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Ecology and the Environment

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Abstract and Keywords

Ecology is the study of the interactions of organisms and their environments. The methods of ecology fall roughly into three categories: descriptive surveys of patterns of species and resource distribution and abundance, theoretical modeling, and experimental manipulations. Ecological systems are “open” systems, and patterns and processes are products of a huge number of interacting forces. Ecology and the environmental sciences have made enormous advances since the mid-twentieth century in the understanding of ecological systems, as well as in the human impact on the environment. Theory in ecology usually centers on the development of models. Environmental outcomes are uncertain and when making decisions under uncertainty, there are a variety of options available. One option is to carry out a cost benefit analysis based upon expected utilities and other is to adopt the precautionary principle. Uncertainty and under determination of theory by evidence is a fact of life in science.

Keywords: ecology, interaction, system, theory, environment, model, science

1. Introduction

Ecology is the study of interactions of organisms and their environments. The term “ecology” (from the Greek *oikos*, which means house or dwelling) was coined by Haeckel in 1866, to refer to the study of “the economy of nature” and “the complex interrelations referred to by Darwin as the struggle for existence.” Ecology's antecedents in plant physiology, biogeography, demography, and evolutionary biology (Edgerton 1976; McIntosh 1985; Kingsland [1985]1995) investigated how individual organisms adapt to their physical environment, how populations grow, and what shapes the patterns of distribution and abundance of different species. Ecology today is a “patchwork” of

subdisciplines (Sarkar 2005): physiological ecology, behavioral ecology, population ecology, community ecology, evolutionary ecology, and ecosystem ecology. Within these subdisciplines, there are even further divisions, e.g., between terrestrial and marine community ecology. McIntosh (1985) calls ecology a “polymorphic” discipline, due in part to the fact that ecology is so diverse in its subject matter.

Ecology is unlike fields such as physics or evolutionary biology, in that there is no central set of laws or principles. In part, this may be due to its diversity of subject matter. However, some have argued that there are no lawful generalizations to be discovered (Shrader-Frechette and McCoy 1993); ecological phenomena, they argue, are simply too historically contingent, unique, or complex. Others contend that there are ecological laws, though the debate has been complicated by the fact that there is very little agreement as to what counts as a law (Ginzburg and Colyvan 2003; Lange 2005; O'Hara 2005). While ecologists can occasionally agree on the truth of descriptive generalizations, *ceteris paribus* (e.g., the species-area law),¹ there is frequently little agreement as to the mechanisms that give rise to them.

The methods of ecology fall roughly into three categories: descriptive surveys of patterns of species and resource distribution and abundance, theoretical modeling, and experimental manipulations, either in the laboratory or in the field. Most models of hypothesis testing in ecology take experimental manipulation and control to be central (Hairston 1989). However, experiment should not be emphasized to the exclusion of all other methods of investigation. Some of the most innovative advances in ecology grew out of carefully done natural history, though some still will claim that this is not “scientific” ecology. There is a long and heated debate among ecologists over the relation between theoretical modeling and empirical tests of hypotheses in the laboratory and field, as will be discussed further below (section 3).

Critical reflection on the concepts, methods, successes, and limitations of ecology is not merely of philosophical interest. The science of ecology has, of course, a great deal of social and political significance. Conservation management strategies depend upon models and predictions in population ecology. Ecological research on the small scale may have implications for the biosphere as a whole (e.g., linking patterns of tree growth in tropical forests to global patterns of carbon dynamics and global climate change; Clark et al. 2003). And it is not only empirical results, but also conceptual questions about defining core terms, appropriate methods of testing hypotheses, and burden of proof that have import for environmental policy. With such pressing problems as global climate change, biodiversity loss, pollution, and the overconsumption of natural resources at stake, the question of what counts as “good science” in the context of ecology and the environmental sciences is an issue that has import for the public at large, not only for philosophers of science.

One of several ways of approaching the variety of conceptual and interpretive issues that arise out of the science of ecology is to examine the history of ecological ideas. Ecology has a particularly rich history, which repays philosophical examination. For instance, a

persistent background assumption among ecologists, as well as in popular culture, is that there is a “balance of nature” (Edgerton 1973). Only relatively recently have ecologists transformed this metaphor into precise hypotheses and subjected them to empirical tests. Many of the purported mechanisms upholding this “balance” have been shown to be questionable (e.g., the diversity-complexity-stability hypothesis) and will be discussed in greater detail below (section 2). This historical case study will serve as a useful entry point for examining a number of core conceptual issues in ecology: (1) the problem of defining ecological terms and concepts, such as “community” and “stability,” (2) the problem of generality and contingency in ecology, and finally (3) the problem of the “natural” and the “normative” in ecology.

