

CHAPTER ONE

Ecological Opportunities, Communities, and Evolution

Spend any time in nature and you quickly notice that even over quite short distances you encounter different creatures in different places. The trees change as you hike from the bottom to the top of a high hill. The understory plants change as you pass from an oak-hickory stand into a pine stand. Different birds are singing in the open field as compared to the forest. The insects in the small creek you jump over are different from those you find in the river miles downstream. The lake at the bottom of the hill has sunfish in it, but the vernal pond at the summit has salamanders instead.

These are the kinds of patterns in nature that fascinate me. Consequently, one question has primarily driven my work: Why do these species live here but not over there, but why do those species live over there and not here? In fact, my very first research project as a budding undergraduate scientist addressed a very simple variant of this question (McPeck et al. 1983). This question continues to beguile me to this day. I am not alone in this quest. Many of those in ecology and evolutionary biology see their task as the explanation of such patterns in the distributions, abundances and diversity of species at one site, at different sites across space, and through time.

To answer this broad and overarching question with appropriate justice, one must consider many different, faceted, and layered questions. The first set of more specific questions necessarily address the ecological bases of these patterns. Are there ecological processes that cause these species assemblages to segregate across the landscape, and if so what are they? In other words, what prevents those particular species from living here? Also, the complementary question is just as essential. What makes species successful (or at least successful enough) to live where you find them? In other words, why do these particular species live here? The answers to these questions establish the ecological processes that maintain these patterns today and into the future.

These answers do not, however, address how these patterns were established in the first place. For this, we need to address a further set of questions. How did

these collections of species come to have the properties that influence where they can and cannot live? More generally, where did these species come from in the first place? These are fundamental questions about the evolution of species individually and of the diversification of the clades in which each has been embedded over long time scales. The contemporary ecological context of these taxa form the foundation on which these evolutionary questions must be built, but we must address the longer-term evolutionary dynamics explicitly for a complete answer to the overarching query.

In designing such a research program, I have always been inspired by two grand metaphors. The first is Stephen J. Gould's (1989) metaphor of playing the tape of evolutionary history over. Gould felt that much of what would evolve would be highly contingent, and the course of evolution would be difficult to predict. I am not nearly as pessimistic as he was that we cannot understand or predict what would happen. Certainly, the exact same creatures would not arise, and the stochastic nature of evolution would set Earth's biota down different paths with each replay. However, the governing principles of ecology and evolutionary biology would apply to every replay of the tape; although we may not be able to exactly predict all the particulars, we should be able to understand and interpret what happens. In my own research, I imagine what would happen if I could go back 10 million years into the past to see which types of ponds and lakes the various taxa of eastern North America inhabit, and then watch what happens to them and their descendants until they and I arrive in the present (e.g., McPeck and Brown 2000).

This evolutionary play unfolds in the ecological theater—this is the second grand metaphor, articulated by G. Evelyn Hutchinson (1965), that inspires this book. The evolutionary trajectories of various species are directed by the ecological interactions they experience each day across the landscape. Each species is an actor on this ecological stage, and their interactions define what they experience, and thus how the play proceeds. What new opportunities do the various actors present to one another? How does each attempt to exploit these opportunities and how must they change to exploit these opportunities? Finally, how do those changes affect their distributions, abundances, and diversity across the theater through time?

The structure of this work is inspired by Hutchinson's and Gould's metaphors. Can we organize and link ecological and evolutionary theory to provide a framework in which we can understand and predict the organization of local communities and regional biotas over evolutionary time? For me, the organizing concept in all this is the ecological opportunity. In ecology, we might call this a niche; in evolutionary biology we might call this an adaptive peak—we'll see. Some species can exploit an opportunity, and others cannot. Whether a species or a lineage can do this may have far-reaching consequences for the organization of

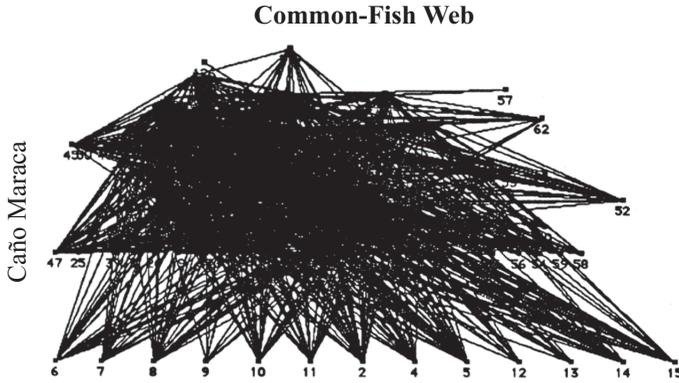
the local community, the evolutionary trajectory of that taxon, and the structure of the regional biota.

WHAT DO REAL COMMUNITIES LOOK LIKE?

If you stop at any spot along a trail through the woods, you will encounter a dizzying collection of species that are interacting with one another under the abiotic conditions at that site. In fact, an immense amount of work is required to characterize the web of interactions among all the species found in a patch of forest, or in a stream or lake, and the network of connections are typically very dense and complex (e.g., Winemiller 1990, Martinez 1991, Dunne et al. 2002, Bascompte et al. 2003). For example, figure 1.1 reproduces the figure constructed by Winemiller (1990) that depicts the trophic interactions among 63 aggregated taxa found in the Caño Maraca swamp creek in western Venezuela; this work represents one of the best characterized food webs in ecology. Each dot in the figure is either one of these 63 aggregated taxa or 62 common fish species (of the total 121 fish species collected there), and lines connect taxa that are consumer and resource (one species that feeds on another), based on diet information.

Because Winemiller was interested in the fish assemblage, he identified all fish to species. However, nodes representing the aggregate taxa are not species at all, but rather broad taxonomic groups (e.g., diatoms, chironomids, odonates) and a few categories of detritus (fig. 1.1). This figure also omits the bacteria that process the detritus, viruses, pathogens, and parasites that plague all species, as well as the many species such as kingfishers, herons, and raccoons that come to forage but do not live in the swamp. Pictorially depicting this trophic web in a way that illustrates structure clearly shows the complexity of the entire system, even with most of the taxa being pooled into such broad categories. In fact, each dot for an aggregated taxon represents a few (e.g., 35 palaemonid shrimp), to tens (e.g., 49 mosquito larvae), to hundreds (e.g., 47 chironomid larvae) of species (fig. 1.1, and fig. 6 and Appendix A in Winemiller 1990).

