CONCEPTUAL SYNTHESIS IN COMMUNITY ECOLOGY

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abstract

Community ecology is often perceived as a "mess," given the seemingly vast number of processes that can underlie the many patterns of interest, and the apparent uniqueness of each study system. However, at the most general level, patterns in the composition and diversity of species—the subject matter of community ecology—are influenced by only four classes of process: selection, drift, speciation, and dispersal. Selection represents deterministic fitness differences among species, drift represents stochastic changes in species abundance, speciation creates new species, and dispersal is the movement of organisms across space. All theoretical and conceptual models in community ecology can be understood with respect to their emphasis on these four processes. Empirical evidence exists for all of these processes and many of their interactions, with a predominance of studies on selection. Organizing the material of community ecology according to this framework can clarify the essential similarities and differences among the many conceptual and theoretical approaches to the discipline, and it can also allow for the articulation of a very general theory of community dynamics: species are added to communities via speciation and dispersal, and the relative abundances of these species are then shaped by drift and selection, as well as ongoing dispersal, to drive community dynamics.

Introduction

COMMUNITY ECOLOGY is the study of patterns in the diversity, abundance, and composition of species in communities, and of the processes underlying these patterns. It is a difficult subject to grasp in its entirety, with the patterns of interest seemingly contingent on every last detail of environment and species interactions, and an unsettling morass of theoretical models that take a wide variety of forms. Fifteen years ago, Palmer (1994) identified 120 different hypotheses to explain the maintenance of species diversity, and the list would no doubt be even longer today. However, despite the overwhelmingly large number of mechanisms thought to underpin patterns in ecological communities, all such mechanisms involve only four distinct kinds of processes: selection, drift, speciation, and dispersal.

Many biologists will recognize these four processes as close analogues of the "big four" in population genetics: selection, drift, mutation, and gene flow. Many ecologists, however, might be skeptical that such a simple

organizational scheme is applicable to the more complex subject of community ecology. Population genetics, despite being faced with essentially the same problem as community ecology—that is, understanding the composition and diversity of alleles in populations—is an easier subject to grasp, and I submit that the reason for this is not because of any fundamental difference in the complexity of the subject matter, but because of the coherence and simplicity of its theoretical foundation. Every detail of the complex interactions between species and their environments that are studied by ecologists can also be important agents of natural selection, but it is quite useful to begin by recognizing just that: such interactions mostly fall under the single conceptual umbrella of selection. Add the relatively simpler processes of drift, gene flow, and mutation to the mix, and you have the Modern Evolutionary Synthesis, which remains a robust, general, and widely accepted theoretical foundation for population genetics and microevolution, notwithstanding arguments about whether it fully encompasses all facets of modern evolutionary biology (Pigliucci 2007).

The perspective that synthesis in community ecology can be achieved by organizing processes into the four categories of selection, drift, speciation, and dispersal flows directly out of a sequence of conceptual developments that occurred over the last half century. In the 1950s and 60s, G. Evelyn Hutchinson and Robert MacArthur ushered in an era of community ecology in which the discourse was dominated by the deterministic outcome of local interactions between functionally distinct species and their environments—i.e., selection. Initial developments of mathematical theory in community ecology had occurred decades earlier (e.g., Lotka 1925), but, by all accounts, the 1960s marked the period during which theoretical development in community ecology flourished (Kingsland 1995; Cooper 2003). The importance of selective processes in local communities ruled the day, and the vast body of theoretical and empirical research in this vein has been dubbed "traditional community ecology" (Lawton 1999; see also Brown 1995).

In response to the emphasis on local-scale selective processes almost to the exclusion of other factors, Ricklefs (1987) and others (Ricklefs and Schluter 1993; Brown 1995) argued for and successfully sparked a shift in emphasis to a more inclusive approach in community ecology, explicitly recognizing the importance of processes occurring at broader spatial and temporal scales for understanding local-scale patterns. One key contribution here was the recognition that the composition and diversity of species, even at a local scale, depend fundamentally on the composition and diversity of the regional pool of species, which, in turn, depend on the process of speciation. Just as mutation is the ultimate source of genetic variation, so too is speciation the ultimate source of the species that make up ecological communities.

The next key addition to the mix was ecological drift. Ecologists have long recognized that changes in the composition and diversity of species can have an important stochastic element (e.g., Chesson and Warner 1981). However, it was not until Hubbell (2001) imported the neutral theory of population genetics into ecology that drift was incorporated into theory as something much more than "noise" in an otherwise deterministic world. Pure ecological drift happens when individuals of different species are demographically identical, which is exceedingly unlikely. But drift need not be the only active process in order to be an important process, and, in many groups of species that show only modest functional differentiation, drift may indeed be quite important (McPeek and Gomulkiewicz 2005). The fact that neutral theory was imported into ecology essentially unchanged from population genetics suggests the possibility of a broader synthesis of processes in both population genetics and community ecology, neutral and otherwise (Vellend and Geber 2005; Hu et al. 2006; Vellend and Orrock 2009).

The final key process is dispersal—the ecological equivalent of gene flow in population genetics. Dispersal has been incorporated into ecological theories of all kinds over the past fifty years, but, in recent years, it has been brought to the forefront in the form of

the metacommunity concept (Holyoak et al. 2005), which is explicitly concerned with the role of dispersal among local communities in influencing community patterns at multiple scales. The movement of organisms across space can have a variety of important consequences in communities.

For each of the latter three processes—speciation, drift, and dispersal—conceptual developments were motivated by a perceived lack of emphasis in the literature on the importance of the process in question. Selection, in the form of deterministic interactions among species and between species and their environments, was always recognized as important. With the additions of speciation, drift, and dispersal, we now have a logically complete set of process categories within which all other more specific processes can be placed. I believe that organizing the overwhelming number of specific ecological theories for communities under this scheme can help achieve at least two important goals. First, the essential similarities and differences between different ecological models can be clarified in fairly straightforward terms, thereby making the full set of models easier to understand, apply, and teach to students. Second, we can articulate a very general theory of community dynamics, which may on the surface sound obvious and too generalized to make any specific predictions, but may, nonetheless, serve the same critical function as foundational theory in population genetics.

Before proceeding, I should emphasize that I am not arguing that the parallels between processes or models in population genetics and community ecology are perfect. For example, selection among individuals across species can be manifested in ways that are rare or absent within species (e.g., trophic or parasitic interactions), and speciation is a far more complicated process than mutation. The list could go on. Rather, my argument is that we can define a similar set of four logically distinct processes in community ecology in order to provide a coherent conceptual framework for the discipline.

The rest of this paper is structured as follows. I first specify more precisely the motivation for conceptually organizing the material in community ecology, and provide operational definitions of important terms. I then illustrate, with separate sections on theory and data, how the subject matter of community ecology can be presented using the proposed organizational framework, describing the ways in which selection, drift, speciation, and dispersal influence communities. I then touch on some of the general patterns that community ecologists have traditionally been interested in, and I discuss how pattern is connected with process. Finally, I compare the framework presented here with other conceptual frameworks in community ecology.

Community Ecology Is a Mess

Based largely on empirical results, Lawton (1999) famously called community ecology "a mess," and ascribed this mess to the inherent contingency of ecological patterns on the details of how the underlying processes or rules act. "The rules are contingent in so many ways . . . as to make the search for patterns unworkable" (Lawton 1999:181). One source of motivation for the present paper is that even theoretical community ecology can be considered a mess for much the same reason: each and every twist added to theoretical models seems to matter, making an overarching treatment of the subject very difficult. Consider the number of different models that can be constructed from the simple Lotka-Volterra formulation of interactions between two species by layering on realistic complexities, one by one. First, there are at least three qualitatively distinct kinds of interactions (competition, predation, mutualism). For each of these, we can have either an implicit accounting of basal resources (as in the Lotka-Volterra model), or we can add an explicit accounting in one particular way. That gives six different models so far. We can then add spatial heterogeneity or not ($\times 2$), temporal heterogeneity or not ($\times 2$), stochasticity or not ($\times 2$), immigration or not ($\times 2$), at least three kinds of functional relationships between species (e.g., predator functional responses; $\times 3$), age/size structure or not ($\times 2$), a third species or not

(×2), and three ways that the new species may interact with one of the existing species (×3 for the models with a third species). Having barely scratched the surface of potentially important factors, we have 2304 different models. Many of them would likely yield the same predictions, but, after consolidation, I suspect there still might be hundreds that differ in ecologically important ways. As Lawton (1999) put it, "the necessary contingent theory looks unworkably complicated" (p. 180).

