Introduction

Eugene Odum has called ecology the link between the natural and the social sciences. While that may be a little strong, ecology does probably have more in common, conceptually and methodologically, with the social sciences than with any other natural science, and in this respect it occupies a unique position among the span of scientific disciplines. Furthermore, the history of ecology is rich in foundational controversy and philosophical debate. Finally, given ecology's fundamental role in the design and implementation of environmental policy, it is hard to imagine a science that has more social and practical relevance. For these reasons, one would expect ecology to be one of the more visible targets for the philosophy of science. However, philosophers have been slow to turn their attention toward ecology; there has been very little sustained examination of foundational controversies in the discipline. This book contributes toward filling that void. It does so primarily by examining a number of central foundational issues in ecology; in the process, both the nature of ecology as a scientific field and its role in the process of environmental decision making are clarified.

To a first approximation, issues in the philosophy of ecology can be divided into two groups. In one group, the questions are *internal*. They involve uncertainty over the nature of genuinely ecological questions, conflicting visions of sound ecological practice, and related matters. The *external* questions come in all shapes and sizes, but for the most part, they involve a relationship between a core notion of ecology and other kinds of scientific disciplines and programs of inquiry. They are questions that involve levels of organization along (at least) spatial and temporal dimensions. For the most part, internal questions are conceptually prior to external questions – one must be clear on the nature of ecology before examining relationships with disciplinary neighbors. The work to follow is part of a larger project involving, in the first stage, the investigation of a number of significant internal questions for philosophy of ecology, followed in the second stage by the application of the results to significant external questions. With the exception of a brief look ahead in the Epilogue, this book is directed toward the first part of the project – the internal questions. Before looking at these internal questions, let me first say something about the external questions.

Imagine a square kilometer of the earth's surface and follow the happenings there for a year or so. We can get some initial sense of level of organization by asking what might seem a rather odd question. The question, which we can ask for individual scientific disciplines, is this: How densely populated is that region with the kinds of events that your discipline studies? There are, for example, more instances of chemical interaction throughout this region during this time period than there are interactions between organisms. Presumably the landscape ecologists would find even less going on. Of course, these higher levels of inquiry do recognize that there is lots going on at the lower levels, that sometimes the details of lower-level processes make a difference for their own work, and perhaps even that there is some sense in which higher levels are nothing but the lower levels. The significant point, however, is that higher levels can get by, in large part, ignoring the details of lower-level processes. That is what gives us levels.

The standard gloss on what levels there are goes something like this:

Physico-chemical interactions
Individual organismic behavior
Population phenomena
Community structure
Landscapes
Ecosystems

One set of external questions in the philosophy of ecology concerns the relationship among these levels of inquiry. To begin with, there are questions about the list itself. Do landscapes belong, for example? Are some levels the epiphenomenal products of interactions at lower levels? Is, for example, community structure simply settled by the population behavior of organisms? There are also questions of integration. G. E. Hutchinson, way back in the 1940s, used to speak of the two central modes of ecological inquiry. He called them the *biogeochemical* and the *biodemographic*. He wanted to unify the two and, ever since, ecologists have pursued this elusive unification. How are we to bring together the physico-chemical perspective of ecosystem ecology with the organismic focus of population/community ecology?

These are some of the central external questions for philosophy of ecology that are generated by what might be called issues of spatial scale (see, for example, Allen and Hoekstra, 1992, for a good, though partisan, discussion of these matters). Questions of temporal scale generate external questions as well. Another highly touted but elusive unification has been between population genetics and population ecology (see Lewontin, 1985, for the pessimistic line). Certainly the disciplines have moved toward one another. From the evolutionary direction, ecological genetics has demonstrated that evolutionary processes intrude into what we might call ecological time. From the ecological side, evolutionary ecology has been busy demonstrating the adaptive character of the properties and behaviors of organisms. But questions remain. Is ecological genetics simply a powerful instance of interfield inquiry, or is it what much of ecology, at least population ecology, is destined to become? Has evolutionary ecology largely morphed into the study of adaptation, a project more appropriate for evolutionary studies than for ecology? Just *what is* the relationship between ecology and evolutionary biology?

These external questions are both tough and important. This book answers none of them in a philosophically thorough way. I bring them up here for three reasons. First, it is worth something just to get them on the table. Second, I believe that the work to follow does advance the investigation of these questions, even if it never manages to get all the way there; I discuss some of the implications in the Epilogue. Finally, recognizing these questions helps make sense of the overall strategy of the book. I will explain this last point momentarily, but first consider some of the significant internal questions for philosophy of ecology.

One of the most long-standing controversies in the philosophy of ecology concerns, in a broad sense, the idea of a balance of nature. The controversy takes on a number of distinct forms – sometimes as debate on density dependence, sometimes surrounding the question of whether competition is the queen of ecological factors, sometimes involving equilibrium, stability, and cognate notions. Closely related to these debates is the question of just how much order is to be found in ecological phenomena. Are there ecological laws? How much general ecological knowledge is possible? Is ecology essentially a historical science? These questions, in turn, lead to a series of further questions surrounding the process of model building in ecology. What is the point behind this activity? Or are there a number of points and a number of model building strategies as vehicles for pursuing these distinct cognitive aims? If the latter, how are we to characterize this variety? How do we test models? How is model building related to more empirically oriented ecological endeavors such as the accumulation of descriptive statistical patterns and experimental results?

Though not an exhaustive list, these are some of the central internal questions that the book *does* investigate. In the course of wrestling with foundational problems in ecology, the book also tackles a number of vexing problems in the philosophy of science. What is a law of nature? Are there laws in the biological sciences such as ecology? What cognitive role does theoretical modeling play in a science like ecology, where the phenomena are exceedingly complex and the existence of fundamental laws can be questioned? Does model building in such circumstances amount to the search for predictive instruments, or is it a genuinely explanatory enterprise and, if the latter, what kind of explanation is involved? Each of these questions points toward an active area of inquiry in the philosophy of science; for the most part there are no settled and widely accepted positions on any of these matters. Yet the analysis of ecology cannot proceed without philosophical tools. Thus it will be necessary, during the course of the investigations to follow, to develop working accounts in each of these philosophical areas.

Returning now to the idea that the external questions are important for understanding the strategy of the book, here is the story. The book is structured around the search for an adequate definition of ecology. In fact, it was first conceived as one long argument to the effect that Haeckel's original definition, which sees ecology as the science that studies the Darwinian struggle for existence, remains a good abstract characterization of the science. There are two reasons for adopting such a strategy. First, much foundational controversy has been fueled by uncertainty over just what ecology is supposed to be about. What sorts of phenomena appropriately fall under the domain of ecological study? Investigating the soundness of the Haeckelian definition provides the occasion for clarifying the scope of ecology as a scientific field, as well as its relationships to other closely allied fields. A second and related reason is that the search for an adequate definition can itself be a valuable tool for foundational inquiry. Because a definition is supposed to abstract away less relevant detail, leaving behind the essential relationships, objections to a proposed definition often reveal differences of opinion at a very fundamental level. Such is the case with Haeckel's definition.

Unfortunately, using the adequacy of Haeckel's definition as a tool to probe for foundational controversy has yielded an embarrassment of riches. Put another way, if this book is, in a sense, one long argument for that definition, then it never gets to the end of the argument. In part, this is because the book spends a good deal of time clarifying issues in the philosophy of science proper. In part, it traces back to the complexity of the foundational controversies that are explored. In any case, dealing with the foundational issues internal to the practice of ecology, which has a kind of conceptual priority over examining the relationships between ecology and its disciplinary neighbors, has proven to be handful enough for one book. I will say something in the Epilogue about how I think the argument should go forward, and about the progress that has been made. However, tackling the sorts of external questions mentioned here must remain a project for another day. I conclude with a brief summary of the part of the argument that the book does make.

The first chapter of the book describes the Darwinian conception of the struggle for existence and the emergence of Haeckel's definition of ecology from this conceptual backdrop. It also serves as an introduction to the overall project by (1) explaining the way in which the examination of Haeckel's definition serves as a tool for probing foundations, (2) providing an initial formulation of the foundational controversies at issue, and (3) outlining the response that will ultimately be developed for each of the foundational problems. The second chapter also has two central goals. The first is to provide a brief, historically oriented description of the field of ecology – a primer those familiar with ecology might choose to avoid. The second goal is to provide a historical introduction to the foundational issues, both internal and external, described earlier.

Chapter Three takes up the old balance of nature idea. There is really a cluster of related issues involved here. To what extent are natural populations regulated? What is the relative significance of density-dependent over density-independent factors? What is the relative significance of biotic over abiotic factors? To what extent should we expect certain kinds of ecological interactions, such as interspecific competition, to play a dominant role in shaping the ecological world? To what extent are ecological communities structured by relatively invariant rules for community assembly? All of these questions have been, for significant periods of the history of the discipline, loci for heated debate in ecology. For an outsider, the most striking feature of this debate is the inability of the discipline to let empirical evidence settle what are so obviously empirical questions. The explanation for this tendency to rush to judgment is complicated, and parts of it, such as the desire to solidify evolutionary foundations and the pursuit of mathematical theory, are taken up in later chapters. But there are more immediate reasons as well. One is the belief that there are certain broad ecological claims, such as the inevitability of population regulation, that can be established on purely logical grounds, by arguments *a priori*, as it were. Chapter Three reconstructs and critically evaluates these attempts to establish, by deductive means, substantial conclusions about the degree of biological organization of ecological phenomena and the causes that must lie behind it.

A second reason behind this "balance of nature" debate traces back to the desire to establish the scientific legitimacy of ecology, and to misguided expectations, largely imported from a philosophy of science that has taken physics as its exemplary science, about the kinds of ecological laws required to secure this legitimacy. Chapter Four addresses this issue by developing a philosophical framework for thinking about generalizations in ecology, one that avoids the extreme views – both the belief in MacArthur's "perfect crystals" and the contemporary celebration of the contingency and historicity of ecological phenomena – by developing the machinery for recognizing that there are degrees of contingency among ecological generalizations.

The next four chapters are devoted to the controversies surrounding mathematical modeling. Chapter Five begins with a detailed survey of the various empirical and philosophical challenges that have been leveled against the modeling tradition. It then turns to the responses that have been made to these criticisms by the theoreticians themselves. In some cases, the challenges point up genuine weakness in the early theoretical work, and the response has been to modify model building practice, for example, by adopting a more pluralistic attitude toward theory and calling for the construction of more mechanistic models. In other cases, the theoreticians have met the skeptical challenges head-on, often with considerable success. Arguments that the critics have often misunderstood the cognitive role of mathematical models are an example here. Overall, the debate has had a salubrious impact on the theoretical tradition. But significant philosophical problems remain. The most fundamental of these is that theoretical ecologists tend to believe (1) that successful theoretical models are genuinely explanatory and (2) that there are no fundamental ecological laws for theoretical models to capture. But most philosophical accounts of theoretical explanation hold that theories explain by virtue of capturing laws. If there are no ecological laws for ecological theories to approximate, then how do ecological theories manage to be explanatory? Chapters Six through Eight explore this and related problems and develop an account of scientific explanation that escapes the dilemma, further clarifying the cognitive role of theoretical models in the process.

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This book is part of a larger project in the philosophy of ecology that I have been working on for a very long time. I have had so many conversations with colleagues on the themes of this project that I now find it impossible to disentangle all of the threads. I can only say that I am grateful for every opportunity. I would specifically like to thank Philip Kitcher for helping me get started down this path, and John Beatty for making sure that I didn't lose my way. I owe a special debt of gratitude to Robert Brandon, Janis Antonovics, and the other members of the philosophy of biology reading group at Duke University. Most of what appears here has had the benefit of close scrutiny from that group, though I know that, despite my best efforts, I have not addressed all of the shortcomings that were unearthed. Special thanks also to Michael Ruse whose bird-dog tenacity, together with generous measures of support and encouragement, is the real reason these ideas have found their way into print.

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1

The Struggle for Existence

1.1 INTRODUCTION

Most foundational controversies involve, sooner or later, questions of disciplinary identity. It must be part of the philosophical project, therefore, to say something about what ecology is. The strategy I have chosen is to defend a particular definition of ecology – the Haeckelian definition of ecology as the science that studies what Darwin calls the struggle for existence. I am interested in defending the definition, but, at the same time, the defense of the definition serves as the occasion for a larger, and ultimately more important, project – the examination of two fundamental foundational controversies that have featured prominently throughout the history of ecology. The two issues are (1) the interminable debates over competition, density dependence, the role of biotic versus abiotic factors, and the idea of a balance of nature, and (2) the controversies over theoretical modeling.

This first chapter sets up the issues and outlines the central course for the remainder of the book. Specifically, it describes Haeckel's original definition (sections 1.2 and 1.3), defends the idea of worrying about a definition (section 1.4), describes four basic ways in which Haeckel's definition can be seen as inadequate (section 1.5), and outlines four foundational controversies that underlie these objections, together with a brief description of how the controversies can be handled so as to pose no problems for Haeckel's definition (section 1.6). Following a deeper look into the controversies in Chapter Two, subsequent chapters will examine the two foundational issues described in the previous paragraph.

1.2 DARWINIAN ORIGINS

For Darwin, the struggle for existence follows from the Malthusian insight that populations increase geometrically whereas their resources do not. In Darwin's words:

> A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase. Every being, which during its natural lifetime produces several eggs or seeds, must suffer destruction during some period of its life, and during some season or occasional year, otherwise, on the principle of geometric increase, its numbers would quickly become so inordinately great that no country could support the product. Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. (Darwin 1859: 78)

Of course it is this struggle, together with the fact that some organisms come better equipped to face the struggle than others, as well as the fact that these advantageous traits can be passed on to offspring, that is responsible for evolutionary change by natural selection.

These evolutionary changes, and their implications for the diversity of living beings, were obviously Darwin's central concern. Still, he recognized that the struggle itself represented an interesting and important domain of biological phenomena. He made some concrete forays into this territory – with earthworms, for example – but his general discussions are also sprinkled with insights about the nature of this struggle. A typical example is his anticipation of what has come to be known as the distinction between r-selected and K-selected species. As Darwin puts it, in the former, "A large number of eggs is of some importance to those species which depend on a fluctuating amount of food, for it allows them to rapidly increase their number" (Darwin 1859: 80), while in the latter, "If an animal can in any way protect its own eggs or young, a small number may be produced, and yet the average stock be fully kept up" (Darwin 1859: 80).

Darwin viewed the struggle for existence as both orderly and exceedingly complex. In a famous passage he gives the following description:

> When we look at the plants and bushes clothing an entangled bank, we are tempted to attribute their proportional numbers and kinds to what we call chance. But how false a view this is! Everyone has heard that when an American forest is cut down, a very different vegetation springs up; but it has been observed that the trees now growing on the ancient Indian mounds, in the Southern United States, display the same beautiful diversity and proportion of kinds as in the surrounding virgin forests. What a struggle between the several kinds of trees must here have gone on during long centuries, each annually scattering its seeds by the thousand; what war between insect and insect – between insects, snails, and other animals with birds and beasts of prey – all striving to increase, and all feeding on each other or on the trees or on their seeds and seedlings, or on the other plants which first clothed the ground and thus checked the growth of the trees! Throw up a handful of feathers, and all must fall to the ground according to definite laws; but how simple is this problem compared to the action and reaction of the innumerable plants and animals which have determined, in the course of centuries, the proportional numbers and kinds of trees now growing on the old Indian ruins! (Darwin 1859: 86)

The tangles in the "entangled bank" are intricate indeed, but not chaotic, as the convergence of the Indian mounds to the surrounding vegetation demonstrates.

The struggle for existence is a nice image. But is it more than an image? What is this order that is grounded in a complexity which exceeds the grasp of even our most sophisticated physics? Darwin admits that the struggle for existence is a metaphor. The notion comes closest to being literal when it describes physical combat, as when two coyotes battle for the last scraps of a mule deer carcass, but it is intended to reach out metaphorically to all kinds of trials and tribulations. Here is one last lengthy Darwin quote:

> I should premise that I use the term Struggle for Existence in a large and metaphorical sense, including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny. Two canine animals in a time of dearth, may be truly said to struggle with each other which shall get food and live. But a plant on the edge of a desert is said to struggle for life against the drought, though more properly it should be said to be dependent on the moisture. A plant which annually produces a thousand seeds, of which on an average only one comes to maturity, may be more truly said to struggle with the plants of the same and other kinds which already clothe the ground. The mistletoe is dependent on the apple and a few other trees, but can only in a far-fetched sense be said to struggle with these trees, for if too many of these parasites grow on the same tree it will languish and die. But several seedling mistletoes, growing close together on the same branch, may more truly be said to struggle with each other. As the mistletoe is disseminated by birds, its existence depends on birds; and it may metaphorically be said to struggle with other fruit-bearing plants, in order to tempt birds to devour and thus disseminate its seeds rather than those of other plants. In these several senses which pass into each other, I use for convenience sake the general term of struggle for existence. (Darwin 1859: 77)

As a metaphor, the struggle for existence is obviously laden with all sorts of social or cultural associations (Beer 1985). I do not propose to discuss such matters here. I am concerned, instead, with the extent to which the Darwinian metaphor succeeds in pointing to a coherent and significant domain of biological phenomena. Here it must be admitted that we have something more than metaphor. There are examples of Darwin's investigations of particular concrete instances of the struggle for existence. From these one gets a sense of how to render the metaphor more concrete in other sorts of cases. There are also general insights about the nature of the struggle sprinkled throughout Darwin's writings; the distinction between r and K species was mentioned above. Finally, there is the connection with what Darwin calls the "conditions of life" – those factors which, to put it somewhat anachronistically, are "causally relevant" to the flourishing of the organisms. The struggle for existence is the confrontation between the organism and its conditions of life. Thus, the pieces are there, in Darwin, for sharpening the metaphor by providing a general account of the struggle for existence. Of course, given the fearful complexity of the relations that comprise the tangled bank and the dearth of studies directed toward these phenomena in Darwin's day, such an account would still have had a decidedly speculative air. Perhaps a less cautious Darwin would have taken the bait. In any case, it wasn't long before Ernst Haeckel, for whom caution never seemed to be an obstacle, put the pieces together and offered a general account of the struggle for existence and named the science that might study it.

1.3 THE SCIENCE OF THE STRUGGLE FOR EXISTENCE

Just seven years after the appearance of *The Origin* (Darwin 1859), Haeckel published his *Generelle Morphologie der Organismen*. As the title suggests, this was primarily a study in morphology from the new Darwinian perspective, but in a short passage the book defined a distinct domain of biological inquiry, which Haeckel christened "Ökologie," as the scientific study of the struggle for existence. Three years later, in an inaugural lecture at Jena, he gave his most quotable (and quoted) formulation:

> By ecology we mean the body of knowledge concerning the economy of nature – the investigation of the total relations of the animal both to its inorganic and to its organic environment; including, above all, its friendly and inimical relations with those animals and plants with which it comes directly or indirectly into contact – in a word, ecology is the study of all those complex interrelations referred to by Darwin as the conditions of the struggle for existence. (quoted in Stauffer 1957: 141)

This short version of the definition, though an accurate representation of Haeckel's position, doesn't really go much beyond Darwin's metaphor. The earlier book had more to say and is worth quoting at some length:

> By ecology, we mean the whole science of the relations of the organism to the environment, including, in the broad sense, all the "conditions of existence." These are partly organic, partly inorganic in nature; both, as we have shown, are of the greatest significance for the form of organisms, for they force them to become adapted. Among the inorganic conditions of existence to which every organism must adapt itself belong, first of all, the physical and chemical properties of its habitat, the climate (light, warmth, atmospheric conditions of humidity and electricity), the inorganic nutrients, nature of the water and of the soil, etc.
>
> As organic conditions of existence we consider the entire relations of the organism to all other organisms with which it comes into contact, and of which most contribute either to its advantage or its harm. Each organism has among the other organisms its friends and its enemies, those which favor its existence and those which harm it. The organisms which serve as organic foodstuff for others or which live upon them as parasites also belong in this category of organic conditions of existence. In our discussion of the theory of selection we have shown what enormous importance all these adaptive relations have for the entire formation of organisms, and specially how the organic conditions of existence exert a much more profound transforming action on organisms than do the inorganic. The extraordinary significance of these relations does not correspond in the least to their scientific treatment, however. So far physiology, [the science] to which this belongs, has, in the most one sided fashion, almost exclusively investigated the conserving functions of organisms (preservation of the individual and the species, nutrition, and reproduction), and among the functions of relationship [it has investigated] merely those which are produced by the relations of single parts of the organism to each other and to the whole. On the other hand, physiology has largely neglected the relations of the organism to the environment, the place each organism takes in the household of nature, in the economy of all nature, and has abandoned the gathering of the relevant facts to an uncritical "natural history," without making an attempt to explain them mechanistically.
>
> This great gap in physiology will now be completely filled by the theory of selection and the theory of evolution which results directly from it. It shows us how all the infinitely complicated relations in which each organism occurs in relation to the environment, how the steady reciprocal action between it and all the organic and inorganic conditions of existence are not the premeditated

> arrangements of a Creator fashioning nature according to a plan but are the necessary effects of existing matter with its inalienable properties and their continual motion in time and space. Thus the theory of evolution explains the housekeeping relations of organisms mechanistically as the necessary consequences of effectual causes and so forms the monistic groundwork of ecology. (Haeckel, translated in Stauffer 1957: 140–141)

This is a rather remarkable passage in the history of science. In the first place, Haeckel is defining an entire field of scientific study which, at that time, does not exist. Nor was it "right around the corner," so to speak. As we will see in the next chapter, the first exemplary ecological works, except for Darwin, were still about thirty years away (e.g., Schimper 1898, Warming 1895), the emergence of ecology as a self-conscious discipline still about forty years away. To be sure, there is a long tradition of natural history studies that antedates the definition, but as Haeckel points out, this "uncritical" accumulation of information is not the same as the scientific pursuit of mechanistic explanations. In the second place, the discipline is being defined by someone who had not been, and would not be, a practitioner in that discipline. In fact, Haeckel was downright antagonistic toward the quantitative distributional studies, such as Hensen's (1887) pioneering work with plankton, that were to become one of the central elements in ecological inquiry (Stauffer 1957). Finally, the Haeckel passage is remarkable for a third reason. It remains today, nearly a century and a half later, a good abstract characterization of what ecology is all about. The scientific practice that has come to be ecology is essentially directed at the same phenomena that Haeckel identified in the Darwinian scheme.

This last point will be controversial. In a broad sense, this controversy is the central theme around which this book is organized. Before turning to these matters, however, there is a prior issue to address. Why care about a definition of ecology in the first place?

1.4 WHAT'S IN A DEFINITION?

It might be thought that the attempt to define a field of scientific inquiry is wrong-headed from the start. At best, it is a waste of time, since any acceptable definition will have to be so abstract that it will carry little real information. At worst, it is positively misleading because it attempts to impose an arbitrary conceptual structure on a domain which is fluid and continuous, both in terms of its relationships with other disciplines and in terms of its historical development. And in any case, as the history of debates over definitions of

ecology reveals, the enterprise is destined to become entangled in a morass of semantic squabbles that have little relevance beyond its own self-defined project. What matters, so the objection continues, is not the philosophical attempt to abstractly carve out a chunk of disciplinary space as characteristically ecological, but an examination of what ecologists actually do. The place for philosophy of ecology to begin is with ecological practice itself. What do the scientists that call themselves ecologists actually study? What kinds of methodological and conceptual issues are obstacles to the smooth progression of these studies? Perhaps the individual practices that fall collectively under the rubric of ecology will ultimately lend themselves to concise definition, perhaps not. Surely that is a question to be answered after the spadework has been done.

This objection makes a good deal of sense and therefore deserves a response. My response, to be developed in this section, will be in terms of the following points. First, while the bottom-up, case-by-case approach recommended above certainly makes sense as a philosophical strategy in general, there are considerations that militate against it in the present context. Specifically, the heterogeneity of ecology, the immaturity of the philosophy of ecology, and my desire to locate the philosophical discussions in at least a thinly historical context all work together to render an exhaustive examination of the various subfields of ecology impractical. Second, it *is* both possible and valuable to reason abstractly about the structure of interdisciplinary space. Third, the search for an adequate definition can actually function as a tool for probing foundational issues in the discipline. Finally, when definitional inquiry is used in this way, as a guide to the major controversies within a field, it is the foundational investigations themselves that are central; the emergence of a satisfactory definition, if one does in fact emerge, is an ancillary, though welcome, consequence. Let me address each of these points in turn.

The central obstacle standing in the way of any attempt to move directly from the various ecological practices to a comprehensive examination of issues in the philosophy of ecology is the enormous variety in types of inquiry that have been classified as ecological. Part of the problem is the plasticity of the term *ecology*, and in particular, the tendency to apply the ecological label to work that might more properly be thought of as environmental philosophy. I have in mind here studies with an essentially normative component – from investigations of ecosystem health and integrity (e.g., Costanza et al. 1992) to deep ecology (Naess 1973). But even if one manages to sort ecology the science from these broader concerns, the heterogeneity is still staggering. To illustrate, Robert Ricklefs (1979) influential textbook, which he titles simply

Ecology, is nearly 1,000 pages long, yet there are central subfields in ecology, such as limnology, that are not even discussed.

