of these additions can be thought of as adding complexity to the basic formation, which, as can be seen, is a necessity to avoid critical structural instability (Vandermeer and Lin 2005).

7.9 DISCUSSION

The forests of lowland humid tropical regions have long been known for their rich diversity. The question addressed by Darwin and Wallace had to do mainly with the origin of this diversity, and the answer was a complex equation (made especially complex at the time because of a misunderstanding of genetics) of adaptation and ecological niches (Lewontin 2000). Modern ecology has reformulated much of Darwin's original foray into the problem of ecological niches. Today this problem is sometimes dichotomized when recognizing the two ends of a continuum. At one end of the continuum is the idea that, much as ecological theory predicts when species occupy distinct niches, tree species in a tropical rain forest are sufficiently distinct from one another that they effectively occupy distinct niches. If this is so, the expectation is that they all will form an equilibrium state in which all species will be buffered against local extinction over the long run. This end of the continuum contains, as a complex intellectual heritage, ideas of density dependence, dynamic equilibrium, and minimum niche overlap resulting from a limit on ecological similarity it is the Yodzis category of dominance control.

At the other end of the continuum is the idea that, much as common sense suggests, the basic biology of trees predicts that they all occupy the same (or very similar) niche. If this is so, the expectation is that they will form a nonequilibrium state (more accurately referred to as a multistable state) in which population densities of all but a single species will decline to zero. This end of the continuum contains as an equally complex intellectual heritage, ideas of density independence, nonequilibrium dynamics, and maximum niche overlap resulting from ecological similarity it is the Yodzis category of founder control.

Most practitioners today would argue that the nature of the tropical world is somewhere between these two continua, thus relegating the interesting intellectual debate to a liberal resolution of a little bit of this side and a little bit of that. Indeed, the most ardent proponent of the founder-controlled community would admit that some trees are undoubtedly pioneers and others undoubtedly characteristic of old-growth forest. Nevertheless, they hold that it is within the category of old-growth habit that hyperdiversity cannot be explained by distinct niches. Similarly, the most ardent proponents of the dominance-controlled community would admit that probably some groups of species occupy very similar niches in the context of the old-growth forest. Nevertheless, they hold that the pioneer/old-growth dichotomy is just the first rough cut in recognizing

what must be important niche differences among all species. So the debate actually boils down to a question of whether the forest is "mainly" dominance-controlled or "mainly" founder-controlled.

In this chapter, some data from a post-hurricane forest in Nicaragua supports (albeit perhaps only weakly) the founder-controlled end of the continuum. This support stems from the notion that if a community is founder-controlled, some trajectories ought to be located in different basins of attraction than other trajectories. In the forest damaged by Hurricane Joan in Nicaragua, a natural yet catastrophic event, early forest succession, not dominated by pioneers, suggests that some of the sample plots are located in distinct basins of attraction from one another, a signal expected from a founder-controlled community.

Among the most popular ideas of rain forest dynamics, not necessarily associated with either end of the dominance versus founder-controlled continuum, is what has come to be called the "enemies hypothesis." Originating with some early ideas of Janzen (1970) and Connell (1971), it has become a centerpiece of thinking about rain forest dynamics. The idea is a simple one in principle. If an individual tree (seed, seedling, sapling, or adult) is located in a high-density clump of conspecifics, it will be an obvious target for natural enemies (seed predators, herbivores, and diseases), especially specialist natural enemies. This enemies hypothesis leads logically to a theoretical structure that is not yet universally recognized. Well known by theoretical ecologists, it has to be with heteroclinic cycles, and leads to some interesting constraints on how communities can be organized by this mechanism.

The idea of a heteroclinic cycle is well known in theoretical ecology (Hofbauer and Sigmund 1989, Kirlinger 1986, Huisman and Weissing 2001a, b, Vandermeer and Pascual 2006). Its mathematical form is quite obvious. The output from a saddle point is connected to the input of another saddle point and vice versa. The basic idea is evident in May and Leonard's classic (1975) analysis of a three-species competitive system where there are three saddle points (1,0,0; 0,1,0; and 0,0,1). As the system approaches the equilibrium 1,0,0 (say) it approaches near the inset of that saddle point, yet it ultimately flies by that saddle point as it comes under the influence of the outset of that same point. It then approaches the second point, 0,1,0, but does the same thing, thus being thrown into an approach to the third point, 0,0,1. In this way the trajectories move from approaching point 1 to point 2 to point 3, to point 1, and so forth.

Heteroclinic cycles can be stable or unstable. In a stable heteroclinic cycle the trajectories approach ever closer to their defining saddle points. If a zero population density is one of the values of one of the populations at the saddle point, this means that that population becomes ever closer to zero as the cycle progresses. This point was emphasized by May and Leonard (1975), where they emphasized the ultimate biological outcome of such a cycle is extinction, even though the mathematics predicts "persistence" (Kirlinger 1986) (i.e., since the population becomes arbitrarily close to zero, it must be biologically extinct even though it is mathematically persistent). On the other hand, a stable heteroclinic

cycle defines a region within which the system cannot escape, and can thus be thought of as a basin boundary or separatrix. Here, the reverse dynamics is apparent. Using the same example as above, if the three species system is set near point 1 (1,0,0), say about (0.99999999, 0.000000001, and 0.0000000001) each subsequent time around the cycle, it moves away from that point. Thus, the cycle formed by the output of point 1 connecting to the input of point 2 and the output of point 2 connecting to the input of point 3, and the input of point 3 connecting to the output of point 1, cannot be breached. It is as if the trajectory is on the edge of the rim of a bowl, and corresponds to the basic idea expressed long ago by Lewontin (1969) of "stability away from the edges."

Heteroclinic cycles can become visually complicated when the system involves natural enemies. Natural enemy systems are inherently oscillatory and thus the saddle points associated with them are frequently saddle cycles rather than points. However, the qualitative nature of the underlying dynamics remains the same, with the added complexity that as a fixed point is approached, the approach itself is oscillatory. This results in oscillations that seemingly are damped, but suddenly veer off and begin an approach to some other saddle point (which also could be oscillatory). This structure is presented in Figures 7.4 and 7.6b.

Given the reality of heteroclinic cycles in many ecological models, and the fact that their existence is more likely as systems become larger (Hofbauer and Sigmund 1998), the basic structure, proposed by many authors, of natural enemy control over founder-controlled communities would seem inevitably to involve heteroclinic cycles. Indeed, some basic patterns involving heteroclinic cycles arise logically from what is known about the dynamic behavior of founder-controlled communities constrained by natural enemies (popular theme amongst tropical ecologists), as presented graphically in Figure 7.3.

Part of the logical structure that emerges derives from the extensive literature on "control from above" when applied to founder-controlled communities. That is, authors from Darwin to contemporary sages, note that there is some likelihood that natural enemies of some sort may distort the underlying inevitability of competitive exclusion in founder-controlled communities (see literature reviewed in the introduction). However, it is a general rule (under the assumption of classical dynamics) that (1) generalist natural enemies cannot change the qualitative outcome expected from founder-controlled communities and (2) a minimum of n specialist natural enemies is necessary to counter competitive exclusion in a founder-controlled community of n competitors (Schreiber 1997, 1998). To appreciate this latter point it is important to add that if, in a founder-controlled community, a single competitor species lacks any natural enemy control, the entire community, all competitors save the dominant, and all their natural enemies will go extinct. In this sense, a community in which a single competitor species has only a single specialist predator can be thought of as "structurally unstable" since a stochastic extinction of its predator would result in collapse of the entire system.

Thus, the theoretical literature on the enemies hypothesis suggests that neither complete generalist nor complete specialist predators can create conditions for which a founder-controlled community will not collapse. There appear to be two solutions to this theoretical conundrum: (1) nature is far more complicated and if we add things like population structure, storage, space, stochasticity, and more nonlinearities, the underlying problem disappears and (2) intermediate levels of polyphagy can result in structurally stable maintenance of a founder-controlled community. The first of these solutions is, of course, a hodgepodge of issues that are not included in the most elementary models and that may very well represent the final answer to the original question of maintenance in a founder-controlled community. However, this "retreat into complexity," begs the question. Is it, with the classical formulation of the models, absolutely necessary to add such complexities to solve the problem? One issue that remains within the simplicity of the classical modeling approach is that of intermediate polyphagy (Vandermeer and Pascual 2006), recalling the queries made by Haldane in 1944 (Anonymous 1944; also see introduction).

Empirically, it is not difficult to construct models in which intermediate levels of polyphagy will allow for coexistence in a system in which both fully generalist and fully specialist predators are not capable of deterring the inevitability of competitive exclusion. One such example is presented in Figure 7.5. In such examples, it is frequently the case (perhaps always the case) that there is a bifurcation point at some critical level of polyphagy at which a critical heteroclinic cycle transforms from a stable cycle (in which most species go extinct) to an unstable cycle (in which the cycle contains a portion of space, maintaining the system within that space), as explained qualitatively in Figure 7.7. Such a structure may or may not be associated with a chaotic attractor also.

There are certainly practical consequences to these theoretical results. If tropical rain forests are in fact basically founder-controlled, any force that limits the natural enemies associated with them may result in the loss of polyphagous control, thus ultimately resulting in the collapse of the community due to competitive exclusion. One could speculate that perhaps some of the still enigmatic "monodominant" tropical forests could be examples of this phenomenon. For example, the palm *Raphia taedigera* occurs in almost monodominant stands in isolated pockets of swamps in the Neotropics (Urquhart 1999). There are sites in Costa Rica in which it occurs in small isolated swamps, but not in other isolated swamps that appear perfectly suitable for it. It is likely that its absence in these latter swamps is due to dispersal limitation (Hartshorn, personal communication), since it has no known dispersal mechanism. Where it does occur, it dominates the forest, which is thus not very diverse. Where it does not occur, a relatively high diversity forest emerges. Is this a case in which a particular species, *R. taedigera*, lacks natural enemies (which, in fact, seems to be the case) and the potential community of hundreds of species of trees has "collapsed"? Other similar examples could be cited (e.g., Torti et al 2001, but see also Gross et al. 2000).

There is also a practical side to this issue. Much as small pockets of swamps may or may not contain a particular species, as the lowland tropics become fragmented, each small fragment may be subjected to random extinctions, not of the trees themselves (which, of course, could also occur) but of the all-important natural enemies. Might it be the case that only highly generalist natural enemies are capable of avoiding the stochastic extinctions that are inevitable in smaller patches of habitat? If this were the case, we might expect higher levels of extinction in the long term, than would be expected from a metapopulation-type model that had incorporated only purely stochastic extinctions in its dynamics. Stochastic extinction at the level of natural enemies could have the effect of switching the overall level of polyphagy such that what was an unstable heteroclinic cycle becomes stable, and the system collapses to a very low biodiversity. This is, of course, purely conjecture, but may be added to the variety of other possible mechanisms of sudden extinction (McCann and Yodzis 1994, Nee and May 1992) previously proposed.

7.10   ACKNOWLEDGMENTS

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CHAPTER 8

EMERGENCE IN ECOLOGICAL SYSTEMS

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8.1 ABSTRACT

The quest to understand animate nature, its origins, current state and future course, its dynamical underpinnings and interface with the physical world, is surely the tacit aspiration of contemporary ecology. As a field of inquiry, academic ecology emerged in earnest from the descriptive realm of natural history in the late nineteenth century when observers of nature, pondering similarity and difference, sought cause. Adopting the classic approach to science, ecologists further described, but also dissected, modeled, conceptualized, and manipulated the parts of ecological systems. What emerged is the modern framework of ecology, built upon the struts of population dynamics and tempered by interactions between species, all within an environmental context.

   Yet with the Earth as a laboratory containing millions of extant and evolving species, the number and variety of plausible ecological studies is functionally inexhaustible. A quick glance through any ecological journal reveals surprising novelty and nuance at every turn. Hence, one is compelled to ask whether progress in ecology is best served by strict adherence to a reductionistic program and unending description, or whether this approach should be blended with more general and epiphenomenological complements. This question is apropos to all of science. Attempts at such a synthesis are well underway sparked by the realities of a complex and decidedly nonlinear nature. In this complex nature *one + one* need not always equal *two*, and the simple logical operator *if–then* requires *else*. In ecology, *if* and *then* produces a highly contingent mapping of their own accord. Add *else*, and we have the fundamental reason for the diversity of nature and the nuance of its expression. What then are mechanisms, the holy grail of reductionist ecology, but manifestations of an emergent nature? Nature can be described by the action of mechanisms explicit in our logical operator. Yet understanding nature requires a deeper knowledge of how the action of the mechanism emerged.

   Here we present a solution to the recalcitrant problem of true or hard emergence, the existence of which has been debated, demonized, and exalted for centuries. We suggest that emergence is hidden within the attractor space of dissipative dynamical systems, or more precisely the interaction between multiple attractors. Our arguments while tentative, suggest that two independent systems can interact in the attractor space and produce a persistent attractor that is essentially an offspring of the parents. Emergence in this case is absolute because no trajectories exist linking the child to either parent. You cannot get there from here. Our arguments are based on a long series of experimental studies that have explored the assembly or construction of ecological communities. We offer this notion of emergence as a general solution to all things emergent independent of any particular system.

Regarded from the broadest possible viewpoint, the vegetation of the earth presents itself as a flowing stream, undergoing constant change. It is not a simple stream but a "braided" one, of enormous complexity, with its origin in the far distant past. . . . Vegetation as we see it today is thus a mere cross section of this complex stream. W.S. Cooper (1926)

8.2   INTRODUCTION

The singular ambition of science rests in the orchestration of two distinct yet entangled constructs, the realization of pattern, structure and process, and its antecedent implicate cause. Yet, as with any human concern, perception and description are intrinsically subjective. Despite attempts to address nature from within structured intellectual formalisms such as the scientific method, reality is simultaneously elusive and readily apparent, the observers' perspective making it so. In many cases, increasingly precise measurement and finer-scale description serves the observer well, by revealing the internal workings of some larger system. However, it is often the case that some macroscale behavior fails to yield to dissection, it is irreducible and the pieces belie the whole. It is here where traditional approaches to science falter. When further reduction proves inadequate, intellectual patches are developed within the existing framework of understanding, or the problem is cast aside as unsolvable or deemed beyond the domain of science. The epicycles of Ptolemy serve as a fundamental lesson. Ptolemy gave elegant structure to patterns observed in the night sky, referential to a central and stationary Earth. Increasingly anomalous observations, however, forced Ptolemy into increasingly convoluted machinations in order to preserve his geocentric cosmology. The cataclysmic revelation of Copernicus, that the Earth was but an inconsequential spot in the cosmos shuddered the foundations of science and society.

In science, progress is typically slow and methodical peppered with bursts of insight and rapid evolution—punctuated thought as it were (Kuhn 1962). Modern science seems to be in the midst of such a revolution, driven by the profound realization that nature in all its forms exhibits fundamental similarities despite profound differences in the system at hand. Time and space are one, nature is fractal and self-organizing, networks emerge with common architecture, and structure can be simultaneously complicated, complex, and simple. Are there fundamental organizing rules at play, and if so what are they and how can they be revealed? Surprisingly, ecological systems provide the ideal platform from which to address this question. Not because they are simple and readily manipulated but because they have proven so difficult to understand. There is

no contradiction here because the analytical difficulties posed by these systems are a direct reflection of their complex nature.

Ecological systems are temporally and spatially contingent, a reflection of history tempered by contemporary mechanism and process. The building blocks that comprise these systems are not fixed entities; they reproduce, move, evolve, and interact in myriad fashion. As such, the rules that govern system structure and function, and define the realized attractor space, are continually rewritten. This fluidity is constrained in a fashion similar to Jacob's (1977) evolutionary tinkerer, and as such new rules do not necessarily imply complete novelty in structure and behavior (Solé et al. 2003). Moreover, ecological systems are embedded within a complex and fluctuating physical environment that exacts a substantial controlling function. Consequently, systems observed today have derived much of their structure from history to such a degree that experimentation in real time is largely incapable of distinguishing between the cause and maintenance of structure (Drake et al. 1996). This epistemological dilemma is further amplified in the arena of evolutionary time, exemplified by questions about the origin and maintenance of recombination and the construction of phylogenies. The *ghost of systems past* has proven to be a serious impediment to understanding nature, and remains a fundamental challenge as we evaluate proximate explanation and hypothesis in the face of a complex ecology (Ulanowicz 1997, 2000, Wagner 1999, cf. Leibniz 1697).

Our present goal is to offer an exemplar for understanding the sources of irreducible complexity in ecological systems. Our concept of emergence is founded on the nature and behavior of attractors, and interactions between attractors that occur in dynamical systems with many degrees of freedom. Recent theoretical and empirical studies in nonlinear dynamics have revealed startling intricacies and unfathomable behaviors during the temporal evolution of even the simplest of dynamical systems. Attractors collide and annihilate one another; fragments of trajectories wander through an infinite space, and attractor basins contain holes sharing solutions with other basins. We suggest that hidden deeply within the exotic behavior of such systems rest the keys to understanding the genesis of emergent properties *and* structure. As a foundation to our arguments, we provide perspectives on two essential issues: first, a brief account of emergence highlighting our perception of this crucial phenomenon; and second, a discussion of the general nature and operation of ecological systems.

8.3   A BRIEF ACCOUNT OF EMERGENCE

In a colloquial venue, the terms *complex* and *complicated* are often synonymic. Within the realm of dynamical systems, however, these terms assume unique meanings. Complicated systems may actually be quite simple, while simple systems may be complex. Systems that are complicated are typically deemed so because they contain a dizzying array of constituent parts. Yet a mapping of these parts, linking piece to piece much like an auto mechanics repair guide or

architect's blueprints, completely describes such systems. Such systems are simple. Complex systems, on the other hand, cannot be so readily decomposed, even if they contain but a few pieces. They comprise a class of systems that self-organize, exhibit nonlinearities, nonequilibrium behavior, and feedbacks across scales that, in concert, are expressed in some macroscopic fashion. Most importantly perhaps, they are historically contingent systems. For example, the butterfly attractor of Lorenz with its fractal structure, food web topologies that confer invasion resistance, the existence of alternative community states, and indeed life itself are all macroscopic reflections of mathematically permissible dynamical themes. It is important to note that historical contingency, determinism, and in fact moderate doses of randomness are not at all mutually exclusive.

How do even simple levels of organization, structure, and pattern arise to acquire a dynamical character in the first place? One means is through self-organization, which has been posited as a process capable of producing such structure from simpler entities (e.g., Ashby 1947, Nichols and Prigogine 1989, Solé and Bascompte 2006). It is a generative device of nature, and all definitions of self-organization contain the following premise—structure and organization develop in the absence of external impositions or forcing functions providing directionality. Implicit is the requirement that thermodynamic realities, particularly the envelope of constraint created by entropy, and the existence of an inviolate mathematics are internal to the system. Whatever the pieces of the system, and the manner in which they encounter one another, entropic realities and mathematic plausibility are capable of selectively identifying and distinguishing between alternatives. The only directionality provided is one of information gain against the gradient provided by entropy, and the constraints imposed by historical contingency. Viewed in this fashion, self-organization is a system's response to its own existence rather than a process per se. When bits and pieces of nature interact, a manifold or space is created which outlines plausible configurations and behavior. Self-organization is some vector of movement on that manifold.

Self-organization produces a structure, collective or ensemble that exhibits properties in addition to those of the constituent pieces. Organisms, for example, have properties lacking in their constituent parts—genes, cells, and molecular pathways. It is here that we encounter the concept of emergence and two irreconcilable schools of thought. All definitions of emergence have at their core some form of irreducibility, whereby properties manifest at a given level of organization are not present at lower levels of organization. The reductionist school readily accepts the existence of such properties but with two important caveats. First, these properties are either a consequence of hierarchically organized structures or are a statistical function of large-number systems. Second, they are irreducible only in the sense that they are manifest at specific levels of organization. While these macroscopic properties vanish at lower levels of organization, the parts of the system contain all the information needed to understand the property. This form of emergence has been variously termed

and conceived as *soft, weak, incomplete, aggregative, contingent*, or *contextual* emergence (e.g., Simon 1962, 1996, Wimsatt 1997, Davies 2004, Emmeche et al. 1997). The complex-holist school, however, suggest that a more formidable form of emergence exists in nature where irreducibility is inviolate. Termed hard or strong emergence, the essential feature of such systems is a complete mechanistic decoupling between the property and the elements of the system, a phenomenon captured by the common phrase "the whole is more than the sum of the parts."

At first glance, hard emergence seems nonsensical, invoking wizardry and in violation of foundational mathematics. How is it possible that the very pieces that comprise a system cannot be used to explain the properties and even perhaps the structure of that system? Confronted with such a system and property, the reductionist school argues that it is a contingent class of properties awaiting explanation, and a consequence of observer naiveté, or that it simply is an intractable problem for the moment (Crutchfield 1994). For example, before the airfoil was understood, bird flight was thought to be the result of so much of wing flapping. Of course this view ultimately implies that given any set of pieces, all possible macroscopic behaviors can be predicted (cf. Davies 2004). If so it should be possible to fully map the neural network of an individual and thereby understand sentience, or given a handful of atoms, distinguish between that which will produce a frog, a bird or some inanimate object (cf. Borges 1941). Whether such a feat is logistically possible is immaterial to the argument, systems exist that cannot be approached through the myopia of reductionism.

Distinguishing between something that might be softly emergent, but not yet understood, and the antithetical postulate of hard emergence creates a kind of Gödelian conundrum. One that cannot be resolved until the system either yields to decomposition, or it is proven that decomposition fails and the genesis of the property is otherwise understood. It is insufficient in our view to simply state, or even demonstrate that a property is emergent having dissected the system to the very asymptotic levels of existence. Nature is simultaneously pieces and wholes with primacy belonging to neither. Uncovering the means by which pieces and wholes generate properties and structure of the hard kind is central to comprehending the nature of nature (Laughlin et al. 2000).

Approaches to understanding the evolution of emergence have had a long and discursive history in virtually every academic field. The result being a vast and intriguing literature, one that is frequently insightful and elegant but often burdened by obfuscation, assertion, philosophical meandering, and even mysticism. Among the more promising efforts, emergence has been cast in terms of a grammar, a set theoretic, an entropic consequence, a quantum phenomenon, a formal logical device, a dynamical consequential, an information theoretic, and a system of variously interacting agents to name but a few. It is not possible for us to provide a conceptual review of such approaches here; hence we invite the motivated reader to explore the works of Mill 1843, Pepper 1926, Ablowitz 1939, Blitz 1992, Rosen 1985, 1991, Klee 1984, Baas 1994, Collier and Muller 1998, Solé et al. 2003, Emmeche et al. 2000, Bonabeau et al. 1995, Schneider and

Kay 1994, Holland 1998, Salthe 1985 and Bar-Yam 2004. And from there, step through the door, or perhaps the looking glass, into discourses on one of the most captivating and beguiling concepts of human thought.

8.4   A VIEW OF ECOLOGICAL SYSTEMS

Ecology is a singular yet synthetic discipline, a blend of biology, mathematics, the physical sciences, and philosophy. Consequently, the fundamental nature of ecological systems remains open to definition, a fact reflected by vastly different conceptualizations. Many believe that ecological systems, communities for example, are compositionally limited by the challenges of the physical environment and dispersal. Surely the environment and species source pool play a powerful role, but such a view fails to explain the vast differences in community organization observed in apparently similar environments. Those who see the world in stochastic and neutral terms have invoked a chance to explain such differences, and indeed chance does play a powerful role in nature. Yet alternative states are recurrent themes and $N!$ states are not observed. In a similar fashion, some see a largely idiosyncratic nature that is hopelessly complicated by historical contingency. Contingently driven, yes, idiosyncratic, perhaps on occasion, but in general this idiosyncrasy stems from a lack of historical information. Most see a finer structure to nature, one driven by mechanisms such as competition and predation, variously tuning food web patterns and directing successional change. Often, however, the focus of this approach is necessarily limited to the presently observed state.

Stephan Forbes, Frederic Clements, Umberto D'Ancona, Lorenzo Camerano, Eugene Odum, and Ramon Margalef among others anticipated many of the more refined notions of ecological reality long ago. While the ideas have been there, the quantitative information and analytical machinery needed to exploit those ideas, is only now becoming available. We now have much more sophisticated models and the computational power needed to explore their ideas. We have numerous journals full of experimental results and an explicit understanding of many mechanisms and processes. Yet we have little generality. Ecology is replete with examples and counterexamples such that any premise is laden with qualification. Predation, competition, and disturbance, behave in one fashion here but not there, and relative abundance and diversity correlate with variables X here and Y there. As a result some have suggested that nature is highly idiosyncratic, dooming ecology to a science of case studies. This challenge, in a very real sense, provided the impetus behind macroscale approaches (Brown 1995, Brown and Maurer 1989, Gaston and Blackburn 2003). Still, the cogs and gears of ecology's own epicycle burden attempts at synthesis because the systems are being approached as if they were simply complicated and in reductionistic fashion.

What we see in the real world—species, individuals, populations, guilds, communities, mechanisms, and processes—are all transient and at radically

different scales. A community described a century ago is no longer as described, and the community described today is in route elsewhere. While concepts like species evolution and community succession have played a role in ecological thought for over a century, the paradigms of ecology remain largely structured around short-term, readily observable phenomena. Any given system can be described in considerable detail over some period of years, perhaps decades; but such analyses constitute a mere snapshot in time. As a result, examinations of the role of competition, predation, and invasion reveal a contingent explanation of those dynamics. We have argued elsewhere that the most significant question is not precisely *how* a mechanism operates here and there, but rather the ontological production of that mechanism (Drake et al. 1996). This does not diminish the primacy of ecological experimentation in academic ecology, but rather it places it into an essential and broader developmental context (Ulanowicz 1997).

We view ecological systems as dissipative, self-organizing, historically derived, nonlinear systems that are typically far from equilibrium. Living systems not only exist within the context of entropic reality (Schneider and Kay 1994), they exploit it. Structure and organization are hierarchical, spanning many levels of organization linked by direct and indirect interactions and accompanied by positive and negative feedbacks. These feedbacks provide integrative information across scales, tuning observed structure and adjusting hierarchical organization. Within and between these levels, self-organization and the dynamical constraints and opportunities imposed by nonlinearity couple with natural selection, and constrain system development to a finite range of structures and behaviors or attractor basins. The manners in which the mechanisms of ecology operate are so defined, with observed structure and pattern as a consequence.

So described, these systems exhibit sensitive dependence to events occurring in system development creating a multiplicity of possibilities (Cushing et al. 2003). Even apparently inconsequential differences in the initial abundance of a population can lead to radically different behaviors, the signature of chaotic population growth (Costantino et al. 1997, Hastings et al. 1993, May 1974, 1976). While there is no single solution or even a fixed attractor for real ecological systems, there are recurrent themes. For example, we see regularities in food web patterns, species relative abundance, and evolutionary convergence to similar solutions. But even these recurrent themes give way to new solutions as the context of the system changes. The environment, the appearance of evolutionary novelties, and species invasion, are all eminently capable of changing the rules and overriding the control exacted by an attractor.

Ecological attractor basins typically contain multiple local attractors, producing the alternative states commonly observed. The realization of one state with deference to another occurs for many reasons ranging from even the most trivial of variations in initial conditions, to chance events with subsequent

dynamical consequences, and the relative roles of determinism and indeterminism during system development. For example, many studies have shown that simple modifications in the timing of species arrival in a community enable new portions of the attractor space that were previously unavailable (Drake 1991, Drake et al. 1993, 1996, Fukami 2004a). The consequence of this adjustment in the attractor is profound, influencing species diversity, productivity, invasibility, the action of mechanisms, and patterns of species coexistence (Gamarra et al. 2005, Fukami and Morin 2003, Cardinale et al. 2002, McGrady-Steed et al. 1997).

As species evolve, invade, or disappear from a system, the rules may change to such an extent that the original attractor is destroyed all together and is replaced by a new one. For example, during assembly studies Drake (1991) found that alternative attractors arose due to small variation in the number of eggs carried by colonizing *Daphnia*. Despite identical population sizes upon invasion, this difference in fecundity led to sustained oscillations in one treatment while no such oscillations occurred in other treatments. A consequence of this difference was variation in community vulnerability to invasion. Even in the absence of these structural changes, *crises* can arise in nonlinear dynamical systems that have profound consequences for system development and subsequent structure (Vandermeer and Yodzis 1999, Gamarra et al. 2001). If all of these sources of complexity were not enough, the collective and emergent properties inherent in an ensemble of species further refines and controls structure. Hence, we have an immensely complex nature manifest in millions of species.

This leads us to suggest that attractor mechanics, the dynamics of dynamics, is the key to a deeper ecological understanding. The answers are partially found in mathematics and its rich catalog of dynamical behavior. The relevance of these formal axiomatic systems has been established by a number of recent studies that have compared model expectation with real world behavior. For example, clear evidence exists documenting the existence of chaotic dynamics (Costantino et al. 1995, 1997), and behavior similar to a Hopf bifurcation (Fussmann et al. 2000) in real populations. Self-similarity has been observed in both structure and time series in plant biophysical geometry (Enquist and Niklas 2002, West et al. 1999a, b), and landscape structure reflects fractal pattern (Milne 1992, Solé and Manrubia 1995). The pieces of ecological systems and the systems themselves *can* behave as offered by contemporary mathematics. Yet an essential element is missing: a developmental complement to natural selection and self-organization. We offer that this element is deeply hidden in the fundamental nature of attractors and is manifest as hard emergence.

We are cognizant of the pitfalls that accompany assertions that some property or structure is emergent. However, we have additional insight from direct experimentation that we believe points the way to an explanation of emergence (Drake 1991, Drake et al. 1993, Cadotte and Fukami 2005,
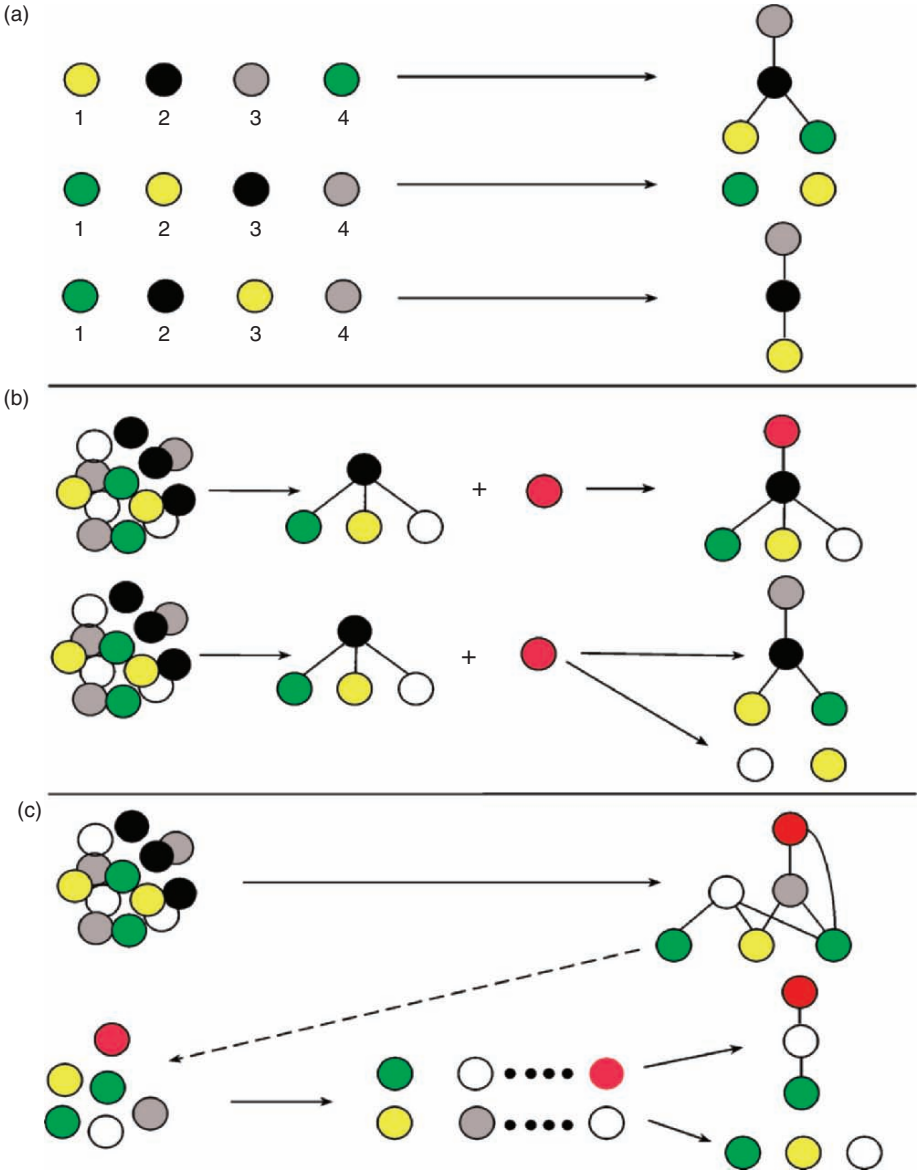
Figure 8.1. Experimental results depicting the rich dynamical behavior exhibited during the construction or assembly of ecological communities. A fixed species pool, depicted as the cluster of species in panel *b*, was established from which populations of each species were introduced to an initially sterile environment. Using different invasion sequences (e.g., species *one* colonizes at time *t*, species *two* colonizes at time *t+1*, and so on) as treatments, the mechanics of community assembly were explored. Panel *a* documents the effect of altering colonization history. Alternative community states are readily generated, representing the activation of specific attractors within the basin of

Cadotte in press, Fukami 2004a, b, Fukami and Morin 2003; see also Drake 1990, Warren et al. 2003). These experiments focused on the construction or assembly of ecological communities in the highly controlled confines of the laboratory (Figure 8.1). For example, vastly different ecological communities can be generated from a finite species pool, as a function of colonization sequence and sensitive dependence to initial conditions (Figure 8.1). In fact sensitive dependence need not be constrained to some starting point, rather it exists in compound fashion in time series and is readily switched *on* and *off* by events as mundane as the order and timing of species colonization and hidden differences in fecundity. This switch is capable of inducing purely deterministic and indeterministic behavior from the same set of species and without exogenous forcing.

