

REVIEW

Trade-offs in community ecology: linking spatial scales and species coexistence

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Abstract

Trade-offs in species performances of different ecological functions is one of the most common explanations for coexistence in communities. Despite the potential for species coexistence occurring at local or regional spatial scales, trade-offs are typically approached at a single scale. In recent years, ecologists have increasingly provided evidence for the importance of community processes at both local and regional spatial scales. This review summarizes the theoretical predictions for the traits associated with trade-offs under different conditions and at different spatial scales. We provide a spatial framework for understanding trade-offs, coexistence and the supportive empirical evidence. Predictions are presented that link the patterns of diversity observed to the patterns of trade-offs that lead to coexistence at different spatial scales. Recent evidence for the evolution of trade-offs under different conditions is provided which explores both laboratory microcosm studies and phylogenetic tests. Examining trade-offs within a spatial framework can provide a strong approach to understanding community structure and dynamics, while explaining patterns of species diversity.

Keywords

Coexistence, community ecology, diversity, local and regional scales, metacommunity, spatial scales, species traits, trade-offs.

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INTRODUCTION

In evolutionary biology, the ‘Darwinian demon’ reigns supreme in the world of life histories, by asexually reproducing with immeasurable frequency and number while living forever. Trade-offs between survival and reproduction, however, constrain any organism from realistically resembling that creature. Similarly, community ecology could have its analogous, ‘Hutchinsonian demon’, whereby one species in a community dominates because it is the best at colonizing new patches, utilizing all the resources, avoiding predators and resisting stresses (Tilman 1982 termed these ‘superspecies’). Here, interspecific trade-offs are invoked to tame this demon, in that the benefits of performing one ecological function well (e.g. consuming one type of resource) comes at a cost of performing another function (e.g. consuming a different type of resource). Trade-offs within this community context represent niche differentiation among species, which emerge from individual-level constraints within an environmental context (e.g. resources, abiotic factors, presence of competitors or predators; Chase & Leibold 2003).

Trade-offs are ultimately exhibited as a negative functional interaction between traits (e.g. growth and reproduction; Stearns 1989; Zera & Harshman 2001). These differences in life-history traits can have consequences for population parameters (growth rate and carrying capacity), body size differences and ecological traits (MacArthur & Wilson 1967; Pianka 1970; Boyce 1984; Gleeson & Tilman 1990). For example, the trade-off between seed size and seed number has been used as a proxy for the competition–colonization trade-off for species coexistence (Turnbull *et al.* 1999; Levine & Rees 2002); competitive ability is enhanced by production of fewer, larger seeds, whereas colonization ability is improved by production of many small seeds. Other examples include allocation to aboveground–belowground growth (e.g. Gleeson & Tilman 1990) and power-efficiency growth (growth at low and high resource levels; e.g. Sommer 1985). However, it is not always necessary to invoke character divergences because habitat characteristics (e.g. refugia; Mouquet *et al.* in press) and neutral models (e.g. Hubbell 2001) can also explain coexistence. Nevertheless, we argue that niche differences exhibited as trade-offs among species provide a more convincing explanation for

species diversity patterns, especially when viewed within a spatial context.

Interspecific trade-offs are typically thought to be a requirement for species coexistence in communities at small spatial scales (MacArthur 1972; Tilman 1982, 2000; Petraitis *et al.* 1989; Tilman & Pacala 1993; Chesson & Huntly 1997; Grover 1997). Examples of local-scale trade-offs include differential use of resource types (MacArthur 1972; Tilman 1982), susceptibility to predators (Holt *et al.* 1994; Leibold 1996), and fitness in a temporally variable environment (Chesson & Huntly 1997). Recent studies, however, have focused on larger spatial scales, and in particular, the relative importance of processes acting at the local and regional scales (Caswell 1978; Ricklefs 1987; Cornell & Lawton 1992; Ricklefs & Schluter 1993; Tilman & Kareiva 1997; Loreau 2000).

A meta-community contains a group of species that potentially interact, and that are spatially segregated into distinct patches connected by dispersal (Wilson 1992). Within the meta-community context, trade-offs are still often heralded as essential for coexistence at a regional scale rather than local scale (but see Bell 2001; Hubbell 2001). For example, species can trade-off in their relative ability to compete and persist in patches and to colonize new patches (e.g. the competition–colonization trade-off; Levins & Culver 1971; Slatkin 1974; Hastings 1980; Tilman 1994; Yu & Wilson 2001). Similarly, species can be favoured in some habitats and disfavoured in others, and thus coexist either regionally as a result of partitioning of habitats (Tilman 1982; Chase & Leibold 2003) or locally as a result of source–sink

relationships (Loreau & Mouquet 1999; Amarasekare & Nisbet 2001; Mouquet & Loreau 2002, 2003).

Despite the recognition that trade-offs can lead to coexistence at different spatial scales, theoretical and empirical studies have largely examined trade-offs for one spatial scale or the other (Amarasekare 2003). Hubbell (2001) has challenged the notion that trade-offs are necessary for understanding broad patterns of species diversity and relative abundance (see also Bell 2001). As a means to open a dialog, and provide a null model for communities, Hubbell developed a ‘neutral’ model which assumes that species have equal per capita fitnesses: species have no niche differences, and thus no trade-offs. In this article, we argue that a better understanding of the range, variation and interactions of trade-offs at multiple spatial scales will allow the development of a more synthetic view of diversity; within this explicit spatial framework, this niche theory provides an alternative to neutral models to explain high levels of diversity at different spatial scales (Fig. 1).

There have been several summaries of theoretical and empirical support for trade-offs in specific systems (insects: Futuyma & Moreno 1988; desert mammals: Kotler & Brown 1988; Vincent *et al.* 1996; plants: Gleeson & Tilman 1990; Tilman 1990; Tilman & Pacala 1993; Grover 1997; aquatic animals: McPeck 1996; Wellborn *et al.* 1996; microbes: Bohannan *et al.* 2002). Therefore, to avoid redundancy, this review will emphasize the conceptual aspects of trade-offs and spatial scale while using empirical studies to better understand this relationship. Additionally, as we are not trying to explain patterns of diversity across

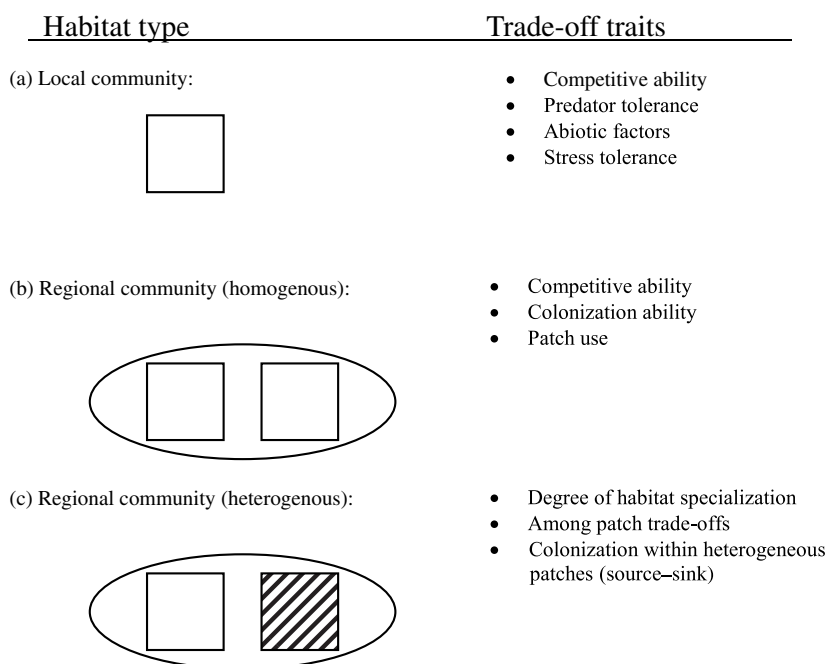


Figure 1 Habitat type and possible traits associated with trade-offs that lead to coexistence at that scale. Trait trade-offs at lower organizational levels are included in higher levels.

