CHAPTER 15

The State of Theory in Ecology

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> There is a need to subject current theory to stringent empirical test, but ecology can never have too much theory.
>
> MacArthur 1972

An article in *Wired Magazine* proclaimed in its title "The End of Theory: The Data Deluge Makes the Scientific Method Obsolete" (Anderson 2008). The basic premise of that essay was that evolving computational capabilities will allow large and heterogeneous datasets to be mined efficiently and effectively. The result would be the production of pattern without the need of hypothesis formation and testing, so much so that correlation would supersede causation. Science would "advance without coherent models, unified theories, or really any mechanistic explanation at all." Although advanced cyberinfrastructure will revolutionize much of the scientific enterprise as it relates to data collection and visualization, the overarching thesis of the article invites replies on many levels. Rather than do so here, we use that statement as a springboard from which to emphasize the unsophisticated view held by many that there is but one scientific method and that the accuracy and utility of models are the essential characteristics of theory. Indeed, perusal of the preceding chapters in this book or the influential tome by Pickett et al. (2007) suggests that Anderson's (2008) conceptualization of theory is flawed from many perspectives. Mark Twain, upon reading his obituary in a New York journal, is quoted as having replied, "The reports of my death are greatly exaggerated." So too, this is our response to Anderson's contention. Theory in general, and theory in ecology in particular, are alive and flourishing, providing much impetus to deepen and broader our understanding of the natural world. Our goal in this chapter is to briefly summarize where the discipline now stands with regard to that understanding.

The hierarchy of ecology

The domain of a theory defines its central focus. In the case of a general theory, that domain also circumscribes a scientific discipline. In Chapter 1, we defined the domain of the theory of ecology as the spatial and temporal patterns of the distribution and abundance of organisms, including their causes and consequences. Nonetheless, this definition requires additional exposition to understand the nature of the patterns and processes under consideration (Kolasa and Pickett 1989). The brief definition of ecology's domain does not address the nature of the interactions that define the levels of the ecological hierarchy, and how that hierarchy fits within the relationships and interactions that define the rest of the domain of biology (Fig. 15.1; Scheiner 2010).

Our hierarchical perspective makes clear that ecological theory is directed at understanding biological entities at or above the level of individuals. The birth, death, growth, and movement of individual organisms give rise to the complex spatial and temporal tapestry of life that is the focus of ecological studies, and these basic attributes arise from the dynamics involved in the acquisition of energy and nutrients from the environment. Most of the chapters in this book focus on the middle of that hierarchy: populations (Hastings Chapter 6; Holt Chapter 7), single communities (Chase Chapter 5; Pickett et al. Chapter 9), or collections of communities (Leibold Chapter 8; Sax and Gaines Chapter 10; Fox et al. Chapter 13; Colwell Chapter 14).

A few chapters examine theory associated with the ends of the hierarchy. At the level of individuals, the domain of the theory of ecology intersects with the domain of the theory of organisms (Scheiner 2010; Zamer and Scheiner in prep.), resulting in such disciplines as physiological ecology. The theories that define those disciplines are examples of how the domains of a constitutive theory can overlap the domains of more general theories. In this book, the individual-level perspective is represented by foraging theory (Sih Chapter 4), which is representative of the broader domain of behavioral ecology.

At the other end of the hierarchy, the theory of ecology overlaps with theories from the geological sciences. Ecological processes have a dramatic effect on the distribution of biologically important chemicals (e.g., C, N, P, O). Over billions of years, ecological interactions have transformed the planet from an

