

# Introduction



## CHAPTER 1

# A General Theory of Ecology

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In the absence of agreed protocols and overarching theory, Ecology with its numerous subdisciplines, can sometimes resemble an amorphous, post-modern hotel or rabbit warren with separate entrances, corridors and rooms that safely accommodate the irreconcilable.

Grime 2007

The development of theory in ecology is a lively and robust enterprise (Pickett et al. 2007). Despite claims to the contrary, the science of ecology has a long history of building theories that fruitfully guide research and deepen understanding. Our goal with this book is to reveal a selection of those theoretical structures. In doing so, our hope is that ecologists will better appreciate the theoretical frameworks within which they do research, and will more thoroughly engage those theories in designing observational, experimental, and modeling components of their research. Many theories in ecology contain unspoken or even subconscious assumptions. By bringing such assumptions to the forefront, we can understand their consequences, and discover new mechanisms, patterns, and linkages among theories. Theory sometimes seems to be distant or disconnected from everyday practice in ecology. By the end of this book, the relevance of theory to understanding in ecology and its role in advancing science should become clear.

In this chapter, we present a general theory of ecology that serves as the supporting framework—a conceptual infrastructure—for the constitutive

theories that appear in subsequent chapters. Although those chapters span the disciplinary range of ecology, they are representative rather than comprehensive. We could not possibly synthesize the full richness of ecological theory in a single book without it becoming encyclopedic. We encourage others to continue the process of theory development in other venues, and to reengage theoretical discourse with ecological research (e.g., Pickett et al. 2007).

We do not claim novelty for the general theory of ecology that we put forward. Quite the contrary, the elements of the general theory have existed for at least 50 years. Many of its principles are implicit in the tables of contents of most ecology textbooks, although our previous treatise (Scheiner and Willig 2008) was their first formal explication. In this chapter, we expand our earlier discussion of the structure of theories and the framework that underlies theory in ecology, providing a foundation for the chapters that follow.

Importantly, we do not claim that the theory presented here is a final version. Rather, it should be considered provisional and ever changing, a general characteristic of theory that is often misunderstood by nonscientists. Indeed, the list of fundamental principles that we present will require additions, deletions, or refinements as ecological theory matures and is confronted by empirical evidence. Critically, this debate can occur only after explication of the theory. In the process of assembling this volume, we convened a workshop of the contributors at the Center for Environmental Sciences and Engineering of the University of Connecticut. At that workshop, a fundamental principle emerged that was not considered in our previous paper (Table 1.3, number 3 below). The theory of ecology is, in turn, embedded within an even broader theory that encompasses all of biology (Scheiner 2010). As that broader theory continues to evolve it may alter the structure of or our understanding of this theory.

### The structure of theories

Before we present our general theory of ecology, we must describe the essence of theory and its structure (Tables 1.1 and 1.2). Theories are hierarchical frameworks that connect broad general principles to highly specific models. For heuristic purposes, we present this hierarchy as having three tiers (a general theory, constitutive theories, and models); however, we do not suggest that all theories fit neatly into one of these three categories. Rather, the framework will often stretch continuously from the general to the specific. The three tiers illustrate that continuum, and provide a useful way of viewing that hierarchy. The definitions and principles of the general theory are meant to encompass a wide variety of more specific constitutive theories, which in turn contain

**Table 1.1** A hierarchical structure of theories including their components. A general theory creates the framework within which constitutive theories can be articulated, which in turn sets the rules for building models. Conversely, tests of models may challenge the propositions and assumptions of its constitutive theory, which in turn may result in a change in the fundamental principles of the general theory. See Table 1.2 for definitions of terms.

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### General Theory

Background: domain, assumptions, framework, definitions

Fundamental principles: concepts, confirmed generalizations

Outputs: constitutive theories

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### Constitutive Theory

Background: domain, assumptions, framework, definitions

Propositions: concepts, confirmed generalizations, laws

Outputs: models

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### Model

Background: domain, assumptions, framework, definitions, propositions

Construction: translation modes

Outputs: hypotheses

Tests: facts

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families of models. This view of constitutive theories as families of models is consistent with how theories are treated across all of biology and in other sciences (van Fraassen 1980; Giere 1988; Beatty 1997; Longino 2002; Pickett et al. 2007; Wimsatt 2007; del Rio 2008; National Research Council 2008).