trophic levels, we limit discussion to trade-offs among competing species within a trophic level. This review addresses four main points. First, we will summarize the trade-offs expected to lead to coexistence at a variety of spatial scales. The mathematical details of each model will not be discussed; our emphasis will be on the assumptions of the models that predict certain species traits. Secondly, the empirical evidence is also assessed for consistency with trade-off predictions, as well as their implications for community structure. Additionally, we address what these studies tell us about trade-offs and the scale of coexistence. Thirdly, we make predictions for the relationship between scale-dependent trade-offs and species diversity at multiple spatial scales (e.g. alpha, beta, and gamma diversity, *sensu* Whittaker 1972; Lande 1996; Loreau 2000). Finally, we discuss how evolutionary processes may influence trade-offs at multiple scales, and suggest avenues for future theoretical and empirical studies.

TRADE-OFFS AND SCALE

Local-scale coexistence and trade-offs

The reductionist paradigm which focuses on controlled experimentation has dominated community ecology for over 25 years (e.g. Simberloff 1983; Strong *et al.* 1984): until recently, community ecology has focused on local-scale phenomena, implicitly assuming that systems are closed and that spatial processes are unimportant. The simplest of the models predict that in a spatially homogeneous locality, the number of coexisting species should be equal to or less than the number of limiting factors (MacArthur & Levins 1964; Levin 1970; Armstrong & McGehee 1980; Tilman 1982). This idea is a simple extension of the competitive exclusion principle as tested by Gause (1934).

A wide variety of limiting factors, and trade-offs among them, have been discussed as prerequisites for coexistence at local spatial scales (Fig. 1). Some of the most common, and potentially important, trade-offs among species include differential utilization of resources (i.e. different nutrients or prey items), susceptibility to predators, use of the abiotic environment (e.g. soil pH or temperature) and responses to disturbance or stress (Fig. 1). We briefly overview the traits associated with these trade-offs.

Resources

When a community is composed of a single trophic level, coexistence is possible between two species when there is more than one resource for which those species compete (MacArthur 1972; Tilman 1982). For example, each species' ability to persist and compete for limiting resources can be derived by the amount of resource where a species' death rate is exactly replaced by its birth rate. This level of

resource, known as a species' R^* , represents the equilibrium level of resource expected when consumers have population growth, and the resource is depletable (Tilman 1982; Grover 1997; Chase & Leibold 2003). If there are two limiting resources, the species can coexist only when one species has a lower R^* (superior competitive ability) for one resource, and the other has a lower R^* for the other resource. Note, however, that this trade-off alone does not guarantee coexistence, as the ability of species to reduce resources, and the relative supply of the two different resources also influences coexistence.

Numerous empirical tests have been conducted to measure trade-offs among species' use of resources (see review in Grover 1997). Most evidence comes from freshwater microorganisms (algae) that coexist under certain ratios of differentially used nutrients (Tilman 1982; Grover 1997). Some direct evidence for trade-offs among resource use in other systems (plants and animals) is weaker, some direct evidence exists for such trade-offs (e.g. Rothhaupt 1988), along with considerable indirect evidence (e.g. Werner & Platt 1976; Brown & Davidson 1977; Gleeson & Tilman 1990).

Resources and abiotic factors

Abiotic factors in communities can also influence interactions between species (Dunson & Travis 1990). For example, species can trade-off in their ability to utilize a limiting resource or to tolerate a stressful abiotic factor such as temperature, drought, or pH (Tilman & Pacala 1993; Chase & Leibold 2003). While abiotic factors are different from resources in that they are not consumed, the basic conclusion that such a trade-off is necessary for coexistence holds. Empirical evidence for such trade-offs include trade-offs between resource use and thermal tolerance (ants: Bestelmeyer 2000; invertebrates: Bengtsson 1991) or desiccation tolerance (marine invertebrates: Connell 1961; mosquito larvae: Juliano *et al.* 2002).

Resources and predation

A trade-off between competitive ability and predator invulnerability among species is often required for species to coexist; good competitors are negatively affected (individual or population growth rate) by predation and poor competitors are less vulnerable to predation (Paine 1966; Vance 1978; Armstrong 1979; Holt *et al.* 1994; Leibold 1996; Uriarte *et al.* 2002). Predator invulnerability can be exhibited in a variety of ways, including avoidance, tolerance, or resistance (Brooks & Dodson 1965; Fritz & Simms 1992; Wellborn *et al.* 1996; Strauss & Agrawal 1999; Chase *et al.* 2000a; Tiffin 2000). These invulnerability traits then inhibit the prey species' ability to gather resources, reduce their growth rates, or require higher levels of resources, which ultimately reduces its competitive ability.

Although the interaction between predation and competition can result in coexistence by several related trade-offs and mechanisms, they only promote coexistence under certain circumstances (Abrams 1999; Chase *et al.* 2002).

Direct empirical evidence for this trade-off is common across terrestrial and aquatic systems (Leibold 1989; Balciunas & Lawler 1995; Kraajeveld & Godfray 1998; McPeck 1998; Schmitz 1998; Baldwin & Hamilton 2000; Bohannan & Lenski 2000a,b; Peacor & Werner 2001; Steiner 2003), and indirect evidence, in the response of different groups of species to removal of predators or increases of resources, is also prevalent (Paine 1966; Morin 1983; Lewis 1986; Leibold 1999; Carson & Root 2000; Chase *et al.* 2000b; Chase 2003).

Temporal variation

When there is temporal variation in environmental conditions, and when species trade-off in their ability to thrive under those different environmental conditions, many species can persist on few resources because of their being differentially favoured in different temporal windows (Chesson & Warner 1981; Caceres 1997; Chesson & Huntly 1997; Chesson 2000). One such mechanism by which such temporal variation can allow species to coexist is the 'storage effect' (Chesson & Warner 1981; Warner & Chesson 1985). The storage effect allows species to persist during unfavourable time periods by reproducing and growing rapidly during favourable time periods. Persistence during unfavourable time periods requires the organism to have some life-stage that can withstand the unfavourable conditions. For example, many organisms have resting eggs or dormant seeds, and others have long-lived adults that can persist during times of famine. Empirical examples of local coexistence thought to occur by means of mechanisms similar to the storage effect include two species of *Daphnia* that persist in the long term because of temporal variation in recruitment from resting eggs which result from environmental fluctuations (Caceres 1997), and several species of desert annual plants that vary in their recruitment and levels of seed dormancy among years with highly variable amounts of rainfall (Pake & Venable 1995, 1996).

Local trade-offs in a spatial context

All of the trade-offs at the local level discussed above can be used to help explain diversity at larger spatial scales. If the environmental factors or resources are spatially variable, then different species can be favoured in different localities, and thus can coexist regionally. For example, a plant species will be favoured when the ratio of two limiting nutrients, such as phosphorus and nitrogen, is low, and a different species will be favoured when the ratio is high. In a region where some localities have low N : P and others high N : P

both species can persist. Similarly, when prey show a trade-off between competitive ability and predator resistance, the stronger competitor is favoured in environments with low resource supply, the more resistant species is favoured in environments with high resource supply and predators, and the species can coexist in regions that have both low and high resource localities with and without predators (Holt *et al.* 1994; Leibold 1996). In fact, Chase & Leibold (2003) have shown that these basic principles hold for a wide variety of combinations of limiting factors, including resources, predators and stresses. This simple result crystallizes the problem of scale in the principle that 'the number of species coexisting cannot exceed the number of limiting factors' (Levin 1970). Instead, when there is spatial heterogeneity, there can be many more species coexisting regionally than the number of limiting resources. Empirical evidence is provided by studies in several systems (Tilman 1982; Kotler & Brown 1988; Sommer 1993, 1994; Wellborn *et al.* 1996).