Are these behaviors the result of emergent properties and the emergence of structure? We believe so because the structures ultimately produced by assembly, and the dynamical differences that developed, could not be recreated using only those species present in the final community state. These structures represent pure irreducible novelty, because the final community state is fully decoupled from the attractor series that created it. The system effectively does not contain a solution to itself; hence the pieces cannot describe the whole. In what follows we provide a solution to the genesis of emergence.

8.5 ATTRACTOR PROCESSES: INADVERTENT AUTHORS OF EMERGENCE

An attractor is not as simple to define as reason might suggest. As ecologists, we have a fundamental feel for the term acquired through our cognitive, semiotic and derivative philosophical perspectives (Beisner et al. 2003, Cuddington 2001, Egerton 1973). We perceive change in nature—population growth and decline, succession, convergence, divergence, evolution, species turnover, and extinction—trends in one direction or another. As mathematicians our formal axiomatic constructs offer explicit, though varied, definitions of this dynamical consequence (Ruelle 1981, Milnor 1985, Strogatz 1994). In general, dynamical systems possess one or more attractors, solutions to the dynamics towards which the system evolves over time. For example, the familiar

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attraction. Further, some assembly sequences were perfectly replicable resulting in identical communities. However, other assembly sequences were never replicable because the dynamical space created by the sequence effect was either indeterministic or *apparently* indeterministic. Panel *b* illustrates the occurrence of assembly trajectories derived from alternate invasion sequences that crossed in time. That is, at a common point in their development these communities converged to the same structure. In both cases the communities were probed by introducing that same species, illustrated using the red dot. In one trajectory the invader was always successful, while in the other it always failed. Panel *c* presents the *Humpty Dumpty* effect. Here, an assembly trajectory was employed that produced perfectly replicable end-point communities. Subsequently, a species pool was recreated from these species alone (follow the dashed line), after which an attempt was made to reconstruct the end-point community. Reconstruction proved impossible.

carrying capacity (K) of a population growing logistically in continuous time is an attractor of the dynamics. Much like the course of a marble released into a bowl at various starting points within that bowl, a population's initial size creates an alternative trajectory or route to the attractor.

The set of all possible initial conditions defines a basin of attraction, a virtual asymptotic roadmap of the dynamics. This roadmap may lead exclusively to a fixed point like a carrying capacity, or to a repeating sequence of states as in the case of a limit cycle (Ruelle and Takens 1971). The attractor can also be *strange*, having a noninteger dimension or exhibit chaotic dynamics. In nonlinear systems, an attractor basin's, boundary is often a place of extraordinary events, ranging from trajectory leaps into alternative domains of attraction to collisions with the boundary itself inducing bifurcation and subsequent chaos. In the case of our bowl analogy this boundary is clearly defined in the three-dimensional space of human experience. Should another bowl be present, our marble is at the basin boundary if it has a limit of points within each of the basins. But where the marble goes from there becomes a complicated and even complex mathematical situation (Greborgi et al. 1983a, b, c, Alexander et al. 1992).

Of course there are considerable differences between the marble and its animate analogue. Species interact with other species and in so doing create a high dimensional system. This situation is akin to our marble variously interacting with other marbles. Even more of an aberrant, species evolve; hence the marble changes mass or shape, and as a consequence the attractor and its basin change (Wright 1932, Van Valen 1973, Gavrilets 2004). In many systems reducing dimensionality for the sake of tractability is a simple task. While common practice in both theoretical and experimental ecology, such dimensional reduction is simultaneously an essential and dangerous practice. Our *ecology* is based on tractable mathematics and logistically feasible experimentation. In light of these additional complexities, we find it essential to offer a hybrid view of the attractor and a series of conjectures, which we outline below. This view is attentive to the mathematics, but not fully constrained by the limits of our experimental, mathematical, and computational circumstance.

Because attractors are invariant to the dynamics, asymptotic solutions have until recently been the natural focus. However, complex systems demand both a finer and broader scale of observation. Classically, the dynamical middle ground has been viewed as the means to an end, rather than the source of mechanism, structure, and process. Hastings (2004) provides an excellent review of this issue, pointing out that transient dynamics are entirely relevant to understanding systems at commonly viewed time scales (Hastings 2001, Hastings and Higgins 1994). We take Hastings view a step further and suggest that asymptotic behavior is seldom realized in the real world because *nature* happens. Invasion, disturbance, evolution, species movement, and fluctuating resources to name a few, variously eliminate, reshape, and replace attractors altogether. One might ask then, what value is there in understanding

an attractor's short-term behavior or long-term solution given this fickle nature? The answer to this query is a simple duality with profound implications. An attractor is defined by the components of some system under plausible dynamics and attractors interact and evolve in space and time.

8.5.1 A scenario

Consider the behavior of Verhulst's logistic model of population growth brought to fruition by May 1976 (see also Verhulst 1845, 1847, Feigenbaum 1978, 1979). Many excellent expositions of the properties of this and allied systems are available and we refer the interested reader to May 1976, Strogatz 1994, and Ott et al. 1994. This simple equation cast as a quadratic recurrence equation, has the form:

$$X_{n+1} = \lambda X_n (1 - X_n) \tag{8.1}$$

which is typically referred to as the logistic map. The behavior of the logistic map can be visualized by iteration assuming some starting value of x_n, the populations abundance, across some range of values of λ, the growth rate. For example, the first three iterates are:

$$x_1 = \lambda x_0 (1 - x_0)$$
$$x_2 = \lambda^2 (1 - x_0) x_0 (1 - \lambda x_0 + \lambda x_0^2)$$
$$x_3 = \lambda^3 (1 - x_0) x_0 (1 - \lambda x_0 + \lambda x_0^2)(1 - \lambda^2 x_0 + \lambda^2 x_0^2 + \lambda^3 x_0^2 - 2\lambda^3 x_0^3 + \lambda^3 x_0^4)$$

For a range of values of λ over x (where $x \approx 3.569$), no simple attractor exists as can be seen in the well-known period doubling route to chaos (Figure 8.2). Among the more interesting properties observed in nonlinear models such as the logistic map is the occurrence of extraordinary dynamical changes over time, periods of chaotic and regular behavior, and the sudden appearance of persistent cycles over some ranges of λ. While indeed complex there is also generality. For example, any system that can be described by a logistic map follows a period doubling route to chaos in identical fashion yielding a similar fractal structure (Feigenbaum 1978, 1979, Grossmann and Thomae 1977, Coullet and Tresser 1978). Scaling relationships such as this are suggestive of common developmental themes and underlying general rules.

At this point we explore a simple scenario. Consider two independent systems X and Y each residing somewhere on some attractor. Each system has the form of Eq. (8.1) with unique parameter values. If an interaction develops between these systems the dynamics become coupled and the individual attractors vanish. We now have a system of two equations:

$$X_{n+1} = \lambda_x X_n (1 - x_n)(1 - q) + q\lambda_y Y_n (1 - y_n) \tag{8.2}$$

$$Y_{n+1} = \lambda_y Y_n (1 - y_n)(1 - q) + q\lambda_x X_n (1 - x_n) \tag{8.3}$$
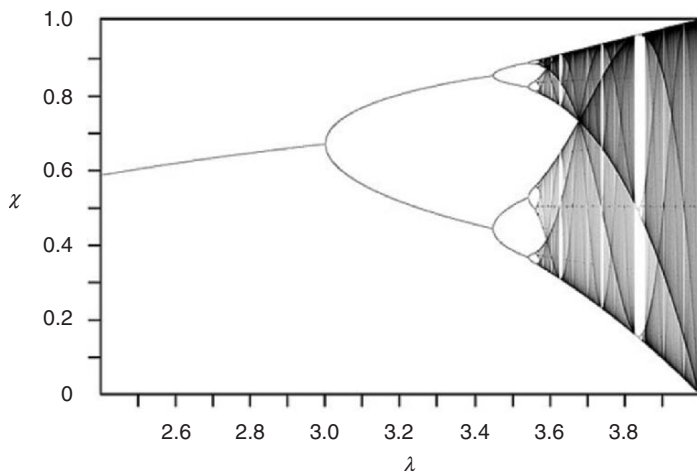
Figure 8.2. The classic logistic bifurcation map revisited. This common numerical simulation illustrates a period-doubling route to chaos that results as a single parameter is tuned.

where q is some coupling value. Clearly when $q = 0$ there is no coupling and populations are independent. When $q = 1$ the equations are coupled and become a reciprocal input-output pair. Coupled forms of nonlinear models have received considerable attention revealing intricate and surprising dynamics (Kaneko 1989, Heagy et al. 1994, Strogatz and Stewart 1993). However, defining appropriate coupling functions remains guesswork despite the fact that this term is at least as important as the base equations. It is possible that the dynamics observed in nature are those that "play well" with the universe of plausible coupling functions. Regardless, the properties of such mathematical representations can be reconstructed because time is fully reversible. This fact limits the emergence of properties of such systems to the soft form, regardless of the dimensionality of the system and its spatial extent. Whether or not such feats are computationally feasible is irrelevant.

Now imagine two sets X and Y, where $X = \{x_a, y_a\}$ and $Y = \{x_b, y_b\}$, each containing a pair of identical uncoupled systems with unspecified but deterministic dynamics. Assume X and Y are replicates, with the members of each set serving as precursors to the establishment of metaset dynamics. In the uncoupled state the paired systems are autonomous but upon interaction this autonomy is lost, and as above we have coupled equations. Assuming identical initial conditions the trajectories of each system are mirror images, moving in lockstep on the attractor. If the initial conditions of x_a and x_b vary, the models exhibit sensitive dependence but the attractors and their basins remain identical, only the route to the solution has changed. This symmetry occurs whether x_a or x_b become coupled with their counterparts at $t = 0$ or some $t > 0$, such points remain initial conditions in X and Y.

However, relaxing the temporal congruity among $\{x_a, x_b\}$ and $\{y_a, y_b\}$ such that coupling occurs at different points during the evolution of each system, redefines the plausible trajectories to the attractors. Destroying the lockstep symmetry observed above. If, for example, x_a of pair $\{x_a, y_a\}$, had begun to exhibit period four oscillations, while x_b of pair $\{x_b, y_b\}$ was in a regular or chaotic realm, upon initiation of their respective metastructures the newly coupled systems exhibit *phenotypic* differences.

Consider what happens when two previously independent systems such as X and Y interact. For example, suppose two previously independent communities are connected, such that individuals can migrate from one community to the other. If the dynamics of the two systems differ (as above), the influence of one community on the dynamics of the other may be asymmetrical. For example, different population dynamics (e.g., limit cycles versus chaos) generate different rates of reproduction. If the rate at which colonists arrives from system X to system Y is determined by the reproduction rate, than the system with the higher rate will exert a greater influence on the dynamics of the coupled metasystem. For a given species, such asymmetry may mean the difference between invasion success and failure. Criminale et al. (2004) have provided support for this notion (Matthews et al. 1991, Pastor et al. 1993). They examined the "competitive interaction" between the dynamics of a set of coupled systems, where one system exhibited a strange attractor and the other a limit cycle. In the absence of external forcing (such as an imposed signal), they found a striking asymmetry in effect contingent upon which attractor type forced the other.

Laboratory experimentation conducted by members of the Complex Systems Group has demonstrated that attractor forcing similar to that above occurs in ecological communities (Cadotte 2005, Cadotte in press, Drake et al. 1993, Fukami and Morin 2003, Cadotte and Fukami 2005). For example, Drake et al. 1993 constructed sets of interconnected community patches that were derived from a common species pool (Figure 8.3). Movement of species occurred as discrete unidirectional events from the source pool to increasingly distant patches, similar to the scenario posed above. This was accomplished by transferring a small subsample from a source community to an adjacent "downstream" community. The rate at which different species arrived at a given downstream patch was not manipulated and tended to be proportional to the species population density in the source pools. Population and community dynamics occurring in source communities served as forcing functions to the dynamics occurring in downstream or target systems, and so on throughout the landscape of patches. Differences among replicate source communities sometimes developed suddenly, most likely because sensitive dependence was induced by small variation in subsamples. As one might expect, differences readily appeared among previously identical target systems.

Time remains reversible in our model, but we now have a means of generating a visible distortion between pairs of dynamical systems. Are there circumstances
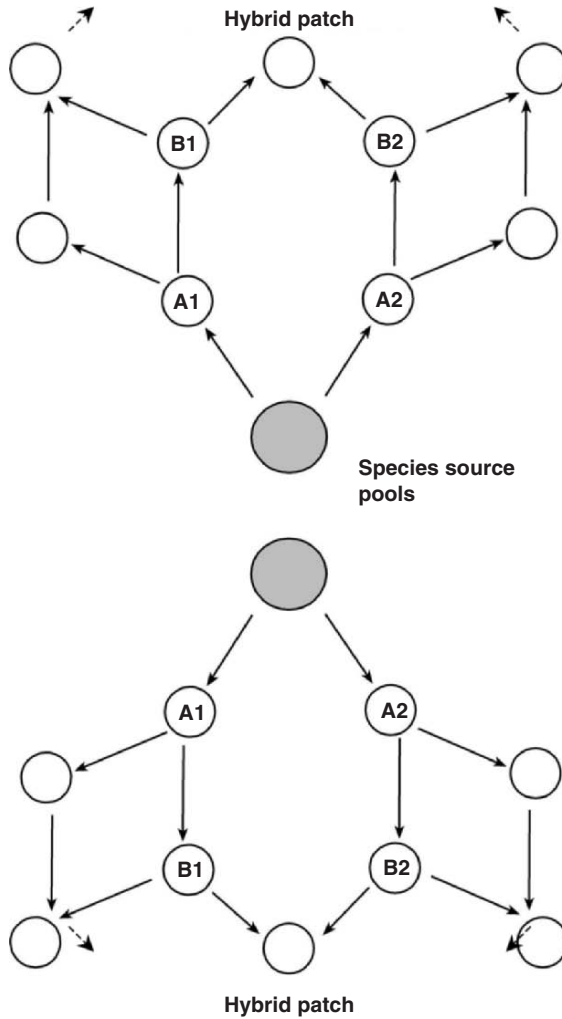
Figure 8.3. A small portion of the landscape topology from a set of experimental studies that explored a spatially extended, laboratory based ecological landscape. Species source pools (grey circles) were assembled by sequentially adding species from a defined species pool of common pond organisms. Arrows indicate colonization pathways. Community patches (A1, A2) were the source of entry into various landscape segments. Assembly processes eventually produced differences in the dynamics of A1 and A2 community patches, patches that interacted via colonization events with developing B level patches. Similarly, B level communities developed alternative dynamics resulting in differences in species composition and relative abundance. Blending B level communities into hybrid patches did not result in convergent structure among hybrid patches.

under which time can become functionally irreversible, or where some forward and reverse operation on a system produces solutions that differ in their stability? The phenomenon of hysteresis provides a well-known example of such an asymmetry (Krasnosel'skii and Pokrovskii 1989). Here, a system subject to a symmetric change in some controlling parameter fails to return to its original state. Rather like increasing the volume of a radio by say 10 dB, but upon reducing the volume 10 dB the result is something other than the volume that existed before the operation was performed. Of course hysteresis generally refers to the behavior of a particular dynamical system. In our scenario, irreversibility arises because the dynamical system itself has changed, such changes may also occur in coupled hysteretic systems.

8.5.2 Uncharted territory

8.5.2.1 *Transience, dynamical capture and collapse*

Systems develop organization, structure, and pattern by gaining and losing elements through a series of coupling and decoupling events. This is effectively an assembly process and it is driven by an exceedingly complex mechanics (Drake et al. 1996). Of particular interest is the dynamical nature of transients that accompany each assembly step—a coupling or decoupling. Transients may be long-lived expressing different dynamics along their course. Hence, the properties of a system far from an attractor can differ markedly from that observed upon closer approach to its attractor (Manrubia and Mikhailov 2000, Hastings 2001). For example, the oscillations characteristic of some predator and prey interactions are preceded by entirely different dynamics. Our experimental work has shown that the transient behaviors that accompany assembly steps in some developmental trajectories can be a rich source of variation. In other such trajectories no variation of consequence is permissible. Based on these results we suppose that the transient dynamics initiated by coupling or decoupling within a metasystem contain several temporally distinct regions of behavior.

Immediately upon coupling, the metasystem enters into a relatively short-lived stage, reflecting a temporary loss of coordination among and within system components as previous dynamical controls collapse. As coordination is asserted under the new dynamics, the residual information contained in the precoupled systems is dissipated. Once dissipated, the dynamics of the coupled system are fully engaged under the new dynamics. We suspect that a system in this early stage will respond differently to exogenous effects than it would once dynamical control has been asserted. By the same token, a system entering into this stage may exhibit sensitive dependence such that residual dynamics are dissipated differently and potentially with alternative solutions. In such a case the systems that comprise the coupled unit, define a family of possible approaches to the attractor, and in fact multiple attractors.

While the earliest events in the life of transients remain unexplored, many studies have documented their long-term behavior (Koelle and Vandermeer 2005, Hastings and Higgins 1994, Ermentrout and Kopell 1994, Pikovsky and Maistrenko 2003, Chazottes and Frenandez 2005). Here, it is not uncommon to observe sequential or cyclic transitions through various limit cycles, quasiperiodic, regular, and chaotic behaviors—all occurring in route to a stable or quasistable attractor that was born by a coupling event. In nature there are no rules demanding that subsequent coupling events must wait until a system reaches its attractor. Hence, the outcome of coupling depends upon the dynamical nature of both systems at the time. The possible variation is striking and exploitable by self-organizing systems of nature.

The route to hard emergence requires the occurrence of events or processes that lead to irreversible steps in time. Emergence derived otherwise is necessarily soft. Any given deterministic system is of course reversible by definition, however this condition is one that is localized in the dynamics. That is, given some arbitrary dynamics the route from the any plausible initial conditions to the attractor(s) and back again can be retraced. Altering system dynamics modifies this localization, with the processes or events responsible for that alteration becoming a feature of the new dynamics. While the system has changed, it remains reversible with reference to the alteration. Here we draw a fine, yet critical line. Self-organized, assembled, or evolutionary systems can potentially lose this localization when historically contingent events like coupling initiate a dimensional collapse during development. At the community level, for example, a dimensional collapse will result if an invading species induces extinctions. Subsequent development will most likely restore or surpass the system's previous dimensionality, though species composition may vary.

Whether or not an interaction develops between systems is contingent on many factors. In nature the opportunity to couple might depend upon chance events placing systems in close spatial proximity, or on the presence or absence of other systems. Dynamical considerations exist as well. The relative location of systems in their respective phase space, a kind of dynamical synchrony, strongly regulates the likelihood of coupling when the opportunity is presented. For example, a predator that encounters a potential prey species whose population happens to be in a dynamical trough, may very well leave the system. Yet that same predator may engage the system if the potential prey has some other abundance. In this case the cause of specific prey population dynamics becomes an indirect mechanism involved in coupling. Our predator may colonize the system because a competitor of its prey has vanished or diminished in numbers. Should the development of an interaction be contingent on itinerant dynamics or events, further system development may result in a system whose representation is irreducible (Kamp and Reyle 1990, Fulton and Harris 1991). Essential components of development cannot be recovered.

A contingent event that permits or prohibits colonization by some species acts as a dynamical switch. When the result of coupling is a new system

whose dimensionality is less than or equal to that of the precoupled systems, a dynamical collapse has occurred. For example, a change in system dynamics can easily lead to extinctions. Should that extinction involve the switch, the reduction in dimensionality yields a system whose remaining parts may contain insufficient information to recreate *self*. This is effectively a distortion in the correlation between microscopic (within system) properties and macroscopic (whole system and its time series) properties. Alteration of the macroscopic state, as in the sequence of events described above, leaves microscopic properties only partially correlated to subsequent macroscopic states. Historical contingency can become embedded within such systems (Kaneko 1998), but it may not be recoverable. To an external observer with complete historical insight, these fleeting events permit a causal understanding. While the system can be recreated from this vantage point, reconstruction cannot be accomplished with the pieces that comprise that system alone. As such the system and its properties are fully emergent in the hard sense.

Such historical contingency is a key feature in higher dimensional nonlinear systems. These systems appear to be dominated by Milnor attractors, which have the curious property of being asymptotically unstable (Milnor 1985, Kaneko 1997). Milnor attractors can dominate significant regions of a multi-attractor basin, yet they are unable to hold all orbits in their local neighborhood. In the absence of disturbance, the system behaves as if it were a classic multistable system, but given arbitrarily small disturbance the trajectories can escape. Under such conditions periodic disturbance has a clear and significant effect. For example, Tsuda and Umemura (2003) show that the existence of Milnor attractors, and their riddled basins, leads to phase shifts or chaotic cycling and itinerancy. Trajectories visit attractor after attractor, exhibiting equilibrium behavior but without the presence of equilibria. Milnor attractors create a situation of extended transience with abrupt discontinuities in the trajectory as it wanders among attractors.

Should the location of previously visited attractors drift, for whatever reason, it becomes impossible to reproduce a system governed by Milnor attractors. Given that systems in early transient stages are at the most malleable stage of their evolution, systems dominated by Milnor attractors should be capable of producing extraordinary novelty. Coupling in such systems should have the same effect as described above, a system whose organization and properties are owed to past transient phases. Further, it is plausible that the trajectory of the system may visit regions of phase space that lay *outside* of the original attractor basin of one or more of the precoupled systems. That is, the coupled system contains space (realizable configuration of structure) that does not exist in the uncoupled state for one of the subsystems. A coupling induced dimensional collapse is a reduction in the degrees of freedom in such a region, and could leave a former system element beyond the confines of its dynamically specified basin. While we are uncertain of the consequences of such a condition, the orphaned system element remains susceptible to coupling to, or *dynamical*

capture by, other systems. If this should prove possible, such dynamical capture immediately generates hard emergence.

8.5.2.2   *Interactions in the attractor space*

Our search for just such a route to emergence began after noticing a curious experimental and theoretical result (Drake 1990, 1991, Drake et al. 1993). Ecological communities can sometimes be assembled that cannot be reconstructed from their constituent parts. This *Humpty Dumpty* effect is a direct result of historical contingency driven by system development in the face of coupling and decoupling. The presence of one or more transient species, or their dynamics, is required to generate the final community state. The mechanics are simple. The presence of transient species at specific times during development actualizes new regions of state space while eliminating others. The result is a modification of the attractor and its equilibria. Among the many consequences associated with such a reconfiguration are changes in species composition, relative abundance, species-specific community invasibility, and the mode of action of specific mechanisms.

After the system has entered a newly created region of phase space, and the species that defined that region is uncoupled from the system, the attractor again changes. Does it return precisely to its previous configuration? Not necessarily so. For example, the timely presence of some species may mitigate the effects of preexisting dynamics such as competition long enough for an alternative outcome to occur. A competitor headed for extinction, but rescued by a transient species, owes its existence to the altered attractor space produced by that species. It would seem that the residence time of transient species is somehow correlated with the probability of such novelty occurring. When the transient species are absent from the final state, the *Humpty Dumpty* effect emerges. Within the dynamical realm, the final community state has no solution to its own structure.

Such dynamics are consistent with the presence of Milnor attractors that route trajectories first here and then there much like the action of the cushion of a billiard table. Imagine the game of billiards where portions of the table cushion occasionally shift from a reflective to an absorbing boundary—so determined by the relative position of balls on the table at each step. Assuming the ball reappears on the table, the dynamics have clearly changed for further play. In direct analogy, our experiments have shown that the same fixed species pool that created the *Humpty Dumpty* effect also contains routes to fully reconstructible community solutions. These systems are not emergent in any sense, and their nature can be fully exposed by reductionistic methodologies. On theoretical grounds it follows that two communities comprised of the same species can exist, where one exhibits emergence while the other does not. This duality suggests that emergence can be something more than a system-level property as defined by the elements that compose the system. Dynamics are involved and the existence of alternative dynamical realms, not simply different dynamics as a function of time, may underlie much of the variation

in community assembly patterns observed in nature. We are suggesting that emergence is a function of the manner in which systems are created, and ultimately the outcome of interactions between attractors.

This leads us to the question of how interactions occur between dynamical systems, while each system's generative dynamics remain autonomous and uncoupled. At first glance contemplating such an interaction seems contrary to experience and untenable. If an interaction exists, that interaction must explicitly exist in the underlying equations. After all two species cannot compete unless they are competing for something, and in that case terms are readily specified. Indeed this is the case, and many interactions are appropriately modeled with coupling terms. However, it is also plausible that interactions can occur vicariously in the attractor spaces of dynamical systems where direct interaction terms are inappropriate. Here, the generative dynamics of one system modifies the attractor space of another system precluding previously viable trajectory routes and creating others. In ecological systems, where spatial extents are explicit, such processes surely exist when two or more communities serve as source pools for the creation of a new community.

As an example, consider two or more rule-based cellular automata (CA) operating independently but on the same grid or lattice. In such a system, an occupied or open cell, produced by the evolution of one system potentially modifies the developmental trajectory of others (Figure 8.4). There can be no doubt that each system will evolve in a fashion that differs from the situation when they are operated on independent grids. Certain trajectories are preempted while others are created to such an extent that the familiar "creatures" (e.g., gliders, blinkers) produced by a single rule base may no longer evolve in the coupled system. Our thought experiment suggests that coexisting yet autonomous systems, can distort the available attractor space by functionally eliminating solutions to some trajectories while enhancing others. This distortion is a source of novelty capable of creating dynamical opportunities that could not otherwise exist.

It is important to recognize that an attractor's character is defined at multiple levels of scale that are discordantly viewed by constituents of the system. In the absence of hard emergence, the system expresses collective dynamics, and its constituents, express dynamics decomposable from the system. Thus the constituents define a basin of attractor and the subsequent movement of that system in space and time. But what of systems where collective dynamics are irreducible, creating caveats in the fundamental mathematical operators of $(=, +, -)$, and simply eliminating associative and commutative algebras?

8.6   CONCLUSIONS: WHEN YOU CAN'T GET THERE FROM HERE!

Inquiry in science generally proceeds by noting some macroscale pattern, structure, or phenomena, followed by dissection of the system in question. The observer, armed with information about interrelationships among pieces that
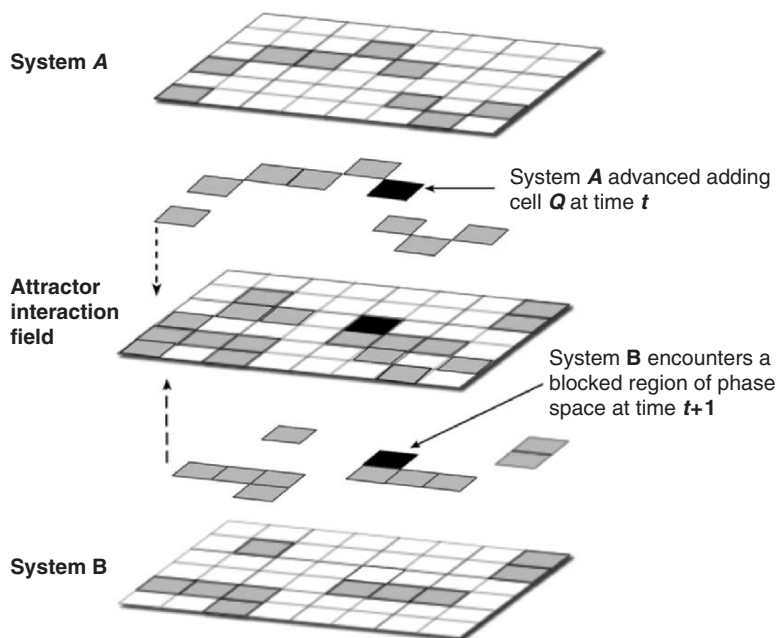
Figure 8.4. The interaction between two systems without explicit dynamical coupling is most easily visualized by considering two two-dimensional cellular automata. Systems, *A* and *B*, are shown developing independently in the top and bottom lattices. However, the *attractor interaction field* represents a situation where both systems coexist on the same lattice. System *A* and *B* come into conflict over cell *Q* which system *A* occupied immediately before the trajectory of system *B* reached that location. This situation effectively represents a change is the boundary conditions of system *B*.

comprise the system, variously manipulates those pieces with the explicit aim of implicating the mechanisms and processes responsible for observation. This approach works exceedingly well in a broad class of simple hierarchically structured systems, and provides some degree of operational adequacy. However, this approach stumbles when confronted with complex systems, retreating to statistics, and the contingent level of understanding available by focusing on the maintenance of structure. Maintenance and cause represent two very different levels of understanding, one proximate and one fundamental. There is a limit, an asymptote if you will, to the knowledge attainable given our predisposition to reduction. While the decomposition of a complex system can lead to a level of mechanical operability, it does so at the expense of understanding.

Pattern and structure arise via many processes and mechanisms inextricably woven together with emergence. Self-organization and chance create opportunity that subsequently derives directionality from assembly mechanics while being tested by natural selection. The operation of process and mechanism is ultimately shaped by system-level constraints operating at various scales

of organization. As such, the mode of action permitted under the dynamics, and plausible under the constraints, is but the phenotype of causal processes that are historically derived.

We began this paper based upon conjectures we have developed to explain the intriguing behavior of the assembly experiments discussed above. These experiments have shown that (1) the attractor space is richly varied and complex, (2) a portion of this space is deterministic, while a portion is indeterministic, (3) attractors can dynamically break, after which there may be no link, trajectory or solution from the original attractor or parent to the new or child attractor. The *Humpty Dumpty* effect is real. The only explanatory recourse remaining is to conclude that hard emergence exists, and that its source is in the creation, evolution, destruction, and interaction of dynamical attractors. Hence, emergent properties and structures are not magical or mystical manifestations, they are not simply systems that push the bounds of human logistical and computational limits, nor are they philosophical or linguistic constructs of the mind. Routes to emergence necessarily exist because emergent systems exist, and as such emergence can be understood. Nevertheless, the parts of such systems in extant reality cannot explain the whole.