Each theory or model applies to a domain. The domain defines the universe of discourse—the scope of the theory—delimiting the boundaries within which constituent theories may be interconnected to form coherent entities. Constitutive theories are often most fruitful when they focus on one or a few phenomena in need of explanation (e.g., Hastings Chapter 6; Sax and Gaines Chapter 10). Without such boundaries, we would be faced with continually trying to create a theory of everything.

Nonetheless, we recognize that domains are somewhat arbitrary conceptual constructs and that theories or models may have overlapping domains. Changing the domain of a model can be a fruitful avenue for juxtaposing phenomena or processes that had been considered in isolation. For example,

**Table 1.2** Definitions of terms for the theory components in Table 1.1 (modified from Pickett et al. 2007).

Component	Definition
Assumptions	Conditions or structures needed to build a theory or model
Concepts	Labeled regularities in phenomena
Confirmed generalizations	Condensations and abstractions from a body of facts that have been tested
Definitions	Conventions and prescriptions necessary for a theory or model to work with clarity
Domain	The scope in space, time, and phenomena addressed by a theory or model
Facts	Confirmable records of phenomena
Framework	Nested causal or logical structure of a theory or model
Fundamental principle	A concept or confirmed generalization that is a component of a general theory
Hypotheses	Testable statements derived from or representing various components of the theory or model
Laws	Conditional statements of relationship or causation, or statements of process that hold within a universe of discourse
Model	Conceptual construct that represents or simplifies the natural world
Translation modes	Procedures and concepts needed to move from the abstractions of a theory to the specifics of model, application, or test

microeconomic theory uses three concepts—utility, income, and price—to understand consumer choices (Henderson and Quandt 1971; Mansfield 1979). Choices are assumed to maximize utility, subject to income and price constraints. Behavioral ecologists study the economics of choice for nonhuman animals and have applied conceptual constructs and mathematical models from economics to understanding foraging ecology and space utilization (Stephens and Krebs 1986; see Sih Chapter 4). Recent examples of such borrowing of models across domains include the use in ecology of maximum entropy from thermodynamics theory (Harte et al. 2008; McRae et al. 2008) and connectivity models from electrical circuit theory (McRae et al. 2008).

All theories and models contain simplifying assumptions so as to focus other characteristics of a system. The problem with many assumptions is that they are unstated, even subconscious. Making such assumptions explicit sometimes may change the focus of the theory. For example, a fundamental principle of ecology is that ecological traits arise through evolution, but nearly always this is an unstated and ignored assumption. Models of community assembly usually ignore phylogenetic relationships among species. Recently, models that incorporate phylogenetic relationships have added substantially to our understanding of community assembly (e.g., Kraft et al. 2007).

Sometimes, such unstated assumptions can turn around and bite us. Most models of life history evolution assume that organisms can always adopt the optimal phenotype, instantaneously reallocating resources from growth to reproduction, and so ignoring evolutionary and developmental constraints. Ignoring this assumption led to predictions that were biologically improbable, e.g., an organism should allocate 100% of its resources to reproduction one day after devoting 100% of its resources to growth (Schaffer 1983), or an annual plant should switch multiple times between growth and reproduction (King and Roughgarden 1982).

### *Principles and propositions*

When asked to describe a theory, we often think of a set of broad statements about empirical patterns and the processes that operate within a domain. For the sake of clarity, we use different terms to refer to those broad statements when we speak of general theories (fundamental principles) versus when we speak of constitutive theories (propositions). In part, fundamental principles are similar to propositions. Each can be a concept (labeled regularities) or a confirmed generalization (condensations of facts). They differ in that fundamental principles are broader in scope, often encompassing multiple inter-related patterns and mechanisms. Because constitutive theories are meant to guide the building of specific models, their propositions should be more precise statements that represent the potential individual components of those models.

Propositions can be laws: statements of relationship or causation. The propositions are where the fundamental principles of the general theory are integrated. For the general theory of ecology, some of the principles involve patterns, others involve processes, many involve both (see below). Thus, the causal linking of process and pattern, the lawlike behavior that we look for in theories, occurs through the propositions of the constitutive theories.

Laws reside within constitutive theories, and not as part of the general the-

ory, because no single law is required for the construction of the models in all of ecology's subdomains. Several chapters show, however, that ecology is rich in laws that hold within more limited domains (see discussion in Willig and Scheiner Chapter 15). A brisk debate has occurred over whether ecology has any laws at the level of its general theory (e.g., Lawton 1999; Murray 2000; Turchin 2001; Berryman 2003; Simberloff 2004; O'Hara 2005; Pickett et al. 2007; Lockwood 2008), which is related to the debate about laws across all of biology (e.g., Beatty 1997; Brandon 1997; Mitchell 1997; Sober 1997). The continuing search for such laws is an important aspect of a theory's evolution.