While this aggregation is frequently unavoidable, particularly for questions about interaction networks, much of community ecology is directed at explaining features and patterns pertaining to the species themselves. We ask questions about factors influencing the number of species of a particular type that can live in an area, whether some collection of species can coexist with one another, or whether some species can exploit a particular ecological opportunity. Such questions can only be addressed if individuals are identified to species. Moreover, these problems multiply when one realizes that no simple answer exists for the question of what a species is.



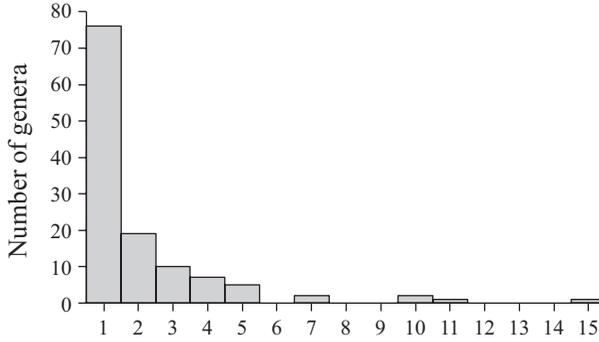
Numeric code	Web node	Numeric code	Web node
2	Fine detritus (organic mud component)	39	Ephemeroptera (mayfly nymphs)
3	Larval anurans (Amphibia)	40	Odonata nymphs
4	Coarse detritus	41	Other aquatic Hemiptera
5	Vegetative detritus	42	Corixidae (aquatic Hemiptera)
6	Diatoms	43	Gerridae (aquatic Hemiptera)
7	Desmids and unicellular green algae	44	Trichoptera larvae
8	Filamentous algae	45	Aquatic Coleoptera, larval forms
9	<i>Chara</i> sp. (macroscopic filamentous algae)	46	Adult aquatic Coleoptera
10	Aquatic macrophytes	47	Chironomid larvae (Diptera)
11	<i>Wolffia</i> spp. and <i>Lemma</i> spp.	48	Other aquatic Diptera larvae
12	Terrestrial vegetation	49	Mosquito larvae (Diptera)
13	Fruits (soft tissues) and flowers	50	Aquatic Neuroptera larvae
14	Seeds and nuts	51	Unidentified aquatic insects
18	Other Protozoa	52	Unidentified terrestrial insects
19	Difflugiid Protozoa	53	Hymenoptera
20	Rotifera	54	Orthoptera
21	Nematoda (non-parasitic forms)	55	Terrestrial Coleoptera
22	Hydracarina (water mites)	56	Lepidoptera larval forms
23	Nematophora (horsehair worms)	57	Hirudinea (leeches)
24	Annelida (earthworms)	58	Lepidoptera adults
25	Gastropoda (snails, Mollusca)	59	Terrestrial Diptera
26	Bivalvia (clams, Mollusca)	60	Terrestrial Hemiptera
27	Thoracica (shipworms, Mollusca)	61	Isoptera (termites)
28	Copepoda (microcrustacea)	62	Arachnida (spiders)
29	Cladocera (microcrustacea)	77	Adult anurans (Amphibia) (only eaten at C. Volcan, dry season)
30	Amphipoda (Crustacea)	99	Lizard (Gekkonidae) (only eaten at C. Agua Fria, wet season)
31	Eubranchiopoda (Crustacea)	122	Turtle flesh (<i>Trachemys scripta</i>) (only at C. Maraca, wet season)
32	Ostracoda (microcrustacea)	123	Bird flesh (only eaten at C. Maraca, wet season)
33	Isopoda (Crustacea)	124	Mammal flesh (only eaten at C. Maraca, wet season)
34	Unidentified microcrustacea		
35	Palaemonid shrimp (<i>Macrobranchium</i> spp.)		
36	Crabs (<i>Dilocarcinus</i> and <i>Callinectes</i> spp.)		
37	Collembola (springtails)		
38	Plecoptera (stonefly nymphs)		

FIGURE 1.1. Representation of the trophic interaction web for the Caño Maraca swamp creek in western Venezuela. Each node in the web represents an aggregated group of taxa (many of which are identified in the accompanying table) and individual species of fish. Lines identify trophic links between taxa. From figure 6 of Winemiller 1990. *Ecological Monographs* (reprinted with permission from John Wiley and Sons).

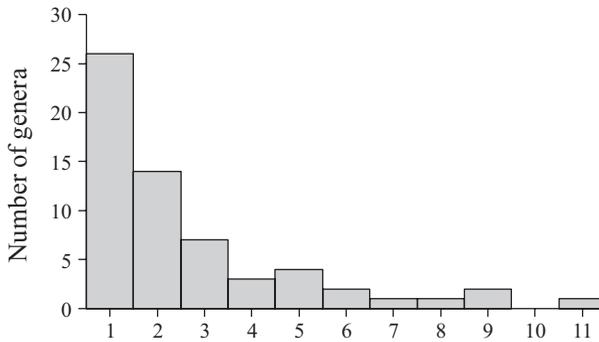
Therefore, it would be instructive to actually look at what is inside those aggregated taxa in the trophic web. Because Winemiller (1990) only identified fish to species, we cannot crack open any of his specific aggregated taxa, but species data on some of these taxa in other systems are available. For example, consider the phytoplankton that forms the base of many aquatic communities. In figure 1.1, phytoplankton are represented by three aggregate taxa. Figure 1.2A presents data on the number of species per genus for phytoplankton in Peter Lake, northern Wisconsin, United States, in samples taken from 1984 to 1995 (data downloaded 6 April 2016 from <https://lter.limnology.wisc.edu/datacatalog/search>). In this lake, 257 total species in 123 genera have been identified. Many genera are represented by a single species, but many others have multiple species living together in the lake, including one (*Dinobryon*) with 15 species. Likewise, chironomids (the midge family of dipterans) are typically a species-rich group in aquatic habitats. Figure 1.2B presents the same information for chironomids for a 100-meter stretch of a first-order mountain creek in Granada, Spain (Casas and Langton 2008). In this short stretch, 163 species in 61 genera were found in samples taken biweekly over four years. Again, some genera were represented by a single species, but many were represented by multiple species, with one (*Eukiefferiella*) having 11 species living together in the stream reach. Finally, figure 1.2C presents the same information from my own work on odonates found in Palmatier Lake, Michigan, United States. I have collected 53 species in 26 genera at this lake over the years (M. A. McPeck, unpubl. data), with almost half of the genera having two or more representative species, and one genus (*Enallagma*) having 12 species living together. Thus, if fully resolved to species, the trophic web depicted in figure 1.1 would have thousands of connected nodes.

