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ORIGINAL PAPER

A general theory of ecology

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Abstract Ecologists bemoan the dearth of theory in ecology, in particular, the lack of an overarching, general theory. These complaints largely are unjustified. The components of a general theory of ecology have existed for the past half century; ecologists simply have failed to explicitly recognize them. We present a general theory of ecology and show how it relates to ecology's numerous constituent theories and models. The general theory consists of a description of the domain of ecology and a set of fundamental principles. The domain of ecology is the spatial and temporal patterns of the distribution and abundance of organisms, including causes and consequences. Fundamental principles are broad statements about the patterns that exist and the processes that operate within a domain. The seven fundamental principles of the theory of ecology are: the heterogeneous distribution of organisms, interactions of organisms, contingency, environmental heterogeneity, finite and heterogeneous resources, the mortality of organisms, and the evolutionary cause of ecological properties. These principles are the necessary and sufficient elements for a general theory of ecology. The propositions of any constituent theory of ecology can be shown to be a consequence of these fundamental principles along with principles from other science domains. The general theory establishes relationships among constituent theories through shared fundamental principles. The next challenge is to develop and integrate unified, constituent theories and to establish the relationships among them within the framework established by the general theory.

Keywords Conceptual framework · law · model · theory

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Introduction

Like the emperor who had no clothes, ecology often is criticized as lacking the theoretical adornments of the physical sciences. Indeed, for many years ecologists have decried the fact that we have no general theories. Often, this debate is framed as whether ecology has laws (e.g., Lawton 1999; Simberloff 2004), a necessary component of a well-developed theory. We contend that pessimism about the theoretical foundations of ecology is ill founded: ecology has had a robust theoretical framework for many years. We ecologists simply have not recognized that fact, in part because we have misunderstood the nature and form of a comprehensive theory. Given a proper understanding of the nature and form of an overarching theory, exposing a general theory of ecology becomes less challenging. The goal of this paper is to present the fundamental principles of such a theory so as to further its development.

What is a theory?

A theory is a framework or system of concepts and propositions that provides causal explanations of phenomena within a particular domain (Hempel 1965; Suppe 1977; Miller 1987; Giere 1988). The purpose of a theory is to provide a set of linkages for observations and lower-level models or theories of those observations. Confusion exists because the term “theory” is used in reference to a variety of kinds of systems at different levels of specificity. Moreover, the nature of theory differs at each level. In this context, we recognize three levels of theory.

At the broadest level, a general theory consists of an entire domain of science and a set of fundamental principles (e.g., the theory of evolution, Darwin 1859; Mayr 1982; Kutschera and Niklas 2004). That is the type of theory that we present, a general theory of ecology. A general theory does not make specific predictions. Rather, it provides the scaffolding on which the components of more specific, constituent theories are assembled and integrated. It exposes assumptions that are sometimes hidden at the level of models or constituent theories and identifies areas that are ripe for theoretical development. In addition, it provides the interconnections that link constituent theories to each other. A mature or fully developed general theory enhances understanding at the broadest of levels and facilitates prediction and forecasting via well articulated models and constituent theories.

At the intermediate level are constituent theories, which set boundaries and identify parameters for particular interest, guiding model development. Constituent theories can overlap in domain and differ in scope. Depending on the form and domain of a constituent theory, it may make no predictions, or it may make qualitative predictions. Most important, a constituent theory unifies a set of interrelated models. For example, Scheiner and Willig (2005) present a constituent theory in ecology that pertains to variation in species richness along environmental gradients and show how a number of models are derived from its propositions.

At the most specific level, models are instantiations of a constituent theory. At this level, predictions are formalized and causal understanding motivates the process. Most references to theory in ecology actually relate to one of these instantiations (Ives and Agrawal 2005, and related papers). We prefer the word “model” for these theories to indicate that the domain is relatively narrow and predictions are contingent on well-specified conditions. Models often are referred to as theories and are the theories that are most familiar to ecologists. We emphasize that this is not the level of theory that we present here.

If quantitative predictions occur at the level of models, what is the utility of the other levels? That question is easy to answer for constituent theories. Such theories identify the necessary structure for models to address a particular issue (e.g., diversity along gradients). Such guidelines make model development easier and more complete, and can reveal interrelationships among seemingly disparate models. For example, Scheiner and Willig (2005) demonstrate how an articulated theory can be used to guide model development.