In this discourse we have offered the essential key and some of the foundational elements necessary to understanding emergent property and structure. Without doubt our framework is incomplete and additional elements remain hidden waiting to be uncovered. Considerable work also remains in developing a robust mathematical approach to attractor interactions, beginning first with interactions among low-dimensional systems and then approaching more realistic high-dimensional systems. Academic ecology, one of the driving forces behind the movement known as complexity, is at a critical intellectual juncture along with a handful of other scientific disciplines. While more case studies and documentation are indeed valuable, we are now in a position to step past pure dissection and description, and realize the promise of a causal understanding; arguably, for the very first time in human history. Emergence is at the center of this foray and within an understanding of this dynamical realm is the solution to nature.

8.7 ACKNOWLEDGMENTS

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CHAPTER 9

DYNAMIC SIGNATURES OF REAL
AND MODEL ECOSYSTEMS

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9.1   ABSTRACT

Model systems can be used to generate time series. Given that specific structures predominate in food webs (e.g., a food chain lies within every food web) and that such ubiquitous structures have characteristic spectral signatures, then we ought to also expect to find these signatures in real time series. Not long ago, it was shown that chaotic solutions to autonomous discrete-time models for single populations tend to have "blue" spectral densities or blue signatures, in which high-frequency fluctuations are prevalent. This seems at variance with a number of studies that suggest real biological populations tend to have "red" time series, where low-frequency fluctuations prevail. Here, we argue that blue spectral densities are peculiar to discrete-time, single-population chaos, and that solutions for interacting populations (hence, for populations in nature) tend to have resonant spectra, with fundamental harmonics of relatively low frequency. In the absence of extremely long time series, these spectra will appear to be red.

9.2   DISCUSSION

Something approaching a consensus has been emerging in the literature, concerning the form of the spectral density of population fluctuations. Several studies indicate that the spectra tend to be "red," (e.g., Pimm and Redfearn 1988, Arino and Pimm 1995, Sugihara 1995). Similarly, it has been argued that the environmental variation experienced by natural populations tends to have a red spectrum (Steele 1985, Halley 1996, Vasseur and Yodzis 2004). It seemed inconsistent when Cohen (1995) showed that chaotic solutions to autonomous discrete-time models for single populations tend to have "blue" spectra, with high-frequency fluctuations prevalent. There is, however, evidence that structured models for single populations, for instance, those with spatial structure (White et al. 1996) or time delays (Kaitala and Ranta 1996) have red spectra. We suggest another potentially very powerful mechanism that produces red spectra, and is universal in natural systems, namely, interactions with other populations.

One is accustomed to seeing red spectra for chaotic solutions to continuous time models of interacting populations (e.g., Schaffer and Kot 1986). Is this difference from the blue spectra of discrete-time single-species model due to the differing mathematical artifices employed in the two cases (differential equations on the one hand and difference equations on the other) or to the presence of interactions? Figure 9.1 shows the power spectrum of the resource species N for a chaotic solution to the continuous time food chain model (McCann and Yodzis 1994):
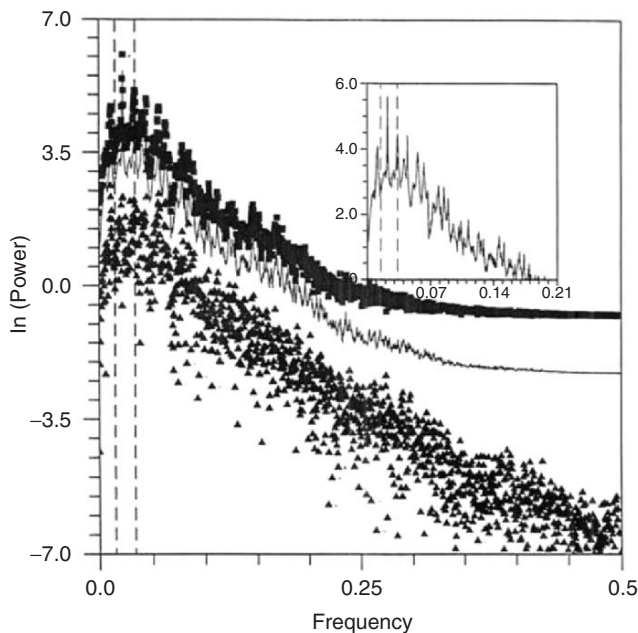
Figure 9.1. Power spectral density of N in the continuous-time food chain model Eq. (9.1).

$$\frac{dN}{dt} = N(1 - N) - 0.804\frac{CN}{N + 0.161}$$

$$\frac{dC}{dt} = -0.4C\left(1 - 2.01\frac{N}{N + 0.161}\right) - 0.4\frac{PC}{P + 0.5} \qquad (9.1)$$

$$\frac{dP}{dt} = -0.08P\left(1 - 5.0\frac{C}{C + 0.5}\right)$$

Plotting the mean (solid curve), maximum (squares), and minimum (triangles) over 100 initial values as Cohen (1995) did for his discrete-time single-species models. The spectrum is red—it falls off at large frequencies.

However, it is not a simple *l/f* spectrum (Halley 1996). As seen most clearly in the inset, which shows just the mean curve at the lower end of the frequency range, there is a peak in the region delineated by two dashed lines. Those dashed lines are the two oscillatory frequencies that are present in this system: (1) the frequency of oscillations in the consumer–resource plane (i.e., the dynamic when the top predator, P, is held at zero) and (2) the frequency of oscillations in the predator–consumer plane (estimated by adjusting a parameter just across the Hopf bifurcation that gives a stable equilibrium in the consumer–resource plane, and a cycle very nearly parallel to the predator–consumer plane—see McCann and Yodzis 1995). The spectrum has a broad resonance, defined by these fundamental harmonics, with a decrease at higher and lower frequencies. Because the fundamental harmonics have relatively low frequencies, it is appropriate to call such a spectrum "red."

We suggest that this behaviour is typical of systems of *interacting* populations generally, be they modeled in continuous time or in discrete time, because such systems are constructed from consumer–resource interactions as basic "building blocks," and these component systems tend to exhibit oscillations with periods ranging, for plausible biological parameter values (Yodzis and Innes 1992), from 3 to 10 years or more. For instance, Figure 9.2 shows the "blue" spectrum for one of the single-species models studied by Cohen (1995):

$$N_{t+1} = 3.7N_t - 2.7N_t^2 \qquad (9.2)$$

Adding a consumer

$$N_{t+1} = 3.7N_t - 2.7N_t^2 - 2.5N_tP_t$$
$$C_{t+1} = 2.5N_tC_t \qquad (9.3)$$

gives the spectrum for N shown in Figure 9.3, and Figure 9.4 shows the spectrum of N if a predator is added to that system (a discrete-time three-species food chain):

$$N_{t+1} = 3.7N_t - 2.7N_t^2 - 2.5N_tP_t$$
$$C_{t+1} = 2.5N_tC_t - 2.75C_tP_t \qquad (9.4)$$
$$P_{t+1} = 2.75C_tP_t$$
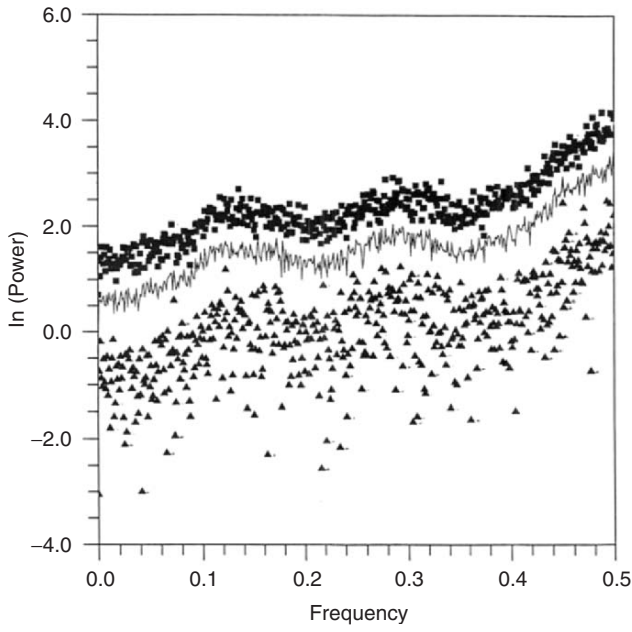
Figure 9.2. Power spectral density of N in the discrete-time single-species model Eq. (9.2).
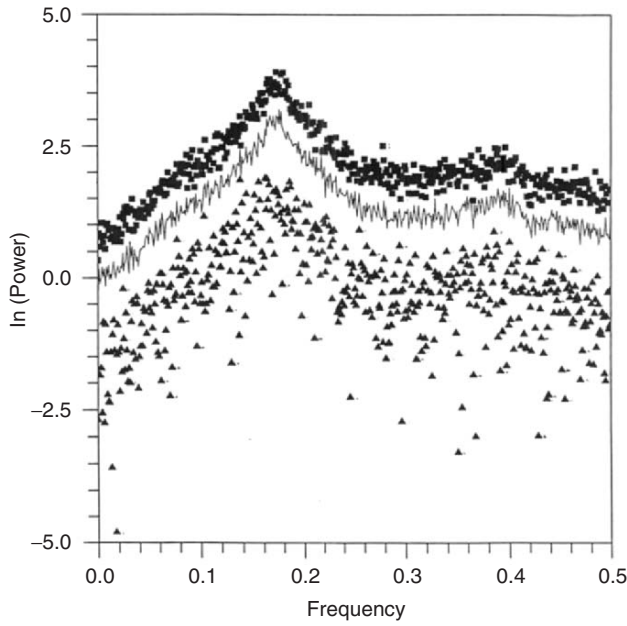
Figure 9.3. Power spectral density of N in the discrete-time predator–prey model Eq. (9.3).
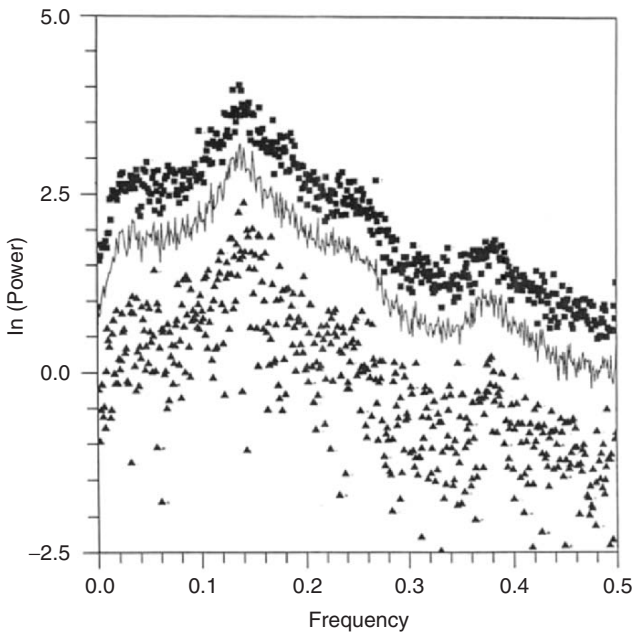
Figure 9.4. Power spectral density of N in the discrete-time food chain model Eq. (9.4).

As in continuous-time systems, interactions produce resonant chaotic spectra, with relatively low frequency fundamental harmonics. Because of their bifurcation structure, underlying oscillatory frequencies for these systems cannot be cleanly extracted, but the resonance occurs in the expected range of frequencies. The blue spectra seen in single-species discrete-time chaos can be understood similarly as deriving from resonance. However, in those systems the fundamental harmonic has frequency 1, and frequencies higher than this are not observable, since the time series is only defined at intervals of one-time unit. Therefore, all frequencies observed are lower than the resonant frequency, so one can only see an increase in spectral power as frequency increases. Since all natural populations interact with other populations, red spectra ought to be typical of oscillatory dynamics in strongly interacting communities. Our results ought to also work for the transient dynamic phase of interacting natural populations since such dynamics frequently display characteristics similar to oscillatory solutions during the transient. This is generally true even if the long-term dynamics are stable equilibrium dynamics since the transient tends to display fluctuations due to the nature of the underlying C–R building blocks.

9.3   ACKNOWLEDGMENTS

9.4   LITERATURE CITED

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CHAPTER 10

EVOLUTIONARY BRANCHING OF SINGLE TRAITS

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10.1 ABSTRACT

In this paper, using the methods of adaptive dynamics, we develop a framework to explain how evolutionary branching of multiple species or types occurs. The biggest difficulty lies in the change in dimensionality of adaptive dynamical systems before and after branching. We introduce a "double-dimension method" to work around this problem, and deduce branching conditions. These conditions comprise a coexistence condition for mutants and their parents, and a saddle condition for the evolutionary equilibrium in the "doubled" system. The results imply that the branching of multiple species leads to their interference with one another by eliminating the coexistence region of other species and their mutants. If they can coexist with their mutants, then they branch independently.

10.2 INTRODUCTION

The observed diversities in ecosystems, and the processes of speciation, have long represented intriguing challenges. Understanding the emergence of new species is crucial to the study of biodiversity, and the study of species inter-actions was the special province of Peter Yodzis. Traditionally, theoretical approaches to ecology and evolutionary biology have been as separate as the timescales on which they are usually assumed to occur. The literature on population interactions and the associated theory of food webs generally take the properties of species as given, and allow no evolutionary modification. On the other hand (Levin 1978), evolutionary theory treats population densities as fixed, and ignores population dynamics. The theory of adaptive dynamics, the focus of this paper, has taken great steps toward unifying these two literatures.

In evolutionary theory, allopatric speciation and sympatric speciation are the two dominating theories, and sometimes even compete. Allopatric speciation means that geographically isolated subpopulations of a species evolve independently into isolated species, while sympatric speciation means that two or more species evolve from a single parent species within its dispersal range. Allopatric speciation is both well studied experimentally (Rice and Hostert 1993) and confirmed in numerous field studies (Joyeux et al. 2001, Bilton et al. 1998).

Sympatric speciation was once thought to be at best rare (Mayr 1963), because of a lack of understanding of appropriate genetic mechanisms, but Maynard Smith (1966) and others showed that sympatric speciation is possible under disruptive selection (Thoday and Gibson 1962, 1970), in which subpopulations dwell in environments in which selection favors the extremes, but disfavors the intermediate genotypes. Although Maynard Smith's model assumed habitat separation, some real populations, like the warblers (MacArthur 1958), Darwin's finches (Lack 1947, Grant 1999), and Arctic charrs (Sandlund et al. 1992) clearly show a relationship between species and the resources they utilize.

It is more natural to assume that the evolution of these systems is driven in large part by resource competition, instead of habitat isolation alone. Rosenzweig (1995), Metz et al. (1996), and Drossel and McKane (2000) showed that competition pressure alone can lead to sympatric speciation. In the adaptive dynamics literature, this phenomenon is referred as *evolutionary branching* (Geritz et al. 1997, 1998, Doebeli and Dieckmann 2000).

However, two problems hinder the application of evolutionary branching theory to the study of systems like MacArthur's warblers, Darwin's finches, and Arctic charrs. Firstly, the speciation of these species involves coevolution and branching of multiple species with multiple traits. Unfortunately, the branching of multiple species is poorly understood, because the branching species may suppress one another, and complicate the analysis (Geritz et al. 1998). Secondly, these species undergo sexual reproduction, and thus can maintain a phenotype distribution that cannot easily be represented by a single trait value, which is required by the current evolutionary branching theory (Geritz et al. 1997, 1998).

The purpose of this paper is to solve the first problem by building on the framework of Metz et al. (1996), Dieckmann and Law (1996), and Geritz et al. (1998)—we explore the coevolution and branching of multiple species, while keeping the assumption that species can be represented by a single trait value.

10.2.1   Modeling the evolution process

Following the framework of Metz et al. (1996) and Dieckmann and Law (1996), we model the evolutionary process with a mutation-based model, where a mutation of a resident species is introduced into the resident community at a specific rate. The biology here is highly simplified. Reproduction is asexual, and real "species" are defined by a simple character. Changing that character, in effect, results in a shift of species.

Assume that we have a coevolving community $\vec{X} = \{X_i\}_{i=1}^{n}$, and environment $\vec{Y} = \{Y_j\}_{j=1}^{m}$, the latter representing resources or species that do not evolve. Each X_i is characterized by a trait $s_i \in \mathbf{R}$. We introduce the notation $\vec{s} = \{s_i\}_{i=1}^{n}$, to represent the vector of traits that characterize the current community, and are permitted to change through an evolutionary process to be described. We call the set of all the possible traits $\vec{s}$ the *trait space S*. The population dynamics are given by:

$$\dot{Y}_j = F_j(\vec{X}, \vec{Y});\tag{10.1}$$

$$\dot{X}_i = X_i r_i(\vec{X}, \vec{Y}; s_i, \vec{s}).\tag{10.2}$$

where $F_j(\vec{X}, \vec{Y})$ are continuous functions defining the rates of change in Y_j, and the functions $r_i(\vec{X}, \vec{Y}; s_i, \vec{s})$ define the growth rates of the evolving species X_i.

If species X_i and X_j satisfy $s_i = s_j$ (i.e., they share the same trait value), and $X_i(t) = X_j(t)$ for all time t, then X_i and X_j are called *equivalent*. Indeed, species X_i and X_j have identical inter- and intraspecific interactions, and hence it is not

necessary to distinguish them as two different species. We can therefore treat such X_i and X_j as a single species, and reduce the dimensionality of the dynamics by one.

The evolutionary process: The standard method of adaptive dynamics theory requires separation of ecological and evolutionary timescales. On the fast (ecological) timescale, the system is assumed to reach an equilibrium, determined by the fixed traits, which are allowed to vary only on the slow (evolutionary) timescale. On this scale, at random, an individual of a resident species s_i produces a mutant s'. The mutation process is a Poisson process, with a rate γ_i per individual of species s_i. Thus, the mutation rate for species s_i is $\gamma_i X_i$, and the mutation process for each species is independent of the mutations of other species. When a mutant is introduced, its trait s' is drawn from a normal distribution with mean s_i (the trait of its parent species), and a fixed variance σ^2. The population dynamics and the evolutionary process thus are coupled. We assume that both inter- and intraspecific interactions of the mutant s' are only slightly perturbed from those of the parent s_i, so that the growth rate of s' has approximately the same functional form as that of s_i. Thus, the population dynamics of s' are given by:

$$\dot{X}' = X' r_i(\vec{X}, \vec{Y}; s', \vec{s}).$$

We make three basic assumptions. It must be emphasized that these are assumptions, not facts, and that in some cases these assumptions may be called into question.

Assumption 1: The system (10.1) and (10.2) has a unique nonnegative equilibrium $(\vec{X}^*, \vec{Y}^*)$. Furthermore, this equilibrium is globally asymptotically stable (GAS).

Assumption 2: The evolutionary timescale is much longer than the population dynamic timescale, i.e., $\gamma_i \ll 1$, so that the system can be considered resting at the GAS equilibrium when a mutant is introduced. This assumption decouples the population dynamics and the evolutionary process. The traits become parameters in the equations governing the population dynamics, and the population sizes that are crucial to determining the mutation rates of species become the equilibrium population sizes, which are deterministic functions of the traits.

Assumption 3: The mean mutation step size σ is small.

The population equilibrium $(\vec{X}^*, \vec{Y}^*)$ is the unique solution of

$$r_i(\vec{X}, \vec{Y}; s_i, \vec{s}) = 0,$$
$$F_j(\vec{X}, \vec{Y}) = 0.$$

Thus, $(\vec{X}^*, \vec{Y}^*)$ is uniquely determined by $\vec{s}$.

If s_i mutates to s$'$ with a population size X' that is close to 0,

$$\frac{\dot{X}'}{X'}\Big|_{X'=0} = r_i(\vec{X}^*, \vec{Y}^*; s', \vec{s}).$$

s' can invade if and only if $r_i(\vec{X}^*, \vec{Y}^*, s', \vec{s}) > 0$. Since $\vec{X}^*$ and $\vec{Y}^*$ are totally determined by $\vec{s}$ at equilibrium, we can simply rewrite $r_i(\vec{X}^*, \vec{Y}^*; s', \vec{s})$ as $r_i(s' | \vec{s})$. We can understand this term as the intrinsic growth rate of s' when it interacts with a resident community that has traits $\vec{s}$. The sign of $r_i(s' | \vec{s})$ determines whether the mutant s' can invade. Hence, we call this function as the *invasion function* (or, as sometimes referred to by other researchers, the *fitness function*).

Thus, assumptions 1 and 2 ensure that when a species mutates, the state of the system is uniquely determined by $\vec{s}$. The set of traits in trait space S that satisfy assumption 1 is called the *coexistence region*, which is denoted as C.

In the coexistence region, since system ((10.1) and (10.2)) is at equilibrium, for all i,

$$r_i(s_i | \vec{s}) = 0.$$

Thus, when s' is very close to s_i, we can replace $r_i(s' | \vec{s})$ by the linear approximation[1]:

$$r_i(s' | \vec{s}) \approx \frac{\partial r_i}{\partial s'}(s_i | \vec{s})(s' - s_i). \tag{10.3}$$

Equation (10.3) shows that s' can invade from the right ($s' > s$) if $\frac{\partial r_i}{\partial s'}(s_i | \vec{s}) > 0$, and can invade from the left ($s' < s$) if $\frac{\partial r_i}{\partial s'}(s_i | \vec{s}) < 0$.

If a mutant s' of s_i successfully invades a community $\vec{s}$, can it coexist with its parent? To answer this question, we need to check the reciprocal ability of s_i to invade the community $\vec{s}' = (s_1, s_2, \ldots, s_{i-1}, s', s_{i+1}, \ldots, s_n)$. If s_i cannot invade $\vec{s}'$, then the boundary equilibrium ($X_i = 0$) is asymptotically stable. Because of assumption 1, it is GAS. Thus, in this case the mutant s' will replace its parent s_i. On the other hand, if s_i can invade $\vec{s}'$ while s' invades $\vec{s}$, then the mutant s' coexists with s_i.

We can show (Appendix A) that, if $\frac{\partial r_i}{\partial s}(s_i | \vec{s}) > 0$, then s_i will be replaced by mutants with larger trait values, and that if $\frac{\partial r_i}{\partial s}(s_i | \vec{s}) < 0$, s_i will be replaced by those with smaller trait values.

The replacement argument in Appendix A requires that s' and s are very close, which is not always true under the assumption that the mutant trait distribution is normal. However, when the variance of the normal distribution (the mutation step size) $\sigma \to 0$, the probability that the replacement argument holds converges to 1. Thus, with the small mutation step assumption, the replacement argument is true with probability tending to 1 as the mean mutation step size goes to 0.

A complication of the analysis is that, when a mutant s' is introduced, it will be represented by only a few individuals. Thus, differential equations may not provide a good approximation of the population dynamics; it is more appropriate to model the invasion using stochastic population models. Dieckmann and Law (1996) showed with stochastic models that if a mutant s' of s_i can invade, i.e., $r_i(s' | \vec{s}) \approx \frac{\partial r_i}{\partial s'}(s_i | \vec{s})(s' - s_i) > 0$, it invades with a probability

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[1] $\frac{\partial r_i}{\partial s'}(s' | \vec{s})$ refers to the derivative with respect to the first variable s'; $\frac{\partial r_i}{\partial s_i}(s' | \vec{s})$ refers to the derivative w.r.t. the i-th component of the vector $\vec{s}$; for any function $f(x)$, $f(x)_+ = \max\{f(x), 0\}$.

proportional to $r_i(s'|\vec{s})_+$ because of stochastic perturbations. Thus, more generally, we assume that a mutant invades with probability $\beta r_i(s'|\vec{s})_+$.

It remains to examine the case $\frac{\partial r}{\partial s'} = 0$, for which invasion is still possible.

We call the strategy s_i that satisfies:

$$\frac{\partial r_i}{\partial s'}(s_i|\vec{s}) = 0 \qquad (10.4)$$

an *evolutionary singular strategy*, at which the ability of the mutant s' to invade cannot be determined by the gradient of r_i.

We stop the replacement process when either the biomass is 0, or the condition (10.4) is satisfied. However, if we consider all the evolving species together, we must be aware that when a species s_i approaches the evolutionary singular strategy, it takes a very long time for a mutant s' of s_i to replace it, because the probability that s' invades is close to 0. While other species are still evolving, the movement of $\vec{s}$ may push the species s_i away from the critical point corresponding to condition (10.4). So the system either does not settle down at all, or else reaches a state where all species reach singular strategies. If the latter case applies, we say that the system state $\vec{s}$ is *singular*. If the system evolves into a singular state, we call the singular state *attracting* (or convergence stable). If the system evolves away from a singular state, we call the state *repelling*.

Thus, before the system evolves to an evolutionary singular state, the evolution process is a continuous time Markov chain in trait space. Let $w(\vec{s}'|\vec{s})$ be the transition rate of the system jumping from state $\vec{s}$ to $\vec{s}'$, and let $P(\vec{s},t)$ be the probability density of the system being in state $\vec{s}$ at time t. Then, because of the Markov property, we have (Dieckmann and Law 1996):

$$\dot{P}(\vec{s},t) = \int w(\vec{s}|\vec{s}')P(\vec{s}',t) - w(\vec{s}'|\vec{s})P(\vec{s},t)\mathrm{d}s'_1, \ldots, \mathrm{d}s'_n. \qquad (10.5)$$

Suppose that at any time there is at most one mutant produced, then

$$w(\vec{s}'|\vec{s}) = \sum_{i=1}^{n} w_i(s'_i, \vec{s}) \prod_{j \neq i} \delta(s'_j - s_j). \qquad (10.6)$$

where $w_i(s'_i, \vec{s})$ is the probability of species s_i jumping to s'_i. A species s_i jumps to s' if and only if s_i produces a mutant s' and s' can replace its parent s_i. Let $Q_i(s', \vec{s})$ be the probability density of species s_i producing a mutant s' in a community $\vec{s}$. As assumed, Q_i is normal, i.e.,

$$Q_i(s', \vec{s}) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(s'-s_i)^2}{2\sigma^2}}.$$

The replacement probability is $\beta r_i(s'|\vec{s})_+ \approx \beta \left[\frac{\partial r_i}{\partial s}(s_i|\vec{s})(s'_i - s_i)\right]_+$. So we have

$$w_i(s'_i, \vec{s}) \approx \gamma_i X_i Q_i(s'_i, \vec{s}) \beta \left[\frac{\partial r_i}{\partial s}(s_i|\vec{s})(s'_i - s_i)\right]_+. \qquad (10.7)$$

Thus, in summary we have modeled the evolution process with Eqs. (10.5), (10.6), and (10.7). This model is only well defined in the coexistence region, where the traits $\vec{s}$ uniquely determine the states of the system (10.1) and (10.2) when a species mutates.

10.2.2 Adaptive dynamics of single trait systems

The adaptive dynamics approximation of the evolutionary process was introduced by Metz et al. (1996) and Dieckmann and Law (1996). They use the method of moment closure to compute the dynamics of the mean traits: the mean can be written as:

$$\langle \vec{s} \rangle = \int_{-\infty}^{\infty} \vec{s} P(\vec{s}, t) \mathrm{d}\vec{s}. \tag{10.8}$$

Take the derivative with respect to t on both sides of Eq. (10.8), and get

$$\left\langle \frac{\mathrm{d}}{\mathrm{d}t} \vec{s} \right\rangle = \int_{-\infty}^{\infty} \vec{s} \frac{\mathrm{d}}{\mathrm{d}t} P(\vec{s}, t) \mathrm{d}\vec{s}. \tag{10.9}$$

By substituting Eqs. (10.5) and (10.7) into (10.9), and ignoring all the second and higher moments, they obtained the approximation of the mean path,

$$\frac{\mathrm{d}}{\mathrm{d}t} \langle s_i \rangle = \frac{\sigma^2 \beta}{2} \gamma_i X_i \frac{\partial r_i}{\partial s'} (\langle s_i \rangle | \langle \vec{s} \rangle). \tag{10.10}$$

We call this dynamical system (10.10) as *adaptive dynamics*; it describes the dynamics of trait evolution. The adaptive dynamical system (10.10) is only well defined in the coexistence region C, where the notation $r(s_i | \vec{s})$ is meaningful.

The evolutionary strategies, i.e., the traits that satisfy the singular condition (10.4), are the equilibria of the adaptive dynamics. Thus, the adaptive dynamical systems fail at equilibria, because the Markov property (10.5) fails.

10.2.3 Coexistence condition

The condition (called a *coexistence condition*) that ensures s_i can produce a coexisting mutant at a point $\vec{s}$ in trait space is important because, in our mutation-based framework, this is the only way evolutionary branching can occur. If no mutant can coexist with the parent, there is certainly no branching; coexistence of mutants and parents is possible only when $\vec{s}^*$ is at evolutionary equilibrium.

Geritz et al. (1998) deduced the coexistence condition for a species and its mutants using the traditional *pairwise invasibility plot* method. The pairwise invasibility plot indicates the sign of the invasion function $r(s'|s)$ for all possible values of the resident phenotype values s and the mutants s', in a plane where x-axis is s' and y-axis is s. The boundary of the positive and negative regions

are the curves such that $r(s'|s) = 0$. Since $r(s|s) = 0$, $s' = s$ is always a boundary. From the Taylor expansion of $r(s'|s)$,

$$r(s'|s) \approx \frac{\partial r}{\partial s'}(s|s)(s'-s) + \frac{1}{2}\frac{\partial^2 r}{\partial s'^2}(s|s)(s'-s)^2,$$

we can see that, around $s' = s$, the other boundary is a curve tangent to

$$\frac{\partial r}{\partial s'}(s|s) + \frac{1}{2}\frac{\partial^2 r}{\partial s'^2}(s|s)(s'-s) = 0.$$

The intersections of this curve and $s' = s$ are the points such that $\frac{\partial r}{\partial s'}(s|s) = 0$, i.e., the evolutionary equilibria.

Because of assumption 1 (GAS equilibrium of the population dynamics), a mutant and its parent can coexist if and only if they can mutually invade, specifically, if the positive regions of $r(s'|s)$ and $r(s|s')$ have a nonempty intersection. Note that $r(s'|s)$ and $r(s|s')$ are symmetric with respect to $s' = s$, around an evolutionary equilibrium s^*, s and s' can mutually invade if and only if the straight line $s - s^* = s^* - s'$ is contained in the intersection of the positive regions of $r(s'|s)$ and $r(s|s')$. So s^* is a local minimum of $r(s'|s)$ along $s - s^* = s^* - s'$, which leads to the coexistence condition for s and s':

$$\frac{\partial^2 r_i}{\partial s' \partial s_i}(s_i^*|\vec{s}^*) < 0. \tag{10.11}$$

Condition (10.11) only ensures the coexistence of mutant s' and the parent s_i if all other species are fixed at the singular strategy. If more than one species satisfies the coexistence condition, ecological constraints may prohibit coexistence of all species. Geritz et al. (1998) presented an example of patch selection, where a system with N patches can support not more than N species. He showed through numerical simulation that when $N = 3$, starting with one species, the system can branch into two, then both satisfy the coexistence condition; but they cannot coexist with their mutants, because otherwise there would be four species coexisting on three patches, which is impossible.

10.2.4 Branching

A strategy in trait space is called an *evolutionary branching point* if a mutant of one species can invade and coexist with it, and then the traits of the mutant and the parent move apart from each other; such points are necessarily evolutionary equilibria. Furthermore, we are only interested in attractive equilibria, because they are evolutionarily reachable.

For the evolution of a single species s, an attractive evolutionary equilibrium s^* is approached from the left if $s < s^*$, and from the right if $s > s^*$. Thus, in the pairwise invasibility plot, the positive region is above $s' = s(s > s')$ on the left-hand side of $s^*(s' < s^*)$, and below $s' = s(s < s')$ on the right-hand side of $s^*(s' > s^*)$.

An attractive equilibrium s^* falls into one of three cases: (1) there is no coexistence region (which implies that s^* is evolutionarily stable, as we show later); (2) there is a coexistence region but s^* is evolutionarily stable; and (3) there is a coexistence region and s^* is not evolutionarily stable.