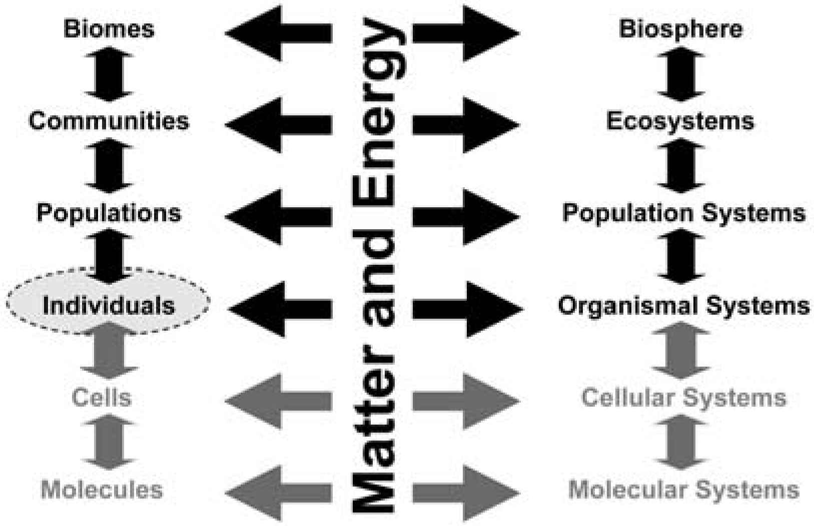

Figure 15.1 One way of organizing living systems is as a hierarchy that extends from molecules to biomes. At each level, biological entities (e.g., cells, individuals, communities) interact with matter and energy (double-headed horizontal arrows) to form living systems. The domain of ecology is defined by interactions at the level of individuals and higher (signified by black rather than gray lettering), and is characterized by an organismal perspective (signified by the shaded ellipse at the individual level). Each level in the biological hierarchy is associated with other levels (e.g., populations comprise individuals of the same species and populations of different species comprise communities) in the hierarchy (represented by vertical arrows on the left). Additional connectivity among levels occurs because the matter and energy that fuel the activities of all biological entities flow and cycle, respectively, in biological systems regardless of level in the hierarchy (indicted by vertical arrows on the right). Moreover, then nature of the ecological entities and their interactions changes over time as a consequence of evolution, resulting in complex dynamics and multiple feedbacks. (Modified from Odum 1971.)

environment with high ultraviolet radiation, low availability of oxidizing and reducing ion pairs, and few energy sources to an environment with low ultraviolet radiation, high availability of oxidizing and reducing ion pairs, and a diversity of energy sources (Burke and Lauenroth Chapter 11). Moreover, the interplay between matter and energy with the biotic portions of the environment creates dynamic interacting systems at all levels of the ecological hierarchy (e.g., organismal systems, population systems, ecosystems) that can play out over global scales (Peters et al. Chapter 12). This framework makes clear that the study of ecosystems (i.e., community systems) is an integral part of the domain of ecology. Ecosystems arise from the interactions of communities with matter and energy, and the resultant cycles, flows, and pools or standing stocks are consequences, to at least some extent, of the activities of the biota.

Implicit in our definition of ecology is an emphasis on spatial and temporal perspectives. As elucidated in many of chapters in this book, ecological relationships can vary as a function of the scales of space or time, and environmental drivers that strongly affect variation at one scale may be markedly different from those at other scales. Consequently, ecological understanding, especially predictive understanding, is a challenge when the form or parameterization of a relationship may differ across scales, or when the identity of the dominant driver of a pattern changes with scale. One of the central challenges in ecology is the development of theories and models that integrate across levels in the biological hierarchy (Fig. 15.1). In this book, the only theories that explicitly integrate across the hierarchy are metacommunity theory (Leibold Chapter 8), succession theory (Pickett et al. Chapter 9), and island biogeography theory (Sax and Gaines Chapter 10), each of which integrates population- and community-level processes, and global change theory (Peters et al. Chapter 12), which integrates from individuals to the biosphere. Other chapters (e.g., Fox et al. Chapter 13; Colwell Chapter 14) hint at such integration, but do not explicitly model it.

