

(To appear in *Encyclopedia of the Philosophy of Science*, edited by Sahotra Sarkar, Routledge Press)

Ecology

A Polymorphic Science

Ecology is composed of a remarkably diverse set of scientific disciplines. There are many different sub-fields in ecology—physiological, behavioral, evolutionary, population, community, ecosystem, and landscape ecology. Clearly, no summary will do them all justice. However, for the present context, ecology as a science can be divided into three basic areas—population, community, and ecosystem ecology. This entry will introduce some of the fundamental philosophical issues raised by these three disciplines.

The first order of business is to ask what is the science of ecology, and more importantly, what is it *not* (see Brennan 1988). Sometimes the term ‘ecology’ is treated as synonymous or coextensive with three different concepts or sets of concepts:

- The science of ecology: the study of organisms and groups of them and their relation to their environment.
- Environmentalism: a set of sociopolitical views about the right relationship between humans and nature.
- The ecology of an organism, population, or community: in the case of organisms, roughly the life-history of that organism.

This entry will focus only on ecology in the first of these senses—as a set of scientific disciplines. It should be noted, however, that there are important questions about how the science of ecology is related to environmental ethics and public policy (see Ludwig, Mangel, and Haddad 2001).

Metaphysics and Ecological Communities

One of the standard topics of ecology is *succession*. Succession concerns the structural and compositional changes that occur in communities and ecosystems as populations and species replace each other. Traditionally, succession is broken into three types of stages. There is a *pioneer* stage in which the first colonizers arrive in an area, there are the subsequent stages called *seres*, and there is a final, relatively stable stage called a *climax*. Succession is either *primary* or *secondary*. Primary succession involves the colonization of bare ground where no ecosystem was present. Examples of areas where primary succession occurs are sand dunes, volcanic flows, mud flats, or glacial tills. Secondary succession involves the replacement of communities after some disturbance that may involve abandoned fields, wind-blown gaps in forests, or wildfires. An example of temperate terrestrial secondary succession is the sequence of annual weeds, perennial weeds, shrubs, young pine forest, and oak forest with a well-defined canopy.

One of the foundational controversies in community ecology arose between Frederic Clements (1916) and Henry Gleason (1917) concerning succession and the nature of communities. Clements argued that communities follow a very specific sequence of stages that can be characterized in terms of nutrient cycling, species diversity, and biomass. He claimed there is a single climax community that is self-perpetuating and tightly integrated as the result of biotic interactions between species. Clements considered communities to be “superorganisms”:

The developmental study of vegetation necessarily rests upon the assumption that the unit or climax formation is an organic entity. As an organism the formation arises, grows, matures, and dies... The life-history of a formation is a complex but

definite process, comparable in its chief features with the life-history of an individual plant (1916, 16).

Gleason considered Clements' views to be without empirical support, and argued that succession results from individual species' physiological requirements and local climatic conditions.

[I]t may be said that every species of plant is a law unto itself, the distribution of which in space depends upon its individual peculiarities of migration and environmental requirements (1917, 26).

Hence, Gleason's views were more "individualistic." Likewise, he did not think that there is a final climax community, but rather communities are continually changing and non-equilibrial. These two approaches to succession and communities continue to be of influence in contemporary ecology (see Levins and Lewontin 1980 [1993], Simberloff 1980).

Nonetheless, one is still left wondering what communities are. Ecologists have conceived of communities in roughly three different ways (Shrader-Frechette and McCoy 1993, 11–31);

- Communities are groups of species at particular places and times and nothing more.
- Communities are functionally interrelated groups of species.
- Communities are groups of species that are organism-like entities.

Biologists grant that an ecological community is minimally a set of species. However, what else if anything is required? As Shrader-Frechette and McCoy write:

Envision a group of species occurring in the same place at the same time. Conceptually, what attributes might be used to link these species together, such that they could be distinguished from other similar groups? (1993, 13)

Better sense can be made of these three different concepts of communities by considering some metaphysics.

Objects, except possibly for the simplest, are composed of parts. Those parts may or may not be related to each other. Objects can be classified by the relations that exist between their parts. These different types of objects will be called *aggregates*, *wholes*, and *individuals*. If an object is an *aggregate*, then its parts bear little or no causal relations to one another. Thus, aggregates are not causally integrated at a time or over time. If an object is a *whole*, then certain causal relations exist between its parts. Wholes exist as causally structured entities that are minimally integrated at a time and through time. Finally, an *individual* is an object whose parts bear causal relations to one another such that the object is highly structured and integrated. The differences between aggregates, wholes, and individuals concern the causal relations amongst their parts and the strength of those relations. These objects form a continuum and the differences between them are of degree.