If s^* is an evolutionarily stable strategy, then no mutants can invade s^*; and thus in the pairwise invasibility plot, the vertical line $s' = s^*$ lies completely in the negative region. Hence, for an attractive equilibrium, if there is no coexistence region around s^*, i.e., the diagonal line $s - s^* = s^* - s'$ lies completely in the negative region, then the vertical line $s' = s^*$ has to lie in the negative region. This means that the absence of a coexistence region implies evolutionary stability. Moreover, $r(s' | s^*) < 0$ for all $s \neq s^*$ implies that s^* is a local maximum of $r(s' | s^*)$. Hence, the condition for s^* to be evolutionarily stable is

$$\frac{\partial^2 r}{\partial s'^2}(s^* | s^*) < 0.$$

But if there is a coexistence region, the pairwise invasibility plots become less helpful to investigate the evolution, because when a mutant coexists with its parent, it also changes the invasion function and hence the plot. Geritz et al. (1998) showed heuristically that the existence of a coexistence region, and hence the absence of evolutionary stability, implies evolutionary branching. However, a rigorous proof would involve complex perturbations to the invasion function, and is hard to obtain. The same problem arises when we use the pairwise invasibility plot method to investigate the branching of multiple species: branching of other species changes the invasion function of other species.

This is why we need to use more sophisticated tools, especially, the method of adaptive dynamics, to study the branching of multiple species. As the system evolves to an equilibrium, the adaptive dynamical system (10.12) governs the evolution. But at the branching point, a mutant and its parent coexist. Thus, the evolutionary process is not a Markov process any more: the dimensionality has changed, so the approach of adaptive dynamics fails. Once the system moves away from the branching point, the system becomes a new system with more species; mutants and their parents cannot coexist anymore. Thus, the adaptive dynamics framework once again applies. In Section 10.3, we develop a method to avoid the problem of change in dimensionality.

10.3 BRANCHING THEORY

Suppose there exists an evolving system that can be described by the adaptive dynamical system

$$\dot{s}_i = \gamma_i X_i \frac{\partial r_i}{\partial s'}(s_i | \vec{s}). \tag{10.12}$$

Since we are interested in evolutionary branching, we assume that the system evolves to an evolutionary equilibrium $\vec{s}^*$ (which is thus attractive).

To avoid the change in dimension after branching, consider that each species s_i consists of two identical virtual species u_i and v_i, where $u_i = v_i = s_i$, with identical biomasses $U_i = V_i = X_i/2$. Now, there are $2n$ species in the system. Next perturb (u_i, v_i) slightly away from (s_i^*, s_i^*). Since the system is no longer at the equilibrium, we can apply the adaptive dynamics to the new system.

If $\vec{s}^*$ is a branching point, there must be some subspecies u_i and v_i that coexist and then evolve away from the equilibrium. So the equilibrium $(\vec{s}^*, \vec{s}^*)$ has an unstable manifold. But, when restricted to the subspace $\{u_i = v_i\}_{i=1}^n$ the doubled system is actually the original one, which has $\vec{s}^*$ as a locally asymptotically stable equilibrium. So $(\vec{s}^*, \vec{s}^*)$ must be a saddle with the unstable manifold transverse to $\{u_i = v_i\}$. On the other hand, if $\vec{s}^*$ is an evolutionarily stable strategy, all perturbed subspecies u_i and v_i either cannot coexist, or coevolve back into the equilibrium. Thus, in this case, the equilibrium $(\vec{s}^*, \vec{s}^*)$ is a stable node. This means that the strategy $\vec{s}^*$ is a branching point if and only if the $2n$-dimensional system satisfies two conditions: (1) there exists a region where some species u_i and its mutant v_i can coexist and (2) the equilibrium $(\vec{s}^*, \vec{s}^*)$ is a saddle with an unstable manifold lying within the coexistence region.

Suppose the invasion functions for each species, after we double the dimension, are $\tilde{r}_i(u_i | \vec{u}, \vec{v})$ and $\tilde{r}_i(v_i | \vec{u}, \vec{v})$.[2] Then, the adaptive dynamics are given by

$$\dot{u}_i = \gamma_i U_i \frac{\partial \tilde{r}_i}{\partial s'}(u_i | \vec{u}, \vec{v}), \tag{10.13}$$

$$v_i' = \gamma_i V_i \frac{\partial \tilde{r}_i}{\partial s'}(v_i | \vec{u}, \vec{v}). \tag{10.14}$$

Random initial condition: Because of the randomness of the mutant trait, the initial condition is a random vector $(\vec{u}(0), \vec{v}(0))$ near the equilibrium $(\vec{s}^*, \vec{s}^*)$. Since the adaptive dynamical system ((10.13) and (10.14)) is only well defined within the coexistence region $\mathcal{C}$, we assume $(\vec{u}(0), \vec{v}(0)) \in \mathcal{C}$.

When restricted to the subspace $\{u_i = v_i\}_{i=1}^n$, the doubled dimension system (10.13) and (10.14), is indeed the original system. Therefore, the subspace $\{s_1 = s_2\}$ is invariant, i.e.,

$$\tilde{r}_i(s_i | \vec{s}, \vec{s}) = r_i(s_i | \vec{s}); \; \frac{\partial^2 \tilde{r}_i}{\partial s'}(s_i | \vec{s}, \vec{s}) = \frac{\partial^2 r_i}{\partial s'}(s_i | \vec{s}); \; \frac{\partial^2 \tilde{r}_i}{\partial s'^2}(s_i | \vec{s}, \vec{s}) = \frac{\partial^2 r_i}{\partial s'^2}(s_i | \vec{s}); \tag{10.15}$$

$$\left[\frac{\partial^2}{\partial s' \partial u_i} + \frac{\partial^2}{\partial s' \partial v_i} \right] \tilde{r}_i(u_i | \vec{u}, \vec{v})\big|_{\vec{u} = \vec{v} = \vec{s}} = \frac{\partial^2 r_i}{\partial s' \partial s_i}(s_i | \vec{s}). \tag{10.16}$$

Thus, under the doubled system, the coexistence condition (10.11) becomes

$$\left[\frac{\partial^2}{\partial s' \partial u_i} + \frac{\partial^2}{\partial s' \partial v_i} \right] \tilde{r}_i(u_i | \vec{u}, \vec{v})\big|_{\vec{u} = \vec{v} = \vec{s}^*} < 0. \tag{10.17}$$

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[2]We have changed the notation of the growth rate to $\tilde{r}_i$, because it is a function that depends on both $\vec{u}$ and $\vec{v}$. However, it is related to r_i as described later.

10.3.1 Branching of a single species

Although the branching of a single species has been studied by Geritz et al. (1997) and Geritz et al. (1998), and the branching condition given, applying the proposed doubled dimension method to the branching of a single species not only can illustrate the method, but also can give us a geometric view of how evolutionary branching occurs. Thus, to begin, consider the single-species system:

$$\dot{s} = X \frac{\partial r}{\partial s'}(s \mid s), \tag{10.18}$$

where $r(s \mid s)$ is the exponential growth rate. Assume the system has reached an attractive evolutionary singular strategy s^*, where $\frac{\partial r}{\partial s'}(s^* \mid s^*) = 0$, and because of attraction, $\frac{d}{ds}[\frac{\partial r}{\partial s'}(s \mid s)]|_{s=s^*} < 0$.

Now we assume that the system consists of two virtual species, u and v, with population sizes U and V. The two-dimensional adaptive dynamical system (i.e., the "doubled" system) can be written as:

$$\dot{u} = U \frac{\partial \tilde{r}}{\partial s'}(u \mid u, v), \tag{10.19}$$

$$\dot{v} = V \frac{\partial \tilde{r}}{\partial s'}(v \mid u, v), \tag{10.20}$$

The equilibrium corresponding to s^* in the one-dimensional system is (s^*, s^*). Since there are only two species u and v in the doubled system, the existence of the coexistence region is solely determined by the coexistence condition (10.17).

The stability of (s^*, s^*) is determined by the eigenvalues of the Jacobian matrix:

$$\begin{bmatrix} U^*(\frac{\partial^2 \tilde{r}}{\partial s'^2} + \frac{\partial^2 \tilde{r}}{\partial s' \partial u})(s^* \mid s^*, s^*) & U^* \frac{\partial^2 \tilde{r}}{\partial s' \partial v}(s^* \mid s^*, s^*) \\ V^* \frac{\partial^2 \tilde{r}}{\partial s' \partial u}(s^* \mid s^*, s^*) & V^*(\frac{\partial^2 \tilde{r}}{\partial s'^2} + \frac{\partial^2 \tilde{r}}{\partial s' \partial v})(s^* \mid s^*, s^*) \end{bmatrix}.$$

Since u and v are simply new names for s^* when $u = v = s^*$, we have

$$\frac{\partial^2 \tilde{r}}{\partial s' \partial u}(s^* \mid s^*, s^*) = \frac{\partial^2 \tilde{r}}{\partial s' \partial v}(s^* \mid s^*, s^*).$$

Also, since we assumed $U^* = V^* = X^*/2$, one eigenvalue is

$$\lambda_1 = \frac{X^*}{2} \frac{\partial^2 \tilde{r}}{\partial s'^2}(s^* \mid s^*, s^*) = \frac{X^*}{2} \frac{\partial'^2 r}{\partial s'^2}(s^* \mid s^*),$$

which is associated with the eigenvector $(-1, 1)^T$. Because $s_1 = s_2$ is an invariant line of the doubled system (10.19) and (10.20), the other eigenvalue is

$$\lambda_2 = \frac{X^*}{2}(\frac{\partial^2}{\partial s'^2} + \frac{\partial^2}{\partial s' \partial u} + \frac{\partial^2}{\partial s' \partial v})\tilde{r}(s^* \mid s^*, s^*) = \frac{X^*}{2}(\frac{\partial^2}{\partial s'^2} + \frac{\partial^2}{\partial s' \partial s})r(s^* \mid s^*),$$

associated with eigenvector $(1,1)^T$. On the invariant set $u = v$ the doubled system is actually the original one-dimensional system (10.18). So λ_2 is the eigenvalue associated with the equilibrium s^* of the original system (10.18). Since s^* is assumed to be stable, $\lambda_2 < 0$. Thus, the stability of (s^*, s^*) is determined only by λ_1.

Case 1: $\lambda_1 < 0$. When $\lambda_1 < 0$, (s^*, s^*) is a stable node. We will show that it cannot be a branching point.

When the coexistence condition (10.11) holds, i.e.,

$$\frac{\partial^2}{\partial s' \partial s} r(s^* | s^*) = \frac{2(\lambda_2 - \lambda_1)}{X^*} < 0,$$

u and v can coexist in a region around (s^*, s^*). As long as they coexist, u and v will evolve along the eigenvector that corresponds to the eigenvalue with the smallest absolute value, toward the equilibrium (s^*, s^*). In this case, $0 > \lambda_1 > \lambda_2$, so u and v evolve along $(-1,1)$. When they evolve back into the equilibrium (s^*, s^*), they become indistinguishable, because their traits are identical. That is, they collapse into a single species. At this point, a new mutant can invade and push the system away from the equilibrium (s^*, s^*). Hence, the system is repeatedly pushed away from the equilibrium and then evolves back. By definition, the equilibrium is not an evolutionarily stable strategy. But when mutation steps are small, the mutant and the parent species are almost indistinguishable and stay very close to the equilibrium.

When the coexistence condition (10.17) is not satisfied, in the neighborhood of the equilibrium (s^*, s^*), no two species u and v can coexist except for $u = v$. That is, when species s in the original one-dimensional system evolves to equilibrium s^*, no mutant can invade and coexist with it. So, by definition, again, s^* is not a branching point.

Hence, when $\lambda_1 < 0$, the equilibrium is not a branching point.

Case 2: $\lambda_1 > 0$. When $\lambda_1 > 0$, (s^*, s^*) is a saddle. Furthermore, since $\lambda_2 < 0$,

$$\frac{\partial^2}{\partial s' \partial s} r(s^* | s^*) = (\lambda_2 - \lambda_1)\frac{2}{X^*} < 0.$$

Thus, the coexistence condition (10.11) holds. Hence, around the equilibrium (s^*, s^*) there is a coexistence region for species u and v. As shown by Geritz et al. (1998), the unstable eigenvector $(1, -1)$ lies in the coexistence region. This means that as long as they coexist, u and v will leave the equilibrium along the unstable eigenvector $(1, -1)$, as illustrated in Figure 10.1; that is, the two traits split with the same speed. In other words, when $\lambda_1 > 0$, the strategy s^* is a branching point.

Case 3: $\lambda_1 = 0$. In this case, the evolutionary equilibrium (s^*, s^*) is a degenerate equilibrium. This degenerate case is more complex. Since

$$\frac{\partial^2}{\partial s' \partial s} r(s^* | s^*) = (\lambda_2 - \lambda_1)\frac{2}{X^*} = \frac{2\lambda_2}{X^*} < 0,$$
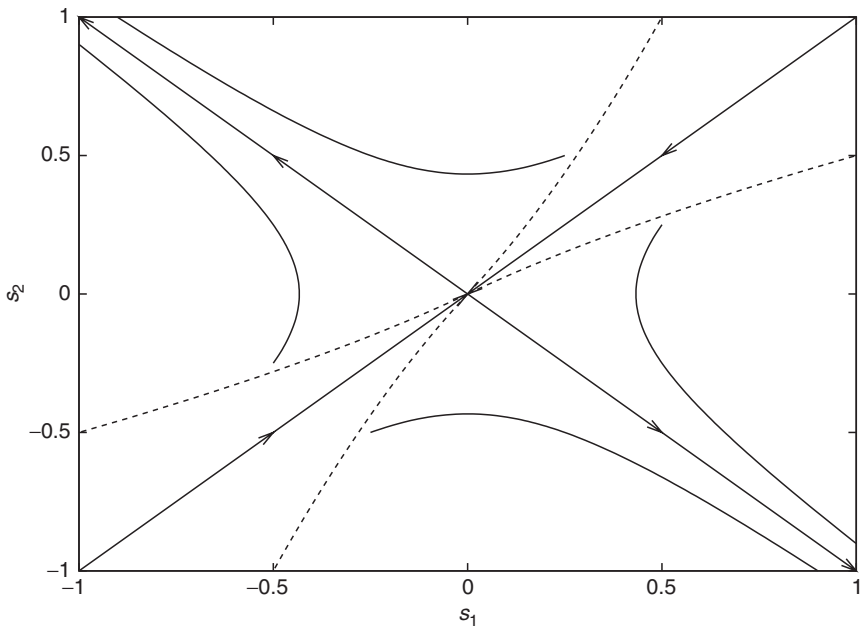
Figure 10.1. Phase portrait of the doubled system (10.13) and (10.14) around the equilibrium (s^*, s^*) when $\lambda_1 > 0$. The equilibrium is a saddle. The eigenvector $(-1, 1)$ lies in the coexistence region, with boundary marked by the dotted lines. If a mutant can coexist with its parent, they will coevolve away from (s^*, s^*) along the unstable eigenvector $(-1, 1)$.

the coexistence condition holds. Hence, there is always a coexistence region around (s^*, s^*). The branching therefore is determined by the stability of the equilibrium (s^*, s^*), which, in turn, is determined by the direction of flow of trajectories along the eigenvector $(-1, 1)$. Along this eigenvector, the adaptive dynamical system (10.19) and (10.20) becomes

$$\dot{x} = X \frac{\partial \tilde{r}}{\partial s'}(s^* + x \,|\, s^* + x,\, s^* - x), \tag{10.21}$$

where $(u = s^* + x,\ v = s^* - x)$. Because the system ((10.19) and (10.20)) is symmetric about $u = v$, system (10.21) is symmetric about $x = 0$. Thus

$$\frac{\partial^{2k-1}\tilde{r}}{\partial s'^{2k-1}}(s^* \,|\, s^*, s^*) = 0.$$

So the stability of $x = 0$ is determined by the sign of the first nonzero even-order derivative $\frac{\partial^{2k}\tilde{r}}{\partial s'^{2k}}(s^* \,|\, s^*, s^*)$ for $k > 1$. If the sign is positive, $x = 0$ is unstable, so (s^*, s^*) is unstable; s^* is thus a branching point. If the sign is negative, (s^*, s^*) is stable, so s^* is not a branching point. Varkonyi (2006) presented an interesting example of this case: the emergence of asymmetry by branching of symmetry at a degenerate evolutionary equilibrium.

However, if we consider higher-order moment approximations, when $\lambda_1 = 0$, the variances may have a larger effect on the dynamics of system (10.21) than the higher-order terms. In this case, the adaptive dynamical system (10.19) and (10.20) may no longer provide an appropriate approximation of the system. Hence, we need higher-order moment closure approximations in the case of $\lambda_1 = 0$.

The branching condition is the same as the one that Geritz et al. (1998) deduced. Therefore, the doubled dimension method is valid to study evolutionary branching. It also makes clear what has happened at the branching point: the attractive evolutionary equilibrium s^* of the single-dimensional adaptive dynamics becomes a saddle in the doubled system; the doubled system restricted to the stable manifold $s_1 = s_2$ of the saddle is the original one-dimensional system. Furthermore, there is a coexistence region around the saddle: a species evolves along the stable manifold toward the saddle, until a mutation pushes the system away from the stable manifold into the coexistence region. After the system enters the coexistence region, it is effectively two-dimensional and evolves away from the saddle along the unstable manifold, which is tangent to $s_1 - s^* = s^* - s_2$; thus, the traits of the two species move away from each other.

10.3.2   Multiple species branching

In this section, we apply the same method to multispecies systems. Assume that the adaptive dynamical system (10.12) evolves into an asymptotically stable equilibrium $\vec{s}^*$. Denote the eigenvectors as $\vec{w}_i$, with associated eigenvalues θ_i. Since $\vec{s}^*$ is asymptotically stable, all θ_i have negative real part. Then, we double the dimension and get the system ((10.13) and (10.14)).

For this system, $(\vec{s}^*, \vec{s}^*)$ is also an equilibrium. The Jacobian matrix of the adaptive dynamic system at $(\vec{s}^*, \vec{s}^*)$ is

$$\begin{bmatrix} U_1^*(\frac{\partial^2 \tilde{r}}{\partial s'^2} + \frac{\partial^2 \tilde{r}}{\partial s' \partial u_1}) & \cdots & U_1^* \frac{\partial^2 \tilde{r}}{\partial s' \partial v_1} & \cdots \\ \vdots & \ddots & \vdots & \ddots \\ V_1^* \frac{\partial^2 \tilde{r}}{\partial s' \partial u_1} & \cdots & V_1^*(\frac{\partial^2 \tilde{r}}{\partial s'^2} + \frac{\partial^2 \tilde{r}}{\partial s' \partial v_1}) & \cdots \\ \vdots & \ddots & \vdots & \ddots \end{bmatrix}.$$

Because the subspace $\{\vec{u} = \vec{v}\}$ is invariant and, when restricted to this invariant subspace, the doubled system is indeed the original system (10.12), for each i, (w_i, w_i) is an eigenvector of the doubled dimensional system, with associated eigenvalue θ_i.

We can check that $\vec{z}_i = (e_i, -e_i)$ are also eigenvectors, with associated eigenvalues

$$\lambda_i = \frac{\partial^2 \tilde{r}}{\partial s'^2}(s_i^* | \vec{s}^*, \vec{s}^*),$$

where e_i is the vector whose components are all zero except the i-th component, which is one. So the eigenvalues λ_i determine the stability of the equilibrium $(\vec{s}^*, \vec{s}^*)$. According to the relation (10.15), $\lambda_i = \frac{\partial^2 r}{\partial s_i'^2}(s_i^* | \vec{s}^*)$.

If a species s_i does not satisfy the coexistence condition (10.17), it cannot produce a coexisting mutant s_i'. Thus, by definition, species s_i cannot branch. So only the species that satisfy condition (10.17) may branch.

In the case of the evolution of a single species, $\lambda_1 > 0$ implies condition (10.17). But if we have multiple evolving species, this is not true any more. This can be illustrated by the following example:

We consider a predator–prey system, with population dynamics

$$\dot{R}_i = r_R R_i \left(1 - \sum_j \alpha(s_{R_i}, s_{R_j}) R_j - \sum_j \beta(s_{R_i}, s_{C_j}) C_j \right), \qquad (10.22)$$

$$\dot{C}_i = r_C C_i \left(-1 + \gamma \sum_j \beta(s_{R_j}, s_{C_i}) R_j \right). \qquad (10.23)$$

where $\alpha(s_{R_i}, s_{R_j}) = h e^{-s_{R_i} s_{R_j}}$ are the inter-$(i \neq j)$ and intra-$(i = j)$ species interaction coefficients between prey species, and

$$\beta(s_{R_i}, s_{C_j}) = e^{(a^2 s_{R_i}^2 + 2 b s_{R_i} s_{C_j} + d^2 s_{C_j}^2)/2}$$

is the predation term between predator species C_j and prey species R_i. The adaptive dynamics are:

$$\dot{s}_R = r_R \left[s_R \frac{\alpha}{\gamma \beta} - (a s_R + b s_C)(1 - \frac{\alpha}{\gamma \beta}) \right], \qquad (10.24)$$

$$\dot{s}_C = r_C (b s_R + d s_C)(1 - \frac{\alpha}{\gamma \beta}). \qquad (10.25)$$

Thus, $(s_R = 0, s_C = 0)$ is an equilibrium. If we take $a = -1$, $b = 3$, $d = -4$, $h = 0.5$, $\gamma = 1$, the Jacobian at $(0, 0)$ is:

$$\begin{bmatrix} \frac{\alpha}{\gamma \beta} - a(1 - \frac{\alpha}{\gamma \beta}) & -b(1 - \frac{\alpha}{\gamma \beta}) \\ b(1 - \frac{\alpha}{\gamma \beta}) & d(1 - \frac{\alpha}{\gamma \beta}) \end{bmatrix} = 0.5 \begin{bmatrix} 0 & -2 \\ 2 & -1 \end{bmatrix}.$$

Thus, $(0, 0)$ is asymptotically stable. We can check that

$$\lambda_R = \frac{\partial^2 r^R(s_R | s_R, s_C)}{\partial s^2} \Big|_{s_R = s_C = 0} = -a(1 - \frac{\alpha}{\gamma \beta}) = 0.5 > 0;$$

$$\frac{\partial^2 r^R(s_R | s_R, s_C)}{\partial s \partial s_R} \Big|_{s_R = s_C = 0} = \frac{\alpha}{\gamma \beta} = 0.5 > 0;$$

$$\lambda_C = \frac{\partial^2 r^C(s_R | s_R, s_C)}{\partial s^2} \Big|_{s_R = s_C = 0} = d(1 - \frac{\alpha}{\gamma \beta}) = -2 < 0.$$
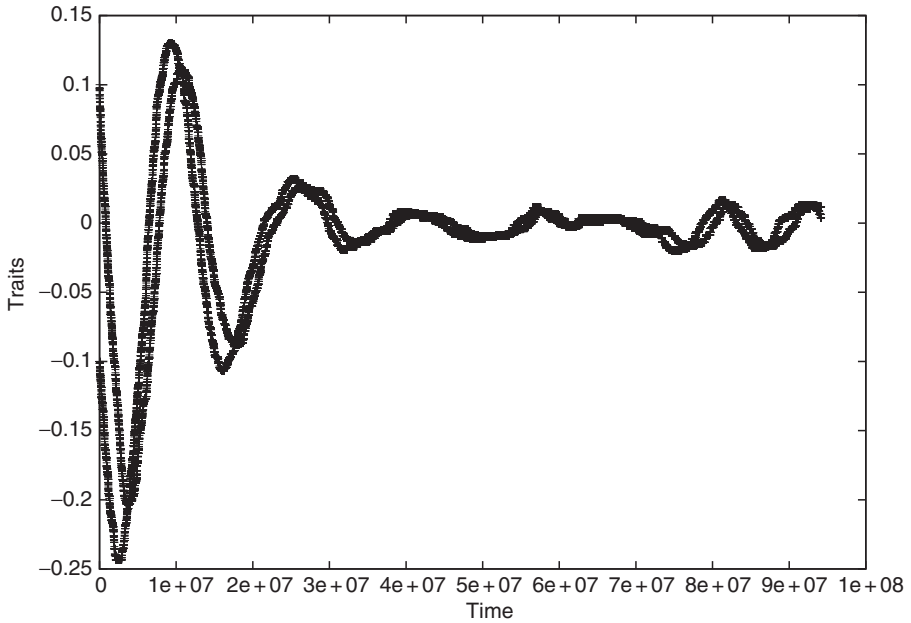
Figure 10.2. A realization of the evolution process corresponding to the example (10.24) and (10.25) with two traits plotted against time. $a = -1$, $b = 3$, $d = -4$, $h = 0.5$, $\gamma = 1$. No branching happens even though $\lambda_R > 0$, because there is no coexistence region for prey species R. However, the system cannot settle down at equilibrium $(0, 0)$ because near the equilibrium $(0, 0)$ mutants constantly invade and replace the parent species, and then push the system away from $(0, 0)$. On the other hand, $(0, 0)$ is GAS, so the system keeps evolving back, before being kicked away.

Thus, the prey species R satisfies $\lambda_R > 0$, but does not satisfy the coexistence condition (10.11). Thus, species R cannot branch at all, as confirmed by simulation (Figure 10.2).

Hence, it is important to check condition (10.17) for each species. If none of the species satisfies condition (10.17), no species can branch. For those species that satisfy the condition, we consider three cases:

Case 1: $\lambda_i < 0$ for some i. In this case the subspace $u_i + v_i = 2s_i^*$ is tangent to the stable manifold of the equilibrium $(\vec{s}^*, \vec{s}^*)$. Since $u_i = v_i$ is also in the stable manifold, u_i and v_i coevolve toward $(\vec{s}^*, \vec{s}^*)$. So species s_i will not branch.

Case 2: $\lambda_{vi} > 0$ for some i. In this case the equilibrium $(\vec{s}^*, \vec{s}^*)$ is a saddle. If u_i and v_i can coexist, they will coevolve along the unstable eigenvector $(e_i, -e_i)$, which implies that they will evolve away from each other. That is, if u_i and v_i can coexist, s_i will branch. However, as we have seen in Section 10.2.3, even if the species s_i satisfies the coexistence condition (10.17), u_i and v_i may not coexist

with other branching species. This is because when another species s_j branches into $s_j - \delta$ and $s_j + \delta$, the community has moved away from the singular strategy. Yet, the condition (10.17) only works when all the species are close to the singular strategy. Hence, if s_j branches first, the condition (10.17) may not ensure that s_i can produce a coexisting mutant. In this case the branching of s_j interferes with the branching of s_i.

In Appendix B, we show that the interference between s_i and s_j is independent of the branching of any other species. Let $\hat{r}_i(s'_i | \vec{s}, s'_j)$ be the intrinsic growth rate of the mutant s'_i invading a community of $\{\vec{s}, s'_j\}$, where s'_j is a mutant of s_j. We derive the independent branching condition in Appendix B:

$$\left[\frac{\partial}{\partial s'} - \frac{\partial}{\partial s_i}\right]\left[\frac{\partial}{\partial s_j} - \frac{\partial}{\partial s'_j}\right]\hat{r}_i(s^*_i | \vec{s}^*, s^*_j) = 0, \tag{10.26}$$

i.e., if this condition is satisfied, then the branching of s_j does not affect the branching of s_j.

Case 3: $\lambda_i = 0$ for some i. In this case the equilibrium $(\vec{s}^*, \vec{s}^*)$ is degenerate. As for case 3 of the single-species branching, the direction of flow of trajectories along the eigenvector $(e_i, -e_i)$ may be affected by the dynamics of variances.

In summary, a species s_i may branch if and only if it can produce a coexisting mutant near $\vec{s}^*$ and $(\vec{s}^*, \vec{s}^*)$ is unstable. Specifically, all the species s_i that satisfy the coexistence condition (10.11), and

$$\frac{\partial^2}{\partial s'^2}\tilde{r}_i(s^*_i | \vec{s}^*, \vec{s}^*) > 0, \tag{10.27}$$

may branch. But the branching of one species may suppress the branching of another. If s_i and s_j may both branch, the independent branching condition (10.26) is satisfied, and then the branching of s_j will not affect the branching of s_i.

10.4   CONCLUSIONS AND DISCUSSION

We have modeled the process of evolution as a stochastic process that is coupled with population dynamics. By assuming that the evolutionary timescale is much longer than the population dynamic timescale, we can decouple the evolutionary process from the population dynamics. Then, by requiring small phenotype variation and a unique GAS equilibrium for the population dynamics, we ensure that the invasion of the mutants always kills the parent species before the system reaches the evolutionary equilibrium. This implies that the evolutionary process can then be written as a continuoustime Markov process. By using the method of moment closure and ignoring the third and higher moments of this Markov process, we can deduce the adaptive dynamical system.

The branching conditions, which describe a saddle condition of the evolutionary equilibrium, and a coexistence region condition, can be naturally deduced using the double-dimension method. This method provides a clear geometric view of what happens at the branching point. Actually, when a system branches, the dimension of the system changes; thus in order to maintain the continuity in dimension, we view each species as consisting of two virtual identical species before branching. The branching process can then be viewed as the evolutionary process of the doubled system, with a random initial condition very close to the evolutionary equilibrium.

We see that the branching of one species in some cases can suppress the branching of other species, but this is because of the ecological constraints that prevent all the branching species and their mutants from coexisting together. As long as the mutants and parents of each branching species can coexist, they will branch independently. Otherwise, the evolutionary outcome is randomly dependent on which species branches first. The complexity of real ecosystems suggests that the evolutionary outcomes are random rather than deterministic; thus, predicting exactly what will happen is impossible. Yet the theory is still useful to explain what might have happened in real systems.

In this work, the evolutionary model is based on mutation. However, as shown by Charlesworth (1990), Abrams et al. (1993), and Abrams (2001), as long as the phenotype variance (mutation step in this model) is small, it gives rise to the same dynamical systems as that of the quantitative genetic models. Thus, the results we deduced in this chapter are general, as long as the phenotypic variance is small.

10.5   ACKNOWLEDGMENTS

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APPENDIX A   REPLACEMENT OF RESIDENT SPECIES BY THEIR MUTANTS

The condition for s_i to invade $\vec{s}'$ is, as always mentioned,

$$r_i(s_i|\vec{s}') > 0.$$

We also have $r_i(s'|\vec{s}') = 0$, thus,

$$r_i(s_i|\vec{s}') \approx \frac{\partial r_i}{\partial s'}(s_i|\vec{s})(s_i - s') + [\frac{\partial^2 r_i}{\partial s'^2}(s_i|\vec{s}') + \frac{\partial^2 r_i}{\partial s'\partial s_i}(s'|\vec{s})](s_i - s')]^2.$$

Hence, we have $r_i(s_i|\vec{s}') \approx -r_i(s'|\vec{s})$. Thus, if s' is very close to s_i, $\frac{\partial r_i}{\partial s'}(s_i|\vec{s})(s' - s) > 0$, it implies that $r_i(s'|\vec{s}) > 0$ and $r_i(s_i|\vec{s}') < 0$. Thus, s' can invade $\vec{s}$, but s_i cannot invade the community $\vec{s}'$. Similarly, $\frac{\partial r_i}{\partial s'}(s_i|\vec{s})(s' - s) < 0$ implies that $r_i(s'|\vec{s}) < 0$ and $r_i(s_i|\vec{s}') > 0$; thus, s' cannot invade $\vec{s}$, but s_i can invade the community $\vec{s}'$. Hence, s' and s can never coexist as long as $\frac{\partial r_i}{\partial s'}(s_i|\vec{s}) \neq 0$: either the mutant s' cannot invade, or if it can it replaces the parent species s_i. In particular, if $\frac{\partial r_i}{\partial s'}(s_i|\vec{s}) > 0 (< 0)$, s_i will be replaced by mutants $s' > s_i (s' < s_i)$.