The issue of prediction is separate from the existence of a well-developed theory. A theory can provide understanding without prediction. Precise predictions may be difficult or impossible for many reasons, including context dependency, scale dependency, nonequilibrial dynamics, and the importance of historical contingency. Ecological theories—both general and constituent—are often probabilistic rather than deterministic, identifying the contexts within which particular patterns or process are more likely to manifest. To the extent that theory drives research, constituent theories make clear where assumptions lie, the sorts of predictions that are possible, and criteria for evaluating the relative merits of different lines of inquiry.

The utility of a general theory may be less apparent because it is two levels removed from the quantitative predictions that rigorously evaluate theories and test models (Ives and Agrawal 2005). Consequently, we address this issue at the end of this essay, once we have clarified the nature of a general theory and have articulated a theory of ecology.

A general theory of ecology

A general theory consists of a domain plus a set of fundamental principles. Fundamental principles are broad statements about empirical patterns and the processes that operate within a domain. The domain and fundamental principles of a general theory of ecology are presented below. We do not present the fully amplified theory with all of its components. Such an endeavor would take an entire book. Rather, our goal is to present its basic premises in sufficient detail so that others understand their meaning and reasons for inclusion within the theory. Clarification of the nature of those premises results in a framework for theories in ecology. Having such a framework and articulating the theories within it will help to catalyze the unification of theory in ecology.

We do not claim that the general theory of ecology is novel. Quite the contrary, its elements have existed for at least the past 50 years. However, it has never been described formally and concisely, although many of its principles are implicit in the table of contents of most ecology textbooks (see references in Table 1). Nor do we claim that the theory, as presented here, is the final version. Rather, it should be considered provisional and evolving. The list of fundamental principles may require additions, deletions, or refinements. Critically, this process can occur only after the theory has been formalized and discussed in an open scientific forum.

Table 1 Definitions of ecology as presented in various textbooks

Source	Definition
Odum (1971)	[T]he study of the structure and function of nature
McNaughton and Wolf (1973)	[The] scientific study of the relationships between organisms and their environments
Ricklefs (1979)	[T]he study of the natural environment, particularly the interrelationships between organisms and their surroundings
Colinvaux (1986)	[T]he study of animals and plants in relation to their habits and habitats
Ehrlich and Roughgarden (1987)	[T]he study of the relationship between organisms and their physical and biological environments
Stiling (1992)	[T]he study of interactions between organisms and between organisms and their environments
Dodson et al. (1998)	[T]he study of the relationships, distribution, and abundance of organisms, or groups of organisms, in an environment
Krebs (2001)	[T]he scientific study of the interactions that determine the distribution and abundance of organisms
Begon et al. (2006)	[T]he scientific study of the interactions between organisms and their environment
Gurevitch et al. (2006)	[T]he study of the relationships between living organisms and their environments, the interactions of organisms with one another, and the patterns and causes of the abundance and distribution of organisms in nature
This paper	The study of the spatial and temporal patterns of the distribution and abundance of organisms, including causes and consequences

The domain of ecology

Before we synthesize and make explicit the structure of this general theory, we need to define its domain. Although domains are artificial constructs, they serve as foci for organizing theories into coherent entities. The domain of ecology and its general theory is the spatial and temporal patterns of the distribution and abundance of organisms, including causes and consequences. Although our definition of the domain spans the definitions found in most textbooks (Table 1), it is different in two respects. First, our definition includes the phenomena to be explained (i.e., spatial and temporal patterns of abundance of organisms) and the causes of those phenomena. Some definitions include only the latter (i.e., interactions of organisms and environments). Second, and most strikingly, our definition explicitly includes the study of the consequences of those phenomena, thereby embracing much of ecosystem sciences.

The rules governing fundamental principles

Fundamental principles can be determined by a simple set of rules, although we recognize that the application of the rules is open to debate and disagreement. Here, we present the rules in the abstract; they are made more concrete when applied to the principles of the theory of ecology.

Fundamental principles are of two general types: those unique to the domain of consideration, and those shared with other domains. If a fundamental principle is unique to a domain, it must meet one of two criteria, either the principle is shared by many constituent theories within the domain, or the principle is necessary for distinguishing competing general theories. We refer to the former criterion as the inclusionary rule and the latter as the exclusionary rule. Inclusionary principles must be broad, whereas exclusionary principles may be narrow and can often be the result of the history of debates about a theory. If a fundamental principle is shared with another domain, it must be a consequence of mechanisms from another domain and have domain-specific causal significance. We refer to this criterion as the causal rule.