One important manifestation of this mess is that textbook treatments of community ecology and their associated university courses—that is, the vehicles by which the subject matter is taught to students—have a structure whose logic is not easy to discern. Section or chapter topics typically fall loosely under one or more of the following headings: community patterns, competition, predation (plus other enemy-resource interactions), niches, food webs, and issues of space and time (e.g., Putman 1994; Morin 1999; Ricklefs and Miller 1999). This is a confusing list because it includes unlike entities—patterns, processes (competition, predation), concepts (niches, food webs), objects of study (food webs), or a consideration that is always important to think about (space and time) (Vellend and Orrock 2009). In contrast, books and courses in population genetics (e.g., Hartl and Clark 1997) are based upon a structure that is easier to follow, with a consistent focus on the four processes of selection, drift, gene flow, and mutation, and how these processes either individually or jointly determine patterns of genetic variation. In my opinion, ecology textbooks and courses are a fairly accurate reflection of the way in which practicing community ecologists have self-organized around particular research topics or themes, but I am not convinced that this is the best way to organize the subject matter for facilitating synthetic and integrated understanding by students and practitioners alike. As elaborated below, selection, drift, speciation, and dispersal may not be of equal importance in understanding ecological patterns, but they fully represent the logically distinct categories of important processes in community ecology.

A Theory of What Is Possible

Amazingly, the foundation of theoretical population genetics was built in the near absence of data on patterns of genetic variation in natural populations—the very subject matter of the discipline (Provine 1971). Perhaps for this reason, at least in part, a theoretical foundation was built to describe a logically complete range of the basic possible processes that could cause evolutionary change, rather than a theory skewed towards an emphasis on those processes that are actually important in nature. The latter is an empirical rather than theoretical issue. In contrast, long before the existence of ecological theory, patterns in nature were well-known to any keen observer. Allen and Hoekstra (1992) describe ecology as a discipline "whose material study is part of everyday encounters: birds, bees, trees, and rivers" (p. 1). They go on to argue, albeit in a somewhat different context, that "It is, however, a mistake to imagine that this familiarity makes ecology an easy pursuit. . . .the very familiarity of ecological objects presents the difficulties" (Allen and Hoekstra 1992:1). I argue that this everyday familiarity with ecological patterns pushed ecological theory down the path of emphasizing particular viewpoints on the processes that are actually most important in nature, rather than emphasizing a logically complete set of possible processes that must play at least some role in community dynamics. The emphasis in ecology, therefore, has been on pattern before process (Roughgarden 2009; Vellend and Orrock 2009). Using the structure of population genetics theory as a guide, with details altered where necessary for communities, the following presents an organizational scheme for community ecology, within which all specific models and frameworks can be described.

DEFINITIONS

Table 1 provides operational definitions of the key terms used in this paper. With respect to the definition of community, there has been considerable debate in ecology concerning the degree to which ecological communities are sufficiently co-

TABLE 1
Definitions of terms

Term	Definition
Community	A group of organisms representing multiple species living in a specified place and time
Community ecology	The study of patterns in the diversity, abundance, and composition of species in communities, and the processes underlying these patterns
Community dynamics	Changes over time in the relative abundances of species in a specified area, including extinctions and species additions via dispersal or speciation
Species composition	For a given community, a state defined by the abundances of all species
Species relative abundance	The proportion of all organisms in a given area that are of a given species; equivalent to species frequency.
Species density	The number of organisms of a given species per unit of space
Community size	The total number of organisms in a community
Coexistence	The indefinite persistence of a specified set of species in a specified area
Absolute fitness	The quantity of offspring produced by an individual organism per unit of time, including survival of the organism itself
Relative fitness	The absolute fitness of a given organism divided by the mean absolute fitness across all individuals in the community
Species fitness (absolute or relative)	The mean fitness (absolute or relative) across all individuals of a given species in the community; for absolute fitness, this is equivalent to the species per capita population growth rate.
Selection	A deterministic fitness difference between individuals of different species
Drift	Random changes in species relative abundances
Neutrality	A state in which all individual organisms share identical demographic properties
Speciation	The creation of new species
Dispersal	The movement of organisms across space

herent entities to be considered appropriate objects of study (reviewed in Ricklefs 2008). The definition of community used here—that is, a group of organisms representing multiple species living in a specified place and time—bypasses this issue by recognizing that properties of communities are of central interest in ecology, regardless of their coherence and integrity. This definition of community also implicitly embraces all scales of space and time. Studying communities in 1m² plots or across entire continents requires different methods, and the relative importance of different processes likely varies across scales, but we are often interested in understanding the same kinds of patterns (e.g., diversity, composition) at these different scales. This represents an expansion of the purview of community ecology beyond its traditional focus on relatively small scales, without applying a new name to the discipline (e.g., studies in "macroecology" of species diversity are considered part of community ecology here).

The Four Processes of Community Ecology: Theory

selection

Use of the term "selection" to describe deterministic fitness differences among individuals of different species (Table 1) requires some explanation, as it is not yet commonplace in ecology (but see Loreau and Hector 2001; Norberg et al. 2001; Shipley et al. 2006; Bell 2008). Although the term is used in biology most often with respect to evolutionary dynamics within species, the definition of selection in no way restricts its application as such. Selection occurs when individuals in a population vary in some respect, and when different variants reproduce or replicate themselves at different rates (Darwin 1859; Bell 2008; Nowak 2006). In its most generalized form, the con-

cept of selection—and, more broadly, evolutionary change—can be applied "based only on the assumption of a population of things that leave descendants and have measurable phenotypes" (Rice 2008:4).

Applying the concept of selection to species in a community rather than to alleles in a species' population requires two changes to the frame of reference. First, rather than invoking selection at any level higher than that of the individual organism, we simply define the "population" as containing individuals of multiple species; we call this population a community. Second, the phenotype of interest, which may be under selection, is most often just the species identity. The species identity is a categorical phenotype, assumed to have perfect heritability, except when speciation occurs, after which new species identities are assigned (just as mutation changes the identity of an allele). In the same way that selection may favor allele A over allele a within a species' population, selection may favor species X over species Y in a community. It is important to note that although the concept of selection in communities is easier to envision for species on the same trophic level than for species on different trophic levels, the difference is one of degree and not kind. For example, a lynx and a hare are very different organisms, but selection still favors hares when lynx are declining, and it favors lynx when hares are abundant (Krebs et al. 2001).

Rather than focusing only on species identities, it is also possible to define each species by one or more traits (e.g., beak depth, leaf thickness) (McGill et al. 2006) and to then apply tools from quantitative genetics at the community level (e.g., Norberg et al. 2001; Shipley et al. 2006). This opens the door to simultaneous consideration of selection both within and among species. However, to simplify the discussion and focus attention most sharply at the community level, I henceforth address selection in communities by assuming that individuals of a given species have the exact same phenotype (e.g., the species identity). Relaxing this assumption forms the basis of a very active area of research (e.g., Hughes et al. 2008), but, before doing so, it is first necessary to establish the basic building blocks of community ecology, with species as the fundamental category of accounting in the assessment of community-level phenomena.

In a community context, there are three relevant forms of selection: (1) constant, (2) frequency- or density-dependent, and (3) spatially- or temporally-variable selection. Constant selection is simple: if relative fitness is constant in space and time, independent of species' densities but variable across species, the species with the highest fitness will exclude all others (Figure 1A). The other forms of selection, however, are more complicated.