The concept of hierarchical levels as applied to ecology (Odum 1971) has long been recognized in many realms of the natural and social sciences, along with important philosophical considerations (e.g., Novikoff 1945; Feibleman 1954; Greenberg 1988). In addition to facilitating communication and classification in ecology, the integrative levels of organization in that hierarchy suggest that moving from individuals to communities involves increases in complexity, and that properties at higher levels can emerge from lower levels. At each level in the ecological hierarchy, emergent characteristics manifest that cannot be predicted or fully understood based on just the patterns and processes at lower levels. Moreover, interactions are horizontal, among entities at the same level (e.g., different species interact within a community) as well as vertical. In addition, influences are fully complementary, in that processes at higher levels can affect properties at lower levels (e.g., communities affect populations). For these reasons, both reductionist and system approaches to ecological understanding are by themselves insufficient and sometimes misleading. In ecology, an inability to clearly and unambiguously identify the spatiotemporal limits of entities at each hierarchical level (e.g., individual, population, community) may conspire to further challenge the development of predictive understanding. For example, we may find it easier or less arbitrary to distinguish unitary individuals than to distinguish unitary communities, making it progressively more complicated to understand the linkage between pattern and process as we traverse up the ecological hierarchy.

The development of theory

The chapters in this book represent a diversity of ecological theories that differ greatly in content and scope, as well as in their degree of theoretical maturation. The chapters also differ in the extent to which their syntheses summarize, clarify, amplify, integrate, or unify theoretical constructs to the advancement of ecological understanding. In Chapter 1 we presented a hierarchical view of theory consisting of three tiers: general theories, constitutive theories, and models (Table 1.1). We noted, however, that this division into three tiers was arbitrary. The hierarchy is really a continuum. About half of the chapters primarily focus on the model end of this continuum because they provide explicit directions for the building of models: foraging theory (Sih Chapter 4), niche theory (Chase Chapter 5), population dynamics theory (Hastings Chapter 6), enemy-victim theory (Holt Chapter 7), island biogeography theory (Sax and Gaines Chapter 10), and ecological gradient theory (Fox et al. Chapter 14). The others—metacommunity theory (Leibold Chapter 8), succession theory (Pickett et al. Chapter 9), ecosystem theory (Burke and Lauenroth Chapter 11), global change theory (Peters et al. Chapter 12), and biogeographical gradient theory (Colwell Chapter 14)—are much more like general theories because their propositions are closer in nature to fundamental principles and define the domain of their models rather than provide explicit rules for model building. So, even for the constitutive theories presented in this book, additional constitutive theories could be developed that are either narrower in scope and act to unify some particular set of models or are broader in scope and aim at uniting other constitutive theories.

To some extent the tendency of a chapter to be at one end or the other of that continuum from general to specific is a function of the maturity of the theory. Foraging theory, population dynamic theory, enemy-victim theory, and island biogeography theory are all quite mature and the authors of those chapters focused on models. In contrast, metacommunity theory, global change theory, and biogeographical gradient theory are less mature and those authors presented more general views of their topics. In some cases, the very maturity of the theory in combination with the complexity of the domain led to a chapter that was more general in focus (succession theory and ecosystem theory). In other cases, the theories arose out of attempts to synthesize across competing models, leading to a more model-focused approach of a less mature theory (niche theory and ecological gradient theory).

Theories may assume a number of different roles (R. Creath, unpublished ms.). They represent generalizations that extend the scope of the particular data that espoused those generalizations. They generate concepts that extend beyond what can be expressed in observation alone. In these two capacities, theories are primarily descriptors of the world. In addition, theories are a framework for guiding and evaluating research paradigms sensu Kuhn (1962) or research traditions sensu Laudan (1977). To a greater or lesser extent, all of the constitutive theories in this book play each of these roles.

Many controversies arise within a domain because of a failure to differentiate between a core concept that is neutral and broad on the one hand, and various incarnations of that concept that may be narrow and specific on the other. The differences among particular models allow the more general theory to be broadly applicable, depending on circumstances defined by the distinguishing assumptions of those models. Understanding the features that favor one model over another thereafter becomes a unifying strength of the theory to account for myriad empirical observations. The framework for understanding disturbance and succession (Pickett et al. Chapter 9) exemplifies this process. The frameworks for niche theory (Chase Chapter 5), enemy-victim theory (Holt Chapter 7), and metacommunity theory (Leibold Chapter 8) perform similar unifications.