Ecology is the study of the patterns of interactions of organisms with their environments; of course, this includes our own species. So ecologists are often (p. 506) called upon to address questions concerning not only how humans do, but how they ought to, relate to their environment (Kingsland 2005; Mitman 1992). Before the late nineteenth century, this question was framed in terms of what was “natural,” where humans were understood as somehow standing outside of or apart from nature. Ever since Darwin, biologists have understood that humans are simply one among many species and no less “natural” than blowflies or beetles, but popular conflation of the “natural” with normative ideals of the environment absent human impact continues (Sober 1986). Since the 1960s, ecologists have responded to the concerns about human impacts on the environment and formed ties with other disciplines in order to better understand human-induced factors influencing climate change, emerging diseases, extinction risk, and exotic invasions. Ecology is one of several fields under the umbrella of the “environmental sciences,” which also encompasses the fields of chemistry, biology, climatology, epidemiology, geography, demography, oceanography, and geology. Ecology has, more by accident than by design, been called upon to serve as a bridge among these many disciplines. The interdisciplinarity of the environmental sciences is an experiment in progress and a model for the future course of science. A philosophical investigation of this new interdisciplinary breed of inquiry may yield interesting insights about not only the internal practice of science, but also the fraught border between science and policy. How are theories confirmed that draw so broadly on so many different fields? Can we have a predictive science of the biosphere, and what will it look like?² What standards of certainty should we expect and demand in the environmental sciences, in making choices about environmental policy? The problem of decision making with respect to uncertainty in the environmental context will be addressed in the final section (section 4).

2. A Balance of Nature? History of the Idea

When one visits a tropical forest, one may be struck by the sense that it is a well-ordered household, in which it seems that each species keeps within a relatively limited boundary in abundance. One may further be struck by the chains of interdependence among

species. For instance, epiphytes attached to the branches of tropical trees take advantage of soil particles blown through the canopy, supply needed nutrients to canopy trees, and serve as a home for tree frogs, mosquitoes, flatworms, snails, salamanders, and even some crabs (Kricher 1997). These and similar observations of apparent “balance” in the sense of species constancy and coadaptation inspired natural theologians in the eighteenth century to comment, “The Balance of the Animal World is, throughout all Ages, kept even, and by a curious Harmony and just Proportion between the increase of all Animals ... the (p. 507) World is through all Ages well, but not overstored,” and “every distinct Part of Nature's works is necessary for support of the rest” (Derham 1714, p. 171; Bradley 1721, p. 159 cf. Edgerton 1973). Similar claims of balance by natural historians can be traced back to antiquity.

In contrast, one might be struck by the dynamic features of the forest; each individual seems to struggle to reproduce as much as possible as light gaps open and are filled. If one observes over a long enough time span, the composition of the assortment and chains of causation between different species can change radically over time. Species go extinct, or they come to dominate a landscape, or they exclude other species in competition for similar resources. These and similar observations prompted Wallace, Darwin's contemporary and co-discoverer of the theory of natural selection, to comment: “Some species exclude all others in particular tracts. Where is the balance? When the locust devastates vast regions and causes the death of animals and man, what is the meaning of saying the balance is preserved?” (Wallace, in McKinney 1966, 345–46; cf. Edgerton 1973). Wallace draws attention to the dynamism, rather than stability, of communities.

These two perspectives illustrate a persistent divide in the history of ecology, over whether and to what extent communities are more or less stable or balanced. The notion of a “balance of nature” has been called a “background assumption” and an “orientation toward ecological phenomena” (Edgerton 1973; McIntosh 1985). Edgerton describes it as one of those concepts in the history of science “that have remained as background assumptions for long periods of time without anyone thinking that they needed testing” (Edgerton 1973). The idea that nature was somehow in balance had, for a long time, the status of dogma, guiding belief and practice in ecology, without quite rising to the status of a testable hypothesis before the mid-twentieth century.

One may distinguish two components of the idea: a descriptive thesis (or, rather, theses) and a hypothetical explanation, usually either “externalist” or “internalist.” Cuddington (2001) describes three main descriptive theses: (1) the claim that natural populations have more or less constant numbers of individuals, (2) the claim that natural systems have more or less constant number of species, and (3) the claim that communities of species maintain a “delicate balance” of relationships, where removal of one species could cause collapse of the whole. As for explanations of these theses, in externalist explanations, some power or factor outside of the phenomenon of interest controlling or regulating its orderly behavior was appealed to. In internalist explanations, some internal factor of self-regulation was invoked. Until the late nineteenth century, the externalist

explanations were appeals to either God or gods' role(s) in ordering the natural world, which Edgerton calls "providential ecology" (1973, p. 330). On the alternative, internalist account, nature itself was viewed as a kind of "superorganism."

In the twentieth century, ecologists advanced several explicit empirical hypotheses about the role of density dependence in governing population sizes, the role of competition in structuring communities, and the role of diversity and complexity in community stability, and subjected them to empirical test.³ Debates (p. 508) over these questions were surprisingly heated and persistent over decades (Cooper 2003; Cuddington 2001). Several explanations are available for this: First, these seemingly straightforward empirical questions bear on a normative question. Are ecological systems, absent human interference, in some sense more stable than those that have been subjected to such interference? When forests are cut, cities or dams are built, it is evident that the environment changes and, therefore, perhaps is more subject to disturbance of various kinds (invasions, extinctions). This commonsense observation stands behind the a priori assumptions that ecologists and proto-ecologists frequently have made about the stability of ecological communities (Cooper 2003).