A few brave souls try to make sense of these huge webs of interactions, but inquiry at this level is almost exclusively done with taxonomically aggregated nodes (e.g., Winemiller 1990, Martinez 1991, Dunne et al. 2002, Bascompte et al. 2003, Allesina et al. 2008). In contrast to those cited, most community ecologists limit the problems they address to a small subset of interacting species embedded in the broader interaction web—what Holt (1997a) has called the *community module*. As Holt (1997a, p. 333) notes, “the hope is that modules may, at the very least, illuminate general processes and qualitative features of complex communities.” It is at this level that questions are addressed regarding coexistence, limits on the numbers and types of species that can live together, and the exploitation of ecological opportunities. Furthermore, if we are interested in understanding how ecological interactions shape the evolution of species, and how the evolution of species in turn shapes the community in which they are embedded, we must limit our inquiry to these smaller pieces. This is the level on which I focus in this book.

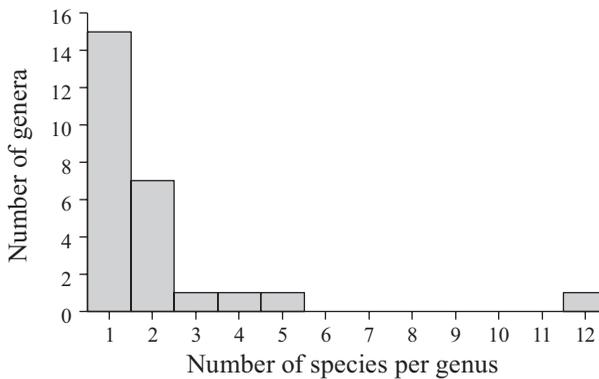
A. Phytoplankton in Peter Lake, Wisconsin



B. Chironomids in 1st order stream, Granada



C. Odonates in Palmatier Lake, Michigan



WHAT IS AN ECOLOGICAL OPPORTUNITY?

Each species in the interaction web of a community is potentially exploiting an ecological opportunity. Before the subject of ecological opportunity can be considered, it must be defined. I define an *ecological opportunity* as a functional position within a community. I will come to what I mean by “functional position” in the coming pages. This definition seems simple but implies a number of important ecological and evolutionary issues. From the outset, let me define a *community* as the species found together in a local area that directly or indirectly interact with the local abiotic environment, and with one another, to thereby affect each other’s fitness (Fauth et al. 1996). Thus, community in the sense used in this analysis is necessarily a local community. The central issue that this definition raises is species coexistence (MacArthur 1972, Holt 1977, Chesson 2000, Adler et al. 2007, Siepielski and McPeck 2010).

An ecological opportunity may be exploited by a species or may be available but unexploited. The processes by which an ecological opportunity can be exploited by a single or multiple species are of critical importance. These processes include immigration from outside the community under consideration, or the origination of new types of organisms from an existing community member (e.g., genetic differentiation within one species across geographic regions or sympatric speciation to create a new species in one place). How opportunities are exploited over ecological and evolutionary time defines the process of community assembly and shapes community structure on both local and regional geographic scales and through time.

The most proximate concern in evaluating an ecological opportunity is whether a new species can invade a community and establish a viable population to exploit the opening. Some invading species will have a positive population growth rate from the instant they establish a population. Such an invading species, call it species i with abundance N_i , would have a positive population growth rate $dN_i/dt > 0$ at a population size of $N_i \approx 0$. As it increases in abundance, the invading species may simply take its place in the community with only quantitative adjustments in the abundances of other species, or other species may be driven extinct by direct

FIGURE 1.2. Numbers of genera with different numbers of species that inhabit communities for representative taxa from three different locations: (A) phytoplankton found in Peter Lake, Wisconsin, United States (data from <https://lter.limnology.wisc.edu/datacatalog/search/>); (B) chironomid midges (Diptera: Chironomidae) from Río Albuñuelas, a permanent first-order creek in Spain (taken from data in Casas and Langton 2008); and (C) the Odonata in Palmatier Lake, Michigan, United States. (Taken from data in McPeck 1990b, 1998; Stoks and McPeck 2003; and M. A. McPeck, unpubl. data.)

interactions with species i , or by the indirect interactions that propagate through the community. By invading, this new community member may also alter the kinds of ecological opportunities for subsequent invaders.

For species that already reside together, the same issue must be considered because these demographic conditions (i.e., $dN_i/dt > 0$ at $N_i \approx 0$) exactly state the criterion of *invasibility*, which is the theoretical benchmark used by community ecologists to evaluate whether an assemblage of species coexist with one another (MacArthur 1972, Holt 1977, Chesson 2000, Adler et al. 2007, Siepielski and McPeck 2010). To an ecologist, *coexistence* has a very precise meaning that differs from the term's more general usage. If the species found living together in a community are coexisting, then they all must be able to pass the invasibility criterion. To experimentally test whether a set of species are coexisting, one would evaluate whether each species in turn can increase in population size when (a) it is removed from the community, (b) the other species come to their new abundances because of its absence, and (c) it is then allowed to reinvade. In practice, invasibility has only been evaluated on the most simple of ecological systems, and so remains mainly a conceptual ideal (Siepielski and McPeck 2010). In the context of ecological opportunities, invasibility will probably also be a conceptual ideal, but it identifies the tangible hurdle that a species faces when invading a new community to exploit some ecological opportunity.

The invasibility criterion of community ecology is equivalent to stating that the average fitness among the individuals in the invading population is greater than replacement; that is, $\ln(\bar{W}_i) > 0$ or $\bar{W}_i > 1$, where \bar{W}_i is the average fitness of the individuals (Lande 1982). When restated in this way, the implications for natural selection and local adaptation become readily apparent. As it increases in size, this invading population may adapt to the natural selection pressures imposed by the local abiotic environment and by the interactions with species in the new ecological regime. In so doing, it may cause further changes in the abundances and phenotypic traits of the other community members.