These criteria mean that a principle taken unchanged from another domain need not be specified within a theory. We take as given the fundamental principles of any other general theory. We recognize the general tenet of consilience, that the entire set of scientific theories must be consistent with each other (Whewell 1858). Theories may clash, but such clashes indicate foci of research that advance understanding. In general, theories inhabiting different domains will not clash directly, although results from one domain can point to problems with theories in other domains. For example, studies of geographical distributions of clades of organisms, within the domain of historical biogeography, became important evidence for the theory of continental drift, a part of the domain of geology. In that instance, the need for a causal mechanism to explain distribution patterns (the causal rule) was one factor that led to the development of new fundamental principles in another domain.

The fundamental principles of ecology

The general theory of ecology consists of seven fundamental principles (Table 2). These principles were in place by the 1950s and were widely accepted by most ecologists after the coalescence of the field of ecosystem ecology and the cementing of the Modern Synthesis in evolutionary biology. Of course, the roots of all of the principles go back much further.

The first fundamental principle—the heterogeneous distribution of organisms—is a refinement of the domain. It encompasses the basic object of interest and its most

Table 2 The seven fundamental principles of the general theory of ecology and the rules that determine their inclusion

Seven fundamental principles
1. Organisms are distributed in space and time in a heterogeneous manner. [inclusionary rule]
2. Organisms interact with their abiotic and biotic environments. [inclusionary rule]
3. The distributions of organisms and their interactions depend on contingencies. [exclusionary rule]
4. Environmental conditions are heterogeneous in space and time. [causal rule]
5. Resources are finite and heterogeneous in space and time. [causal rule]
6. All organisms are mortal. [causal rule]
7. The ecological properties of species are the result of evolution. [causal rule]

important property. The heterogeneity of distribution is one of the most striking features of nature: all species have a heterogeneous distribution at some, if not most, spatial scales. Arguably, the origins of ecology as a discipline and the first ecological theories can be traced to its recognition (Forster 1778; von Humboldt 1808). This heterogeneous distribution is both caused by and a cause of other ecological processes. The fundamental principles are not independent causal mechanisms, rather, the mechanisms that they encompass interact.

The second fundamental principle—interactions of organisms—includes within it the vast majority of ecological processes responsible for heterogeneity in time and space. Many definitions of ecology are equivalent to this principle (Table 1). Within this principle, particular interactions that are part of constituent theories act to unpack the general theory (see Constituent theories section).

The third fundamental principle—contingency—represents either the inclusionary rule or the exclusionary rule, depending on views of the history of theories in ecology. We discuss the exclusionary nature of this principle at the time of its genesis (see Competing general theories section). Since that time, recognition of the importance of contingency in all ecological processes has increased steadily and now appears in a wide variety of constituent theories and models. Contingency is an important cause of the heterogeneous distribution of organisms, both at very large extents of time and space (e.g., a particular species arose on a particular continent) and at very small extents (e.g., a seed lands in one spot and not another).

We speculate that general theories of all domains include some version of this principle (e.g., genetic drift in evolution; quantum theory in physics). Thus, it might be considered fundamental to all scientific theories. This principle demonstrates that the decision to include a fundamental principle and the type of rule that is the basis for inclusion are not always clear and may be subject to debate by scientists, historians, and philosophers.

The fourth fundamental principle—environmental heterogeneity—is a consequence of processes from the domains of the earth and space sciences. For example, seasonal variation in temperature is the result of orbital properties of the Earth, whereas a variety of geophysical processes create heterogeneity in environmental stressors like salt (e.g., wave action near shores) or heavy metals (e.g., geologic processes that create differences in bedrocks). It is beyond the scope of this paper to detail all of those processes and their domains. Indeed, this principle encompasses many constituent theories and contains a broad class of underlying mechanisms for the heterogeneous distribution of organisms. As with the second principle, particular mechanisms pertain to particular constituent theories. Again, the fundamental principle captures a wide range of theories and mechanisms so as to provide a unifying framework.

The fifth principle—finite and heterogeneous resources—is again a consequence of processes from the domains of the earth and space sciences. Although variation in resources is similar to variation in environmental conditions, a fundamental distinction is the finite nature of these resources. Unlike an environmental condition, a resource is subject to competition. For example, seasonal variation in light and temperature are caused by the same orbital mechanisms, but light is subject to competition (e.g., one plant shades another), whereas temperature is a condition and not subject to competition. This distinction in the nature of environmental factors with regard to competitive processes can result in very different ecological outcomes (e.g., patterns of â diversity in plant communities, Scheiner and Rey-Benayas 1994). Whether a particular environmental factor is a condition or a resource can be context dependent. For example, water is sometimes a resource subject to competition (e.g., plants in a desert), and sometimes a condition (e.g., fish in the ocean).