Second, the debates required the formalization and operationalization of key ecological terms and concepts, such as "stability" and "equilibrium." This turned out to be surprisingly difficult, what Sarkar (2005) has called the "formalization indeterminacy problem." Further, the debates occurred in a wider context concerning the historical contingency of ecological systems. If populations or communities are not "self-regulated" either by density-dependence or competition, then some ecologists were concerned that there may be no general "laws" governing ecological systems. And, if there are no laws of ecology governing ecological communities, i.e., if there are no higher-level properties or systematic laws of organization and behavior of these entities, then perhaps communities and ecosystems are not natural kinds. One may see how these questions arose and were resolved below, in a survey of the history of the idea of the balance of nature, in two phases, 1859–1950 and 1950–2000.⁴

2.1. The balance of nature in community ecology, 1859–1950

In the late nineteenth century, recognition of large-scale geological change and the fact of extinction caused natural historians to rethink the indefinite "stability" of ecological communities. However, even among those who recognized the fact of extinction, appeal to the balance of forces regulating population abundances was common.⁵ Darwin comments that the "forces" governing population sizes and species composition are "so nicely balanced, that the face of nature remains uniform for long periods of time." Nonetheless, he notes that "the merest trifle" can upset this balance, giving "victory to one organic being over another" (1859, 73). Darwin seems to emphasize the struggle between species for survival over their harmony.⁶ He does, however, invoke the superorganismic view of ecological communities when he speaks of species being akin to

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the “organs in the same body” (cf. Edgerton, 1976, 341). Darwin's theory did not replace the balance-of-nature idea so much as provide a theoretical framework for subsequent advocates of the idea of community self-regulation.

Many early community ecologists imagined that competition or natural selection somehow regulated population sizes. For example, Forbes (1887) and (p. 509) Clements (1916) made claims to the effect that there is an “economy” or “balance” of nature. While they occasionally used these terms interchangeably, there are a variety of different plausible senses of both an “economy” and “balance” of nature. For example, by “economy,” one might mean specified roles in some system of interchanges—for example, one assumes that there are specified niches out there to be filled. By “balance,” one might mean species constancy, or constancy of species' interrelationships, or both. Perhaps, for genuinely stochastic, historical reasons, it may be that those taxa which occupy those niches do so fleetingly. Hence, you could have an economy but not balance in the sense of species constancy.⁷ Forbes' and Clements' explanations tended to be internalist ones, in that there were forces of self-regulation governing population abundances and species composition. Both suggested that the lake or plant community functions as a superorganism, with coadapted parts, each serving their separate functions.

Forbes famously described the lake as functioning as a “microcosm,” an organic unit, “like a single organism” (Forbes 1880; cf. McIntosh 1985), and argued that “a steady balance of organic nature ... holds each species within the limits of uniform average number, year after year” (1887, 549). Forbes undertook a careful analysis of the food webs connecting insects, birds, and fish in a lake community. Forbes suggested that natural selection somehow adjusted reproductive rates in species so that they did not overpopulate. In this way, “beneficent order is maintained,” and “an equilibrium has been reached and steadily maintained that actually accomplishes for all the parties involved the greatest good which the circumstances will all permit” (Forbes 1887, 549–50). Forbes was particularly subject to slipping between the natural and the normative; he not only described “a general community of interests” among species, but also suggested that a similar “harmonious balance of competing interests” might be achieved in “human affairs.” One of the concerns motivating much of his work was that wild nature exhibited relative balance and homeostasis, as compared to areas inhabited by or affected by humans and their domesticated plants and animals. Forbes is exemplary of a tradition in ecology of seeing the community as highly integrated and self-regulating.

This idea was shared, but advanced beyond mere metaphor, by Clements. Clements studied grasslands and conifer forests in the West and developed a theory of the plant community as governed by deterministic laws of succession leading to a stable “climax community” (Clements 1916). Clements believed that the community could be analyzed as a superorganism with both a structure and a function, as well as a natural birth, development, and death. Moreover, a climax formation could “reproduce” itself, “repeating with essential fidelity the stages of its development” (Clements 1936, 261). Clements introduced an elaborate series of distinctions between stages of community

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development (preclimax, proclimax, subclimax, disclimax, postclimax), classified different kinds of plant associations, and did detailed work on the specific species compositions of these different types. Clements' work was thus an advance over Forbes, insofar as he urged more quantitative sampling and viewed himself as testing hypotheses, as opposed to merely giving descriptions of plant formations. He called his approach "dynamic ecology," (p. 510) which he contrasted with merely "descriptive ecology." There is no doubt that ecology was emerging out of natural history and becoming a more self-conscious science at this stage (McIntosh 1985, 76-85). Key to the superorganismic view that Clements popularized were three ideas: communities were bounded, they were governed by laws of succession, and these laws were due to internal, structural features of the type of community one was investigating.⁸

The superorganismic view was challenged on both empirical and conceptual grounds, first by Gleason (1926) and, somewhat later, by Arthur Tansley (1935). Tansley argued that the idea of the community as a "complex organism" has at best heuristic value; while he did not dispute that vegetational associations are typical of some regions (there are "formations" of regional vegetation associated with different climates), he disputed the notion of a monoclimate, or the characterization of succession as a progress toward a single equilibrium. Tansley also drew attention to the boundary problem, i.e., it is difficult to make clear distinctions between, or draw discrete boundaries around, different communities or, in his preferred language, ecosystems. An ecosystem, in Tansley's view, could be as small as a drop of pond water or as large as an ocean; which kind of ecosystem one chooses to study is dependent on the interests of the scientist. Nonetheless, Tansley also claimed: "[T]he longer vegetation is left alone ... the more it tends to form well-defined communities, and the more these develop relatively constant and well-defined 'structures' in relatively stable equilibrium with their conditions of life" (Tansley 1935, 215).