However, not all invading species may be so fortunate. Other invading species may initially have a negative population growth rate (i.e., $dN_i/dt < 0$, and so $\ln(\bar{W}_i) < 0$), but may nonetheless be able to adapt quickly so as to become a viable population. To exploit an ecological opportunity in this case, species i must evolutionarily adapt to this new environment quickly enough to stop its numbers from declining and begin increasing; in other words, the invader initially could not satisfy the invasibility criterion, but was able to adapt to the local conditions soon enough that it then does satisfy the invasibility criterion. This process necessitates a race between adaptation and population extinction (Gomulkiewicz and Holt 1995). Obviously, the more maladapted the initial colonizing population is (i.e., the more negative $\ln(\bar{W}_i)$ is initially), the less likely that the population will

succeed in sufficiently adapting before its demise. Also, greater levels of immigration will impede the necessary local adaptation (Holt and Gomulkiewicz 1997). These considerations additionally imply that we cannot truly speak of the properties of an entire species. Local populations of species may have differentiated to some degree because of adaptation to local ecological conditions in different communities (Thompson 2005). If this differentiation proceeds far enough, speciation may occur (Schluter 2000, Nosil 2012).

These processes over the long term will define evolutionary trajectories for the component species and the phenotypic diversity present in communities and regional biotas. Conceptually, the invasibility criterion is used in community ecology as a retrospective test, in the sense that it is applied to species that are already found living together. For those species found to be coexisting today, we can infer that in the past they each colonized the ecological opportunity that they now exploit. To make this inference, one would need data on contemporary communities to test whether species today are coexisting, as well as evolutionary analyses based on historical, paleontological, or phylogenetic data to test for such an invasion in the past. For example, in my own work, I have used systematics analyses to infer the sequence of habitat shifts that must have occurred in various damselfly lineages to account for the distributions of species along habitat gradients today, and the adaptive evolutionary changes that were associated with each invasion of a new habitat (McPeck and Brown 2000, Stoks and McPeck 2006). Each one of these habitat shifts represented a lineage invading a new ecological opportunity, and by inserting a new functional group into a community each would have changed how the system responded to perturbations. We will consider these matters in more depth in the following pages.

WHO ARE THE MEMBERS OF A COMMUNITY?

The idea of a set of coexisting species will be an important organizing concept throughout these pages. However, this does not mean that each of the thousands of species in the interaction web depicted in figure 1.1 can satisfy its local invasibility criterion. Far from it! By identifying which species are coexisting and what the phenotypic and evolutionary properties of those species must be, one is also identifying the criteria for species that are not coexisting in the strict sense used by ecologists. I use the term *co-occurring* to identify those species in a community that are not coexisting (Leibold and McPeck 2006). All communities are heterogeneous mixtures of many coexisting and co-occurring species.

Moreover, admitting that some (or many) of the species in the community are merely co-occurring immediately forces one to consider that each large and

complex local community is embedded in a larger regional system of communities; this system is known as a *metacommunity* (Holyoak et al. 2005), in which dispersal among communities can play a pivotal role in shaping both local and regional community structure. Metacommunities are themselves embedded in an even larger regional biogeographic system. Successful movement of species among metacommunities is quite rare but important when it does happen. I will consider aspects of the consequences of a local community being embedded in larger systems at these two scales.

Four types of species, based on their population dynamical properties, are found in a community: coexisting, neutral, sink, and walking dead species. Conceptualizing these categories is easy, but identifying any particular species to one of these types can be exceedingly difficult in practice. Moreover, some reflection will also identify that these categories are not necessarily mutually exclusive. Also, any particular species will occupy different categories in different communities.

The first and obviously fundamental species type to consider, based on the above discussion, is the *coexisting species*. As stated above, these are the species that can satisfy the invasibility criterion. Note that my definition of ecological opportunity is also based on defining functional groups, rather than species, within a community. I define a single *functional group* as a set of species that are ecologically quite similar to one another and are therefore exploiting the same ecological opportunity. Ecological similarity is defined by the ways individuals respond to and interact with the abiotic conditions and other species in the system. I think of ecological similarity in the context of an Eltonian definition of the niche. Elton (1927) conceptualized the niche of a species as its “occupation”—that is, what individuals of a particular species are capable of doing, and the species’ place in the community. I think of these as the abilities of individuals comprising a species to perform in the various interactions with the abiotic environment and with other species, and the resulting demographic consequences of these interactions.

In this context, ecological similarity must be measured in the totality of abiotic and biotic interactions in which a species engages. If two species differ substantially in only one type of interaction (perhaps they eat different resources, or are attacked by different parasites or predators), they are not ecologically similar even if they are identical in all other respects. Obviously, ecological similarity is a measure of degrees, and the degree to which species are similar will be a critical recurring issue throughout this analysis. Species that are too ecologically similar will not coexist in the conceptual sense with which I use the term.

However, strong differentiation in some ecological feature is not a necessary condition of coexistence (e.g., Holt 1977, Tilman 1994, Chesson 2000, McPeck 2012). For example, two species that differ substantially in their abilities to acquire a single essential resource from the environment will not coexist (Tilman 1982).

To coexist, species must differ in particular ways, and these depend on the types of species interactions in which they are engaged. For example, the criteria for these two resource competitors to coexist differ if they have no natural enemies, if they are fed upon by a common predator, or if they each have unique parasites (Tilman 1982; Grover 1994; Holt et al. 1994; McPeck 2012, 2014a). Moreover, how these two species might evolutionarily adapt to acquiring the resource may also differ under these various scenarios. Finally, the number of consumers that can potentially coexist in these scenarios may be quite different. The criteria for coexistence cannot be reduced to platitudes, such as two species must be different to coexist or intraspecific competition must be stronger than interspecific competition. The features favoring coexistence also cannot be generalized across all possible types of species interactions and all community modules. Luckily, as I hope to show, generalities do exist and are based on common features of mechanisms of various species interactions and natural selection.

Species that are ecologically nearly identical to one another comprise the second type of species found in a community—these are *neutral species*. These will follow the neutral dynamics of a random walk in relative frequency, as described by Hubbell (2001). Much of the debate that neutral theory has sparked about the importance of neutral dynamics in communities has constructed the argument as though it were an “either-or” proposition—either all species in a community are coexisting with one another or they are all neutral species. Moreover, almost all analyses addressing these issues construct their tests based on this presumption. If any evidence is found for coexistence of any species in the community, then species in the entire collection are declared to be coexisting, and neutral dynamics are declared completely unimportant.