The sixth fundamental principle—the mortality of organisms—is the result of processes that come from the domain of organismal biology, physiology, and development. By “mortal” we mean that no organism is invulnerable, i.e., any organism might die as the result of predation, stress, or trauma. We do not mean by this principle that all organisms senesce. The senescence of organisms is a more narrow version of this principle that would apply to particular constituent theories. Although the majority of multicellular species apparently senesce, this has not been demonstrated for some multicellular species. We are not aware of an articulated theory of development or physiology that predicts the necessity of or conditions for senescence, but suspect that it could be accomplished given current knowledge of organisms. We will let philosophers argue whether a bacterium that splits into two represents a single, immortal organism or (our position) the end of one individual and the creation of two new individuals. This fifth principle, either in the more general version of vulnerability or in the more narrow version of senescence, forms the basis of a large number of constituent theories concerning phenomena as wide ranging as life histories, behavior, demography, and succession.

The seventh principle—the evolutionary cause of ecological properties—is the result of processes that derive from the theory of evolution. The inclusion of evolution within ecological thinking was an important outcome of the Modern Synthesis. Although evolutionary thinking about ecological processes goes back at least to Darwin (1859), evolutionary thinking had been infusing ecology more widely at least since the 1920s (Collins 1986; Mitman 1992) and its widespread acceptance occurred primarily in the latter half of the 20th century. The acceptance of this principle led to such disciplines as behavioral ecology and population biology, and the demise of the Clementsian superorganism theory (see Competing constituent theories). It is in this latter capacity that this principle can be considered under the exclusionary rule and the causal rule.

The scope of the fundamental principles

These fundamental principles are necessary and sufficient to support a general theory of ecology. One or more of the propositions of each constituent theory of ecology can be shown to be a consequence either of the fundamental principles of ecology, or of principles from other domains. A proposition of a constituent theory can be a consequence of a fundamental principle in three ways. First, a proposition may be a member of a class defined by a fundamental principle. For example, competition, a type of biotic interaction (principle 2), plays a key role in plant succession (Pickett et al. 1987). Second, a constituent theory can identify, define, or refine particular patterns or mechanisms identified in a fundamental principle. For example, variation in dispersal distance, a form of contingency (principle 3), is a component of population dynamic theory (Turchin 2001). Third, a proposition in a constituent theory might be derived formally from a fundamental principle. For example, in food web theory, rules governing food chain length derive from aspects of the second law of thermodynamics (a principle in the domain of physics). In the next section, we examine further the relationship between fundamental principles and the propositions of constituent theories.

To the extent that the fields of ecology can be characterized as a collection of related or overlapping constituent theories, these principles provide the scaffolding for a mature and fully developed theory that applies to all subdisciplines of ecology. The general theory establishes relationships among constituent theories. Linkages occur when constituent theories are derived from one or more of the same fundamental principles. Constituent theories that share fundamental principles must be consistent with each other. If they are not, one or more of those theories may require revision. Some of the propositions may be the consequence of theories in other domains. To be a constituent theory within the domain of ecology, at least one of its propositions would have to be a consequence of the fundamental principles of the general theory of ecology.

The fundamental principles do not include ecological entities or systems, such as populations, communities, or ecosystems. Rather, those entities are a consequence of the mechanisms embodied by the principles. For example, a population and its properties are the consequence of organisms of a single species inhabiting a particular location (principle 1) and interacting with each other (principle 2). Philosophers refer to this derivation of one object from other principles as ontological reduction. Ontological reduction is favored because it results in theory simplification and eliminates ontological primitives that require special explanation.

The fundamental principles do not specify mechanisms. It is the function of constituent theories to explicate the types and appropriateness of particular mechanisms. For example, interactions such as predation, herbivory, competition, mutualism or parasitism might be mechanisms within theories of community structure. Such lack of specificity has two causes. The first relates to the diversity of environmental and historical circumstances which determine the importance of any suite of mechanisms effecting the properties of ecological systems. Any attempt to enumerate the circumstances in which particular biotic interactions dominate would create an unwieldy theory. The second cause relates to the history of ecology, which can be characterized as the accumulation of mechanisms about, and an appreciation for, the complexity of ecological systems. Rather than debates about the existence of mechanisms, disagreements mostly have been about their relative importance, a dispute that occurs at the level of constituent theories, rather than at the level of the general theory.