Now consider the sort of community that Gleason had in mind:

Are we not justified in coming to the general conclusion, far removed from the prevailing opinion, that an association [i.e., community] is not an organism, scarcely even a vegetation unit, but merely a *coincidence*? (1926, 16).

Communities, according to Gleason, are composed of whatever species coexist in space and time. This we might call a *Gleasonian Community*.

A *Gleasonian community* is a group of species in a particular area at a particular time.

In effect, this type of community consists of aggregates—objects whose parts bear few if any causal relations to one another.

Now consider those communities that exist as wholes. Here there are a set of species that exists as a structured entity—there are causal relations that at least weakly integrate the species at a time and through time. This type of community concept is

sometimes associated with George Evelyn Hutchinson. Hutchinson thought of communities as having feedback loops that assure their self-regulation and persistence.

What sorts of causal relations or “feedback loops” might bind species in a community? One candidate is the various interspecific interactions that exist amongst organisms and populations. Between any two species, we can classify these interactions as either positive (+), negative (−), or non-existent (0) depending on how they affect the growth or abundance of the respective species. These relations include competition [−,−], predator-prey [−,+], mutualisms [+,+], amensalisms [−,0], and commensalism [0,+]. Likewise, some interactions take place between more than two species. These *indirect effects* occur when a donor species’ influence is transmitted through at least one transmitter species to a receiver species. Finally, pairwise interactions themselves may be *non-additive* if the interaction between the pair changes as the number of species in the community changes. If there are interspecific interactions between species that integrates the species into something more than an aggregate—a whole—then this community will be called a *Hutchinsonian community*.

A Hutchinsonian community is a group of species that at least weakly interact with one another and no others.

The community exists as a group of species structured by various interspecific causal relations. One can also see why some ecologists are skeptical of the existence of plant communities and animal communities, respectively, since they leave out causally salient parts.

Finally, a *Clementsian community* is a tightly integrated group of species that bear various causal relations between its component species. The community forms an individual like that of a multi-cellular organism. So,

A *Clementsian community* is a group of species that strongly interact with one another.

Communities can exist as aggregates, wholes, or individuals.

It is certainly an empirical issue whether any of these community concepts apply to any group of species. Nonetheless, some progress has been made in understanding what ecological communities *might* be. Next, several arguments will be considered for why one might think ecological communities do not exist. Here is one such argument. Communities are real only if they have distinct boundaries. However, many purported communities do not have distinct boundaries. Hence, many purported communities are not real (see Simberloff 1980, 16–17; Levins and Lewontin 1980, 54).

There are several general points to be made about this argument. By all accounts, a community consists in a group of species. Moreover, the community exists wherever those species exist. Thus, its boundary consists of its outermost species. So, though it may be difficult to determine, a community's boundary is determined by its species' boundaries. However, putatively different communities blend continuously into one another unless there is some *ecotone*—a relatively discrete zone of transition (Figure 1). If they blend continuously, then it is not clear where the communities begin and end.

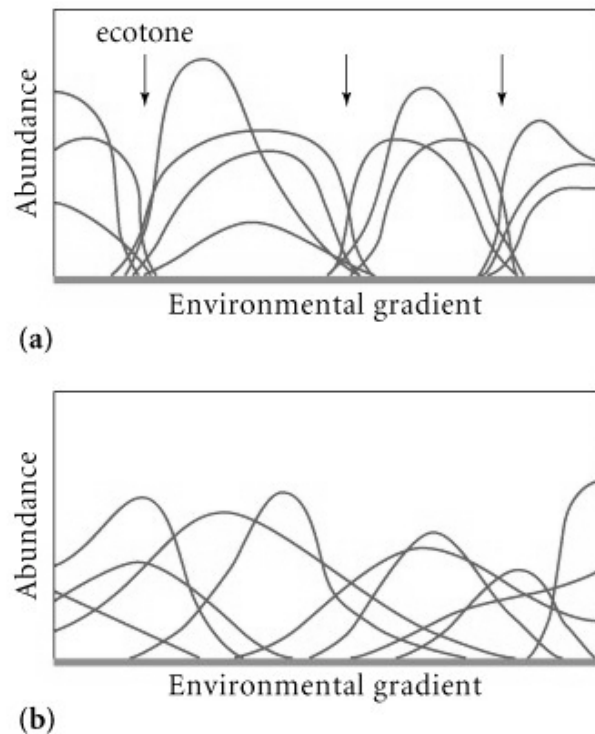


Figure 1. (a) Ecotones generating discrete boundaries between groups of species. (b) No ecotones generating discrete boundaries between species (from Ricklefs and Miller 2000, 524).