The conception of community structure in the context of coexisting and neutral species that I want to present is much more nuanced and layered. Specifically, a single functional group may contain multiple neutral species. Again, the definition of ecological opportunity given above does not use the word species—this was intentional. If species in some collection are ecologically identical or nearly so, the rest of the community will experience them as though they represent a single ecological entity. To see this, consider the following simple model of a food web with three trophic levels:

$$\begin{aligned}\frac{dP}{dt} &= P\left(\sum_{j=1}^q n_j m_j N_j - x\right) \\ \frac{dN_j}{dt} &= N_j (b_j a_j R - m_j P - f_j), \\ \frac{dR}{dt} &= R\left(c - dR - \sum_{j=1}^q a_j N_j\right)\end{aligned}\tag{1.1}$$

where R , N_j , and P are, respectively, the abundances of a basal resource, q intermediate-trophic-level consumers ($j = 1, 2, \dots, q$), and a top predator (see also Leibold 1996, Siepielski et al. 2010). In this model, the basal resource has logistic population growth in the absence of any of the consumers, where c is the intrinsic growth rate when rare, and d is the strength of density dependence in its growth rate. The top predator and all consumers have linear functional responses, where a_j and b_j are the attack rate and conversion efficiency, respectively, of consumer j feeding on the resource; and m_j and n_j are the attack rate and conversion efficiency, respectively, of the predator feeding on consumer j . Additionally, the top predator and consumers have density-independent mortality rates of x and f_j , respectively. If the consumers are all ecologically different from one another, meaning that at least some of the parameters in their population dynamics in equations 1.1 are different, at most two can coexist with the resource and the predator (Holt et al. 1994; Leibold 1996; McPeck 1996b, 2014a). Moreover, they will respond differently to perturbations that affect the equilibrium abundance of the resource or the predator.

However, if all the consumers are ecologically equivalent, meaning that they have exactly the same parameters (e.g., $a_1 = a_2 = \dots = a_q = a$), notice what happens to this system of equations:

$$\begin{aligned} \frac{dP}{dt} &= P \left(mn \sum_{j=1}^q N_j - x \right) \\ \frac{dN_j}{dt} &= N_j (baR - mP - f) \quad . \\ \frac{dR}{dt} &= R \left(c - dR - a \sum_{j=1}^q N_j \right) \end{aligned} \quad (1.2)$$

In this case, all the ecologically equivalent consumers (i.e., all N_j) in the community act as a single dynamic unit—a single functional group—and the ecological interactions and population dynamics of the community respond to the sum of their abundances (i.e., $\sum_{j=1}^q N_j$) (Siepielski et al. 2010). In fact, this system sets the equilibrium abundance of the consumers at $\sum_{j=1}^q N_j = x/(mn)$. The relative abundances of the consumers will drift according to a random walk within this constraint on total abundance. Over time, consumer species will be lost randomly from the system based on the rate of drift, which depends on their summed abundances, until only one consumer species remains (Chesson and Huntly 1997, Hubbell 2001). In other words, collections of neutral species that follow the dynamics described by Hubbell (2001) are easily embedded in more complex food webs that follow the strictures of coexistence (Leibold and McPeck 2006).

The presence of neutral species makes the assignment of coexisting and neutral descriptions to each species ambiguous. If the consumers in equations (1.1)

are ecologically distinct, and hence only two are present with the predator and resource in this diamond-shaped community, we can easily stipulate that every species in this community is coexisting; that is, each species will satisfy the invasibility criterion (Leibold 1996). However, this is not true if the consumers are ecologically identical. Imagine applying the invasibility criterion to a community described by equation (1.2) with four consumers. Initially, the community would come to a stable equilibrium with $N_1 + N_2 + N_3 + N_4 = x/(mn)$. Then remove consumer 3 from the community and allow the remaining species to re-equilibrate; now $N_1 + N_2 + N_4 = x/(mn)$. When consumer 3 is reintroduced it will have $dN_3/dt = 0$ at $N_3 \approx 0$.

Thus, any single neutral species is not coexisting in this community, which is reassuring given the definition of coexistence. However, the entire collection of neutral species—the functional group that they comprise—is coexisting with the rest of the community. To me, functional groups coexist, and so two species that coexist with one another are in two different functional groups exploiting two different ecological opportunities. If all members of a functional group were missing, then the first member that invades would satisfy the invasibility criterion. However, once the first species enters and establishes itself, subsequent invaders that are ecologically identical to the first would have exactly the same demographic performance as the ones already present, and so would not satisfy the invasibility criterion.

My work on the odonates found in lakes across eastern North America sheds some light on this issue. A summary of the taxonomic diversity of the Odonata at any lake across eastern North America from the Gulf of Mexico to northern Canada would look very similar to that for Palmatier Lake, Michigan (fig. 1.2C). Palmatier Lake harbors 53 species in 26 genera (McPeck 1990b, 1998; Stoks and McPeck 2003; and McPeck, unpubl. data). Fifteen genera are represented by a single species, whereas the other genera have multiple species present, including one (*Enallagma*) with 12 species. Extensive field experiments on three of these genera show that the 12 *Enallagma* are neutral species occupying a single functional group, whereas genera differ in ways that match the requirements for coexistence (McPeck 1998, Siepielski et al. 2010, Siepielski et al. 2011b, Siepielski and McPeck 2013). In other words, for odonates in lakes, each genus seems to be a different functional group within the community, whereas species within a genus are neutral within the same functional group. Given that the last common ancestor of those 12 *Enallagma* species dates to approximately 10 million years ago, these species must have been neutral members of the local communities for all that time (McPeck and Brown 2000, Turgeon et al. 2005).

I am sure that the taxonomic predictability of coexisting and neutral species I have found in the odonates of lakes is not a general rule. For example, thorough

field experiments have shown that two barnacle species in different genera are neutral species in the intertidal zone of the Pacific coast of Chile (Shinen and Navarrete 2014). In contrast, four *Daphnia* species clearly coexist by segregating spatially within the same lakes inhabited by *Enallagma*, and these *Daphnia* species therefore coexist as four separate functional groups in these communities (Leibold and Tessier 1991, Tessier and Leibold 1997). It is probably a loose but general rule that the more phylogenetic and taxonomic distance between two species, the greater the ecological dissimilarity between them. However, as these three examples illustrate, this assumption is by no means inviolate.