Frequency- or density-dependent selection is central to the vast majority of theoretical models with species interactions in community ecology. For simplicity, I will only use the term "density-dependent," given that most ecological models include densities rather than frequencies—a key distinction from the tradition in population genetics (Lewontin 2004). If community size is constant, density and frequency are equal (as in Figure 1, for simplicity of presentation). Density-dependent selection occurs when individual fitness in a given species depends at least in part on the density of that species, as well as the densities of other species. For two species, negative density-dependent selection favors species when they are at low density and is thus capable of maintaining stable coexistence (Figure 1B), whereas positive frequency-dependent selection favors species at high density and cannot maintain stable coexistence (Figure 1C). Selection can also depend on species densities in more complex ways, possibly allowing more than one stable state at which coexistence can be maintained (Figure 1D), or creating repeated oscillations in interacting species' abundances (Morin 1999). A major challenge in ecology is presented by the nearly limitless variety of configurations that the full set of intra- and interspecific density dependencies can take in a species-rich community.

The nature of density-dependent selection between pairs of species depends on the qualitative ecological relationship between them (e.g., competition, predation,
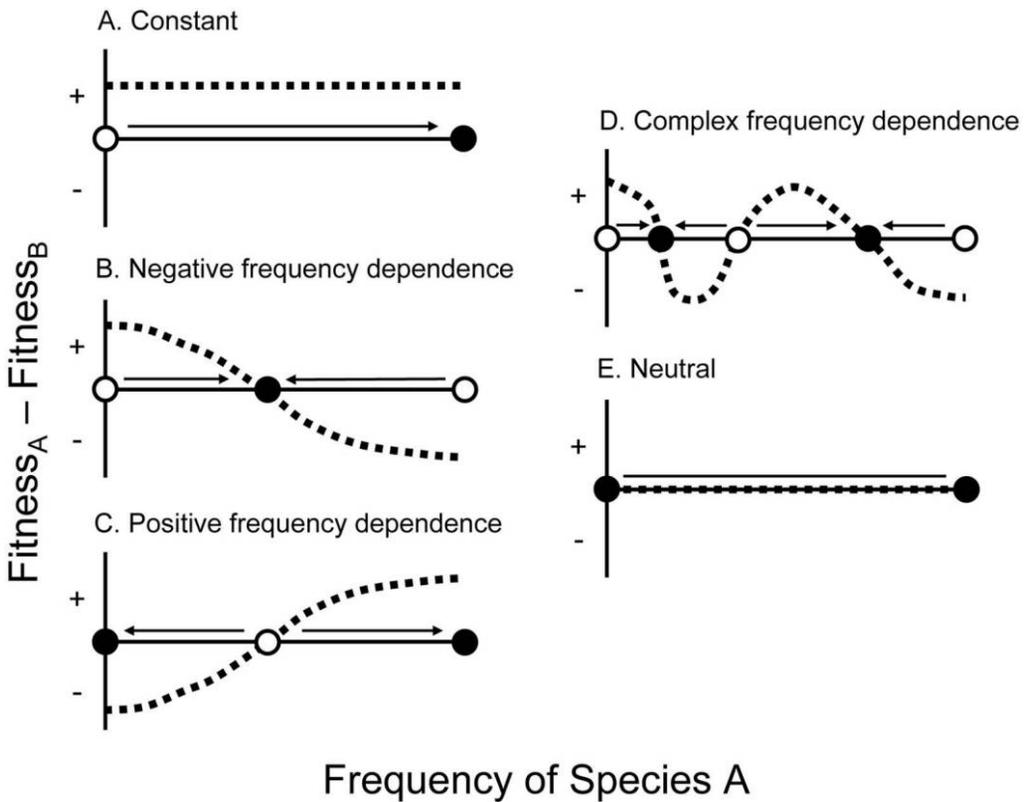
Figure 1. Expected Dynamics and Equilibria between Two Species

Examples for species A and B in a community of constant size are shown under (A) constant selection favoring species A, (B) negative frequency-dependent selection, (C) positive frequency-dependent selection, (D) complex frequency-dependent selection, and (E) no selection. Solid and open circles indicate stable and unstable equilibria, respectively. Dotted lines indicate the difference between the fitness of species A and species B. Arrows indicate the change in species' frequencies. These figures are modeled after Nowak (2006). Note that when species densities (rather than only frequencies) are of central interest, as in most models of trophic interactions, each species density would need to be represented by a separate axis rather than along a single axis, as in these simplified examples.

mutualism, and disease) and the quantitative form of this relationship. With more than two species, indirect interactions can arise whereby fitness in one species depends on the density of a second species not because of a direct interaction, but because each of the two species interacts directly with a third (Strauss 1991). Even the nature of the direct interaction between two species can be influenced by other species, amplifying even further the number of ways a community can be configured. A massive edifice of theoretical research has addressed the community consequences of different forms of density-dependent interactions among species (Morin

1999). From a given set of initial conditions, outcomes such as the exclusion of all but one species, the indefinite coexistence of all species, complex temporal fluctuations, or entirely different equilibrium patterns depending on initial conditions are possible.

Selection, whether constant or density-dependent, may vary across space or time, with potentially important consequences for community dynamics. Most importantly, the behavior of such models can deviate qualitatively from spatiotemporally invariant models when the relative fitness of different species switches in different places or times, thereby allowing for coexistence among species that would oth-

erwise not be possible (Levene 1953; Chesson 2000). More generally, species coexistence always depends on trade-offs of some kind, with different species having fitness advantages under different sets of conditions, specified by some combination of the abiotic environment and the densities of the species themselves (Chesson 2000).

DRIFT

Because birth, death, and offspring production are inherently stochastic processes, changes in any community with a finite number of individuals will also have a stochastic component. This is ecological drift. If individual-level demographic parameters are identical across all individuals in a closed community, drift is the only driver of community dynamics (i.e., there are no deterministic changes in abundance; Figure 1E) and, eventually, all but one species will drift to extinction. The probability of each species reaching monodominance is equal to its initial frequency, and the rate at which this is achieved is negatively related to community size (Figure 2). As such, declines in community size (i.e., disturbance) may increase the importance of drift. Importantly, drift need not act alone to have an important impact on community dynamics. The interaction of drift with speciation and dispersal (Hubbell 2001) will be described in subsequent sections; here, I address the interaction of drift and selection.

If selection is relatively strong and the community size is large, selection will override any effects of drift. But if selection is relatively weak and the community size is small, drift can override the effects of selection. Between these two extremes, selection makes some community outcomes more likely than others, but it does not guarantee any particular outcome (Nowak 2006). For example, even with constant selection favoring one of two species, there is some probability that the species with the higher fitness will drift to extinction (Figure 2).

SPECIATION

Most treatments of community ecology inherently exclude from their purview the question of how the species in a given area arose in the first place, leaving such questions to the fields of biogeography and macroevolution (Ricklefs 1987; Brown 1995). From the perspective of understanding how species interactions play out in homogeneous, small-scale localities, this is entirely defensible, because the origin of the local species pool does not matter; what does matter is that the species are present locally and possess a given set of traits. But to compare community patterns across different regions, and even across environmental gradients at quite local scales, it may be important to incorporate the biogeographic and macroevolutionary context in which the species pool originated (Ricklefs 1987; Ricklefs and Schluter 1993; Pärtel 2002). We can no more afford to exclude speciation from community ecology than we can afford to exclude mutation from population genetics, even if speciation is a far more complex process.

I deliberately focus on speciation rather than embracing extinction under this umbrella as well, because, with an expanded spatial and temporal scope of community ecology (see DEFINITIONS section above), extinction is best considered as an outcome of selection and drift, rather than as a distinct process in and of itself. When the last individual of a species dies, the species is extinct, and while the decline to extinction may have many specific causes, they must either be deterministic (selection) or stochastic (drift). Even major geological events (e.g., glaciation) are distinguished from more subtle environmental changes (e.g., slight acidification of a lake) as agents of selection by the rate, magnitude, and spatial scale of change, rather than by a qualitatively distinct influence on communities. Such environmental changes may also alter the effects of drift via changes in community size.