The exact list of fundamental principles of ecology certainly will be the subject of debate. Recently, a partial form of our general theory was advanced by Lawton (1999) as a list of "universal laws that underpin all ecological systems" that are equivalent to principles 2 and 7. He included other principles such as the first and second laws of thermodynamics and the conservation of mass. We did not include those principles because they were taken unchanged from the domain of physics. He also included physical principles governing a broad set of properties which underpin the physiology of organisms. Those were not included because we consider the physiology of organisms to be outside the domain of ecology. The effects of principles in that domain appear in our theory in the guise of principle 6. Otherwise, those principles might play roles in more specific, constituent theories. Our effort also differs from that of Lawton by providing a set of rules by which one can decide whether a principle should be included within the general theory.

Constituent theories

A general theory of ecology should be able to construct and accommodate all constituent theories within the domain of ecology. We demonstrate this accommodation and the way in which their propositions are consequences of fundamental principles by examining two constituent theories. Turchin (2001) presented a theory of population dynamics consisting of various models of population growth, which he referred to as laws and enunciated several propositions that form the bases of those laws. The propositions, which he called "foundational concepts," are: exponential population growth, self-limitation, and trophic oscillations. These propositions are a consequence of fundamental principles 2–6. The pattern of exponential population growth is a function of the birth and death (principle 6) of individuals, but can also be affected by environmental heterogeneity (principle 4) and various types of contingency (principle 3). Population self-limitation occurs because resources are finite (principle 5). Trophic oscillations occur because of interactions among species (principle 2). Although not expressed precisely within the conceptual framework presented here, Turchin's ideas amount to a constituent theory that it is quite mature.

This example also demonstrates how fundamental principles can set boundaries on the form of constituent theories and models. Turchin (2001) explains how a system that contained an additional proposition involving spontaneous generation would result in different models of population growth, linear rather than exponential. Clearly, however, the proposition of spontaneous generation is not supported by any fundamental principle in any general theory of biology.

Scheiner and Willig (2005) presented a theory of diversity gradients consisting of four propositions: limiting resources (a consequence of principle 5), species pools (principle 1), environmental variation (principle 4), and population or organismal trade-offs (principles 6 and 7). Those propositions, in turn, embody a large variety of models. While those models have been presented as contradictory or in opposition, when presented as part of a framework of propositions their commonalities become clear. Levins (1968) pointed out that no model can simultaneously maximize generality, precision, and realism. At most, a model can strive to maximize two of these qualities, and the majority of models are a compromise among all three. Since there is no best all-purpose model, theory unification permits one to choose which among a variety of models is most appropriate for a given situation, while allowing one to relate model results to those of other models. In a similar fashion, a general theory exposes commonalities among constituent theories.

Ecology contains a plethora of constituent theories that differ in maturity (Table 3). Some, such as the equilibrium theory of island biogeography, are mature. Substantial effort has refined the mathematical models of that theory and demonstrated its empirical utility. Other constituent theories are promising but underdeveloped. For example, the metabolic theory of ecology currently consists of a single model and lacks a broader unifying set of propositions that would facilitate the building of alternative models.

For any of these constituent theories, we could go through a similar exercise of explicating their propositions and showing how those propositions are a consequence of the fundamental principles of ecology. Our claim is that one or more of the fundamental principles are necessary to any of ecology's constituent theories, and the fundamental principles of the entire set of general theories in science are sufficient to derive their propositions. It is beyond the

Table 3 Selected constituent theories of ecology

Theory	Stage of maturity	Reference
Island biogeography theory	More complete	MacArthur and Wilson (1967)
Foraging theory	More complete	Stephens and Krebs (1986)
Succession theory	More complete	Pickett et al. (1987)
Metapopulation theory	More complete	Hanski (1999)
Population dynamic theory	More complete	Turchin (2001)
Niche theory	More complete	Chase and Leibold (2003)
Food web theory	Intermediate	Pimm (1982)
Theory of latitudinal gradients of diversity	Intermediate	Willig et al. (2003)
Metabolic theory of ecology	Intermediate	Brown et al. (2004)
Unified theory of diversity gradients	Intermediate	Scheiner and Willig (2005)
Metacommunity theory	Less complete	Leibold et al. (2004)

The associated reference is illustrative rather than definitive or comprehensive.

scope of this paper to verify this claim in an exhaustive fashion, although that is a paramount task for further development of a general theory of ecology.