APPENDIX B   DERIVATION OF THE INTERFERENCE CONDITION

Our model predicts that the branching is determined by the adaptive dynamics of the doubled system on the unstable manifold of $(\vec{s}^*, \vec{s}^*)$, and branching interference is caused by the change in coexistence region. Hence, we will only discuss the coexistence region on the unstable manifold. Let the set J be the index of all the species s_i that satisfy the saddle condition (10.27) and the condition (10.17). These are the species that may branch. If all the other species $s_j \neq s_i$ in J (we denote $J_i = J \setminus \{i\}$) have produced a coexisting mutant s'_j, we want to understand how this affects the coexistence of s_i and s'_i. Since we restrict ourselves to the unstable manifold, we want to study the coexistence of $s_i^* - \delta_i$ and $s_i^* + \delta_i$ in the presence of the species $s_j^* - \delta_j$ and $s_j^* + \delta_j$ for all $j \in J_i$. Let $\vec{u} = \{s_j^* - \delta_j\}_{j \in J_i}$; $\vec{v} = \{s_j^* + \delta_j\}_{j \in J_i}$; $\vec{u}^* = \vec{v}^* = \{s_j^*\}_{j \in J_i}$.

We know that $s_i^* - \delta_i$ and $s_i^* + \delta_i$ can coexist if and only if $s_i^* - \delta_i$ can invade the community $\{s_i^* + \delta_i, \vec{u}, \vec{v}\}$, while $s_i^* + \delta_i$ can invade the community $\{s_i^* - \delta_i, \vec{u}, \vec{v}\}$. Let $\hat{r}_i(s'_i | s_i, \vec{u}, \vec{v})$ be the intrinsic growth rate of the mutant s'_i in the community of $\{s_i, \vec{u}, \vec{v}\}$. Then we require:

$$r_i(s_i^* + \delta_i | s_i^* - \delta_i, \vec{u}, \vec{v}) > 0, \tag{10.28}$$

$$r_i(s_i^* - \delta_i | s_i^* + \delta_i, \vec{u}, \vec{v}) > 0. \tag{10.29}$$

We expand Eq. (10.28) in a Taylor series around $\{s_k^*\}_{k \in J}$:

$$\hat{r}_i(s_i^* | s_i^*, \vec{u}^*, \vec{v}^*) + \left[\frac{\partial}{\partial s'} - \frac{\partial}{\partial s_i} \right] \hat{r}_i(s_i^* | s_i^*, \vec{u}^*, \vec{v}^*)$$

$$+ \sum_{j \in J_i} \left[\frac{\partial}{\partial u_j} - \frac{\partial}{\partial v_j} \right] \hat{r}_i(s_i^* | s_i^*, \vec{u}^*, \vec{v}^*) \delta_j$$

$$+ \left[\frac{\partial}{\partial s'} - \frac{\partial}{\partial s_i} \right] \left[\frac{\partial}{\partial s'} - \frac{\partial}{\partial s_i} \right] \hat{r}_i(s_i^* | s_i^*, \vec{u}^*, \vec{v}^*)$$

$$+ 2 \sum_{j \in J_i} \left[\frac{\partial}{\partial s'} - \frac{\partial}{\partial s_i} \right] \left[\frac{\partial}{\partial u_j} - \frac{\partial}{\partial u_j} \right] \hat{r}_i(s_i^* | s_I^*, \vec{u}^*, \vec{v}^*) \delta_i \delta_j$$

$$+ \sum_{j,k \in J_i} \left[\frac{\partial}{\partial u_j} - \frac{\partial}{\partial v_j} \right] \left[\frac{\partial}{\partial u_k} - \frac{\partial}{\partial v_k} \right] \hat{r}_i(s_i^* | s_i^*, \vec{u}^*, \vec{v}^*) \delta_j \delta_k + o\left(\sum_{j \in J} \delta_j^2 \right) > 0.$$

For any $s_i, \vec{u}$ and $\vec{v}$, we have:

$$\hat{r}_i(s_i | s_i, \vec{u}, \vec{v}) = 0. \tag{10.30}$$

Hence, for all $j \in J_i$,

$$\frac{\partial}{\partial u_j} \hat{r}_i(s_i | s_i, \vec{u}, \vec{v}) = \frac{\partial}{\partial v_j} \hat{r}_i(s_i | s_i, \vec{u}, \vec{v}) = 0; \tag{10.31}$$

and for any $j, k \in J_i$,

$$\left[\frac{\partial}{\partial u_j} - \frac{\partial}{\partial v_j} \right] \left[\frac{\partial}{\partial u_k} - \frac{\partial}{\partial v_k} \right] \hat{r}_i(s_i | s_i, \vec{u}, \vec{v}) = 0. \tag{10.32}$$

If we differentiate Eq. (10.30) with respect to s_i, we get

$$\left[\frac{\partial}{\partial s'} + \frac{\partial}{\partial s_i}\right]\hat{r}_i(s_i \,|\, s_i, \vec{u}, \vec{v}) = 0;\tag{10.33}$$

$$\left[\frac{\partial^2}{\partial s'^2} + 2\frac{\partial^2}{\partial s'\partial s_i} + \frac{\partial^2}{\partial s_i^2}\right]\hat{r}_i(s_i \,|\, s_i, \vec{u}, \vec{v}) = 0.\tag{10.34}$$

Furthermore, since $\vec{s}^*$ is a singular strategy,

$$\frac{\partial}{\partial s'}\hat{r}_i(s_i^* \,|\, s_i^*, \vec{u}^*, \vec{v}^*) = 0.\tag{10.35}$$

From Eqs. (10.33) and (10.35) we have

$$\frac{\partial}{\partial s_i}\hat{r}_i(s_i^* \,|\, s_i^*, \vec{u}^*, \vec{v}^*) = 0.\tag{10.36}$$

From Eq. (10.34) we have

$$\left[\frac{\partial}{\partial s'} - \frac{\partial}{\partial s_i}\right]\left[\frac{\partial}{\partial s'} - \frac{\partial}{\partial s_i}\right]\hat{r}_i(s_i^* \,|\, s_i^*, \vec{u}^*, \vec{v}^*) = -4\frac{\partial^2}{\partial s'\partial s_i}\hat{r}_i(s_i^* \,|\, s_i^*, \vec{u}^*, \vec{v}^*).\tag{10.37}$$

From Eqs. (10.30)–(10.32) and (10.35)–(10.37), the Taylor expansion is simplified to

$$-4\frac{\partial^2}{\partial s'\partial s_i}\hat{r}_i(s_i^* \,|\, s_i^*, \vec{u}^*, \vec{v}^*)\delta_i^2 + \sum_{j\in J_i}\left[\frac{\partial}{\partial s'} - \frac{\partial}{\partial s_i}\right]\left[\frac{\partial}{\partial u_j} - \frac{\partial}{\partial v_j}\right]\hat{r}_i(s_i^* \,|\, s_i^*, \vec{u}^*, \vec{v}^*)\delta_i\delta_j > 0.$$

Similarly, from Eq. (10.29) we can derive

$$-4\frac{\partial^2}{\partial s'\partial s_i}\hat{r}_i(s_i^* \,|\, s_i^*, \vec{u}^*, \vec{v}^*)\delta_i^2 - \sum_{j\in J_i}\left[\frac{\partial}{\partial s'} - \frac{\partial}{\partial s_i}\right]\left[\frac{\partial}{\partial u_j} - \frac{\partial}{\partial v_j}\right]\hat{r}_i(s_i^* \,|\, s_i^*, \vec{u}^*, \vec{v}^*)\delta_i\delta_j > 0.$$

Hence, the species $s_i - \delta_i$ can coexist with $s_i + \delta_i$ and all the other species and their mutants $s_j \pm \delta_j$ if and only if

$$-4\frac{\partial^2}{\partial s'\partial s_i}\hat{r}_i(s_i^* \,|\, s_i^*, \vec{u}^*, \vec{v}^*)|\delta_i| > \sum_{j\in J_i}\left[\frac{\partial}{\partial s'} - \frac{\partial}{\partial s_i}\right]\left[\frac{\partial}{\partial u_j} - \frac{\partial}{\partial v_j}\right]\hat{r}_i(s_i^* \,|\, s_i^*, \vec{u}^*, \vec{v}^*)|\delta_j|.\tag{10.38}$$

When $\delta_j = 0$ for all $j \in J_i$, i.e., when all species $s_j \neq s_i$ are at the equilibrium s_j^*, this condition becomes the coexistence condition (10.17):

$$-4\frac{\partial^2 r_i}{\partial s'\partial s_i}(s_i^* \,|\, \vec{s}^*) > 0.$$

The condition (10.38) also immediately implies that for any $j \in J_i$, when

$$\left[\frac{\partial}{\partial s'} - \frac{\partial}{\partial s_i}\right]\left[\frac{\partial}{\partial u_j} - \frac{\partial}{\partial v_j}\right]\hat{r}_i(s_i^* \,|\, s_i^*, \vec{u}^*, \vec{v}^*) = 0,\tag{10.39}$$

the value δ_j will not affect the coexistence condition of $s_i^* \pm \delta_i$; on the other hand, if

$$\left[\frac{\partial}{\partial s'} - \frac{\partial}{\partial s_i}\right]\left[\frac{\partial}{\partial u_j} - \frac{\partial}{\partial v_j}\right]\hat{r}_i(s_i^* \,|\, s_i^*, \vec{u}^*, \vec{v}^*) \neq 0,$$

then for any δ_j there are values of δ_i that do not satisfy the condition (10.38), which means that the coexistence of $s_i^* \pm \delta_i$ depends on the state of the species $s_j^* \pm \delta_j$. In this case, the branching of species s_j may affect the coexistence of $s_i^* \pm \delta_i$, and thus interfere with the branching of s_i^*.

Hence, for any $i, j \in J$, the condition (10.39) determines if the branching of s_j affects the branching of s_i. This condition is independent of any other species.

CHAPTER 11

FEEDBACK EFFECTS BETWEEN THE FOOD CHAIN AND INDUCED DEFENSE STRATEGIES

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11.1   ABSTRACT

Recently it has been shown that inducible defenses in species at the bottom and middle of three-species food chains promote stability and typically allow all trophic levels to increase in response to fertilization. However, that past work did not allow prey individuals to optimize their responses to the levels of resources and predator density, and hence ignored the effects of optimal defense induction on trophic structure. In the present work, we studied such feedback effects in a food chain containing a predator, a prey with an inducible defense, and a resource. Both ordinary differential equations and their individual-based analogs were used to investigate food chain behavior under enrichment. The individual-based implementation simulated many competing prey strains, each with a different parameter value for responsiveness to predator density in its function for inducible defense. Eventually, a single prey strain remained. Simulations suggested that the prey evolved toward an evolutionarily stable strategy (ESS) for this defense parameter, which simultaneously produced an ideal free distribution (IFD) of individuals between the defended and undefended states. This was confirmed by further analysis. In our model system with prey defenses at ESS and IFD, only the abundance of the prey responded to enrichment. In contrast, when prey did not use the ESS and a source–sink relation existed between defended and undefended prey types, all trophic levels increased in response to enrichment. This response pattern is frequently observed in the field and laboratory.

11.2   INTRODUCTION

During the past decade or so, theoretical ecology has witnessed an explosion of interest in the interactions between the adaptive traits of individuals, the forces of natural selection acting on them, and population dynamics. In his book, *Introduction to Theoretical Ecology*, Peter Yodzis (1989) had already forecast this trend:

> There are, broadly speaking, two ways that theory can develop. One way is to follow through on the consequences of a current set of [population level] hypotheses. The other way is to seek to explain the current hypotheses themselves on the basis of some "deeper," "underlying" processes ... Up to now, we have been following mostly the first course. Assuming certain population growth rates and interactions, we have deduced certain phenomena. In this enterprise, the population parameters have been treated as given quantities ... (I)n this part, we are going to seek restrictions on the population parameters due to a process distinct from population dynamics, namely microevolution (p. 247).

What Peter Yodzis said and provided as a basis in 1989 is now canonical. For example, Levin (1998) noted that "ecosystems are prototypical examples of complex adaptive systems, in which patterns at higher levels emerge from localized interactions and selection processes acting at lower levels." Through combining classical models and techniques of adaptive dynamics, structured

population modeling, individual-based modeling (IBM), and experimental approaches, ecologists are focusing on understanding how patterns at the levels of populations and communities emerge from the traits of individuals. In particular, some of the generalizations that have been deduced from the study of population dynamics models are now being challenged by more sophisticated models that take into account the phenotypic variation within populations, the adaptive nature of individuals, or both (Abrams 1995, Abrams and Vos 2003, Bolker et al. 2003, Loeuille and Loreau 2004).

One of the classical generalizations regarding food webs is well known as the exploitation ecosystem hypothesis (EEH), which specifies how top-down control affects the responses of trophic level abundances to enrichment (Oksanen et al. 1981, Leibold 1989, Oksanen and Oksanen 2000). For bitrophic systems in stable equilibrium the model predicts that autotroph biomass is exclusively controlled by herbivores and will not respond to enrichment. Similarly, equilibrium herbivore biomass is exclusively controlled by carnivores in tritrophic systems and should not respond to increases in primary productivity, though autotroph and carnivore biomass will increase. This EEH pattern of trophic level responses has been observed to occur, for example, in a river system in which primary productivity was limited by a light gradient (Wootton and Power 1993).

However, field studies show that this pattern should not be expected in all cases (Mittelbach et al. 1988, Akcakaya et al. 1995, Brett and Goldman 1997, Kaunzinger and Morin 1998, Chase et al. 2000, Oksanen and Oksanen 2000). Discrepancies between EEH predictions and both laboratory and field observations require an evaluation of important ecological factors not present in the Oksanen et al. (1981) model that potentially affect trophic level biomass responses in nature. Theory has already provided a variety of explanations for the lack of the strict top-down control predicted by Oksanen et al. (1981). These explanations include direct density dependence influencing consumer dynamics (Gatto 1993, Akcakaya et al. 1995), adaptive foraging behavior by the consumers on middle or lower levels (Abrams 1984, 1995, 1996, Loeuille and Loreau 2004), and heterogeneity within trophic levels (Abrams 1993, Leibold 1989, 1996). We will focus on the last of these explanations, but will examine a different type of heterogeneity than has been examined in previous models. The community-level consequences of having different species within a given trophic level have been discussed by Leibold (1989, 1996), Power (1992), Abrams (1993, 1995), Grover (1995), Leibold et al. (1997), Oksanen and Oksanen (2000), Agrawal (2001), and Steiner (2001). The presence of both edible and inedible autotroph species introduces heterogeneity within that trophic level, and such heterogeneity has been predicted to change biomass responses to enrichment (Leibold 1989, 1996, Abrams 1993).

Inducible defenses constitute an important source of heterogeneity within prey species in food webs. In aquatic planktonic systems, herbivore-released infochemicals may induce colony formation in algae (Hessen and Van Donk 1993, Lampert et al. 1994, Van Donk et al. 1999, Tang 2003). Such an increase

in size makes algal particles more difficult to handle and/or ingest, and thus changes herbivore functional responses and per capita consumption rates. Karban and Baldwin (1997) discuss induced resistance in more than 100 terrestrial plant species, while inducible defenses in animals include behavioral, life history, and morphological changes. Kats and Dill (1998) list predator-induced changes in more than 200 animal species (also see Harvell 1984, Havel 1987, Tollrian and Harvell 1999, DeMeester et al. 1999, Turner et al. 2000, Vos et al. 2002, 2004a, Dahl and Peckarsky 2002, Johansson and Wahlstrom 2002).

The work described here was motivated by experiments and modeling by Verschoor et al. (unpublished) and by Vos et al. (2004a, b), who examined the effects of induced defenses in terms of stability and in relation to EEH predictions. While Vos et al. were simply interested in how induced defenses influence food webs, we are interested here in the specific details of the inducible defense response to consumer density and how optimization of this response by individuals feeds back into population dynamics and trophic structure. First we briefly review the work of Vos et al. Then, we describe a slight variation on their model in which only the autotrophs can be in a defended or undefended state. We develop an individual-based analog of the model, so that individual autotrophs can be allowed to vary in their responses to herbivore density. This IBM is used to examine natural selection operating in response to herbivory within the autotroph strain. Normally, the outcome of such selection is expected to be an ESS or an evolutionarily stable polymorphism. After finding the evolutionary stable state, the dynamical properties and trophic structure of this system are studied.

Vos et al. (2004b) investigated how inducible defenses affect changes in the distribution of biomass over the trophic levels when the system is enriched. The authors focused on three aspects of inducible defenses that have been shown to be important in a variety of empirical studies, but that have not been investigated in concert in theoretical studies. (1) The induction of defenses depends on consumer density (e.g., Anholt and Werner 1999, Kuhlmann et al. 1999, Van Donk et al. 1999), (2) both undefended prey and prey with induced defenses may be present at a given moment, over a range of consumer densities (Hessen and Van Donk 1993, Lampert et al. 1994), and (3) defended prey are not invulnerable (Jeschke and Tollrian 2000).

Vos et al. (2004a, b) incorporated these aspects of inducible defenses into a classical food chain model (Rosenzweig and MacArthur 1963, Rosenzweig 1971, 1973, Oksanen et al. 1981, Kretzschmar et al. 1993). They studied this model analytically and parameterized it for well-studied bitrophic and tritrophic systems to investigate the effects of inducible defenses in an ecologically relevant domain and to provide an example where theoretical results could be amenable to empirical testing. They addressed the following question: does an increase in primary productivity cause biomass increases of adjacent trophic levels, when inducible defenses are incorporated in the classical Oksanen et al. (1981) food chain model? Their model analyses answered that question affirmatively.

11.3 METHODS

The basic food chain model that we consider here is a nutrient–autotroph–herbivore chain. We follow Vos et al. (2004a, b) in incorporating inducible defenses in the above system by allowing both an undefended and a defended component in the autotroph population (Figure 11.1). This modified model has the set of equations:

$$\frac{dN}{dt} = Q_I(N_0 - N) - \frac{(f_1 P_1 + f_2 P_2)N}{k_1 + N} \tag{11.1a}$$

$$\frac{dP_1}{dt} = \frac{f_1 P_1 N}{k_1 + N} - \frac{v_1 H P_1}{1 + v_1 h_1 P_1 + v_2 h_2 P_2} - s_1 P_1 + D_1 P_2 - I_1 P_1 \tag{11.1b}$$

$$\frac{dP_2}{dt} = \frac{f_2 P_2 N}{k_1 + N} - \frac{v_2 H P_2}{1 + v_1 h_1 P_1 + v_2 h_2 P_2} - s_2 P_2 + I_1 P_1 - D_1 P_2 \tag{11.1c}$$

$$\frac{dH}{dt} = \frac{c_1(v_1 P_1 + v_2 P_2)H}{1 + v_1 h_1 P_1 + v_2 h_2 P_2} - s_3 H \tag{11.1d}$$
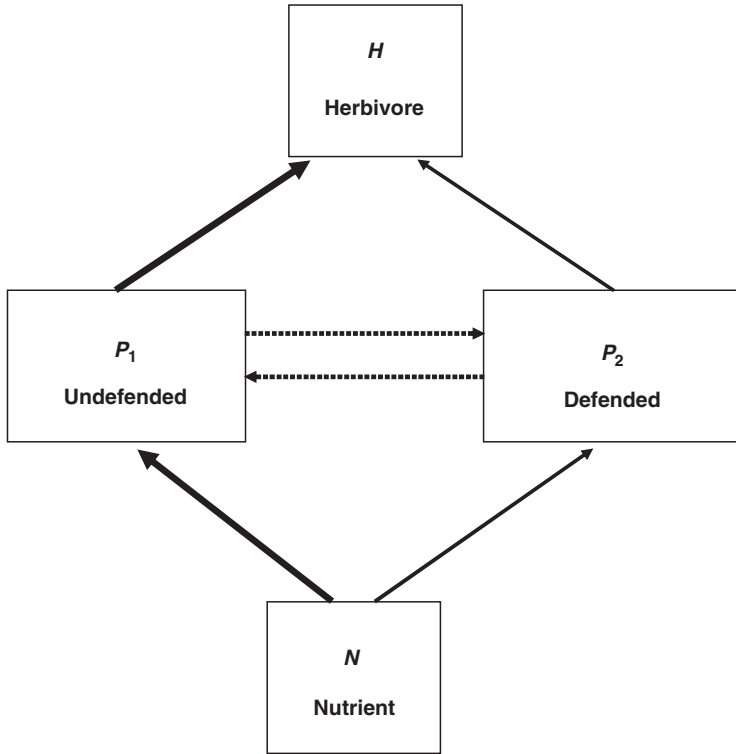
Figure 11.1. Schematic of nutrient–phytoplankton–herbivore chain in which phytoplankton can switch between defended or undefended states.

where N is the limiting nutrient concentration, P_1 and P_2 are the undefended and defended autotrophs, and H is the herbivore. P_1, P_2, and H are expressed in terms of their limiting nutrient; so all variables have units of nutrient per unit area.

The parameter Q_I represents the flux of water into the system and N_0 is the input nutrient concentration. Nutrient recycling within the system is not considered. The parameters f_1 and f_2 are rates of nutrient uptake by the undefended and defended plants, respectively, and k_1 is a half-saturation coefficient. The herbivore–autotroph interaction parameters are v_i, the herbivore search rate, and h_i, the herbivore handling time. The s_i values are mortality rates, and c_1 is the efficiency of plant conversion into herbivore biomass. Consumption rate of plants by the herbivore follows a multispecies Holling type II functional response. Defended plants P_2 impose a decreased capture rate v_2 on herbivores, relative to the higher v_1 of undefended plants P_1. As a trade-off, we assume that undefended autotrophs are more efficient at nutrient uptake; i.e., $f_1 > f_2$. For present purposes, we assume that $h_1 = h_2$ and $s_1 = s_2$. The rate coefficient for the induction of defenses is I_1, and the rate coefficient for the decay of defenses is D_1, and both are assumed to be functions of herbivore density. Induction is a process that subtracts from the undefended part of the resource population and adds to the defended part. Decay of defenses takes away from the defended part of a prey population and adds to the undefended part.

By definition, a food chain without defenses is composed of only P_1, while a food chain with all permanently defended autotrophs would have only P_2. It is unlikely in nature that induction or decay occur at razor-sharp values of herbivore density, because members of the autotroph population will not all sense the same herbivore density. Therefore, it is preferable to model these fluxes as continuous functions of herbivore density. Induction of defenses is assumed minimal at low herbivore densities and maximal at high herbivore densities. The reverse is true for the decay of defenses. According to this model, fluxes in both directions are usually occurring simultaneously. We assume that the induction and decay rates are sigmoidal in shape and have the specific mathematical forms:

$$I_1(H) = i_1 \left(1 - \left(1 + \left(\frac{H}{g_1} \right)^{b_1} \right)^{-1} \right)$$

$$= \text{induction rate of autotroph defenses} \qquad (11.2a)$$

$$D_1(H) = i_1 \left(1 + \left(\frac{H}{g_1} \right)^{b_1} \right)^{-1} = \text{decay rate of autotroph defenses} \qquad (11.2b)$$

where g_1 is the density of herbivores at which autotroph defense induction reaches half its maximum rate (thus can be called a "half-saturation" constant), and b_1 is a shape parameter of the defense induction and decay functions
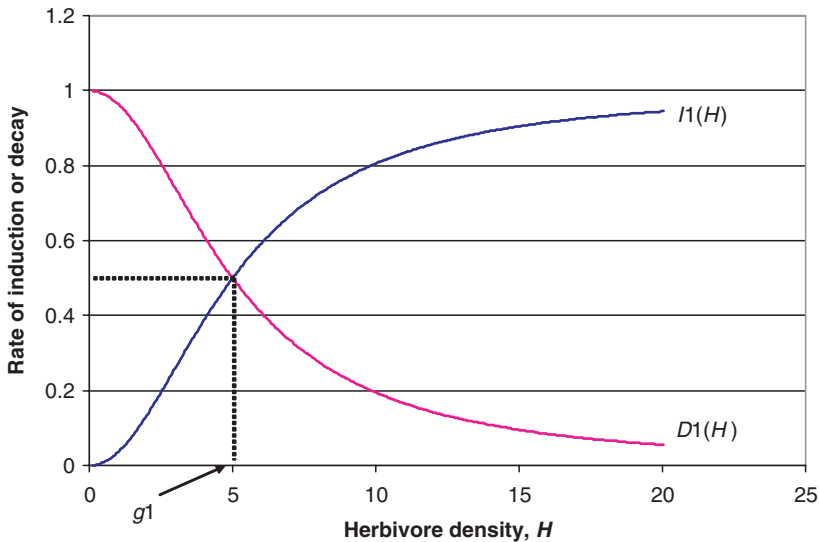
Figure 11.2. Rate coefficients for defense induction and decay as functions of herbivore density ($g_1 = 5.0$ and $b_1 = 2.05$).

(Figure 11.2). We have made the simplest assumption, that b_1 and g_1 are the same for induction and decay in the absence of more precise knowledge. Note that $I_1(H) + D_1(H) = i_1$. The fluxes (11.2a, b) ensure that eventually all autotrophs become undefended when no herbivores are present. When herbivores are present, a balance of defense induction and decay will be approached at a rate that is set by parameter i_1.

In this system, when all autotrophs are either undefended or defended and cannot change, the variables N, P, and H respond to a change in nutrient input, N_0, according to the EEH (Figure 11.3). When all autotrophs have the ability to switch between the defended and undefended states, the total autotroph biomass increases over the whole range of values of N_0 (Figure 11.4a, b). This increase occurs for the productivity range in which the fraction of defended autotrophs increases from 0 to 1. The nutrient input range for which both defended and undefended autotrophs are present widens as the value of the parameter b_1 decreases. Within this productivity range total plant biomass increases continuously with enrichment. This shows that inducible defenses have the effect of modifying the top-down control by the herbivore such that the herbivore does not control the total biomass of the autotrophs.

11.3.1   Adaptive evolution of the induction and decay functions

The food web model represented by Eqs. (11.1a, b, c, d) and (11.2a, b) incorporates inducible defenses by the autotrophs, and describes the dynamics of
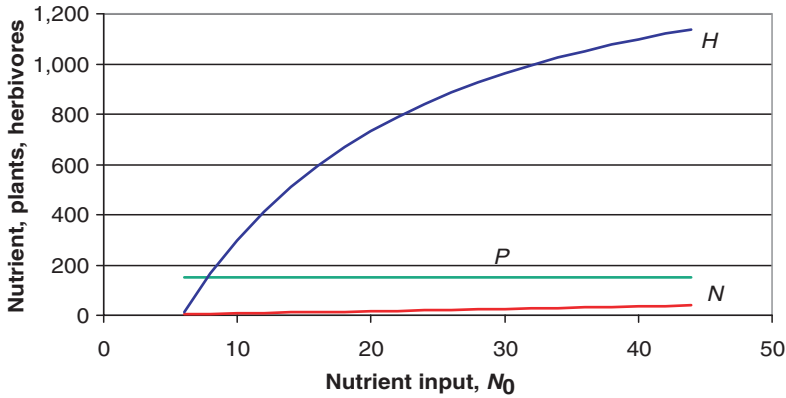
Figure 11.3. Behavior of trophic levels as a function of nutrient input concentration, N_0, when there is no defense induction. $f_1 = 1.45$.

undefended and defended fractions of the population through time, as well as the dynamics of the nutrient resource and of the herbivore population. However, this model makes an assumption concerning switching between states that needs to be evaluated further. The induction and decay functions contain a parameter g_1, which is a behavioral parameter of the autotrophs governing the likelihood of switching at a given herbivore density H. For values of herbivore density, $H > g_1$, the probability of an individual changing from undefended autotrophs to defended autotrophs is greater than a transition in the opposite direction, whereas for $H < g_1$, the reverse is true. The value of g_1 in the simulations shown in Figure 11.4 was chosen arbitrarily as $g_1 = 5$. While assignment of g_1 to any positive value correctly reflects the observed qualitative fact that the probability for induced defense increases with higher herbivore density, it leaves open the question of whether a particular saturation constant value, g_1, is optimal for individuals. This can be examined by allowing g_1 to itself be a variable in the simulation. In particular, many different plant genotypes can be modeled, each with a different value of g_1, to determine which has the highest fitness. This allows us to address adaptive change in the induction and decay functions, which was not included in the model of Vos et al. (2004b). This is done here using an IBM approach. This model, described in Section 11.3.2, is designed to determine how natural selection acting on the individual trait g_1 affects the dynamics and trophic structure of the system.

11.3.2   Individual-based version of the model

To investigate the induction and decay strategy at the level of individuals, we developed an IBM that is an analog of the model incorporated in Eqs. (11.1a, b, c, d) and (11.2a, b). In this model the nutrient resource and the herbivores
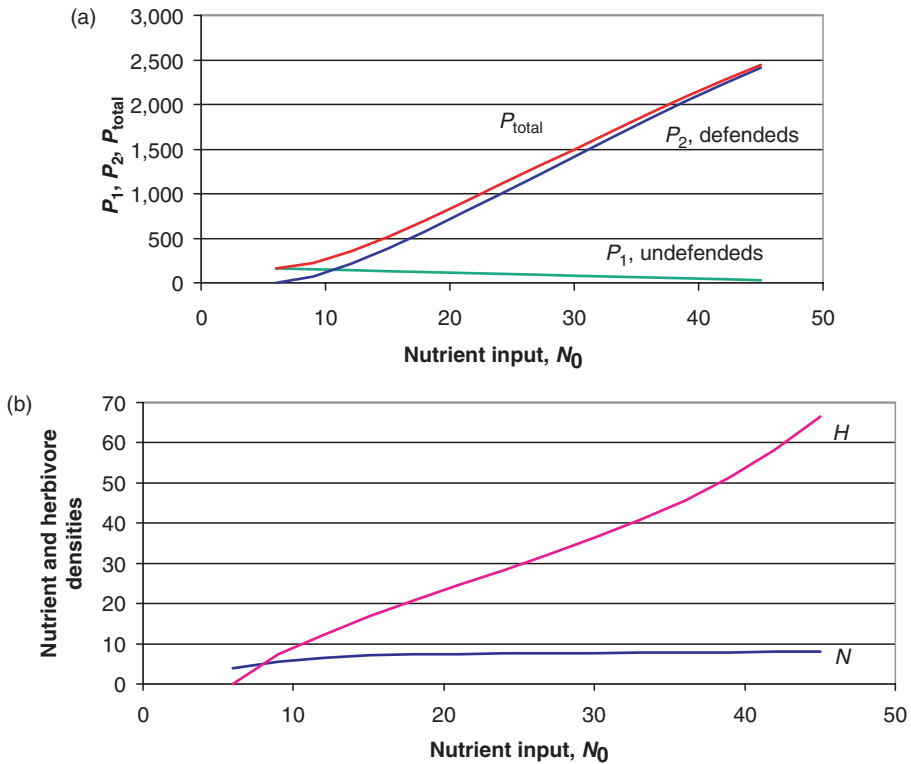
Figure 11.4. Behavior of trophic levels as a function of nutrient input concentration, N_0, when there is defense induction. (a) Behavior of P_1, P_2, and P_{total}. (b) Behavior of N and H. This is from a simulation run with g_1 having an arbitrary value. $f_1 = 1.45$, $g_1 = 10$, $f_2 = 1$. Other parameter values are given in Table 11.1.

continue to be represented by single variables, but the autotrophs (phytoplankters) are modeled as individuals. In this way each individual can be one of a large variety of genotypes. Each genotype has its own value, g_{1i}, of the switching parameter g_1.

The phytoplankters are discretized in the following way:

- Each phytoplankter is modeled as an individual cell with a given genotype, i, where the different genotypes differ only in their values of the switching parameter, g_{1i}.
- Phytoplankton cells grow and reproduce by fission. Daughter cells have the same genotype as the parent cell.
- The initial size of a cell is one biomass unit. On each time step, each cell grows by an amount $[f_j N/(k_1 + N)]\Delta t$, where Δt, is the size of the time step. The parameter f_j is the phytoplankton growth rate coefficient, which depends only on whether the individual phytoplankter is in the undefended ($j = 1$) or defended ($j = 2$) state. When a cell reaches two biomass units, it splits into two

daughter cells, each having the size of one biomass unit. Daughter cells are assumed to initially have the same state, defended or undefended, as the parent.