The difficulty is compounded by the need to incorporate history. The "historical turn" in the philosophy of science involves, in part, a recognition that foundational inquiry can be deepened and enriched by considering the historical development of the issues under investigation. For ecology this presents special problems because large portions of the relevant history have not yet been written. In the most comprehensive history of ecology to date, Robert McIntosh confronts what we might call the complexity problem. Here is what he says:

> The intrinsically polymorphic nature of ecology as a science, the widespread distortion of its content and competence which accompanied its meteoric rise in public awareness during the period of environmental concern, or crisis, of the 1960s and 1970s, and the lack of historical studies combined to allow diverse, even contradictory, opinions to persist about the roots or origins of ecology. Hence, what I call *retrospective* ecology encounters problems in identifying roots because ecology is, to continue the botanical metaphor, more a bush with multiple stems and a diverse rootstock than a tree with a single, well-defined trunk and roots. (McIntosh 1985: 7)

McIntosh responds to the problem by doing a kind of phenomenology of the history of ecology; he charts the temporal pattern of significant events while remaining relatively silent on the causal story that underlies that pattern. Thus he describes his work as dealing with the "antecedents" of ecology rather than the history of the discipline. The situation is rapidly improving, as historians break off bits and pieces of the discipline and do the relevant history (e.g., Kingsland 1985, Hagen 1992, Golley 1993), but the parts that have been tackled do not yet add up to the whole.

Setting the historical problems to one side, it would be possible to take a more direct, bottom-up approach to the conceptual and methodological problems of ecology if there were more shoulders to stand on. If the philosophical spadework were done for the various styles and domains of ecological investigation, then a more comprehensive treatment could be constructed on this foundation. Unfortunately, that is not the case. Confining attention to book length treatments, there are just three works that systematically attempt to apply the conceptual tools of philosophy of science to the foundational problems of ecology.[1]

The most recent work, by Pickett et al. (1994), does an admirable job both of identifying significant philosophical issues that an adequate philosophy of ecology must address, and also of canvassing relevant work in the philosophy of science. But it is overly catholic in appropriating ideas from philosophy, incorporating positions that, from the viewpoint of those working in the philosophical trenches, are not compatible in any obvious sense (see Cooper 1996). In fairness to the authors, they explicitly announce that this is a book "by practicing ecologists for practicing ecologists" (Pickett et al. 1994: xi), and their work is to be commended for introducing fresh ideas from philosophy of science into the ecological arena. Even so, because these ideas lack philosophical cohesion, the work represents more a McIntosh-style phenomenology of issues in the philosophy of ecology than a philosophical treatment that can serve as the foundation for further philosophical inquiry. A second work, Shrader-Frechette and McCoy (1993), is more explicitly concerned to apply a coherent and defensible philosophical position; however, it is also more narrow in its focus. The authors are primarily concerned with the role of ecology as a guide to environmental policy and less directly with the broader sweep of issues in the philosophy of ecology as such. Like the episodic histories mentioned above, Shrader-Frechette and McCoy are pursuing a divide-and-conquer strategy, isolating a particular cluster of issues and subjecting them to detailed investigation. The third book, Peters (1991), *is* an attempt to be both comprehensive and philosophically grounded. Unfortunately, as we see in Chapter Five, it is grounded in a rather impoverished view of science as a cognitive activity, a view that takes predictive success as the sole criterion for genuine science. This positivist legacy may provide shoulders to stand on, but they are narrow shoulders indeed.

Thus, the heterogeneity of ecology as a scientific discipline, together with the relatively underdeveloped nature of both historical and philosophical studies of the field, conspire to discourage a comprehensive approach to the philosophy of ecology, especially one that is grounded in a kind of seriatim investigation of the various cognitive projects that have been classified as

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[1] I leave out the work by Tim Allen and his colleagues (for example, Allen and Hoekstra 1992) because, while clearly directed at foundational problems, it makes little attempt to explicitly incorporate the machinery of philosophy of science. The volume by Haila and Levins (1992) contains valuable philosophical work, and the orientation of this book is largely sympathetic to the perspective they adopt; however, the overall focus of their work is on the social context of ecological science. There are several anthologies that make important contributions. The massive compendium of classic papers with commentaries edited by Real and Brown (1991) is a tremendous source for the historical development of key ideas. A recent volume on ecological experimentation (Resetarits and Bernardo 1998) focuses on an important area of ecological methodology. However, neither volume contains much by way of explicit deployment of philosophical ideas. The recent anthology by Keller and Golley (2000) does the best job, in both terms of scope and the blending of ecological and philosophical ideas.

ecological. However, at this juncture the philosophy of ecology needs, in my judgment, something more comprehensive. Clearly, it is crucial that any philosophical inquiry into the foundations of a science be as informed by, and as faithful to, the practice of that science as possible. That desideratum is kept in the forefront throughout the course of this study. Furthermore, given the variety of associations that the term *ecology* calls to mind in contemporary intellectual (and not so intellectual) culture, it is important to indicate, at least in broad outlines, the various kinds of scientific activities that have traditionally been classified as ecological. Chapter Two presents such an overview. But it still remains necessary, for the reasons that have just been given, to structure the investigations around an organizing framework; the search for an adequate definition is the framework I shall use.[2]

Thus goes the argument that, given the contemporary situation, a comprehensive examination of the philosophy of ecology must take a kind of top-down approach to the field. I now want to argue that such an approach can be valuable in its own right. Over roughly the last two decades, the investigation of the disciplinary structure of science has become an important domain of inquiry for science studies. Three broad areas of investigation can be recognized: (1) what Bechtel (1986b) calls the "cognitive" aspect, (2) the social and institutional aspect, and (3) the historical aspect. Within the cognitive domain we can, following Kuhn (1962), distinguish between the substantive and the methodological. What I am arguing is that philosophical investigation of the substantive/cognitive structure of interdisciplinary space can be a useful tool for exploring foundational controversies. I will illustrate with three examples.

As a graduate student in philosophy of science making my initial forays into ecology, I was astonished to find, on opening the massive *Principles of Animal Ecology* by Allee et al., a definition of ecology by Rudolf Carnap. I had been attending rather closely to Carnap's work and I had no idea that he knew anything about ecology. As it turns out, I was right; he didn't know anything about ecology the discipline, about ecological practice. He had, instead, deduced in an *a priori* fashion, in the course of developing his program of unified science, that there was a significant domain of phenomena here that ought to be the target of a scientific field. Here is the definition Allee et al. are referring to:

> Carnap (1938) recognized "physics" as a common name for the nonbiological field of science and stated that "the whole of the rest of science may be called biology (in the large sense)." He immediately saw the necessity of dividing this wider biology into two fields, the first of which contains "most of what is usually called biology, namely, general biology, botany, and the greater part of zoology." The second part "deals with the behavior of individual organisms and groups of organisms within the environment; with the dispositions to such behavior, with such features of processes in organisms as are relative to the behavior, and with certain features of the environment which are characteristic of and relevant to the behavior, e.g., objects observed and work done by organisms." . . . He continues by saying that "there is no name in common use for this second field." (Allee et al. 1949: 13)

Carnap's definition is not bad for someone essentially clueless about the practice; it illustrates the power of an abstract interdisciplinary perspective. Allee et al. draw a similar moral:

> Thus, in the late 1930s, a philosopher of high attainments compounded logical necessity with ignorance of the history and present development of biological ideas, and announced as new the discovery of the field of "bionomics," "ethology," "ecology," or "relations physiology." This happened at the University of Chicago, where research and teaching concerning the relations between organisms and their environments had been an active feature of the biological program since the late 1890s. . . . Carnap's statement . . . demonstrates anew that ecology fills a natural niche in biological science. It also gives warning of the lack of general knowledge among scholars as to the mass of information in this field. (Allee et al. 1949: 13)

Of course, philosophical approaches to foundational problems in the special sciences do get better if they actually pay attention to scientific practice, and there is good work in this domain to which we can point. Bechtel's (1984, 1986b) use of cognitive/substantive considerations to explain the emergence of biochemistry as a distinct scientific field, and the papers in the Bechtel (1986a) volume generally, illustrate the utility of looking at foundational issues from the standpoint of the structure of interdisciplinary space. The examination of proposed definitions of a discipline is a natural place to begin such an inquiry. The search for an adequate definition for the field is just where one would expect differences about the substantive/cognitive component of the field to emerge – after all, a definition seeks to abstract away details to isolate what is essential.

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[2] As noted in the preface, this book has not managed to be as comprehensive as it set out to be. Obviously the case for structuring the investigations around Haeckel's definition of ecology would be stronger were this book to tackle not only internal questions in the philosophy of ecology but the significant external questions as well, those questions that pertain to the relationship between ecology and its close disciplinary neighbors.

Some might think I have fussed too much over the justification for structuring the book around the search for an adequate definition of ecology. But the issues discussed in this section serve a second purpose; they also clarify both the context and the orientation of the philosophical project that is to follow. For others, perhaps, no amount of fussing will do; the question of a definition of ecology is simply uninspiring. There is a fallback argument for those who find none of the foregoing convincing. The bulk of the book looks at issues that have featured prominently throughout the history of ecology. Those issues should be seen as worth addressing by anyone concerned with the advancement of the science, even if they are not much given to searching for an adequate definition.

1.5 FOUR FUNDAMENTAL OBJECTIONS

Haeckel finds, in Darwin, a vision of what the science of ecology should be about. However, though the term stuck, the vision has not played a very prominent role in the subsequent development of the discipline. Major textbooks either fail to mention Haeckel altogether (Putman and Wratten 1984) or they give only a brief nod in his direction as the one who coined the name of their discipline (Ricklefs 1979, Krebs 1978). There is the occasional polemic to the effect that ecologists should pay more attention to their Darwinian roots (e.g., Harper 1967), but even here the emphasis tends to be more on the larger Darwinian enterprise than on the more restricted science that Haeckel defines. Haeckel never really engaged in ecological investigation, and the definition antedated the emergence of the discipline by close to half a decade – two points that go some distance toward explaining this lack of attention. A detailed historical study would, I am sure, turn up other reasons as well. But part of the explanation traces to conceptual problems with the definition itself. This section outlines four such objections. Subsequent sections of this chapter look at the four objections in more detail, and subsequent chapters examine the foundational issues that underlie these objections, though, as I have said, I do not get to them all.

As the passages quoted above reveal, Darwin viewed the struggle for existence as involving both biotic and abiotic factors. Two canines may struggle with one another for the last morsel of food, but the plant growing on the edge of the desert also struggles, albeit more metaphorically, with the climate. Still there can be little doubt that Darwin regarded competition among organisms, especially among closely related forms, as the most significant factor in the struggle for existence. He says, for example, that "not until we reach the extreme confines of life, in the Arctic regions or on the borders of an utter desert, will competition cease" (Darwin 1859: 89). Darwin was also famously fond of the idea of an "economy of nature" – the notion that through the workings of a kind of biological hidden hand, the struggles of the various individuals produce an overall balance or order in the entangled bank. As he puts it, "Battle within battle must be continually recurring with varying success; and yet in the long-run the forces are so nicely balanced, that the face of nature remains for long periods uniform" (Darwin 1859: 85). Sometimes the two ideas, the struggle for existence and the economy of nature, are explicitly related to one another. Thus, he says, "For as all organic beings are striving, it may be said, to seize on each place in the economy of nature, if any one species does not become modified and improved in a corresponding degree with its competitors, it will soon be exterminated" (quoted in Stauffer 1957: 139 from the first edition of *The Origin*).

This emphasis on the importance of biotic factors and on the economy of nature is preserved in Haeckel's extended definition. Thus in the passage quoted above he emphasizes how "the organic conditions of existence exert a much more profound transforming action on organisms than do the inorganic," and he sees the role of ecology as the investigation of "the place each organism takes in the household of nature, in the economy of all nature." And here we have the basis for the first objection, what we might call the "biotic bias" objection. Do biotic factors really have this tendency to swamp abiotic factors in the struggle for existence? Is competition really so ubiquitous? Do the complex organic relations among beings really generate the biological hidden hand that smooths over the influences of local history? Is there a balance of nature? The biotic bias objection worries that at least some of these questions should be answered in the negative, and that, as a result, Haeckel's definition is flawed.

The second objection, which I will call the "theory bias" objection, is rather difficult to state succinctly. We can get an initial sense for the problem by proceeding indirectly, via the convergence of two relatively distinct lines of argument. The first begins with some criticisms developed by Peters in his book on the philosophy of ecology (Peters 1991). In that work, he is concerned to argue against the misuse of what he calls "logico-deductive argument" in ecology. Peters has no problem when "practitioners wisely explore potential new routes for research logically, before expending resources to examine them empirically" (Peters 1991: 60). But, on his view, this deductive, *a priori* approach has closed in on itself to become a kind of self-perpetuating enterprise, insulated from empirical criticism because it is predictively barren and wasteful of the resources for ecological investigation. The merits of Peters's critique will be taken up in the second half of the book. The important point for now is that he sees this theoretical dead end as having its roots in the attempt to establish a Darwinian origin for ecology. In his review of Peters's book, McIntosh puts the matter as follows: "Because the original definition of ecology was predicated on Darwinian ideas of struggle for existence, it is no surprise that Peters describes natural selection as 'one of the major influences making ecology a new scholasticism' (p. 60), and a failure as a theoretical predictive science" (McIntosh 1992: 495–96). So, on the first line of argument, the attempt to erect a definition of ecology within the Darwinian theoretical framework is inevitably biased in favor of a particular tradition of deductive theorizing in ecology, and one, on Peters's view at any rate, that has been singularly unproductive.

Admittedly, Peters is something of an iconoclast; neither his views about ecology, nor the philosophical positions that underlie them, represent anything near the mainstream of either discipline. Thus it is appropriate to examine another way of formulating the theory bias objection. In 1934 the Russian ecologist G. F. Gause published a book that explicitly recognized the Darwinian roots of ecology. The book was, in fact, titled *The Struggle for Existence*. Lamenting the fact that "our knowledge of the struggle for existence has since Darwin's era increased to an almost negligible extent," Gause resolved to investigate "the elementary processes in the struggle for existence," and to do so for the most elementary cases so that, at least for these simple cases, "we can give a clear answer to Darwin's question: why has one species been victorious over another in the great battle of life?" (Gause 1934: 1–2) The book was a brilliant synthesis of two emerging research traditions: the experimental study of populations in the laboratory (e.g., Chapman 1931) and the mathematical modeling of populations based on the seminal work of Lotka (1925) and Volterra (1926). In the present context, I want to focus on this second tradition.

In the course of his investigations, Gause made a connection between the concept of the niche as Elton had used it (e.g., Elton 1927) and the mathematical representation of competition between two species. Eltonian niches were very much like the "stations" in the Darwinian economy of nature discussed above. Here is Gause's interpretation, together with the qualitative insight about the struggle to occupy these stations that traces back to Darwin: "A niche indicates what place the given species occupies in a community, i.e., what are its habits, food and mode of life. It is admitted that as a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain peculiar kinds of food and modes of life in which it has an advantage over its

competitor" (Gause 1934: 19). The connection with mathematical competition theory is as follows: "It is the place to note here that the equation (12) as it is written does not permit of any equilibrium between the competing species occupying the same 'niche,' and leads to the entire displacing of one of them by another. This has been pointed out by Volterra ('24), Lotka ('32b) and even earlier by Haldane ('24), and for the experimental confirmation and a further analysis of this problem the reader is referred to Chapter V" (Gause 1934: 48).[3] As the quote indicates, Gause was not the first to point out that the early competition models gave quantitative expression to the insight about competition for "stations"; however, perhaps because of the "empirical confirmation" of the idea with his laboratory populations of protozoans, his name became intimately bound up with the notion of competitive exclusion. Gause's principle, the idea that organisms occupying identical niches cannot coexist in the same environment, became the fundamental theoretical principle of the science of the struggle for existence. As such, it was to become the foundation of a flourishing tradition of theoretical model building in ecology, extending through the seminal work of G. E. Hutchinson and Robert MacArthur to contemporary theoretical ecology.

We can now formulate the second line of argument behind the theory bias objection. It is, in brief, that the Haeckel definition, through the connection with Gause and his investigations of the struggle for existence, singles out this highly visible theoretical tradition as being in some sense paradigmatic of ecological inquiry, and it does so at the expense of other forms of ecological investigation. In other words, defining ecology as the science of the struggle for existence, given the role of this idea in the historical development of the science, comes too close to defining ecology as the theoretical investigation of the consequences of competitive exclusion. We can also see how this line of argument converges with the earlier argument – that the definition gives pride of place to deductive theorizing in ecology. It does so because, for the most part, the tradition that Peters singles out as the "new scholasticism" coincides with the tradition of theoretical ecology that has grown out of the Gausian focus on the struggle for existence.

In contrast to complaints about biotic bias and theory bias, the third and fourth objections can be succinctly put. The third objection, which we can label the "autonomy threatened" objection, is just this: under the proposed definition, ecology loses its status as an autonomous discipline and becomes instead a subdiscipline of a subdiscipline of evolutionary theory. Specifically, ecology becomes that part of the theory of natural selection, itself a part of the

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[3] With "equation (12)," Gause is referring to the standard Lotka-Volterra competition equations.

theory of evolution, that deals with the circumstances that generate selection pressures. How is this supposed to follow? The argument is straightforward. The struggle for existence is the engine that drives natural selection. Ecology is the science of the struggle for existence. So, ecology is part of the theory of natural selection. Furthermore, since the theory of evolution is concerned with evolutionary change, understood as change in gene frequencies, and since natural selection is one mechanism for changing gene frequencies, the theory of natural selection is part of the theory of evolution. Thus, ecology is a branch of a branch of evolutionary biology. But, so the objection goes, there are lots of ecologists who do not consider themselves evolutionary biologists, and therein lies the flaw in the definition.

The fourth objection is the "levels of organization" objection. The central idea is that there are all sorts of practices that are properly seen as ecological but that are not captured by the Haeckelian definition. I will mention two examples, both ultimately based on the idea that the definition is too organism centered. The first complains that, by focusing entirely on the demographics of individual populations, the Haeckel definition rules out *a priori* the possibility of genuine community level properties, and therefore the existence of a legitimate body of ecological inquiry that focuses on this level of organization. A second sort of complaint is that the definition completely excludes ecosystem ecology. There is, after all, no mention of the flow of energy and/or materials through ecosystems. Given the historical context from which this definition emerges, this should come as no surprise, but it does represent, so this objection goes, a fatal flaw in the definition.

1.6 FOUR FOUNDATIONAL ISSUES

The four objections discussed in the previous section are largely hypothetical in the sense that they cannot be located in specific discussions of the adequacy of Haeckel's definition. But that is a reflection of the paucity of serious examinations of Haeckel's definition, not the centrality of the objections. We can be confident of the following counterfactual: were Haeckel's account to be put forward as an adequate abstract characterization of what the science of ecology is about, the objections raised earlier would be offered in response. The reason we can be confident in such a counterfactual is that the objections themselves are grounded in foundational controversies that have dogged ecology throughout its history. The next chapter substantiates this claim and, in the process, looks in more detail at the nature of these foundational issues. Before turning to that discussion, however, I conclude this chapter by presenting

a preliminary outline of the foundational issues involved. In the case of the first two objections, I also give a preliminary indication of the kind of response that can be made on behalf of the Haeckelian definition. A detailed investigation of the third and fourth objections is beyond the scope of the present work; however, I return to these issues for a brief look forward in the Epilogue.

1.6.1 Biotic Factors, Density Dependence, and the Balance of Nature

On the face of it, the biotic bias objection seems to turn on straightforward empirical considerations. It is an empirical question whether organisms mostly struggle with one another or with the abiotic factors in their environment; whether, among the biotic relationships, competition is the dominant force; whether populations are regulated in such a way as to produce finely balanced communities. Such questions are foundational in the sense that they raise fundamental issues about the nature of ecological organization, but they do not appear to be foundational in the sense that they turn on philosophical considerations. At one level, this impression is accurate; this is a debate that should be settled on empirical grounds. But there is a philosophical side to the matter as well. When it comes to this particular cluster of issues, ecologists have had an especially difficult time letting nature settle the matter. Why, throughout the history of the discipline, has there been such a strong propensity to adopt, as an article of faith or an *a priori* axiom, an extreme stance on these matters? There are a number of reasons (Cooper 1993), of which I discuss two. Let me say something about each in turn.

What I call the "balance of nature argument" is a pattern of reasoning that has been influential in shaping the controversies associated with the biotic bias objection. It is hard to find versions of the argument explicitly stated, but it often lurks in the background, shaping expectations about the determinants of ecological phenomena. The argument begins by pointing to an obvious empirical fact – by and large, populations manage to persist, or, as Darwin put it, the face of nature remains relatively unchanged for long periods. But this would be impossible, so the reasoning goes, were it not for density-sensitive processes regulating population size and/or community structure. From here the argument can go in several (not mutually exclusive) directions. Since this balance is supposed to be the product of natural selection, we should look toward biotic interactions, and perhaps competition in particular, for these density-dependent factors. The existence of this density-dependent regulation might also be used to justify the assumption of equilibrium as a kind of "zero force state" for populations and/or communities. This way of thinking has, of course, generated substantial controversy throughout the history of ecology.

Closely related to this question of the degree of biological organization in ecological phenomena is a second issue, one that comes in more directly from the philosophy of science. The issue concerns the status of ecology as legitimate science, and particularly, expectations about the kind of general knowledge ecology must produce in order to solidify its status in the scientific pantheon. For a variety of reasons, not the least of which has been a philosophy of science that has typically looked to physics as its model science, the standards have been perceived to be quite demanding. Real science produces laws, and laws are special – they are spatio-temporally universal, support counterfactuals, can be confirmed with just a few positive cases, and so forth (see van Fraassen 1989 for a general discussion). With the bar set so high, it is not surprising to find ecologists exploiting *a priori* strategies to increase generality, looking to equilibrium to erase the effects of history, and generally, relying on natural selection to produce the nomothetic structures that would sustain the genuine laws that a *science* of ecology needs. The consequence, once again, has been a tendency to rush to judgment about the relative importance of biotic over abiotic factors, about the significance of competition as an ecological determinant, and about the prevalence of stability and balance in ecological situations. Unlike the *a priori* argument from persistence, however, this pursuit of ecological generality cuts both ways. Those arguing that abiotic factors, such as climate, are the truly important determinants of ecological phenomena have frequently been just as dogmatic in their attempt to project limited studies across the broad sweep of ecological situations.

Chapters Three and Four are devoted to diffusing the two sources of controversy that have just been described. Chapter Three begins by taking a close look at the pattern of reasoning associated with various versions of the balance of nature argument. A detailed reconstruction and examination of the relevant arguments reveals that there is no *a priori* route to the balance of nature, to the prevalence of density dependence, or to biotic bias generally. The discussion then turns, in Chapter Four, to the question of ecological generalizations. Here the debate over biotic bias and the balance of nature makes contact with larger issues. A number of influences have come together to suggest that there might be something of a revolution afoot in ecology. Recent philosophy of biology has begun to press the idea that there really are no laws in biology (Beatty 1995, Gould 1989). It has become fashionable to see ecology itself as an essentially historical science (Kingsland 1995 and references therein, Kritcher 1998). Botkin (1990) and others (see papers in *Duke Environmental Law & Policy Forum*, vol. 7) have come to view the balance of nature idea as a dominating myth that has distorted ecological inquiry, and that must be outgrown if the science is to advance. From the philosophy of ecology itself (Shrader-Frechette and McCoy 1993) we get the idea that ecology is destined to become a science of case studies, with little real prospect for the generation of portable ecological knowledge that can be applied across a range of situations. Even among theoretical ecologists themselves, where we might expect the pursuit of generality to be strongest, there is a call for pluralism and a view of theories as little more than a collection of tools (Roughgarden 1984, Diamond and Case 1996, Loehle 1983, Haila 1988). Ecology once had aspirations of becoming a genuine nomothetic science; the pendulum seems to have swung quite dramatically in the other direction.

The issues raised by this celebration of contingency and historicity spill over into other controversies beyond the scope of this book, but clearly questions about the nature of ecological generalizations lie close to the heart of the matter. Thus it is important to develop a conceptual framework for thinking about ecological generalizations not just as a means to resolve conflicts about biotic bias but also as a resource for dealing with this larger (and related) cluster of issues. Chapter Four develops such a framework. Specifically, through an examination of ecological methodology and an analysis of the concept of a law of nature, the chapter supplies a way of thinking about ecological generalizations that does the following. First, it clarifies the various kinds of general knowledge claims that ecologists pursue. Second, it locates these various kinds as part of a larger cognitive endeavor. Third, it develops a conception of lawfulness (what I will call "nomic force") that recognizes that the nomicity of ecological generalizations comes in degrees and with domain restrictions – one acknowledging that while there might not be anything in ecology to match the nomicity of physics and chemistry, it does not follow that everything in ecology is equally contingent.

Returning, then, to worries about how the definition of ecology as the science of the struggle for existence might illicitly incorporate a bias in favor of biological factors, I argue the following. There are good reasons to worry about the problem; there has been a historical pattern of controversy between those who emphasize the biological organization underlying ecological phenomena and those who deny it, and the struggle for existence idea has mostly been associated with the former. However, the nature of the determinants of ecological phenomena is an empirical question that can be decided only by looking at those phenomena. Released from any *a priori* baggage that for historical reasons it might be carrying, and placed in a framework where misguided philosophical expectations no longer distort the pursuit of general ecological knowledge, the struggle definition is no longer susceptible to the biotic bias objection.

1.6.2 *The Controversies Surrounding Theoretical Modeling*

The theory bias objection really involves two distinct objections, corresponding to the two lines of argument used to describe the objection initially. The worry that Haeckels' definition gives unwarranted pride of place to the Gause/Hutchinson/MacArthur theoretical tradition is closely related to the constellation of issues just discussed. There is a tendency, in this tradition, to emphasize biotic factors, population regulation, and the kind of equilibrium or balance that erases local history – all the factors that make the world a friendlier place for theory (Kingsland 1985). In part, then, the theory bias objection can be seen as a reluctance to settle these empirical issues prematurely by the definition one gives of ecology. As such, the appropriate response is the same as before – a bias toward balance and biotic factors is not essential to the definition of ecology as the science of the struggle for existence.