I focus here on some of the simplest ways that speciation has been incorporated into theoretical community models, as well as some empirically-motivated conceptual models. At large spatial scales, such as entire continents, the rate of speciation can enter mathematical models directly as a key determinant of community dynamics. For example, Hubbell (2001) considered a neutral community of fixed size in which the
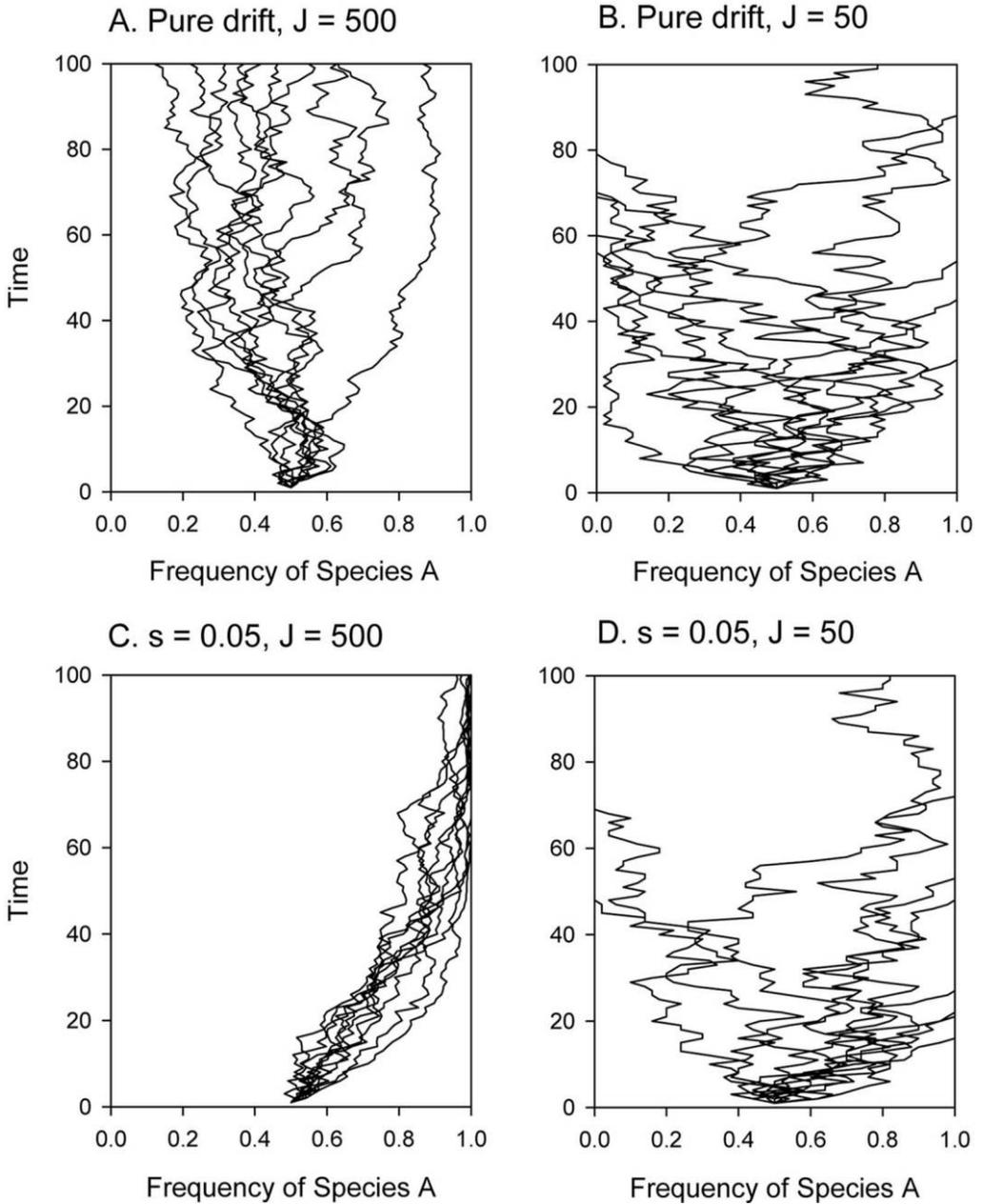
FIGURE 2. FREQUENCY DYNAMICS OF TWO SPECIES UNDER DRIFT AND SELECTION

Dynamics are shown for two species, A and B, with non-overlapping generations in 10 simulated communities of constant size, J, with (A) no fitness differential and J = 500, (B) no fitness differential and J = 50, (C) a 5% fitness advantage to species A and J = 500, and (D) a 5% fitness advantage to species A and J = 50.

speciation rate is constant, with the rate of extinction due to drift increasing with the number of species because, with more species, each species' population must be smaller. Alternatively, MacArthur (1969) posited that both speciation and extinction rates increase

with the number of species, but with the increase decelerating for speciation and accelerating for extinction, thus resulting in an equilibrium number of species in the region. These models correspond to drift-speciation balance and selection-speciation balance, respectively, and, in both cases, a greater rate of speciation leads to a larger species pool, all else being equal. In a model of multiple local communities connected by dispersal along an environmental gradient, McPeek (2007) found that the nature of the speciation process influenced local species diversity: greater ecological similarity between new and existing species extended times to extinction, thereby elevating local species diversity at any given time. More conceptual (rather than mathematical) models address the consequences of variation in the rate at which species that are adapted to particular conditions (e.g., regionally common or rare abiotic conditions) are produced. The term "species pool hypothesis" has been used to describe this type of conceptual model (Taylor et al. 1990). Through its effects on the regional species pool, speciation then indirectly becomes a potentially important determinant of community dynamics and patterns, even at a local scale where the rate of speciation is negligible relative to other processes (e.g., Ricklefs and Schluter 1993; Pärtel 2002).

DISPERSAL

Dispersal involves the movement of organisms across space, and, thus, its influence on community dynamics depends on the size and composition of the communities where the dispersers come from and of those in which they disperse to (Holyoak et al. 2005). As such, the community consequences of dispersal can only be addressed in relation to the action and results of other processes, selection and drift in particular. The construction of theoretical community models addressing the role of dispersal usually specifies whether organisms are distributed continuously across space or in discrete patches. The latter type of distribution will be adopted here for the sake of simplicity and clarity.

With respect to the relative sizes of the source and recipient communities for dispers-

ers, two kinds of models represent the ends of a continuum. Mainland-island models assume one-way dispersal from a source community of effectively infinite size (the mainland) to one or more smaller, discrete local communities (the islands, or localities). These models assume that community dynamics in small localities are sufficiently rapid relative to those on the mainland, such that the composition of the pool of dispersers is effectively constant. In contrast, island models assume a network of small local communities linked by dispersal among them, with no distinct mainland. Such networks of local communities may be called "metacommunities" (Holyoak et al. 2005).

Dispersal can interact with drift and speciation. In a mainland-island model with local drift but no speciation or selection, dispersal increases local species richness and causes local community composition to converge with that of the mainland. For a given level of dispersal, the number of new species introduced per unit of time will decrease as local species richness increases, because fewer and fewer of the dispersers will represent new species in the locality. With fixed local community size, greater species richness necessitates smaller population size per species, so that the rate of species extinction increases with species richness, at some point equaling the rate of species introduction, and thus determining an equilibrium number of species whose identities nonetheless change through time. This is the simplest form of the theory of island biogeography (MacArthur and Wilson 1967). In an island model with local drift but no speciation or selection, dispersal increases local diversity by countering drift, and causes the similarity in composition among localities to increase (Wright 1940). Without input via speciation or dispersal from a separate metacommunity, all but one species will ultimately drift to extinction. In a model with drift, speciation, and dispersal but no selection, all community patterns are determined by the size of the local communities, the size of the entire metacommunity, and the rates of speciation and dispersal (Hubbell 2001).

Not surprisingly, the range of outcomes when dispersal interacts with selection is vast. The nature of selection among species in one

locality can take many different forms, and dispersal implies multiple localities, each of which may represent a unique selective environment. The consequences of dispersal depend on these details. Also, in addition to the many kinds of trade-offs in different models of pure selection, dispersal ability itself may vary among species, possibly with a trade-off involving other aspects of fitness. Enumerating all possible ways that dispersal can interact with selection and drift is well beyond the scope of the present paper, but three generalized examples will provide us with a glimpse into how selection and dispersal can interact. First, if selection via competition or predation causes a species to go locally extinct, that species may nonetheless persist regionally, along with its competitor/predator, if it has a superior ability to disperse to "open" sites where the superior competitor/predator has gone extinct due to either an absence of prey or for other reasons (Caswell 1978; Tilman 1994). Second, if selection favors different species in different patches, dispersal can nonetheless maintain persistent local populations of species, even in patches where they are at a fitness disadvantage (Levene 1953). If species vary in their mean fitness across patches, then very high dispersal will allow the species with the highest average fitness to exclude all others. Finally, in a mainland-island context, dispersal to the island determines the species pool in a way closely analogous to the role of speciation on continents.