The third type of community member are *sink species*, which are present only because of continual immigration from other communities (Shmida and Ellner 1984, Pulliam 1988). If immigration were prevented, sink species would eventually go extinct locally because local average fitness is lower than what is needed to maintain the population (i.e., $\ln(\bar{W}_i) < 0$). A sink species is maintained in the community at a population abundance for which decline due to local average fitness balances immigration rate (Pulliam 1988). Clearly, sink species do not coexist in the local community, since by definition they would have a local negative population growth rate due to local ecological conditions. However, sink species are still interacting with the other species in the community (e.g., utilizing resources, being fed upon by predators, interacting with mutualists) and so can have appreciable effects on the ecological and evolutionary dynamics of other community members.

The presence of sink species highlights the importance of considering how a community is embedded in a larger regional metacommunity (Holyoak et al. 2005). Because a sink species is maintained by continual immigration, those immigrants must come from nearby communities, and these species must have source populations (i.e., $\ln(\bar{W}_i) > 0$ when rare, which means that they are coexisting) in some of those nearby communities. Moreover, the continual gene flow from the source populations would retard or prevent adaptation of the sink population to local ecological conditions under most conditions (Holt and Gomulkiewicz 1997).

Although many extinctions occur via stochastic processes (Raup 1992), many species are driven extinct by ecological interactions with the abiotic environment and other species. This fourth type of species I call the *walking-dead species*, a term first attributed to Daniel Janzen. They have also been called the “extinction debt” of the community (Tilman et al. 1994), and the “living dead” (Hanski 1998). These are species that are slowly being driven extinct by the ecological conditions they experience in the community, and immigration from elsewhere in the metacommunity will not rescue them or prevent their demise. Consequently, they must have a long-term negative population growth rate ($dN_i/dt < 0$) and thus a long-term average fitness less than replacement ($\ln(\bar{W}_i) < 0$). (Note that in

the long term, most neutral species are expected to go extinct, but via a random walk with $\ln(\bar{W}_i) = 0$ [Hubbell 2001].) For walking-dead species, extinction has a temporal dynamic specified by their long-term population growth rate, with more negative long-term population growth rates causing species to go extinct more rapidly (Lewontin and Cohen 1969, Turelli 1977, McPeck 2007). Despite their ultimate demise, species that are destined for extinction do not simply give up and throw themselves on their swords. Until the last individual dies, these species will still be present in some number of communities, and they may remain for a very long time if their rate of population decline is quite slow. Spatial and temporal variability in demographic rates may also greatly obscure when species are the walking dead.

A walking-dead species also undergoes another potential outcome; namely, it may adapt to the system sufficiently to experience a positive population growth rate and thereby evolve to be a coexisting or neutral member of the community. Were it to not adapt, the species would eventually be driven extinct. However, adaptation can rescue walking-dead species, and as we will see, this process has been a prevalent mode of ecological speciation.

ARE COMMUNITIES “REAL”?

Ecologists have debated for nearly a century whether there is such a thing as an ecological community. The debate embarked in earnest in the 1910s and 1920s with the views exchanged between Frederic Clements and Henry Gleason regarding plant communities and succession (Clements 1916, Gleason 1926). Clements saw plant communities as integrated units, whereas Gleason argued that plant communities were merely collections of individual species that were all acting largely autonomously. This debate has been a perpetual feature of community ecology and continues to this day (Whittaker 1953, Goodall 1963, Shipley and Keddy 1987, Callaway 1997). In this vein, a critique by Ricklefs (2008) argued for the “disintegration of the community as a central concept.” His argument for the abandonment of the concept is that an ecological community is not an integral entity. Instead, the species found at a local site are the result of regional processes that control the “distribution of populations over ecological and geographic gradients.” In fact, in chapter 4 I will summarize much paleoecological and phylogeographic work that indicates Gleason and Ricklefs are correct in arguing that communities are not integral entities. Moreover, I wholeheartedly agree with Ricklefs’ call for more emphasis on regional, historical, and phylogenetic processes in the study of ecological communities (see also Ricklefs 1987, 1989). Those ideas are at the core of what I am trying to accomplish with this work.

However, I obviously do not agree with the characterization of community as an invalid concept about nature. I hold this view because assemblages of species show regular and predictable patterns of distributions and abundances across the local landscape in all ecological systems. Moreover, myriad experimental studies have shown that local species interactions drive much of this distributional patterning; it is not simply the result of each species' physiological abilities to deal with the abiotic conditions found at some site. In the system I know best, characteristic assemblages of most animal taxa, including snails, leeches, beetles, mayflies, stoneflies, true bugs, damselflies, dragonflies, salamanders, frogs, fish, and so forth, are found segregating along the ecological gradients in ponds and lakes of eastern North America (Wellborn et al. 1996). Taxa do differ in their breadth of distribution along these gradients. For example, different sets of *Enallagma* and *Lestes* damselfly (Odonata: Zygoptera) species are found in ponds and lakes depending on whether fish or dragonflies are top predators and whether the pond has water that continuously or periodically dries up (McPeck 1990b, 1998; Stoks and McPeck 2003, 2006). However, the same *Ischnura* species are found in all these pond types (McPeck 1998). Water bodies with these various ecologies are interspersed across the landscape.

If bluegill sunfish (*Lepomis macrochirus*) are experimentally introduced to a pond where large dragonflies are the top predators, the fish quickly kill all the large dragonflies and the *Enallagma* and *Lestes* species that are specialists living with those large dragonflies (Crowder and Cooper 1982, McPeck 1990b, Werner and McPeck 1994, Stoks and McPeck 2003). Over the next 20 to 30 years the *Enallagma* and *Lestes* species that are specialists in living with fish colonize and increase in abundance (M. A. McPeck, pers. observation). Moreover, removing fish completely from a pond or lake will reverse this process; large dragonflies will colonize, kill the *Lestes* and *Enallagma* species that specialize in living with fish, and the species specialized in living with large dragonflies will colonize (M. A. McPeck, pers. observation). Thus, adding or removing a single species to or from a pond will dramatically and predictably change large suites of other species, and this experimental result explains the natural variation among ponds and lakes. It is true that the same *Ischnura* species will be present in both of these situations, but the source of their mortality and how their population abundances are controlled are substantially changed by switching the top predator (McPeck 1998).

Such patterning of local species assemblages across the landscape is everywhere around us, and innumerable experimental studies over the past 70 years have demonstrated how abiotic factors and species interactions generate these patterns. Zonation patterning of species distributions in the marine intertidal are classic examples of the maintenance of this strong patterning, and these are over mere centimeters of tidal height (Connell 1961, Payne 1966, Dayton 1971, Menge

1976, Sousa 1979). Plant assemblages in local areas strongly depend on whether grazers have access to forage in these areas (Harper 1969). Similar patterning to what I described for damselflies in the littoral zones of ponds and lakes also occurs for the zooplankton found in the pelagic zones of these same lakes (Brooks and Dodson 1965, Dodson 1970, Sprules 1972, Vanni 1988).