The theory bias objection as illustrated by Peters's criticism is a different matter. In this case, the objection is to a particular style of ecological investigation – the deductive elaboration of theoretical ideas, or what we might call model building. In the extreme form of Peters, it is an objection to the tradition of theoretical model building – period – on the grounds that it does not constitute legitimate science. But we should be prepared to recognize milder forms of the objection as well. For example, there are potential objections that have no complaint about theoretical model building in principle, but that do worry about the way it has been practiced in ecology. Finally, there are objections that worry not about the legitimacy of theoretical modeling, even as practiced, but about the way in which the struggle definition appears to place this style of ecological inquiry on center stage. Let me grant at the outset that Haeckel's definition does conjure up images of a competition-based theoretical ecology. There are good historical reasons for these images, just as there are for the association between the struggle for existence and an emphasis on competition and biotic factors generally; but there is no essential connection in either case. I am more interested here in potential complaints that are grounded in the controversies over model building itself, because it is these controversies that form the second of the foundational issues to be examined.

The tradition of theoretical modeling in ecology has been challenged on a wide variety of grounds and, as the previous paragraph suggests, some of these challenges have been more extreme than others. The more extreme challenges tend to be grounded in one of two ways. The first is empirical and reflects a

basic skepticism about the susceptibility of ecological phenomena to the kind of theoretical systematization that the abstract model builders pursue. This is connected to the celebration of contingency and historicity mentioned above; model building, on this view, is doomed to failure because of the uniqueness and/or causal complexity of ecological situations.

A second grounding, for the more extreme challenges, comes from philosophy. Peters is the example I have been using, but there are a number of distinct views here. What they share is a commitment to philosophical positions that leave little room for the scientific legitimacy, or at least the explanatory potential, of theoretical modeling as a cognitive activity. The less extreme criticisms are more concerned with the particular way the tradition of model building in ecology has developed. They criticize the way in which theoretical enterprises tend to float free of the evidence, explain patterns that are not really there, and idealize their way into irrelevance. In general, they raise questions about the role of model building in ecology and about its relationship to other, more empirically oriented styles of ecological investigation.

Chapter Five takes an extensive look at the various kinds of criticisms that have been leveled against the model building tradition, and then examines some of the ways theoreticians have responded to these challenges. It argues that many of these criticisms have been successfully addressed, either through direct philosophical argument or through recent modifications in the practice of model building, such as the call to build more mechanistic models and the tendency to look at model building as the construction of a kind of theoretical tool kit. However, while many of the challenges have been addressed, at a deeper level fundamental philosophical questions remain. Here is a sampling. In what sense are theories tools? Is this classical instrumentalism? Are theoretical models genuinely explanatory, or is their value heuristic in nature? How do we understand the call for more mechanistic models in the overall context of theoretical modeling as an explanatory enterprise? If testability is overblown and deductivism fails, then what is the relationship between theoretical models and the underlying phenomena they are supposed to systematize? Finally, perhaps the most fundamental question stems from the fact that one can make a decent case for each of the following propositions: (1) some theoretical models are genuinely explanatory, (2) there are no fundamental nomological truths (i.e., laws) for ecological theory to capture, and (3) laws are a necessary condition for successful theoretical explanation. The problem, of course, is that the three propositions are not mutually consistent.

The next three chapters (Chapters Six through Eight) turn to the philosophical literature to provide the resources for wrestling with these difficult problems. In effect, what is needed is a philosophical clarification of the "theories as tools" idea that is so prevalent among the model builders. Chapter Six surveys the resources in current philosophical theory for such a project and finds them wanting. Chapter Seven then develops a theory of explanation that explicitly recognizes two independent sources of explanatory virtue – explanation as telling the causal story and explanation as unification. Finally, Chapter Eight clarifies the role of model building in the pursuit of theoretical explanation. Taken together, the three chapters provide a way of understanding the idea of theories as tools, a way that answers the questions raised in the previous paragraph. I will not try to summarize the position here. Suffice it to say, for now, that this view of theoretical modeling also generates a response to the theory bias objection. Understood correctly, the Haeckel definition sees model building as *one way* to study the struggle for existence.

1.6.3 Ecology and Evolution

The "autonomy-threatened" objection, as formulated above, is a rather abstract worry. Perhaps no ecologist would be troubled by the problem put in quite this way. Still, there is a long history of ambivalence among ecologists about the relationship between their discipline and evolutionary biology. Defining ecology in this Darwinian way, in terms of the study of the struggle for existence, is bound to resonate with some and raise the hackles of others. Once again, this is symptomatic of a foundational issue that is yet to be satisfactorily resolved.

In this case, there appear to be two potential interlopers – evolutionary ecology and ecological genetics. Begin with evolutionary ecology. Early work by David Lack (1947) and Lamont Cole (1954) introduced the concept of strategic thinking into ecology. Very roughly, strategic thinking involves viewing the traits of organisms, including behavioral traits, in terms of their impact on the fitness of the organism. Cole in particular pointed to the tight connection to be expected between life history strategies and the demographic patterns that are the province of population ecologists. This connection between evolution and ecology bore further fruit in the "selection thinking" of MacArthur and Pianka (1966) and ultimately in the appropriation of the methodology of optimality modeling. This research tradition, which has come to be known as evolutionary ecology, has undergone tremendous growth over the last two decades. Might it be seen as an appropriate locus for the autonomy threatened objection? After all, its Darwinian pedigree is impeccable, and as McIntosh points out: "A major aspect of current ecology hopes to develop ecological theory from the life history properties of organisms [life history theory is one of the central elements of evolutionary ecology]" (McIntosh1985: 11). Certainly

ecologists have shown tremendous interest in evolution-based approaches to traditionally ecological domains of study; optimal foraging theory is an example. Textbooks that cover the standard ecological fare are often given titles like *Evolutionary Ecology* (Pianka 1983). Papers written from the perspective of evolutionary ecology frequent and sometimes dominate journals that have historically been venues for ecological work. One might be tempted to think that the phrase "evolutionary ecology" has become redundant, and that the appropriateness of a definition of ecology in terms of the struggle for existence is simply symptomatic of that fact. It is just such a temptation that the autonomy-threatened objection is supposed to reflect.

I mentioned above that there is a second potential interloper. There is a style of investigation that combines the biometrical approach of agricultural genetics with field studies of evolution tracing back to E. B. Ford and his students. I call this field "ecological genetics," but some may prefer a different name (e.g., "quantitative genetics"). Though I must paint in rather bold strokes here, a sense of the relationship between ecological genetics and more traditional domains of ecological inquiry can be gained by comparing the former with both evolutionary ecology (as defined above) and population genetics (where there is explicit representation of genetic loci). Evolutionary ecology studies the ways in which the sources of selection pressures play themselves out in evolutionary time, yielding the adaptive traits of organisms, but it fudges the genetics. Population genetics studies the ways in which the consequences of selection pressures (among other factors) play themselves out in evolutionary time, yielding changes in gene frequencies, but it fudges the ecological story. By focusing on phenotypic performance as a kind of universal measure, ecological genetics studies both stories at the same time. Using statistical and/or experimental methods to create a kind of stable background, it manages to identify significant patterns of statistical relevance that can be partitioned into two fundamental categories of causal relevance – the genetic and the environmental. Put another way, ecological genetics focuses on empirical patterns at the expense of a detailed understanding of the causal processes that underlie those patterns and, in this way, is able to investigate simultaneously both ecological and genetic phenomena. Ecological genetics is, in a sense, the econometrics of evolutionary biology.

The techniques of ecological genetics can be quite powerful. Consider the following idealized example of ecological inquiry. Suppose one has a population of clones and a sequence of environments that are perfectly homogeneous except for one ecologically relevant factor, which itself varies across the environments. Let the clones live out their lives in the various environments and then measure ecological performance (i.e., short-term survival

and reproductive success). Here one has as good an empirical measure of the
ecological relevance of the varying factor as one can get (see Brandon 1990 for
more detailed discussion and some real examples). Of course the tables can be
turned; phenotypic performance can be used to study genetic changes as well.

Unfortunately, the response to this objection involves a detailed look at
the relationship between ecology and evolutionary biology. While such an
investigation is beyond the scope of the present work, I will return to these
potential interlopers in the Epilogue, indicating there the direction that a
response to this objection is likely to take.

1.6.4 *Levels of Organization*

It is a commonplace, these days, that ecology is a hierarchical science. The
familiar image is that ecology studies systems at various points along the
hierarchical scheme from individual organisms to populations to communi-
ties to ecosystems; recently there have been attempts to wedge another level,
the landscape level, in between the community and the ecosystem. But this
easy recognition of hierarchical structure conceals underlying foundational
problems. There has been, for example, a long history of controversy sur-
rounding the existence of the ecological community as a legitimate level of
ecological organization. No one, of course, doubts that there are, in some
sense, ecological communities; what they have doubted is whether such com-
munities are more than fortuitous assemblages of populations that happen to
be living in the same place. A second area of perpetual frustration involves the
relationship between the ecology of organisms (the first three levels in the hi-
erarchy) and the ecosystem perspective, which embodies a physico-chemical,
as opposed to an organismic, stance toward ecological systems. There have
been continued calls for integration between these two points of view (Allen
and Hoekstra 1992, Pickett et al. 1994), but little real progress has been made.

The "community autonomy" issue arises in ecology in two ways – one for
plant ecologists and another for animal ecologists. The issue in plant ecology
has venerable roots. In 1905, Frederick Clements developed what has come
to be known as the superorganism view of ecological communities. On this
view, communities have a cohesiveness akin to the cohesiveness of organ-
isms, and for this reason they are just as legitimately seen as natural kinds as
are organisms. This view held sway for quite some time until, around mid-
century, plant ecologists began to seriously question whether these natural
kinds were so natural after all. We will discuss these ideas in the next chapter;
the important point here is that for plant ecologists this issue has been largely
a descriptive one: When we describe existing patterns of vegetation across

regions, do we find the regular associations that would be required if commu-
nities were really natural units? For the animal ecologists, on the other hand,
the problem has taken a more theoretical cast. Here the issue was clearly for-
mulated first by Charles Elton. He asked the question of limited membership:
Why are communities only a limited subset of the kinds of organisms that
might be found together? The theoretical problem for community ecology,
from the animal ecology perspective, has been to find those "assembly rules"
that govern the development of ecological communities such that the end
result is this limited sample from the regional fauna. Though both issues are
discussed in subsequent chapters, I confine my attention in this chapter to the
second version of the community autonomy problem.

In starkest terms, the discussion on this issue has been dominated by two
camps. One group holds that organisms interact, primarily by competition,
so as to carve up the potential niches that a community presents, and that
it is ultimately the availability of these niches that determines community
membership – the assembly rules are to be found in the partitioning of re-
sources. The other group doubts that there are any assembly rules to be found
at all, and thus that there is really any legitimate domain of phenomena for
community ecology to study: organisms simply do not interact in the kinds of
regular and systematic ways that would be necessary for the existence of any
kind of community *Bauplan*. The issue is, at bottom, a question of levels of
causal organization, and as we see in the Epilogue, the account developed in
this book does help clarify the matter. However, problems surrounding the
relationship between individual, population, and community ecology will not
be taken up in detail.

Perhaps the most dramatic gulf in the hierarchical scheme of ecology arises
with the transition from communities to ecosystems, or as described above,
between the organismic and ecosystemic perspectives. The fundamental prob-
lem is that the two approaches sort nature in terms of fundamentally distinct
categories – the demographics of organisms versus the flow of energy and the
cycling of matter. We get a deeper view of the problem in the next chapter
so I do not dwell on it here. Once again, while a thorough treatment of this
issue would require a deeper investigation of the levels problem than this book
provides, the outlines of a response will be developed in the Epilogue.

1.7 A CONCLUDING COMMENT

I have tried in this first chapter to lay out the overall structure of the argu-
ment that this book develops, including the central conclusions that will be

defended. It is, of course, risky business to present the conclusions before the arguments have been made. I have had to speak, at times, rather dogmatically, and at other times, I fear, rather cryptically. Still it can be useful as a point of orientation to know where the argument is headed, and if the discussion is provocative enough to prompt the reader to press on, so much the better.

It is perhaps even riskier to end a book on a speculative note, yet that is what the Epilogue will do. This book set out to address a number of significant external questions for philosophy of ecology that proved, ultimately, beyond its scope. Still the analysis that is developed does, in a sense, prepare the ground for that work. For that reason, I have kept these issues as part of the discussion in this chapter, explore them in a historical context in the next chapter, and return to them at the end of the book.

2

The Roots of Controversy

2.1 INTRODUCTION

The previous chapter outlined four basic objections to the definition of ecology as the science of the struggle for existence. Not surprisingly, these four objections correspond to four enduring foundational issues in the practice of the discipline itself. The goal of the present chapter is to deepen the analysis and to gain a clearer picture of what is at stake with each of these issues while, at the same time, substantiating the claim that each of these four areas has indeed been a significant locus for ecological controversy. The strategy is to look ultimately at some of the ways these foundational controversies have been manifest in the history of ecology, and I do this in two ways: first, by outlining the historical development of the various intellectual traditions that collectively comprise the field of ecology (section 2.3), and second, by exploring a series of eruptions of foundational debate that Robert May has dubbed ecology's twelve-year cycle (section 2.4). Before embarking on the historical study, some time is devoted to clarifying the philosophical framework for the investigations; attention is devoted, in particular, to the concept of a scientific field. This is the task of section 2.2.

2.2 FROM THEORIES TO FIELDS

For most of its early history, philosophy of science has been preoccupied with the scientific theory as the unit of scientific structure most germane to philosophical analysis. The interesting questions all seemed to involve theory in one form or another. What is the structure of a scientific theory? How are theories, which typically involve unobservables, connected to the empirical basis of a science? How are scientific theories tested? What makes a theory genuinely explanatory? Explications of scientific disciplines involved the axiomatization of the theories characteristic of that discipline. Even questions of interdisciplinary relationship were approached in terms of the inferential connections (such as deductive subsumption) that could be demonstrated to hold between the characteristic theories of the disciplines involved.

However, beginning in the 1960s, the picture began to change. With the publication of Kuhn's (1962) seminal work and with the increasing infusion of a historical perspective into the philosophy of science that this work stimulated, philosophers began to pay closer attention to the actual practice of science. In the process, they began to recognize interesting structure beyond the scientific theory. Practitioners in a scientific discipline may be wedded by commitment to certain fundamental theories, but they typically share much more than that, including the commitment to regard certain exemplary achievements in the field as "paradigmatic" of successful inquiry, the commitment to certain kinds of broad methodological norms, a shared framework for determining which kinds of questions are worth pursuing, and a common set of presuppositions about the entities and properties that comprise the domain of phenomena for the field.

Since this "historical turn" in the philosophy of science, there has been a great deal of work on the structure of scientific disciplines, on the way in which this structure changes over time, and on the various kinds of interactions that occur between disciplines (Shapere 1974, Darden and Maull 1977). I will adopt an essentially Kuhnian view, the view associated with his original concept of the scientific paradigm and later articulated in terms of the idea of a disciplinary matrix (Kuhn 1970). Following Bechtel (1986b:10), the relevant considerations can be distilled into the following three categories: (1) characteristic problems, (2) methodological practice, and (3) laws and theories. Commitments in these three categories go a long way toward determining the cognitive identity of a discipline; they form what we might call the constitutive basis for the field. The overall goal of section 2.3 is to describe, in a general way, the commitments of ecology in these three areas, with emphasis being given to the first area – to the questions that have typified ecological inquiry. Before turning to these matters, however there are several further preliminaries to address.

First, there is a question of terminology. The proliferation of investigations of disciplinary structure has been accompanied by a proliferation in terms for describing the basic units of the scientific enterprise. As mentioned, Kuhn initially talks about the *paradigm* but later shifts to *disciplinary matrix* in response to ambiguities in the former term. Once the philosophers got busy in this area, further terms were introduced: *domain* (Shapere 1974), *field* (Darden and Maull 1977), *research programme* (Lakatos 1970), *discipline* (Bechtel 1986b), *practice* (Kitcher 1993), and this list is not exhaustive. There are, of course, important differences among these concepts, but for our purposes we can understand all these terms as referring to a unit of scientific structure that is constituted by commitments in the three categories just mentioned.

Second, there are problems with the individuation of fields. As Bechtel (1986b) points out, the degree of disciplinary structure that can be distinguished depends on the level of resolution of the investigation – from the broad categories such as physics, chemistry, and biology at one extreme to Price's (1961) "invisible colleges" at the other. Except, perhaps, for the lowest level, turning up the resolution always reveals fields within fields. As we will see, this can generate foundational confusion in a number of ways. Practitioners in one subfield might fail to appreciate the work of others in a different subfield of the same discipline because they see their own work as constitutive of the discipline. In the other direction, practitioners who happen to be working in the intersection of two fields may undervalue work that fails to integrate because they have come to see the interfield work as constitutive of one of the originally distinct fields. To further complicate matters, sometimes the kinds of judgments that have just been described as mistakes, based on the misapprehension of disciplinary space, are actually correct because the nature of that space has changed – disciplines can merge, bifurcate, and so on. Some of the foundational controversies in ecology actually trace back to these kinds of differences in the perception of the structure of disciplinary space. The present chapter attempts to steer clear of these matters as much as possible, presenting instead a generic overview of the kinds of investigations that have typically been classified as ecological.

Finally, there is a potential objection that must be anticipated. The idea, broached in the previous paragraph, of there being a *correct* account of the structure of disciplinary space might give pause to some. The objection really comes in two forms. The strong version holds that while there might be all sorts of interesting ways to classify and categorize the larger scientific enterprise, there is no basis for grounding judgments about the correctness or incorrectness of particular accounts. A milder version acknowledges that there is something to get right here but maintains that it has nothing to do with foundational investigation. Rather, it is a matter of getting the sociological and institutional facts straight – memberships in professional societies, journal affiliations, patterns of correspondence and citation, student-teacher relationships, and the like. I do not find the first objection persuasive, though I will not argue the matter here. The second objection is more interesting.

One of the legacies of the "historical turn" in the philosophy of science has been an increased recognition of the importance of the social aspect of science. While I agree that there is interesting material to investigate here and that it can be relevant to the kinds of questions I want to pursue, I do not think it constitutes the entire story. Because I am a realist about ecological (and related) phenomena and believe that these various kinds of phenomena cleave into fundamental types or categories, I treat the social and institutional phenomena, in the best cases, as a useful guide to the foundational study and in the worst cases, as noise to be filtered out in the philosophical analysis. To put the matter another way, I believe it is perfectly possible for a scientific field, *qua* sociological entity, to misconceive either its own phenomena or its relationship to other fields and that there is, as a result, more to the matter than just sociology.

2.3 AN OVERVIEW OF THE FIELD OF ECOLOGY

This section tackles rather big game. By focusing primarily on the kinds of questions being put to nature and to a lesser degree on methodological practice and characteristic laws and theories, it identifies a number of relatively distinct programs of investigation that have come together to form ecology as a scientific discipline. Of course the story is vastly more complex than the thumbnail sketch that is provided here. I have attempted to paint in bold strokes, and I have chosen to emphasize historical development rather than the contemporary scene; by and large, I have not attempted to push the historical discussion much beyond the 1950s. The goal of this section is to generate an image of the science of ecology that can function as an adequate background for the foundational investigations that are to follow.[1]

2.3.1 *Conditions of Existence*

Ecology has sometimes been defined as scientific natural history (see, e.g., Elton 1927). Though this does accurately reflect the natural history roots of the discipline, it is not a very satisfying definition. To begin with, just what constitutes natural history is not immediately apparent. We can attempt to spell this out, for example, by saying that natural historians are interested

in what organisms there are, in where they live, and in how they live. But when we do so, natural history does not appear as the unique antecedent of ecology; the three questions associated with early natural history have evolved into relatively distinct scientific fields – namely, systematics, biogeography, and ecology. So the proposed definition is too broad. But it is also too narrow. If we confine attention to that part of natural history concerned with how organisms live, we miss a great deal of what has traditionally been thought of as ecological inquiry. Even if the scientific natural history definition does not work as a comprehensive account, however, it surely does capture a significant aspect of ecology. The goal of the present section is to elaborate on this aspect of ecological investigation.

As McIntosh (1985) points out, the emergence of ecology as a science represents the crystallization of a number of distinct intellectual traditions. One of the strongest channels of influence is through physiology. We have already seen that in Haeckel's view, ecology is physiology taken out of the laboratory and into the field; and he was not alone in adopting this perspective. In one of the earliest histories of ecology, Thomas Park (in Allee et al. 1949) discusses the emergence of ecology from physiological studies in some detail. He suggests that the effect of the environment on the organism can be classified roughly in terms of whether it has morphophysiological consequences or behavioral consequences. (For Park, these were both aspects of physiology; he called the former developmental, maintenance, and/or toleration physiology and the latter response physiology.) The distinction, as Park points out, is neither sharp nor mutually exclusive, but it is useful nonetheless. The distinction also has important implications. First of all, it is a distinction about the physiology of *organisms*, not *organs*. The separation of these two aspects of physiology was recognized by K. G. Semper in 1881. He claimed that the physiology of *organisms* was concerned with "reciprocal relations which adjust the balance between the existence of any species and the natural, external conditions of its existence, in the widest sense of the term" (Semper 1881). As this passage reveals, this "new" physiology focuses attention on the relationship between organism and environment. Although Semper never used the term *ecology*, the connection is obvious between these studies and the investigation of the "conditions of existence" that Haeckel targeted as the subject matter of ecology.

This physiology in the field is one of the earliest manifestations of the scientific natural history theme. The question, then, is what were these biologists doing as they worked in traditions that came together to be called ecology? What kinds of questions were they asking? How were they attempting to arrive at answers to these questions? The short answer is that

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[1] For those who would like to see more of the history, I recommend Kingsland (1995), McIntosh (1985), Hagen (1992), and Golley (1993); for those who want an overview of the contemporary science, I recommend the most recent editions of introductory texts such as Ricklefs (1979) or Krebs (1978).

they were using the techniques of experimental physiology to study the effects of environmental factors on the morphological, physiological, and behavioral properties of organisms. I do not intend to discuss this literature in any detail, but a few examples illustrate the kinds of questions that were being addressed.

One of the environmental factors that attracted interest was salinity. Experiments were conducted to determine the consequences of various degrees of salinity on a variety of organisms (e.g., amoebae, freshwater flagellates), and sufficient research had been done by the turn of the century to enable C. B. Davenport (1897) to conclude that "the capacity for resistance to stronger salt solutions seems to be closely correlated with the conditions of the medium in which the organism has been reared" (reprinted in Allee et al. 1949). As evidence for this generalization he referred to field experiments on mollusks from environments with varying salinity and laboratory experiments that radically altered the "natural" salinity tolerances of organisms by raising them in settings in which the salt content of the environment was gradually altered. Other features of the environment that attracted interest were light (e.g., the consequences of wavelength for photosynthesis), heat (e.g., the acceleration of growth accompanying an increase in temperature), air (e.g., the effect of changes in barometric pressure on oxygen tension), and water (e.g., the mechanical consequences of its movement). The many investigations undertaken and the information amassed enabled Davenport (1897) to generalize at a bit higher level: "When dynamic conditions vary quantitatively, a quantitative variation in metabolism will follow such that metabolism begins to slow down as limiting conditions are approached" (reprinted in Allee et al. 1949). Earlier work on the relationship between soil minerals and plant growth resulted in a related generalization, one of the first of many ecological "laws," known as Liebig's "law of the minimum." Roughly, this "law" states that "the rate of any process is limited by the least, or slowest, factor affecting it" (McIntosh 1985: 149). Later, V. E. Shelford (1911) expanded Liebig's idea of limiting factors in his "law of toleration," which included the ideas of maximum and optimum values. The principle remains today and, according to Krebs, it is "the major conceptual tool of the physiological ecologist." In its modern guise it receives the following formulation: "The distribution of a species will be controlled by that environmental factor for which the organism has the narrowest range of adaptability or control" (Krebs 1978: 20).

As already mentioned, there is, in retrospect, an obvious connection between this field physiology and the investigation of the conditions of existence that form the basis of the Haeckelian definition of ecology. Yet this experimental tradition and the Darwinian-based discipline described by Haeckel

never really managed to connect. Why? No doubt this is an involved story, but there are two salient differences between the two traditions that had an impact, and that have continued to play a role, in the emergence of ecology. The first one concerns the nature of the environmental factors against which organisms were seen to struggle. The physiological focus was on the role of the physical, or abiotic, environment. The reasons for this emphasis, whether grounded in a conviction that these factors are the most causally relevant or in the amenability of physical factors to mensuration and experiment, are hard to disentangle. In any case, as we have seen, the Darwin/Haeckel emphasis was just the opposite (Coleman 1986, McIntosh 1985). They emphasized the interaction with other organisms – the biotic environment – as exerting the dominant influence in the organisms' struggle to exist. A second important difference concerns the notion of adaptation. The experimental physiologists were interested in how the properties of organisms served to adapt them to their environment. But whereas Darwin, and Haeckel behind him, had definite ideas about where these adaptations came from, the experimental physiologists tended to have a far less critical attitude toward the mechanisms generating adaptations. They talked about "adaptations," but this should not be construed as implying a firm commitment to the Darwinian tradition. In addition (and sometimes in opposition) to natural selection, they frequently accepted various means of direct action by the environment (e.g., Buffon's principle of environmental induction or Lamarck's principle of the inheritance of acquired characteristics) as a major source of adaptation. But more important, it was the properties of the organisms themselves rather than the historical causes responsible for these properties that were the primary objects of interest.