Roles of theory in ecology

The body of theory in ecology accounts for our observations about the natural world and gives us our predictive understanding through the use of models. It organizes those models into constitutive domains that provide a robust intellectual infrastructure. That organizational framework provides a blueprint of the strengths and weaknesses of our understanding, motivating future empirical and theoretical work and catalyzing research agendas. Refinements of theory can identify the mechanistic bases of patterns and processes about which we have considerable confirmation, as well as distinguish the ideas and relationships that are in flux or about which there is considerable uncertainty.

In the title to his chapter, Kolasa (Chapter 2) emphasizes that "theory makes ecology evolve." Using a historical perspective, he identifies the genesis of the ideas that formed the bases of the fundamental principles of the domain of ecology (Table 1.3). He forcefully argues that theory and empiricism are inextricably intertwined, not mutually exclusive undertakings, and that theory is a vehicle for sharing knowledge across domains as well as for targeting efforts to fruitfully deepen or broaden the scope of ecological understanding. This too is the broad perspective that can be gleaned from other chapters in this book. It is a basis for our contention that the proclamation about the death of theory (Anderson 2008) is fatally flawed, even in an age of cyberinformatics. Given the deluge of data, theory helps winnow out data that are irrelevant to a particular domain of interest while highlighting that which advances understanding. Theory helps to organize multiple lines of evidence in an efficient manner. Theory provides connections among ideas and concepts within and among domains. Theory provides insights into new data requirements needed to distinguish among or resolve differences among competing views of the world.

Odenbaugh (Chapter 3) clarifies the nature of a unifying theory, and reinforces Kolasa's contention that models alone, no matter how mathematically elegant or predictive, are incomplete aspects of a mature theory. Odenbaugh challenges ecologists and evolutionary biologists to further integrate disciplinary understanding with a goal of exposing the spatiotemporal interdependence of ecological and evolutionary processes: current ecological processes are in play because of past evolutionary processes and current evolutionary processes are in play because of past ecological processes. He illustrates past efforts in this area by focusing on the work of MacArthur and his collaborators. Odenbaugh argues that although their ideas were formative and stimulatory to generations of ecologists, they did not succeed in unifying ecology, despite their intentions. Rather, their work provided the discipline with natural selection thinking, a focus on model building, and a strategy aimed at predictive understanding and generality, instead of only descriptive understanding, as in natural history. This same tension between predictive understanding and descriptive natural history helped shape the origins of ecology as a discipline at the beginning of the 20th century (Hagen 1992). As evidenced by the chapters in our book, this striving towards predictive understanding continues.

Multicausality

Ecological systems have a critical property—multicausality—that affects the structure and evaluation of ecological theories (Pickett et al. 2007). In general, multicausality (Fig. 15.2A) occurs when more than one driving factor (Xs in figure) effects an outcome (Y in figure). For heuristic purposes, we distinguish a number of general types of multicausality. First are instances where variation in a particular characteristic arises as a consequence of variation in only a subset of the possibilities driving factors (Fig. 15.2B). For example, each of three factors (e.g., X_1, X_2, or X_3) could affect an outcome, but they do not all do so in concert in all circumstances. In some circumstances, only X_1 and X_2 might effect the outcome whereas in other circumstances, only X_1 might do so. From