Theories differ in their level of generality. We classify a theory as a constituent theory if it meets one of two criteria: the theory serves to unite many models that attempt to explain a single phenomenon (e.g., the theory of diversity gradients), or a single model is portrayed as explaining a broad range of phenomena (e.g., the metabolic theory of ecology). Otherwise, the theory is likely a model within a more general constituent theory, or a nascent constituent theory.

The nature and benefits of a general theory of ecology

What we term "constituent theory" is what ecologists often refer to as "theory" with all of its components, including facts, generalization, laws, models and hypotheses (Pickett et al. 1994). A general theory is sparser, consisting of a domain and a set of fundamental principles, which together define a framework. For a general theory, the other components are encapsulated within its constituent theories. A general theory is mature only to the extent that its constituent theories are mature and their interrelationships are clear. In this regard, the general theory of ecology is an adolescent, some of its constituent theories are quite mature, while others are still under ripe, and the interrelationships among them are not well established.

Competing constituent theories

A general theory provides several benefits. It helps scientists decide between competing constituent theories. For example, in plant ecology in the first half of the twentieth century, two competing theories considered the nature of communities. These two extreme viewpoints differed in the importance they ascribed to biotic versus abiotic factors, and predictable versus random processes in shaping community structure.

The first theory, proposed by Clements (1916), saw plant communities as highly organized entities made up of mutually interdependent species. Communities were superorganisms—the analogue of individual organisms—that are born, develop, grow, and eventually die. Two of the hallmarks of the superorganism concept were the presence of very tight linkages among species within communities and cooperation among the species in a community for the benefit of the entire community.

The alternative theory, put forward by Gleason (1917; 1926), posited that communities are the result of the interactions of each species and the environment (biotic and abiotic factors) in combination with chance historical events. Each species has its own environmental tolerances and thus responds in its own way to environmental conditions. The implication was that along an environmental gradient, different species would have their boundaries at different places. Not only were communities not tightly linked superorganisms, but defining the collection of species living together in a particular place as a community was an arbitrary human construct.

These two theories disagreed on a number of grounds that can be seen within the framework of the general theory. For example, they held to different ideas about how evolution shapes ecological traits (principle 7). They differed in the nature of environmental heterogeneity (principle 4), and they differed in the nature of interactions among organisms (principle 2). If the general theory of ecology had been formalized while those theories were being debated, it might have made the nature of the disagreements clearer, focused the disagreements along productive lines of inquiry, and pointed to the evidence needed to decide between them.

Competing general theories

Formalizing a general theory facilitates an assessment of the merits of competing general theories. Competing general theories are distinguished by either requiring, rejecting, or altering the form of fundamental principles. The shift in ecology from an equilibrium paradigm to a nonequilibrium paradigm illustrates this process. In terms of our general theory, one aspect of this shift was the recognition of the importance of contingency through the addition of the third principle. A general theory of ecology that posits that the world is in equilibrium, while potentially recognizing a role for contingency, would not see contingency as being a major mechanism. Rather, the equilibrium paradigm included a strongly deterministic viewpoint, and principle 3 was simply part of particular models rather than a fundamental principle. We realize that this example is oversimplified and does not capture the complexities of the debate. McIntosh (1985) provides a detailed discussion of the history of this conceptual shift.

A general theory also highlights the nature of disagreements about mechanisms. In the general theory of ecology, no biotic mechanism is given primacy. During the 1970s and 1980s, a debate raged among ecologists about the primacy of competition in structuring communities (McIntosh 1985). The outcome of that debate was an agreement that competition is an important process, but that other processes can be of equal or greater importance in many circumstances. In the context of the general theory of ecology, the debate was whether the set of fundamental principles was insufficient and needed an additional statement about the primacy of competition, with the conclusion being that no such principle was warranted.

Whither ecology?

We recognize that ecology presents challenges for unification—the vast number of objects (e.g., taxa) to be considered leads to an extreme diversity of disparate models. All the more reason to reiterate our previous call for ecologists to develop and integrate unified, constituent theories (Scheiner and Willig 2005). The general theory presented here should help guide that process. We ecologists need no longer argue among ourselves about the strength of the theoretical underpinnings of our discipline. The components of a general theory have existed for many years. The next challenge is to establish the relationships among ecology's constituent theories. Indeed, the cries that the empress has no clothes were myopic. Now fully vested, it is clear: ecology is a well dressed lady, as elegant as any of her sister disciplines in the sciences.

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