RELATING EXISTING THEORIES TO THE FOUR PROCESSES

Four processes—or any four items—can be considered singly or in combination in 15 different ways: each of the four alone, six pairwise combinations, four trios, and all four together. However, it is impossible to build a theoretical community model with only speciation and/or dispersal without specifying the fate of new species or dispersers, particularly with respect to selection or drift. Thus, the four processes can form the basis of theoretical models in 12 different ways.

Table 2 relates many of the influential and familiar theories, models, and concep-tual frameworks in community ecology to their emphasis on selection, drift, speciation, and dispersal. Briefly, the idea of species "niches" (Chase and Leibold 2003) is essentially synonymous with selection, and many models of species interactions represent different manifestations of selection. Adding demographic stochasticity to selection-based models represents a combination of drift and selection (e.g., Tilman 2004), as do models proposed under the rubric of a niche-neutral reconciliation (e.g., Shipley et al. 2006; Adler et al. 2007). The species-pool hypothesis (Taylor et al. 1990) and the broader conceptual framework, based on the interaction between local and regional processes (Ricklefs and Schluter 1993), represent the interaction between speciation and selection and, to some degree, dispersal. Classic island biogeography theory (MacArthur and Wilson 1967) represents a balance between drift and dispersal, and the full version of Hubbell's (2001) neutral theory represents the combined influence of drift, dispersal, and speciation. Meta-community theory (Holyoak et al. 2005) and the many specific models that fall into this category, such as those involving colonization-competition tradeoffs or "mass effects," emphasize dispersal first and foremost, and how dispersal interacts with selection and drift.

THE FOUR PROCESSES OF COMMUNITY ECOLOGY: DATA

A vast amount of empirical literature addresses the processes underlying the dynamics of ecological communities. The purpose of this section is to illustrate the kinds of evidence available from lab experiments, field experiments, and observations of nature that speak to the importance of various forms of selection, drift, speciation, and dispersal in communities.

SELECTION

Case studies of selection in ecological communities number in the thousands, and most communities documented in these studies appear to be characterized by unique combinations of selective factors (Diamond and Case 1986; Putman 1994; Lawton 1999; Morin

TABLE 2

Twelve combinations of selection, drift, speciation, and dispersal, and the ways in which existing ecological theories relate to these combinations

Combination	Selection	Drift	Speciation	Dispersal	Theories and models	Representative references
1	×				Niche models of all kinds (e.g., resource competition, predator-prey, food webs)	Tilman (1982); Chase & Leibold (2003)
2		×			Neutral theory I (demographic stochasticity)	Hubbell (2001)
3	×	×			Niche-neutral models (any niche model with demographic stochasticity)	Tilman (2004); Adler et al. (2007)
4	×		×		Historical/regional ecology I (species pool theory, diversity on gradients, speciation-selection balance)	MacArthur (1969); Ricklefs (1987)
5		×	×		Neutral model II (non-spatial)	Hubbell (2001)
6	×			×	Metacommunities - deterministic (spatial mass effects, spatial food webs)	Holyoak et al. (2005)
7		×		×	Neutral model III (island biogeography)	MacArthur & Wilson (1967); Hubbell (2001)
8	×	×	×		Historical/regional ecology II	Ricklefs (1987)
9	×		×	×	Historical/regional ecology III	Ricklefs (1987)
10		×	×	×	Neutral model IV (spatial)	Hubbell (2001)
11	×	×		×	Metacommunities - stochastic (colonization-competition tradeoffs, stochastic versions of six)	Holyoak et al. (2005)
12	×	×	×	×	The theory of ecological communities	This paper

1999). Important factors that underlie the influence of selection on community patterns include species' responses to the abiotic environment, the disturbance regime, the types of direct interactions between organisms (e.g., competition, predation, parasitism, herbivory, mutualism), the functional or behavioral responses of organisms to different densities of interacting species, the degree of specialization in interspecific interactions, the number and types of limiting resources (e.g., renewable or non-renewable), and the presence and nature of indirect interactions among species (Putman 1994; Morin 1999; Ricklefs and Miller 1999). The following handful of examples focuses mostly on competition and trophic interactions to illustrate the basic types of selection (Figure 1) and the range of outcomes of selection in local communities, such as the exclusion of some species by oth-

ers, the stable coexistence of species, complex fluctuations in abundance over time, or alternation between different stable states. I focus on studies in which the outcome of selective processes is measured as changes in the abundances or diversity of species, rather than in the responses, such as individual growth rates or body size, of focal species, which are often measured under the assumption that they may have consequences at the community level (e.g., Van Zandt and Agrawal 2004).

Species can exclude each other; while selection in any real situation is unlikely to be constant across all species' densities (Figure 1A), one species may be at an advantage across the full range of possible densities. Lab experiments have demonstrated competitive exclusion between species of paramecium (Gause 1934), phytoplankton (Tilman 1977), and flour beetles (Park 1948), among many others, as well as the exclusion of prey species by a predator (Gause 1934; Huffaker 1958). Similarly, field experiments have revealed competitive exclusion—for example, between barnacle species at particular tidal depths (Connell 1961), or plant species under particular resource conditions (Tilman 1982, 1988). In many cases of competitive exclusion, the winner in competition depends on environmental conditions, thus establishing the possibility (in lab experiments) or existence (in field studies) of spatially-variable selection. Many species distribution patterns have been interpreted as evidence of competitive exclusion between functionally similar species (e.g., Diamond 1975), although it is very difficult to confidently infer process from pattern in such cases (Strong et al. 1984). Regardless of the strength of direct interspecific competition, past environmental change (e.g., glacial cycles) has acted as an agent of selection among species, favoring some but causing others to decline, sometimes to the point of extinction (McKinney 1997; Williams et al. 2004).

Competing species often exist in stable combinations via negative density-dependent selection. With multiple limiting resources and two phytoplankton species, Tilman (1977) found that one species (*Asterionella formosa*) was a superior competitor for the resource most limiting to the other species (Si) and vice versa (*Cyclotella meneghiniana*, and P), resulting in stable coexistence via negative density-dependent selection at intermediate Si/P ratios. Coexistence among grassland plant species via the same mechanism has been found in field experiments as well (Tilman 1988). A trade-off between competitive ability and colonization ability can create negative density-dependent selection contributing to the coexistence of protozoans and rotifers in lab microcosms (Cadotte et al. 2006), although field evidence for this mechanism is more ambiguous (e.g., Levine and Rees 2002). Temporally variable selection via environmental fluctuations can lead to stable coexistence of diatoms under variable temperatures in the lab (Descamps-Julien and Gonzalez 2005), and also appears to be a likely explanation for the coexistence and fluctuation of grassland plants in variable climatic conditions in Kansas (Adler et al. 2006). Patterns of species composition are often closely correlated with environmental conditions, with spatially-variable selection almost certainly playing an important role (Whittaker 1975).

Trophic interactions among species can lead to coexistence with fluctuations over time via complex forms of density-dependent selection. Predators and their prey can coexist over the long term with regular cycles, both in lab microcosms, such as those with different species of mites (Huffaker 1958) or rotifers and algae (Fussman et al. 2000), as well as in field populations, such as snowshoe hares and lynx in the boreal forest (Krebs et al. 2001). Density-dependent species interactions can also lead to complex, chaotic dynamics with species persistence in aquatic laboratory food webs (Benincà et al. 2008).