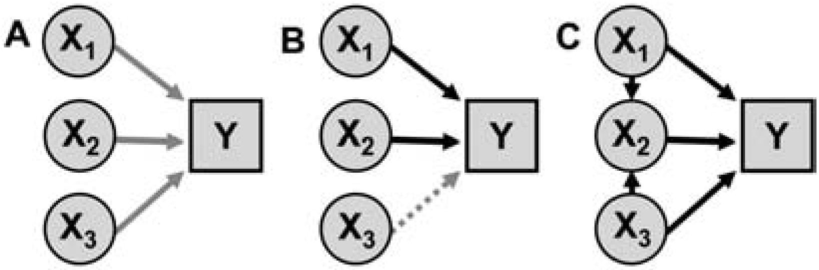

Figure 15.2 These diagrams represent various types of multicausality, a situation in which more than one driving factor (represented by Xs) effects variation in focal characteristic (represented by Y). (A) A general model that defines the candidate driving factors (solid grey lines) and the responding characteristic of interest. (B) Only a subset of the possible driving factors have an effect depending on particular circumstances (represented by solid arrows). In this case, the model is additive and multivariate, but under other circumstances it could be univariate. (C) All of the candidate driving factors have an effect on the responding characteristic of interest. In this case the effects of the factors are interactive. Even more complex situations can arise, where only subsets of the candidate driving factors come into effect in particular circumstances, and the factors interact in a non-additive way, including direct and indirect effects.

an analytical perspective, this results in multivariate causation in the former situation and univariate causation in the latter situation. Second are instances where all of the driving factors in concert effect an outcome (Fig. 15.2C). The multiple driving factors could act together in an additive manner or could do so in complex ways that are nonlinear and include direct and indirect effects.

These aspects of multicausality are important for the structure of ecological models and their evaluation. If a model includes all of the multiple causes, it will provide robust predictions or explanations. For multicausal models of the first type (Fig. 15.2B), it is necessary that the model include only the particular driving factors acting in a particular situation, but the causes that are included in the model may differ from situation to situation. Thus, it is not necessary to know all of the possible causes in all situations, just the ones that are important in the situation under consideration. For models of second type (Fig. 15.2C), it is necessary to know all of the driving factors in advance of model construction.

For all types of multicausality, if a model does not include all causes, the utility of the model depends on whether those causes have additive or nonadditive (i.e., interactive) effects on the outcome. When effects are additive (Fig. 15.2B), conclusions about the relative magnitudes of the processes included in the model are robust. The excluded factors may affect absolute predictions of a model, but not relative ones. On the other hand, if the causes interact (Fig. 15.2C), then the magnitudes and rank orders associated with one causative mechanism may depend on those of another. At minimum, it is necessary to acknowledge that this is an inherent assumption in particular models.

In this book, we find both types of multicausal models. Models that deal with independent, additive causes are exemplified by niche theory (Chase Chapter 5), population dynamics theory (Hastings Chapter 6), enemy-victim theory (Holt Chapter 7), island biogeography theory (Sax and Gaines Chapter 10), and ecological gradient theory (Fox et al. Chapter 13). Interactive causes are notable in foraging theory (Sih Chapter 4), metacommunity theory (Leibold Chapter 8), ecosystem theory (Burke and Lauenroth Chapter 11), global change theory (Peters et al. Chapter 12), and biogeographic gradient theory (Colwell Chapter 14). Perhaps the most extreme version of such interactions is found in succession theory (Pickett et al. Chapter 9).

When evaluating models, the two types of multicausality and the details of their interactions have important implications for how an experiment would be designed. For the first type of multicausality with additive effects, rigorously holding constant all factors other than those under investigation would be most informative. Even with nonadditive effects, an experiment would manipulate just a few factors. Most laboratory and greenhouse experiments are of these types. For the second type of multicausality, unless one knew all of the necessary causes and their interactions, a field experiment would be more informative. Although one or a few factors might be deliberately manipulated, other necessary factors would also be free to also contribute. Importantly, statistical techniques such as structural equation modeling, which are capable of identifying causal factors and of incorporating direct and indirect effects (Grace 2006; Grace et al. 2010), could be employed with nonexperimental data.

Because of the second type of multicausality, some philosophers of science conclude that we can never determine the true explanation of a phenomenon because multiple alternative explanations always exist (Suppe 1977). In practice, ecologists must often use multiple lines of evidence to discern the relative roles of ecological processes in producing patterns (e.g., Carpenter 1998). See Scheiner (2004a) for a more complete discussion of the use of total evidence in ecology.