Gleason, however, was less willing to grant that equilibrium was a property of ecological systems. In his view, plant associations were a matter of "fluctuating and fortuitous immigration of plants and an equally fluctuating environment" (Gleason 1926, 23). On the Gleasonian "individualistic" view, communities are not natural kinds with distinct functional organization, but rather chance associations of organisms particularly adapted to one or another environment. The distributions of plants one finds in an area is a product of individual life histories and the initial conditions set by the physical environment, not some natural "growth" of a superorganism. Gleason comments:

There is nothing comparable to reproduction in any assemblage of plants Far from being an organism, an association is merely the fortuitous juxtaposition of plants. What plants? Those that can live together under the physical environment and under their interlocking spheres of influence and which are already located within migrating distance. (Gleason 1926, 8-10)

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This divide between Clements and Gleason was not merely a debate over a metaphor, but a debate about the ontology of communities (their boundedness, functional integration) and about the problem of reducibility and generality in ecology. According to the individualistic concept, communities are accidental products of chance and the physical environment, chance products of individual populations' trajectories. On this view, stability is not necessarily a property of communities; their composition or structure can change relatively quickly and (p. 511) may or may not eventuate in a stable association of species. If communities are merely fortuitous associations of plants and animals, and their structure is a by-product of the autecology of individual species in their local environments, then a hope for laws of regulation of communities seems elusive (Cooper 2005). One should focus instead on individual populations and the factors shaping their growth, rather than seek general community-level laws of association. On the other hand, if communities are functional wholes with tightly integrated causal interactions, then one might discover regular laws of succession, and the properties of communities or ecosystems cannot be reduced to the behavior of individual organisms or populations and features of climate and geography. The holistic internalist view of Clements can be contrasted with the more reductionist and externalist view of Gleason, dividing early ecologists over not merely the fact of community boundedness and lawful regulation, but also the very possibility of generalizations in ecology.

Similar debates were found in early population ecology. The debate (Nicholson 1933; Andrewartha and Birch 1954) over whether population sizes are regulated by “density-independent” or “density-dependent” factors, or whether the regulation of population sizes in nature was governed primarily by external forces (climate, etc.) or internal factors (crowding, mate availability, etc.) similarly takes sides on the problem of internal regulation and reducibility. The “forces” at issue governing the purported balance of nature and the phenomena to be explained were different, but the form of explanation was very similar. Cooper (2003) has argued that the tenacity of ecologists in clinging to some version of the a priori argument for internalist, biotic regulation of population sizes is traceable to their belief that such an internalist explanation is necessary for a general science of ecology to be possible. If there are not lawful, deterministic factors internally regulating population sizes, then perhaps there is nothing “really general to learn in ecology” (Cooper 2003, 94).

2.2. Balance of nature: Phase II, 1950-2000

The idea of a balance or economy of nature persisted to some extent into the latter half of the twentieth century. However, the concept subtly changed; the increase in popularity of ecosystem ecology shifted the rhetoric from talk of “harmonious integration” to “cycling,” of nutrients, energy flow, “feedback mechanisms,” and other machine metaphors from cybernetics, physics, and engineering (Kingsland 2005; Taylor 1988). Ecosystem ecology became “big biology” in the 1950s and '60s, with the federal government's funding of the International Biological Program. Tom and Eugene Odum's popular textbook, *Fundamentals of Ecology* (1953), with graphics resembling electrical circuit models, gave the appearance of a more mathematical and theoretical science. The hope was that the huge investment in the IBP would pay for itself with a new predictive ecological theory. There were frequent claims that a new “revolutionary” science of ecosystem ecology could supersede and replace the merely descriptive community ecology of the recent past.

(p. 512)

However, this hope was not fulfilled (see Golley 1994). Despite huge expense and the investment of time and effort of quite a few ecologists, illuminating generalizations about the patterns and processes governing ecosystems were few and rather unsurprising (Sarkar 2005). Further, the same questions about the contingency and historical uniqueness of ecological communities arise in the context of ecosystems. And replacing “balance” with “equilibrium” only counts as an improvement if one gives a definition and operational measure of purported equilibrium. The very same worries that Tansley (1935) raised about community ecology arose again in the context of ecosystem ecology: Do ecosystems have functional integration? Is it meaningful to speak of them in “equilibrium” or as more or less “stable”? How should one define “stability,” “regulation,” and “organization”? Moreover, “function” and “dysfunction” are in part normative notions. While one can measure patterns and processes of nutrient and energy cycling in ecosystems, or features of trophic organization (Naeem et al. 1995), it is not clear how to operationalize ecosystem function in a way that does not import evaluative notions (Brennan 1988).

