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When can competition for resources lead to ecological equivalence?

Casey P. terHorst, Thomas E. Miller and Eric Powell

Department of Biological Science, Florida State University,
Tallahassee, Florida, USA

ABSTRACT

Question: Under what conditions do species using distinct niches evolve and converge to become ecologically equivalent? Does evolution in a community context affect functional group diversity?

Mathematical methods: We simulated the population dynamics and evolution of multiple species competing for discrete, substitutable resources.

Key assumptions: Species' competitive effect and response are based on resource-use overlap. Evolution occurs via selection on mutations of small effect. Intraspecific genetic variation is the same for each species.

Predictions: Evolution of equivalence is possible when species evolve in a community context. A combination of convergence, divergence, and extinctions occurs when the number of species exceeds the number of resources. Species avoid competitive exclusion via convergence or divergence in their resource use. Ecological and evolutionary outcomes depend on an interaction between the rate of evolution and the initial similarity of competitors. The evolution of equivalence determines diversity within functional groups, but niche processes drive diversity among groups.

Keywords: character displacement, competitive exclusion, evolution, evolvability, extinction, functional groups, neutral theory, niche partitioning, theoretical.

INTRODUCTION

Niche partitioning and character displacement have served as the foundation for most theories of biodiversity and are thought to occur in response to competition for limited resources (Chase and Leibold, 2003; Clark *et al.*, 2007). However, niche partitioning alone is often insufficient to explain the high diversity found in many natural systems, where the number of species greatly exceeds the number of limiting resources (McPeek and Brown, 2000; Hubbell, 2001). A more recent concept, the neutral theory of biodiversity, posits that if species use similar resources and are ecologically equivalent, niche partitioning is unnecessary to explain

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Correspondence: C.P. terHorst, W.K. Kellogg Biological Station, Michigan State University, 3700 E. Gull Lake Drive, Hickory Corners, MI 49060, USA. e-mail: casey.terhorst@kbs.msu.edu

patterns of diversity – species co-exist because their similarity precludes competitive dominance (Bell, 2000; Hubbell, 2001).

Evidence of ecologically equivalent species has been found in a variety of systems. Several communities contain complexes of closely related species that are so similar in morphology and ecological roles that they are difficult to distinguish from one another (e.g. Hubbell, 1979; Witt *et al.*, 2003; Siepielski *et al.*, 2010). For example, *Enallagma* damselfly species appear to have diverged via sexual selection and are distinguished only by their reproductive structures (McPeek *et al.*, 2009). Species within this genus are equally adept at avoiding predators and acquiring resources and co-exist within lakes with fish predators (Siepielski *et al.*, 2010). Plant competition experiments have also demonstrated that species can have equivalent competitive effects on other species (e.g. Aarssen and Turkington, 1985; Goldberg and Fleetwood, 1987; Peart, 1989). Furthermore, biologists often lump species into functional groups based on morphological similarities (e.g. Steneck and Dethier, 1994) or similar ecological roles in the community (e.g. Petchey and Gaston, 2002), which suggests co-existence of multiple species within the same niche. For instance, ecologically equivalent *Enallagma* damselflies form one functional group, but a suite of *Ischnura* damselfly species are competitively dominant, but easily consumed by fish, and form a second functional group found only in fishless lakes (McPeek, 1998).

Despite its simplicity and modest empirical support, neutral theory remains divisive for two reasons: (1) literature from the past several decades is rife with evidence for significant niche differences between species (Chase and Leibold, 2003), and (2) there is little theory to explain the origin or maintenance of species equivalence over evolutionary time (but see Hubbell, 2006; Scheffer and van Nes, 2006). One way that ecological equivalence may arise is via convergent evolution. Ecologists have developed significant theory on evolutionary divergence [e.g. character displacement (see Taper and Case, 1992)], but until recently have had little interest in evolutionary convergence (but see MacArthur and Levins, 1967; Abrams, 1987). Fox and Vasseur (2008) used a mathematical model to demonstrate that species competing for essential (i.e. non-substitutable) resources may converge, resulting in more similar, but not ecologically equivalent, species (see also Abrams, 1987). However, both plants and animals frequently compete for substitutable resources and arguments for niche partitioning are largely based on competition for such resources. Plants compete for substitutable resources, such as different depths of soil, light levels in different parts of a forest canopy or time (e.g. different phenologies), while animals compete for substitutable resources in the form of different food types or food available at different times or locations.

Hubbell's (2006) simple verbal model suggests that species competing for substitutable resources might converge in their resource use, resulting in equivalent species. Scheffer and van Nes (2006) used a simulation model to follow the evolution of species along a single continuous resource axis. Convergence in their model requires a large number of species ($n = 200$) with a high degree of initial resource overlap (Fort *et al.*, 2010). Natural communities may be composed of many competing species but it is unlikely that all species compete solely for a single resource with such high species packing, as natural communities are generally dominated by a few strong and many weak interactions (Paine, 1992; Polis, 1994). Re-evaluation of the original model of Scheffer and van Nes (2006) shows that it leads to divergence, rather than convergence, when initial niche overlap is lower (Fort *et al.*, 2010; T.E. Miller, unpublished simulations).

We suggest that attention should now turn to when, rather than if, niche or neutral processes operate, to determine the conditions under which evolutionary convergence occurs. We investigated the conditions under which competing species evolved to converge in their niche use or diverged to utilize distinct niches, using a simulation model to investigate the simultaneous evolution and population dynamics of multiple species competing for discrete, substitutable resources. Each species was allowed to evolve its resource use to maximize its population growth rate, thus decreasing the probability of its extinction. A focal species could decrease competition with an associate species by evolving to minimize resource overlap with the associate species (i.e. niche divergence) (MacArthur and Levins, 1967). Alternatively, the focal species could evolve to use the same resources as the associate species (i.e. niche convergence), thereby decreasing the difference in relative competitive ability between an associate species and itself and increasing the likelihood of co-existence (Aarssen, 1983; Abrams, 1998).