Another aspect of multicausality is that some causal processes are proximate and others ultimate. Consider the question: Why are male lions larger than female lions? A proximate explanation involves development and food intake during growth. A more ultimate explanation involves sexual selection: larger males are better able to monopolize a group of females. Beyond those processes may be phylogenetic effects involving all felids or carnivores. These alternative explanations often derive from different general theories, so a given constitutive theory needs to either draw on those multiple general theories or acknowledge the limitations of its explanatory scope.

Spatial variation, temporal variation, and scale

Environmental heterogeneity, both abiotic and biotic, is core to ecological processes, as shown by its prominence in the theory of ecology (Table 1.3, principles 3, 5, and 6). This heterogeneity creates a central role for the importance of scale in ecological theories.

Geographic space and ecological space are intimately intertwined. This intersection can be seen most clearly in two theories. Biogeographic gradient theory (Colwell Chapter 14) presents a synthetic framework for the creation of a theory of spatial gradients (e.g., latitude, elevation, depth) that operate at broad geographic scales. Broad-scale patterns of species richness and range size are an emergent property arising from the sum of species-specific responses. Metacommunity theory (Leibold Chapter 8) bridges local and regional scales (i.e., mesoscale ecology) by considering the extent to which local filters and dispersal determine the composition and species richness of sets of communities.

Interactions of ecological processes can change over space and time. Within a single community their relationships change as a result of disturbance and succession (Pickett et al. Chapter 9). Those interactions are now mostly understood as befits a theory that has been developing since the origins of ecology in the late 19th century (Cowles 1899; Clements 1916). At the other end of the spatial and temporal scale are those global changes initiated by human activities (Peters et al. Chapter 12). Borrowing concepts from hierarchy theory (Allen and Starr 1982) and landscape ecology (e.g., Peters et al. 2006; Peters et al. 2008), global change theory addresses issues associated with the consequences of large-scale human-initiated disturbances such as global warming, urbanization, and agricultural intensification. This theory is implicitly scale-sensitive, suggesting that fine-scale relationships between pattern and process interact with broad-scale relationships, resulting in spatial heterogeneity and differential connectivity among spatial units.

Conservation, management, and policy

Ecology as a discipline and ecologists as scientists have changed greatly from the middle of the last century, when the Nature Conservancy was formed. That organization was founded by a group of ecologists who were frustrated with their inability to get the leadership of the Ecological Society of America (ESA) to address the practical and policy implications of their science. In contrast, today the ESA has taken a leadership role in translating science into policy.

It is telling, though, that such linkage is mostly absent from this book, despite our instructions to authors that they should address those issues. Only two chapters do so explicitly: island biogeography theory (Sax and Gaines Chapter 10) and global change theory (Peters et al. Chapter 12). It is not surprising that these chapters address those concerns. Island biogeography theory has long been entwined in efforts to determine the best design for nature reserves (Burgman et al. 2005), especially the SLOSS ("single large or several small") debate of the 1980s. Today, global change has become a central focus of both science and public policy. The magnitude and rate of change are both great, and these anthropogenically induced changes will likely affect all levels in the ecological hierarchy, often in dramatic ways and likely over broad spatial extents.

That is not to say that the other theories in this book are not also relevant to applied issues. For example, population dynamics theory (Hastings Chapter 6) is used extensively for population viability analyses. Similarly, enemy-victim theory (Holt Chapter 7) is useful in understanding pathogen-host interactions in agricultural settings as well as the dynamics of infectious diseases as they relate to public health. Rather, we ecologists tend to separate theory development from theory application. The drive for theory development often comes from basic research questions, with application and additional refinement of theory coming later. Global change theory is a notable exception. Its impetus arises from current concerns about where our planet is headed as a consequence of anthropogenic contributions to greenhouse gases and expansive modifications of landscape structure and configuration throughout the world.

Much of the application of theory to questions of management has focused on optimization issues (i.e., maximum sustained yield) related to production of particular agricultural crops or harvests of particular species of wildlife for human consumption or use. A more holistic approach that considers management from an integrated, multispecies ecosystem perspective is gaining ground because of its ability to include both direct and indirect effects on targeted species, the species with which they interact, and the ecosystem services that they provide to humans (Peterson 2005). In many ways, this heralds the emergence of a new scientific discipline—socioecology—at the intersection of the social sciences, environmental sciences, and engineering.