This last point can be seen more clearly if we introduce an important distinction between two kinds of causal processes that might interest the biologist – the distinction between proximate and ultimate causes (Mayr 1961). One may ask why male white-tailed deer typically enter the rut in early November. One answer would be that the shortening periods of daylight at that time of year cause certain hormonal changes in the deer, which in turn are responsible for the behavioral and morphological changes associated with the rut. This answer gives the proximate mechanism at work. But one may also be asking a question about why male white-tails are organized in such a way that the pituitary gland responds in this way to decreasing periods of irradiation of the retina. This is a more difficult question, but it is also a different *kind* of question. It asks not what the properties of the organism are but why they are this way and not some other way. In this particular case the question is, given a cluster of properties of the white-tailed deer such as the kind of mating system they have, the consequences of increased levels of testosterone in the blood, the gestation period, and so on; why does the pituitary gland respond to decreasing photoperiodicity (rather than the opposite, for example)? I do not know the answer, but I can imagine the kinds of considerations that might be involved. For example, it might be that the timing of reproduction is controlled by the timing of estrus in the female and that males who do not synchronize their reproductive readiness with this event are at a distinct disadvantage when it comes to passing on their genes. Or it may be that the timing of the entire process is controlled by the gestation period together with an average fitness advantage enjoyed by young born during a certain period of the year. In any case, the attempt is to understand not what the properties of the organism are but why it has the properties it does.

Returning now to the study of adaptations by the early experimental ecologists, the nonevolutionary flavor of these efforts can be seen as stemming from a preoccupation with proximate, rather than ultimate, questions. Many of these investigators were unconcerned with giving ultimate explanations of the properties of organisms; rather they were preoccupied with understanding the proximate mechanisms at work in the interaction between the organism and its environment. This is not to say that the connection between ecology and evolution was not on the minds of some ecologists. C. C. Adams, for example, published a study of snails in 1915 in which he discussed both evolutionary and ecological issues, and similar examples would not be hard to find. Furthermore, it is not surprising, especially from a contemporary perspective, that such examples exist. The central issue behind the physiological studies was, after all, the environmental limitations on the survival of the organism – the connection with natural selection is obvious.

This interest in the properties of organisms in relation to their environmental circumstances has remained a consistent theme throughout the development of ecology up to the present day. It takes at least the following forms: (1) investigations of the "ecology" of particular species, and (2) more detailed and mechanistic studies in general ecophysiology (e.g., Larcher 1995). However, such studies faded into the background once ecologists began to focus on patterns of distribution and abundance – what Elton called the "population problem." In part this is because of the inherent importance of the latter, and in part it is because looking at patterns of distribution and abundance came to be seen as an alternative way to study the relations between organisms and their conditions of existence without looking directly at environmental physiology. More recently, there has been a resurgence of interest in the properties of organisms. There appear to be two central factors responsible for this development. By far the most significant impetus has been the

emergence of evolutionary ecology, which once again brings the physiological, morphological, and behavioral properties of organisms into focus, this time in an explicitly evolutionary context (Wainwright and Reilly 1994, Krebs and Davies1984, Townsend and Calow 1981). Whether such studies are asking proximate questions about ecological mechanisms or ultimate questions about the Darwinian histories behind the properties of organisms is a difficult and controversial issue, one that lies beyond the scope of the present work. The second, and related, factor involves the pursuit of a more mechanistic understanding of population phenomena – the so-called individual-based approach to population ecology (Schoener 1986a, Lomnicki 1988, Huston et al. 1988, Smith and Huston 1989, Huston 1991).

2.3.2 *A New Natural Kind*

The previous section was devoted largely to the early development of animal ecology, and it emphasized the role of experimental physiology in this process. Physiological considerations were no less important in the emergence of plant ecology. However, plant ecologists developed a conceptual structure with which to systematize their observation much sooner than did animal ecologists. This pioneer ecological theory is the subject of the current section. After an examination of some of the antecedents of this theory, we turn to a brief overview of the theory itself. The section concludes with a look at a major challenge to this theoretical framework, one that has had a significant impact on the development of ecology.

A major impetus to the development of ecology as an autonomous science was the development of a physiologically oriented German botany near the end of the nineteenth century. Of most significance for the emergence of ecology, these investigators were taking their experiments out of the laboratory and turning to the physiological investigation of plants in their natural setting. In this way they provided a conceptual alternative to the floristically oriented natural history tradition, an alternative that saw the approach to plant distribution not in terms of the historical development of the region but in terms of the impact of the current environment on the lives of plants. Among the leaders in this tradition were two German biologists, Andreas Schimper and Oscar Drude. But perhaps the most influential of the group was not a German, but a Dane, Eugenius Warming. In Warming's work we find the "conditions of life" perspective of Semper and Haeckel applied to the problem of distribution. In William Coleman's words: "How, he repeatedly asked, does the structure and physiological capability of a plant or a group of plants fit an organism or a community to a definite place in nature and – this being the essential question – what conclusions can we draw from such knowledge regarding the distribution of plants?" (Coleman 1986: 185–186). For Warming, the way to address this question was to focus on the factors, both biotic and abiotic, causally relevant to the success of the plant.

Whereas Haeckel recognized, in the analysis of Darwin's entangled bank, the conceptual domain of ecology but did not pursue it, and Semper, as we shall see, pursued it but never used the term *ecology*, Warming not only attempted to unravel the tangles but also recognized that "ecology was the science that needed to be invented to deal with these matters" (Coleman 1986: 190). This, together with his subsequent influence, makes him another candidate for the "father of ecology" epithet; in fact, he was designated as such by Tansley (1935). It would be nice if the story were so simple: Darwin setting the conceptual framework and, after a lengthy labor, the birth of ecology, both in name and deed, in the work of Eugenius Warming. Alas, nothing associated with ecology is so straightforward. In this case there are problems both looking backward and looking forward. In the former case, there are at least three considerations that distance Warming and Darwin (Coleman1986). First, Warming, like so many other influential figures in the early history of ecology, was not in step with Darwin on the origin of adaptations. He shared, with others under the sway of physiology, the tendency to put much more stock in the direct action of the environment than we find in Darwin. A related point has to do with the nature of the causes shaping the tangled bank. Coleman, following Ospovat (1981), argues that Darwin settled on a formulation of natural selection that de-emphasized the role of the abiotic environment; the struggle for existence was largely an organism to organism affair. As previously indicated, the early physiologists had quite the opposite orientation. Although Warming did consider biotic factors, his approach is more closely aligned with the latter group. Finally, there is the question of history. As already noted, Warming was after ahistorical explanations. Darwin, on the other hand, was much more directly concerned with the historical causes behind the characteristics of organisms.

Looking forward, Warming does not seem to be squarely in the middle of subsequent developments in ecology. Perhaps the most salient characteristic of early twentieth-century plant ecology is the conception of the biological community as a superorganism. But, as McIntosh (1985: 43) points out, "Warming's emphasis was on the individual plant, and he was critical of higher-level units, such as formations, or causes which could be applied to such entities." For Warming, the goal was "to provide a scientific demonstration of how each member . . . of a community exists *in morphological, anatomical, and physiological agreement with the diverse ecological and social conditions under which it lives*" (Warming 1895: 119–120). As we shall see, this individualistic perspective did not go unrepresented in the early history of plant ecology, but a source must be found for the emergentist perspective that played on center stage during this period, and it is apparently not to be found in the work of Warming.

The man most closely identified with the "community as superorganism" tradition is Frederick Clements, who, together with Henry Cowles, was one of the leaders in establishing plant ecology as an autonomous science in America. Cowles and Clements shared a common emphasis on the physiological nature of ecology, an emphasis that both inherited from the European tradition just discussed. But there were apparently different lines of transmission at work. According to R. Tobey (1981), a historian of this period in American biology, Clements saw Oscar Drude as his intellectual ancestor, whereas for Cowles it was Warming. Furthermore, there was, Tobey argues, a difference in philosophical orientation between Drude and Warming, the former being under the influence of German *Naturphilosophie* and the latter more prone to mechanistic reductionism. The twin influences were explicitly recognized by Cowles (1898): "It may be too early to predict whether the direction of future work in plant geography will be given by Warming or by Drude; and so whether we shall speak of ecology or phytogeography, or of life forms or of vegetational forms, or plant societies or formations is yet to be decided." Tracing the philosophical roots of the holistic and individualistic traditions would be interesting, but it cannot be undertaken here. The important point is the emergence of these two contrasting perspectives in ecology; they serve to divide ecological camps right up to the present day.

To see how the holistic tradition developed, we will take a brief look at the ideas of Clements, in particular as represented in his 1905 *Research Methods in Ecology*. His work represents the first attempt at the construction of a comprehensive theoretical framework in ecology. The guiding idea was that the surface of the planet is divided into distinct natural units that he called plant formations. There are, for example, fourteen such units in North America. Each unit is defined by a climax community, the community that with sufficient time and in the absence of disturbance will occupy the site. The climax community itself is a function of climate. The climax vegetation of a given area is the only plant community that is able to perpetuate itself in that location; so long as climatic conditions do not change, the climax will remain in stable equilibrium. But, as McIntosh points out, Clements's view of the balance of nature was anything but static. The climax formation is the end of a process, a process in which internal structures change in a unidirectional development governed from above by the higher level unit. In short, the plant formation is like an organism:

> The developmental study of vegetation necessarily rests upon the assumption that the unit or climax formation is an organic entity. As an organism the formation arises, grows, matures, and dies. Its response to the habitat is shown in processes or functions and in structures which are the record as well as the result of these functions. Furthermore, each climax formation is able to reproduce itself, repeating with essential fidelity the stages of its development. The life history of a formation is a complex but definite process, comparable in its chief features with the life history of an individual plant. (Clements 1916: 33)

The process of development in plant formations is called *succession*. Whereas the climax community is ultimately determined by climate, succession is driven by the successive modifications of the habitat by each of the stages of the process. An example is perhaps the best way to illustrate how this works. Because succession, in plants at least, is generally a slow process in "academic" time, ecologists tend to look for situations in which several stages are simultaneously present. Warming, the pioneer in developing the concept, found such a place in the dunes on the coast of Denmark. Emulating his approach, American ecologists Henry Cowles and Victor Shelford studied the sand dunes on the southern shore of Lake Michigan (Cowles focused on plants and Shelford on animals). I illustrate succession with a brief description of Cowles's results.

The shoreline of Lake Michigan is in the process of a slow retreat. By moving steadily away from the lake, one starts with young uncolonized terrestrial habitats, the newly formed dunes, and successively enters older habitats. In the process the vegetational cover changes. The barren sand dunes are first invaded by perennial grasses such as bluestem. The rhizomes from these grasses stabilize the dune and the accumulation of organic litter begins. With the increase in soil fertility, colonization by a variety of annual plants becomes possible. Further accumulation of detritus makes the habitat suitable for the growth of shrubs such as sand cherry and juniper. Eventually pines invade, but after several generations they lose out to competitively superior shade-tolerant beech and maple that dominate the climax community of the region. Of course all of this takes a long time, but the results of the process are laid out in the spatial dimension from the lake shore to the inland climax community.

The beech and maple, by shading the forest floor, create a habitat that is more favorable to their own offspring than to any of the colonizing candidates and in this way they are able to sustain their position of dominance. In all

the preceding stages (the entire sequence is called a *sere*, and each stage is a *seral stage*) the invading organisms alter the site in such a way that they eventually put themselves at a competitive disadvantage with respect to potential invaders. Thus, though the outcome is controlled by the climate of the region, the transition between seral stages is determined by events in previous stages. Of course the area around Lake Michigan is not one vast unbroken stand of beech and maple except for the transitional zone around the lake. But this can be explained. The process that has been described is *primary succession*, the successive colonization of a previously uncolonized site. But climax communities do not go undisturbed, nor does the succession of seral stages always proceed without a hitch. These eventualities give rise to the concept of *secondary succession*, meaning the return to the climax following intervention. Possible agents of disruption include fire, wind, frost, and other organisms, most notably that great intervenor, the human. In addition to the climax community, a given area is likely to contain communities that represent various stages in the process of secondary succession.

Only the barest bones of Clementsian-style early twentieth-century plant ecology has been presented. But even here, one sees a theoretical framework in which there is much for ecologists to do. The natural units must be discovered and their relations to climate investigated. The various seral stages that characterized each of the seres must be described and the mechanisms generating the transitions elucidated. But there were problems with the approach. For one thing, the natural kinds were not quite natural enough. A semantic jungle grew up as Clements and his followers attempted to supplant the conceptual scheme with subcategories and what not, so that they might squeeze an increasingly uncooperative natural world into their theoretical mold. Soon there were subclimaxes, disclimaxes, postclimaxes, preclimaxes, pseudoclimaxes, and my favorite, the anticlimax (see Krebs 1978; I have mentioned less than half of the categories he cites.) Another problem was that the tasks of description and classification were so absorbing that there was little time left to look for the underlying causal mechanisms that fueled the process. For all the touting of the physiological nature of the new discipline, there was surprisingly little physiological field experimentation conducted (McIntosh 1985). The organismic analogy may have been a fruitful heuristic in the initial search for patterns, but it offered little assistance in the effort to explain those patterns. When it came to the question of why, for example, the pine-dominated seral stage in the Lake Michigan dune sequence lasted only a few generations, the answers seemed to have a lot to do with the life histories of individual species involved, and little if anything to do with the plant formation as a superorganismic entity giving direction from above. As a result of these problems, some ecologists began to challenge the Clementsia system.

As previously mentioned, the seeds of individualism were already sown, i Cowles for example, and ultimately tracing back to Warming, before Clement began to develop his theoretical framework. But the relationship betwee Cowles and Clements is unclear. The first really clear statement of the in dividualistic alternative, and it comes as a direct response to the excess of the Clementsian approach, is in the work of H. A. Gleason (1926) and Russian ecologist named L. G. Ramensky (1924). I have focused on Gleaso He advanced the *individualistic hypothesis* – in essence, the thesis that pla communities do not come in natural kinds with distinct boundaries but a distributed in a continuous fashion, and that the distributions we find are th result of the individual species' life histories, the vagaries of initial condition and the interactions of plants with the physical environment and with the neighbors. To see what is at issue between the individualistic perspective an the "communities as superorganisms" approach, it is useful to look at a mo contemporary analysis of the situation; the analysis is supplied by Com ecologist Robert Whittaker (1975).

According to Whittaker, two issues are involved. One is the existence of th sharp, well-defined boundaries necessary for discrete community units, a the other is the existence of the close associations between species that wou be required if communities came in distinct kinds. According to the individu istic school, neither of these phenomena is very widespread in nature, where for Clements and his followers, the sharply delineated and tightly integrat community unit forms the backdrop against which community studies a carried out. Whittaker and other plant ecologists, most notably J. T. Curtis Wisconsin, set out to resolve the controversy beginning around 1950.

Whittaker presents the issues in more contemporary dress. One of t features he adds is an account of the mechanisms that would purported be responsible for the discrete boundaries and close associations. Inten competition, excluding one species or another, is the supposed mechanis that would generate the distinct boundaries between community types. T close associations between species in a community type would be the res of co-evolved adaptations for life in the presence of one another. Cleme did not have such an account, cast in terms of specific mechanisms, to prop the assumptions on which his community-unit theory rested. But the theo did have evolutionary underpinnings. One of the characteristics of early ec ogy was a widespread belief in the fine-tuning of higher level biological un (such as communities) by evolution. This belief was, by and large, an article faith because there was little articulation of how this was supposed to co

about. But the faith was strong and it played an important role in shaping the conceptual terrain of theoretical ecology. As with individual organisms, there was a homeostasis of communities, and the designer of the system in each case was evolution. This reliance on a background theory of evolution, undeveloped though it was, was perhaps the most important strand in the conceptual net sustaining the superorganismic view of biological communities. As we shall see, this perspective proved to be very tenacious. Gleason proposed his individualistic hypothesis in 1926, but he was viewed by the ecological community as something of a heretic; as he puts it, he was the "good man gone wrong" of ecology. The serious attempts at resolution that we are about to discuss did not come along for twenty-five years. Why were his views so neglected? It seems likely that the absence of a background theoretical framework comparable to the evolutionary foundations of the Clementsian view played a major role (see McIntosh 1995 for further discussion).

The efforts at resolving the controversy between these two views of community organization focused on the way species were distributed along an environmental gradient (for example, variation in soil moisture). If the community-unit theory is right about the discrete boundaries, then there should be points along the gradient where there is rapid species replacement, and these should be interspersed with longer stretches in which there is little change in species composition. Furthermore, co-evolved members of a community type should have similar patterns of distribution. The consensus that has emerged from observations of species distributions is that in large measure, Gleason was right. Species are distributed individualistically and communities tend to intergrade continuously into one another. There are cases of close distributional association between species and there are cases where there is a sharp discontinuity between communities, but these are special cases that call for special explanations. Furthermore, although it remains useful to classify communities on the basis of certain properties, the nature of the classification has changed. For those who follow Gleason, classification is not a process of describing natural categories; rather, it involves the imposition of conceptual categories, judged primarily by their utility, on a reality of individual populations.

The experimental ecologists discussed in Section 2.3.1 tended to look toward the "response physiology" of the individual *animal*, but the project was, by and large, the accumulation of descriptive information. As pointed out, they lacked a theoretical framework. The work of Clements was essentially a response to the accumulation of descriptive information as well, but the plant ecologists of the day tended to accumulate information on patterns of spatial distribution and the ways in which populations of plants tended to cluster

together into characteristic communities. While the Clementsian theoretic
framework has been largely superseded, the descriptive focus on spatial p
tern has remained. The theoretical structure of Clements has been replaced
a different kind of kind of theoretical structure – the mathematics of statistic
and multivariate analysis. But the goal remains essentially unchanged: W
are the patterns in vegetation? In contrast to animal ecology, plant ecolo
has been infused throughout its development with the conviction that the k
to uncovering underlying mechanisms and processes is first to describe t
distributional patterns that vegetation exhibits.

2.3.3 Charles Elton

As noted, ecology has diffuse beginnings. Although the science did not arise
the minds of a few great thinkers, Charles Elton was perhaps the first ecolog
to supply a conceptual framework that in many ways is still the foundati
for several contemporary ecological traditions. This section departs from t
pattern of the previous sections by concentrating on the work of a sing
individual. It outlines Elton's most significant contributions and in so doi
introduces themes that will become the focus of later sections as we unra
the approaches that have come to characterize contemporary ecology.

In 1927 Elton was "commissioned" by his teacher, Julian Huxley, to wr
a book on animal ecology. In eighty-five days he wrote *Animal Ecology*, an
fluential book that Hutchinson has called one of the greatest biological boo
of the century (see Cox 1979 for details). The significance of this work li
not so much in the novelty of the ideas – as Elton himself points out, eco
ogists had for some time been zeroing in on the principles he enunciates
but in the way they are put together to create a verbal model of the biologi
community. The book offered a conceptual framework that differed fro
the then-dominant Clementsian tradition in the following two ways. First
downplayed the descriptive, species-list approach to communities that h
been so predominant among plant ecologists, offering instead a new set
categories in terms of which communities could be viewed. Second, it su
gested a new way to look at community dynamics. Rather than looking f
the causes of community change in an overarching developmental bluepri
Elton focused attention on the relationships among the populations that ma
up the community, and in particular, on the ways these relationships determ
the sizes of populations.

As we have seen, in the early decades of this century, ecology was f
cused in large measure on physiological limiting factors. This was partic
larly true of animal ecology. There had been efforts to incorporate the data

experimental physiology into the succession/climax framework of the plant
ecologists (e.g., Shelford 1911, and to a lesser degree Adams 1915); however,
they were never to take hold. Elton focused on limiting factors as well. But
he saw the major category of limiting factors not as a set of physiological
constraints, such as tolerance of salinity, pH, and the like, but as a matter
of the "sociology and economics of animals." He recognized, of course, the
role of the physical environment in the lives of organisms, but he was interested in the behavior of populations, initially for the economic implications
of such behavior. On the Clementsian approach, the behavior of populations
is ultimately grounded in physiological response to climate. This might work
for plants, but for Elton, population size in organisms depends significantly
on what he calls "the interrelations between organisms." In his view, animal
ecology was in need of a theoretical framework with which to explore this
important and exceedingly complex phenomenon.

Elton introduces his verbal model of the community as an effort to fill this
void. It is based on four principles, one of which is the *principle of the niche*.
The term *niche* had been used earlier by Grinnell (1917) to refer to the kinds
of environments (in a broad sense) in which an organism could live. He saw
a close correlation (if not an identity) between a species' niche and the set of
environments in which it was actually living. Elton did not use the term in this
way; he thought of niches as being analogous to the professions of a human
society. The species' niche was a function of its relations with other species
in the community. The idea is abstract in the sense that radically different
kinds of organisms (in the taxonomic sense) could inhabit the same niche.
Hummingbirds and bees, for example, to the extent that they are both related
to plants as consumers of nectar and dispersers of pollen, occupy the same
niche.

The principle of the niche can also be used to examine what Elton calls
"community structure," but the structural rules are not like the developmental
constraints of the Clementsian program. For Elton, community structure is a
matter of the ways in which the interactions of the various kinds of organisms
in the community are organized. A simple example, though Elton (1927)
did not give it the status of a principle, is the way in which communities
are organized into patterns of nocturnal and diurnal activity – the different
species of the community can be grouped in terms of the period during the
day/night cycle in which they are active. In the same way, animals can be
grouped in terms of the kinds of interactions they have with other organisms.
Elton had at least two distinct kinds of virtue in mind for this sort of abstract
characterization of community structure; both can be illustrated by recalling
the important concept of limitation.

In addition to recognizing the limiting factors of the experimental phy iologist, Elton extended the notion to include factors that limit membersh in the animal community. The soundness of this move is testified to by th following passage from a contemporary treatment of community ecology:

> It may turn out that there is no unifying theme among the community properties suggested as evidence of structure. However, it seems worth trying to find a unifying theme and the best candidate seems to us to be Elton's (1927) phrase "limited membership": Why is it that what *does* occur together constitutes a limited subset of what *might* occur together? (Roughgarden and Diamond 1986: 335)

If community structure is what limits community membership, then the principle of the niche can give us some understanding of it. Elton argues a follows: "It seems probable that, since the number of niches that exist at a for vegetarian animals in a community is limited, we have a glimpse of wh the number of species is rather limited" (Elton 1933: 28). As we will se in Chapter Four, the idea that available niches limit community membershi was to be a central theme of later ecologists.

As the previous quote illustrates, Elton was preoccupied with the foo niches of animals. His second principle, *the principle of food size*, is a generalization about such food niches. Animals (aside from parasites) typicall feed on prey of a particular size range, usually much smaller than themselve This leads in the following way to the third principle, the principle of foo chains and the food cycle.

> This sort of relation between the sizes of predators and the animals they prey upon is very important in splitting up the animal community into food-niches. The limitations placed by size of food on feeding together with other special food preferences give rise to *food-chains*, leading usually from smaller to larger forms, and starting of course from some herbivorous or scavenging form, which in turn depends directly or indirectly on plants. (Elton 1933: 29)

In other words, the feeding niches of animals are organized into sequences i which one organism is eaten by another, which is in turn eaten by a third, an so on. Among animals, these chains are ultimately grounded in organism that make their living by consuming plants, and as Elton indicates, the siz relations between predator and prey typically issue in chains that procee from smaller to larger organisms. (This idea was anticipated by Semper wi his 10 percent rule.)

It is less clear what Elton had in mind when he talked about food cycle When he first introduced the idea in his 1927 book, he provided two exampl

of food cycles (Elton 1927: 58), but the examples differ from food chains only in complexity. That is, they portend to be fairly complete mappings of the various food relationships of some particular community – a kind of exhaustive description of the trophic structure. The resulting weblike structures are more reminiscent of the food webs that later replaced food chains in the classification of trophic relations. But there is an alternative interpretation, one in which food cycles are not simply complicated patterns of food chains. According to McIntosh:

> *Food cycle* improved on *food chain* in providing the essence of what was to be called the biogeochemical cycle because it integrated the organic food chains with the nonliving environment, an essential attribute of much early ecological thought that was later christened the "ecosystem" (Tansley 1935). (McIntosh 1985: 91)

There is some evidence for McIntosh's interpretation, especially in Elton's discussion of the fourth principle, to which we now turn. We have seen that as one travels up the food chain, the animals typically get larger. There are several factors that, in conjunction with this tendency, act to set upper bounds on the length of food chains. First, there are physical limitations on body size. More important, a limit is placed on population size of higher level predators by the occurrence of a reduction in what Elton calls "the original plant produced living matter" available to each successive link in the chain. The result is the widely recognized phenomenon that Elton dubs the principle of the pyramid of numbers – organisms get less numerous as one proceeds up the trophic ladder, resulting in a kind of pyramid shape when each trophic level is represented in terms of numerical abundance. This pyramid of numbers was to become the pyramid of biomass, once the biogeochemical perspective was explicitly incorporated into ecology. Whether in terms of numbers or biomass, the pyramid is, in Elton's view, a pervasive aspect of community structure; it provides another glimpse of a reason behind limited community membership.

These four principles, then, form the core of Elton's theory of the community. He concludes, "As a result of these principles we find that the organization or structure of an animal community is not widely different in almost any habitat which supports a rich fauna at all" (Elton 1933: 32). It is for these ideas that Elton is most widely known; as we will see, they provide grist for the mills of many subsequent ecologists. Ironically, however, the most influential aspect of Elton's thought may not lie here at all. His focus on the organization of biotic relationships within the community is primarily in service of another end; the end he takes to be the most significant and least understood aspect of animal ecology – the population problem.