The reaction of many to confirmed generalizations is, "Well, isn't that obvious?" In reality, the answer is no. Often such generalizations are obvious only after their explication. Generalizations serve as reminders about assumptions contained in lower-level theories or models. For example, a fundamental principle in ecology is that ecological processes depend on contingencies (see below). Yet many ecological theories and models are deterministic and ignore the role of contingency or stochasticity in molding patterns and processes in nature. Deterministic models are not wrong, just potentially incomplete. Sometimes ignoring contingencies has no effect on model predictions. At other times, the consequences can be profound. As the statistician George E. P. Box is reputed to have said, "Essentially, all models are wrong, but some are useful."

Fundamental principles keep prodding us to test assumptions. For example, one fundamental principle tells us that species are made up of individuals that differ in phenotype. Nonetheless, many ecological theories assume that species consist of identical individuals. Although this is a useful simplification in many instances, it is important to be reminded continually about this assumption and its consequences to predictive understanding. Similarly, many of the fundamental principles consider variation in the environment or species interactions, yet many constitutive theories or models average over that variation (Clark 2010).

Not all assumptions within a constitutive theory derive from the fundamental principles of its general theory. Some assumptions derive from other domains. If an assumption is taken unchanged from another domain it may be unspecified within a theory. For example, all constitutive theories in ecology take as given the conservation of matter and energy, fundamental principles from the domain of physics. We take as given the fundamental principles of any other general theory. As such, we recognize the general tenet of consilience: the entire set of scientific theories must be consistent with each other (Whewell 1858). The decision to explicitly include such assumptions as fundamental principles within the theory under consideration depends on



whether those assumptions are subject to test within that theory. Since no theory in ecology would ever test the conservation of matter, it lies outside those theories.

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 was a factor that led to the development of new fundamental principles in another domain.

### *Models*

At the lowest level of our theory hierarchy are models. Models are where the theoretical rubber meets the empirical road. Many ecological theories are just such models. Although scientific theories encompass a wide variety of types of models, including physical models (e.g., Watson and Crick's ball and wire model of a DNA molecule), in ecology we generally deal with abstract or conceptual models. These models may be analytic, statistical, or computational.

Models are where predictions are made and hypotheses are tested. Those predictions can run the gamut from general qualitative predictions (e.g., increases in primary productivity will lead to increases in species richness) to very specific quantitative predictions (e.g., an increase in soil nitrogen of 5 ppm will result in an increase in average species richness of 4.3 species). The prediction can be a point estimate if the model is deterministic, or it can be a distribution of values if the model is stochastic. The models that make those predictions can be very simple (e.g., equation 7.1 in Holt Chapter 7) or highly complex (e.g., figure 12.4 in Peters et al. Chapter 12). A particular constitutive theory can encompass many different types of models. Because general theories consist of families of models, they very rarely rise or fall based on tests of any one model. Alternative or competing models exist within most theoretical constructs in ecology (e.g., Pickett et al. Chapter 9) allowing a single theory to encompass a diversity of phenomena.

Recognizing that what is often labeled as a theory is but one model within a larger theory can help to clarify our thinking. For example, Scheiner and Willig (2005) assembled an apparently bewildering array of 17 models about species richness gradients into a framework built on just four propositions. A similar process of clarification can be found in Chapter 8, where Leibold shows that all

metacommunity theories can be captured within a single framework of just two characteristics: amount of interpatch heterogeneity and dispersal rate. Other chapters in this book provide further examples of model unification. This process of model unification has begun to take hold in other areas of ecology (e.g., McGill 2010). We disagree, however, with McGill's claim that to be unified a theory can contain just a single model. Rather, a strength of our approach to theory unification is the ability of a theory to embrace model diversity.

Because theories often consist of families of models, it is possible for models to be inconsistent or even contradictory. Sometimes, such inconsistencies point to areas that require additional empirical evaluation or model development. But sometimes contradictory models can be maintained side-by-side because they serve different functions or are useful under different conditions. For example, in some physics models, light is treated as a particle and in others as a wave. There is no need to insist that contradictory models always be reconciled or that one always prevail. Instead, this apparent contradiction is resolved at a higher level in the theory hierarchy by a more general theory, for example one that allows for both wave-like and particle-like behavior of light. The apparently contradictory models are built from differing sets of propositions arising from different assumptions and thus refer to different domains. In a similar fashion, constitutive theories can be contradictory if they are built with different assumptions.