This new discipline explicitly considers coupled human and natural sys-

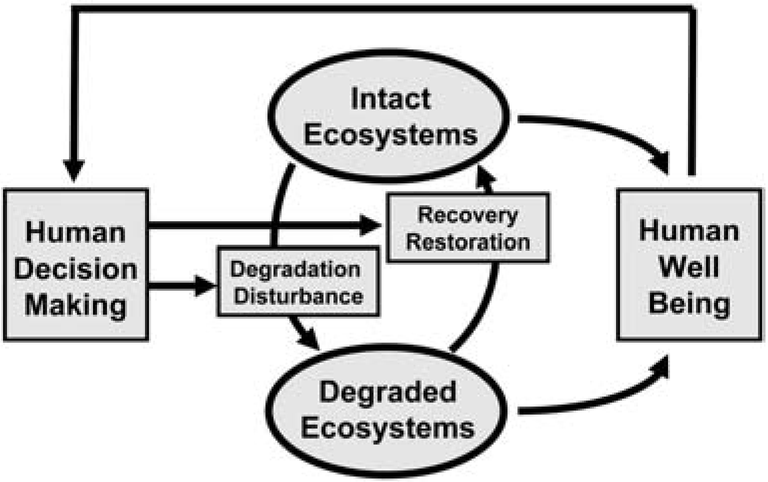

Figure 15.3 This conceptual model illustrates key linkages between natural and human systems that together constitute a socioecological system. It recognizes (1) that the functionality of natural systems varies along a continuum from intact to degraded, with each providing inputs (both positive or negative) to human well-being; (2) that human decisions affect ecosystems positively, via recovery, restoration, or reclamation, or negatively via degradation; and (3) that real or perceived well-being of humans should directly feed back on decision making (policy) so as to adaptively and sustainably manage natural systems.

tems as the domain of interest (Fig. 15.3). At its foundation is the theory of disturbance and succession, with human social systems as both the drivers of and respondents to change. These dynamic feedbacks must be used in policy decisions if they are to lead to adaptive management with a goal of enhancing resilience and long-term sustainability. Such a theory would focus on cycles of disturbance and recovery (succession) within the socioecological system (including its biotic and abiotic constituents), and would rely on an understanding of successional dynamics (Pickett et al. Chapter 9) and ecosystem function (Burke and Lauenroth Chapter 11). In so doing, it considers humans as ecological engineers or drivers of change (disturbance agents) that affect landscape configurations of local ecosystems, each with positive or negative consequences to human well-being. Moreover, it considers human well-being as providing feedback to human actions via policy and management. Perhaps the greatest challenge to face society and science in the 21st century will be developing a predictive understanding of coupled human and natural systems—socioecological systems—so that policy and management can be responsive to long-term goals of sustainability. The further development of theory across all of ecology will play a critical role in the ultimate success of such an endeavor.

Integration and unification: the future of ecology

Despite the different levels in the biological hierarchy that the chapters in this book address, as well as particular interactions that form the focus of their expositions, they share a number of features. Each chapter defines a suite of basic propositions within a particular domain, and combines different state variables or parameters in alternative ways to provide understanding or prediction about central ecological phenomena. Each links the propositions associated with its domain back to the fundamental principles of ecology (Table 1.3). The chapters identify central models within their domains; some are conceptual while others are more precise and mathematical in nature. Thus, these chapters consolidate the state of understanding and accelerate the process of theory unification. In addition, each chapter clarifies connections between its focal domain and the domains of other chapters or subdisciplines of ecology, enhancing integration. Various chapters illustrate how different assumptions lead to different models. A failure to substantiate a particular model does not necessarily mean that the more general theory with which it is associated is wrong or useless. Rather, much of ecology deals with understanding the conditions that favor one model over another, and how these conditions relate to the formalized assumptions of each model.