In its broadest sense, the population problem involves understanding the hows and whys of animal numbers. Elton distinguishes two aspects to the problem: "The statistics are what we find out about animal populations at any one moment. The dynamics introduce movements in time" (Elton 1933: 48). The snapshot view of populations that Elton labels "statistics" is essentially the spatial distribution approach to ecology discussed at the end of the pre- vious section; we will not spend time on it here. The focus on population dynamics, however, is Elton's contribution to a then-emerging tradition that was to become a central theme of ecology. We look at this tradition in the next section, but before doing so, we highlight some of Elton's contributions.

Elton begins his discussion of population dynamics by noting an importan generalization about animal populations. Contrary to the historically popu- lar "balance of nature" view, it must be recognized that animal populations "fluctuate greatly in numbers." The simplest hypothesis is that the caus of these fluctuations lies in the variability of environmental factors such a climate. While this is no doubt a significant factor, it will not do in general be cause there are two other important generalizations that must be recognized. The first is that there is a close interdependence among animal populations. Ecologists, then and now, distinguish two kinds of investigations – *autecolog* and *synecology*. Roughly, the distinction is that the former studies species on at a time and the latter studies species as groups of interacting populations. For Elton, "it is clear that the study of the autecology of the numbers of an species involves inevitably a study of the synecology of the community i which it lives" (Elton 1933: 69). What was clear for Elton has been less tha clear for many subsequent ecologists; the relative merits of autecological an synecological approaches to ecology remain a matter of controversy to thi day, and we will have more to say about the issue later in this chapter an also in the next.

The other important generalization to be reckoned with – and for Elto the element of truth in the balance of nature perspective – is that anim populations are regulated by "automatic control" mechanisms. The relati constancy of species compositions in a community, even though the indivi ual species' populations are fluctuating in size, can be accounted for by th fluctuations' being bounded by these regulating factors. Elton uses the alrea familiar distinction between density-dependent and density-independent fa tors (first discussed by Howard and Fisk 1911) to make the point. In contra to density-independent influences, which exert their effect regardless of po ulation size, density-dependent factors act as a function of population siz In large part, the density-dependent regulating mechanisms involve relatio with other organisms, especially trophic relations. For example, increas

population size might result in a shortage of food or increased levels of predation. Elton also saw behavior as an important density-dependent regulating mechanism. Thus, increased migration rates might be a density-dependent population response to overcrowding in a particular habitat. The upshot is that the existence of these regulating factors provides, for Elton, another reason for thinking that a solution to the population problem presupposes an adequate theoretical framework for dealing with the interrelations of organisms.

This need to do community ecology, even if one's interest is ultimately in the behavior of populations, places Elton among the sources of an important conceptual tradition in ecology. The significance of this early work lies in Elton's emphasis on the importance of synecology and to the way he used his community principles – all of which were already in the literature – to fashion a rudimentary theory of the community. We move next to an area in which Elton's contributions to ecology were something of a novelty.

He begins the last chapter of his 1927 book somewhat apologetically, pointing out that "it may at first sight seem out of place to devote one chapter of a book on ecology to the subject of evolution" (Elton 1927: 179). Indeed, it must have seemed a significant departure when other ecology texts of the day did not even include "evolution" and "natural selection" in their indices (see Chapman 1931 for a typical example and Kingsland 1985: 220, note 11, for further discussion). Elton's views on the relationship between ecology and evolution (in the period under consideration) can only be outlined here. The central argument in the above-mentioned chapter can be paraphrased as follows:

1. Natural selection, though of doubtless importance in the evolution of characters, cannot be used to explain many of the (adaptively insignificant) differences in polymorphic organisms and closely allied species.
2. An alternative explanation is available once it is recognized that the forces responsible for the struggle for existence are the limiting factors studied by the population ecologist, and that in many cases (e.g., rapidly expanding populations) these limiting factors are not exerting their influence.
3. In such cases, nonadaptive characters can spread with impunity (until the checks on population growth – the selection pressures – once again become important).
4. Whether this particular argument works or not, it indicates the general way in which the ecological study of population dynamics is relevant to the study of evolution.

For a number of reasons, then, evolutionary biologists ignore population ecology at their peril.

What about the other direction? Does the study of evolution (especially via the mechanism of selection) have implications for ecology? On this score Elton's views are much more difficult to unravel. At one point he says that the study of special adaptations – for "attack and defense," for example – "form a subject of their own" (Elton 1933: 32). Yet he also points to the need to understand the behavioral adaptations related to competition for mates and the advantages of social organization if one is to have an adequate theory of the organization of the community. It is hard to make a final pronouncement here. Perhaps the best one can say is that Elton dimly perceived but did not exploit the significance of evolution for ecology. We will get to this exploitation later in the chapter. The most important point here, however, is that Elton was one of the first ecologists to recognize explicitly and to put to work the connection between the factors that regulate population size and the circumstances responsible for natural selection.

Elton was truly a man at the crossroads. We have seen his role in the development of "macro-community" theory (with food chains, the pyramid of numbers, etc.); we have seen him as one of the first to recognize the importance of demographic studies and to advocate a synecological approach to the study of animal numbers; we have seen him as one of the pioneers in pointing out the connections between ecology and evolution. Yet he stands as a central figure in the emergence of still another tradition.

Recall McIntosh's suggestion that Elton's food cycles were more than complicated food chains. The something more is supposed to come from the fact that the food cycles integrate the organic and inorganic worlds. When Elton talks about quantities of "living matter," this does seem to suggest thinking of the organic and inorganic as parts of a single system. Just how far Elton pushed these ideas is a matter of controversy. What is important is that in the 1940s a Minnesota limnologist named Raymond Lindemann took Elton's ideas on trophic structure, Tansley's idea of an ecosystem as an integrated unit with biotic and abiotic parts, and his inherited limnological preoccupation with the gross physical features of lakes (which are relatively handy self-contained systems), and executed, virtually single-handedly, a conceptual revolution in ecology. Lindemann's "trophic-dynamic" ecology focused on the flow of energy (in the form of calories) and materials (typically nutrients such as nitrogen and phosphorus) through the lake ecosystem. What is perhaps most revolutionary about this perspective is that it treats the organism as a kind of "black box" transducer of energy and/or nutrients[2], rather than in terms of the more traditional ecological categories, which tend to have their origin in the relationship to life history features of the organism. Thus, a distinction can be made between organism ecology and ecosystem ecology, with the idea being roughly that the former is concerned with organisms *qua* biological entities and the latter with organisms *qua* energy and/or nutrient transforming nodes in a physical system. We look at the emergence of this ecosystem tradition a bit later in the chapter, after examining the other three traditions – population dynamics, community ecology, and evolutionary ecology – to which Elton made seminal contributions.

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[2] More will be said about this idea in section 2.3.6.

2.3.4 *Population Dynamics and Community Ecology*

In the early 1920s ecology was advancing in two fairly distinct areas (Allee et al. 1949, Kingsland 1985). On the one hand, the study of the behavioral, morphological, and physiological properties of organisms from an experimental perspective was accumulating vast catalogues of information. Simultaneously, the study of the distribution and development of biological communities as natural units was generating an ever more cumbersome theoretical apparatus. The former area was dominated largely by animal ecologists, whereas the community approach was, as we have seen, characteristic of plant ecology at the time. But ecologists were becoming increasingly aware that the distinction between the ecology of plants and the ecology of animals was in many ways artificial. The importance of plant/animal interactions is an old insight in ecology, tracing back at least to Darwin. The emergence of an interest in the behavior of populations traces, in part, to the desire to find a middle ground in which the study of organismic function and community dynamics could be related. However, there were other factors that played a role in the development of population ecology.

As previously suggested, the study of the interaction between organism and environment was proceeding at a rapid pace during this period; however, there was little conceptual structure in which to imbed the various bits and pieces of information that were being accumulated. To be sure, many of the investigators talked the language of adaptation, and from our contemporary vantage point, it is tempting to view their efforts as working out the details of particular examples of natural selection. But that would be a mistake in a great many cases. The focus of this era in ecology tended to be on what the properties of an organism were, rather than on *why* they were this way and not that – on proximate rather than ultimate causes.

Evolutionary theory was not in a position to function as a fruitful theoretical framework within which to organize the accumulating mass of experimental data. We have already seen that as late as 1927, Elton felt the need to offer a special justification for concluding his book on animal ecology with a chapter on evolution. We also noted that the first great wave of texts on animal ecology in the late 1920s and early 1930s were conspicuously silent on the subjects of evolution and natural selection. As a final piece of evidence, consider the comments of one of the most influential ecologists of the "experimental physiology" era:

> There are two distinct points of view for biological investigation. One is that of *evolution*; the other, that of *physiology*, or the explanation of the organism in terms of physics and chemistry. . . . In this paper we are concerned with the *physiological relations of animals to natural environments*. (Shelford 1911: 554)

While these experimental physiologists were not directly asking evolutionary questions, evolutionary theory did eventually supply, at least indirectly, a fruitful conceptual framework for animal ecologists – one that had shown itself much earlier in the plant ecology tradition. By the third decade of the century, ecologists were looking with increasing frequency at a certain kind of environmental factor; they were looking at what Semper had called much earlier the "conditions of existence." As Victor Shelford (1918: 21) put it, these factors "are of importance only in so far as they affect the life and death processes of organisms." From a focus on life and death processes, it is a short step to changes in number. Furthermore, the dynamics of populations, at least potentially, brings a certain unity to the otherwise piecemeal investigations of organism/environment interactions. The responses of organisms to environmental factors become important not just from the point of view of understanding the organism but from the point of view of understanding what determines the abundance of the organism. And the latter was important, frequently for economic reasons but also because, as frustrations with the holistic community perspective mounted, the structure of communities began to be seen more and more as a function of the behavior of individual populations.

Additional reasons have been given for the emergence of population ecology. For example, Kingsland (1985) mentions a focus on populations as a way for animal ecologists to assert their autonomy from the community-oriented plant ecology that dominated the ecological scene. In addition, economic ecology has a long history of emphasis on population studies that had a major impact on the emergence of theoretical population ecology (Kingsland 1985, McIntosh 1985, Allee et al. 1949). I will not discuss inputs from these sources, but there is one additional factor that shaped developments in this emerging branch of ecology – namely, the development of mathematical models to represent population processes. It is to this story that we now turn (I present the barest of outlines; for an excellent historical account see Kingsland 1985, and for the models themselves see any introductory ecology text).

In the second decade of this century, and largely at the hands of Raymond Pearl (see, for example, Pearl and Reed 1920), ecology had rediscovered the logistic equation for population growth originally formulated by Verhulst. The equation yields the familiar sigmoid growth curve, with population growth tapering off as population size approaches the carrying capacity of the environment. In the mid-1920s, two non-ecologists (Lotka 1925, Volterra 1926) simultaneously and independently introduced mathematical models extending this modeling strategy to the important ecological interactions of competition and predation. Before long these models came to be seen as the basis for a theoretical framework that could, at last, give some order to the welter of unstructured observational and experimental results that animal ecologists had been accumulating.

In the early 1930s, a Russian ecologist named G. F. Gause undertook a series of laboratory experiments designed to test the logistic model of population growth and its extension to interspecific competition (he also investigated the Lotka-Volterra predator-prey models, but this will not be discussed). By associating the level of toxic wastes (ethyl alcohol) in a growing yeast population with the carrying capacity of the logistic, he was able to create a situation in which all the parameters of the logistic could be measured. Furthermore, by measuring the alcohol-producing capacities of two kinds of yeast, he was able to translate the effects of an individual of one yeast population into the terms of individuals of a second population. Thus, by using the production of ethyl alcohol as the common currency, he was able to assign values to competition coefficients, thereby creating an experimental setup for testing the Lotka-Volterra competition model. The evaluation of Gause's experiments is not a clear-cut matter. In ecology texts the results of these classic experiments are typically represented as achieving a "reasonably good fit" with the predictions of the model. But both the significance of the experiment (Hutchinson 1978) and the underlying details of the experimental setup (Salt 1984) have been criticized. For present concerns, however, it is not the success or failure that is significant. Rather, it is the nature of the experiments and the conclusions that Gause went on to draw.

If Gause's experiments did not issue in resounding success for the logistic-based competition model, they at least revealed what it is like to test the model. In particular, extracting predictions from the model means finding something about organisms or their environment, something that can be measured, to associate with the various parameters of the model. Furthermore, if the test is to have credibility, there must be reasons for thinking that the

associations are appropriate. For example, in Gause's case there were
dependent reasons – an account of the inhibitory effects of alcohol on yea
reproduction (Richards 1928) – for associating alcohol levels with populati
inhibition. When one reflects on the kind of detailed information required
the goings on in Gause's yeast cultures, the paucity of tests involving natu
populations comes as no surprise. When it comes to the complexities of na
ural situations, theoretical models like the Lotka-Volterra competition mod
seem to play a somewhat different conceptual role.

In a sense, the yeast experiments and subsequent experiments with pro
zoans were for Gause an attempt to establish whether the competition mod
at hand was a good way to think about population behavior. There was alrea
an initial plausibility to the model, perhaps deriving in large measure fro
the analogy with physical systems from which the mathematical structu
was obtained. If it could be shown to hold approximately in a few partic
lar cases, even if they involved simple organisms in artificial situations, th
one would be justified in using this tool to address broader concerns, such
the nature of the forces structuring biological communities. The concept
role of theoretical models is taken up in detail in later chapters; for now I ha
simply focused on the significance that Gause attached to his experimen
investigations.

Gause drew two conclusions that are of particular significance for t
present study. First, he linked the model to the concept of the ecologi
niche, drawing his famous (though by no means original) conclusion that n
species occupying the same niche cannot coexist. As he put it,

> It seems as that the central ecological problem of regulation in the composition
> of complex biotic communities is in these analytical investigations reduced
> to simplest terms. In light of all this evidence [essentially the mathematical
> analysis and the laboratory experiments] one may claim that if two or more
> nearly related species live in the field in a stable association, these species
> certainly possess different ecological niches. (Gause 1939: 255)

Gause's second conclusion concerned the relationship between ecology a
evolution. He regarded the Lotka-Volterra models as a way to quantify on
ecological scale the struggle for existence that drives Darwinian selection.
we will see, both of these conclusions – the principle of competitive exclus
and the idea that the factors determining the fates of populations are the sa
forces that are responsible for Darwinian selection – were to have a signific
impact on the course of ecology.

The population studies that flourished following the development of
abstract mathematical framework for thinking about population phenom

have been characterized as the "Golden Age" of theoretical ecology (Scudo
and Ziegler 1978). This framework gave ecologists a way to present the
dynamics of populations as sensitive to population densities – both intraspe-
cific and interspecific. Thus it brought the idea of population regulation, long
an element of the background picture in ecology, into the forefront of ecologi-
cal consciousness. The principle of competitive exclusion, and the associated
idea of the niche as the key to community structure, also had a profound
effect on the development of animal ecology. It focused ecologists' atten-
tion on the competitive relationships that govern the ways organisms carve
up the resources available in a locality. Together with the theoretical mod-
els of predator-prey relationships, ecologists could begin to unravel how the
interactions among organisms give shape to ecological communities; they
now had the tools to begin executing the Eltonian program of determining the
ground rules for community structure. Some of the manifestations of this pro-
gram will be described in Chapter Four. For now, I simply want to emphasize
that one of the central consequences of these developments was an ecology
that placed considerable emphasis on population regulation, density depen-
dence, biotic interactions, and in a general sense, on the idea of a balance of
nature.

With the publication of *The Distribution and Abundance of Animals* in
1954, H. G. Andrewartha and L. C. Birch presented a systematic alternative
to the conceptual framework that ecology, in its "Golden Age," had devel-
oped for thinking about population and community structure. In the process,
they also attempted, for all practical purposes, to put community ecology
out of business. At bottom, the complaint of Andrewartha and Birch embod-
ies an old empirical challenge. It represents the same response to perceived
overzealousness on the part of theoreticians that we saw earlier in the case of
Gleason. The difference is mainly in the target: for Gleason, the issue was the
Clementsian account of spatial distributional patterns; in the present case, it
is the mathematical representation of temporal dynamics, and specifically the
preoccupation with synecology and density dependence. To see the nature of
this challenge, we must return to the idea of population regulation. A second
major work of 1954, *The Natural Regulation of Animal Numbers*, published
by David Lack, illustrates the population regulation perspective.

Lack begins with a simple observation: "Most wild animals fluctuate
irregularly in numbers between limits that are extremely restricted compared
with what their rates of increase would allow" (Lack 1954: 1). He calls this
the population problem; in its barest terms, it resolves into the following
question: How is it that such a balance between replacements and losses is
achieved? Lack found his answer in the density-dependent population models

of A. J. Nicholson (Nicholson 1933, Nicholson and Bailey 1935). The central idea is that stability of numbers suggests regulation, and regulation implies sensitivity to population densities. That is, populations must be subject to determining factors that are functionally dependent on population levels. Andrewartha and Birch had a different view of this argument. The reasoning, as they reconstruct it, is as follows:

> In a favorable "environment," numbers would go on increasing without limit (until they "filled the universe") unless they were prevented from doing this by some density-dependent factor. Alternatively, in an unfavorable "environment," numbers would go on decreasing indefinitely until the population became extinct unless the "environment" were ameliorated by a "density-dependent factor." When stated in this way, the fallacy of this view is apparent. In nature the conditions of life do not remain continuously favorable or continuously unfavorable. Circumstances are perpetually changing. (Andrewartha and Birch 1954: 21)

This passage is instructive for at least two reasons. First, it reveals a theme played out again and again in the subsequent history of this controversy, namely, missing the point of the opponent's argument. The observation underlying the population regulation view is not simply that populations have upper and lower bounds, but that they seem to be bounded in such a way that numbers remain relatively constant from year to year. In the absence of further argument, this fact is not explained by simply pointing out that in nature, the conditions of life are always changing. To answer the argument, Andrewartha and Birch must either repudiate this observation or explain it in the terms of their own theory.

This leads to the second way in which this passage is important; it expresses the cornerstone of the authors' theory in the idea that population phenomena are essentially responses to fluctuations in the conditions of life. These conditions include other organisms, but the other components of the environment – food, weather, and shelter – are given a major role in determining population behavior. For Andrewartha and Birch, populations are structured primarily by *autecological* factors rather than *synecological* factors. The patchiness, in both space and time, of autecologically favorable conditions is what limits population growth and ultimately, what produces the various types of population behavior we find in nature.

Much more could be said about the details of Andrewartha and Birch's approach, but with this brief overview we can see that a major part of their objection to theories that rely heavily on density-dependent processes such as competition is based on a different conception of the nature of the causes that underlie population level regularities. Thus it comes as no surprise that they find the basic Lotka-Volterra competition model "so unreal as to hold practically no interest for a biologist" (Andrewartha and Birch 1954: 411). Their evaluation of the model makes reference to specific considerations, such as its being based on the logistic equations that they also find unrealistic and concerns that the competition coefficients of the model are not likely to be constant in nature; but the real issue is that they do not see competition as an especially useful category when it comes to sorting out the forces that drive demographic change.

The Gausian program suggests – even demands – a kind of reductionist approach to community ecology. Community structure emerges out of the behaviors of the component populations, and – in principle at any rate – the population interactions can be represented with competition models, predator-prey models, and the like. But what if the interactions among populations are only weakly responsible for community structure? What if the fates of populations of one kind of organism depend very little on the fates of populations of the other kinds of organisms that might be about? One could still do community ecology in the sense that one could pick out geographical areas and do the population ecology of the species one found there; but that is all one would be doing – the ecology of this particular set of populations. Theoretical community ecology would seem to be out of business in such a world because there would be no phenomena to theorize about. It is in this sense that Andrewartha and Birch's challenge to the density-dependent population regulation tradition is, at bottom, a challenge to the entire program of a population-based answer to the Eltonian question, "What limits community membership?"

2.3.5 *Ecology and Evolution*

We have already seen that among the earliest antecedents of ecology – for example, among plant ecologists such as Semper and Warming – the connection with evolution was quite strong, even if not self-consciously so. As ecology began to take on more of the character of experimental field physiology, this link began to weaken; the investigations tended to be directed at proximate questions about organism/environment interaction. This was not the situation for long however, at least not for plant ecology. The introduction of the Clementsian paradigm brought with it an explicit evolutionary orientation. As Lewontin points out, the Clementsian view "is nothing if not an evolutionary theory of the community" (Lewontin 1969: 13). Evolutionary it was; but it was not very Darwinian. Clements was deeply committed to Lamarkianism, believing that individual plants adapted directly to the environment, and even that the environment could induce speciation in just a few generations (Hagen 1992).

Clements's evolutionary views were not something he took lightly. He conducted transplant experiments that he believed, demonstrated the Lamarkian influence, and he took a great deal of criticism late in his career for his evolutionary views – criticism that he weathered, characteristically, with an unbending resolve. Clements was perhaps atypical in this respect. Much of early ecology was related in a rather loose way to evolutionary views. For example, ecologists even into the 1960s tended to be rather profligate about levels of selection. Whereas Darwin clearly thought long and hard about whether natural selection occurs above the level of the individual organism, ecologists tended to be rather cavalier about invoking the good of the species, and even the community, in their evolutionary reasoning. Even Lamont Cole, who did as much as anyone to galvanize the connection between ecology and evolution, expressed confidence in these higher levels of selection (Cole 1957). The matter came to a head in 1962 with the publication of Wynne-Edwards's book on dispersion and social behavior. The blatantly group selectionist character of the account, together with the existence of a recently emerged self-conscious tradition of evolutionary ecology (to be described shortly), resulted in a serious stock taking (Williams 1966) and ultimately in a much tighter relationship between ecology and evolution. And where did this new evolutionary ecology come from? It is to this story that we now turn.

As mentioned above, when Elton wrote his 1927 book on animal ecology, he felt the need to apologize for including a chapter on evolution. It did not take long for matters to change significantly. Within a decade or so, Elton's central argument of that evolutionary chapter had itself been incorporated into theoretical population ecology and was one of the central connections being pursued. Recall that Elton had argued for a restriction in the scope of selectionist accounts. In his view, natural selection is at work shaping the traits of organisms only when populations are straining against the carrying capacity of the environment. When this is not the case – and for Elton, with his preoccupation with population cycles, it frequently is not – then nonadaptive traits can "spread with impunity" through the population. The upshot, as was pointed out in section 2.3.3, is that an ecological understanding of population dynamics is essential to unraveling the evolution of traits. A very similar view emerged from the population models of an Australian ecologist named A. J.Nicholson.

Nicholson's primary focus was on the idea of population regulation; however, he also had a long-standing interest in the problem of adaptation. His position (see, for example, Nicholson 1933, 1954, 1960, and Nicholson and

Bailey, 1935) is roughly as follows. To begin with, he took as "axiomatic" (as did Lack) that populations must be regulated by density-dependent factors; he saw this as the only possible explanation for the stability of natural populations. Nicholson made another fundamental assumption: the regulation of population size is accomplished by competition among the members of the population. Obviously, competition would increase in severity as the population became more and more crowded; thus it would act in just the way that a density-dependent regulating factor should, exerting its strongest influence at high densities and relaxing as density decreased. But if competition was the direct cause of population regulation, it was not itself a direct cause of mortality. Nicholson saw population regulation as a matter of inhospitable environments impinging on a population when density-induced competition crowds some of the members into these less hospitable portions of the environment. Thus the environment – physical factors and trophic relationships – acts only indirectly, when competition forces organisms under its sway. Though the environment acts only indirectly in the regulation of population size, it is directly responsible for natural selection; after all, this is where the mortality is. When competition becomes strong enough, it forces organisms under the eyes of natural selection, and here is where the significant (for the species) adaptations take place. Organisms also evolve in response to the competition with one another to remain invisible to the selection forces (the environment), but Nicholson viewed this as less significant – a kind of fine tuning; in a later work (Nicholson 1960: 507) he referred to this fine-tuning as "hyperadaptation" and defined it as "biological improvement [as a result of natural selection] beyond that necessary for the maintenance of the stability of a species in its existing environment."

Nicholson's position on the interaction between population regulation and natural selection is somewhat idiosyncratic and was not well received (Kimler 1986). It led him to the view that paradigm "adaptations" such as mimicry were, in fact, not significant adaptations at all but cases of the fine-tuning just mentioned. However, I will not spend more time unraveling Nicholson's views. What is of significance here is that he exemplifies the Eltonian idea that one cannot understand natural selection without knowing something about the ecology of populations. On the face of it, there is an even stronger similarity with Elton. Recall that Elton had urged the efficacy of selection only during the crunches associated with high population density, for it is only then that the species could really be said to *struggle* for existence. Nicholson likewise used population dynamical considerations to restrict the scope of natural selection – in his case, he decoupled the force (primarily intraspecific competition) responsible for population regulation and balance from the selection forces that produced the traits enabling populations to successfully exploit their environments.

Both Elton and Nicholson are in a sense exploiting Gause's idea that in modeling the dynamics of populations one is modeling the struggle for existence on which Darwin based his notion of natural selection (though Elton obviously did not have Gause's work in mind). However, the reasoning involved falls somewhat short of actual theoretical integration. To begin with, the inferences run in only one direction – from ecological considerations to evolutionary ones. More important, the arguments express only a negative relationship between ecology and evolution, a limitation on the phenomena that ought to be regarded as falling under the domain of the theory of natural selection. For a positive exploitation of Gause's connection we must turn to David Lack.