This may be an epistemological problem for ecologists, but from a metaphysical point of view it need not be. For example, if two Hutchinsonian or Clementsian communities share common habitat they still are distinct in virtue of the causal interactions between their respective species. As Richard Levins and Richard Lewontin write, “The question of boundaries of communities is really secondary to the issues of interaction among species” (1980 [1993], 54). Hence, the problem of continuous overlap need not be a particular problem for the Hutchinsonian and Clementsian approaches.

There does seem to be reason for denying the existence of Gleasonian communities. Recall that a Gleasonian community is a set of species in particular area at a particular time. Suppose we have a group of n species at a particular place at a

particular time. If the group is a Gleasonian community, then we can properly ask why some other $(n + 1)$ -th species is *not* a member of the community. If we were taking one of the other approaches, the answer would be given by the causal interactions of the n species. The $(n + 1)$ -th species would be excluded from such interactions. However, on the Gleasonian approach, it appears that the membership of the community is not secured by mind-independent causal interactions but rather by the ecologist's choice about spatial and temporal boundaries. However, if Gleasonian communities objectively exist, they must exist mind-independently. The communities depend on ecologists' decisions—arbitrary or not—as to what species to consider members of the community. Hence, they do not objectively exist. This in effect was the view of the ecologist Robert MacArthur:

Irrespective of how other ecologists use the term “community”—and there are almost as many uses as there are ecologists—I use it here to mean any set of organisms currently living near each other and about which it is interesting to talk... (1962, 189–190).

Likewise, something is *natural* only if it does not depend on human activities. Hence, even if Gleasonian communities exist, they would be non-natural in this sense. Hence, they either do not objectively exist or are non-natural.

This discussion has considered the nature of ecological communities and has only skimmed some of the issues. There are, however, many conceptual and metaphysical problems concerning ecological entities. Here are some others. *Token* ecological communities may exist; however, what about *types* of communities or *biomes*—do temperate grassland, chaparral, savanna, deserts, taiga, and tropical rain forests exist as well? Much of early community ecology consisted in classifying communities and traditional accounts of succession seem to depend on such classifications. Do other ecological entities like ecosystems or guilds exist? If ecosystems exist, do they possess

fashionable properties like *health* and *integrity*? As ecosystem ecologist Howard Odum eloquently notes, “The intriguing question is, do mature ecosystems age, as organisms do?”

A Balance of Nature?

One might consider it “folk wisdom” that flora and fauna exhibit a “balance of nature” (Egerton 1975, Pimm 1993). Ecologists have often thought that the more diverse or complex a community or ecosystem is, the more stable it would be. This section will consider the diversity/complexity-stability hypothesis conceptually.

As was mentioned in the introductory section, ecologists have debated the meanings of *community* for some time. Similarly, *stability* has been construed as the return of species abundances to their pre-perturbation equilibrium values, resistance of invasion by exotics, and the persistence of species composition of the community after a disturbance. At first glance, one might conclude that ecology is in conceptual disarray, since ecologists cannot even agree on what they are theorizing about (Shrader-Frechette and McCoy 1993).

To formulate diversity-stability hypotheses carefully, ecologists have provided precise notions of ecological stability. We can understand this hypothesis as the following claim:

As the diversity or complexity of a community increases, so does the stability of the community.

However, this is really a schema for a variety of hypotheses depending on how one characterizes ‘stability’, ‘diversity’, and ‘complexity’. In order to understand the

concept(s) of *stability*, it is useful to begin with an examination of the work of Stuart Pimm (1984a, 1984b, 1991).

Pimm distinguishes *complexity*, *stability*, and *variables of interest*. The complexity of a community can be defined in terms of species richness, connectance, interaction strength, or evenness. Species richness is the number of species in a community. Connectance is the number of interspecific interactions divided by those possible. Interaction strength is the mean magnitude of interspecific interaction; i.e., the size of the effect of one species' density on the growth rate of another species. Species evenness is the variance of the species abundance distribution. The variables of interest are individual species abundances, species taxonomic composition, and trophic level abundance. One important issue to note is that diversity (species richness and evenness) forms a proper part of the complexity concept. Hence, as ecologists have moved from evaluating "diversity-stability" hypotheses to "complexity-stability" hypotheses, they have broadened the very nature of their hypotheses.

The 'stability' of a community is characterized in one of the following ways (1984b, 322):

- *Stability*: a system is stable just in case all the variables return to their initial equilibrium values following a perturbation
- *Resilience*: how fast the variables return to their equilibrium following a perturbation
- *Persistence*: how long the value of a variable lasts before it changes to a new value
- *Resistance*: the degree to which a variable is changed following a perturbation
- *Variability*: the degree to which a variable varies over time

The number of options for formulating a complexity-stability hypothesis has the three dimensions of complexity, stability, and variables of interest. There are four definitions of complexity, five of stability, and three variables of interest. Thus, there are an extremely large number of contenders for the complexity-stability hypothesis.