During discussions at the workshop that preceded this book and during the process of articulating the various constitutive theories, a common claim was that one person's theory was central to all of ecology and that all other domains could be viewed as ancillary to her or his domain. Such viewpoints are to be expected as we attempt to build a set of integrated constitutive theories. Our general theory tells us that the constitutive theories must be linked to each other. As noted in the various chapters, each constitutive theory links directly with numerous other theories. In some cases the theories share similar propositions. Some of this sharing is expected and obvious [e.g., population dynamics theory (Hastings Chapter 6) and enemy-victim theory (Holt Chapter 7); ecological gradient theory (Fox et al. Chapter 13) and biogeographical gradient theory (Colwell Chapter 14)]. In other cases, overlaps become more apparent after propositions are formalized, for example the role of connectivity in metacommunity theory (Leibold Chapter 8) and global change theory (Peters et al. Chapter 12). In yet other cases, the propositions of one theory can point to ways that other theories can be modified, for example the role of species interactions in niche theory (Chase Chapter 5) as a guide to adding such interactions to island biogeography theory (Sax and Gaines Chapter 10) or ecological gradient theory (Fox et al. Chapter 13). No single constitutive theory is at the center of ecology. Rather all are connected and overlap to some degree and together define the science of ecology.

A more comprehensive unification and integration of ecology would be advanced by applying these approaches to domains of ecology beyond those considered in this book (e.g., competition, mutualism, food webs, and landscapes). For example, the metabolic theory of ecology (West et al. 1997; Brown et al. 2004) currently consists of a single model that has been applied to a variety of questions (e.g., Allen and Gillooly 2009). Progress would be furthered through the articulation of the propositions that underlie that model coupled with an attempt to develop alternative models derived from those same propositions. Such alternative models would help to clarify the debate around this theory (Hawkins et al. 2007; del Rio 2008). It would lead to the testing of alternative hypotheses, going beyond the current practice of simply fitting data to a single model, as is frequently done across all of ecology.

We do not mean to imply that ecology will advance or mature only via a single approach, such as that advocated in this book. Indeed, understanding within a domain evolves via a variety of activities. Such a diversity of approaches can lead to robust formulations of the intellectual framework—the theory—that distinguishes ecology, integrates its components, and identifies lacunae in understanding or shortcomings in empirical validation.

The past 50 years in ecology have seen the development of two contrasting approaches to model development. One is the ecosystem approach, exemplified by the work of Odum and his collaborators (Odum 1971), which attempts to build models that are highly complex and specific. The other is the evolutionary ecology approach, exemplified by the work of MacArthur and his colleagues (Odenbaugh Chapter 3), which aims to build very simple and general models. Although often seen as antithetical (Odenbaugh 2003), the theoretical framework presented in this book can encompass both modeling approaches (e.g., Holt Chapter 7, Burke and Lauenroth Chapter 11). The challenge for all modeling approaches is to determine the underlying propositions that provide the theoretical framework for a set of models. For simple, general models moving to more general propositions is relatively straightforward, although still not a trivial exercise, as was discovered by the contributors to this book. For complex, specific models, deriving general propositions is less straightforward. Recent advances in structural equation modeling (Grace et al. 2010) provide one avenue by which such models can be united within a general framework.

In summary, the process of unification and integration is well under way within the various domains of the constituent theories of ecology, as well as at the level of the general theory, including its integration with the rest of biology (Scheiner 2010). An uber-theory, in the sense of an all-encompassing model or mathematical formulation, is unlikely to characterize ecology in its full diversity of content based on the hierarchy of interacting systems.

We are hopeful that from these modest beginnings, advances in ecological understanding will be accelerated by a faithful and consistent application of integrative and unifying approaches to the development of theory, such as those considered in this book. We trust that these chapters will strengthen the foundations of ecological understanding and help to herald a time of an intensified interest in ecological theory. We are not viewing the death of theory. Borrowing from Winston Churchill (10 November 1942), "his is not the end. It is not even the beginning of the end. But it is, perhaps, the end of the beginning" of a revitalization in the advancement of theory as a vehicle for promoting deep understanding of ecological systems.

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