Positive and negative density-dependent selection over different ranges of species' densities can lead to switches between multiple states with respect to community composition. Changes in the initial abundances of species in aquatic microcosms can lead to very different and seemingly stable final species compositions (Drake 1991)—a result that has been found in a variety of lab and field experiments (Schröder et al. 2005). In

natural, nonexperimental systems, a change in the abiotic environment can act as a selective force that changes species composition, which, in some cases, may not be reversible just by returning the environmental condition to its original state (Scheffer et al. 2001). In lakes, for instance, nutrient input can push species composition towards a new stable state that is not reversible unless nutrients are reduced to much lower levels than those at which the initial change took place (Dent et al. 2002).

The range of detailed mechanisms underlying the influence of selection on communities is vast. In a nutshell, almost any kind of selective interaction between species can be found in some community on earth, or can be recreated in the laboratory. Likewise, many case studies have been able to reject hypotheses based on particular forms of selection, although such rejections typically apply only to the system under study, rather than representing a general refutation of a hypothesis. Ecologists working in different kinds of communities have traditionally emphasized the importance of particular processes (e.g., competition among terrestrial plants vs. trophic interactions among aquatic animals), although it is not clear whether these reflect real differences among communities or logistical constraints to studying different processes in different systems.

DRIFT

Testing for ecological drift among species presents considerable empirical challenges. First, pure ecological drift—without any selection—seems unlikely given the myriad differences between species. Second, while selection is relatively easy to detect as a consistent fitness difference between species across observational or experimental units, the unexplained variance across such units cannot automatically be attributed to drift. This is because of the entirely plausible possibility that much of the unexplained variance is due to minor differences in uncontrolled factors, such as environmental parameters. One can always dream up a deterministic explanation for apparent randomness. Indeed, the discussion sections of many ecological papers implicitly attribute low

values of r^2 to unmeasured but deterministic factors, rarely entertaining the possibility that the unexplained variation is truly random—that is, due to ecological drift. Nonetheless, in a world of finite size, drift is a fact of life, and there are in fact many empirical studies in which a compelling case can be made for drift as an important process underlying community dynamics.

Experiments by Thomas Park (1948) and colleagues (Mertz et al. 1976) with *Tribolium* flour beetles demonstrated a competitive advantage of one or another species depending upon conditions of temperature and humidity, but they also discovered conditions under which the outcome was indeterminate. Sometimes *T. castaneum* wins and sometimes *T. confusum* wins, despite seemingly identical conditions across replicate microcosms. It has been suggested that differences in the genetic composition of populations can provide a selective explanation for the seemingly indeterminate results (Lerner and Dempster 1962), but, ultimately, it appears that under particular conditions the two species are sufficiently close to competitive equivalency that ecological drift does indeed play an important role in the outcome of competition (Mertz et al. 1976). More recently, density manipulation experiments with *Enallagma* damselflies strongly suggested ecological equivalence between two species, with no obvious advantage to either species at low relative abundance, but strong sensitivity of demography to total density across the two species (Siepielski et al. 2010).

I know of few other examples where conclusive evidence has been found that drift does indeed play a dominant role in community dynamics, but a number of studies have reported seeming competitive equivalence between species under particular conditions, in organisms ranging from vascular plants (Goldberg and Werner 1983) to salamanders (Fauth et al. 1990). Hubbell (2001, 2005) has vigorously advanced the hypothesis that many tropical tree species are effectively ecological equivalents, with their community dynamics determined by drift and dispersal in the short term, along with speciation in the long term. Some tropical tree species show clear evidence of

ecological differences in traits, such as a trade-off between survival versus growth rate in gaps (Hubbell 2005) and environment-dependent fitness (John et al. 2007), thus suggesting an important role for selection in community dynamics. However, hundreds of co-occurring species of any particular ecological "type" still remain, indicating a potentially important role for drift, even though it is clearly not the only important process at work in tropical forests. In many data sets, species composition is strongly related to environmental conditions (indicative of selection), but variation in the compositional similarity between sites is also related to spatial proximity independent of environment, and this is an indirect indication of drift (Cottenie 2005). For species engaged in trophic interactions, the concept of pure neutrality does not apply, although changes in predator and prey abundances almost certainly have an important stochastic component in many cases (Chesson 1978).

SPECIATION

Speciation is obviously an important determinant of the number and types of species found in large regions, such as entire continents, as well as on isolated islands (MacArthur 1969; Losos and Schluter 2000; Ricklefs 2008). Although the distinction of discrete spatial scales is largely arbitrary (Ricklefs and Schluter 1993), the present discussion focuses on circumstances under which speciation exerts an important influence on community patterns at comparatively small scales.

Speciation appears to be critical to our understanding of at least two kinds of species diversity patterns. First, why do equal-sized areas under very similar environmental conditions but in different geographical regions contain different numbers of species? These have been dubbed "diversity anomalies" (Ricklefs 2008). For example, across a range of scales, equal-area portions of eastern Asia contain about twice the number of plant species as in eastern North America, despite similar environmental conditions and strong taxonomic affiliations between the two regions (Ricklefs et al. 2004). Increased opportunity for speciation in eastern Asia due to greater physi-

ographic heterogeneity appears to be an important contributor to this pattern (Qian and Ricklefs 2000). More generally, many studies report linear increases in local species richness with increasing regional species richness (Srivastava 1999), thus suggesting an important influence on local diversity of processes, such as speciation and dispersal, that determine the regional species pool.

The second kind of species diversity pattern for which speciation can be a key underlying process is the relationship between species diversity and local environmental gradients (Ricklefs 2004). Such patterns are widespread (Rosenzweig 1995), and, before assessing the underlying processes at work here, it is important to consider that the species in lower diversity areas may not just be a subset of the species in higher diversity areas. For example, while the number of species per unit of area may change with elevation up a mountainside, one must take into account that there are different sets of species living at the base and at the top of the mountain (Whittaker 1975). If we take the regional species pool as a given and assume that all species have been able to reach different areas, selection must be an important process underlying the composition-environment relationship. However, why should we find different numbers of species at different elevations or different levels of productivity? For productivity gradients in plants, for instance, one selection-based explanation is that high productivity fosters dominance by fast-growing species, thereby limiting species diversity under such conditions (Grime 1973). But again, why should there be relatively few species capable of exploiting high productivity conditions or, more generally, any particular set of conditions (Aarssen and Schamp 2002)?

One potentially important part of the answer is that different sets of environmental conditions have been represented to variable degrees over time, such that speciation has produced many species that are adapted to common, widespread conditions, but far fewer that are adapted to rarer conditions (Taylor et al. 1990). For example, in regions where relatively high soil pH has predominated, plant species diversity tends to be positively correlated with pH, whereas in regions

where relatively low soil pH has predominated, the opposite is true (Pärtel 2002). Even if different habitats have been equally available over time, current species richness might be greatest in conditions under which a particular group of organisms initially evolved and, therefore, where diversity has had more time to accumulate via speciation. For example, Wiens et al. (2007) found similar rates of diversification at different elevations for a clade of tropical salamanders, but they noted that mid-elevation habitats were colonized earliest in the evolution of the clade, thus helping explain a mid-elevation peak in species richness patterns. In summary, although selection is a key determinant of compositional change along gradients, speciation is likely a critical process contributing to many diversity-environment relationships (Ricklefs 2004).

DISPERSAL

Dispersal can have manifold consequences for community patterns at multiple spatial scales. First, much like speciation, dispersal is a key contributor to the regional species pool and, consequently, the various community consequences that it entails (Ricklefs and Schluter 1993).

From the local habitat perspective, a common empirical result is that increasing dispersal into the locality increases species diversity. For areas undergoing primary succession, such as Krakatau following its volcanic eruption, dispersal is required in order to establish a community and increase diversity (Whittaker et al. 1989). In the field, experimental dispersal via seed addition into established plant communities often results in increased species diversity (Turnbull et al. 2000), and the proximity of an island or habitat patch to potential sources of dispersers often correlates positively with local species diversity in a wide range of organisms (e.g., MacArthur and Wilson 1967). For amphibians in a network of ponds, for instance, increased connectivity positively influenced species turnover, suggesting that dispersal can affect not only species composition and diversity, but their temporal rates of change as well (Werner et al. 2007a).