Physicist-turned-ecologist Robert May (1973) was one of the first to explore precisely the connections between complexity and stability with what are called *local stability analyses*. May assumes that there is a community of species described by a set of nonlinear first-order differential equations. To determine the joint equilibrium density N_i^* of the species, their growth rates ($dN_i(t)/dt$) are set equal to zero and the equations are solved. One must then determine whether the joint equilibrium density is stable or not. That is, if the species were perturbed in a relatively small way from that joint density, would they return in the limit? If the community would return, then it is asymptotically locally stable, and is not locally stable otherwise.

May constructed his model communities with S species by choosing the interaction coefficients a_{ij} , a parameter measuring the effect of species j on species i , at random. Thus, some species interaction coefficients were greater than, less than, or equal to zero, and hence, some species pairs interacted as competitors, predator and prey, and mutualists. He defined the connectance C of the community as the proportion of interspecific interactions a_{ij} not equal to zero. The intensity I of the interspecific interaction a_{ij} was a random variable with a mean of zero and a variance of I^2 . May infamously demonstrated that a community is qualitatively stable if, and only if,

$$I(SC)^{1/2} < 1$$

Hence, an *increase* in the number of species, connectance, or interaction strength all lead to a *decrease* in the stability of a community. May's result has not gone uncriticized. Nonetheless, more realistic models lead to the same general result that stability decreases with increasing complexity.

Stuart Pimm (1984) investigated larger perturbations of a different kind than the arbitrarily small demographic ones of May's analysis. Pimm's larger perturbation was the deletion of single species from the community. Informally, a community is *species deletion stable* if, and only if, following the removal of a species from the community all of the remaining species are maintained at a new locally stable equilibrium. Pimm found with qualifications that the number of interactions decreases the community's species deletion stability.

Empirically oriented ecologists have not always looked favorably on the work of May and his mathematical cohorts. For example, J. S. McNaughton argued that the truth of the diversity-stability hypothesis depends on empirical tests, all else are "acts of faith, not science" (1977, 516). One study he and his colleagues conducted was on the grasslands in the Serengeti-Mara ecosystem in Tanzania and Kenya. McNaughton examined the effect of the grazing African Buffalo *Syncerus caffer* on the grasslands. He found that species diversity in the more diverse stands decreased more than in the less diverse stands because of grazing. Amazingly though, the more diverse community suffered less of a reduction in primary production (biomass) than the less diverse community. McNaughton concluded from his study that, "[t]he weight of evidence resulting from explicit tests of the diversity-stability hypothesis...suggests, not that the hypothesis is invalid, but that it is correct" (1977, 522). It thus seemed that species

diversity stabilizes ecosystem properties like primary production, and so the diversity-stability hypothesis is true and the recent models incorrect.

In 1983, Pimm and Anthony King replied to McNaughton's work, attempting to "resolve this apparent contradiction between theory and empiricism." Pimm and King devised grazing food web models with n plant species and one herbivore. They examined the models with respect to three types of complexity—species richness, connectance, and species diversity. Pimm and King found that for each type of complexity, complexity increases relative biomass stability, which is the ratio of total plant biomass without the herbivore and the total plant biomass with the herbivore. They also found that if stability is determined by species composition of the community, then stability decreases with increasing complexity. So Pimm and King's and McNaughton's results generally coincide.

Pimm and King argue that McNaughton was incorrect in supposing that either the field ecologists or the mathematical modelers were right. There are different types of stability and increasing complexity can increase or decrease those different types of stability independently. The conflict between the work of McNaughton and the modelers was only apparent.

Since 1982, David Tilman has continued the work of May, Pimm, and McNaughton by conducting large-scale experiments at Cedar Creek Natural History Area in Minnesota. These experiments have shown that species richness is positively correlated with plant community stability—there is a decreased coefficient of variability of plant community biomass with increasing numbers of species. However, diversity does not seem to have much effect on the variability of the component populations. There is

still much controversy over whether increasing diversity *causes* decreasing plant biomass variability.

Lastly, Kristin Shrader-Frechette and Earl McCoy argue (1993) that the terms *stability* (and *community*) are “ambiguous, imprecise, and inconsistent.” They claim that if community ecology is to produce predictive, general theories that are adequate for environmental applications, then the foundational concepts of ecology must be clear and precise. Otherwise, there will be conceptual confusion, and different interpretations of those concepts will lead to different conservation strategies (1993, 54, 57-58). They conclude that the theories of community ecology are not well equipped for conservation purposes (for a response, see Odenbaugh 2001).