Lack's book on the regulation of natural populations combined an interest in the "population problem" (i.e., the nature of the factors that regulate population size) with a long-standing interest in the evolutionary significance of the traits of organisms. His views on population dynamics were very much influenced by Nicholson through a close association with G. C. Varley, who had been one of the first to investigate Nicholson's population models experimentally (cf. Kingsland 1985). Lack agreed with Nicholson that populations must obviously be regulated by density-dependent factors, but he was never overly enthusiastic about the efforts of the mathematical model builders. In a discussion of the logistic model he comments, "The Pearl-Verhulst logistic curve was valuable in introducing precision in a new field of biology, and its use has greatly stimulated further research on populations. But undue veneration has sometimes been paid to it and it does not, of course, 'explain' population growth" (Lack 1954: 17). What kind of approach is needed? He says, "A simple and unifying theme is . . . needed in population research. The approach attempted in this book is factual and analytical, not abstract or mathematical, the facts being organized round the biological concepts of competition, natural selection, and the interaction of predators and parasites with their prey. For this reason, the best introduction to the subject is still that given in Chapter 3 of *The Origin of Species*" (Lack 1954: 4).

In short, understanding ecological phenomena for Lack means incorporating them into the framework of Darwinian evolutionary theory. In explaining the nature of his project, he trots out the familiar distinction between proximate and ultimate causes discussed in the previous section, indicating that his interest is primarily in the latter. His contribution to the task in the 1954 volume concerned the determination, by natural selection,

of clutch size in birds. He argued, largely on empirical grounds, that clutch size was regulated by selection so as to maximize the number of offspring successfully raised to independence. The details of his argument must be passed over in favor of attending to its significance. Here I want to emphasize two points (Lack 1954: 5). First, if the reproductive rate (clutch size) of the species is set by natural selection (and this is individual-level Darwinian selection), then it is not, as had been supposed, adjusted to the mortality rate of the species. If populations are regulated, then it is not accomplished by a species-level adjustment of reproduction and mortality. In fact, and this is the second important point, the population regulation must be accomplished by density-dependent mortality factors.

The first point is significant because it exemplifies the treatment of an important population parameter from an evolutionary perspective and thus is an example of the kind of unification that Lack was urging. It challenged the established tradition of theoretical population ecology to think about ecological phenomena in evolutionary terms – to exploit Gause's theoretical connection between the determinants of population dynamics and the conditions that underwrite the Darwinian struggle for existence, rather than retreat to the "good of the species" perspective that had so typified the evolutionary thoughts of ecologists. The second point, the commitment to density-dependent population regulation, is significant because it entangled Lack in the then-raging debate over the reality of density-dependent population regulation discussed in the previous section.

Before turning to the consequences of Lack's challenge to theoretical population ecology, we should briefly explore the implications of this second point – the entanglement in the density-dependence debate. From Darwin forward there has been a strong association between natural selection and the following two intuitions. First, there is a kind of balance to nature: populations and communities are stable sorts of things, and to be stable they must be regulated by various factors that act to keep them in roughly the same configuration. Second, the factors that achieve this kind of orderly behavior are mostly complex clusters of interrelationships among organisms (Darwin's "entangled bank"). This is just the kind of evolutionary conception Lack is pushing. As we saw in the last section, Andrewartha and Birch deny both of these Darwinian intuitions. Thus, the density-dependence debate, in essence, spills over into the question of the relationship between ecology and evolution. Lack is now at odds with Andrewartha and Birch not just over density dependence but over the evolutionary character of population and community ecology as well. This is, in fact, just how Gordon Orians diagnoses the situation. In a review of these matters, Orians makes the following claim: "The rejection of community ecology by Andrewartha and Birch is the corollary of a still more basic position, namely, that evolutionary concepts have no place in ecological theory" (Orians 1962: 258). I think Orians is correct to make the connection, but I believe he has the order of dependence just backward. Birch, for example, was ahead of his time in warning ecologists about the possibility of genetic changes in the organisms during the course of an ecological study (Birch 1960). Furthermore, as Collins (1986) points out, both ecologists had been sensitized to this possibility of "ecological time" evolution by their encounters with evolved resistance to insecticides in agricultural pests. Andrewartha and Birch are not suggesting that ecologists have no business paying attention to evolutionary considerations; rather, they are proposing that one should not import a particular stance on the factors of ecological significance simply to solidify the evolutionary foundations of ecology.

Lack's first theme, treating significant population parameters from an evolutionary perspective, fell on more fertile soil. That same crucial year, 1954, saw the publication of an important paper by Lamont Cole treating significant demographic characteristics from an evolutionary point of view. Cole's paper was probably more influential in this respect because he made explicit connections with demographic theory whereas Lack, never a big fan of mathematics, simply pointed in the appropriate directions. Cole's paper signals the birth of the important area of life history theory in evolutionary ecology (there were of course other influences – see Collins 1986 and Korfiatis and Stamou 1994 for more of the history). Three years later, Williams (1957) applied the methodology of "selection thinking" – the view of organisms as strategies for solving the problem of reproduction – to the phenomenon of senescence. Evolutionary ecology was off and running.

This emerging connection with evolutionary biology has bequeathed a kind of schizophrenia to ecology. In 1959, Hutchinson published his famous "Homage to Santa Rosalia" paper that asks, Why are there so many kinds of animals? The question inspired a generation of ecological investigation. But the question also contains a fundamental ambiguity; we can use the proximate/ultimate distinction to get an initial sense of the possibilities. It might be asking about the ultimate causes of the diversity we find in nature – a kind of macroevolutionary question. It might also be asking about the proximate mechanisms responsible for the level of diversity that we find in the communities around us – a question of Eltonian limited membership. Of course, it is always possible that these are in some sense the same question. I will not speculate here on what Hutchinson had in mind. The moral for now is that the question is not as simple as it might first appear. Things are not always as they seem; after all, as Lewin (1983) points out, Santa Rosalia was a goat.

2.3.6 *Ecosystem Ecology*

As discussed in the previous chapter, there appears to be a curious tension in Darwin's thought. On the one hand, there is the image of individual organisms struggling for existence both with one another and with their physical circumstances, a largely competitive nature, red in tooth and claw, in which no quarter is given, and none expected. On the other hand, there is the balance of nature, with the various components of the entangled bank so exquisitely fashioned to suit one another that the face of nature remains largely unchanged, at least at the scale of human observation. How could such stability emerge from such unbounded struggle? These days, as we will see, it has become fashionable to question the existence of this stability. But it was clearly part of the Darwinian canon, and the idea has exerted a profound influence on the development of ecology. We have already seen its influence in the Clementsian view of the community as a superorganism and in the Eltonian view of community structure; in this section we will see that it is the seed from which ecosystem ecology has grown as well.

Our story begins with one of the remarkable figures in the early history of the discipline – Stephen Forbes. Forbes, a midwesterner with virtually no formal training, used his gifts as a natural historian, together with a solid grasp of Darwinian principles, to emerge as one of the most prescient thinkers among nineteenth-century ecologists. Though his direct influence was limited by the rather obscure places in which his work was published, he clearly articulated themes that were to occupy ecologists far into the future. His most famous work, "The Lake as a Microcosm" (Forbes 1887), is of particular relevance here.

In this essay, Forbes emphasizes the interdependence of lacustrine phenomena, not just the complex web of biotic interactions among the organisms living there but also the impact of the physical circumstances of the environment. The consequence of this interdependence is that one cannot hope to study parts of the aquatic system in isolation from the whole; rather, to understand some component one must "run through the whole complicated mechanism of the aquatic life of the locality" (Forbes 1887: 537). This focus on an ecological community in the context of its physical setting is perhaps the first expression of the ecosystem perspective in ecology. In fact, as Golley (1993) points out, Forbes actually goes beyond the recognition of the ecosystem as a significant ecological entity. Thus he speaks of the way in which matter circulates in the system, an idea that was to resurface much later as one of the central themes of ecosystem studies.

Forbes's view of the lake as a microcosm also illustrates a second theme that has been important throughout the course of ecosystem ecology. He was very much under the sway of Darwinian ideas, especially as these ideas had been developed at the hands of Spencer, and like Spencer, he was prepared to see the struggle for existence as producing order at a variety of levels of organization. According to Forbes, "Perhaps no phenomenon of life . . . is more remarkable than the steady balance of organic nature, which holds each species within the limits of a uniform average number, year after year, although each one is always doing its best to break across boundaries on every side. The reproductive rate is usually enormous and the struggle for existence is correspondingly severe, . . . yet life does not perish in the lake, nor even oscillate to any considerable degree, but on the contrary the little community secluded here is as prosperous as if its state were one of profound and perpetual peace" (Forbes 1887: 549). What explains this balance? "Two ideas are thus seen to be sufficient to explain the order evolved from this seeming chaos; the first that of a general community of interests among all the classes of organic beings here assembled, and the second that of the beneficent power of natural selection which compels such adjustments of the rates of destruction and of multiplication of the various species as shall best promote this common interest" (Forbes 1887: 550). In short, the various organisms share a common interest in the stability of their aquatic world, and natural selection has shaped the life histories of the various organisms so that this common interest is served.

Thus, two important themes emerge from Forbes's work. First, a complete ecological understanding can be achieved only if we look at ecological communities as complex systems of interaction, where the influences flow not just between the organisms living together, but also between the organisms and the abiotic circumstances in which they live. Second, there is a kind of organic unity or balance that emerges at the level of the biological microcosm itself; the eyes of natural selection are not just on the individual organisms but on these more holistic ecological entities as well.

This view of the unity of the biota and their physico-chemical circumstances lay fallow for close to fifty years until, in 1935, Tansley introduced the concept of the ecosystem. Tansley was motivated by worries of a metaphysical nature. Specifically, he was concerned that the dominant view of communities of the time, the Clementsian superorganism view, was being saddled with a scientifically suspect holism. The immediate catalyst was an exposition of Clements's ideas in a series of papers by John Phillips that employed

the holistic philosophical ideas of Jan Christian Smuts (see Golley 1993: 11ff. for the full story). Tansley's ecosystems were an antidote to these perceived philosophical excesses because they connected ecology not to the ethereal domain of holistic entities, but to the solid structures of physics and chemistry. The ecosystem was seen as the sum total of the physical, chemical and biological entities and processes in a given place, with emphasis on the interactions between the physico-chemical and biological components.

Though Tansley never explored them himself, this emphasis on the connection between the biota and their abiotic circumstances opened up avenues for the exploration of biological processes in physico-chemical terms. Circumstances were ripe for such exploration. We have already seen how Elton's ideas on trophic structure (e.g., food cycles and the pyramid of numbers) point in the direction of physical and chemical processes playing a constraining role on the structure of ecological communities. At the same time, and for many years prior, limnologists had been developing a physico-chemical framework for exploring Forbes's lacustrine microcosms. Finally, the Russian polymath, Vladimir Vernadsky (1944), had recently outlined a new field of scientific inquiry – he called it biogeochemistry. Biogeochemistry looked at these same interactions between physics and chemistry on the one hand and the biota on the other, though at perhaps broader temporal and spatial scales.

All three of these influences came together in the work of a single individual – G. E. Hutchinson. There can be little doubt of Elton's influence on Hutchinson; in fact, he called Elton's first book (Elton 1927) one of the greatest biological books of the century. But Hutchinson was also a limnologist and one of the central figures in that field during the period in question. Finally, he was quite familiar with Vernadsky's work on biogeochemistry; interestingly, Vernadsky's son was one of Hutchinson's colleagues at Yale (see Hagen 1992 for a more complete account of Hutchinson's role in the emergence of ecosystem ecology). Hutchinson was able to bring these influences to bear to supply a firmer physico-chemical grounding of the Clementsian community than Tansley had been able to supply. Clements was enamored with physiology, and he believed that ultimately a kind of superorganismic physiology drove the process of succession toward the climax state. Hutchinson was now able to supply the underlying "physiological" mechanisms – the "energetics" of ecological systems. In other words, the fundamental processes at work in ecosystems could now be seen in the capture of solar radiation and the transfer of this energy across trophic levels, and in the cycling of materials (e.g., nitrogen) across these levels. These nutrient cycles and energy flows could be seen as the province of Vernadsky's new science of biogeochemistry, and Hutchinson could now claim that there are two central "modes" of ecological inquiry – the *biogeochemical* and the *biodemographic* (Hagen 1992: 68).

Hutchinson worked on these ideas from an abstract and mathematical perspective. He and his students did carry out intensive studies of Linsley Pond, and of course limnologists in general could, with some justification, claim that they had been adopting the biogeochemical perspective for decades; but for the first work from this perspective that had a serious impact on the entire discipline of ecology we must turn to Raymond Lindeman. Lindeman was a graduate student at the University of Minnesota and he did his graduate research on Cedar Bog Lake, a small senescent lake in the region. In this work he introduced his trophic-dynamic concept, which involved sorting the organisms in the lake not in terms of taxonomic affinities but by their feeding habits; he then located these "trophic levels" in the context of the lake as a physical system that both received and exported energy and nutrients from its external surroundings, and then empirically tracked the energy flows and nutrient cycles within the system. For the first time an entire ecosystem was being studied, and it was being studied *qua* ecosystem, that is, as a physico-chemical system of energy and nutrient transfers in which the organisms were essentially assigned the role of black box transducing nodes that influence these flows and transfers.

In his insightful history of ecosystem ecology, Golley offers the following summary of Lindeman's impact:

> With Raymond Lindeman we see for the first time a deliberate effort to implement Tansley's ecosystem concept. His focus was on the dynamic processes of the ecosystem. The idiom in which he expressed this process was energy. Lindeman introduced most of the major questions and concepts of modern ecological energetics, including questions about the length of food chains, the efficiency of trophic transfers, the storage of energy at different levels, the rates of primary productivity, the problems of correcting energy values for losses due to respiration, predation, and decomposition, and the role of bacteria and microorganisms in cycling dead organic matter. In addition, he made clear the idea that ecosystems develop through ecological succession and are tied to the energy dynamics of the system and the concept that nutrient cycling, as food cycling, is linked to the wider biogeochemical cycles coupling one ecosystem with another. (Golley 1993: 59–60)

Unfortunately, Lindeman never lived to pursue the agenda that his work laid out for ecosystem ecology. He died even before his most famous article appeared in print, the paper that set out his trophic dynamic approach (Lindeman 1942). Nor did his ideas fall immediately on receptive ears; the

paper just cited was widely panned by the influential limnologists of the day as being too theoretical, and a concerted effort by Hutchinson was required to get the paper published (for the details of this fascinating story, see Cook 1977). However, ecosystem ecology was not without its apostles. Following World War II, Eugene and Howard Odum took up the cause. Eugene Odum's influential textbook (Odum 1953), which used the ecosystem as its central organizing concept, was especially effective in spreading the word about the virtues of ecosystem level analyses. By exploiting the physico-chemical perspective of the ecosystem, Odum was able to articulate a number of principles that could give shape to ecological studies. At last ecology had its hands on some general truths. Never mind that the principles, at least the most defensible ones such as the laws of thermodynamics, were not really biological principles at all.

The development of ecosystem ecology at the hands of the Odums and others and its fling with big biology in the International Biological Program is an interesting tale that, fortunately, is ably told in two recent histories of the ecosystem approach (Hagen 1992, Golley 1993). Suffice it to say here that ecosystem studies flourish today as an established domain of scientific inquiry. What is important here is that the two fundamental areas of controversy that have dogged the ecosystem approach throughout its history continue to be sources of difficulty to the present day. Recall Forbes's two fundamental claims: (1) to understand any part of an ecological community one must grasp the entire system, both organic and inorganic, of which it is a part – put anachronistically, one must adopt the ecosystem perspective; and (2) from this more holistic perspective, one sees a kind of balance or order that is not visible when one's attention remains focused on the parts. In each of these claims lie the seeds of controversy; let us reflect for a moment on each.

The ecosystem perspective can be adopted, in any practical sense, only with the appearance of the conceptual framework developed by Lindeman. He provides the tools for systematically adopting what Hutchinson calls the biogeochemical mode of inquiry. Speaking of this biogeochemical mode, V. I. Vernadsky says: "The single living organism recedes from view; the sum of all organisms, i.e., living matter, is what is important" (Vernadsky 1944: 487). This shift away from the life history struggles of individual organisms and even from the population dynamics that record these struggles is clearly the central feature of Lindeman's ecosystem approach. As Hagen points out, "Lindeman criticized earlier ecologists for taking a too biological perspective on their work. In important ways Lindeman removed the traditional biological orientation from ecology" (Hagen 1992: 98). And here we have the raw materials for our first controversy. Is ecosystems studies a field of biological inquiry or is it not? Put another way, how are we to reconcile, within a single scientific discipline, both the biogeochemical and the biodemographic modes of inquiry that Hutchinson recognized?

Turning to the second of Forbes's fundamental claims, we recognize immediately a hoary philosophical problem – the problem of emergentism. We have already seen this issue in the debate between the superorganisms of Clements and the individualistic approach of Gleason, and in a way, it is not surprising to find it resurfacing here. As our brief history reveals, the ecosystem approach, in at least some of its manifestations, is the intellectual heir to the Clementsian view; the developmental blueprint shaping the superorganism has been replaced by a robust notion of ecosystem function. But the same difficult questions arise. What is this ecosystem function? Where does it come from? Does natural selection really see through to a community of interests among the members of an ecosystem, as Forbes suggests?

2.4 ECOLOGY'S TWELVE-YEAR CYCLE

In March 1981, a conference was held at Wakulla Springs, Florida, on some conceptual and methodological issues that had been vexing community ecologists. As is so often the case when scientists turn to an explicit discussion of foundational controversies, the attempt to shed some light on the problems generated considerable heat as well. The papers presented at that conference were collected for publication in the usual way, and the task fell to Robert May to write the introductory overview for the volume. May's (1984) piece was clearly an ecumenical attempt to build a conceptual tent commodious enough to house all of the disputants, and part of his strategy for doing so was to locate the debates in more familiar terrain. To this end, he pointed out that the Wakulla Springs conference was just the latest installment in what he dubbed "ecology's 12-year cycle." Previous manifestations of the cycle included the 1944 meeting of the British Ecological Society, the famous 1957 Cold Spring Harbor Symposium, and the Brookhaven Symposium of 1969 on the "Diversity and Stability of Ecological Systems." Each of these meetings, he claims, involved debate on broadly similar themes, with the Wakulla Springs conference representing the latest go-round.

There is clearly a tongue-in-cheek element behind May's elaboration of the cycle, and I would not want to be counted among his "naive and eager pattern-seekers." Still, there is an element of truth to the observation as well. A number of fundamental issues have divided ecologists for a long time. These issues do tend to remain in the background throughout the normal course of ecological inquiry, and the meetings May singles out served as

occasions where these issues emerged into the foreground of self-conscious debate. In particular, the four foundational issues described in Chapter One have been at the center of these episodic debates. This is not to say that these conferences were the only occasions where these foundational issues came to the fore; in particular, there is no suggestion here that 1944 is when the issues in question first became controversial in ecology – quite the contrary. As our brief historical survey reveals, these foundational problems trace back for, the most part, to the very origins of the discipline. Nor am I suggesting that these issues were the only issues involved during the controversial conferences, though I do believe they were among the central issues. Finally, the four foundational issues were not equally central to each of the conferences. For example, uncertainty about the relationship between organismic ecology and systems ecology was not even a possible issue at the first or even the second – though other manifestations of the levels of organization issue were involved. Still, with these caveats in place, we can use the twelve-year cycle to gather together the various manifestations of the four central areas of controversy as they have appeared in the historical outlines just completed, and at the same time, to substantiate the claim that these have been resilient and enduring issues in the history of ecological investigations.

The first episode in May's cycle, the 1944 meeting of the British Ecological Society, was titled "Ecology of Closely Allied Species." Specifically, the central focus of the conference was on the Gausian principle of competitive exclusion. According to an account of the events published in the *Journal of Animal Ecology* (Anon. 1944), there were six central protagonists. Lack, Elton, and Varley argued for the validity of the Gausian notion, and Blackman, Diver, and Spooner argued the other side; a host of others also contributed to the "lively discussion" that followed, in which "the arguments pro and contra were fairly evenly balanced" (Anon. 1944: 177). Unfortunately, only the papers by Lack and Elton were published, so the resources for an analysis of the debate are rather limited; we are forced to rely on these papers, the brief report on the session, and various recollections of the event, such as in Lack's short autobiography (Lack 1973).

Still, there is enough material to get a pretty clear sense of the issues fueling the debate. The contribution by Lack was his first attempt to present the implications of two ideas he had "rediscovered" in 1943 (Lack 1973): the first was Gause's principle itself, and the second was the idea, introduced by Huxley (1942), that size differences between related species living together might have been evolved to reduce competition. Elton's paper shares a similar focus, with the emphasis on Gause's principle of competitive exclusion. Reports of the discussions reveal that resistance to this principle traces back to two familiar sources: the venerable balance of nature theme and a more recent set of worries involving the relevance of the new abstract mathematical approach to ecological theory. In the first case, an emphasis on the significance of competitive exclusion seemed to presuppose a particular image of ecological phenomena, one that emphasizes population regulation by density-dependent factors and the central importance of biotic interactions, especially competition, in the determination of ecological phenomena. The criticisms of mathematical theory, pressed largely by Cyril Diver, also echoed a perennial theme – the mathematical models leave out too much relevant biology.

Perhaps the most novel aspect of the conference involved another side to Gause's work. As noted earlier, he saw his work in population ecology as an investigation into the workings of the Darwinian struggle for existence. The second central question under debate, the evolutionary significance of phenotypic differences (e.g., in size) among closely related sympatric species, suggests that ecologists were beginning to pay more than lip service to their Darwinian roots. In particular, the Lack/Elton/Varley camp appeared to be exploiting a fundamental implication of the Gausian perspective: if ecological factors express the struggle for existence, then it should make sense to look for the evolutionary consequences of the operation of these factors. It should be possible, in other words, to do a kind of evolutionary ecology. Subsequent ecologists have taken up this theme in spades, to the point that evolutionary ecology is considered in some circles to be simply another name for ecology in general. However, this increased activity at the interface between ecology and evolutionary biology has not always clarified the relationship between the two fields, and in some respects it has muddied the waters even further. Unfortunately, a detailed investigation of this controversy lies beyond the scope of the present work.[3]

The next installment of the cycle occurred in 1957. In that year, demographers, mathematicians, ecologists, and evolutionary biologists gathered at Cold Spring Harbor for a symposium on the population problem. The most conspicuous feature of the conference was the heated debate over the nature of the factors that determine population size; the participants formed, in Hutchinson's words, "a heterogeneous and unstable population." At the heart of the debate was the old balance of nature theme once again: specifically, the issue of population regulation via density-dependent (primarily biotic)

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[3] Much contemporary work in evolutionary ecology is devoted to answering ultimate evolutionary questions rather than proximate ecological questions. In the Epilogue, I suggest that much of this investigation is more properly seen as falling within the broad field of evolutionary biology rather than ecology proper.

factors versus population control at the hands of density-independent (primarily abiotic) factors such as the weather.

The central protagonists in this debate were Nicholson on the one hand, and Andrewartha and Birch on the other. Particularly revealing was an exchange between Nicholson and Birch following the presentation of Birch's paper, which argues that for some populations of grasshoppers the weather, and not any density-sensitive mechanism, determines patterns of distribution and abundance (Cold Spring Harbor 1957: 216–217). Nicholson objects that the persistence of these populations in such a circumstance would require a miracle, whereby the destructive influence of the weather should, by some supernatural serendipity, just manage to counterbalance the capacity for increase in the population. For Nicholson, "The fact that grasshoppers, and other animals, do exist in a stable state in environments with widely different degrees of favorability shows that something adjusts the forces which oppose multiplication at an intensity which just counters the tendency to multiply indefinitely" (Cold Spring Harbor 1957: 216). Such an adjustment is possible only if this "something" is responsive to the density of the population, and the most likely mechanism is competition. Birch replies, with equal trenchancy, that "the chance of a grasshopper finding food is independent of the number of grasshoppers searching for food" (Cold Spring Harbor 1957: 217). We will look in detail at this impasse in Chapter Three.

Though the Cold Spring Harbor conference is perhaps most remarkable for the intensity of the debate over density-dependent regulation, there was also a fairly extensive critical examination of the utility of the abstract theoretical approach to population ecology. Andrewartha presented a paper largely critical of this enterprise, and in the discussion that followed he succinctly summarized his central reason for rejecting these abstract population models: "I discard them because they are so unrealistic that one can not find a way to test them against a natural population. If a hypothesis cannot be tested empirically what is the use of framing it?" (Cold Spring Harbor 1957: 234). Birch was a bit more conciliatory. Responding to the point that population models without density dependence predict unreasonable population trajectories, he says:

> These mathematical propositions are, I do not doubt, accurate representations of very simple models of population growth and dispersal. I think they have their usefulness as starting points in helping us to build a more complex and realistic picture, if not mathematically, then at least in imagination. However, I cannot see how they can be used in themselves to inform us as to what should happen in natural populations of animals. Many more factors come into operation in the natural populations than are considered in these simplified hypothetical

> situations . . . The models may be true as far as they go. I cannot see that they go as far as the natural population or anywhere very near it. (Cold Spring Harbor 1957: 217)

The debates surrounding population regulation and the role of abstract theoretical models were undoubtedly the most significant aspects of the Cold Spring Harbor Symposium, at least for our story. Before moving on to the next episode in the cycle, however, I will mention one final passage that has some bearing on the foundational issues under study. Commenting on the population regulation debate that dominated the conference, the evolutionary biologist, Theodosius Dobzhansky, says:

> To a non-ecologist, the controversy that has made our sessions so lively is, I confess, somewhat bewildering. . . . Being a geneticist, I am most interested in the bearing of this issue on evolutionary problems. We have been brought up, or at least I have been brought up, to believe that natural selection, and hence the evolutionary process, are the outcome of "competition" and therefore are governed by density-dependent factors. This evokes the shadows of Malthus, of Darwin's dependence on Malthus, and of the "social Darwinists." (Cold Spring Harbor 1957: 235)

Dobzhansky acknowledges that there appear to be selection pressures that do not operate in a density-dependent fashion and he urges the evolutionary investigation of such processes. That is sensible advice, but it is not the point I want to emphasize here. The passage is significant because it illustrates why there has been some reticence, among ecologists, to embrace the evolutionary side of their discipline. Adopting the Darwinian perspective has been implicitly associated, because of the historical connections referred to by Dobzhansky, with taking the side of those who would emphasize the role of competition, density dependence, and so on, in the debate over the determination of demographic behavior. Those who have doubts about this ecological picture have at times been led to downplay the evolutionary connections as well.