Trade-offs along multiple axes

Trade-offs are typically addressed among two traits, but there are potentially numerous environmental conditions along which species can segregate (Grime 1977; Tilman & Pacala 1993). These trade-offs are predicted to lead to coexistence at different spatial scales, but without any explicit connection among the scales. As examples, we consider McPeck's studies of interspecific interactions among larval damselflies living in lakes, and Tilman's studies on herbaceous plants living in old fields. Among genera of damselflies in the family Coenagrionidae, McPeck (1998) has found that species within genera trade-off in their relative ability to compete for limiting resources (zooplankton) and to avoid predators. This work illustrates how it allows certain groups of damselfly species to coexist within a single lake. However, the story gets more complicated, because different types of lakes have different types of predators: dragonflies or fish. Some species within the genera have avoidance strategies that are effective against dragonflies, but ineffective against fish, and other species have the opposite set of traits. Thus, these species coexist regionally by partitioning habitats with different types of top predators.

In a similar manner, Tilman and colleagues have discussed a variety of trade-offs in which herbaceous plant species trade-off in their ability to compete for nutrients and compete for light (Tilman 1982, 1988; Gleeson & Tilman 1990; Wedin & Tilman 1993), colonize new habitats (Tilman 1994), or their susceptibility to herbivores (Ritchie *et al.* 1998). Trade-offs in a meta-community with heterogeneous local communities may not necessarily require explicit dispersal among patches. These examples point to a

potential explanation for high diversity: heterogeneity of local patches which results in different types of trade-offs required for coexistence among patches.

Regional-scale coexistence and trade-offs

When a system is spatially explicit, additional trade-offs can be incurred where space can also be partitioned (see reviews in Kareiva 1990; Tilman & Pacala 1993; Tilman & Kareiva 1997; Amarasekare 2003). Effectively, space increases the dimensionality of a community where interactions occur within local communities and differential dispersal or movement may occur among local communities (Fig. 1).

Competition-colonization

This trade-off holds that species differ in their ability to disperse to and colonize new habitats vs. their ability to compete once in a habitat; strong competitors are weaker colonizers (dispersers) and weak competitors are strong colonizers (dispersers; Hutchinson 1951; Skellam 1951; Levins & Culver 1971; Slatkin 1974; Armstrong 1976; Hastings 1980; Hanski 1983; Nee & May 1992; Tilman 1994; Kinzig *et al.* 1999; Yu & Wilson 2001; Chave *et al.* 2002; Levine & Rees 2002; Wang *et al.* 2002). Coexistence among the species then occurs at the regional scale. For species that show this trade-off, there must be a rate of extinction of the superior competitor species within patches that exceeds the rate of colonization and competitive exclusion of the inferior competitor. This allows the better colonizer to persist as a fugitive in those habitats where the superior competitor has recently gone extinct or not yet colonized. Although originally envisioned at a patch level, where entire populations of species have colonization and extinction probabilities (Levins & Culver 1971; Horn & MacArthur 1972), this trade-off has also been used to discuss coexistence at scales where patches consist of a single species, such as a sessile plant, that has a probability of establishing at a site and a probability of death at that site (Hastings 1980; Loreau & Mouquet 1999).

Dispersal ability is a difficult trait to measure as it occurs over large spatial and temporal scales. In theoretical studies, the better disperser arrives in empty patches by colonizing (1) more distant patches (Levins & Culver 1971; Holmes & Wilson 1998), or (2) new patches more quickly (Armstrong 1976; Tilman 1994). This may be achieved by occupying more patches in a region, producing numerous propagules, or having greater movement rates. The direct measurement of dispersal is for most organisms and systems a logistical nightmare. Consequently, empirical studies have used numerous surrogates for dispersal ability. Some have measured developmental and allocation strategies of individuals: early reproduction (Armstrong 1976), seed size and number (Turnbull *et al.* 1999), allocation to aboveground

tissue in plants (Gleeson & Tilman 1990), and development rate (Sevenster & van Alphen 1993). Other studies measure dispersal directly or indirectly by clonal spread (Brewer *et al.* 1998), distance (Rabinowitz & Rapp 1981; Lei & Hanski 1998), regional distribution (Hanski & Ranta 1983; Yu *et al.* 2001), propagule number (Marino 1991a,b), or arrival time at a patch (Bengtsson 1991; Marshall *et al.* 2000; Miller & Kneitel in press). These measures have their own biases, and multiple measurements should be considered when determining a species' colonization ability (Higgins & Cain 2002). In addition, colonization rates must be interpreted in the context of the temporal scale of competitive exclusion (Hanski 1983; Kneitel & Miller 2003) and the spatial movement of colonists (Higgins & Cain 2002).

Most studies do not find the competitive/dispersal ability trade-off, but instead find species' differences in habitat use (Marino 1991a,b; Harrison *et al.* 1995; Turnbull *et al.* 1999; Amarasekare 2000; Marshall *et al.* 2000; Yu *et al.* 2001). These cases (along with those with similar conclusions at the local scale) point to the potential importance of spatial heterogeneity for species coexistence in many communities (Levine & Rees 2002); care must be taken to understand the scale at which organisms disperse and interact with their environment. Finally, as there are many systems in which species interact and coexist at different scales, empirical studies need to examine the potential for species trade-offs at different scales.

The interaction between local and regional trade-offs

Where environments are heterogeneous and patchy, species can exhibit trade-offs in their ability to utilize local habitats and to exploit patches regionally. In these cases, the interaction between local and regional trade-offs can complicate patterns of coexistence. For example, Mouquet & Loreau (2002, 2003) have discussed a theoretical framework where organisms differ in their ability to utilize different habitat types and also in their ability to disperse among habitats. In this model, when dispersal rates are low, each species persists only in the habitat type in which they are favoured; local diversity is low (one per patch type), but regional diversity is high (equal to the number of patch types). With intermediate rates of dispersal, however, local diversity increases, because species are able to persist as sink populations in patches where they are unfavoured if they have migration from source populations where they are favoured. Finally, at the highest rates of dispersal, species that are better at colonizing empty patches can dominate and drive other species extinct, even though those species could persist in the local habitat in the absence of spatial effects.

Variation among habitat patches in the presence or absence of top predators can also create a situation where

local and regional trade-offs interact. Theoretically, the presence of a keystone predator can release the constraint that a competition–colonization trade-off is necessary for coexistence (Shurin & Allen 2001); also see Shurin (2001) for experimental results in support of this model with aquatic zooplankton. Similarly, an empirical study on protists that interact and coexist at different spatial scales in the water-filled leaves of pitcher-plants indicated that trade-offs at local and regional scales may both be exhibited, potentially allowing these organisms to coexist at both scales (Miller & Kneitel in press).