Since species vary in their propensity for dispersal, the proximity of a locality to potential source habitats can also influence species composition, with distant localities containing a preponderance of good dispersers (e.g., Kadmon and Pulliam 1993). With variation in local species composition created by dispersal, either related to locality isolation or stochastic variation, density-dependent selection via species interactions can further magnify local variation in species composition, as in freshwater communities of zooplankton and their insect or fish predators (Shurin 2001).

Dispersal can interact with selection or drift to influence community patterns at the regional scale as well as at the local scale. In an experimental metacommunity of protozoans and rotifers, local species richness was maximal at intermediate rates of dispersal (Cadotte 2006a). The shift from low to moderate dispersal increases the rate of addition of new species to localities and allows competitively inferior species to find temporary refuges, whereas the shift from moderate to high dispersal allows superior competitors to dominate across the metacommunity. In the same experiment, compositional variability among localities was maintained to the greatest degree with low to moderate dispersal, thus maximizing richness across the entire metacommunity (Cadotte 2006a). A meta-analysis of similar experiments found that local diversity was generally maximized at intermediate dispersal rates in animal communities, but, at the highest dispersal rates in plants, there was either a negative effect on regional diversity or no effect was observed at all (Cadotte 2006b). For the pond amphibians mentioned above, species turnover was strongly influenced by both connectivity and environmental factors, thus suggesting an important interaction between dispersal and selection (Werner et al. 2007a,b).

The body of research on the community consequences of dispersal and its interaction with selection is still comparatively small. As with selection, it seems likely that any theoretically plausible effect of dispersal on community dynamics will be found in some experimental or natural community, while at the same time, many hypotheses concerning

the consequences of dispersal will be rejected in particular systems.

General Patterns and the Pattern-Process Relationship

In this paper, I have argued for a conceptual organization of community ecology based on the recognition of four fundamental classes of process. However, research directions in community ecology have seldom begun by starting first from principles and then asking what patterns in nature we expect to see based on the action of elementary processes. More often, patterns are observed in nature, after which explanations are sought. Patterns that have received considerable attention include the distribution of species' relative abundances; the relationship between species diversity and area, latitude, elevation, productivity, disturbance, or spatial heterogeneity; the relationship between local and regional species diversity; patterns in connectance, as well as other properties, of food webs; and temporal changes in species composition during succession (Diamond and Case 1986; Rosenzweig 1995; Morin 1999; Ricklefs and Miller 1999).

A major source of debate in community ecology is the fact that most such patterns have multiple explanations. As such, finding a particular pattern in a given system often reveals very little about the important processes at work in that system. Species-area relationships provide an illustrative example. According to the theory of island biogeography, large islands contain larger populations of component species, so the rate of extinction due to drift is lower than on smaller islands, thus leading to a greater number of species on large versus small islands (MacArthur and Wilson 1967). It is also possible that larger islands provide a bigger target for dispersing organisms, such that the rate of immigration, and therefore species richness, is greater on large islands as compared to small ones (Gilpin and Diamond 1976). The environmental heterogeneity of an island also tends to scale positively with island area, such that spatially variable selection allows more species to coexist on large rather than small islands (Whittaker and Fernandez-Palacios 2007). Finally, opportunities for speciation may be greater on large islands, thereby contributing
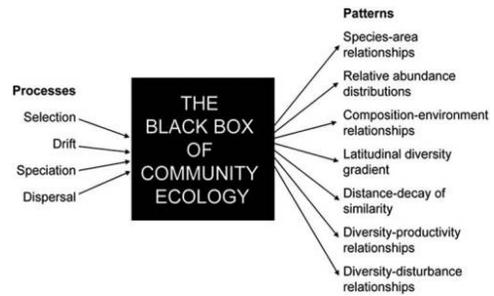

Figure 3. The Black Box of Community Ecology

Community ecology has a straightforward set of processes that have created some general patterns in nature, but there are innumerable ways to get from process to pattern.

to positive species-area relationships (Losos and Schluter 2000). Thus, drift, dispersal, selection, and speciation can all explain or contribute to the species-area relationship. Similar arguments pertain to other common community patterns.

As such, perhaps the greatest challenge in community ecology is drawing the link between process and pattern. Community ecologists have, in fact, risen impressively to this challenge, by developing a suite of experimental and observational methods to tease apart the workings of particular communities in particular places, often providing critical guidance to applied management efforts (Simberloff 2004). It is, therefore, fairly straightforward to study processes at relatively small scales, or to document broad-scale community patterns. The "mess" stems from our inability to make general statements about process-pattern connections (Lawton 1999; Simberoff 2004). Thus, there is a kind of black box in community ecology, within which lie the innumerable ways to get from process to pattern (Figure 3), and it is disconcerting to many that when we peer into the box, what we see seems to be fundamentally system-specific. Lawton (1999) takes this as a lesson that local experimental studies are no longer a fruitful avenue for pursuing generalities in ecology. Alternatively, it could be taken as a lesson that seeking generalities of the form "pattern X has a broadly applicable explanation in simple theory Y" or "process Q is always the key to

understanding community patterns" is bound to fail in community ecology. Generalities of the form "community patterns can be understood as the outcome of interacting processes A, B, and C" seem more likely to hold. This paper is about defining the ABC's of community ecology in the simplest possible, logically complete way.

Existing Organizational Frameworks in Community Ecology

A number of different frameworks have been put forth aimed at the conceptual organization of community ecology, or at least major parts of community ecology, with which the present framework can be compared. Ecology has a long history of debates centered around whether or not populations and communities reach some kind of equilibrium state—that is, a "balance of nature" (Kingsland 1995). The conceptual framework presented here is silent on this issue—and, indeed, on any issue regarding what has most often actually happened in nature—but is focused on conceptually organizing the processes that can influence what happens in communities, whether they are at equilibrium or not.

At least three fairly recent conceptual frameworks have gained popularity in the contemporary literature: equalizing vs. stabilizing mechanisms of coexistence (Chesson 2000), local vs. regional controls on community structure (Ricklefs and Schluter 1993), and the metacommunity concept (Holyoak et al. 2005). With respect to models of species coexistence, Chesson (2000) recognized two fundamental classes of mechanism: those that equalize fitness differences, thereby slowing competitive exclusion and possibly enhancing drift, and those that stabilize coexistence via negative density dependent selection. This framework is reflected in many of the recent efforts at synthesis under the rubric of niche-neutral reconciliation (e.g., Shipley et al. 2006; Adler et al. 2007), and has proven very useful, but its domain is restricted to competitive coexistence and is focused almost entirely on local selection and drift.

The emphasis on historical and regional processes (Ricklefs and Schluter 1993) was developed to underscore the importance of processes occurring at broader spatial and temporal scales than are typically considered in traditional community ecology—namely, speciation and long-range dispersal. The framework presented here shares much in common with the perspective of Ricklefs and Schluter (1993). The graphical representation of their perspective shows regional diversity determined by input via biotal interchange and species production, and output via mass extinction; local diversity is determined by input via habitat selection and output via stochastic extinction, competitive exclusion, and predatory exclusion (Figure 30.1 in Ricklefs and Schluter 1993:351). This perspective is quite similar to a common type of graphical model that shows a local community as the outcome of a series of filters, including dispersal, the abiotic environment, and biotic interactions (e.g., Morin 1999). The conceptual framework presented here takes these a step further by recognizing four distinct classes of process, within which all others fall and which thereby allows for a more comprehensive and logically complete framework. For example, biotal interchange and habitat selection (as used by Ricklefs and Schluter) both fall under dispersal, and competition and predation are only two of many deterministic factors that can exclude species, all of which fall under selection.

The metacommunity framework explicitly encompasses drift, selection, and dispersal (Holyoak et al. 2005). Speciation is not explicitly excluded, but is, for the most part, absent from this framework. Within the metacommunity framework, four perspectives are recognized: neutrality, patch dynamics, species sorting, and mass effects. These correspond loosely to theoretical constructs or formalisms around which practicing ecologists have self-organized, but, in my opinion, they do not represent fundamental, logically distinct classes of ecological process. Mass effects, for example, include species sorting, and patch dynamics models can be neutral. The metacommunity perspective also excludes from its purview community dynamics that do not involve dispersal as a key component. For these reasons, the present framework is distinct from the metacommunity

perspective, although metacommunity models fit comfortably within it.