- Each cell has a probability of being consumed on each time step, given by $[v_j H/(1 + v_1 h_1 P_1 + v_2 h_2 P_2)]\Delta t$, where P_1 and P_2 are the number of cells in the undefended and defended states, respectively. The predation probability coefficient, v_j, depends only on whether the phytoplankton cell is in the defended or undefended state. Each cell also has a probability, $s_{11}\Delta t$, of natural mortality at each time step.

- Each individual has a probability, on each time step, of switching between the undefended state and defended state. The probability of switching from the undefended to the defended state is given by $I_1\Delta t$, while the reverse is given by $D_1\Delta t$. The parameter i in I_1 and D_1 was adjusted so that switching was not likely to occur more than a few times in the lifetime of an individual.

- One further difference between the differential equation model and the IBM is that both f_j and v_j were increased by 50% in the latter to reflect that the average cell is somewhere between 1.0 and 2.0 biomass units.

The IBM is simulated by using small discrete time steps, rather than as a continuous process; thus, the equations for nutrient and herbivore densities are described by difference equations rather than differential equations. This allows there to be a small probability each time step for phytoplankton individuals to die, be consumed, or to switch states. The variables, N and H, are updated each time step. The internal nutrient pool receives external input and losses by flow through, as well as uptake by plants. The herbivore component is able to assimilate an amount, c_1, times the number of phytoplankton consumed each time step, times their biomass units.

The IBM differs in two major respects from the differential equation model. First, the individual phytoplankters are given simple life cycles, and second, switching by individuals is explicitly modeled. Other differences are, of course, that the model now has difference rather than differential equations for N and H, and that the phytoplankters are individuals, which introduces demographic stochasticity. However, only the first two changes might be expected to make noticeable systematic differences in the variables between this model and that of Eqs. (11.1a, b, c, d) and (11.2a, b) when simulations are performed.

To test this, a simulation was performed in which the set of parameters used for Figure 11.4 was employed, but adjustment was made on the switching rate, using parameter i_1. For comparison, the output of P_1 and P_2 from both the differential equation and IBM simulations is shown in Figures 11.5a, b. The plot of defended and undefended individuals in Figure 11.5b shows slightly lower values than the differential equation model (Figure 11.5a). The deviation is not unexpected, as the IBM is not a perfect analog of the differential equation model. We considered the IBM to be a useful device to explore the effects of variation within the phytoplankton population, which can then be tested more rigorously through other means. Thus, there was no need for the IBM to precisely duplicate the differential equation model.
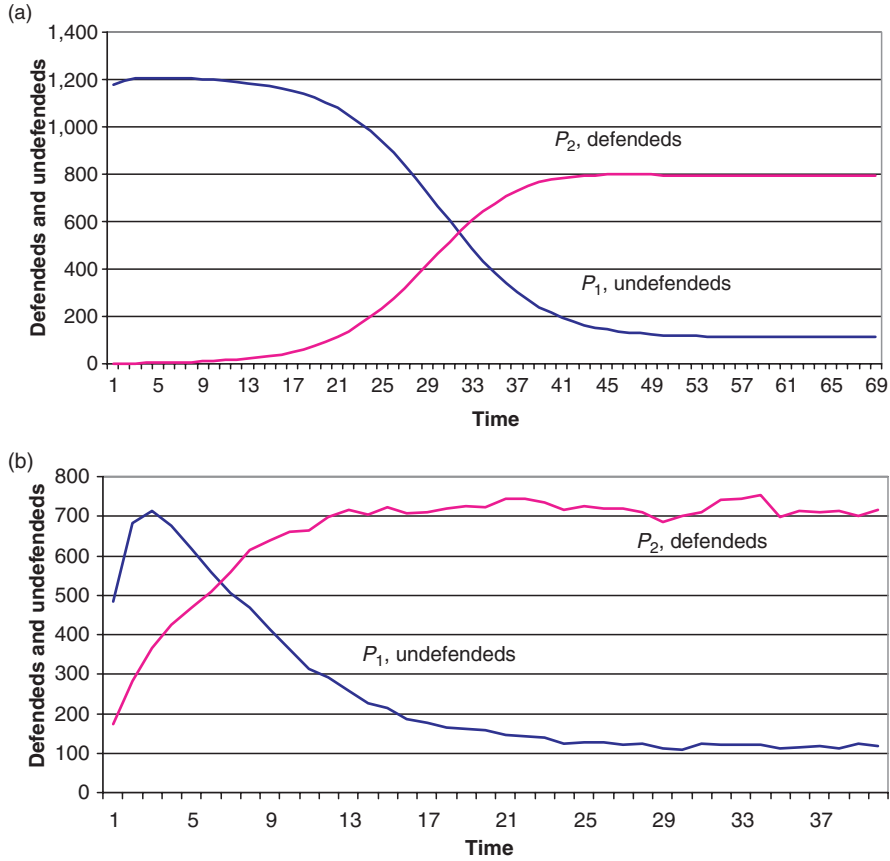
Figure 11.5. (a) Numerical solution of differential equation model for P_1 and P_2 through time; for $f_1 = 1.45$ and $f_2 = 1.00$, $g_1 = 5.98$. (b) Simulation of analog individual-based model for P_1 and P_2. $f_1 = 1.45$, $f_2 = 1$, $g_1 = 5.98$.

11.4 RESULTS

Simulations were performed using the same set of parameter values shown in Figures 11.4 and 11.5, except that simulations were initiated with a set of 400 individuals, each of which was one of 40 different genotypes, having 40 different parameter values, $g_{1i} = 0.1, 0.5, 1, 1.5, \ldots, 19.5$. The genotypes were assigned randomly to individuals by choosing pseudorandom numbers in the interval $(0,1)$ and letting each of the 400 initial individuals have a 0.025 chance of having any given value of g_{1i}. In the simulation, offspring were assumed to have the same genotype as the mother cell.

The parameter values used in the simulations also differed from Figures 11.4 and 11.5 in that results for a variety of different values of the parameters f_1 and f_2 were explored. The results of a typical simulation are shown in Figures 11.6a, b, c, d. Figure 11.6a shows the numbers of individuals in each genotype surviving as a function of the number of time steps. We observed stabilization over time of the resource level and herbivore density (Figure 11.6b), the numbers of undefended and defended individuals (Figure 11.6c) and the fluxes of individuals
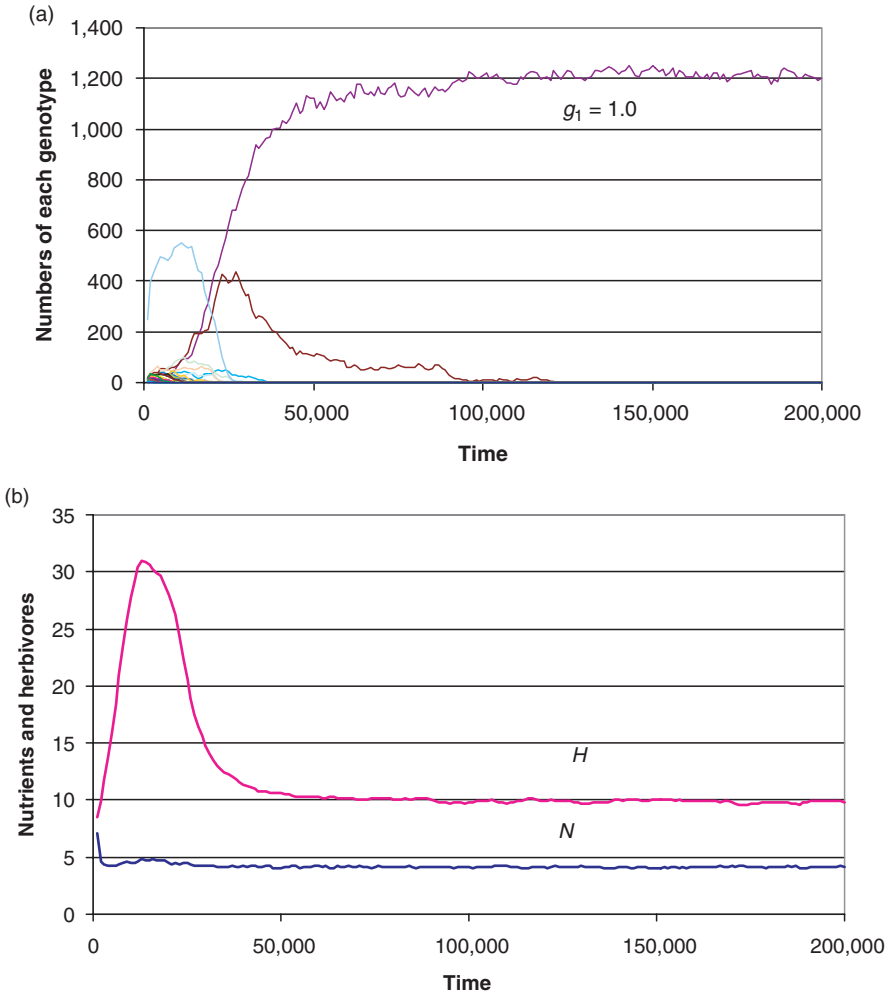
Figure 11.6. Simulation of individual-based model for the case in which 40 initial phytoplankton lineages are in competition. Parameters $f_1 = 1.40$ and $f_2 = 1.38$. Other parameter values are given in Table 11.1. (a) Numbers of phytoplankton with various genotypes. (b) Values of N and H.
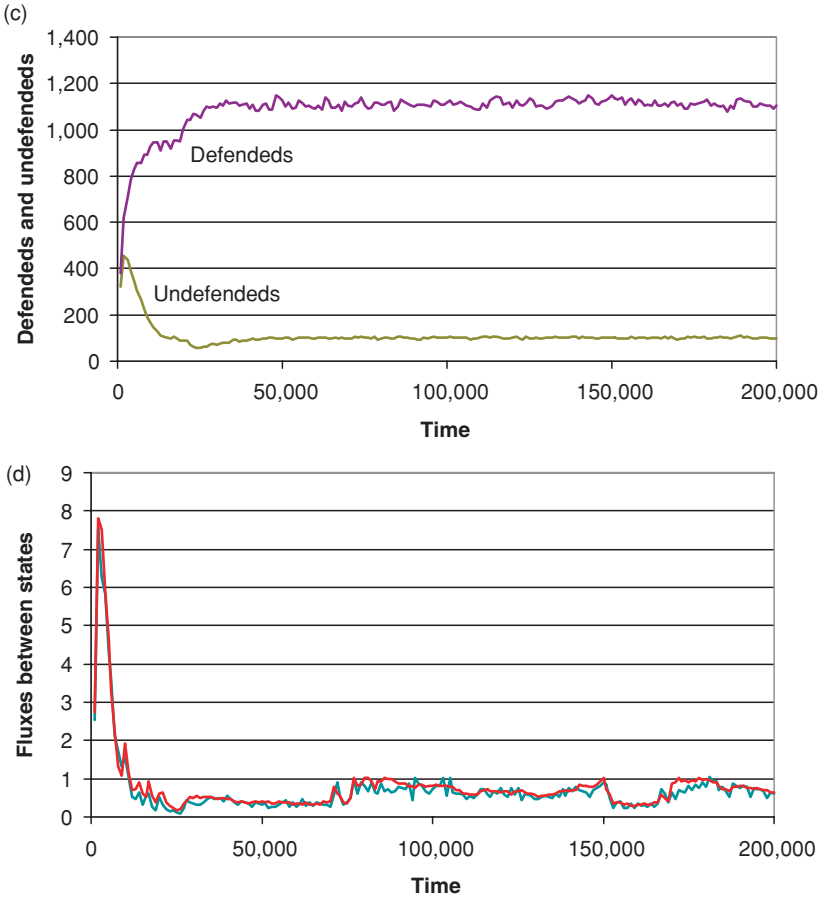
Figure 11.6. (*Continued*) (c) Numbers of P_1 and P_2. (d) Fluxes between defended and undefended states. $f_1 = 1.40$ and $f_2 = 1.38$.

between the defended and undefended states (Figure 11.6d). In all simulations one genotype eventually dominated, and that value of g_1 depended on the particular values of f_1 and f_2 in the simulation.

An interesting outcome of the individual-based simulation was that the system approached a steady state in which the fluxes between defended and undefended components in the population appear to be approximately equal (see Figure 11.6d). We performed numerous simulations, with different values of f_1 and f_2, in which the same result occurred. When the system was allowed to evolve toward a dominant genotype, this always resulted in an approximate balance of fluxes between defended and undefended individuals, whereas, if g_1 was chosen arbitrarily, there was more likely to be a net flux from one state to another. That is, in the ESS, it appeared that $I_1 P_1 = D_1 P_2$. This equality has a

Table 11.1. Parameter values used in model

$Q_I = 30.0$
$N_0 = 20.0$
$k_1 = 10.0$
$f_1 = $ various values between 1.00 and 1.45
$f_2 = $ various values between 0.70 and 1.40
$v_1 = 0.20$
$v_2 = 0.0125$
$h_1 = 0.5$
$h_2 = 0.5$
$s_1 = 0.4$
$s_2 = 0.4$
$s_3 = 0.95$
$c_1 = 0.5$
$i_1 = $ various values from 0.01 to 1.0
$b = 2.05$

further implication. The first three terms on the right-hand side of Eq. (11.1b), divided by P_1, can be thought of as an instantaneous (or very short term) measure of the "fitness" associated with being in the undefended state. The first three terms on the right-hand side of Eq. (11.1c), divided by P_2, can similarly be thought of as the instantaneous "fitness" associated with being in the defended state. (Note this short-term measure of fitness associated with being in a given state, defended, or undefended, is not to be confused with the fitness associated with being a certain genotype with a particular value of g_1, and having the freedom to switch between states.) If it is true that $I_1 P_1 = D_1 P_2$, then in steady state the fitnesses associated with the defended and undefended states would be equal, both $I_1 P_1$ and $D_1 P_2$ being zero. This equality would correspond to an IFD between the defended and undefended states. Since our assumption that $I_1 P_1 = D_1 P_2$ is based only on observations of numerical model output, we next attempted to confirm this more rigorously.

11.4.1 Does the evolutionarily stable state correspond to an ideal free distribution?

The ESS corresponds to an IFD if the fitnesses of defended and undefended phenotypes are the same at equilibrium. From Eq. (11.1), this is the same as $P_1 I_1(H) = P_2 D_1(H)$ being true. If this equality is assumed in the differential equation model, then it is easy to solve Eqs. (11.1a, b, c, d) and (11.2a, b) analytically to obtain the steady state values

$$N^* = (v_2 s_1 - v_1 s_2) k_1 / (v_2 f_1 - v_1 f_2 + v_1 s_1 - v_2 s_1)$$
$$P_1^* = A_4 / A_3$$
$$P_2^* = (s_2 k_2 - A_1 P_1^*) / A_2$$
$$H^* = [f_1 N^* / (k_1 + N^*) - s_1][1 + v_1 h_1 P_1^* + v_2 h_2 P_2^*] / v_1$$

where

$$A_1 = c_1 v_1 - s_3 v_1 h_1$$
$$A_2 = c_1 v_2 - s_3 v_2 h_2$$
$$A_3 = A_2 f_1 - A_1 f_2$$
$$A_4 = A_2(k_1 + N^*)Q_I(N_0 - N^*)/N^* - f_2 s_3$$

We can then use $I_1(H) = D_1(H)$ to solve g_1 that corresponds to the IFD;

$$g_{1,\text{IFD}} = H^*(P_1^*/P_2^*)^{1/b}$$

Now we are in a position to find the values of $g_{1,\text{IFD}}$ corresponding to the IFD for any set of model parameters. For example, holding all parameters (including f_1) constant except for f_2, which is allowed to take values from 1.43 to 0.61, we find a set of values of $g_{1,\text{IFD}}$, forming a curve, that correspond to IFDs (Figure 11.7).

It is now possible to determine whether the resultant values of $g_{1,\text{IFD}}$ in Figure 11.7 are ESSs in addition to being values that correspond to the IFD. We did this for some parameter combinations by performing simulations with the set of Eqs. (11.1a, b, c, d) and (11.2a, b), which was extended in order to model the existence of both a resident and an invading strain or genotype. The resident genotype had the parameter value $g_{1,\text{IFD}}$, whereas the invader had some other genotype g_1 value. We simulated all possible combinations of resident and invader strategies on the grid shown in Figure 11.8, starting with the equilibrium values of the resident strategies and small initial populations of the invaders.
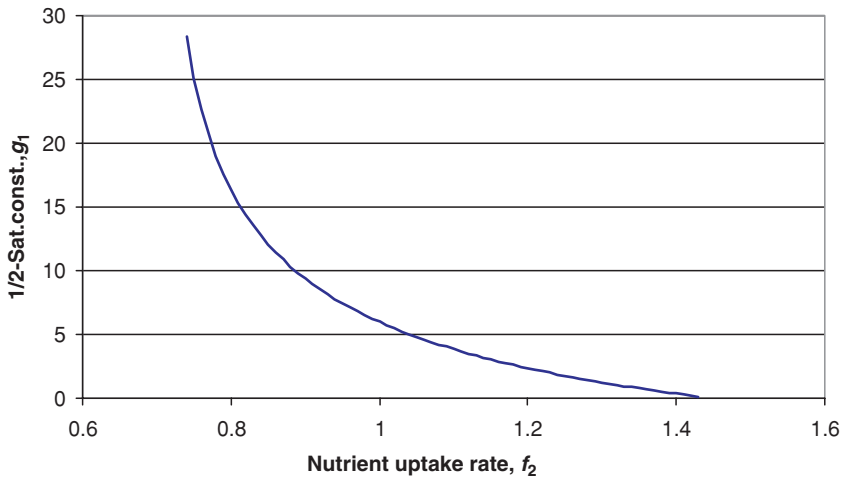
Figure 11.7. Plot of $g_{1,\text{IFD}}$ (the value of g_1 that produces IFD) versus nutrient uptake rate, f_2, from the analytic model. $f_1 = 1.45$.
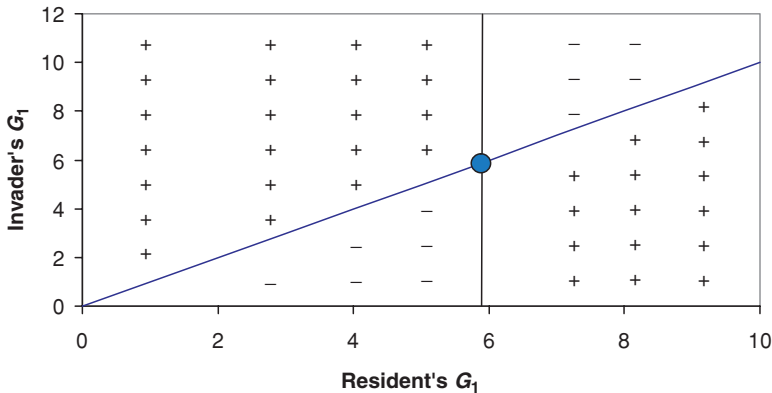
Figure 11.8. Invasion plot for testing whether the IFD is also an ESS. Example for $f_1 = 1.45$ and $f_2 = 1$. For these values, $g_{1,\text{IFD}} = 5.98$.

Plus signs show the combinations for which the invaders were successful and minus signs show the combinations for which the residents were successful. This pattern corresponds to an ESS. It also corresponds to "convergence stability," because the strategy is not only stable against invasion, but can also be reached through the course of evolution. That is, given some resident strategy that is not an ESS, a mutant strategy that lies closer to the ESS can always invade (e.g., Dieckmann 1997, Geritz et al. 1998, Doebeli and Dieckmann 2000).

A more general theoretical approach to the relationship between an IFD and ESS has been described in the analogous situation of animals moving between two different habitats in space. In such situations, it has been proven that an IFD for the population corresponds to an ESS for individuals (McPeek and Holt 1992, Cressman et al. 2004). A similar proof of the identity of the IFD and ESS can be produced for the case of a population with inducible defenses, but we will not present it here.

11.4.2   Implications of g_1 as an adaptive trait

Now, by believing that the $g_{1,\text{IFD}}$ is also $g_{1,\text{ESS}}$, we can assume that it is possible for $I_1 P_1 = D_1 P_2$ to hold if natural selection can act on the parameter g_1 such that $g_1 = g_{1,\text{ESS}}$. Suppose now the environmental conditions change through time, causing such parameters as nutrient input, N_0, to change. The population of autotrophs could respond through changes in g_1. If natural selection can occur on a timescale as fast as the changes in N_0, then it will always be true that $g_1 = g_{1,\text{ESS}}$, and hence $I_1 P_1 = D_1 P_2$. This has the interesting implication that, as N_0 changes, the two states, defendeds and undefendeds, will behave during this process as if there is no net flux, and hence no interaction, between them. In other words, the inducible defense model should behave as if it were a

"diamond-shaped" food web; that is, one with two prey species sharing one resource and preyed on by one predator species.

To confirm this, we repeated the enrichment manipulations that were carried out earlier by increasing N_0 (see Figure 11.3) and letting the system come to steady state for each incremental change in N_0. What happened was that neither N nor H increased with increasing N_0 (Figure 11.9a). Instead, P_1 decreased and P_2 increased (Figure 11.9b). This is exactly the type of response that Abrams (1993) demonstrated in an analysis of many different three-level food webs. Leibold (1996) also showed that in a "diamond-shaped" food web (i.e., with one resource, two consumer–prey species, and one predator) "the predator and resource densities are buffered against such variation in productivity...but the intermediate consumer–prey species are not." Abrams and Vos (2003)
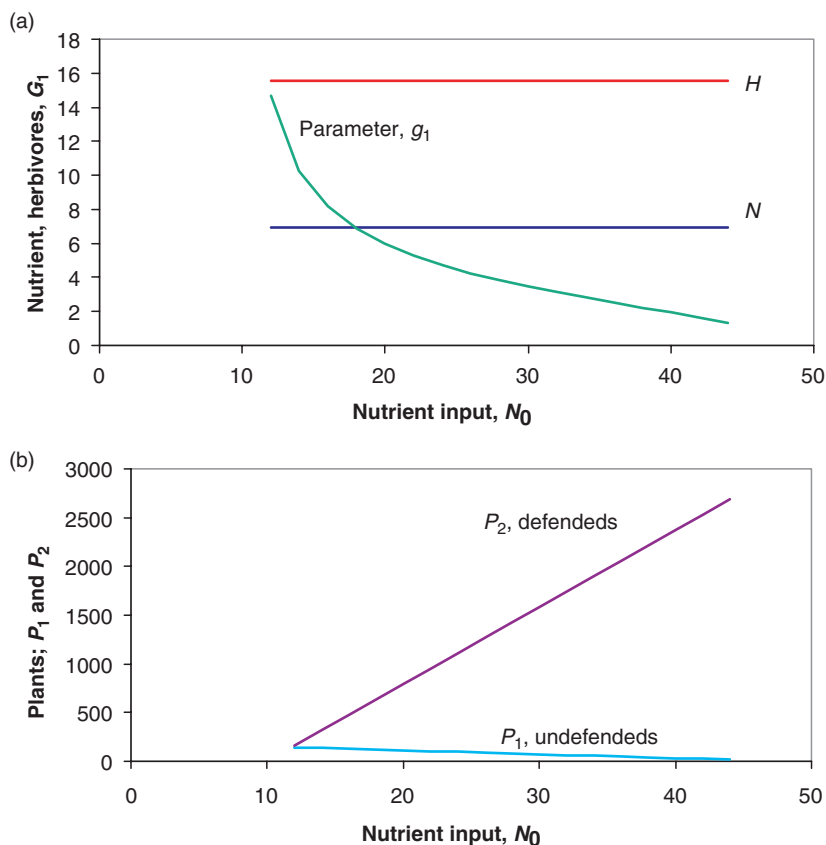
Figure 11.9. (a) Plot of N and H as a function of nutrient input, N_0, when $g_1 = g_{1,IFD}$. Note that g_1 changes through time to maintain the ideal free distribution. (b) Plot of P_1, P_2, and P_{total} as a function of N_0. $f_1 = 1.45$, $f_2 = 1$.

investigated a three-species food chain with adaptive behavior by the middle (prey) species. They showed that, when prey has a continuously variable defensive trait that is adjusted optimally, there is no response of equilibrium predator and resource abundances to resource productivity when there is a linear trade-off between resource capture and vulnerability to the predator. Here, we have obtained similar results for a three-species food chain with a different kind of defensive trait; i.e., one that allows the prey species to switch between two states, defendeds and undefendeds. It is interesting to note that the ESS criterion in the present model corresponds to the optimization condition in Abrams and Vos (2003), and the presence of only two phenotypes implies a linear relationship between the mean vulnerability to herbivores and the mean capture rate of nutrient in the autotroph (prey) population.
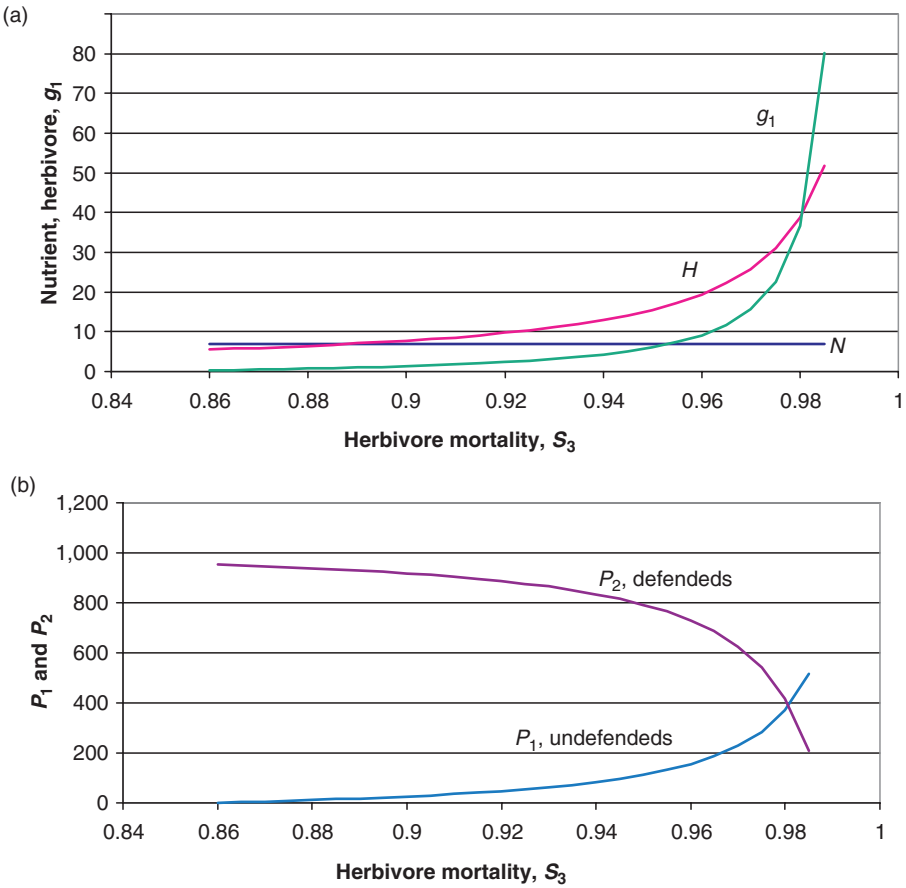
Figure 11.10. (a) Plot of N and H as a function of herbivore mortality, s_3, when $g_1 = g_{1,\text{IFD}}$. (b) Plot of P_1, P_2, and P_{total} as a function of s_3. $f_1 = 1.45$, $f_2 = 1$.

We also examined the system when the herbivore mortality, s_3, was changed, with all other parameters remaining constant, and the system allowed to reach steady state for each change in s_3. These results are shown in Figures 11.10a, b. The herbivore biomass increases as herbivore mortality increases. This indicates that, at least for some sets of parameter values, increases in predator death rate can lead to increases in predator density as well as in total prey density. This surprising result, though new in context, is also not new in type. Abrams and Vos (2003) pointed out that models with an adaptively induced defense polymorphism have properties very similar to those in which all individuals adjust a continuous defensive behavior adaptively. Abrams and Matsuda (1997, 2005) pointed out that this reduction in predator density with increased predator mortality can occur in food chains with either a single adaptive prey species or in a system with two competing prey species and one predator.

11.5   DISCUSSION

This work has focused on the well-known property that the presence of predators can induce defenses against predation in many prey species. We have explored the food web consequences of the prey optimizing their switching to defense with respect to predator density. The main conclusions of this work are as follows:
- If selection is allowed to act on the parameter g_1, for half-saturation of defense induction, the phytoplankton population will move toward an ESS.
- This ESS corresponds to an IFD with respect to the two phenotype states; defendeds and undefendeds.
- If g_1 is allowed to adjust adaptively, then the bitrophic system with induced defenses behaves like a simple "diamond-shaped" food web.

There are some ways in which the work might be extended in the future. These include the following:
- Examining effects of b_1 in the induction/decay functions as well as other forms of this function.
- Examining other types of alternate traits within a population than induced defenses.
- Examining cases with more than two possible states; that is, more than just "defense" or "no defense." Work of this type has already been done by Abrams and Vos (2003) and Loeuille and Loreau (2004), but both of these papers implicitly assume a narrow distribution of states within the prey population.
- Examining situations that are more complex environmentally and taxonomically.

The present work explores only one of a variety of processes by which a given trophic level can become better defended, which includes the following. Individuals within species can alter their behavior. Developmental changes can produce better-defended individuals within species on a slightly slower

timescale. Evolutionary change can do the same thing on a longer timescale. Replacement of poorly defended species by better-defended species may also occur. Models of all of these processes typically assume, as we do here, that there is a cost to defense in terms of growth rate or resource utilization. It is therefore not surprising that all processes may have similar ecological consequences in terms of the responses of equilibrium trophic level abundances to fertilization. The lack of predator and resource response to enrichment in our ESS model has also been observed in food web models that lack adaptation and have only two species on the middle level (Leibold 1989, Abrams 1993). The same lack of predator and resource response is also seen in models with behavioral flexibility, but a linear trade-off between a growth parameter and predator vulnerability (Abrams and Vos 2003). However, optimal adjustment of nonlinear behavioral trade-offs (Abrams and Vos 2003), or the presence of many potential species whose growth and defense properties are described by a similarly nonlinear trade-off (Leibold 1996) predict increases in all trophic levels following enrichment. Presumably, a model in which a number of different degrees of defense could be induced would produce a similar result. Therefore, our model results appear to be one example of a general phenomenon that occurs in food webs.

But it is still important to ask whether the adaptive adjustment of the parameter g_1 that is assumed here actually occurs in the parameters of induced defenses (or of the parameters for other adaptations for that matter). One reason that optimization might not be achieved is that organisms are usually unable to accurately determine the exact state of the environment and thus to tune their behavior accordingly. Another reason is that food webs are dynamic and changing continuously over the seasons, years, and decades, and thus adaptation might not be able to keep up with the changing biotic environment. The nonadaptive Vos et al. (2004b) pattern is in agreement with the pattern that is almost exclusively observed in the field (all levels increasing under enrichment). It should be noted, of course, that the pattern in the field is also consistent with many models other than that of Vos et al., in which the autotroph exhibits continuous variation in a parameter (Abrams and Vos 2003, Loeuille and Loreau 2004), and there are many other (nonevolutionary) explanations for this pattern (Abrams 1994). In any case, the pattern of changes in food web trophic structure when the induced defense is adaptive (Figure 11.9) is not observed empirically. Adaptive arguments narrow down parameter space from all that is possible to what is likely in an ecologically realistic domain. However, most communities change faster than it is likely to take ESS types to "arrive" based on random mutation and selection.

Most food webs are probably highly dynamic relative to the speed of arrival of potential "ESS" mutations. For example, during the late Pleistocene, a mere 12,000 years ago, most modern ecological communities did not exist in their present locations, or consist of the particular mixture of species that coexists today (e.g., Davis 1986). In addition, community assembly and compositional change in communities may be cyclic (see e.g., Steiner and Leibold

2004). An ESS approach is essentially based on an equilibrium view of the world. Change (and dealing with it) is the essence of life/nature. Evolution is a process that tracks change, but it is still an open question to what extent it optimizes.