The scale at which coexistence occurs is more easily seen with certain trade-offs than others. Several types of trade-offs potentially allow coexistence at the local or regional scales. Although the colonization–extinction trade-off has been primarily discussed as a concept relevant to sessile organisms (e.g. trees), or organisms that live their entire lives within a patch, similar trade-offs have been discussed in the context of differential exploitation of patches by mobile organisms. Examples of these trade-offs include desert rodents, which have been classified as having a ‘cream-skimmer-crumble-picker’ trade-offs (Kotler & Brown 1988), and marine and freshwater snails, which have been classified to have a ‘digger-grazer’ trade-off (Wilson *et al.* 1999; Chase *et al.* 2001). In these examples, foragers trade-off the ability to find new patches (the cream-skimmer or grazer) with the ability to consume resources down to low levels once in a patch (the crumble-picker or digger), and qualitative patterns of coexistence are quite similar to that predicted from the colonization–extinction trade-off (similar trade-offs include milker–killer, van Ballen & Sabelis 1995; sitter–rover, Sokolowski 1980; gleaner–exploiter, Fredrickson & Stephanopoulos 1981).

A related trade-off occurs between species that differ in their ability to consume resources when resources are abundant vs. rare (Tilman & Pacala 1993; Tessier & Woodruff 2002). Thus, when resources are very abundant, as they would be in a previously unoccupied habitat or in recently created forest gaps awash with light, some species are superior competitors for this abundant resource (Pacala & Rees 1998; Bolker & Pacala 1999). These species have a set of traits that allow them to exploit very abundant

resources, such as steep functional responses. Other species, however, are more efficient at consuming resources when they are rare, and exhibit traits such as low metabolism and resource extraction efficiency. In such cases, the former species can occupy and outcompete the latter species early, but not late, in the successional process. Likewise, they can only coexist regionally because of variation in the abundance of resources and the time since colonization (Whittaker & Levin 1977). In many ways, this trade-off is mechanistically similar to the competition–colonization trade-off and even the predictions of *r*-*K* selection strategies (MacArthur & Wilson 1967; Pianka 1970). Finally, this sort of trade-off can allow two species to coexist on a single resource when their consumption of that resource causes it to cycle between high and low abundances (Armstrong & McGehee 1980; Huisman & Weissing 1999; Abrams & Holt 2002).

TRADE-OFFS AND PATTERNS OF DIVERSITY

The interaction between local and regional scale trade-offs are also reflected by a characteristic pattern of alpha (local) and beta (compositional turnover) diversity (Table 1; see also Mouquet & Loreau 2002, 2003). When trade-offs are primarily at the local scale, alpha diversity should be relatively high, because these trade-offs often promote local coexistence. Beta diversity, however, is expected to be low because there should be little turnover in species composition because coexistence is primarily at the local scale. Alternatively, when trade-offs are primarily at the regional scale, alpha diversity should be relatively low, as only the good competitors or good dispersers inhabit each locality. However, beta diversity should be relatively higher because there is turnover in species composition across patches that result from species differences in dispersal rates (homogeneous patches) or specialization (heterogeneous patches; Table 1). High beta diversity could also be produced if environmental conditions vary among different patches and different species are favoured under different environments. Finally, a combination of trade-offs at local and regional scales will produce coexistence at the local community scale (high alpha diversity) along with high turnover among patches (high beta diversity; Table 1).

Coexistence scale	Trade-off	Expected pattern of diversity		
		α	β	γ
Local	Resources, predator invulnerability, abiotic factors	High	Low	–
Regional	Homogeneous or heterogeneous local communities	Low	High	–
	Mixture (local and regional)	High	High	–

Table 1 Expected patterns of diversity resulting from the trade-offs that lead to coexistence. See text for specific information on trade-offs at different scales

A similar argument presented by Frank & Amarasekare (1998) predicted that an increase in dimensionality (number of resources available for specialization) would alter the types of traits that were expected, the scale at which dynamics were important, and the resulting pattern of diversity. As dimensionality increased, control of community dynamics was predicted to shift from local (competition) to regional (specialization and dispersal) processes. Furthermore, the patterns in diversity were predicted to shift from high local diversity to low local diversity with an increase in regional diversity because of specialization (trade-offs among patches; Frank & Amarasekare 1998). Thus, linking species traits with emergent coexistence patterns should be reflected in the diversity patterns at different spatial scales. These patterns merit further empirical and theoretical exploration.

Species can coexist at the local and regional scale by specializing on a specific habitat (Futuyma & Moreno 1988). Specialists, by definition, have highest fitness in a particular habitat and the trade-off is then exhibited across habitat types, whereas generalists do not exhibit trade-offs across habitat types (McPeck 1996; Caley & Munday 2003). However, within any given community type, trade-offs are required between the specialist and generalist for coexistence (Fig. 2). The expected composition of communities should then include coexistence of a habitat specialist and generalist whose identity can differ depending on the type of community (presence of different predators, resources, etc.; McPeck 1996). Therefore, coexistence at the local scale will occur between habitat generalists and specialists, while regional scale coexistence will occur between different habitat specialists and possibly generalists (Fig. 2).

Dispersal rates among patches can also play an important role in affecting patterns of alpha, beta and gamma (regional) diversity, interacting with local and regional

trade-offs (Loreau 2000; Kneitel & Miller 2003). For example, increasing connectedness among patches may decrease beta diversity and increase alpha diversity in certain situations (Loreau & Mouquet 1999; Mouquet & Loreau 2002, 2003); dispersal rates essentially shift the relative importance of local and regional scale trade-offs. However, the neutral theory (e.g. Hubbell 2001), which assumes no local or regional trade-offs, can predict similar patterns under varying rates of dispersal. Therefore, diversity variation cannot be used to determine the specific mechanisms of trade-offs that create patterns of coexistence in the absence of other information.

EVOLUTION OF TRADE-OFFS

The evolution of ecological traits in a community context has had a long and contentious history in ecology (e.g. Strong *et al.* 1984). In recent years, the evolution of trade-offs has been specifically addressed both theoretically and empirically (Futuyma & Moreno 1988; Bohannan & Lenski 2000a,b; Bohannan *et al.* 2002). Furthermore, understanding this in the context of community dynamics is one of the most difficult, but important challenges for community ecology (Bohannan & Lenski 2000a,b; Thompson *et al.* 2001; Bohannan *et al.* 2002; Tessier & Woodruff 2002).

Evidence for the evolution of trade-offs has come from a variety of studies in experimental microcosms. For example, there is good evidence for the evolution of the competitive ability-predator invulnerability trade-off in simple artificial communities using different genotypes of bacteria (Shikano *et al.* 1990; Nakajima & Kurihara 1994; Bohannan & Lenski 1999, 2000a,b), algae (Yoshida *et al.* 2003), and *Drosophila melanogaster* (Kraaijeveld & Godfray 1998). Mutations that lead to 'predator' resistance in these studies have come at the cost of their efficient use of resources. In addition, the bacterial studies have shown complex interactions and feedback between these traits and community dynamics.

Rainey and colleagues' (Rainey & Travisano 1998; Buckling *et al.* 2000; Kassen *et al.* 2000) studies on the bacteria *Pseudomonas* spp. have shown that in a spatially heterogeneous environment, different morphologies emerge that allow them to utilize different parts of the environment better. Although there is no specific evidence for trade-offs leading to these different morphologies, the indirect evidence is quite compelling; for example, the number of morphologies that emerge depend on the level of resources in the habitat (Kassen *et al.* 2000) and the degree of heterogeneity (Rainey & Travisano 1998; Buckling *et al.* 2000).

Another approach to the evolution of trade-offs in communities stems from a historical perspective (Ricklefs

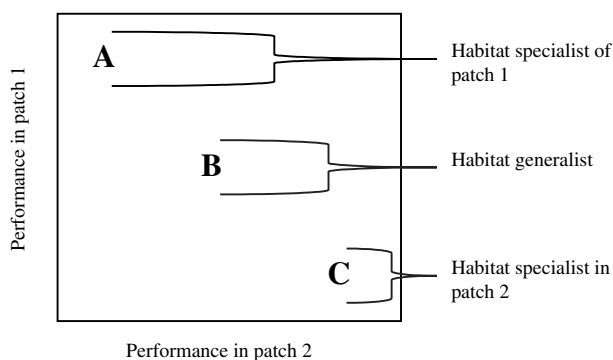


Figure 2 Species A–C ranked in their performances in two patch types. Species A and C are habitat specialists in having high fitness in a respective patch or trait, but poor performance of the other patch or trait. By comparison, species B is a generalist of both patches or traits.