I take the fact that we can make regular and predictable changes in the composition and abundances of many species across disparate taxa at a very local scale by experimentally manipulating the presence/absence of one or a few species as strong evidence that local species interactions are a primary determinant of the distributions and abundances of species across the landscape. Note that I say *a* primary determinant, and not *the* primary determinant. It is this importance of local species interactions that causes most ecologists to think the concept of a community has significant utility. The fact that species composition does not change wholesale or that the local assemblage does not form a completely integrated unit seems immaterial to whether local species interactions play a substantial role in determining which species are there and what their abundances are. How could it be expected to change wholesale when composed of not only coexisting, but also neutral, walking-dead, and sink species? Also, like *Enallagma* and *Ischnura* damselflies, different species will be members of different collections of local communities. The definition of community needs no statement about integration or boundaries.

Moreover, that which shapes the population abundance of a species at each locality within the geographic region must control the “distribution of populations over ecological and geographic gradients.” These controls are precisely the set of abiotic conditions and other species that are found at a local position in space and time and with which the species in question directly and indirectly interacts. A species is found in a local area if it can support a population because of favorable local demographic conditions (i.e., coexisting or neutral species), by continual immigration from other local areas (i.e., sink species), or if it cannot support a population there but has not yet gone extinct (i.e., walking-dead species). Sorting through these possibilities requires one to consider ecological issues at both local and regional scales.

Rather than dismissing local interactions and the community concept, I think a better approach is to consider how processes operating at the local and regional scales interact. As with issues of coexistence and neutrality, this is not an “either-or” proposition. Both are important in fundamental ways, and I want to shift the argument to say that you cannot understand one without the other. I find it hard to imagine a scenario in which a species will be found in a region unless it has at least one local source population within that region—that is, it is a coexisting or neutral member of a functional group in at least one community

(but see Roy et al. 2005). Moreover, explaining why a species is present in some local areas may necessitate considering other areas (i.e., sink species). I hope in this work I can make a more concrete connection between local and regional processes that shape patterns of biodiversity across the landscape and through time.

WHAT ARE THE SOURCES OF NEW SPECIES?

The biodiversity present today in a community comes from two sources. Species may have immigrated in from outside, or the species may have arisen within. Thus, biogeographic-scale immigration and speciation are the two critical sources of species to fill ecological opportunities, or at least to try and fill them.

Today, the field of conservation biology is quite concerned with “invasive” species, and the surrounding ecological issues (Elton 1958, Davis 2009, Simberloff 2012, Valéry et al. 2013). In the present work, I will consider the ecological and evolutionary dynamics caused by immigrating species. This would be equivalent to a “foreign” invading species, but this is not a statement about the debate that continues in conservation biology regarding what constitutes an “invasive species” (e.g., Davis 2009, Simberloff 2012, Valéry et al. 2013). Fundamentally, the species that are considered by invasion ecology today are undergoing the same ecological and evolutionary processes that taxa filling ecological opportunities in the past also experienced (Richardson and Pysek 2006, Strauss et al. 2006). Therefore, while not the focus of this work, I hope that the models and results discussed here can contribute to studies of “invasive species,” however they are defined.

More broadly, I will take a more thorough view of deep time to consider how local ecological interactions spread across a landscape shape local community development and regional patterns of biodiversity; this view involves invasions and internal lineage diversification over long expanses of evolutionary time. The source of a new species will influence how similar it will be on average to those already present, and thus will affect the likelihood of initial invasion success. For example, an invader from outside the system will have phenotypic properties and ecological performance capabilities that are essentially random with respect to what is needed to fill some ecological opportunity. Thus, an approach of adding species with random phenotypes to a system would suffice for this immigration scenario.

Species do not have to be from some other biogeographic region to essentially be from outside the system. Consider, for example, the *Enallagma* damselflies I described above. Ponds and lakes with fish as the top predator harbor one set of *Enallagma* species, whereas ponds and lakes with large dragonflies as the top

predators (and therefore lacking fish) harbor a different set of *Enallagma* species (Johnson and Crowley 1980; McPeck 1990b, 1998). For many (but not all) species, these two habitats operate as separate metacommunities, despite the fact that they are interspersed across the landscape. Shifts between them are exceedingly rare over evolutionary time (e.g., three are apparent over the *Enallagma* clade's ~10 million year history, and two over the *Lestes* clade's ~6 million year history), despite the fact that these habitats may often be separated by only a few meters, and founder populations are probably being established each year across these boundaries in both directions (McPeck and Brown 2000, Turgeon et al. 2005, Stoks and McPeck 2006).

These invasions from outside the community may result in a new species being formed if the invading populations must significantly adapt to the new ecological milieu and in so doing become reproductively isolated from their ancestral populations. This is essentially the process of ecological speciation (Schluter 2000, Nosil 2012).

However, ecological differentiation is not the only mode of speciation, and not all new species come from outside the system. In fact, speciation is caused by myriad processes that generate reproductive isolation, and these processes generate varying levels of ecological differentiation, from producing new coexisting species to those that are ecologically identical but reproductively isolated (Dobzhansky 1937a, Mayr 1942, Coyne and Orr 2004). As you might imagine, the degree of ecological differentiation at the time of speciation can have a tremendous effect on the resulting structure of communities and regional assemblages as well as the macroevolutionary structure of diversifying clades (McPeck 2007, 2008).

An analogous argument to the “local versus regional” perspective of community ecology also can be made about considerations of the short-term versus long-term evolutionary dynamics of populations, species, and clades—“micro-” and “macro-” evolutionary dynamics, respectively. The distinction that is usually made to distinguish these two is that microevolution encompasses the evolutionary processes that occur within a species (i.e., mutation, genetic drift, gene flow, and natural selection), and macroevolution involves the processes driving speciation, extinction, and thus long-term clade diversification. Paleontologists have debated for years whether macroevolutionary dynamics are simply the natural extension of microevolution or whether there are processes unique to macroevolution (Erwin 2000). I believe there are unique events and processes that are only seen on a macroevolutionary scale, but here again, I think the important issue is not the primacy of one over the other, but rather how they interact to produce a biota. Ecological interactions, adaptation, dispersal, speciation, and extinction all go hand in hand. This perspective will be the premise of this work.