Ecological Theories: Contingency, Predictive Accuracy, and Explanation

This section will consider various methodological problems that have haunted ecological theory. Ecology has not suffered from a lack of theories. However, these models and the practice from which they arise have been heavily criticized (Peters 1991, Shrader-Frechette and McCoy 1993). As Daniel Simberloff writes,

Ecology is awash in all manner of untested (and often untestable) models, most claiming to be heuristic, many simple elaborations of earlier untested models. Entire journals are devoted to such work, and are as remote from biological reality as are faith-healers (1981).

Critics have been skeptical of the construction of theory for these and other reasons. Whatever its merits, this skepticism does force us to wonder how the success of model building, if it is successful, *could* arise. Put dramatically, how is it distinct from a sort of numerology? This section will consider three questions:

- Can ecologists build *successful* theories and models?

- How should ecologists *evaluate* their theories and models?
- Can ecological theories or models be *explanatory*?

For want of space, the treatment here will consider some characteristic answers and is not intended to be exhaustive.

Can ecologists build successful models and theories? Ecologists have long desired general theories that account for the behavior of populations, communities, and ecosystems. More than any other ecologist, MacArthur has been associated with the building of such theories, often in mathematical form. He argues that ecologists are in the business of finding and explaining general patterns in the distribution and abundance of organisms. They should seek theories that minimize history and emphasize the equilibria so dear to their hearts.

However, if a research program like MacArthur's is to succeed, the biological world must cooperate. Philosophers and ecologists have suggested two problems with such theorizing. First, there is the problem of *contingency* (Sterelny 2000). One can argue that there simply are no general patterns about which ecologists can theorize. For example, historical accidents of distribution involving geographic barriers can play important causal roles in determining which species occur where. Australia, for instance, has bats and marsupials but very few other mammals. As Kim Sterelny writes:

The worry posed by extreme versions of the contingency hypothesis is that there are no patterns at all. The thought here is that membership and abundance within a community is sensitive to so many causal factors that we cannot project from one community to another (2001, 158–159).

More generally, ecological systems can be sensitively dependent on their prior states. This means that if the system's state at time t had been otherwise, then the system at $t + \Delta t$ would be significantly different. However, if ecological systems exhibit this

“sensitive-dependence” or if history matters, then ecologists should provide narratives, not mathematical models. At least in part, ecology would consist in labor-intensive case studies (Shrader-Frechette and McCoy 1993).

The second problem is that of *complexity*. Ecological systems can be exceedingly complex. They have large number of parts that usually interact in nonlinear ways. Moreover, ecologists themselves are limited cognitively. First, there are limitations that arise from the inability to manipulate experimentally the systems as directly as is desirable. In the field, there are multifarious factors at work and only some of them are recognized at any given time. Second, there are limitations in the ability to use our mathematical representations of the systems of interest. Present capacities for storing and retrieving information, carrying out various inferences, and abstracting from details make it difficult for us to use certain types of mathematical formalisms. Hence, ecological modeling may be too labor intensive and mathematically intractable to be of any use for prediction (Levins 1966). There may be general ecological patterns that we cannot discern or explain.

In light of the problems of contingency and complexity, many ecologists have accepted *theoretical pluralism* (McIntosh 1987). First, metaphysically, ecologists must grant that there is no single biotic or abiotic process that is responsible for ecological patterns. Second, models must be built with differing degrees of realism, generality and precision. Some models should be more mechanistic and some more phenomenological. Moreover, one may have to trade these desiderata off as Levins (1966) has long suggested. Finally, methodologically there must be a dynamic division of labor amongst modelers, laboratory experimentalists, and field workers.

How should ecologists evaluate their theories and models? There are two issues to consider here concerning the role of prediction in modeling.

- Should ecological models be evaluated on the basis of their predictive accuracy and that alone?
- Provided that some models make predictions that can be tested, how should those predictions be evaluated?

Critics of ecological modeling offer the following argument. If models are going to be epistemically successful, then these theoretical hypotheses must be empirically testable. However, models are not straightforwardly testable. They either make *no* predictions, *no testable* predictions, or testable *false* predictions. Ecologist R. H. Peters writes,

Ecology seeks to predict the abundances, distributions and other characteristics of organisms in nature... This book contends that much of contemporary ecology predicts neither the characteristics of organisms nor much of anything else. Therefore it represents neither ecological nor more general scientific knowledge (1991, 17).

Therefore, theoretical models are not a successful part of ecology.

Different critics recommend different ways of coping with the predictive failure of models. Even without delving into those proposals, serious problems can be seen with the preceding argument. First, some ecological models can accurately represent some empirical systems. Second, the argument assumes that predictive accuracy is the most important function of models. However, models, even empirically inaccurate ones, can be used for a variety of purposes. For example, they allow ecologists to explore possibilities, clarify ecological concepts, and provide conceptual frameworks for experimentation and fieldwork. As theoretical ecologist Hal Caswell (1988) argues, it is false to think that

- the only important thing to do with theories is to test them
- that refuted theories must be abandoned

- idealizations are a “methodological evil.”