The notion of stability has proven extremely difficult to operationalize consistently. The debates over the relationships among community stability, complexity, and diversity illustrate the intractability of the formalization indeterminacy problem (Sarkar 2005). The idea that complexity or diversity somehow yields more stable communities is a fairly intuitive one, first articulated by MacArthur (1957) and Elton (1958). MacArthur explained, “If each species has just one predator and one prey the stability should be minimum, say zero, and ... as the number of links in the food web increases the stability should increase (there is a compensatory response to species loss)” (MacArthur 1958). Likewise, Elton reasoned that the more pathways available for energy to reach a consumer, the less severe the consequences of losing one pathway. Some have called this

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the “redundancy” theory, i.e., more-diverse ecosystems with more trophic interactions have a greater “buffering” effect for species loss than less diverse, simpler systems. As evidence for his theory, Elton noted that agricultural monocultures are more prone to pest outbreaks than mixed communities, that pest outbreaks are rare in tropical ecosystems (more diverse than temperate), that population cycles occur primarily in species-poor ecosystems (arctic regions), and finally, that invasion by new species is easiest in oceanic islands that are species-poor.

From the 1950s through the '70s, most ecologists accepted that more-diverse or complex communities were more stable. However, May proposed in 1973 that increased complexity in fact jeopardizes stability. More precisely, May constructed model food webs comprising a number of species and investigated the way in which the population sizes of each species changed in the neighborhood of its equilibrium abundance. He found that three key parameters, S , the number of species; C , the “connectance” of the web; and β , the average interaction strength of interactions, all tended to *decrease* stability. Or, disturbed populations would be *less* likely to return to equilibrium abundance when these parameters took high values. Stability (p. 513) decreased as diversity, connectance, or interaction strength increased (Begon et al. 1996). May's work seemed to undermine the conventional wisdom about diversity-stability-complexity, and led to a long debate in the literature. The debate was complicated by the fact that different authors adopted different definitions of ecological stability, diversity, and complexity (Pimm 1991). May defined “diversity” as simply species number (also called “species richness”). However, one might also define “diversity” using a variety of other criteria, (abundance, chances of interaction, etc.) (Sarkar 2005). Depending upon how one defines diversity, stability, or complexity, one arrives at entirely different conclusions regarding their relationships (Justus forthcoming; see also Ives 2005).

Some (Shrader-Frechette and McCoy 1993, 57) conclude on the basis of these terminological difficulties that the idea of stability is “conceptually incoherent.” However, once measures of stability are made precise, testable predictions about the relationships among different aspects of complexity, diversity, and stability are possible. Moreover, communities may be stable in some sense, but not in others; or diversity in some sense may contribute to stability, but not in others (Ives 2005). The controversy is not over, but the most reasonable conclusion to draw is as follows. The relationship between the complexity of a community and its stability appears to vary with the type of community (grasslands, intertidal zones), with the way in which the community is perturbed, and with the ways in which stability is assessed (see Lehman and Tilman 2000; Pfisterer and Schmid 2002; Sarkar 2005).

What is the upshot? Environmental ethicists have frequently sought support for their views about our moral obligations to the natural world in the environmental sciences. For instance, appeals to the “good” of an individual organism, species, or ecosystem are often founded on more or less scientifically grounded conceptions of organismic fitness or ecological balance. Yet, it is not clear whether these sciences have any implications to the effect that individual organisms, species, or whole ecosystems have a “good” (Cooper

1998). For that matter, even if there were a “natural” course that any particular species or collection of species heads toward, it is unlikely that environmentalists would regard it as desirable. Most species in the history of life on Earth have gone extinct. Ecological communities are dynamic; like species, communities have gone extinct and been replaced by new communities, alongside changes in geology and climate.⁹ Surely, extinction is not the end that environmental ethicists are endorsing.

A challenge for philosophers of the environmental sciences is to provide a clearer understanding of the science of the environment for those who wish to preserve it. Is the environment “fragile,” or are varieties of species of plants and animals living in a “delicate balance”? As reviewed above, this debate has been made more precise and split into a variety of different debates in the science of ecology, and generalizations about community stability are elusive. With a better understanding of the history of this idea and of its variety of manifestations, environmentalists will perhaps be more cautious in their appeals to the environmental sciences and in their use of terms like fragility and balance.¹⁰

(p. 514) 3. Methodological Challenges for Ecology

The balance-of-nature debate illustrates a number of persistent methodological challenges in ecology. Ecological systems are “open” systems, and what patterns and processes we see are products of a huge number of interacting forces. So, holding factors constant and testing hypotheses about various relationships between different factors, or estimating even simple ecological parameters in the field, are all difficult. There are a few well-studied (often highly controlled) environments, but field ecology is difficult to fund and frequently undersupported. Moreover, ecological terms and concepts, such as community and stability, have been defined in a variety of different ways, which has complicated the search for ecological generalizations. Developing well-confirmed general hypotheses about ecological systems has proven to be difficult. Ecologists have become increasingly aware that ecological associations are “contingent” (in the sense of being products of historical forces) and “local” (in the sense that local associations have specific characteristics relative to local climates or geological conditions). However, it does not follow that generalized skepticism about the science of ecology is in order, for two reasons. First, most sciences are subject to some of the same difficulties of uncertainty and formalization, though in different respects and to different degrees. Second, ecology and the environmental sciences have made enormous advances since the mid-twentieth century in our understanding of ecological systems, as well as in the human impact on the environment. Despite the many challenges to a science of the environment, scientists are optimistic about developing more-predictive models (Moorcroft, forthcoming) and integrating data from a wide variety of fields (Clark and Gelfand, forthcoming).