### The domain of ecology

The domain of ecology 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 (Pickett et al. 2007; Scheiner and Willig 2008), it differs in two respects. First, our definition includes the phenomena to be understood (i.e., spatial and temporal patterns of the 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, such as the flux of matter and energy.

In general, the domain of a theory defines the objects of interest and their characteristics. Ecological theories make predictions about three types of objects: species, individuals, and traits or consequences of individuals. Parts of ecology (e.g., ecosystem theory) also make predictions about fluxes and pools of elements and energy. However, what makes these theories part of the do-

main of ecology is that those fluxes and pools are controlled or affected by the activities, abundances, and distribution of organisms. Thus, they are aggregate consequences of species, individuals, or the traits of individuals. Otherwise, ecosystem theory would reside firmly in the domain of the geosciences.

All three types of objects share an important property, variability (see below). This collection of objects distinguishes ecology from other related and overlapping domains. The theory of evolution makes predictions about species and the traits of individuals. Its domain differs from that of ecology in that predictions are always about collections of individuals (e.g., gene frequencies), never about a single individual. In contrast, theories in ecology may make predictions about either collections of individuals or a single individual (e.g., Sih Chapter 4). Because a given object may be part of multiple domains, understanding of that object and its characteristics depends on examining it within the context of all of those domains.

Just as a general theory has a domain, each constitutive theory or particular model has a domain. Explicitly defining each such domain is important for two reasons. First, a domain defines the most central or general topics under investigation. Second, a clear definition indicates which objects or phenomena are excluded from consideration. Many protracted debates in ecology have occurred when proponents or opponents of particular theories or models have attempted to make claims that fall outside a theory's domain. For example, the extensive debates over the causes of large-scale patterns of plant diversity (e.g., Huston 1994; Waide et al. 1999; Mittelbach et al. 2001; Mittelbach et al. 2003; Whittaker and Heegaard 2003) are based on extrapolating to continental and global scales, models that are valid only at a regional scale (Fox et al. Chapter 13).

### Overlapping domains

The domain of the theory of ecology overlaps substantially with several other domains (Scheiner 2010). Of course, all scientific domains overlap in some fashion, but we speak here of those domains that make predictions about some of the same objects of study as does the theory of ecology, or constitutive theories that use fundamental principles from other domains. A constitutive theory can straddle two or more general theories if some of its models ultimately address a central question of each general theory. One way to decide whether a constitutive theory straddles two general theories is to consider the assumptions of those general theories. If the constitutive theory simply accepts all of the assumptions in a particular general theory and never questions or tests them, it likely is not a member of that general theory.

A corollary of the previous statement is that any given model of necessity explores or tests one or more of the assumptions, fundamental principles or propositions of a theory. For example, a continuing issue in ecology concerns the identity of parameters that can be treated as constants and those that need to be treated as variables in a particular theory or model. If a parameter is treated as a constant, the average value of that parameter is assumed to be sufficient because either the variation has no effect or acts in a strictly additive fashion relative to the causative mechanisms under examination.

In some instances, ecologists make assumptions without ever testing them. For example, it is reasonable to assume that we can average over quantum fluctuations (from the domain of physics) in ecological processes. On the other hand, the physiological variations that occur in a mammal so as to maintain body temperature (from the domain of the theory of organisms) (Scheiner 2010; Zamer and Scheiner in prep.) may matter for ecological processes and should not be averaged in some instances. For example, basal metabolic rates in large mammals can vary substantially between winter and summer. Failure to account for this variation can seriously overestimate winter energy expenditures and underestimate summer energy expenditures and the concomitant consequences for food intake requirements (Arnold et al. 2006).

A subdomain can overlap two domains. For example, ecosystem science has some constituent theories that are part of ecology and some that are part of the geosciences. Such overlaps can extend to the level of individual models. For example, foraging theory (Sih Chapter 4) contains some models that are ecological, others that are evolutionary, and others that are both. This sharing of subdomains shows that the boundaries of domains are not distinct and can be somewhat arbitrary.

A domain as defined by a general theory, constitutive theory, or model should be a coherent entity. Some named areas are not domains, but collections of domains. For example, evolutionary ecology consists of a set of constituent theories, some of which are within the domain of the theory of ecology and others that are within the domain of the theory of evolution.