Models must be evaluated for performing the tasks for which they are designed. Theoretical ecologists like Caswell have argued that “theories are tools”—they are theoretical instruments that allow biologists to further their cognitive goals. These goals include predictive accuracy but not exclusively so. As philosopher William Wimsatt (1987) has suggested, “false models can lead to truer theories.” Ecologists and philosophers however have been slow to explain how the heuristics of model building works and what its standards are.

These pragmatists have also suggested that model building is *inescapable* for ecologists. For example, Charles Elton, without mathematics, suggested that communities that are more complex are more stable. Through the work of May and Pimm, it can be seen that there are many different ways of characterizing stability, complexity, and variables of interest. As Caswell writes:

None of these distinctions were, or could have been, drawn by Elton. Their importance became apparent only as the original verbal theory was studied using mathematical models (1988, 35).

The same is true in more applied matters. One recent trend in applied ecology is *population viability analysis* (Boyce 1992). Ecologists utilize simple logistic equations, Leslie projection matrices, and probabilistic models of demographic and environmental stochasticity to simulate the expected time to extinction of various species. These tools are needed since the relevant autoecological data is lacking and, if conservation is at stake, it is impossible to perturb experimentally these demographically depressed populations. There is no choice but to predict the fates of endangered species with mathematical models even if they are not especially accurate. Thus, model building is an essential part of theoretical and applied ecology.

Turning to the question of how the predictions of models should be tested, one of the most cantankerous debates in ecology concerns *null hypotheses* (Gotelli and Graves 1997). In essence, the debate arose concerning how important interspecific competition is in structuring properties of organisms such as body size and resource use. This debate also led to more general issues surrounding how should ecological theories be tested and evaluated. In 1975, ecologist and physiologist Jared Diamond published a study on the distribution of bird species among fifty islands in the Bismarck Archipelago near New Guinea (Diamond 1975). Diamond recognized that certain combinations of species were never found together in the archipelago. For example, two species of cuckoo-dove, *Macropygia nigriostris* and *M. mackinlayi*, occur on six and fourteen islands respectively (Figure 2). However, they never co-occur on any island.

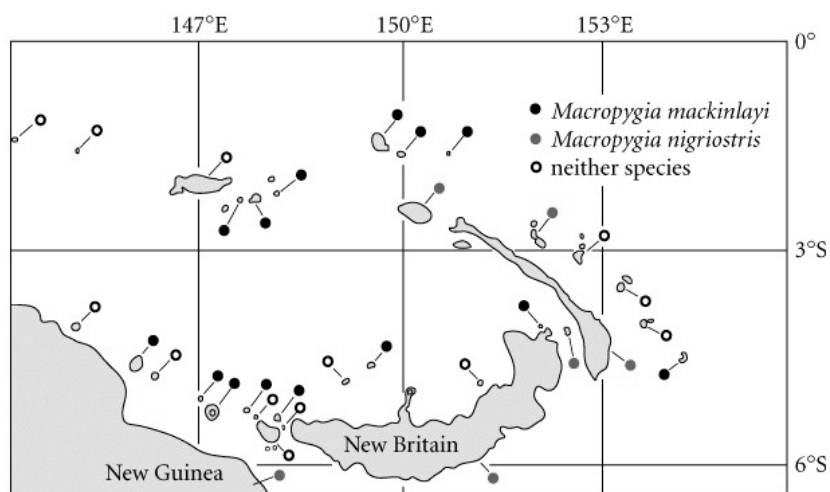


Figure 2. The Distribution of *Macropygia* species in the Bismarck Archipelago (from Ricklefs and Miller 2000, 613).

This “checkerboard pattern” or complementary distribution suggested that interspecific competition was at work through niche differentiation.

In the late seventies, Edward Connor and Daniel Simberloff (1979) argued that Diamond's work was seriously flawed. They suggested that the checkerboard distribution could have resulted from random colonization rather than competition. They devised *neutral* or *null models* of communities that retain certain features of the communities such as the number of species per island, the relative abundances of species, and their incidence functions (the probability of a species occurring on an island given the total number of species on that island) but reassemble the rest at random excluding the effects of competition. If the actual data differ in statistically significant ways from the null hypothesis, then the null is rejected and the interaction is strongly suggested. Simberloff and his colleagues claimed that null hypotheses were more parsimonious and "logically prior" to competitionist hypotheses. Contrary to a Popperian philosophy that Simberloff and Connor's adopted, Diamond looked for confirming evidence as opposed to trying first to refute a null hypothesis.