Some ecologists, noting the contingency and uniqueness of communities, have argued that there are no lawful regularities to be discovered in ecology. On the one hand, some (Lange 2005; Ginzburg and Colyvan 2004, 2003) have argued that ecology does have laws, though these laws frequently are subject to exceptions. On the other hand, “law skeptics” (McIntosh 1985 Peters 1991; O'Hara 2005) argue that there are very few candidates for lawful regularities in ecology, given the complexity, uniqueness, and contingency of ecological systems. Part of the difficulty in resolving this debate is that there continues to be controversy over how to define a law of nature. Theory in ecology usually centers around the development of models, so perhaps it would be more fruitful for philosophers to examine the roles of models and theoretical modeling in ecology. The attempt to force models into the confines of the classical model of laws (i.e., as exceptionless generalizations) has proven especially difficult in ecology.

Theoretical modeling has a long tradition in ecology, primarily in population ecology, where the “golden age” of mathematical ecology originated. Population ecology uses deterministic and stochastic models to represent population dynamics (p. 515) over time, for single species and for species pairs, such as the famous Lotka-Volterra predator-prey model. Lotka-Volterra is a population-level model, representing population sizes of prey as functions of the density of predator populations, and as such, it makes a number of idealizing assumptions. For instance, the model assumes that the growth of populations is exponential in the absence of predators and that the predator and prey encounter one another randomly in a homogeneous environment, and it treats individuals in both populations as identical.

Structured, or “individual-based” population ecology models relax some of these assumptions. For instance, they assume that individuals vary by sex, age, and health, and they might represent the environment as heterogeneous, so that predator and prey do not encounter one another at random. Thus, the latter models are more “realistic,” in the sense of dropping false or idealized assumptions. One might consider this an advantage. However, there is some controversy on this point. A model that includes more of the relevant details and drops idealizing assumptions may have a number of limitations. It may be difficult to estimate the large number of variables and parameters in the field (Odenbaugh 2005). And, such models might be analytically intractable, though computer simulations may be helpful in this regard. On the other hand, the value of population-level models turns upon whether there are, in fact, population-level properties to discover and whether these are causally related to other such properties. In other words, is the “identical individuals” assumption a harmless one? Do individual-level interactions wash out, so that population-level models capture general properties of a larger number of systems? This is an empirical question, and it seems that, until it is decided, it may be wise to pursue both individual- and population-level models (Odenbaugh 2005).

The question of whether we ought to prefer individual- versus population-level models, it seems, turns on what we want them for. Whether the identical-individuals assumption is harmless really turns on how much precision we require, and what we need the models to do for us. Models serve a variety of functions, but in the main are used to consider in

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simplified form the essential factors governing complex systems. Models are tools, but they are also representations of systems of interest. This is the crux of the difficulty of modeling; insofar as models serve as tools, they need to be user-friendly, and simpler models are easier to manipulate and understand. However, complex models are more likely to be more accurate representations of systems of interest, insofar as they include more of the moving parts or more of the causal details. It follows, according to Levins (1966), that there are tradeoffs in choosing a model; generality, realism, and precision, he claims, cannot be maximized simultaneously. One must choose, or so he claims, between different goals.

Levins argues that there are three strategies of model building in population ecology: modeling that sacrifices generality for the sake of realism and precision (what he calls Type I), modeling that sacrifices realism for generality and precision (Type II), and modeling that sacrifices precision for generality and realism (Type (p. 516) III). There has been a series of replies and exchanges in the literature on what he might mean and whether his insights can and should be preserved. Orzack and Sober (1993) argue that Levins is mistaken. They define the terms “generality,” “precision,” and “realism” as follows:

- (G)** If one model applies to more real world systems than another, it is more general.
- (R)** If one model takes account of more independent variables known to have an effect than another model, it is more realistic.
- (P)** If a model generates point predictions for output parameters, it is precise. (534)

Given these definitions, they claim that there are not necessarily tradeoffs among these three virtues in model building. For instance, they show that one model may be both as general and more realistic (in their senses of the terms) than a second model if, for instance, the latter is a special case of the former. Thus, generality and realism can be maximized simultaneously. (Their example is density-independent versus density-dependent models of population growth. The former can be “nested” in the latter, or it is an instance of the more-general case, only the value of the variable describing the effects of density is zero.) Moreover, they show how we may increase realism, and make no sacrifice in generality or precision in a model, simply by adding new independent variables. In other words, they show how, in some cases at least, it is possible to maximize all three virtues.

In reply to Sober and Orzack, Odenbaugh (2003) argues that Levins' claim is about the pragmatics of model building. Levins (1993) also remarks in his reply to Sober and Orzack that model building is a process, and the process can be developed along different lines to meet different needs. Levins claims that, on Orzack and Sober's “formalist” view, we construct models and then proceed to determine whether they fit the world. Better or worse fit can be engineered by adding or removing variables, or by making models more or less realistic or precise. Levins explains that, for some purposes, one may be satisfied if a simple, general model can answer a number of questions about the general dynamics

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of a system given certain assumptions, and in such cases, a sacrifice of precision is not necessarily a loss.