1987; Webb *et al.* 2002; Losos *et al.* 2003). Advances in phylogenetic analyses have facilitated these new approaches to understanding patterns of diversity in communities (Losos 1996; McPeck & Brown 2000; Webb *et al.* 2002). One recent example, Silvertown *et al.* (1999) found trade-offs among plant species along moisture gradients in meadow communities. To better understand the nature of these trade-offs in structuring this community, Silvertown *et al.* (2001) calculated niche overlap among all 64 species and compared the pattern of overlap at different taxonomic levels to determine where niche differentiation occurred. Understanding contemporary trait differences of coexisting species within this larger phylogenetic framework will certainly contribute to a broader understanding of the role of evolution in niche differentiation in structuring communities (Webb *et al.* 2002; Losos *et al.* 2003).

The study of the evolution of trade-offs could be advanced along two fronts. First, simple systems can be further explored while increasing the complexity in community structure (Bohannan *et al.* 2002). This would most easily be performed in microcosm experiments where the interplay between species traits and community dynamics could be easily followed. Adding more competing species into these communities that are less related or different types of predators may expand our understanding of the emergence and maintenance of trade-offs. Secondly, the evolution of trade-offs needs to be explored further in natural communities that include different species. Much of the work in this field has been conducted on different genotypes of a species. Comparative approaches can also be used to examine differences in selection regimes in guilds of coexisting species.

CONCLUSIONS

Trade-offs among ecological traits at some spatial scale are a prerequisite for species coexistence in the majority of community ecology theories. In many ways, we are revisiting old questions when it comes to thinking about the trade-offs in community ecology as it relates to ecological niches (Chase & Leibold 2003, and Fig. 2). Our current understanding of communities has, in recent years, integrated processes at different spatial scales (e.g. Ricklefs & Schluter 1993; Tilman & Kareiva 1997). Further, alternative trade-off predictions have recently been proposed for empirically testing mechanisms of coexistence in a spatial community (Amarasekare 2003). We have argued that this momentum should also extend to linking species traits to diversity patterns by examining the trade-offs that lead to coexistence at local (e.g. Tilman 1982; Leibold 1996) and regional scales (e.g. Levins & Culver 1971; Slatkin 1974; Tilman 1994).

Hubbell (2001) has challenged the view that niche differences are important for understanding broad patterns of species diversity and relative abundance (see also Bell 2001). Although quite contentious (Abrams 2001; Enquist *et al.* 2002; Whitfield 2002; Norris 2003), Hubbell's neutral model has achieved some success in a variety of systems (Hubbell 1979; Hubbell *et al.* 1999; Bell 2001; Hubbell 2001; Volkov *et al.* 2003), but less success in other systems (Condit *et al.* 2002; McGill 2003; Tuomisto *et al.* 2003). One of the primary motivations for Hubbell's neutral model was because of the perception that there is too much diversity in many natural systems (particularly tropical forests) to be explained by traditional equilibrial models of niche differences and trade-offs.

In an attempt to reconcile niche and neutral theories, Hubbell (2001) proposed that trade-offs among species could be the very mechanism that leads to fitness equality under neutral dynamics. This is because life-history trade-offs (e.g. growth vs. survival) act to make all organisms fitness' approximately the same in a given environment. However, for long-term coexistence, two processes are required: equalizing and stabilizing effects (Chesson 2000). Hubbell is right that life-history trade-offs, which are characteristic of niche models, can lead to equalizing effects. However, the types of trade-offs that we have discussed here and the differences in the scale at which they are manifested, lead to stabilizing effects (e.g. density and frequency dependence). These stabilizing effects allow species to coexist in the long term, whereas all but one species will eventually go on a random walk to extinction if just equalizing effects are present (Chesson 2000).

In contrast to Hubbell's neutral theory, we argue that species traits are meaningful relative to its environmental context, and that these differences along with habitat heterogeneity can explain patterns of diversity; the evidence for habitat segregation and changes in relative abundance among species are clear in numerous systems (e.g. Kotler & Brown 1988; Wellborn *et al.* 1996; McPeck 1998). When trade-offs are considered in an explicitly spatial context (both local and regional trade-offs as well as their interactions), many more species can coexist locally and regionally than predicted from the classical niche theory that was based on local species interactions (e.g. Gause 1934; Levin 1970). Furthermore, recent analyses based on trade-offs, including colonization-competition dynamics (Chave *et al.* 2002) and source-sink interactions (Mouquet & Loreau 2003), as well more generalized models of species interactions (Wilson *et al.* 2003), can provide predictions nearly indistinguishable from those predicted by the neutral theory. Placing these theoretical predictions into a spatial framework will provide insight into the scale or scales of coexistence, as well as to compare among the various

mechanisms that create and maintain species diversity and composition in communities.