### The fundamental principles of ecology

The general theory of ecology consists of eight fundamental principles (Table 1.3). The roots of these principles can be traced to the origins of ecology in the 19th century. They were in place and widely accepted by the 1950s, were recently codified as the components of a general theory (Scheiner and Willig 2008), and continue to evolve (compare this treatment with somewhat different versions in Scheiner and Willig 2008, and Scheiner 2010). In par-

**Table 1.3** Eight fundamental principles of the general theory of ecology (modified from Scheiner and Willig 2008; Scheiner 2010)

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1. Organisms are distributed in space and time in a heterogeneous manner.
  2. Organisms interact with their abiotic and biotic environments.
  3. Variation in the characteristics of organisms results in heterogeneity of ecological patterns and processes.
  4. The distributions of organisms and their interactions depend on contingencies.
  5. Environmental conditions as perceived by organisms are heterogeneous in space and time.
  6. Resources as perceived by organisms are finite and heterogeneous in space and time.
  7. Birth rates and death rates are a consequence of interactions with the abiotic and biotic environment.
  8. The ecological properties of species are the result of evolution.
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ticular, we have added an eighth fundamental principle (number 3), so that the numbering of this set differs somewhat from our previous list, and revised the wording of several others.

### *Heterogeneous distributions*

The first fundamental principle—the heterogeneous distribution of organisms—is a refinement of the domain of the theory of ecology. The heterogeneity of distributions is one of the most striking features of nature: all species have a heterogeneous distribution at some if not most spatial scales. Thus, this principle encompasses a basic object of interest, is its most important property, and serves to guide the rest of the theory. All of the other parts of the theory of ecology serve to either explain this central observation or to explore its consequences. 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 patterns and processes.

### *Environmental interactions*

The second fundamental principle—interactions of organisms—includes within it the vast majority of ecological processes responsible for heterogene-

ity in time and space. They include both intraspecific and interspecific interactions such as competition, predation, and mutualism, as well as feedbacks between biotic and abiotic components. Within this principle, particular interactions that are part of constituent theories act to elaborate the general theory (see later chapters). Many definitions of ecology are restatements of this principle (Scheiner and Willig 2008).

### *Variation of organisms*

The third principle—the variation of organisms—is the result of processes that derive from the theory of organisms (Scheiner 2010; Zamer and Scheiner in prep.). Ecological theories make predictions about the characteristics or aggregate properties of species, individuals, or traits. The majority of ecological theories make predictions about species or collections of species (e.g., species richness of communities; see Chapters 8–10, 13, 14). Some theories, such as population ecology and behavioral ecology, concern themselves with predictions about individuals or collections of individuals (e.g., numbers of individuals in a population; see Chapters 4–8). Some theories make predictions about the properties of individuals or species (e.g., body size distributions; see Chapters 4, 5, 8, 10, 13, 14). Finally, some theories make predictions about the aggregate properties of individuals or species (e.g., ecosystem standing biomass; see Chapter 11).

Groups of species or individuals share the property that the members of those groups differ in their characteristics, even though many theories and models assume invariance. For example, one of the most common hidden assumption in models of species richness is that all individuals within a species are identical (e.g., Fox et al. Chapter 13). Such assumptions may be reasonable for the purposes of simplifying models. Violations of this assumption may not substantially change predictions. However, in some cases relaxing this assumption has led to substantial changes in predictions. For example, when the chances of survival are allowed to vary among individuals within a population, treating all individuals as identical turns out to substantially misestimate the risk of local extinction from demographic stochasticity; depending on the model used for reproduction, treating all individuals as identical can over- or underestimate that risk (Kendall and Fox 2003).

### *Contingency*

The fourth fundamental principle—contingency—has grown in importance in ecological theory and now appears in a wide variety of constituent theories

and models. By contingency we mean the combined effects of two processes—randomness and sensitivity to initial conditions. Contingency is an important cause of the heterogeneous distribution of organisms, both at very large and very small extents of time and space (e.g., a seed lands in one spot and not another; a particular species arises on a particular continent). This principle exemplifies the dynamic nature of a theory. A theory is constantly evolving, although substantive change typically occurs over decades. One hallmark of that dynamic is the emergence of new principles, such as this one, which arose during the 1960s to 1980s.