This debate connects to a larger debate about empiricism, the role of theory, and the perils and profits of model building in ecology. McIntosh (1987) describes a turning point in ecology in the 1960s and '70s, when many ecologists imagined that the development of information theory, systems analysis, and mathematical models would turn ecology into a “hard” science, with more predictive power. This was exemplified in the then-rapid growth of mathematical ecology and systems ecology and the hope for a general, unifying theory of ecosystem functioning. However, he notes that these heady days have been followed by a period of “retrenchment” in ecology, where ecologists have started to grant that “pesky ‘biological details matter a lot,” and the individuality of species responses and the heterogeneity of ecological community types has served to complicate the hopes for a general theory in community ecology.

(p. 517)

In response to these and similar criticisms of theory within ecology, Roughgarden (1984), Haila (1988), and May (1981) provide a defense of theory in ecology. Theoretical models are, admittedly, sometimes simply either quasi-analytic truths (e.g., species number on islands is a function of immigration and extinction) or hold only of organisms in highly controlled environments (e.g., the logistic model of population growth). However, such models serve as “conceptual devices” (Haila 1988) or as frameworks for developing more context-sensitive models and testable hypotheses. Roughgarden (1984) also argues that models are “collections of tools” that help one to “visualize” phenomena, “sensitize” us to potential hypotheses, and aid in “understanding.” Wimsatt (1987) has argued that idealized models or, in his words, models that are, strictly speaking, false, can be important tools for arriving at “truer” theories.

Cooper (2003) calls this the “heuristic” role of models or the “theory-as-tools” perspective. He explains, “The point is not that theories should be allowed to float free of empirical constraints but that the emphasis on immediate and rigorous testing of theoretical ideas [is a] misunderstanding [of] the cognitive roles that theories play” (Cooper 2003, 170). On this heuristic account, models are ways of allowing one to see the likely consequence of making this or that assumption about the dynamics of a system of interest, in however an idealized fashion. Lewontin makes a similar point with respect to theoretical modeling in population genetics, “The delineation of the prohibited and the possible is the function of population genetic theory. The revelation of the actual is the task of population genetic experiments” (Lewontin 1985, 11).

In sum, theoretical modeling serves a variety of functions, from addressing “what if” questions (conditional on certain assumptions, what pattern or process might we expect?) to setting problems for empirical investigation.

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There has been a divide between those ecologists who are promoting a “mechanistic” and “experimental” approach to ecology, against what they see as the excesses of theory. This has been helpful, insofar as it has spurred more experimental work in ecology. However, theoretical modeling can serve important functions. Levins' claim that there is no “single, best all-purpose model” (1966, 7) should perhaps be understood as follows. Models are tools; different tools serve different purposes. Excesses of theory are only problematic when and if they do not assist in developing testable hypotheses or in enhancing understanding by uncovering conditional truth claims about ecological system dynamics.

4. Environmental Decision Making

Many environmental outcomes are uncertain. We do not know the exact costs of our actions. For instance, we do not know the exact risk posed to biodiversity, coastal cities, or agriculture by global climate change. However, we do know that (p. 518) there is a nonnegligible risk. When making decisions under uncertainty, there are a variety of options available. One option is to do a cost-benefit analysis based upon expected utilities. Bayesian decision theorists calculate the expected utility of each course of action, and then choose the course of action that has the highest expected utility. Expected utilities are calculated by multiplying the value assignments of each outcome/action pair by the estimated probability of some state of affairs coming to pass. Then, they add the products for each possible choice.

For instance, suppose one is deciding whether to try river rafting for the first time. Suppose one is going with a relatively experienced guide and estimates that the chance of falling out and having to swim is about 10%. Of course, going for a swim is the least-favorable option, worth, let's say, 1 out of 100 points. Not rafting were the trip to be perfectly safe and pleasurable would be unfortunate (there would be an "opportunity cost") but not, of course, as unfortunate as the first scenario; so, the value of this option is 30 out of 100 possible points. Not rafting when a fall is imminent is the second-best favorable option, worth, say, 60 out of 100 points. Finally, rafting and having a safe and pleasurable trip is the most-favorable option, thus, we shall assign it 100 out of 100 points. The expected utility of taking the trip is thus $(.80 \times 100) + (.10 \times 1) = 80.1$, versus $(.80 \times 30) + (.10 \times 60) = 30$, for not taking the opportunity to raft. Based on this calculation, one should take the river rafting trip. Of course, a great deal depends upon what value we assign to each of the options. So there are two sources of uncertainty: In addition to the uncertainty surrounding the question of what will happen, there is uncertainty surrounding what we value. One might be willing to absorb the opportunity cost in this case, given the risk, however small. This procedure is called "decision making under uncertainty."

Arguably, many environmental problems are unlike ordinary decision making under uncertainty in at least one important respect: The consequences may be irreversible. So not only is there difficulty in estimating the probability of various events coming to pass and in assigning values to various options, there is the added problem that if we make a wrong choice, the consequences are irreversible or, as some say, catastrophic. Thus, some argue that ordinary cost-benefit analysis based upon expected utilities is the wrong way to make decisions in such cases. Unlike cases where we can reasonably estimate costs and benefits over the long run, environmental problems may have no long run. Some have called environmental dilemmas such as these "zero-infinity" dilemmas (Norton 1987) or cases where the uncertainty of risks is high and the cost of failing to change behavior may be catastrophic.