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REFERENCES

- Abrams, P.A. (1999). Is predator mediated coexistence possible in unstable systems? *Ecology*, 80, 608–621.
- Abrams, P.A. (2001). A world without competition. *Nature*, 412, 858–859.
- Abrams, P.A. & Holt, R.D. (2002). The impact of consumer-resource cycles on the coexistence of competitors. *Theor. Pop. Biol.*, 62, 281–295.
- Amarasekare, P. (2000). Coexistence of competing parasitoids on a patchily distributed host: local vs. spatial mechanisms. *Ecology*, 81, 1286–1296.
- Amarasekare, P. (2003). Competitive coexistence in spatially structured environments: a synthesis. *Ecol. Lett.*, 6, online publication.
- Amarasekare, P. & Nisbet, R.M. (2001). Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. *Am. Nat.*, 158, 572–584.
- Armstrong, R.A. (1976). Fugitive species: experiments with fungi and some theoretical considerations. *Ecology*, 57, 953–963.
- Armstrong, R.A. (1979). Prey species replacement along a gradient of nutrient enrichment: a graphical approach. *Ecology*, 60, 76–84.
- Armstrong, R.A. & McGehee, R. (1980). Competitive exclusion. *Am. Nat.*, 115, 151–170.
- Balciunas, D. & Lawler, S.P. (1995). Effects of basal resources, predation, and alternative prey in microcosm food chains. *Ecology*, 76, 1327–1336.
- Baldwin, I.T. & Hamilton, W. (2000). Jasmonate-induced responses of *Nicotiana sylvestris* results in fitness costs due to impaired competitive ability for nitrogen. *J. Chem. Ecol.*, 26, 915–952.
- van Ballen, M. & Sabelis, M.W. (1995). The milker-killer dilemma in spatially structured predator-prey interactions. *Oikos*, 74, 391–400.
- Bell, G. (2001). Neutral macroecology. *Science*, 293, 2413–2418.
- Bengtsson, J. (1991). Interspecific competition in metapopulations. *Biol. J. Linn. Soc.*, 42, 219–237.
- Bestelmeyer, B.T. (2000). The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. *J. Anim. Ecol.*, 69, 998–1009.
- Bohannan, B.J.M. & Lenski, R.E. (1999). Effect of prey heterogeneity on the response of a model food chain to resource enrichment. *Am. Nat.*, 153, 73–82.
- Bohannan, B.J.M. & Lenski, R.E. (2000a). The relative importance of competition and predation varies with productivity in a model community. *Am. Nat.*, 156, 329–340.
- Bohannan, B.J.M. & Lenski, R.E. (2000b). Linking genetic change to community evolution: insights from studies of bacteria and bacteriophage. *Ecol. Lett.*, 3, 362–377.
- Bohannan, B.J.M., Kerr, B., Jessup, C.M., Hughes, J.B. & Sandvik, G. (2002). Trade-offs and coexistence in microbial microcosms. *Annot. van Leeuw.*, 81, 107–115.
- Bolker, B.M. & Pacala, S.W. (1999). Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *Am. Nat.*, 153, 575–602.
- Boyce, M.S. (1984). Restitution of r- and K-selection as a model of density-dependent natural selection. *Ann. Rev. Ecol. Syst.*, 15, 427–447.
- Brewer, J.S., Rand, T., Levine, J.M. & Bertness, M.D. (1998). Biomass allocation, clonal dispersal, and competitive success in three salt marsh plants. *Oikos*, 82, 347–353.
- Brooks, J.L. & Dodson, S.I. (1965). Predation, body size and composition of plankton. *Science*, 150, 28–35.
- Brown, J.H. & Davidson, D.W. (1977). Competition between seed-eating rodents and ants in desert ecosystems. *Science*, 196, 880–882.
- Buckling, A., Kassen, R., Bell, G. & Rainey, P.B. (2000). Disturbance and diversity in experimental microcosms. *Nature*, 408, 961–964.
- Caceres, C.E. (1997). Temporal variation, dormancy, and coexistence: A field test of the storage effect. *Proc. Natl. Acad. Sci. USA*, 94, 9171–9175.
- Caley, M.J. & Munday, P.L. (2003). Growth rates trade off with habitat specialization. *Proc. R. Soc. Lond. B Biol. Sci.*, 270, 175–177.
- Carson, W.P. & Root, R.B. (2000). Herbivory and plant species coexistence: community regulation by an outbreeding phytophagous insect. *Ecol. Monogr.*, 70, 73–99.
- Caswell, H. (1978). Predator-mediated coexistence: a nonequilibrium model. *Am. Nat.*, 112, 127–154.
- Chase, J.M. (2003). Strong and weak trophic cascades along a productivity gradient. *Oikos*, 101, 187–195.
- Chase, J.M. & Leibold, M.A. (2003). *Ecological niches*. University of Chicago Press, Chicago, IL.
- Chase, J.M., Leibold, M.A. & Simms, E. (2000a). Plant tolerance and resistance in food webs: community-level predictions and evolutionary implications. *Evol. Ecol.*, 14, 289–314.
- Chase, J.M., Leibold, M.A., Downing, A.L. & Shurin, J.B. (2000b). The effects of productivity, herbivory, and plant species turnover in grassland food webs. *Ecology*, 81, 2485–2497.
- Chase, J.M., Wilson, W.G. & Richards, S.A. (2001). Foraging trade-offs and resource patchiness: theory and experiments with a freshwater snail community. *Ecol. Lett.*, 4, 304–312.
- Chase, J.M., Abrams, P.A., Grover, J.P., Diehl, S., Chesson, P., Holt, R.D. *et al.* (2002). The interaction between predation and competition: a review and synthesis. *Ecol. Lett.*, 5, 302–315.
- Chave, J., Muller-Landau, H.C. & Levin, S.A. (2002). Comparing classical community models: theoretical consequences for patterns of diversity. *Am. Nat.*, 159, 1–23.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Ann. Rev. Ecol. Syst.*, 31, 343–366.
- Chesson, P. & Huntly, N. (1997). The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am. Nat.*, 150, 519–553.
- Chesson, P. & Warner, R.R. (1981). Environmental variability promotes coexistence in lottery competitive systems. *Am. Nat.*, 117, 923–943.

- Condit, R., Pitman, N., Leigh, E.G., Jr, Chave, J., Terborgh, J., Foster, R.B. *et al.* (2002). Beta-diversity in tropical forest trees. *Science*, 295, 666–669.
- Connell, J.H. (1961). The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*, 42, 710–723.
- Cornell, H.V. & Lawton, J.H. (1992). Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *J. Anim. Ecol.*, 61, 1–12.
- Dunson, W.A. & Travis, J. (1990). The role of abiotic factors in community organization. *Am. Nat.*, 138, 1067–1091.
- Enquist, B.J., Haskell, J.P. & Tiffney, B.H. (2002). General patterns of taxonomic and biomass partitioning in extant and fossil plant communities. *Nature*, 419, 610–613.
- Frank, S.A. & Amarasekare, P. (1998). Increasing resource specialization among competitors shifts control of diversity from local to spatial processes. *Ecol. Lett.*, 1, 3–5.
- Fredrickson, A.G. & Stephanopoulos, G. (1981). Microbial competition. *Science*, 213, 972–979.
- Fritz, R.S. & Simms, E.L. (1992). *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics*. University of Chicago Press, Chicago, IL.
- Futuyma, D.J. & Moreno, G. (1988). The evolution of ecological specialization. *Ann. Rev. Ecol. Syst.*, 19, 207–233.
- Gause, G.F. (1934). *The Struggle for Existence*. Williams and Wilkins, Baltimore.
- Gleeson, S.K. & Tilman, D. (1990). Allocation and the transient dynamics of succession on poor soils. *Ecology*, 71, 1144–1155.
- Grime, J.P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.*, 111, 1169–1194.
- Grover, J.P. (1997). *Resource Competition*. Chapman and Hall, London.
- Hanski, I. (1983). Coexistence of competitors in patchy environment. *Ecology*, 64, 493–500.
- Hanski, I. & Ranta, E. (1983). Coexistence in a patchy environment: three species of *Daphnia* in rock pools. *J. Anim. Ecol.*, 52, 263–279.
- Harrison, S., Thomas, C.D. & Lewinsohn, T.M. (1995). Testing a metapopulation model of coexistence in the insect community on ragwort (*Senecio jacobaea*). *Am. Nat.*, 145, 546–562.
- Hastings, A. (1980). Disturbance, coexistence, history, and competition for space. *Theor. Popul. Biol.*, 18, 363–373.
- Higgins, S.I. & Cain, M.L. (2002). Spatially realistic plant metapopulation models and the colonization-competition trade-off. *J. Ecol.*, 90, 616–626.
- Holmes, E.E. & Wilson, H.B. (1998). Running from trouble: long-distance dispersal and the competitive coexistence of inferior species. *Am. Nat.*, 151, 578–586.
- Holt, R.D., Grover, J. & Tilman, D. (1994). Simple rules for interspecific dominance in systems with exploitative and apparent competition. *Am. Nat.*, 144, 741–777.
- Horn, H.S. & MacArthur, R.H. (1972). Competition among fugitive species in a harlequin environment. *Ecology*, 53, 749–752.
- Hubbell, S.P. (1979). Tree dispersion, abundance and diversity in a tropical dry forest. *Science*, 203, 1299–1303.
- Hubbell, S.P. (2001). *The Unified Neutral Theory of Species Abundance and Diversity*. Princeton University Press, Princeton, NJ.
- Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B. *et al.* (1999). Disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science*, 283, 554–557.
- Huisman, J. & Weissing, F.J. (1999). Biodiversity of plankton by species oscillations. *Nature*, 402, 407–410.
- Hutchinson, G.E. (1951). Copepodology for the ornithologist. *Ecology*, 32, 571–577.
- Juliano, S.A., O'Meara, G.F., Morrill, J.R. & Cutwa, M.M. (2002). Desiccation and thermal tolerance of eggs and the coexistence of competing mosquitoes. *Oecologia*, 130, 458–469.
- Kareiva, P. (1990). Population dynamics in spatially complex environments: theory and data. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 330, 175–190.
- Kassen, R., Buckling, A., Bell, G. & Rainey, P.B. (2000). Diversity peaks at intermediate productivity in experimental microcosms. *Nature*, 406, 508–512.
- Kinzig, A.P., Levin, S.A., Dushoff, J. & Pacala, S. (1999). Limiting similarity, species packing, and system stability for hierarchical competition–colonization models. *Am. Nat.*, 153, 371–383.
- Kneitel, J.M. & Miller, T.E. (2003). Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. *Am. Nat.*, 162, 165–171.
- Kotler, B.P. & Brown, J.S. (1988). Environmental heterogeneity and the coexistence of desert rodents. *Ann. Rev. Ecol. Syst.*, 19, 281–307.
- Kraaijeveld, A.R. & Godfray, H.C.J. (1998). Trade-off between parasitoid resistance and larval competitive ability in *Drosophila melanogaster*. *Nature*, 389, 278–280.
- Lande, R. (1996). Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos*, 76, 5–13.
- Lei, G. & Hanski, I. (1998). Spatial dynamics of two competing specialist parasitoids in a host metapopulation. *J. Anim. Ecol.*, 67, 422–433.
- Leibold, M.A. (1989). Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *Am. Nat.*, 134, 922–949.
- Leibold, M.A. (1996). A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *Am. Nat.*, 147, 784–812.
- Leibold, M.A. (1999). Biodiversity and nutrient enrichment in pond plankton communities. *Evol. Ecol. Res.*, 1, 73–95.
- Levin, S.A. (1970). Community equilibria and stability, and an extension of the competitive exclusion principle. *Am. Nat.*, 104, 413–423.
- Levine, J.M. & Rees, M. (2002). Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. *Am. Nat.*, 160, 452–467.
- Levins, R. & Culver, D. (1971). Regional coexistence of species and competition between rare species. *Proc. Nat. Acad. Sci. USA*, 68, 1246–1248.
- Lewis, S.M. (1986). The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecol. Monogr.*, 56, 183–200.
- Loreau, M. (2000). Are communities saturated? On the relationship between α , β , and γ diversity. *Ecol. Lett.*, 3, 73–76.
- Loreau, M. & Mouquet, N. (1999). Immigration and the maintenance of local species diversity. *Am. Nat.*, 154, 427–440.
- Losos, J.B. (1996). Phylogenetic perspectives on community ecology. *Ecology*, 77, 1344–1354.