   We cannot resolve this question here. In this paper we have explored, following the ideas of Peter Yodzis, some of the consequences of allowing microevolution in a population model. It is best to allow Yodzis (1989) to have the last words, although he wrote them more than 15 years ago: "In the light of these considerations, it would be foolish to insist that microevolution necessarily will result in an optimal final state for each and every 'evolutionary problem' that we can contemplate. However, while the objections to optimization theory show that optima need not necessarily be attained, there is no proof that optima will never be attained or that they will seldom be attained. . . . it seems prudent then, to suspend judgment for the time being while we explore this powerful methodology, see what it predicts, and compare those predictions to what we see in nature" (p. 251).

11.6   ACKNOWLEDGMENTS

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CHAPTER 12

EVOLUTIONARY DEMOGRAPHY: THE INVASION EXPONENT AND THE EFFECTIVE POPULATION DENSITY IN NONLINEAR MATRIX MODELS

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12.1 ABSTRACT

The invasion exponent plays a critical role in life history theory. It measures the rate at which a new phenotype would grow if introduced at low densities into a population of a resident phenotype, which is on an attractor (equilibrium, cycle, invariant loop, or strange attractor). Only if the invasion exponent is positive will selection favor the phenotypic change represented by the difference between the invader and the resident. The selection gradient on the trait is measured by the sensitivity of the invasion exponent to a change in that parameter. This chapter reviews results on invasion exponents calculated from linear and non-linear matrix population models. In addition to changing the parameter, a successful invasion will also lead to a new attractor, and thus affect population

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density. When the resident phenotype is at a stable equilibrium, the sensitivity of the invasion exponent is equal to the sensitivity of an effective equilibrium density, which is a weighted sum of the equilibrium stage densities. The weights measure the effect of the stage on density dependence and the effect of the density dependence on population growth rate. This chapter presents a new analysis, extending these results to invasions when the resident is on a periodic attractor, an invariant loop, or a strange attractor. In each case, the selection gradient is equal to the sensitivity of an effective average density, which is a weighted average over the attractor. The weights reflect the effect of each stage on the vital rates and on density dependence.

12.2 INTRODUCTION

Tucked away among Peter Yodzis's more significant contributions to ecology is a short paper (Yodzis 1981) on the sensitivity analysis of matrix population models. In it, he took issue with a paper of mine (Caswell 1980) that had criticized a paper of Schaffer (1974) on the equivalence of maximizing fitness and maximizing reproductive value. My goal had been to generalize Schaffer's theorem from age-classified to stage-classified life cycles, but instead I had found that it seemed to apply only under very restrictive conditions. Yodzis questioned my conclusions, and we corresponded back and forth about the calculations and their interpretation. Our communication was memorable for his perceptiveness, clarity, and openness. Philosophers claim that critical discussions under these conditions lead to scientific progress. They certainly did in this case; Yodzis's critique not only resolved the dispute,[1] but, once I understood it, provided the insight I needed to generalize Schaffer's theorem (Caswell 1982).

Yodzis correctly recognized the importance of Schaffer's result, which connected demographic parameters (the age-specific reproductive value schedule, which is determined by age-specific survivorship and fertility) and evolutionary optimization. This connection permits predictions about how natural selection should influence life history traits.

Today, such evolutionary questions would probably be studied in terms of invasion (e.g., Maynard Smith 1982, Yodzis 1989), now termed "adaptive dynamics." Imagine a population with a phenotype given by θ_0 (e.g., clutch size, or age at maturity). Suppose that mutation or recombination introduces a new phenotype, $\theta_0 + \Delta\theta$. If this new phenotype increases in frequency relative to the resident phenotype, we say that it can invade. An evolutionary stable strategy (ESS) is a phenotype that can invade, but cannot be invaded by, any alternative phenotype. See Metz et al. (1992), Rand et al. (1994), Ferriére and Gatto (1995), and Diekmann (2004) for thorough discussions, emphasizing the importance of invasion analysis in evolutionary ecology. Evolution, from this perspective, is a sequence of replacements of one phenotype by another.

[1]It all depended on how one interpreted the optimization problem.

The key to understanding this sequence of replacements is the rate of growth of the invading phenotype relative to that of the resident. Consider the simplest case: a scalar population growing exponentially. The resident grows at a rate λ_1, the invader grows at the rate λ_2. The long-term growth rate of the relative frequency of the two types is

$$\log \lambda_I = \lim_{T \to \infty} \frac{1}{T} \log \frac{N_2(T)}{N_1(T)} \tag{12.1}$$

$$= \lim_{T \to \infty} \frac{1}{T} (\log N_2(0) + T \log \lambda_2 - \log N_1(0) - T \log \lambda_1) \tag{12.2}$$

$$= \log \lambda_2 - \log \lambda_1. \tag{12.3}$$

The quantity $\log \lambda_I$ is known as the *invasion exponent*. The invasion is successful if and only if $\log \lambda_I > 0$; i.e., if the growth rate of the invader exceeds that of the resident (cf. Yodzis 1989, p. 253).

Invasion analysis is a powerful idea, but in order to use it we need a demographic model from which the invasion exponent can be calculated. For applications in life history evolution, that means a structured rather than a scalar model, because life history traits express themselves within the life cycle. In Section 12.3, I consider the calculation of the invasion exponent from a density-dependent stage-structured matrix population model. The nature of the invasion exponent depends on whether the resident population is at an equilibrium, cycling, or undergoing quasiperiodic or chaotic fluctuations.

12.3 INVASION EXPONENTS AND ATTRACTORS

Consider a population governed by a nonlinear stage-structured matrix population model

$$\mathbf{n}(t+1) = \mathbf{A}[\theta, \mathbf{n}(t)]\mathbf{n}(t), \tag{12.4}$$

where $\mathbf{n}$ is a vector whose entries are the densities of the stages and $\mathbf{A}$ is a projection matrix that depends on a parameter θ and on population density. Such models can exhibit a variety of attractors, including equilibria, cycles, invariant loops (generating quasiperiodic dynamics), and strange attractors (generating chaotic dynamics). See Cushing (1998) or Caswell (2001, Chap. 16) for details.

In such a model, invasion is analyzed assuming that the resident phenotype is at an attractor. Since an attractor is bounded, the long-term growth rate of the resident on its attractor is 0, and the invasion exponent is simply the growth rate of the invader. Because mutation produces new phenotypes in extremely low densities relative to the resident phenotype, the invasion depends on the linear growth of the invader in an environment characterized by the resident population on its attractor. Thus the invasion problem is one of linear growth in an environment that depends on the attractor being invaded (Metz et al. 1992).

Invading an equilibrium: The resident is at $\hat{\mathbf{n}}_1$; the invader is at $\mathbf{n}_2 \approx 0$. The projection matrix for the invader depends on the densities of both the resident and the invader: $\mathbf{A}[\theta_2, \mathbf{n}_1(t), \mathbf{n}_2(t)]$. The invasion exponent is the growth rate of the invader,

$$\log \lambda_I = \log \lambda (\mathbf{A}[\theta_2, \hat{\mathbf{n}}_1, 0]), \tag{12.5}$$

where λ is the dominant eigenvalue of $\mathbf{A}$. The invasion is successful if $\log \lambda > 0$.

Invading a cycle: Suppose that the resident is on an attracting p-cycle, $\hat{\mathbf{n}}_1, \ldots, \hat{\mathbf{n}}_p$. The invader now grows in density-independent fashion in a periodic environment characterized by the cyclic density of the resident; its average growth rate in this periodic environment is

$$\log \lambda_I = \frac{1}{p} \log \lambda \left(\mathbf{A}[\theta_2, \hat{\mathbf{n}}_p, 0] \ldots \mathbf{A}[\theta_2, \hat{\mathbf{n}}_1, 0] \right), \tag{12.6}$$

where λ is the dominant eigenvalue of the periodic matrix product characterizing the periodic attractor.

Invading an invariant loop or strange attractor: On an invariant loop or strange attractor, the dynamics of the resident phenotype produce a time-varying but aperiodic environment for the invader. Let $\hat{\mathbf{n}}_1(t)$, $t = 1, 2, \ldots$ denote a sequence of points on the attractor in the absence of the invader. The invading phenotype is introduced at such low densities that its effects on the resident are negligible; the long-term growth rate of the invader is then given by

$$\log \lambda_I = \lim_{T \to \infty} \frac{1}{T} \log \| \mathbf{A}[\theta_2, \hat{\mathbf{n}}_T, 0] \ldots \mathbf{A}[\theta_2, \hat{\mathbf{n}}_1, 0] \hat{\mathbf{n}}_1 \| . \tag{12.7}$$

This conclusion relies on the matrix ergodic theorems of Furstenberg and Kesten (1960) and Oseledec (1968). The mathematical conditions required of a strange attractor to guarantee the convergence of $\log \lambda_I$ to the same value for any initial population are difficult, but it seems likely that we can rely on the result for most ecological cases (Ferriére and Gatto 1995).

12.3.1 Sensitivities and selection gradients

Consider a population with phenotype value θ_0. If an invasion by a phenotype $\theta_0 + d\theta$ is to succeed, the change $d\theta$ must increase $\log \lambda_I$; i.e., the invasion will succeed if and only if

$$\left. \frac{\partial \log \lambda_I}{\partial \theta} \right|_{\theta_0} > 0. \tag{12.8}$$

Thus the sensitivity of the invasion exponent determines the direction of evolution. Under certain assumptions, it also determines the speed with which the phenotype θ will increase (if $\frac{\partial \log \lambda_I}{\partial \theta} > 0$) or decrease (if $\frac{\partial \log \lambda_I}{\partial \theta} < 0$) through repeated invasions (Vincent et al. 1993, Getz 1999). Thus, we can define the

sensitivity of $\log \lambda_I$ (12.8) as the *selection gradient*, in analogy to quantitative genetics (Lande 1982).

Since, depending on the attractor, λ_I is an eigenvalue or a stochastic growth rate, it is straightforward to calculate the selection gradient in all these cases (Caswell 2001, p. 564). In particular, it is no longer necessary to use numerical perturbations (e.g., Grant and Benton 2003) to make these calculations.

12.3.2 Invasion and population density

A successful invasion, replacing one phenotype by another, changes the dynamics of the population and thus has consequences for population density. The earliest studies of density-dependent selection (MacArthur 1962, Roughgarden 1971) emphasized effects on equilibrium population size ("K-selection"). Consider an unstructured, scalar model

$$N(t + 1) = \lambda(\theta, N)N(t), \tag{12.9}$$

where the per capita growth rate λ depends on both the phenotype θ and the population density. An equilibrium $\hat{N}$ must satisfy $\lambda(\theta, \hat{N}) = 1$. Differentiating implicitly with respect to θ gives

$$\frac{\partial \lambda}{\partial \theta} = -\frac{\partial \lambda}{\partial N} \frac{\partial \hat{N}}{\partial \theta}. \tag{12.10}$$

That is, the sensitivity of the invasion exponent to θ (i.e., the selection gradient on θ) is directly proportional to the sensitivity of the equilibrium density to a change in θ. The proportionality constant, $-\partial \lambda / \partial N$, is a measure of the strength of density dependence. If $\partial \lambda / \partial N < 0$; i.e., if increased density reduces fitness, then a successful invasion will always *increase* equilibrium density, and an ESS will maximize equilibrium density. This conclusion has led to a long-standing interest in the conditions under which selection at the individual level will lead to increases in population density.

This relationship is important because it links demography (the effect of the life history parameter θ on the population growth rate λ), the ecology of resource use and competition (the effect of N on λ), and evolution (the direction and rate of evolutionary change in the phenotype θ).

12.4 INVASION OF EQUILIBRIA IN STAGE-STRUCTURED MODELS

To make the relationship between selection and population density useful, it must incorporate more detail than is present in Eq. (12.9). This detail comes in two pieces. First, there is the description of the life cycle, recognizing the stage specificity of the vital rates. Second, there is the description of density dependence. Different stages in the life cycle are differentially sensitive to density, and different stages also contribute differentially to density.

Examples are not hard to think of. The survival and growth of a tadpole might be affected by the density of tadpoles, but probably not by the density of adult frogs. Similarly, frogs are unlikely to be affected by the density of tadpoles. Large trees affect small trees more than vice versa. Density dependence may operate through competition for food, space, or nesting sites, or through cannibalism, allelopathy, or interference, each of which is likely to be stage-specific in its own way.

To accommodate this range of possibilities, we begin with a stage-structured, nonlinear matrix population model written as

$$\mathbf{n}(t+1) = \mathbf{A}[\theta, f(\mathbf{n})]\mathbf{n}(t). \tag{12.11}$$

The projection matrix $\mathbf{A}$ is written as a function of a parameter θ, which could describe any demographic trait, and of a function $f(\mathbf{n})$ that measures "density." An equilibrium $\hat{\mathbf{n}}$ of Eq. (12.11) must satisfy

$$\hat{\mathbf{n}} = \mathbf{A}[\theta, f(\hat{\mathbf{n}})]\hat{\mathbf{n}}. \tag{12.12}$$

The invasion exponent is given by the dominant eigenvalue λ of $\mathbf{A}[\theta, f(\hat{\mathbf{n}})]$. A series of theorems have resolved the question of how density responds to changes in parameters, and the relation of those changes to changes in the invasion exponent.

Takada and Nakajima (1992) considered the special case where $f(\mathbf{n}) = \sum_i n_i \equiv N_{\text{tot}}$. They showed that the sensitivity and elasticity of λ are proportional to the corresponding sensitivity or elasticity of $\hat{N}_{\text{tot}}$. However, while many models in the literature are written as functions of N_{tot}, in reality this can describe density dependence only in the most general qualitative way, because it ignores obvious differences among stages in resource use and competitive impact.

Later, Takada and Nakajima (1998) extended their theorem to the case where $f(\mathbf{n}) = \sum_i \alpha_i n_i \equiv N^*$, which permits different stages to contribute differentially to density effects; the coefficients α_i measure those impacts. They showed that the sensitivity and elasticity of the invasion exponent are proportional to the corresponding sensitivity and elasticity of N^*.

However, not only do different stages contribute differentially to density effects, they also respond differently, so it is unlikely that any single function $f(\mathbf{n})$ will capture the effects of density throughout the life cycle. Caswell et al. (2004) generalized the Takada–Nakajima theorem further, by writing the projection matrix as

$$\mathbf{A}[\theta_0, f_1(\mathbf{n}), f_2(\mathbf{n}), \ldots],$$

where the $f_i(\mathbf{n})$ are arbitrary functions of $\mathbf{n}$ (not restricted to the linear combination N^*). They showed that the sensitivity of the invasion exponent to a parameter is equal to the sensitivity of an *effective population size* $\tilde{N}$ which is a weighted sum of stage densities. The weights depend on the details of the demography and the density dependence. That is,

$$\frac{\partial \lambda(\mathbf{A}[\theta, f_1(\hat{\mathbf{n}}), f_2(\hat{\mathbf{n}}) \dots])}{\partial \theta} = \frac{\partial \mathbf{c}^\top \hat{\mathbf{n}}}{\partial \theta} \tag{12.13}$$

$$= \frac{\partial \tilde{N}}{\partial \theta}, \tag{12.14}$$

where the coefficients are

$$c_i = \left. \left(-\sum_j \frac{\partial \lambda}{\partial f_j} \frac{\partial f_j}{\partial n_i} \right) \right|_{\theta_0, \hat{\mathbf{n}}}. \tag{12.15}$$

The weight on stage i includes the effects of n_i on the density functions f_j and the effects of the f_j on population growth at equilibrium. This theorem includes those of Takada and Nakajima (1992, 1998) as special cases.

Thus, the relationship between the sensitivity of the invasion exponent and the sensitivity of equilibrium density in the simple case (12.10) still holds for stage-classified models, but the definition of "density" changes to reflect the way the stages contribute to density dependence. In particular, successful invasions are still those that increase equilibrium density, and an ESS will still maximize equilibrium density, when density is measured in terms of the effective population.

Note that the terms in c_i can be written as

$$-\sum_j \frac{\partial \lambda}{\partial f_j} \frac{\partial f_j}{\partial n_i} \bigg|_{\theta_0, \hat{\mathbf{n}}} = -\frac{\partial \lambda}{\partial n_i} \bigg|_{\theta_0, \hat{\mathbf{n}}}. \tag{12.16}$$

Thus if $\partial \lambda / \partial n_i \leq 0$ for all i, then the c_i are all nonnegative, and $\tilde{N}$ is a nonnegative weighted density. This is the multistage analog of the negative density-dependence condition for the maximization of $\hat{N}$ in Eq. (12.10).

12.5   INVASION OF NONEQUILIBRIUM ATTRACTORS

The goal of this chapter is to extend these results to nonequilibrium situations characterized by cycles, quasiperiodicity, or chaos. The importance of such calculations has been emphasized by Grant and Benton (2003). They compared the sensitivities of eigenvalues, invasion exponents, and ad hoc measures of density for cyclic population dynamics, but did not arrive at general conclusions. Here, I will derive the relation between the invasion exponent and population density for the special case of a 2-cycle, for a matrix that depends on two functions, $f(\mathbf{n})$ and $g(\mathbf{n})$, of density. The results generalize easily to cycles of arbitrary period and to matrices dependent on an arbitrary number of functions of density. I will present the derivation in detail, because it shows how the generalizations can be accomplished.

Suppose that the population with phenotype θ_0 is on a stable 2-cycle, oscillating between $\hat{\mathbf{n}}_1$ and $\hat{\mathbf{n}}_2$. Thus

$$\hat{\mathbf{n}}_2 = \mathbf{A}[\theta_0, f(\hat{\mathbf{n}}_1), g(\hat{\mathbf{n}}_1)]\mathbf{A}[\theta_0, f(\hat{\mathbf{n}}_2), g(\hat{\mathbf{n}}_2)]\hat{\mathbf{n}}_2. \tag{12.17}$$

To save space, and hopefully without confusion, I will write this as

$$\hat{\mathbf{n}}_2 = \mathbf{A}_1\mathbf{A}_2\hat{\mathbf{n}}_2 \tag{12.18}$$

(the same invasion conclusions result from starting with either $\mathbf{A}_1\mathbf{A}_2$ or $\mathbf{A}_2\mathbf{A}_1$). From Eq. (12.18), it follows that $\hat{\mathbf{n}}_2$ is a right eigenvector of $\mathbf{A}_1\mathbf{A}_2$, with eigenvalue $\lambda = 1$. Let $\mathbf{v}_2$ be the corresponding left eigenvector, scaled so that $\mathbf{v}_2^\top \hat{\mathbf{n}}_2 = 1$. The invasion exponent is the average growth rate over the cycle:

$$\log \lambda_1 = \frac{1}{2} \log \lambda(\mathbf{A}_1\mathbf{A}_2).$$

Now perturb the parameter, so that $\theta_0 \mapsto \theta_0 + d\theta$. The perturbation changes the fixed points, so

$$\hat{\mathbf{n}}_1 \mapsto \hat{\mathbf{n}}_1 + d\hat{\mathbf{n}}_1 \tag{12.19}$$

$$\hat{\mathbf{n}}_2 \mapsto \hat{\mathbf{n}}_2 + d\hat{\mathbf{n}}_2. \tag{12.20}$$

The resulting 2-cycle must satisfy

$$\hat{\mathbf{n}}_2 + d\hat{\mathbf{n}}_2 = \mathbf{A}[\theta_0 + d\theta, f(\hat{\mathbf{n}}_1 + d\hat{\mathbf{n}}_1), g(\hat{\mathbf{n}}_1 + d\hat{\mathbf{n}}_1)]$$

$$\times \mathbf{A}[\theta_0 + d\theta, f(\hat{\mathbf{n}}_2 + d\hat{\mathbf{n}}_2), g(\hat{\mathbf{n}}_2 + d\hat{\mathbf{n}}_2)](\hat{\mathbf{n}}_2 + d\hat{\mathbf{n}}_2) \tag{12.21}$$

Expand $f(\mathbf{n})$ and $g(\mathbf{n})$ in Taylor series to first order; this yields

$$\hat{\mathbf{n}}_2 + d\hat{\mathbf{n}}_2 = \mathbf{A}[\theta_0 + d\theta, f(\hat{\mathbf{n}}_1) + \nabla f^\top d\hat{\mathbf{n}}_1|_{\hat{\mathbf{n}}_1}, g(\hat{\mathbf{n}}_1) + \nabla g^\top d\hat{\mathbf{n}}_1|_{\hat{\mathbf{n}}_1}]$$

$$\times \mathbf{A}[\theta_0 + d\theta, f(\hat{\mathbf{n}}_2) + \nabla f^\top d\hat{\mathbf{n}}_2|_{\hat{\mathbf{n}}_2}, g(\hat{\mathbf{n}}_2) + \nabla g^\top d\hat{\mathbf{n}}_2|_{\hat{\mathbf{n}}_2}](\hat{\mathbf{n}}_2 + d\hat{\mathbf{n}}_2). \tag{12.22}$$

where the gradient vector

$$\nabla f = \left(\frac{\partial f}{\partial n_1} \cdots \frac{\partial f}{\partial n_s} \right)^\top. \tag{12.23}$$

Next, expand each of the matrices to first order; this yields

$$\hat{\mathbf{n}}_2 + d\hat{\mathbf{n}}_2 = \left\{ \mathbf{A}_1 + d\theta \frac{\partial \mathbf{A}_1}{\partial \theta}\bigg|_{\theta_0, \hat{\mathbf{n}}_1} + \nabla f^\top d\hat{\mathbf{n}}_1 \frac{\partial \mathbf{A}_1}{\partial f}\bigg|_{\theta_0, \hat{\mathbf{n}}_1} + \nabla g^\top d\hat{\mathbf{n}}_1 \frac{\partial \mathbf{A}_1}{\partial g}\bigg|_{\theta_0, \hat{\mathbf{n}}_1} \right\}$$

$$\times \left\{ \mathbf{A}_2 + d\theta \frac{\partial \mathbf{A}_2}{\partial \theta}\bigg|_{\theta_0, \hat{\mathbf{n}}_2} + \nabla f^\top d\hat{\mathbf{n}}_2 \frac{\partial \mathbf{A}_2}{\partial f}\bigg|_{\theta_0, \hat{\mathbf{n}}_2} + \nabla g^\top d\hat{\mathbf{n}}_2 \frac{\partial \mathbf{A}_2}{\partial g}\bigg|_{\theta_0, \hat{\mathbf{n}}_2} \right\}(\hat{\mathbf{n}}_2 + d\hat{\mathbf{n}}_2).$$

$$\tag{12.24}$$

Multiplying and retaining only first-order terms yields

$$d\hat{\mathbf{n}}_2 = \mathbf{A}_1 \mathbf{A}_2 d\hat{\mathbf{n}}_2$$

$$+ \left(d\theta \mathbf{A}_1 \left. \frac{\partial \mathbf{A}_2}{\partial \theta} \right|_{\theta_0, \hat{\mathbf{n}}_2} \hat{\mathbf{n}}_2 \right)$$

$$+ \left(\nabla f^\top d\hat{\mathbf{n}}_2 \mathbf{A}_1 \left. \frac{\partial \mathbf{A}_2}{\partial f} \right|_{\theta_0, \hat{\mathbf{n}}_2} \hat{\mathbf{n}}_2 \right)$$

$$+ \left(\nabla g^\top d\hat{\mathbf{n}}_2 \mathbf{A}_1 \left. \frac{\partial \mathbf{A}_2}{\partial g} \right|_{\theta_0, \hat{\mathbf{n}}_2} \hat{\mathbf{n}}_2 \right)$$

$$+ \left(d\theta \left. \frac{\partial \mathbf{A}_1}{\partial \theta} \right|_{\theta_0, \hat{\mathbf{n}}_1} \mathbf{A}_2 \hat{\mathbf{n}}_2 \right)$$

$$+ \left(\nabla f^\top d\hat{\mathbf{n}}_1 \left. \frac{\partial \mathbf{A}_1}{\partial f} \right|_{\theta_0, \hat{\mathbf{n}}_1} \mathbf{A}_2 \hat{\mathbf{n}}_2 \right)$$

$$+ \left(\nabla g^\top d\hat{\mathbf{n}}_1 \left. \frac{\partial \mathbf{A}_1}{\partial g} \right|_{\theta_0, \hat{\mathbf{n}}_1} \mathbf{A}_2 \hat{\mathbf{n}}_2 \right). \tag{12.25}$$

Note that if θ appears in $f(\cdot)$ or $g(\cdot)$, this effect is included in $\partial \mathbf{A}/\partial \theta$. Next, left multiply Eq. (12.25) by the left eigenvector $\mathbf{v}_2^\top$, divide by $d\theta$, and rearrange to obtain

$$0 = \mathbf{v}_2^\top \left\{ \left(\mathbf{A}_1 \left. \frac{\partial \mathbf{A}_2}{\partial \theta} \right|_{\theta_0, \hat{\mathbf{n}}_2} \right) + \left(\left. \frac{\partial \mathbf{A}_1}{\partial \theta} \right|_{\theta_0, \hat{\mathbf{n}}_1} \mathbf{A}_2 \right) \right\} \hat{\mathbf{n}}_2$$

$$+ \mathbf{v}_2^\top \left\{ \mathbf{A}_1 \left. \frac{\partial \mathbf{A}_2}{\partial f} \right|_{\theta_0, \hat{\mathbf{n}}_2} \right\} \hat{\mathbf{n}}_2 \nabla f^\top \left. \frac{\partial \hat{\mathbf{n}}_2}{\partial \theta} \right|_{\theta_0, \hat{\mathbf{n}}_2}$$

$$+ \mathbf{v}_2^\top \left\{ \mathbf{A}_1 \left. \frac{\partial \mathbf{A}_2}{\partial g} \right|_{\theta_0, \hat{\mathbf{n}}_2} \right\} \hat{\mathbf{n}}_2 \nabla g^\top \left. \frac{\partial \hat{\mathbf{n}}_2}{\partial \theta} \right|_{\theta_0, \hat{\mathbf{n}}_2}$$

$$+ \mathbf{v}_2^\top \left\{ \left. \frac{\partial \mathbf{A}_1}{\partial f} \right|_{\theta_0, \hat{\mathbf{n}}_1} \mathbf{A}_2 \right\} \hat{\mathbf{n}}_2 \nabla f^\top \left. \frac{\partial \hat{\mathbf{n}}_1}{\partial \theta} \right|_{\theta_0, \hat{\mathbf{n}}_1}$$

$$+ \mathbf{v}_2^\top \left\{ \left. \frac{\partial \mathbf{A}_1}{\partial g} \right|_{\theta_0, \hat{\mathbf{n}}_1} \mathbf{A}_2 \right\} \hat{\mathbf{n}}_2 \nabla g^\top \left. \frac{\partial \hat{\mathbf{n}}_1}{\partial \theta} \right|_{\theta_0, \hat{\mathbf{n}}_1}. \tag{12.26}$$

The first term in Eq. (12.26) is just

$$\frac{\partial \lambda[\mathbf{A}_1 \mathbf{A}_2]}{\partial \theta} \tag{12.27}$$

(Caswell 1978). The next four lines contain the derivatives of λ with respect to the functions f and g, with the derivative taken at only one of the two matrices A_1 or A_2, treating the other matrix as fixed. In a slight abuse of notation, I will write these derivatives as, e.g.,

$$\mathbf{v}_2^\top \left\{ \mathbf{A}_1 \left. \frac{\partial \mathbf{A}_2}{\partial f} \right|_{\theta_0, \hat{\mathbf{n}}_2} \right\} \hat{\mathbf{n}}_2 = \left. \frac{\partial \lambda}{\partial f} \right|_{\mathbf{A}_2}, \tag{12.28}$$

with similar expressions for the other derivatives. Thus the entire system of equations can be simplified to give

$$\frac{\partial \lambda[\mathbf{A}_1 \mathbf{A}_2]}{\partial \theta} = - \left(\left. \frac{\partial \lambda}{\partial f} \right|_{\mathbf{A}_2} \nabla f^\top |_{\hat{\mathbf{n}}_2} + \left. \frac{\partial \lambda}{\partial g} \right|_{\mathbf{A}_2} \nabla g^\top |_{\hat{\mathbf{n}}_2} \right) \frac{\partial \hat{\mathbf{n}}_2}{\partial \theta}$$

$$- \left(\left. \frac{\partial \lambda}{\partial f} \right|_{\mathbf{A}_1} \nabla f^\top |_{\hat{\mathbf{n}}_1} + \left. \frac{\partial \lambda}{\partial g} \right|_{\mathbf{A}_1} \nabla g^\top |_{\hat{\mathbf{n}}_1} \right) \frac{\partial \hat{\mathbf{n}}_1}{\partial \theta} \tag{12.29}$$

$$= \frac{\partial}{\partial \theta} \left\{ - \left(\left. \frac{\partial \lambda}{\partial f} \right|_{\mathbf{A}_2} \nabla f^\top |_{\hat{\mathbf{n}}_2} + \left. \frac{\partial \lambda}{\partial g} \right|_{\mathbf{A}_2} \nabla g^\top |_{\hat{\mathbf{n}}_2} \right) \hat{\mathbf{n}}_2 \right.$$

$$\left. - \left(\left. \frac{\partial \lambda}{\partial f} \right|_{\mathbf{A}_1} \nabla f^\top |_{\hat{\mathbf{n}}_1} + \left. \frac{\partial \lambda}{\partial g} \right|_{\mathbf{A}_1} \nabla g^\top |_{\hat{\mathbf{n}}_1} \right) \hat{\mathbf{n}}_1 \right\}. \tag{12.30}$$

From this (remembering that $\lambda = 1$) we arrive at the sensitivity of the invasion exponent:

$$\frac{1}{2} \frac{\partial \log \lambda[\mathbf{A}_1 \mathbf{A}_2]}{\partial \theta} = \frac{\partial}{\partial \theta} \frac{1}{2} (\mathbf{c}_1^\top \hat{\mathbf{n}}_1 + \mathbf{c}_2^\top \hat{\mathbf{n}}_2) \tag{12.31}$$

$$= \frac{\partial \tilde{N}}{\partial \theta}. \tag{12.32}$$

where $\tilde{N}$, the effective population density, is a weighted average, over the cycle, of the stage densities:

$$\tilde{N} = \frac{1}{2} (\mathbf{c}_1^\top \hat{\mathbf{n}}_1 + \mathbf{c}_2^\top \hat{\mathbf{n}}_2). \tag{12.33}$$

The vectors of weights are

$$\mathbf{c}_1^\top = - \left(\left. \frac{\partial \lambda}{\partial f} \right|_{\mathbf{A}_1} \nabla f^\top |_{\hat{\mathbf{n}}_1} + \left. \frac{\partial \lambda}{\partial g} \right|_{\mathbf{A}_1} \nabla g^\top |_{\hat{\mathbf{n}}_1} \right) \tag{12.34}$$

$$\mathbf{c}_2^\top = - \left(\left. \frac{\partial \lambda}{\partial f} \right|_{\mathbf{A}_2} \nabla f^\top |_{\hat{\mathbf{n}}_2} + \left. \frac{\partial \lambda}{\partial g} \right|_{\mathbf{A}_2} \nabla g^\top |_{\hat{\mathbf{n}}_2} \right). \tag{12.35}$$

These weights, just as in the case of an equilibrium point, can be interpreted in terms of the two basic processes included in the model: the effect of density on

the vital rates and the effect of those vital rates on λ. Each stage, at each point in the cycle, contributes to $\tilde{N}$. The contribution of stage i to $\tilde{N}$ is

$$\frac{1}{2}\left(c_i^{(1)} + c_i^{(2)}\right) = -\frac{1}{2}\left(\left.\frac{\partial\lambda}{\partial f}\right|_{\mathbf{A}_1}\left.\frac{\partial f}{\partial\hat{n}_i}\right|_{\hat{\mathbf{n}}_1} + \left.\frac{\partial\lambda}{\partial g}\right|_{\mathbf{A}_1}\left.\frac{\partial g}{\partial\hat{n}_i}\right|_{\hat{\mathbf{n}}_1} + \left.\frac{\partial\lambda}{\partial f}\right|_{\mathbf{A}_2}\left.\frac{\partial f}{\partial\hat{n}_i}\right|_{\hat{\mathbf{n}}_2} + \left.\frac{\partial\lambda}{\partial g}\right|_{\mathbf{A}_2}\left.\frac{\partial g}{\partial\hat{n}_i}\right|_{\hat{\mathbf{n}}_2}\right)$$

(12.36)

(where superscripts denote vectors and subscripts vector elements). Thus, stage i makes a large contribution to $\tilde{N}$ if either f or g is very sensitive to n_i, at either $\hat{\mathbf{n}}_1$ or $\hat{\mathbf{n}}_2$, and if λ is very sensitive to f or g at the corresponding point in the cycle.