NATURAL SELECTION, COEVOLUTION, AND COMMUNITY STRUCTURE

Darwin and Wallace (1858) recognized the power of ecological interactions to change the traits and abilities of species over time. Since this original description of evolution by natural selection, evolution has traditionally been assumed to occur very gradually in the wild—almost imperceptibly over the course of a human lifetime—and so population dynamics were assumed to occur on a fast ecological time scale, meaning that species could be assumed to be fixed in their traits and abilities. Important evolutionary change was assumed to occur on a much, much slower evolutionary time scale (Darwin 1859, Mayr 1942, Simpson 1944).

However, we have known for a very long time that this distinction in time scales is not always true; important evolutionary change can happen very rapidly. Darwin's original descriptions highlighted that domesticated animals and plants could be rapidly altered in several to dozens of generations by artificial selection (Darwin 1868). Selection in the wild can be observed to change species' traits significantly in only a few generations (e.g., Reznick 1982, Reznick and Endler 1982, Hendry and Kinnison 1999, Grant and Grant 2002, Ozgul et al. 2009), and significant phenotypic selection can be measured in almost any species one cares to observe (Endler 1986, Kingsolver et al. 2001). Moreover, a dominant pattern of character change in the fossil record is the one termed punctuated equilibrium in which the trait of a new species appears to change almost “instantaneously,” at least given the fossil record's temporal resolution (Eldredge and Gould 1972). Finally, some mechanisms of speciation require only a single generation to create a new species (Rieseberg 1997, Otto and Whitton 2000, Mallet 2007).

The explicit recognition that substantial ecological and evolutionary dynamics can occur simultaneously has renewed interest in the exploration of their joint effects on population dynamics (e.g., Fussman et al. 2000, Yoshida et al. 2003), community structure (e.g., Travis et al. 2014), and ecosystem functioning (e.g., Harmon et al. 2009, Bassar et al. 2012). This has also spawned the coining of many new terms to describe the joint actions of ecological and evolutionary dynamics, including, for example, eco-evolutionary dynamics, eco-evo feedbacks, or ecogenetic links (e.g., Fussmann et al. 2007, Kokko and López-Sepulcre 2007, Schoener 2011). Given that these linkages have always been understood, I see no reason to generate a new jargon and so will refrain from using these terms.

However, this book is about fundamental aspects of the joint dynamics of ecology and evolution in communities. Because these dynamics can be exceedingly complicated, I focus specifically on the joint dynamics of (1) species interactions that regulate their abundances in a community context, and (2) natural selection that shapes the trajectories of their trait evolution. I simplify the analysis by

assuming the standard basis of quantitative inheritance (Lande 1979, Falconer and Mackay 1996). In the following chapters, I explore the theoretical connections among community ecology, evolutionary adaptation, dispersal, and speciation and extinction to understand how local and regional patterns of community structure develop across space and through time. This is obviously a large and expansive undertaking, and I have tried to organize the presentation in a way that makes the interconnections obvious. Also, I cannot cover all types of species interactions. In particular, I do not consider the action of pathogens and disease-causing organisms in a community context (e.g., Ostfeld et al. 2008).

In chapter 2, I develop the purely ecological dynamics of interacting species in many types of community modules. The goal of the chapter is to explore the criteria required for different types of species to coexist in each kind of community module, and also to see how these criteria change as more species are added to some functional position and as new functional groups are added to change the interaction network to a new type of module. By defining what is required for coexistence, we are also defining what types of species would also be walking-dead and sink species.

In chapter 3, I explore how species in simple community modules evolve to adapt to one another. To understand adaptation, I first characterize the three general types of traits that underlie the trophic interactions between predators and their prey. As we will see, the type of traits involved in species interactions have substantial effects on the dynamics of adaptation, the likelihood that species will ecologically differentiate from one another (e.g., character displacement of competitors), and the structure of the resulting communities. I then explore the underlying dynamics of adaptation when all the species in these simple community modules can coevolve, and the influences of various system features on the outcome of this coevolution.

In chapter 4, I evaluate the main processes that operate at the regional and biogeographic scales to ultimately shape local community structure—namely, speciation and biogeographic mixing of taxa. I first consider the definition of a “species.” Next I review the various mechanisms that create new species. In this analysis, I focus on the degree to which the speciation process directly results in differences in ecologically important traits between the progenitor and daughter species, and the geographic configuration of progenitors and daughters relative to one another. The phenotypic differences generated at the time of speciation determine the type of community member the new species begins as, and the geographic configuration of speciation determines whether it is introducing new species into any local communities. Finally, I review paleontological and phylogeographic data to show that past climate change has had an enormous effect on current local and regional community structure by periodic forcing of mass

movements of species across Earth and sparking spikes in speciation and extinction rates. Current community structure cannot be understood without incorporating the massive perturbations that have routinely and regularly occurred over the past few million years.

In chapter 5, I develop explicitly the evolutionary dynamics that follow mixing different types of species together in a community either by invasion or by perturbation, as well as community mixing due to climate change. Specifically, this chapter focuses on the features that promote or retard ecological differentiation of species. Specifically, when will initially neutral species differentiate from one another to convert them into a set of coexisting species, and when will initially differentiated species converge to become ecologically more similar? Here again, we will see that the types of traits that underlie species interactions influence the likelihood and outcome of differentiation. Moreover, trait types also fundamentally shape the community structure that results when species do differentiate from one another.

In chapter 6, I consider the ecological and evolutionary dynamics of species across a metacommunity, and how these dynamics shape regional community structure. I first consider the evolution of dispersal—specifically, when movement between local communities is and is not favored by natural selection, and what these various movement patterns do to local community structure. Necessarily, this is the main area where the existence and evolution of sink species is considered. I then combine consideration of the evolution of dispersal rates among communities along with local adaptation within each to explore a few simple scenarios of how these two trait sets will evolve in a correlated fashion.

In chapter 7 I reflect on what I see as the important insights that emerge from this synthetic analysis of evolution in communities. The dynamics of species' abundances and traits are jointly driven by the same processes, and these dynamics can only be understood in the context of a community of interacting species.

Finally, I have created a website to accompany this book (<http://press.princeton.edu/titles/11175.html>). There you will find animations and games for a visual experience of the abundance and trait dynamics of interacting species that I discuss throughout the book. I hope you will interact with these web games and animations while you read. I also plan to add many features over time to the website, so please visit it periodically for new features.