- Losos, J.B., Leal, M., Glor, R.E., de Queiroz, K., Hertz, P.E., Rodriguez Schettino, L. *et al.* (2003). Niche lability in the evolution of Caribbean lizard community. *Nature*, 424, 542–545.
- MacArthur, R.H. (1972). *Geographical Ecology*. Princeton University Press, Princeton, NJ.
- MacArthur, R.H. & Levins, R. (1964). Competition, habitat selection, and character displacement. *Proc. Nat. Acad. Sci. USA*, 51, 1207–1210.
- MacArthur, R.H. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- McGill, B.J. (2003). A test of the unified neutral theory of biodiversity. *Nature*, 422, 881–885.
- McPeck, M.A. (1996). Trade-offs, food web structure, and the coexistence of habitat specialists and generalists. *Am. Nat.*, 148, S124–S138.
- McPeck, M.A. (1998). The consequences of changing the top predator in a food web: a comparative experimental approach. *Ecol. Monogr.*, 68, 1–23.
- McPeck, M.A. & Brown, J.M. (2000). Building a regional species pool: diversification of the *Enallagma* damselflies in eastern North America. *Ecology*, 81, 904–920.
- Marino, P.C. (1991a). Competition between mosses (Splachnaceae) in patchy habitats. *J. Ecol.*, 79, 1031–1046.
- Marino, P.C. (1991b). Dispersal and coexistence of mosses (Splachnaceae) in patchy habitats. *J. Ecol.*, 79, 1047–1060.
- Marshall, S.D., Walker, S.E. & Rypstra, A.L. (2000). A test for a differential colonization and competitive ability in two generalist predators. *Ecology*, 81, 3341–3349.
- Miller, T.E. & Kneitel, J.M. (in press). Inquiline communities in pitcher-plants as a prototypical metacommunity. In: *Metacommunities* (eds Holyoak, M., Holt, R. & Leibold, M.). University of Chicago Press, Chicago, IL.
- Morin, P.J. (1983). Predation, competition, and composition of larval anuran guilds. *Ecol. Monogr.*, 53, 119–138.
- Mouquet, N. & Loreau, M. (2002). Coexistence in metacommunities: the regional similarity hypothesis. *Am. Nat.*, 159, 420–426.
- Mouquet, N. & Loreau, M. (2003). Community patterns in source-sink metacommunities. *Am. Nat.*, 162, 544–557.
- Mouquet, N., Hoopes, M.F. & Amarasekare, P. (in press). The world is patchy and heterogeneous! Trade-off dynamics in competitive metacommunities. In: *Metacommunities* (eds Holyoak, M., Holt, R. & Leibold, M.). University of Chicago Press, Chicago, IL.
- Nakajima, T. & Kurihara, Y. (1994). Evolutionary changes of ecological traits of bacterial populations through predator-mediated competition. 1. Experimental analysis. *Oikos*, 71, 24–34.
- Nee, S. & May, R.M. (1992). Dynamics of metapopulations: habitat destruction and competitive coexistence. *J. Anim. Ecol.*, 61, 37–40.
- Norris, S. (2003). Neutral theory: a new, unified model for ecology. *Bioscience*, 53, 124–129.
- Pacala, S.W. & Rees, M. (1998). Models suggesting field experiments to test two hypotheses explaining successional diversity. *Am. Nat.*, 152, 729–737.
- Paine, R.T. (1966). Food web complexity and species diversity. *Am. Nat.*, 100, 65–75.
- Pake, C.E. & Venable, D.L. (1995). Is coexistence in Sonoran desert annuals mediated by temporal variability in reproductive success? *Ecology*, 76, 246–261.
- Pake, C.E. & Venable, D.L. (1996). Seed banks in desert annuals: Implications for persistence and coexistence in a variable environment? *Ecology*, 77, 1427–1435.
- Peacor, S.D. & Werner, E.E. (2001). The contribution of trait-mediated indirect effects to the net effects of a predator. *Proc. Nat. Acad. Sci. USA*, 98, 3904–3908.
- Petraitis, P.S., Latham, R.E. & Niesenbaum, R.A. (1989). The maintenance of species diversity by disturbance. *Quart. Rev. Biol.*, 64, 393–418.
- Pianka, E.R. (1970). On r- and K-selection. *Am. Nat.*, 104, 592–597.
- Rabinowitz, D.A. & Rapp, J.K. (1981). Dispersal abilities of seven sparse and common grasses from a Missouri prairie. *Am. J. Bot.*, 68, 616–624.
- Rainey, P.B. & Travisano, M. (1998). Adaptive radiation in a heterogeneous environment. *Nature*, 394, 69–72.
- Ricklefs, R.E. (1987). Community diversity: relative roles of local and regional processes. *Science*, 235, 161–171.
- Ricklefs, R.E. & Schluter, D. (1993). *Species Diversity in Ecological Communities*. The University of Chicago Press, Chicago, IL.
- Ritchie, M.E., Tilman, D. & Knops, J.M.H. (1998). Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology*, 79, 165–177.
- Rothhaupt, K.O. (1988). Mechanistic resource competition theory applied to laboratory experiments with zooplankton. *Nature*, 333, 660–662.
- Schmitz, O.J. (1998). Direct and indirect effects of predation and predation risk in old-field interaction webs. *Am. Nat.*, 151, 327–342.
- Sevenster, J.G. & van Alphen, J.J.M. (1993). A life history trade-off in *Drosophila* species and community structure in variable environments. *J. Anim. Ecol.*, 62, 720–736.
- Shikano, S., Luckinbill, L.S. & Kurchara, G. (1990). Changes of traits in a bacterial population associated with protozoa predation. *Microb. Ecol.*, 20, 75–84.
- Shurin, J.B. (2001). Interactive effects of predation and dispersal on zooplankton communities. *Ecology*, 82, 3404–3416.
- Shurin, J.B. & Allen, E.G. (2001). Effects of competition, predation, and dispersal on species richness at local and regional scales. *Am. Nat.*, 158, 624–637.
- Silvertown, J., Dodd, M.E., Gowing, D. & Mountford, O. (1999). Hydrologically-defined niches reveal a basis for species-richness in plant communities. *Nature*, 400, 61–63.
- Silvertown, J., Dodd, M. & Gowing, D. (2001). Phylogeny and the niche structure of meadow plant communities. *J. Ecology*, 89, 428–435.
- Simberloff, D. (1983). Competition theory, hypothesis-testing, and other community ecological buzzwords. *Am. Nat.*, 122, 626–635.
- Skellam, J.G. (1951). Random dispersal in theoretical populations. *Biometrika*, 38, 196–218.
- Slatkin, M. (1974). Competition and regional coexistence. *Ecology*, 55, 128–134.
- Sokolowski, M.B. (1980). Foraging strategies of *Drosophila melanogaster*: a chromosomal analysis. *Behav. Genet.*, 10, 291–302.
- Sommer, U. (1985). Comparison between steady state and non-steady state competition: experiments with natural phytoplankton. *Limnol. Oceanogr.*, 30, 335–346.
- Sommer, U. (1993). Phytoplankton competition in Pluß see: a field test of the resource-ratio hypothesis. *Limnol. Oceanogr.*, 38, 838–845.