12.5.1 Evolutionary stable strategies and population size

A successful invasion will always increase the average effective population density $\tilde{N}$, and an ESS will maximize $\tilde{N}$. If the elements of $\mathbf{c}_1$ and $\mathbf{c}_2$ are nonnegative, then $\tilde{N}$ is a nonnegative weighted average of the stage densities over the attractor. This is what one usually thinks of as a "density." Sufficient conditions for this are

$$\left.\frac{\partial\lambda}{\partial f}\right|_{\mathbf{A}_j}\left.\frac{\partial f}{\partial n_i}\right|_{\hat{\mathbf{n}}_j} \leq 0 \quad \text{for all } i, j \tag{12.37}$$

$$\left.\frac{\partial\lambda}{\partial g}\right|_{\mathbf{A}_j}\left.\frac{\partial g}{\partial n_i}\right|_{\hat{\mathbf{n}}_j} \leq 0 \quad \text{for all } i, j. \tag{12.38}$$

This is the multistage, nonequilibrium generalization of the "negative density-dependence" condition in (12.10).

12.5.2 Generalizations

The derivation above makes it clear that the results also apply to cycles of arbitrary length p, and to arbitrary numbers of density-dependent functions $f(\mathbf{n})$, $g(\mathbf{n})$, $h(\mathbf{n})$,.... The result is

Theorem 12.1 *Let* $\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$, *where* $\mathbf{A} = \mathbf{A}[\theta, f(\mathbf{n}), g(\mathbf{n}), h(\mathbf{n}),\dots]$ *is a density-dependent population projection matrix depending on a parameter* θ *and an arbitrary finite number of scalar functions f, g, h,..., which are assumed to poses Taylor series expansions. Let* $\hat{\mathbf{n}}_1, \hat{\mathbf{n}}_2,\dots,\hat{\mathbf{n}}_p$ *be a stable cycle of finite period* p, *where* $p \geq 1$. *Then the sensitivity of the invasion exponent,*

$$\frac{\partial\log\lambda_I}{\partial\theta} = \frac{1}{p}\frac{\partial\log\lambda[\mathbf{A}_p\dots\mathbf{A}_1]}{\partial\theta} \tag{12.39}$$

satisfies

$$\frac{\partial \log \lambda_I}{\partial \theta} = \frac{\partial}{\partial \theta} \frac{1}{p} \sum_{i=1}^{p} \mathbf{c}_i^\top \hat{\mathbf{n}}_i \qquad (12.40)$$

$$\equiv \frac{\partial \tilde{N}}{\partial \theta} \qquad (12.41)$$

where

$$\mathbf{c}_i^\top = \left(\frac{\partial \lambda}{\partial f}\Big|_{\mathbf{A}_i} \nabla f^\top|_{\hat{\mathbf{n}}_i} \right) + \left(\frac{\partial \lambda}{\partial g}\Big|_{\mathbf{A}_i} \nabla g^\top|_{\hat{\mathbf{n}}_i} \right) + \left(\frac{\partial \lambda}{\partial h}\Big|_{\mathbf{A}_i} \nabla h^\top|_{\hat{\mathbf{n}}_i} \right) + \cdots \qquad (12.42)$$

Conjecture: I conjecture that this theorem can be extended to invariant loops and strange attractors by taking the limit as $p \to \infty$, provided that the attractor posesses the appropriate ergodic properties for the limit to converge almost everywhere.

The theorems of Takada and Nakajima (1992, 1998) follow as special cases with only a single density function ($f(\mathbf{n}) = \sum n_i$ or $f(\mathbf{n}) = \sum \alpha_i n_i$) and with $p = 1$. The theorem of Caswell et al. (2004) follows as a special case with any number of arbitrary density functions and with $p = 1$.

Example 1: A 2-cycle in the *Tribolium* model

The *Tribolium* model (Dennis et al. 1995; see Cushing et al. 2003 for a comprehensive review) has three stages: larvae, pupae, and adults. Density dependence operates through cannibalism of eggs by larvae and adults, and through cannibalism of pupae by adults. The population projection matrix is

$$\mathbf{A}_n = \begin{pmatrix} 0 & 0 & b\exp(-c_{e\ell}n_1 - c_{ea}n_3) \\ 1 - \mu_\ell & 0 & 0 \\ 0 & \exp(-c_{pa}n_3) & 1 - \mu_a \end{pmatrix} \qquad (12.43)$$

where b is the fertility, c_{ea}, $c_{e\ell}$, and c_{pa} are cannibalism coefficients (of eggs by adults, of eggs by larvae, and of pupae by adults, respectively), and μ_a and μ_ℓ are adult and larval mortality rates. Two functions of density appear in the model, one describing the cannibalism of eggs and the other the cannibalism of larvae:

$$f(\mathbf{n}) = \exp(-c_{e\ell}n_1 - c_{ea}n_3) \qquad (12.44)$$

$$g(\mathbf{n}) = \exp(-c_{pa}n_3) \qquad (12.45)$$

Experimental manipulations and mathematical analysis show that both the population and the model exhibit the full range of dynamic behavior, from stable equilibria to chaos (Cushing et al. 2003). The following parameters, estimated from experiments in Dennis et al. (1995),

$$b = 11.677$$
$$c_{ea} = 0.0110$$
$$c_{e\ell} = 0.0093$$
$$c_{pa} = 0.0178$$
$$\mu_a = 0.1108$$
$$\mu_\ell = 0.5129$$

yield a stable 2-cycle:

$$\hat{\mathbf{n}}_1 = \begin{pmatrix} 325.30 \\ 8.89 \\ 118.46 \end{pmatrix} \quad \hat{\mathbf{n}}_2 = \begin{pmatrix} 18.24 \\ 158.45 \\ 106.42 \end{pmatrix}. \tag{12.46}$$

The population oscillates between being dominated (at $\hat{\mathbf{n}}_1$) by larvae and adults, with few pupae, to being dominated (at $\hat{\mathbf{n}}_2$) by pupae and adults, with few larvae.

Eigenvalue sensitivity analysis (Lesnoff et al. 2003) applied to the product matrix $\mathbf{A}_1\mathbf{A}_2$ gives the sensitivities of the invasion exponent $\log\lambda_I = (1/2)$ $\log\lambda_1(\mathbf{A}_1\mathbf{A}_2)$ to each of the parameters:

<div align="center">Parameter θ</div>

	b	c_{ea}	$c_{e\ell}$	c_{pa}	μ_a	μ_ℓ	
$\left.\dfrac{\partial\log\lambda_I}{\partial\theta}\right|_{\mathbf{n}}$	0.0075	−2.8944	−2.8767	−9.3343	−0.8303	−0.1791	(12.47)

Not surprisingly, the invasion exponent increases with increased birth rate and decreases if cannibalism or mortality increase. Theorem 12.1 says that there should be an effective population density $\tilde{N}$ that changes at the same rate in response to a parameter change.

What is $\tilde{N}$? To calculate it, we need the left eigenvectors,

$$\mathbf{v}_1 = \begin{pmatrix} 5.1065 \times 10^{-4} \\ 9.4179 \times 10^{-4} \\ 6.9686 \times 10^{-3} \end{pmatrix} \quad \mathbf{v}_2 = \begin{pmatrix} 4.5875 \times 10^{-4} \\ 1.0484 \times 10^{-3} \\ 7.7575 \times 10^{-3} \end{pmatrix}, \tag{12.48}$$

the sensitivities of λ to f and g within each of the two matrices $\mathbf{A}_1$ and $\mathbf{A}_2$,

$$\left.\frac{\partial\lambda}{\partial f}\right|_{\mathbf{A}_1} = 0.6346 \qquad \left.\frac{\partial\lambda}{\partial g}\right|_{\mathbf{A}_1} = 0.0689$$

$$\left.\frac{\partial\lambda}{\partial f}\right|_{\mathbf{A}_2} = 0.6346 \qquad \left.\frac{\partial\lambda}{\partial g}\right|_{\mathbf{A}_2} = 1.1042$$

and the gradient vectors,

$$\nabla f^\top|_{\hat{\mathbf{n}}_1} = \begin{pmatrix} -1.227 & 0 & -1.451 \end{pmatrix} \times 10^{-4} \tag{12.49}$$

$$\nabla f^\top|_{\hat{\mathbf{n}}_2} = \begin{pmatrix} -2.435 & 0 & -2.880 \end{pmatrix} \times 10^{-3} \tag{12.50}$$

$$\nabla g^\top|_{\hat{\mathbf{n}}_1} = \begin{pmatrix} 0 & 0 & -2.161 \end{pmatrix} \times 10^{-3} \tag{12.51}$$

$$\nabla g^\top|_{\hat{\mathbf{n}}_2} = \begin{pmatrix} 0 & 0 & -2.678 \end{pmatrix} \times 10^{-3}. \tag{12.52}$$

The weights $\mathbf{c}_i$, calculated from (34) and (35), are

$$\mathbf{c}_1 = \begin{pmatrix} 0.778 \\ 0 \\ 2.410 \end{pmatrix} \times 10^{-4} \qquad \mathbf{c}_2 = \begin{pmatrix} 1.545 \\ 0 \\ 4.784 \end{pmatrix} \times 10^{-3}. \tag{12.53}$$

We finally find that $\tilde{N} = 0.2956$. Since $\mathbf{c}_2 \approx 20\mathbf{c}_1$, the effective population is mostly determined by $\hat{\mathbf{n}}_2$. Since $\hat{\mathbf{n}}_2$ is mostly adults and pupae with few larvae, and the pupae receive no weight in $\mathbf{c}_2$, in this case $\tilde{N}$ is roughly proportional to the density of adults. $\tilde{N}$ is quite different from the total population size, or the average of total population size over the attractor.

Figure 12.1 compares the numerically calculated response of $\tilde{N}$ with the slopes predicted by $\partial \log \lambda_I / \partial \theta$. In each case, the response of the invasion exponent and the effective population size are equal.

12.6 DISCUSSION

Theorem 12.1 shows that there is an intimate relationship between the sensitivity of the invasion exponent and the sensitivity of effective population density. The effective density assigns different weights to different demographic stages and to different points on a cyclic attractor. The weights reflect the impact of the stage densities on the vital rates and the consequences of those impacts on population growth.

Above, I pointed out the value of making both demography and density-dependence stage-specific, to take account of the diverse effects that the densities of some stages can have on the vital rates of others. I must admit, however, that this value is mostly potential. Models including detailed stage-specific density effects are (so far) rare, and the calculations shown in Example 1 will seldom be possible. But it is common to obtain an estimate of a single projection matrix, or a series of a few such matrices, that might be interpreted as describing the population at an equilibrium or on a cycle. When that is possible, Theorem 12.1 guarantees that the linear sensitivity analysis of such a matrix or matrices will provide information on the response to parameter changes of a measure of population density, although the exact nature of that density will be unknown.

What about $\hat{N}_{\mathrm{tot}}$? The effective density is not the total density, and $\hat{N}_{\mathrm{tot}}$ can respond very differently from $\tilde{N}$, even when $\mathbf{c}_i > 0$. The *Tribolium* model provides an example. The sensitivities of $\hat{N}_{\mathrm{tot}}$ to changes in each of the parameters (obtained numerically) are not the same as those of $\tilde{N}$. They are not even
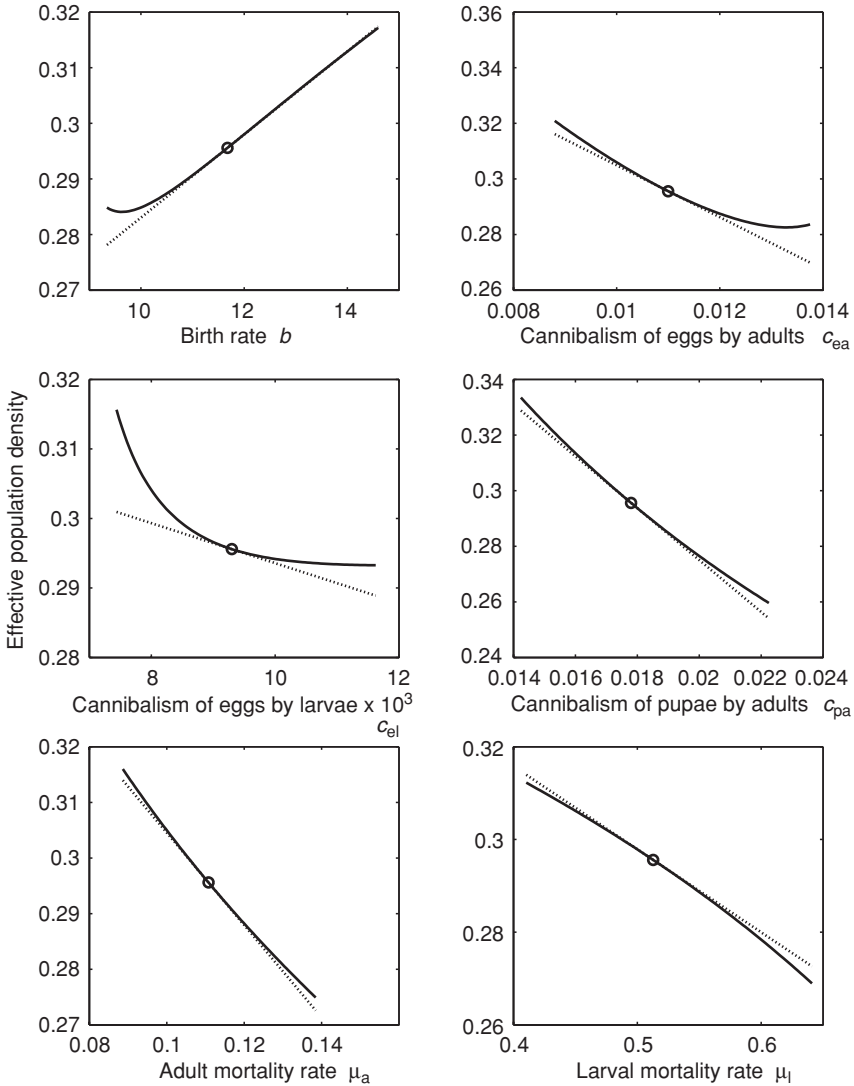
Figure 12.1. The response of the effective population density $\tilde{N}$ to each of the parameters of the *Tribolium* model. The *solid line* shows the response of $\tilde{N}$ in simulations; the *dotted line* shows the slope predicted by the sensitivity of the invasion exponent.

proportional. Figure 12.2 shows the ratios of the sensitivities of $\tilde{N}$ and $\hat{N}_{\text{tot}}$; these ratios would all be the same if the responses of $\tilde{N}$ and $\hat{N}_{\text{tot}}$ were proportional. Worse, they are not even of the same sign! The sensitivity of $\tilde{N}$ (and thus of the invasion exponent) to $c_{e\ell}$ is negative, but the sensitivity of $\hat{N}_{\text{tot}}$ to $c_{e\ell}$ is positive (Figure 12.3).
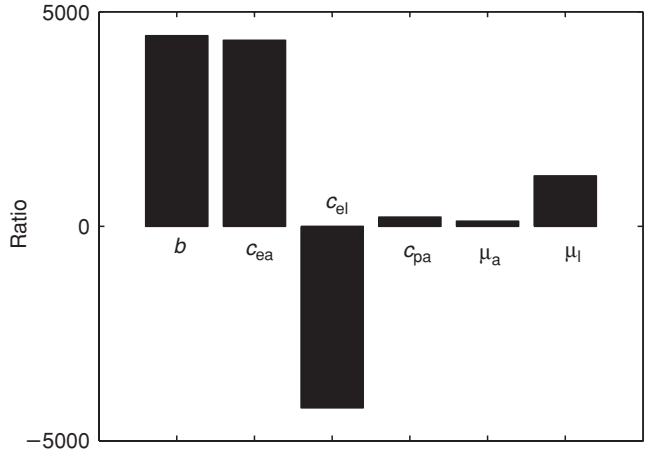
Figure 12.2. The relative sensitivity of N_{tot} and $\tilde{N}$ to each of the parameters of the *Tribolium* model.
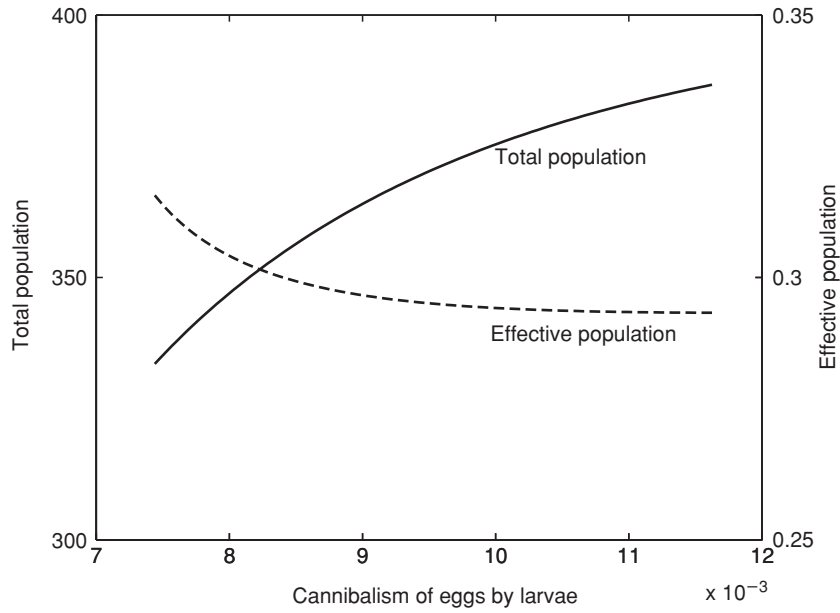
Figure 12.3. The response of the total population density $\hat{N}_{\text{tot}}$ and the effective population density $\tilde{N}$ to changes in the coefficient measuring cannibalism of eggs by larvae.

This implies that an increase in cannibalism of eggs by larvae would not be favored by selection, but it would increase $\hat{N}_{\text{tot}}$. Or, to look at it the other way, a decrease in $c_{e\ell}$, favored by selection, would increase $\tilde{N}$ but reduce $\hat{N}_{\text{tot}}$. This seems counterintuitive. Why would an increase in cannibalism *increase* the total population size averaged over the cycle? Figure 12.4 shows the response of each stage in $\hat{\mathbf{n}}_1$ and $\hat{\mathbf{n}}_2$ to change in $c_{e\ell}$. The adult and larval densities at $\hat{\mathbf{n}}_1$ both increase with $c_{e\ell}$, and the pupal stage receives no weight in $\tilde{N}$. But the component of $\tilde{N}$ due to $\hat{\mathbf{n}}_1$ is much smaller than the component deriving from the response of $\hat{\mathbf{n}}_2$ (Figure 12.4 d, e). In the latter response, adult density increases, but larval density decreases more, so that the net effect on $\tilde{N}$ is negative. The complexity of this response (and this is not a particularly complicated nonlinear model) reflects the nonlinearity of the response of density to changes in parameters throughout the life cycle.

Other than satisfying our natural inclination to count things, N_{tot} has little or no biological rationale. It ignores all ecological differences among stages, adding together the density of tiny seedlings and huge trees, or of larval fish and of
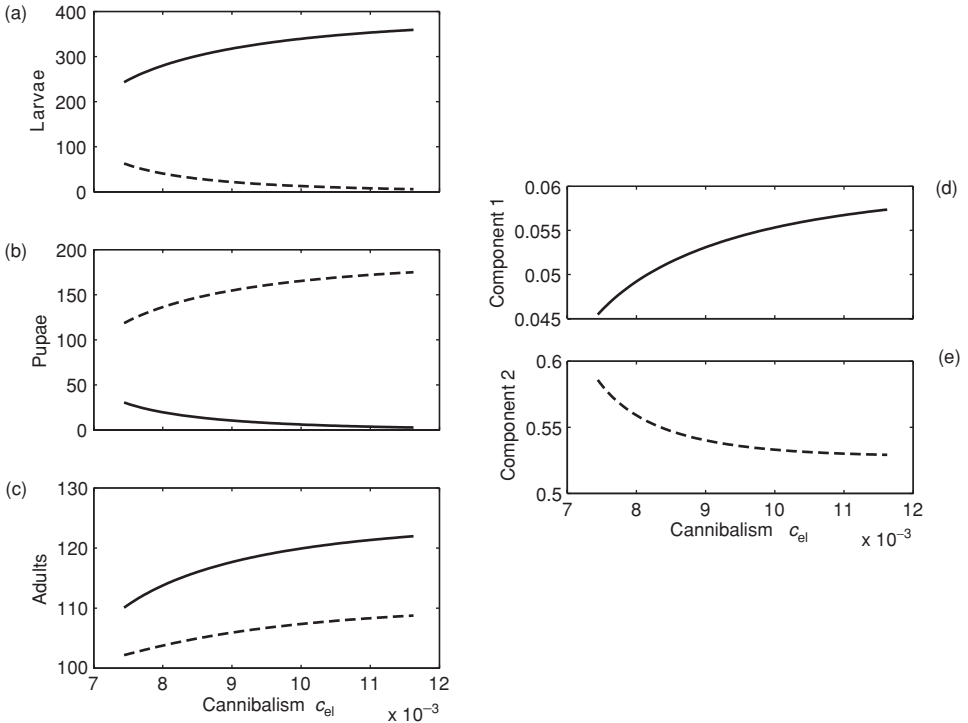
Figure 12.4. (a)–(c) The response of larvae, pupae, and adults to changes in the larval cannibalism coefficient c_{el}. *Solid lines* are $\hat{\mathbf{n}}_1$, *dashed lines* are $\hat{\mathbf{n}}_2$. (d)–(e) The two components of $\tilde{N}$. Component 1 is $\mathbf{c}_1^{\mathsf{T}}\hat{\mathbf{n}}_1$; component 2 is $\mathbf{c}_2^{\mathsf{T}}\hat{\mathbf{n}}_2$.

adult fish weighing a million times more, or of cannibalistic larvae and quiescent pupae. In the *Tribolium* example, nothing in the biology of the organism—not survival, nor fertility, nor development—depends on N_{tot}, so there is no reason to expect N_{tot} to respond in any particular way to parameter changes. The effective density, in contrast, measures density in the same units in which it affects the vital rates of the population.

For similar reasons, N_{tot} is not a particularly useful index of performance for conservation applications, although it is sometimes suggested as such. It does not describe the impact of the population on its environment, nor is it related to the likelihood of extinction or the potential for future population growth (the stable equivalent population, which weights stages by their reproductive value, would do a better job; Keyfitz 1969, Keyfitz and Caswell 2005). However, there is no guarantee that $\tilde{N}$ will do a good job at these tasks either. This suggests the importance of developing a complete perturbation analysis, applicable to *any* specified weighted stage density (Caswell 2006). Not all of these densities will have a simple relationship to the response of the invasion exponent, but that is to be expected, since they will reflect different ecological and demographic processes.

I have focused here on the sensitivities, rather than the elasticities, of $\log \lambda_I$ and of $\tilde{N}$, because the sensitivity corresponds to the selection gradient and appears in evolutionary applications. The elasticities of λ_I and of $\tilde{N}$, however, are proportional to each other;

$$\frac{\theta}{\lambda_I} \frac{\partial \lambda_I}{\partial \theta} = \frac{\theta}{\lambda_I} \frac{\partial \tilde{N}}{\partial \theta} = \tilde{N} \frac{\theta}{\tilde{N}} \frac{\partial \tilde{N}}{\partial \theta} \qquad (12.54)$$

with a proportionality constant equal to $\tilde{N}$ (remember that, on the attractor, $\lambda_I = 1$).

Finally, it is worth noting that these analyses assume that the system is at or near an attractor. Questions of invasion, parameter change, and population density during transient dynamics are important but not well understood.

12.7   ACKNOWLEDGMENTS

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CHAPTER 13

OF EXPERIMENTALISTS, EMPIRICISTS,
AND THEORETICIANS

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13.1   CONCLUSION

Often, edited volumes in the field of ecology seek to bring together disparate subdisciplines under the umbrella of one synthetic idea. It is interesting to consider the idea that this book, in effect, inverts this process. The common thread that unifies the preceding chapters is that the researchers all, at one point, were inspired or informed by the work of Peter Yodzis. To make an irresistible food web analogy, this volume can be viewed as an academic "source web" (sensu Cohen 1978). Peter's source web is just one of three that, though perhaps at odds early in their genesis, have now combined to make ecology a more mature science.

Not too long ago, early in my education as an ecologist, different schools of thought had staked out their territory on the ecological landscape. My introduction to ecology emphasized the utility of carefully designed laboratory experiments for isolating the mechanisms that effect change in nature. I then moved on to McGill University, where I was fortunate enough to overlap with Rob Peters during my Ph.D. This was quite the change from the experimental approach to which I had been indoctrinated. The empirical school of thought dominated the academic atmosphere in the aquatic sciences group at McGill, wherein careful observation of ecological patterns was seen to be the most effective means by which one could predict the behavior of natural systems.

At this point, there was still a contentious debate as to the effectiveness of experimentation versus observation in enabling ecologists to better predict nature. Lost in this debate, especially to the graduate students, was the utility of theory in helping to address ecological problems. This, of course, changed with the arrival of Kevin McCann to the department. Finally, the department had in their hands a theoretical ecologist, and the academic progeny of Peter Yodzis had breached the seemingly impenetrable fortress of empirical ecology. Subwebs were merging into communities, both at McGill and in the ecological community at large.

This is, I would argue, in no small part due to the work of Peter and his colleagues. The elegance of the studies that Peter undertook was twofold: he first asked excellent questions (more on that later), and then in an approach that went beyond the traditional theoretician, he looked to nature for information that would provide constraints for his models. For example, in order to test the hypothesis that natural food webs reside in the neighborhood of equilibrium, Peter used real data from 40 food webs to examine their local stability properties (Yodzis 1981). Later, Yodzis and Innes (1992) used empirical data to constrain consumer-resource models using body size and metabolic type. In order for such advances to continue in ecology, we as researchers must follow this lead and ask questions in a manner that is informed by theory, can be tested experimentally, and can be observed (or not) in the natural world. It is fitting, therefore, that this book is a testament to the fact that experimentalists, empiricists, and theoreticians are beginning to speak one another's languages. Peter Morin provides excellent examples of how theory and experimentation complement each other in advancing ecological knowledge. Kirk Winemiller and John Vandermeer share with us empirical field research that nicely merges theory, observed food web structures and population dynamics. These researchers heed the call of their colleagues in combining approaches in addressing ecological questions.

I might go so far as to argue that theory, observation, and experimentation are inextricably linked and that ecology can only benefit if these approaches are used in concert by ecologists as a community. The perils of not interlinking these approaches have been outlined elsewhere (Belovsky et al. 2004), but they are worth highlighting here. Observation alone lacks mechanism and generality. Experimentation alone lacks predictive power due to simplification and scale issues. Theory, in a vacuum, provides little in the way of context. However, these approaches inform each other (Figure 13.1), and generality can be derived through an iterative process of theorizing, experimenting, and observing. Ecology, therefore, must move forward by adopting all of these approaches, and the better versed in these approaches that researchers are, the more we can hope for generality and predictive power in ecology.

How do we integrate these approaches effectively? First, we must educate our young ecologists in all approaches (the 'good fight' that Peter took on was to promote mathematical literacy). Second, we must take great care in the
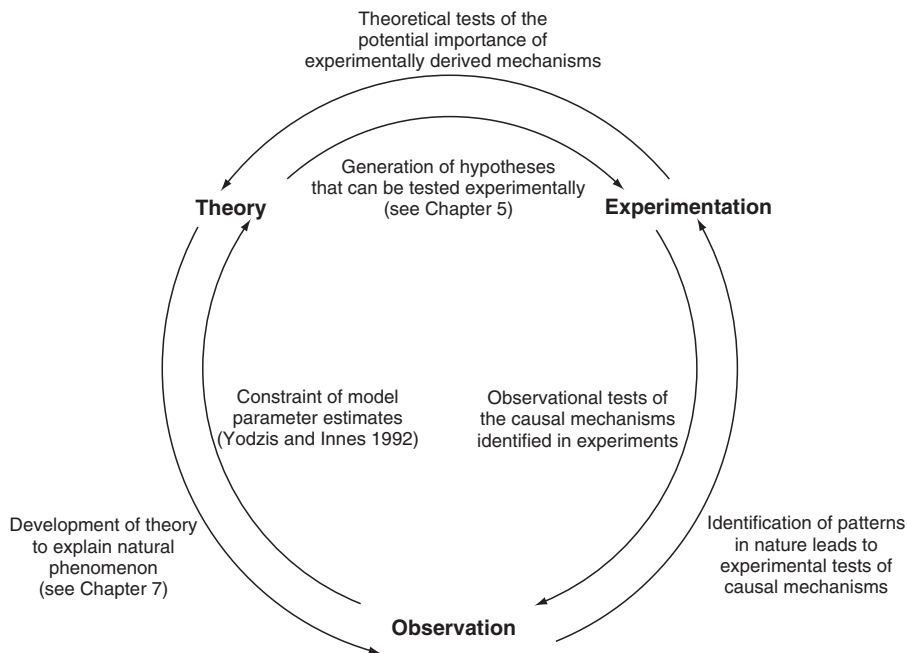
Figure 13.1. The interdependency of theory, experimentation, and observation in ecology.

questions that we ask. Our questions must be both answerable (whether we have the time, resources, calculative capacity, etc.) and relevant. By this, I mean that they should advance our understanding of ecological systems, and facilitate the predictions of the behavior of ecosystems. This is to say that novelty of a question, although enticing, should not be the sole factor determining the validity of a question. Finally, questions must address the issue of the compatibility of temporal and spatial scale. Confusion has often come from researchers obtaining different answers to seemingly the same question, merely because they asked their questions at different spatial or temporal scales.

Peter asked good questions, and then pursued their answers ferociously. His questions were asked such that even the mathematical illiterates among us could grasp the importance and elegance of the question and, perhaps with eyes glazing over the formulae, interpret the results. The extent of Peter's influence on the greater ecological community was made apparent when we organized the first of the Peter Yodzis Colloquia in Fundamental Ecology. Despite the abbreviated time scale on which we had to organize the event, the response was overwhelming. Friends and colleagues from all over the world arrived to see the likes of Don DeAngelis, James Brown, John Harwood, Kirk Winelmiller, and Peter himself give excellent presentations on various areas of ecology. More heartening to us was the presence of young researchers and graduate students

(experimentalists and empiricists as well as theoreticians!) at the colloquium. In contrast to the circumstances under which Peter entered ecology, mathematical literacy is encouraged, if not commonplace among young ecologists today.

It is ironic that one who spent so much of his academic career examining the structure and magnitude of interactions among organisms in food webs should have such an inordinate effect on the structure and function of ecology itself! The introduction of physicist Peter Yodzis and his contemporaries into the field of ecology was a perturbation to the academic system. In 1988, Peter published his best known paper, "The indeterminacy of ecological interactions as perceived through press perturbation experiments." The conclusion, that the consequences of a perturbation on a food web are frequently impossible to determine from short-term observations of the system, has resonated consistently through the food web literature. Similarly, the full consequences of Peter's career in ecology have yet to be determined.

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