Twelve years after meeting at Cold Spring Harbor, the Brookhaven Symposia in Biology addressed the theme of "Diversity and Stability in Ecological Systems" (Brookhaven 1969). When it comes to controversy, Brookhaven was rather tame, at least by Cold Spring standards. It did have its frustrations, however. Many of these can be traced back to the *interdisciplinary* nature of the conference. I emphasize the term because the Brookhaven conference, on the face of things, appears much less interdisciplinary than the earlier Cold Spring Harbor Symposium. The latter placed significantly greater emphasis on human ecology and thus asked questions that brought in the social sciences. Brookhaven, on the other hand, was essentially a collection of biologists. But the first conference still had a cohesion that Brookhaven lacked. In his opening address, Lamont Cole unveiled the unifying theme at Cold Spring Harbor – the "population problem." At bottom, what the group shared was an interest in demography; this can lead to quite distinct kinds of questions, depending on the kinds of populations being studied. Brookhaven was ostensibly about diversity and stability, but these were not as well understood as was the population problem. In effect, the phenomena were just as much at stake as were the investigative strategies for pursuing them. The conference brought together several styles of ecology to discuss diversity and stability, and for the most part that is what they did; but the discussions did not always connect and a considerable amount of time was spent talking about how the phenomena are to be defined within the various investigative frameworks. Brookhaven was interdisciplinary in the sense that there were several established fields of inquiry each vying to *be* ecology.

A look at the first three papers of the conference illustrates the point. The first two papers embody a contrast that is already familiar from the first two episodes of the cycle. The opening paper, by Frank Preston (1969), presents a largely empirical discussion of stability, with numerous concrete examples and little theoretical discussion. The second paper, by Richard Lewontin, is a dramatic contrast. It captures some of the heady optimism of theoretical ecology in the 1960s, an optimism fueled by a concerted effort to incorporate mathematics and evolution into ecology, and aspiring to produce "an exact theory of the evolution of communities of organisms" (Lewontin 1969: 13). According to Lewontin, "Such an exact theory must 'explain' in some sense the present state of the biosphere" (Lewontin 1969: 13). Of course, it must predict and retrodict as well. The fundamental concept required for such an ambitious undertaking, according to Lewontin, is the concept of the vector field in n-dimensional space, and his paper goes on to discuss stability from this abstract theoretical perspective. In the discussion of Lewontin's paper we see the familiar empiricist worries returning: In particular, doesn't this theoretical approach leave out too much relevant biology? We also see that there is apparently more than one way to be exact. In response to Watt's challenge that some of Lewontin's theoretical assumptions might not "correspond to what happens in nature," Lewontin offers the following response: "I don't know whether they correspond or not, and the difference between you and me is that you are used to thinking very exactly about very exact situations" (Lewontin 1969: 24).

The third paper differs just as dramatically from the first two as they did from one another, but along a quite different dimension. This paper, by the

Spanish ecologist Ramón Margalef, applies the ecosystem perspective to the problems of diversity and stability. As Margalef puts it, one "purpose of this paper is to try to link all major 'macroscopic' or synthetic properties of an ecosystem, including especially production, biomass, diversity, and stability, in a single expression" (Margalef 1969: 25). Once again, there are aspirations for a complete ecological theory here; however, for Lewontin the complete theory is supposed to emerge out of a population biology that unites population/community ecology and evolutionary genetics, whereas for Margalef the complete theory comes from embedding all the lower levels into the synthetic perspective of the ecosystem, where the ultimate currency is biomass, energy flows, and the transport of materials.

Further into the volume, evolutionary ecology – the selection thinking mentioned above – makes its appearance. Schoener develops an energy-time optimality study of both diet and body size. Take the case of diet: "An optimal diet is defined as that which yields the greatest net energy per unit feeding time per unit energy requirement" (Schoener 1969: 103). Notice here that Schoener is ultimately interested in "the major ways in which species of a community divide resources" (Schoener 1969: 103); this is a community ecology issue and not an attempt to give what we would these days call an adaptation explanation (Brandon 1990). The paper is not long on concrete examples, but when they are discussed, it is in support of the theoretical treatment, not as the conclusions of explanatory accounts of the evolutionary origins of the traits these organisms exemplify.

We already have three distinct perspectives on the ecological phenomena. The use of optimality to study community organization introduces, in one sense, a fourth style of investigation. It uses an assumption about what evolution is likely to do to support ideas about the processes that shape ecological communities. But in another sense, it does not add anything new because it is thoroughly integrated with the theoretical tradition represented by the Lewontin piece. In any case, the Brookhaven meeting did bring together at least three distinct perspectives that made rather limited contact. But the gulf is not the same in each case. Consider first the empirical and the theoretical. That both perspectives might be represented at the same conference is surely no news. What is significant about Brookhaven is the *distance* between the theoretical and the empirical. One gets the impression of theoretical imaginations relatively more unfettered than might be expected. The gulf between ecosystem ecology and the ecology of organisms, on the other hand, is an ontological divide; the two enterprises sort nature in fundamentally distinct ways.

A final point of significance about the Brookhaven Symposium was its optimistic stance about the balance of nature. As May confesses, "There may

have been too much of a tendency to view communities as orderly, patterned 'systems'" (May 1984: 4). We will return to the balance of nature theme in Chapter Three.

The fourth episode in May's cycle was his own meeting at Wakulla Springs. As suggested by the subtitle of the conference volume (Strong et al. 1984) – "Conceptual Issues and the Evidence" – this was by far the most philosophically oriented debate. Many of these philosophical issues are addressed in subsequent chapters, and for the most part these are themes we have already seen, so I will be brief here.

One perennial issue that prompted recourse to philosophy was the gulf just discussed between theory and empirical reality. Generally, the philosophy of choice was Popperian falsificationism. The way to bring the theoreticians down to earth was to demand that they proffer falsifiable hypotheses, that they seek to falsify these hypotheses, and that they not undertake that process until they have falsified the relevant null hypotheses. The responses from theoretically inclined ecologists were varied; in some cases they attempted to meet the Popperian standards; others accepted falsificationism but denied that the null model has conceptual priority; in still other cases there was rebellion against the Popperian standards, and in some cases, against philosophy itself (Roughgarden 1984).

The second significant issue at Wakulla Springs is a repeat offender as well. A central theme of the conference, and what prompted May to refer to the twelve-year cycle in the first place, is the debate about the significance of density dependence, of biotic factors generally, and of competition in particular in the determination of ecological phenomena. It was perhaps more apparent at the Wakulla Springs conference than at any of the other episodes in our cycle that this balance of nature issue had a distinct conceptual air about it. The theoreticians had been acting as if some things could be figured out *a priori*; we need not dredge every insight up from the data. But more empirically oriented ecologists had seen enough of the *a priori*; hence the turn toward the hammer of Popperian falsifiability. The next chapter examines this issue of the balance of nature and the question of what we can know about it from a conceptual standpoint.

Closely related to issues of density-dependent population regulation and the importance of biotic factors, and included under this broad umbrella that I am calling the balance of nature idea, is the question of community organization. Between the Brookhaven meeting in 1969 and Wakulla Springs, theoretical community ecology underwent a period of intense development. The hope, or perhaps more accurately, the presumption, was that the old Eltonian question of limited membership had an answer. The search was on for the "rules" of community assembly. This was also a locus for controversy. Pitted against the community theorists were ecologists who echoed Gleasonian themes – communities were fortuitous assemblages of species who all happened to be making a living in the same place. Community composition was not dictated by any higher order structural blueprint but instead by the vagaries of dispersal and historical accident, and by the autecologies of the various species involved. As with the population level issues like density-dependent regulation and biotic control, both camps pressed their cases with an assurance that outstripped anything the available evidence would support, suggesting that there were deeper conceptual issues involved.

I have worked through the episodes in May's twelve-year cycle to give something of the flavor of the foundational controversies that have been central to ecology and to support the idea that those we are about to examine are among that group. I do not mean to suggest that these particular episodes are any sort of definitive guide. In fact, they clearly are not. In particular, the tradition of plant ecology is not well represented by this sequence at all. Like everything associated with ecology, including the phenomena it studies, it seems there is always more to the story. The same must be said about the thumbnail historical sketch that has occupied the bulk of this chapter. The goal has been to give some sense for what the discipline is about as well as some substance to the foundational problems we are about to explore. It is time to get on with that task.

3

Must There Be a Balance of Nature?

3.1 INTRODUCTION

The idea of a balance of nature reaches back into antiquity. Egerton (1973) has provided perhaps the most detailed look at this history, tracing the idea from its early manifestations in ancient Greek thought to its most explicit formulations in the ecological studies of the present century. As he points out, however, one of the most striking features of this notion has been its typically implicit character. It usually functions as a background assumption that is rarely brought forward for explicit study. This remains largely true of the balance of nature idea in ecology as a self-conscious scientific field; it has worked in the background, shaping inquiry, but it has rarely been hauled out into the daylight and closely examined.

This chapter does not attempt a comprehensive look at all the various sides of the balance of nature idea (for a comprehensive review see Pimm 1991). Instead, it focuses on one particular aspect – the role that balance of nature plays as the linchpin among a constellation of ideas that jointly served, at least at the hands of some ecologists, to set the course of inquiry for population and community ecology. In keeping with its traditional background role, the balance of nature idea – together with the associated ideas that emphasize the prevalence of biotic interaction, density dependence, and competition – has exerted this guiding influence in a largely implicit fashion. Here I try to reconstruct the inferential tendencies that lie behind this guiding influence, even though, for the most part, these inferential tendencies cannot be traced back to the reasoning of any one particular ecologist. The theme that I defend is that questions about the balance of nature, and about related issues of biotic bias, density dependence, and competition, are at bottom empirical questions to be settled by empirical study rather than conceptual argument. This might seem a truism, but if it is, it has not always been respected as such by the ecologists who have been caught up in this debate. In fact, there has been a significant effort to argue in this area primarily on conceptual grounds. The goal of this chapter is to identify, and to evaluate, the relevant conceptual arguments.

3.2 THE FIRST BALANCE OF NATURE ARGUMENT

The balance of nature idea in population/community ecology is manifest in a number of specific presuppositions or investigative tendencies. Most prominent among these are the emphasis on density-dependent over density-independent factors, the focus on biotic over abiotic factors, the preoccupation with competition, and the tendency to assume equilibrium and stability among ecological phenomena. Those most squarely in the grip of the balance of nature image tend to orient their investigations in light of these background principles. The first task, then, is to say what these various ideas mean and how they are related. Are some more fundamental than others? Do some follow from others?

In fact, there does seem to be a kind of inferential progression involved in this constellation of issues, though it is rarely explicit. Generically, the sequence goes like this. First comes the imputation of balance, stability, persistence, regularity, or some such order-producing concept. Then density dependence and/or biotic control is brought in as a source of this order. Typically, though not always, competition is then invoked as the most likely mechanism for achieving this level of control. Finally, the assumption of equilibrium is justified on the grounds that it is here, in the equilibrium case, that the order-producing forces we are interested in are most fully manifest. It is difficult to document the claim that this schematic chain of reasoning has been historically influential in shaping views about the fundamental nature of ecological phenomena because, as already mentioned, these ideas typically take the form of implicit assumptions. Nonetheless, I believe it has been influential. Specifically, there are two instantiations of this schematic sequence that have shaped, and to some degree continue to shape, the views of some ecologists. They have served as lightning rods for ecological controversy, attracting the attacks of those who do not share the presuppositions involved – controversies that have, no doubt, been fueled by the implicit character of the arguments.

The first instantiation begins with a presupposition that is perhaps closest to the traditional balance of nature idea – the idea that there is a kind of stability and orderliness to the biological world that stands against both the

vicissitudes of abiotic nature and the reproductive potentialities of organisms (Egerton 1973, Botkin 1990). The balance need not be perfect, but as Lack puts it, "Most wild animals fluctuate irregularly in numbers between limits that are extremely restricted compared with what their rates of increase would allow" (Lack 1954: 1). In short, natural populations tend to be regulated. It was this orderliness in nature that, before Darwin, fueled the "argument from design" for the existence of a Divine Creator. After Darwin, of course, responsibility shifts to evolution by natural selection – which brings us to the second step in the sequence. If the processes that yield this stability and order are under evolutionary control, then they must be biotic factors. If natural selection is the "hidden hand" behind the Darwinian economy of nature, then the "market transactions" in nature take place among the organisms themselves. Where this "market" has not been significantly disrupted, in natural populations free from large-scale anthropogenic interference, we should expect to find equilibrium populations (see Hutchinson 1948 for a version of this evolutionary argument). Furthermore, if these biotic interactions are to be effective in achieving control, they must be sensitive to changes in population density; we should expect to find significant density dependence in nature (this idea is perhaps first explicit in Nicholson 1933; see also Nicholson and Bailey 1935). Finally, since the *struggle* for existence is mostly between individuals, both within and across species, for access to the *conditions* for existence, we should expect competition to be the most important mechanism underlying population regulation.

Though something of an idealization, we can put these considerations together in the form of the following inferential tendency:

Balance of Nature Argument I

1. The relative constancy of population sizes, given what the capacity for increase would allow, implies that populations are regulated.
2. Since this order, in the face of a fluctuating abiotic world, is the product of evolution by natural selection, the forces that achieve it must themselves be under evolutionary control – that is, they must be biotic forces.
3. When these biotic forces are unimpeded by noise from the abiotic environment and the vagaries of history, they should issue in equilibrium populations.
4. Effective regulatory control presupposes sensitivity to changes in population density – we should expect these biotic factors to be density dependent.
5. Competition is the most likely mechanism for the implementation of these controls.

I should point out that I am using the term *argument* in a loose sense here. The sequence just described is not an argument in the logician's sense, in which some of the lines express premises and others follow from these by deductive entailment. Rather, it is a constellation of mutually reinforcing ideas that have something of the character of an inferential progression, but the earlier steps, at best, boost the plausibility of later steps; they do not guarantee their truth.

Begin, then, with the first plank in the balance of nature platform: the relative constancy of population sizes as a purported observational fact. There is an initial problem regarding how much temporal variation in population sizes is consistent with the idea of population regulation, and the vagueness of the argument in this regard has certainly contributed to the controversy (see Botkin 1990: 48–49). If we look at further stages of the argument, where the notion of equilibrium population densities comes in, we can perhaps resolve the ambiguity: relatively constant population sizes are those for which the assumption of an equilibrium density is at least approximately true. Understood in this way, the existence of a tendency toward relative constancy of population size is far from an observational given in the eyes of the ecologists who have challenged this argument. Of course, no one doubts the Malthusian observation that populations are, in principle, capable of exponential growth and that such growth is never realized for any significant period of time. But the existence of this ceiling to growth is consistent with all sorts of actual behaviors on the part of populations. As a number of commentators have noticed (e.g., Kingsland 1985), the degree of constancy that one finds in population size appears to depend a great deal on the kinds of organisms one studies. For a variety of reasons, Lack's birds appear to exhibit significantly more demographic stability than the insects that Andrewartha and Birch study. It is an empirical question, and one that appears to be largely still up in the air, whether there are any broad tendencies in either direction among ecological populations overall. Given the ambiguities of the claim, the sweeping character of its scope, and the absence of the kind of comprehensive database that would be required to resolve the matter, the idea of population regulation does not appear to be a promising piece of fundamental background knowledge on which to build expectations about the determinants of demographic phenomena.

Of course, without the idea of rather tightly regulated populations, the second plank in the platform – the existence of biotic regulating mechanisms fashioned by natural selection – is significantly undercut; a reason for supposing that biotic factors will have a special role to play has been removed. The third claim of the balance of nature argument, the preponderance of equilibrium populations, has collapsed into the first on the present analysis because the concept of equilibrium has been used to resolve the ambiguity in the idea

of regulation. Thus, the extent to which populations can be seen as fluctuating around equilibrium densities becomes part of that same unresolved empirical issue discussed in the previous paragraph.

The idea that regulation requires the operation of density-dependent factors, the fourth plank in the platform, traces back to Nicholson (Nicholson 1954, 1957, Kingsland 1985: 119, Cappuccino 1995: 3).[1] One of his images was the governor on a steam engine – any such effective control mechanism must obviously be sensitive to changes of internal state in the system that it controls. Similarly, the biotic forces that produce balance in natural populations must themselves be sensitive to changes in the density of the populations they are controlling. For Nicholson, this was close to a conceptual truth. As he puts it, "Without such density induced governing reaction a species would either multiply indefinitely or dwindle to extinction, unless by chance the ability of the species to multiply were exactly countered by the inherent destructive properties of the environment" (Nicholson 1957: 216). We might call this "the miracle argument" – it would take nothing short of a miracle to get the effect of regulation without the existence of density-dependent factors. For Nicholson, it is hard to imagine how demographic factors could issue in equilibrium densities without functioning as negative feedback processes that are sensitive to population densities.

Note two things about this argument. First, the conceptual link between regulation and density dependence is obviously sensitive to how the ambiguity of "regulation" gets resolved. If regulation is interpreted via the concept of equilibrium, then even if successful, this argument indicates a significant role for density dependence *only* on the assumption that equilibrium populations are the order of the day. Second, there are reasons to think such a large miracle might not be necessary after all to get the effect of regulation in the absence of density dependence. Some have argued (Andrewartha and Birch 1954, 1984, den Boer 1968, Reddingius 1971, den Boer and Reddingius 1996) that local patterns of extinction and colonization can yield a kind of population stability at a more global spatial scale. Recent theoretical work on nonequilibrium dynamics (Caswell 1978) and metapopulations (Hanski 1990, 1991a, 1991b, 1991c, 1996; see Hanski and Gilpin 1997 and Tilman and Kareiva 1997 for overviews) points in a similar direction.

The Nicholson passage is important in another way. I said that the connection between regulation and density dependence was close to a conceptual truth for Nicholson. Of course, it is in the nature of conceptual truths to be

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[1] Nicholson, however, was idiosyncratic in insisting, contrary to the tenor of the above argument, that natural selection did not itself issue in the balance – see Kingsland (1985: 120).

sensitive to how terms are defined. Thus, it is not surprising that the controversy surrounding the issue of population regulation via density-dependent factors has often been denigrated as a purely semantic squabble. Here we have an example of how shifts in meaning can fuel debate. We have already confronted the ambiguity concerning the idea of regulation, resolving it in terms of the existence of equilibrium densities. But the passage Nicholson quoted above suggests a different argument; the very fact that natural populations manage to persist – to avoid the extremes of extinction and perpetual growth – is taken as supporting the inevitability of density-dependent population control. When the argument shifts over to this more liberal notion of regulation, its empirical footing becomes more secure. Just how frequently we should expect to find populations fluctuating around equilibrium densities is an open question, but there is little doubt that most populations manage for considerable periods of time to avoid the two extremes mentioned above. The empirical gains come with a theoretical cost, however; the conceptual ties between density dependence and regulation are considerably weakened. If regulation simply means persistence between the two extremes, then the accomplishment of regulation in the absence of density-dependent negative feedback becomes a much less miraculous affair. Furthermore, the balance of nature position becomes much more difficult to distinguish from opposing views, such as Strong's density-vague dynamics (Strong 1984a, 1986). We take a detailed look at this "persistence" version of the argument in a later section; the important point for now is simply that one cannot argue for the existence of regulation in one sense and use it as a ground for inference in another.

If competition finds its way into the balance of nature argument by being the mechanism that effects the balance, then to the extent that the earlier planks in the balance of nature platform have been undercut, the fifth plank, an emphasis on competition as the most significant ecological factor, suffers as well. But there is a bit more to say on this matter. As we saw in the previous chapter, Nicholson, in addition to being a champion of density dependence, was also one of the strongest proponents of the idea that competition is the only mechanism that could effectively implement the requisite biotic controls (Kingsland 1985: 119). He believed that competition is the only force that, by its very nature, increases in severity as density increases, and therefore the only force that could effectively implement the ceiling on population growth. Population balance, in his view, results from the equilibration between two opposing forces – the tendency toward increase as a function of the suitability of the environment, on the one hand, and the tendency of competition to suppress population growth, on the other. Though less applicable in the case of Nicholson (1960), the tendency to emphasize competition comes also

from (1) the evolutionary character of the first balance of nature argument, together with (2) the fact, to be explored below, that competition has a long history of being seen as the most significant process in the Darwinian struggle for existence. Finally, the emphasis on competition has fueled a strong tradition of theoretical investigation in population and community ecology. No doubt the inertia of this theoretical tradition has itself fostered the tendency to look toward competition as the key to ecological structure.

However, none of these grounds stand up as a justification for holding the unexamined presupposition that competition is likely to be important in system after system. Even granting, for the sake of argument, that population regulation is the norm, Nicholson's claim that competition must be the mechanism involved dramatically underestimates the range of causal possibilities regarding the determinants of population behavior. Nor is there any essential relationship between competition and the struggle for existence. The forces that change population size in ecological time are the forces that drive natural selection, regardless of the mechanisms that underlie these forces. Finally, to pursue competition because that is what has been best articulated theoretically is to follow the drunkard who searches for his keys under the street lamp because the light is better there. Like our earlier questions – the relative constancy of population size, the prevalence of equilibrium populations, and the relative significance of density-dependent demographic forces – the significance of competition among the determinants of population change is an empirical question to be settled not by conceptual argument but by the evidence.

3.3 AN ALTERNATIVE PERSPECTIVE

As already indicated, the balance of nature stance we have been discussing is typically implicit, lurking in the background as an orientation toward ecological phenomena rather than as an articulated body of beliefs about these phenomena (Pickett et al. 1994). In that respect, it is something like a Kuhnian paradigm (Kuhn 1962) or the hard core of a Lakatosian research program (Lakatos 1970). It sets the context for subsequent investigations without itself being put at risk by those investigations, taking on an air of inevitability. When rendered explicit, however, it is revealed as a particular stance on a body of very general empirical issues. The balance of nature camp supposes a level of organization and order in ecological phenomena that may not, as a matter of contingent empirical fact, be there at all. It is guided by the image of nature as full – of populations with boundless reproductive potential being held in check by density-sensitive governors, of communities packed with species like MacArthur's perfect crystals. The opposition is guided by a different image, one of Sysiphean organisms clinging to existence by waging a relentless uphill battle against a hostile and inadequate environment. Here the reproductive potential of the population is spent just managing to persist; times are never good enough, or they are never good enough for long enough, for the Malthusian explosion to be a factor, and communities are fortuitous assemblages of organisms that all happen to be making a living in the same place.

White, a spokesman for this alternative perspective, offers the following:

> Surviving on this earth is, and always has been, especially for the very young, a struggle, a chancey business. . . . Nor is there an "optimum" or "equilibrium" density of a population in nature – only the maximum number that can survive each generation in a population that is pressing hard against the variable but limited supply of resources in its environment. . . . For most the "struggle for existence" is not a tooth and claw business. It is a lonely struggle to live in an inadequate world. They die young, and their passing is passive, solitary, and unnoticed. (White 1993: 5–7)

To get a clearer view of this alternative, consider one of White's favorite illustrations – *Cardiaspina densitexta*, a psyllid (phloem-sucking insect) that feeds on *Eucalyptus*. The females of *C. densitexta* lay their eggs on a single species of *Eucalyptus*, which then becomes the food source for the first instar nymphs. The nymphs encase themselves in a protective cover and feed on the phloem that flows in the leaf, emerging some three to six months later as adults. Here is what White says about the nymphs:

> Most of the first instar nymphs of *C. densitexta* die a day or two after they have settled and started to feed. No predators, parasites, or diseases attacked them, no competitors vied with them for any resource, nor was the weather too hot or too cold, too wet or too dry. And their food was abundant and palatable, but lethally inadequate, so they starved while eating their fill from the phloem. However, a few always chanced to settle where the concentration of nutrients in the phloem was greater. Those few survived. It was the *passive inadequacy* of the environment which killed most of those young animals, not the action of something, living or non-living, in their environment. . . . There is an enormous struggle for survival going on, but it is a struggle by each individual against the inadequacy of its environment, and the struggle of each one is independent of the struggle of every other one. (White 1993: 7, 16)

White's psyllids are, of course, a single example. But they are taken to exemplify a view of ecological organization that stands as an alternative to the

balance of nature perspective. On this view, it is the tremendous reproductive potential of organisms, together with a sprinkling of relatively congenial environmental circumstances in a largely hostile world, that accounts both for population persistence and for the level of numbers that are actually achieved. Reverting to Nicholson's analogy, the governor may or may not be in place, but "in nature rarely is enough steam generated to make the valve operate" (White 1993: 6).

