The Science of the Struggle for Existence

On the Foundations of Ecology

GREGORY J. COOPER
Washington and Lee University

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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]

[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)

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

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.

[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.

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.

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

[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