Simberloff and his group's work has been heavily criticized. First, in traditional Neyman-Pearson statistical testing, one formulates two mutually exclusive and exhaustive hypotheses, the null and the alternative. However, the null hypotheses articulated by the Florida group were not always logically inconsistent with competitionist hypotheses according to Michael Gilpin and Diamond. Key features of the null models—the species pools, dispersal abilities of species, and "incidence functions" of species—could be affected by competition (Gilpin and Diamond 1983). Hence, the "ghost of competition past" might be built into the null model itself and thus it have a "hidden structure". Second, Connor and Simberloff performed their analyses using sets of species that were not restricted to guilds (groups of species that utilize similar resources

in similar ways). Competition is to be expected between two species only if they occupy the same guild. One would thus bury the effects of competition in a morass of irrelevant data (Gilpin and Diamond 1983).

It should be noted that Connor and Simberloff argued even if one could delineate guild assignments with good evidence and had the “checkerboard pattern”, one still could not conclude that interspecific competition had been in operation. Likewise, they argued that Gilpin and Diamond had not provided independent evidence for their “hidden structure” claims (see Strong et. al. 1984 for the details of the debate).

The null model controversy continued in paper after paper and forced ecologists to address subtle issues concerning how predictions of ecological theory should be evaluated. It has invigorated hypothesis testing in ecology and has led to more refined statistical tools for judging theory.

Can ecological theories or models be explanatory? Theories and models in ecology presumably provide scientific understanding of the systems they represent. A common philosophical supposition is that a theory or model explains some event or regularity only if it is true. However, generally ecological models are highly idealized—whatever their virtues, truth is not one of them. Hence, they cannot be explanatory. However, it does appear that ecological models do explain some events and regularities. Thus, models in ecology are not explanatory or truth is not a necessary for successful scientific explanation.

As an example, consider the following why-question, “why is omnivory (feeding on more than one trophic level) rare in vertebrate food webs rather than common?” Pimm and John Lawton (1978), using Lotka-Volterra community models, gave one possible

explanation for this. They demonstrated by computer simulations that food webs with omnivores were generally dynamically unstable. They either were locally unstable, or if locally stable, their return time was excessively long. Hence, vertebrate food webs with omnivores would be unlikely to persist. Thus, a possible answer to the why-question is that vertebrate food webs with omnivores are dynamically fragile and hence do not persist.

Now the Lotka-Volterra community model is a caricature of empirical food webs. Some of the idealizations of the model include assuming that there is no migration, no age or genetic structure in the populations, and the density-dependence is linear. Nonetheless, Pimm and Lawton argued that these dynamical models explain various patterns of food webs including the infrequency of omnivory. The fact that the model is severely idealized does not render it unexplanatory alone.

There are several ways to deal with this problem and I will mention one (see Cartwright 1983 and Wimsatt 1987). Philosopher Greg Cooper (forthcoming) has offered a position that countenances the possibility that false ecological theories and models are explanatory. He argues, following Nancy Cartwright, that ecological models represent the *capacities* or *tendencies* of objects, which is how they would behave if there were no interfering forces. The dynamic equations of the models are true only of these dispositions or propensities. So, for example, the Lotka-Volterra model mentioned above is false of most, if not all, actual food webs though true of “interference-free” food webs. Cooper’s proposal requires that we accept capacities and tendencies exist which may sound implausible to empiricists. However, like Cartwright, he believes that much of science cannot be accounted for without them. Nonetheless, even if we accept the

existence of capacities and tendencies, we still need to understand how idealized models explain ecological dynamics when there are interfering forces.

Conclusion

Ecology presents philosophy with several conceptual and methodological problems. These issues are not just of an abstract bent, but speak to how we should understand the role of science in society (see the Conservation Biology entry). Many issues of importance are connected to the empirical studies and theoretical analyses that ecologists perform. These can be in determining the status of invasive species, considering whether a population is threatened or endangered, and telling us of the risks in losing many of the communities of plants and animals across the globe. To make sense of the roles these ecologists play in policy formation, their scientific activities must also be considered. These issues are enveloped in political and ethical issues of some complexity—all the more reason to exercise philosophical care. After all, how the science of ecology is understood affects both human lives and the environment.