In using White as a spokesman, I am relying on a contemporary source for the development of the antibalance viewpoint. But the view he represents and the clashes between this view and the balance of nature perspective extend deep into the history of ecology (see Kingsland 1985, den Boer and Reddingius 1996 for elaboration). In fact, the venerable nature of the debate might be taken as a basis for criticism of the present analysis. Perhaps White is jousting with a straw man. Perhaps the balance of nature view as I have characterized it is, at best, a crude characterization of a long bygone era. Just how relevant is the balance of nature argument described earlier to contemporary concerns?

Even a cursory look at developments in contemporary ecology would suggest that it is not very relevant at all. As numerous commentators have remarked, there appears to have been something of a paradigm shift in ecology (Kingsland 1995, Colwell 1984, Botkin 1990, McIntosh 1987). The "new" ecology apparently embraces the importance of history over ahistorical equilibria, contingency over "laws" of population growth and community composition, the uniqueness of actual individuals over the homogeneity of the abstract individual, pluralism over monolithic theory, and chance over determinism. Several authors speak explicitly about the emergence of a "nonequilibrium paradigm" in ecology (Pickett et al. 1994, Cappuccino 1995), a paradigm that encompasses all the tendencies just described.

Does this mean that the balance of nature debate has finally been resolved? Is the triumph of the antibalance perspective ecology's version of the oxygen theory ousting phlogiston? There are two reasons for thinking that this is the wrong way to read the situation. First, it is important to recognize that, by and large, the opponents of the balance of nature argument have been just as insistent on the ultimate correctness of their perspective on ecological phenomena as have those on the other side. In its more reasonable incarnations, the nonequilibrium paradigm draws a less dogmatic lesson from the balance of nature debate. It represents a willingness to recognize that the relative importance of abiotic factors over biotic factors such as competition, of density-dependent versus density-independent processes, and of equilibrial versus nonequilibrial situations is likely to depend on the system being investigated.

The very longevity of the debate and the ability of the various protagonists to find ecological examples to support their cause suggest that nature is unlikely to speak with one voice on these matters. The real insight is that we still face fundamental and largely unanswered empirical questions, and the answers, when we finally get them, are unlikely to be univocal. Suggesting that the antibalance perspective has won the day disguises that insight.

The second and more fundamental reason that it would be premature to award victory to the foes of the balance of nature is that debate on this matter remains alive and well in contemporary ecology.[2] To see this we must revisit the argument schema presented at the beginning of this section.

3.4 THE SECOND BALANCE OF NATURE ARGUMENT

The first plank of our original schema posits the pervasive empirical fact that is supposed to underwrite the overall view. In the case of the first balance of nature argument, that premise attributed a strong tendency toward constancy of population size on the part of natural populations. As we have seen, that premise is ambiguous as it leaves open the question of how much variability would actually contravene the claim. Given the demands of other parts of the first balance of nature argument, it seemed best to resolve the ambiguity in terms of the idea of equilibrium densities; but a more liberal and less controversial interpretation of regulation was also discussed. The new and improved balance of nature argument, which I will call the Balance of Nature Argument II, retreats to this much more secure premise: natural populations tend to persist. Who could dispute this? The populations are here and we can point to them; this seems to settle the issue (Royama 1992: 45).

The first balance of nature argument also had an evolutionary flavor, reflected primarily in the second premise. In the second balance of nature argument, this potentially shaky reliance on evolutionary theory is replaced by reliance on solid mathematical fact. Specifically, population densities whose time series can be represented in terms of a random walk are statistically guaranteed to go extinct in the long run. Thus, those that manage to persist must be regulated in the sense that their densities over time must display a kind of statistical stability. Various notions have been proposed as explications of this stability characteristic (see May 1973, Chesson 1981, 1982, Murdoch 1994), but I focus here on the "long-term stationary probability distribution of population densities" (Dennis and Taper 1994, Turchin 1995). A density time series exhibits a stationary probability distribution (SPD) when (1) there exists a mean density level around which the population density fluctuates, and (2) the variance around this mean is itself bounded in the long term. This argument from the inevitability of random walk extinction is intended to put to rest, once and for all, the old arguments over population regulation. As Cappuccino puts it, "Thus the question is no longer 'is it regulated?' but '*how* is it regulated?'" (Cappuccino 1995: 6).

When regulation is understood in this more relaxed statistical sense, the connection between regulation and equilibrium (the subject of the third plank in our original argument) becomes less problematic. In fact, Turchin simply defines equilibrium in terms of the existence of an SPD, which enables him to say that "*being regulated* and *having an equilibrium* are one and the same thing. The whole issue of equilibrium versus nonequilibrium dynamics becomes a semantic argument" (Turchin 1995: 26). This is, in a sense, the converse of the strategy used in the first balance of nature argument. There, a relatively restrictive notion of equilibrium was used to supply a relatively restrictive notion of regulation. Here, a relatively liberal notion of regulation, the manifestation of a statistical return tendency or tendency toward persistence, is used to supply a relatively liberal notion of equilibrium, one so liberal that the distinction between equilibrium and nonequilibrium dynamics loses its force.

This brings us to the fourth plank, the connection with density dependence. Throughout the historical course of this debate there has been a tendency to identify regulation with control by density-dependent factors and to use a version of the miracle argument to establish density dependence directly. We saw this already in the passage quoted from Nicholson in which he says that without density dependence we would have to rely on an incredible serendipity, whereby birth and death processes just happen to cancel one another out. May relies on a similar argument:

> For one thing, no population can be driven entirely by density-independent factors all the time. No matter how severely or unpredictably birth, death, and migration rates may be fluctuating around their long term averages, if there were no density-dependent effects the population would, in the long run, either increase or decrease without bound (barring a miracle by which average gains and losses cancelled exactly). (May 1986: 261)

Against this argument, the antibalance group offers an alternative mechanism, briefly mentioned above, for persistence – the mechanism of spreading

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[2] For a sample of this debate over the last fifteen years, see den Boer (1986), DeAngelis and Waterhouse (1987), Berryman (1987, 1991), Wolda (1989, 1991), Hanski, Woiwood, and Perry (1993), Holyoak and Lawton (1993), Turchin et al. (1993), Wolda et al. (1994), Dennis and Taper (1994), den Boer and Reddingius (1996), Chitty (1996), Murray (1987, 1998), Hunter and Price (1998), Turchin (1995, 1999), Turchin and Berryman (2000), and Ricklefs (2000).

the risk. On this view we must recognize that populations have spatial structure, and often they are better seen as ensembles of subpopulations coupled by migration. Persistence of the overall population – the metapopulation – might be a consequence of the pattern of extinctions and successful migrations among the subpopulations, *even though* the latter are governed in a density-independent fashion. This response was developed first by ecologists who were not really part of the theoretical modeling tradition (den Boer 1968, Reddingius 1971, Andrewartha and Birch 1954, 1984); without the theoreticians on board, it remained a minority voice. More recently, however, there has been a great deal of theoretical interest in nonequilibrium dynamics generally, and especially in the role of spatially heterogeneous population structure (Caswell 1978, Chesson and Case 1986, Hanski 1990, Hanski and Gilpin 1997, Tilman and Kareiva 1997). Not surprisingly, these theoretical breakthroughs have coincided with the announcement in the literature of a paradigm shift and the emergence of the nonequilibrium paradigm.

Does this mean that the connection between regulation and density dependence has been broken? Not necessarily. It has been shown theoretically that if the subpopulations do not have SPDs, then the metapopulation will random walk to extinction as well (Chesson 1981, Cappuccino 1995: 5). For this and other reasons, defenders of the second balance of nature argument reject this move to sever the connection between regulation and density dependence. Turchin, for example, reports that "it is generally accepted that population regulation cannot occur in the absence of density dependence" and that the spreading the risk argument has been rejected "on logical grounds" (Turchin 1995: 20). Later, Turchin explains why density dependence is required. "Simply put, if population density has no effect on the *per capita* growth rate, then there could be no special range of population densities to which the population would return again and again. Therefore, there could be no stationary probability distribution of population densities and, by definition, no regulation" (Turchin 1995: 27). Plank number four in the second balance of nature platform must be, therefore, similar to its counterpart in the first version – namely, that density dependence is a necessary condition for population regulation.

We come finally to the last and most optional line in the schema. In the first version the fifth plank affirms the importance of competition. However, though still deemed a significant interaction, competition no longer has pride of place among the possibilities. There remains, nevertheless, a tendency to locate the regulating forces among the biotic interactions. It is difficult to find this explicitly stated, but it seems to be working as a background premise in arguments such as the following. Having found that population densities of southern pine bark beetles behave phenomenologically as though they are regulated by some delayed density-dependent mechanism, Turchin infers that the dynamics must be driven by "an interaction with some biological factor, such as natural enemies" (Turchin 1995: 32; see also Reeve et al. 1995) rather than by the weather, as had been previously thought. In the absence of further evidence implicating biotic factors, this transition suggests the presence of a background presupposition connecting density dependence and biotic factors. But if the biotic and the density dependent are to be associated in this way, and given the necessity of density dependence for population regulation, it is tempting to think that although competition may have fallen from grace, biotic interactions overall still play the pivotal role, which is what the fifth plank in the second balance of nature platform will have to say.

We can now state the second balance of nature argument thus:

Balance of Nature Argument II

1. Persistence is an ecological fact – the populations are here.
2. Since unregulated populations are statistically destined to random walk their way into extinction, most populations must be regulated (in the SPD sense).
3. Since being regulated *just is* having an equilibrium, most populations are equilibrium populations.
4. Furthermore, since regulation implies density dependence, most populations are under the influence of density-dependent factors.
5. Finally, since biotic forces are the most likely mechanisms for density dependence, we should expect biotic forces to be important determinants of population behavior.

As with the first balance of nature argument, this is more a kind of inferential progression than an argument in the strict sense of the term, and it is also, like the earlier sequence, a reconstruction from the literature. The next task is to evaluate the plausibility of this line of thought.

On the face of it, the first idea is hard to argue with. Certainly extinction is a fact of life, and population explosions are not unheard of, but persistence between these extremes would seem to be the order of the day for most ecological populations. When considered in light of the second plank, however, a potentially troublesome ambiguity once again arises. Persistence is a matter of degree, and what seems to matter is whether populations persist to a greater degree than would be expected if they were executing random walks. Put another way, that random walking populations are committed to extinction in the long run says nothing; they are committed to extinction in the long run in any case. As Grover Maxwell used to say of Bayesian justifications of induction that promise convergence of belief in the long run: "In the long run we are all dead." This criticism of what Strong calls the "old random walk bugbear" has been developed by a number of authors (Reddingius 1971, Andrewartha 1957, Strong 1984a; 1986, den Boer and Reddingius 1996).

Even if one should become convinced that the "long run" is commensurate with reasonable ecological time frames, it is not clear that the random walk argument really does any significant work. Consider White's psyllids once again. Assuming he is right, the dynamics are being driven largely by the stochastic factors of settling sites and nutritionally sufficient veins of phloem. Holding the physiology of the Eucalyptus constant, a strong element of chance determines the fates of individual psyllids and hence the overall density of the population; however, I doubt that White would say the population is executing a random walk. The density of psyllids in a given generation is presumably not statistically independent of the density in the previous generation. White might even be persuaded that small populations are more likely to get larger than smaller, and large populations are more likely to get smaller than larger – that is, the population exhibits a return tendency to at least a broad cloud of "equilibrium" values. Does this mean that White has signed on to the Balance of Nature II program? Perhaps it does. We examine that issue further in a moment. I want to emphasize here that even if this were the case, it would not be random walk worries driving him into the arms of the opposition; believing that stochastic factors dominate changes in population density is not the same as believing that such changes are purely random. Genuinely random phenomena, such as radioactive decay, are not that easy to find (Wimsatt 1980).

Failure of the random walk argument notwithstanding, suppose White grants that psyllid populations exhibit return tendencies, at least in the broad sense just described. Does it follow that such populations are regulated after all? Must he recant his opposition to density-dependent factors? Must he abandon his skepticism about ecological equilibria? The first point to note is that since density dependence is now definitionally equivalent to exhibiting a return tendency, the second question must immediately be answered in the affirmative; the psyllids are governed by density-dependent factors. The second point to note is this: since being regulated and having an equilibrium are definitionally equivalent, the first and third questions collapse into a single question. This question turns on the relationship between exhibiting a return tendency and being regulated, and here there is evidence among the proponents of the second balance of nature argument for two different readings. Turchin (1995: 28) explicitly states that the existence of a return tendency is a necessary but not a sufficient condition for population regulation (see also Berryman 1991: 142). In the same article, however, Turchin (1995: 22) says

the following: "The best way to define population regulation (and regulation in any dynamical system) is to equate it with the presence of a *long-term stationary probability distribution of population densities*" Here, regulation and the existence of a return tendency (SPD) are taken to be definitionally equivalent (see also Cappucino 1995).

If the second option is taken (i.e., regulation is equated with return tendency), then all three of the critical concepts – regulation, equilibrium, and density dependence – have been collapsed into the concept of a return tendency. Once White admits to the existence of a return tendency, he has admitted to all, and the three questions mentioned at the outset of the previous paragraph would all have to be answered in the affirmative. He might, however, be tempted to borrow Bertrand Russell's line here, pointing out that this move has all the advantages of theft over honest toil. Latitude in defining one's terms certainly increases the prospects for logical argument, but the resulting deductive certainty comes at the cost of empirical content. If, on the other hand, the existence of a return tendency is merely a necessary condition for regulation/equilibrium, then from an *a priori* standpoint, the proponents of the second balance of nature perspective have no argument at all. If there are further conditions to be satisfied before the existence of regulation/equilibrium has been established, then in the absence of further *a priori* argument, it becomes an empirical question, as well it should be, whether White's psyllids exhibit this characteristic.

This ambiguity about the relationship between return tendency and regulation/equilibrium has done a great deal to fuel the contemporary debate documented earlier. The tendency to shift back and forth on this issue has, in turn, been fostered by the determination to equate return tendency with density dependence – as we saw with the first balance of nature argument, a tight association between density dependence and population regulation has a venerable history in ecology. So what are the prospects for equating the existence of a return tendency with density-dependent control? Is the connection analytic, as the proponents of the second balance of nature argument have argued? Obviously, that depends on what one means by density dependence.

Three alternatives can be identified in the ecological literature. What I call *phenomenological density dependence* is simply the existence of statistical correlations between population density and the per capita rate of growth. *Weak causal density dependence* is the circumstance whereby population density is itself part of the mechanism determining changes in population size. Obviously, one can have the former without the latter, but not vice versa. Finally, there is an even more restrictive view of density dependence that traces back to the work of Andrewartha and Birch (1954). On that view, which I call *strong causal density dependence*, a population is not under the influence of density-dependent factors unless the "intensity" of these factors is itself a function of the density of the population (see Murray 1982 for a more contemporary exposition of this view). It is perhaps best to illustrate the difference between these last two ideas with an example. Consider a population of birds – perhaps woodpeckers – living in a habitat with a fixed number of nesting cavities. As density increases, the shortage of nesting sites begins to exert a limiting influence on population growth. Weak causal density dependence would see this as a case of density dependence because the causal story behind subsequent changes in population size involves an interaction between contemporary density and the number of nesting sites. On the other hand, because the number of nesting sites is itself constant and is not influenced by changes in population density, this would not be a case of density dependence under the strong causal density-dependence view.

Having these three notions of density dependence on the table has served to muddy the waters further in the population regulation debate. The distinction between weak and strong causal density dependence has been particularly troublesome. However, it is not particularly germane to the matter at hand, so for the purpose of this discussion I simply focus on the contrast between phenomenological density dependence and weak causal density dependence and drop the qualifier "weak" unless confusion threatens.

We can now identify the controversial issue behind the definition of density dependence in terms of the existence of a return tendency. We have already seen Turchin's rationale for this move: "Simply put, if population density has *no effect* on the per capita growth rate, then there could be no special range of population densities to which the population would return again and again" (Turchin 1995: 27, italics added). The problem is with the interpretation of the italicized phrase *no effect*. Under the phenomenological interpretation of density dependence, this passage says that if population density is uncorrelated with per capita rate of growth, there will be no stationary probability distribution. This, I take it, is a mathematical fact. Under the causal interpretation, the passage says that if population density plays no causal role in the determination of per capita rate of growth, then there will be no SPD. But the concept of an SPD is itself a statistical notion. It expresses a view about the kinds of correlations that can be found in a time series of data on population densities. Since one can have correlation in the absence of causal relationship, the second interpretation of the passage cannot be sustained. For the second interpretation to be true, a further premise is needed to the effect that there are independent grounds for believing that the correlations in

question are impossible (or at least unlikely) in the absence of a causal role for population density itself – and this, it seems, is an empirical matter.

This brings us finally to the last line of the second balance of nature argument – the preponderance of biotic factors. It is difficult to find explicit argument for this idea and consequently it is here that the problems of evaluation are most difficult. How might the argument considered so far be seen as enhancing the plausibility that biotic factors have an especially important role to play in the determination of ecological phenomena? Here are two suggestions. We have seen that there has been a long association between the idea of population regulation and the activity of biotic factors. We have also seen that there has been a tendency to identify phenomenological density dependence with population regulation. These two tendencies, together with the idea that the random walk argument establishes the existence of phenomenological density dependence, might bolster the commitment to the importance of biotic factors. A second suggestion involves the failure to maintain a distinction between phenomenological and causal density dependence. If one believes that causal density dependence has been established as a kind of most plausible null hypothesis for populations in the absence of further information, it might seem reasonable to suppose that the interactions among organisms are going to dominate the causal stories behind most demographic behaviors. If the analysis in this chapter is correct, neither of these considerations really provides grounds for a prior presumption in favor of biotic factors.

Let me summarize the critical evaluation of the second balance of nature argument. The persistence of populations, together with the random walk argument, was used to argue to claim the existence of an SPD for most populations. The random walk argument is supposed to add an *a priori* grounding to the argument in favor of regulation, equilibrium, and density dependence. In my view it adds nothing. The long run can be a very long time, and even the most hard-bitten opponent of the balance of nature stance would seem ill-advised to regard changes in population density as a genuinely random phenomenon. Still, the existence of a return tendency, because it has been defined in such a commodious way, does not seem an unreasonable expectation for most populations. Given the existence of return tendencies, four options were considered, two of them sound and two of them unsound. It makes sense to see return tendency as a necessary condition for population regulation, but it is unhelpful to equate regulation with the presence of a return tendency, thereby completely collapsing the distinctions between regulation, equilibrium, and density dependence. It makes sense to equate return tendency with phenomenological density dependence, but it is a mistake to suppose that one has thereby implicated density dependence as a ubiquitous causal mechanism behind demographic change. Finally, stripped of the unsound maneuvers, the second balance of nature argument provides no special grounds for supposing that biotic factors will have a special role to play in the determination of population phenomena.

3.5 CONCLUSION

All the arguments considered here have this in common: they attempt to settle questions about what kinds of ecological factors are most important, as determinants of demographic behavior and/or community structure, from a largely *a priori* perspective, with at best a smattering of empirical cases sprinkled in for good measure. The investigations of these efforts suggest that this is largely a futile endeavor; the questions are empirical and can be settled only by empirical means. One might urge an even stronger response: not only are the questions unresolvable *a priori*, but they are not even well-formed enough to be resolvable empirically. Because of interaction effects, sensitivities to context, and similar issues, there is simply no point to asking "What is the most important kind of ecological factor for X?" In any case, what difference does it make whether we have an answer? After all, we still need to determine the actual ecological factors that are shaping the systems we want to understand.

Taken together with the seemingly interminable debate that has surrounded these issues throughout the history of ecology, such questions prompt one to ask: Why all the fuss? Why such a need to stake out positions, largely in advance of the accumulation of relevant evidence, on questions that are so encompassing that it is not clear what sorts of considerations would eventually settle them in any case? There is no simple answer to this question. At least four factors are involved, each pointing in the direction of a further research project, and I close with a brief comment on each. (These issues are explored in more detail in Cooper 1990, 1993, 1997, 1998, and 2001.)

Since the 1960s, philosophers of science have recognized that the body of scientific beliefs that characterizes a scientific discipline has a kind of hierarchical structure. Some ideas are more fundamental than others, and the most fundamental function to set the very context for disciplinary inquiry. They shape the questions that the discipline deems answerable and worthy of pursuit as well as the kinds of answers that can count as genuine answers. Kuhn is famous for pointing out that the transitions from one set of fundamental presuppositions to another has the character of a revolution. He also argued that it is during such transitions that scientific arguments are least scientific, in the sense of being removed from primarily empirical considerations. Others, such as Lakatos, have attempted to capture some of Kuhn's insights about the structure and development of "research programmes" while avoiding some of the more irrational connotations. Setting aside questions about the individuation of paradigms or research programs in ecology, I believe these ideas are relevant to the question at issue. The arguments between Nicholson and Lack on the one hand and Andrewartha and Birch on the other, for example, seem very similar to arguments for something like distinct research programs. At issue are fundamental ideas about what sorts of expectations should be brought to bear in the investigation of particular ecological phenomena. As is typically the case with such arguments, there is a reaching beyond what any finite body of empirical evidence could ever support. There is perhaps an anology between the issues at stake here and the debate surrounding adaptationism as a research program in evolutionary biology. In the latter case, the driving and at best quasi-legitimate question is whether most traits are adaptive (see Orzack and Sober 1994 for an argument that this question is significant and also should be answered in the affirmative; see Brandon and Rausher 1996 for a dissenting opinion).

Evolutionary biology is more directly implicated in the balance of nature controversy as well. As briefly mentioned at the end of section 3.2, ecologists have often been pushed toward an emphasis on density dependence, regulation, and biotic control by (1) a desire for unification with evolutionary biology, and (2) a general presupposition, typically implicit, that biotic factors such as competition are the central engine behind natural selection. Perhaps the clearest example of the former is a 1962 paper by Gordon Orians that attacks the antibalance perspective, especially as embodied in the works of Andrewartha and Birch. Orians's central reason for siding with Lack over Andrewartha and Birch is that Lack integrates ecology into the theory of natural selection whereas Andrewartha and Birch leave ecology with no theoretical foundation at all. One of the most explicit statements of the tight connection between competition, density dependence, and natural selection, on the other hand, comes not from an ecologist but from the evolutionary biologist Theodosius Dobzhansky. As we saw in the last chapter, Dobzhansky had "been brought up to believe that natural selection, and hence the evolutionary process, are the outcome of 'competition' and therefore are governed by density-dependent factors" (Dobzhansky 1957: 235). The Dobzhansky passage reveals that the evolutionary side of the balance of nature controversy in ecology is itself intimately tied up with the controversy over the prevalence of interspecific competition (for some of the details on this controversy, see Connell and Sousa, 1983, Strong 1984b, Connor and Simberloff 1986, Connell 1990, Cooper 1993, Tilman 1993, 1994a, 1994b, Walter and Paterson 1995).

Orians's worries about the theoretical foundations of ecology reflect a further concern. In addition to threatening the integration of ecology with the theory of natural selection, the very existence of theoretical ecology is at stake in this debate. As he puts it, "The 'theory' of Andrewartha and Birch really states that no general theory of ecology is possible" (Orians 1962: 261). Baldly stated, the established theoretical traditions of ecology, tracing back to the competition and predator/prey models of Lotka and Volterra, deal with the interactions among organisms. If ecological phenomena are largely determined by abiotic factors such as the weather, then the relevance of these theoretical efforts is threatened. In short, this balance of nature debate we have been discussing overlaps to a considerable degree with another long-standing ecological controversy – the controversy surrounding mathematical model building and the development of a general theory of ecology (for discussion, see Gilbert 1980, Shipley and Keddy 1987, Caswell 1988, Tilman 1989, 1991b, Shipley and Peters 1991). The model building controversy is the focus of the second half of the book.

Finally, I believe that the tenacity with which certain ecologists cling to some version of the *a priori* argument for balance/regulation traces back to their belief that it seems to be required for the possibility of general ecological knowledge. If the determination of population behavior and/or community structure is a function of the autecology of individual species in their local settings, then it is hard to see how there could be anything really general to learn in ecology. If ecology is to have genuine laws, there must be the same kinds of processes at work in a variety of cases – density-dependent processes regulating populations around reasonable equilibria and factors such as interspecific competition and trophic relationships producing community structure that "is not widely different in almost any habitat which supports a rich fauna at all" (Elton 1933: 22). To what extent is the possibility of general ecological knowledge held hostage to this view of ecological organization? What does the emergence of the nonequilibrium paradigm, with its celebration of the contingency and historicity of ecological phenomena, imply about the possibility of such knowledge? Again, these are large questions, and ecology is only beginning to work its way through them (for further discussion, see Colwell 1984, Price 1984, Shrader-Frechette 1989, Shrader-Frechette and McCoy 1993, Beatty 1995, Price and Hunter 1995, Cooper 1998, 2001).

None of the four factors just mentioned justifies importing, in *a priori* fashion, sweeping judgments regarding matters that are, at bottom, questions of empirical fact. But they do go some distance in explaining the disposition to do so. It is tempting to suppose that along with such an explanation comes the potential to overcome the disposition – a kind of psychotherapy for

ecological practice. This is doubtless true to some degree, but it is unlikely to be true full stop. Scientists cannot avoid making plausibility judgments; not all hypotheses can be pursued nor can everything be tested at once. Such judgments are grounded in deep-seated beliefs about the nature of the phenomena under scrutiny. It is to be expected, therefore, that ecologists will approach their investigations armed with presuppositions regarding the relative significance of the causal processes in their domain. What we can hope for, perhaps, is a little less dogmatism and a little more recognition that presuppositions, while not put immediately at risk in confrontations with empirical evidence, are fallible nonetheless.