- Sommer, U. (1994). The impact of light intensity and daylength on silicate and nitrate competition among marine phytoplankton. *Limnol. Oceanogr.*, 39, 1680–1688.
- Stearns, S.C. (1989). Trade-offs in life-history evolution. *Funct. Ecol.*, 3, 259–268.
- Steiner, C.F. (2003). Keystone predator effects and grazer control of planktonic primary production. *Oikos*, 101, 569–577.
- Strauss, S.Y. & Agrawal, A.A. (1999). The ecology and evolution of plant tolerance to herbivory. *Trends Ecol. Evol.*, 14, 179–185.
- Strong, D.R., Simberloff, D., Abele, L.G. & Thistle, A.B. (1984). *Ecological Communities: Conceptual Issues and the Evidence*. Princeton University Press, Princeton, NJ.
- Tessier, A.J. & Woodruff, P. (2002). Trading off the ability to exploit rich versus poor food quality. *Ecol. Lett.*, 5, 685–692.
- Thompson, J.N., Reichman, O.J., Morin, P.J., Polis, G.A., Power, M.E., Sterner, R.W. *et al.* (2001). Frontiers of Ecology. *BioScience*, 51, 15–24.
- Tiffin, P. (2000). Are tolerance, avoidance, and antibiosis evolutionarily and ecologically equivalent responses of plants to herbivores? *Am. Nat.*, 155, 128–138.
- Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.
- Tilman, D. (1988). *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, NJ.
- Tilman, D. (1990). Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos*, 58, 3–15.
- Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, 75, 2–16.
- Tilman, D. (2000). Causes, consequences and ethics of biodiversity. *Nature*, 405, 208–211.
- Tilman, D. & Kareiva, P. (1997). *Spatial Ecology*. Princeton University Press, Princeton, NJ.
- Tilman, D. & Pacala, S. (1993). The maintenance of species richness in plant communities. In: *Species Diversity in Ecological Communities* (eds Ricklefs, R.E. & Schluter, D.). University of Chicago Press, Chicago, IL, pp. 13–25.
- Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. (2003). Dispersal, environment, and floristic variation of western Amazonian forests. *Science*, 299, 2414–2444.
- Turnbull, L.A., Rees, M. & Crawley, M.J. (1999). Seed mass and the competition/colonization trade-off: a sowing experiment. *J. Ecol.*, 87, 899–912.
- Uriarte, M., Canham, C.D. & Root, R.B. (2002). A model of simultaneous evolution of competitive ability and herbivore resistance in a perennial plant. *Ecology*, 83, 2649–2663.
- Vance, R.R. (1978). Predation and resource partitioning in one predator-two prey model communities. *Am. Nat.*, 112, 797–813.
- Vincent, T.L.S., Scheel, D., Brown, J.S. & Vincent, T.L. (1996). Trade-offs and coexistence in consumer-resource models: it all depends on what and where you eat. *Am. Nat.*, 148, 1038–1058.
- Volkov, I., Banavar, J.R., Hubbell, S.P. & Maritan, A. (2003). Neutral theory and relative species abundance in ecology. *Nature*, 424, 1035–1037.
- Wang, Z.-L., Wang, F.-Z., Chen, S. & Zhu, M.-Y. (2002). Competition and coexistence in regional habitats. *Am. Nat.*, 159, 498–508.
- Warner, R.R. & Chesson, P.L. (1985). Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *Am. Nat.*, 125, 769–787.
- Webb, C.O., Ackerly, D.A., McPeck, M.A. & Donoghue, M.J. (2002). Phylogenies and community ecology. *Ann. Rev. Ecol. Syst.*, 33, 475–505.
- Wedin, D.A. & Tilman, D. (1993). Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. *Ecol. Monogr.*, 63, 199–229.
- Wellborn, G.A., Skelly, D.K. & Werner, E.E. (1996). Mechanisms creating community structure across a freshwater habitat gradient. *Ann. Rev. Ecol. Syst.*, 27, 337–363.
- Werner, P.A. & Platt, W.J. (1976). Ecological relationships of co-occurring goldenrods (Soldiogo: Compositae). *Am. Nat.*, 110, 959–971.
- Whitfield, J. (2002). Ecology: neutrality versus the niche. *Nature*, 417, 480–481.
- Whittaker, R.H. (1972). Evolution and measurement of species diversity. *Taxon*, 21, 213–251.
- Whittaker, R.H. & Levin, S.A. (1977). The role of mosaic phenomenon in natural communities. *Theor. Popul. Biol.*, 12, 117–139.
- Wilson, D.S. (1992). Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology*, 73, 1984–2000.
- Wilson, W.G., Osenberg, C.W., Schmitt, R.J. & Nisbet, R. (1999). Complementary foraging behavior allows coexistence of two grazers. *Ecology*, 80, 2358–2372.
- Wilson, W.G., Lundberg, P., Vázquez, D.P., Shurin, J.B., Smith, M.D., Langford, W. *et al.* (2003). Biodiversity and species interactions: extending Lotka-Volterra community theory. *Ecol. Lett.*, 6, 944–952.
- Yoshida, T., Jones, L.E., Ellner, S.P., Fussmann, G.F., Hairston, N.G. (2003). Rapid evolution drives ecological dynamics in a predator-prey system. *Nature*, 424, 303–306.
- Yu, D. & Wilson, H.B. (2001). The competition–colonization trade-off is dead; long live the competition–colonization trade-off. *Am. Nat.*, 158, 49–63.
- Yu, D.W., Wilson, H.B. & Pierce, N.E. (2001). An empirical model of species coexistence in a spatially structured environment. *Ecology*, 82, 1761–1771.
- Zera, A.J. & Harshman, L.G. (2001). The physiology of life history trade-offs in animals. *Ann. Rev. Ecol. Syst.*, 32, 95–126.

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