Bibliography

- Boyce, Mark. "Population viability analysis." *Annual Review of Ecology and Systematics* 23 (1992): 481-506.
- Brennan, Andrew. *Thinking About Nature: An Investigation of Nature, Value and Ecology*. Athens: University of Georgia Press, 1988.
- Cartwright, Nancy. *How the Laws of Physics Lie*. Cambridge: Cambridge University Press, 1983.
- Caswell, Hal. "Theory and Models in Ecology: A Different Perspective." *Ecological Modelling* 43 (1988): 33-44, 1988.
- Clements, Frederic. "Plant Succession." Carnegie Institute, Washington Publisher 242 (1916): 1-512.
- Connor, E. F. and Daniel Simberloff. "The Assembly of Species Communities: Chance or Competition?" *Ecology* 60 (1979): 1132-1140.
- Cooper, Gregory. *The Science of the Struggle for Existence: On the Foundations of Ecology*. Cambridge: Cambridge University Press, 2003.
- Diamond, Jared. "Assembly of Species Communities" In *Ecology and Evolution of Communities* (eds.) M. L. Cody and J. M. Diamond. Belknap: Harvard, 1975.
- Egerton, Frank. "Changing Concepts of the Balance of Nature." *The Quarterly Review of Biology* 48 (1973): 322-350.
- Giplin, Michael and Jared Diamond. "Are Species Co-occurrences on Islands Non-random, and Are Null Hypotheses Useful in Community Ecology?" In *Ecological Communities: Conceptual Issues and the Evidence* (eds.) Donald Strong, Daniel Simberloff, L. G. Abele, and A. B. Thistle. Princeton: Princeton University Press.
- Gleason, Henry. "The Individualistic Concept of the Plant Association." *Bulletin of the Torrey Botanical Club* 53 (1926): 7-26.
- _____. "The Structure and Development of the Plant Association," *Bulletin of the Torrey Botanical Club* 44 (1917): 463-481.
- Gotelli, Nicholas. and Gary Graves. *Null Models in Ecology*. Washington, D. C.: Smithsonian Institution, 1996.
- King, Anthony and Stuart Pimm. (1983) "Complexity and Stability: A Reconciliation of Theoretical and Experimental Results." *American Naturalist* 122 (1983): 229-239.

- Levins, Richard. "The Strategy of Model Building in Population Biology," *American Scientist* 54 (1966): 421-431.
- Levins, Richard and Richard Lewontin. "Dialectics and Reductionism in Ecology." In *The Dialectical Biologist*. Cambridge: Harvard University Press, 1993.
- Ludwig, Donald, Mark Mangel, and Brent Haddad. "Ecology, Conservation, and Public Policy." *Annual Review of Ecology and Systematics* 32 (2001): 481-517.
- McNaughton, John. "Diversity and Stability of Ecological Communities: A Comment on the Role of Empiricism in Ecology." *American Naturalist* 111 (1977): 515-525.
- McIntosh, Robert. "Pluralism in ecology." *Annual Review of Ecology and Systematics* 18 (1987): 321-341.
- MacArthur, Robert "Patterns of Terrestrial Bird Communities." In *Avian Biology Vol. 1*, (ed.) Farner, D., King, J. and K. Parkes. New York: Academic Press, 1962.
- May, Robert. *The Stability and Complexity of Model Ecosystems*. Princeton: Princeton University Press, 1973.
- Odenbaugh, Jay. "Ecological Stability, Model Building, and Environmental Policy: A Reply to Some of the Pessimism." *Philosophy of Science*, 68 (2001 Proceedings), S493-S505.
- Peters, Robert. *A Critique for Ecology*. Cambridge: Cambridge University Press, 1991.
- Pimm, Stuart. *Food Webs*. London: Chapman and Hall, 1984a.
- _____. "The Complexity and Stability of Ecosystems." *Nature* 307 (1984b): 321-326.
- _____. *The Balance of Nature?* Chicago: University of Chicago Press, 1993.
- Pimm, Stuart and John Lawton. "On Feeding on More than One Trophic Level." *Nature* 275 (1978): 542-544.
- Ricklefs, Robert and Gary Miller. *Ecology*. New York: W. H. Freeman and Company, 2000.
- Shrader-Frechette, Kristin and Earl McCoy. *Method in Ecology*. Cambridge: Cambridge University Press, 1993.
- Simberloff, Daniel. "A Succession of Paradigms in Ecology: Essentialism to Probabilism to Materialism and Probabilism." *Synthese* 43 (1980): 3-39.
- Sterrenly, Kim. (2001) "Darwin's Tangled Bank." In *The Evolution of Agency and Other Essays*. Cambridge: Cambridge University Press, 2001.

Donald Strong, Daniel Simberloff, L. G. Abele, and A. B. Thistle. *Ecological Communities: Conceptual Issues and the Evidence*. Princeton: Princeton University Press, 1984.

Wimsatt, William. "False Models as means to Truer Theories." In M. Nitecki, and A. Hoffman, (eds.) *Neutral Models in Biology*. London: Oxford University Press, 1987.

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Acknowledgments: I would like to thank Andrew Hamilton and Sahotra Sarkar for extremely helpful feedback on the manuscript. This essay incorporates previously published material from "Ecological Stability, Model Building, and Environmental Policy: A Reply to Some of the Pessimism." *Philosophy of Science*, 68 (2001 Proceedings), S493–S505. I would like to thank the Philosophy of Science Association and the University of Chicago Press for permission to use this material.