### *Heterogeneity of environmental conditions*

The fifth fundamental principle—environmental heterogeneity—is a consequence of the interaction of processes from the theory of organisms and the theories of earth and space sciences when the environmental factors are abiotic, as well as the consequences of the second principle when those factors are biotic. 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). This principle is part of many constituent theories and contains a broad class of underlying mechanisms for the heterogeneous distribution of organisms, as seen in many of the constitutive theories presented in this book. As with the second principle, particular mechanisms pertain to particular constituent theories.

### *Finite and heterogeneous resources*

The sixth principle—finite and heterogeneous resources—is again a consequence of processes from the theory of organisms, and the theories of earth and space sciences or the second principle. Although variation in resources is similar to variation in environmental conditions, a fundamental distinction is the finite, and thus limiting, 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 different ecological outcomes. For example,  $\beta$ -diversity in plant communities is high in warm deserts and low in arctic tundra because diversity in warm deserts is controlled by water, a limiting resource, whereas diversity

in arctic tundra is controlled by temperature, an environmental condition (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). Some heavy metals (e.g., manganese) can be limiting to plants if at low levels, so acting as a resource, and be toxic at high levels, so acting as a condition.

### *Birth and death*

The seventh fundamental principle—the birth and death of organisms—is the result of processes that come from the domain of the theory of organisms (Scheiner 2010; Zamer and Scheiner in prep.). One of the fundamental characteristics of life is reproduction. While birth comes about through cellular and organismal processes, such as fertilization and development, the rate that it occurs depends on interactions of an organism with its environment, such as the uptake of nutrients or mating.

Similarly, a defining characteristic of life is that all organisms are mortal. By “mortal” we mean that no organism is invulnerable, i.e., any organism might die as the result of predation, stress, trauma, or starvation. Thus, the rate of death depends on environmental interactions. We do not mean that all organisms senesce. The senescence of organisms, a decrease in function or fitness with age, is a more narrow version of this principle that would apply to particular constituent theories. This fifth principle forms the basis of a large number of constituent theories concerning phenomena as wide ranging as life histories, behavior, demography, and succession (e.g., Chapters 4, 6, and 9).

### *Evolution*

The eighth 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 influencing ecology widely since at least 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 (Sih Chapter 4) and population biology, and contributed to the demise of the Clementsian superorganism theory (Clements 1916, 1937).

This principle illustrates how theories in overlapping domains can interact



with each other. One of the fundamental principles of the theory of evolution is that evolutionary change is caused primarily by natural selection (Mayr 1982; Scheiner 2010). Fitness differences among individuals, a key component of the process of natural selection, are caused in large part by ecological processes. So ecology drives evolution, which in turn determines ecological properties.

## Overview

This chapter only begins to delve into the many issues that relate to theory structure and development in ecology. For a much more comprehensive discussion, we recommend Pickett et al. (2007). One purpose in articulating a general theory is to clarify thinking, bringing to the fore aspects of science that may not be recognized consciously. For example, it is notable that five of the eight fundamental principles are about variability. Although ecologists sometimes decry the variation among the entities that they study and claim that such variation prevents the development of laws or predictions, we suggest that progress in ecology requires that ecologists embrace this variation and explicitly encompass it in theories. More important, recognizing that variation is a pervasive property of our discipline helps explain why ecologists sometimes have difficulty communicating about ecology to colleagues in other disciplines, where the focus is on the shared properties of organisms rather than on their variability.

From the general overview of the theory of ecology given here, Chapters 2 (Kolasa) and 3 (Odenbaugh) consider the role that theory has played in ecology from the perspectives of a practicing ecologist and of a philosopher of science. Then, the eleven chapters that make up the heart of the book delve into the theoretical underpinnings of a broad range of ecological subdisciplines. Each of those chapters develops a constitutive theory by identifying the domain of the theory, listing its propositions, explaining the structure of the theory, and exploring one or more models that can be derived from that theory. In doing so, they show how theory formalization enhances our understanding of the theory and improves our ability to build models. Finally, we provide a brief synthesis chapter highlighting the linkages among the constitutive theories and exploring their similarities and differences in approach to theory development and structure.

Throughout the process of developing and articulating the general theory and the constitutive theories of ecology, we have been impressed by how often the statement and full consideration of the seemingly obvious can lead to deep insights. The chapters that follow demonstrate that process. Our hope is

that such insights will substantially improve how we do our science. Ecologists often despair over the seemingly endless variety of their science with no clear overarching structure. The theories discussed in this book present a critical set of steps in unifying that structure.

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