In addition to these three conceptual frameworks specifically focused on community ecology, two highly influential theoretical frameworks that cut across sub-fields of biology, but with some connections to community ecology, are worth mentioning: the metabolic theory of ecology (Brown et al. 2004) and ecological stoichiometry (Sterner and Elser 2002). In simple terms, these two approaches explore the consequences of considering organisms essentially as physical entities that process energy optimally given their size (metabolic theory), or that interact with their environment based largely on their chemical composition (stoichiometry). In my opinion, these frameworks are most powerful in aiding our understanding of the functioning of individual organisms or the fluxes of energy and chemicals in whole ecosystems. The contributions of these frameworks to community ecology, such as predictions concerning the effect of temperature on species diversity (metabolic theory) or of plant-herbivore interactions (stoichiometry), fall comfortably within the present framework, usually as mechanisms underlying selection.

IMPLICATIONS

The first goal of this paper was to organize the material of community ecology in a logically consistent way in order to clarify the similarities and differences among various conceptual constructs in the discipline. One motivation was the common criticism that ecologists tend to repeatedly reinvent the wheel: we claim ideas as new that are only subtly distinct, or not distinct at all, from ideas put forth long ago (Lawton 1991; Graham and Dayton 2002; Belovsky et al. 2004). There are likely many reasons for this, but one important reason, at least in community ecology, may be the lack of a coherent framework within which particular perspectives or theories can be described and related. As such, a plethora of terms, each of which sounds new and different, is often used to communicate much the same thing—such as niche processes, species interactions, or species sorting all being used to describe selection. It

does not matter whether selection is the best term for deterministic fitness differences among species, but it is critical to recognize that different mechanisms underlying selection, such as competition or predation, share more in common with one another than either does with drift, dispersal, or speciation.

Recognizing how different theoretical traditions in community ecology relate to one another based on fundamental, logically distinct categories of process can potentially prevent students from concluding from a Web of Science search that research on species sorting or metacommunities goes back no more than 15–20 years. We might also make more modest—and, I believe, realistic—assessments of the degree to which popular areas of research truly represent new paradigms or, more likely, incremental advances on previous work. Placing ecological ideas in their full historical context can curtail wheel reinvention and thus help to advance and expand ecological understanding in the long term (Graham and Dayton 2002).

My hope is that the present framework will be useful to practicing community ecologists as a way to place their research in a process-based context. I also think that this conceptual framework can potentially be of great use in teaching and communicating the subject matter of community ecology to a broader audience. As argued in the introduction, the traditional presentation of community ecology can be confusing because the common threads among topics such as food webs, competitive coexistence, and island biogeography are quite difficult to discern. The essential similarities and differences among these theoretical traditions can be seen quite clearly in the present framework (Table 2). The core subject matter in community ecology need not change, but I believe there can be great benefit to shifting the emphasis away from an organizational structure based on the useful lines of inquiry carved out by researchers, to one based on the fundamental processes that underlie community dynamics and patterns.

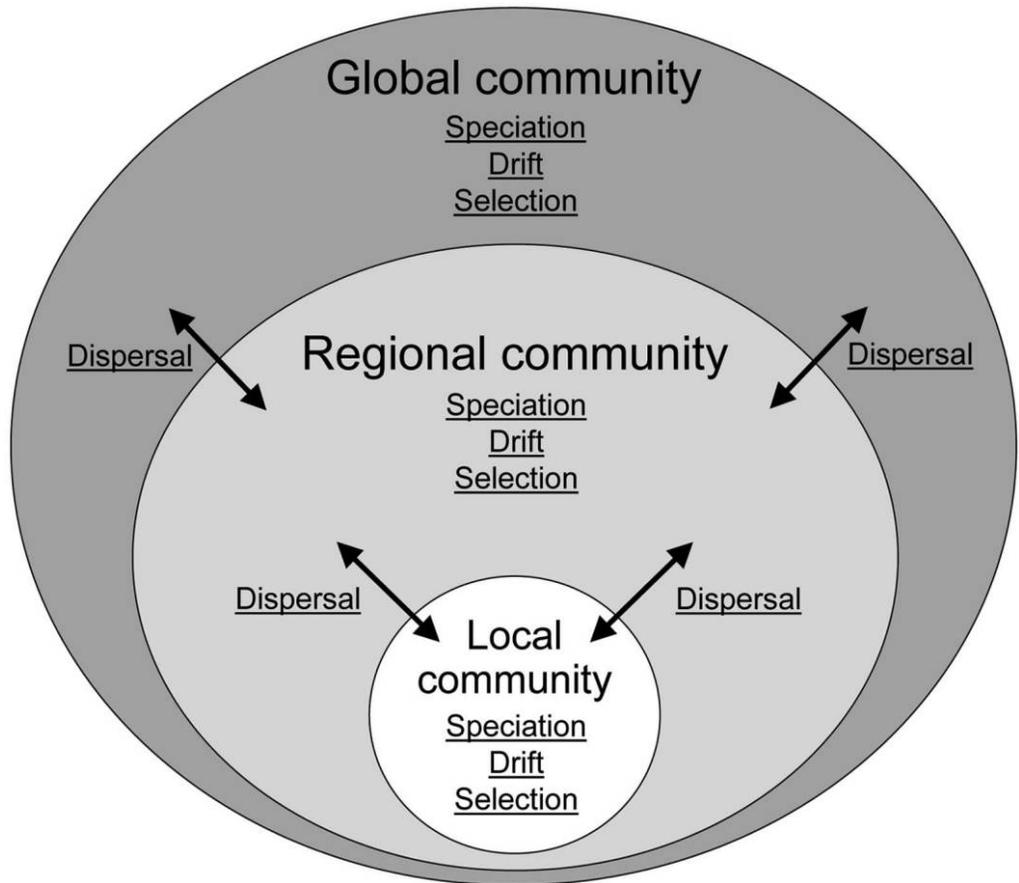The second goal of this paper was to articulate a general theory of community ecol-

FIGURE 4. THE THEORY OF COMMUNITY ECOLOGY
   Selection, drift, speciation, and dispersal interact to determine community dynamics across spatial scales. The delineation of discrete spatial scales is arbitrary, and used only for clarity of presentation. Figure modified from Vellend and Orrock (2009).

ogy. Such a theory might seem so generalized as to be of little use, but the utility of the Modern Synthesis in evolutionary biology—warts and all (Pigliucci 2007)—suggests otherwise. In essence, the Modern Synthesis can be summarized as positing that genetic variation is created in populations via mutation and immigration, and is then shaped by drift and natural selection to drive evolutionary change (Kutschera and Niklas 2004). The fact that the all-important mechanism of heredity was essentially unknown until the rediscovery of Mendel made the construction of the Modern Synthesis a profound scientific achievement in a way that cannot be matched in community ecology, where the

important rule of heredity is decidedly facile: elephants give rise to elephants and daffodils to daffodils. However, on its own, the Modern Synthesis makes no predictions about exactly how processes will interact to determine evolutionary change in any particular situation; rather, it simply establishes the fundamental set of processes that may be at work.
   We can likewise articulate a very general theory of community ecology: species are added to communities via speciation and dispersal, and the relative abundances of these species are then shaped by drift and selection, as well as ongoing dispersal, to drive community dynamics (Figure 4). The

precise way in which these processes interact to determine community dynamics varies tremendously from case to case, just as the processes that determine evolutionary change interact in ways that vary tremendously in each case. Stating a general theory of community ecology in this way echoes the perspective of Ricklefs and Schluter (1993), and I believe that recognizing this perspective as the community ecology counterpart to the evolutionary Modern Synthesis highlights an important sense in which community ecology already has a general theoretical framework that is every bit as robust as that of population genetics. The oft-cited recalcitrance of community ecology to generally applicable theory (e.g., Lawton 1999) seems like a fair assessment if the goal is to be able to make general predictions about how particular processes have shaped real ecological communities. If the goal is to make general statements about the fundamental processes that can underlie community dynamics and the possible ways in which these can interact, then community ecology appears to be in excellent shape.

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