Thus, there are two strategies we might consider. First, one can take the risk of there not being an environmental catastrophe, and simply go ahead and continue as before, on the basis of the following rationale. The intuitive idea is that acting out of fear of the unknown is irrational. Or, it is irrational to take precautions, unless the need for precaution has been established on the basis of rigorous standards of acceptability (Sunstein 2004). So, the burden of proof should be placed on those claiming that there is a very serious risk; we should, on this (p. 519) account, be optimists and assume the best until proven otherwise. Part of the reason for adopting this viewpoint is consideration of the costs of reacting to unknown risk; the annual cost of stabilizing carbon dioxide emissions, for example, has been estimated as 1–3% of the gross domestic product of the entire world, on the order of the entire output of Canada (Economist 1993, 84). With this kind of cost at stake, some, such as the United States, have endorsed a “wait and see” policy. One official, justifying the U.S. failure to sign the Rio Protocol to reduce greenhouse gases, wrote, “Scientific uncertainties must be reduced before we commit the nation's economic future to drastic and potentially misplaced policy responses” (Bernard 1993, 157; cf. Haller 2002).

On the other hand, some endorse the opposite perspective: precaution (Gardiner 2006). The precautionary principle has been given different formulations, often with drastically different implications (Sunstein and Hahn 2005). However, it is, roughly, that one should take precautionary measures in the face of uncertainty. This is a reversal of the standard burden of proof in scientific contexts. For most novel scientific hypotheses, the assumption is that one should be skeptical of their plausibility until proven otherwise. Thus, some claim that to adopt a precautionary principle is “unscientific.” However, there is a variety of different rationales on offer. Some base their preference for the precautionary principle on the maximin rule: “Choose the option with the least worst outcome.” Others argue that the nature of environmental problems as zero-infinity dilemmas is such that precaution is warranted. For, if one must await certainty on environmental questions, it may simply be too late before action to reduce the costs is possible.

The precautionary principle has been controversial because (a) it is vague, and (b) on some formulations, it seems so strong as to set an impossible standard. Zero tolerance for risk would require almost impossible precautionary measures. In its weakest versions, however, the precautionary principle seems to reduce to a matter of cost effectiveness. That is, the only difference between cost-benefit analysis and adopting the precautionary principle is that the latter simply places greater weight on the costs. Thus, the precautionary principle falls prey to many of the same objections that have been raised to cost-benefit analysis, namely, uncertainty in assigning probability of outcomes and difficulties in estimating costs and benefits. Furthermore, many environmental decisions have prisoner's dilemma features, insofar as acting alone, one does not have the assurance of a good outcome; collective action is necessary for everyone to benefit. So it

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seems irrational on this account to act alone with precaution: “Everyone else is polluting, my actions alone will have minimal effect, so why not pollute?”

However, given what we have seen above about the indeterminacy in many ecological questions, from the prevalence of density-dependence to the role of complexity in generating stability, it should not be seen as an impassible obstacle that the answers to many environmental questions do not have the level of certainty hoped for. Uncertainty and underdetermination of theory by evidence is a fact of life in science. Thus, placing an unreasonable burden of proof for hypotheses about global change seems unwise. Ultimately, these decisions come down (p. 520) to whether we are willing to collectively assume the costs of precautionary action. And, once everyone so acts, the prisoner's dilemma disappears, and it becomes rational to act with precaution.

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Notes:

(1.) For a discussion of the species-area law, see Sarkar (2005).

(2.) For a review of these issues, see Moorcroft (2006); (Clark and Gelfand, 2006).

(3.) For excellent historical reviews, see Edgerton (1973), McIntosh (1985), Cooper (2003), and Kingsland (2005).

(4.) Of course, the historical break is arbitrary.

(5.) An example is Spencer, who believed that, as evolution progressed, the forces governing population increase and decrease came into balance (fertility was adjusted to mortality) (Kingsland [1985]1995; Spencer, 1898).

(6.) Thanks to Michael Ruse for pointing this out.

(7.) Thanks to Jay Odenbaugh for this helpful clarification.

(8.) Others had recognized patterns of succession but did not share Clements' superorganismic view of communities. For instance, Cowles (1899) discussed the succession of plant communities, but his emphasis was on the role of geological and climatic features, rather than features internal to the community, and he thought that the successional stages were not linear and deterministic, but could regress and fail to reach the climax state. Some (Tobey 1981) have identified Clements and Cowles as founders of two traditions in ecology—a "holistic" versus an "individualistic" view of communities.

(9.) Odenbaugh notes that the work of Davis (1969) is a good illustration of this point. Davis is a paleoecologist who has analyzed pollen data over the northeastern part of the United States. As the glaciers receded, she has noted, tree species that generally had formed communities—that is, they had occurred together at the same place—migrated north at very different rates. If communities were functionally interdependent, surely their parts would hang together. Thanks to Odenbaugh for this argument.

(10.) One especially pernicious metaphor is Ehrlich and Ehrlich's (1981) rivets metaphor; the extinction of species is like "popping rivets" on a plane, and one such rivet may prove to be the last. For a discussion of the difficulties with this metaphor, see Sarkar 2006.

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