A MODEL OF EVOLUTION IN A COMMUNITY CONTEXT

Ecological effects

We created a computer simulation to construct communities of n species competing for two substitutable resources [the R code for this simulation is available at http://bio.fsu.edu/~miller/HOMEPAGE (R Development Core Team, 2009)]. The basic form of the competition and population growth components of the model were similar to the models of Case (1990, 1991). We modelled the population growth and ecological interactions of each species as a discrete approximation of the continuous Lotka-Volterra competition equation:

$$N_{i,t+1} = N_{i,t}\left[1 + r\left(1 - \frac{\sum_{j=1}^{S} a_{ij}N_{j,t}}{K}\right)\right], \tag{1}$$

where $N_{i,t}$ is the abundance of species i at time t; $N_{j,t}$ is the abundance of any competing species j at time t; r and K are the intrinsic growth rate and the carrying capacity for each species respectively; S is the number of competing species; and a_{ij} is the per capita effect of species j on species i. Species with greater resource overlap had higher interaction coefficients. We let $\mathbf{A}$ denote the community matrix, composed of elements a_{ij}. For simplicity, we set r and K identically for all species ($r = 0.5$, $K = 500$) and sufficient to avoid chaotic population dynamics. The equilibrium states in this equation do not depend on the value of r (Case, 2000).

The competitive interaction strengths a_{ij} are determined by pairwise resource overlap (Levins, 1968; Case, 1990, 1991). We let u_{ij} denote the use of resource i by species j. This is a number between 0 and 10, but we constrained the total resource use of each species to exactly 10 resource units. We let $\mathbf{U}$ denote the matrix with elements u_{ij}. We assigned or randomly chose the initial resource use of each species (u_{ij}), depending on the set of simulations (see below).

The niche width of each competitor is determined by

$$w_{jj} = \frac{1}{\sum_i u_{ij}^2}\,. \tag{2}$$

We let $\mathbf{W}$ denote the diagonal matrix created from equation (2).

According to Levins (1968), we defined interaction strengths as

$$\mathbf{A} = \mathbf{U}\mathbf{U}^{\mathrm{T}}\mathbf{W}. \tag{3}$$

Evolutionary effects

We adapted this basic ecological model of population growth and species interactions to allow species to evolve their resource use (u_{ij}) so as to alter competitive effect and response (a_{ij}) in each generation to maximize population growth rate. We created genetic variation in resource use in each population and selected for the variant with the highest fitness to create evolution in resource use and competitive ability. In each generation, we introduced genetic variation in resource use by increasing or decreasing the resource use of each species by a small amount (δ), which represents the evolvability of resource use (*sensu* Houle, 1992), where the variants represent the centre and the extremes of genetic diversity in the population:

$$u'_{ij} = u_{ij} \pm \delta. \tag{4}$$

With only two resources, this created three variants for each species in each generation (an increase of δ in the use of resource 1, a decrease of δ in the use of resource 1, no change in either resource). Since we constrained total resource use to a constant value (10), trade-offs were inherent; an increase of δ in the use of resource 1 necessitated a decrease of δ in the use of resource 2:

$$\textstyle\sum_{i=1}^{n} u_i = 10. \tag{5}$$

For each variant, we converted a $\mathbf{U}'$ matrix with the variant u'_{ij} into an $\mathbf{A}'$ matrix and used the a'_{ij} elements to calculate the population growth of the variant, using equation (1). We compared the population growth rates of all variant u'_{ij} within a species (including the variant of no change in resource use) and selected the variant u'_{ij} with the highest population growth rate as the new u_{ij} in the next generation, with all other variants going extinct. If all variants produced identical growth rates, resource use remained the same in the next generation. In additional simulations, we resolved these ties by choosing one variant at random, but we found no qualitative effect in simulations with more than one species. This selection on the underlying variation in resource use resulted in evolution of the $\mathbf{U}$ matrix, and consequently the $\mathbf{A}$ matrix and the a_{ij} elements, over time in each simulation, until the community reached a stable state with no further change in the matrices. Co-evolutionarily stable community models have been criticized for assuming that there is no intraspecific frequency-dependent selection, which can result in problematic results when species interactions are asymmetric (Taper and Case, 1992). However, our use of a resource use matrix ($\mathbf{U}$) results in nearly symmetric interaction coefficients and we feel that this serves as a good first-order model.

Model simulations

We followed the evolution of up to eight competing species, although we were particularly interested in the three-species scenario, where the number of competing species becomes greater than the number of resources. In the first set of simulations, we followed the evolution of three species (A, B, C) competing for two resources (1 and 2). Each simulation tracked the fate of each of the three species as a function of varying combinations of two independent variables: the evolvability of resource use (δ) and the initial strength of competition (a_{ij}). Evolvability was varied among simulations by a change of between 0.001 and 0.1 resource units per generation, but was the same for all species within a simulation. We varied the strength of competition by varying the initial resource use of one species. The initial resource use of species A and B was 10 and 8 units of resource 1 (i.e. 0 and 2 units of resource 2), respectively. We varied the initial resource use of species C among simulations by 0.01 resource units across the range of 0 to 10 units of each resource. When the initial use of resource 1 by species C was low, competition was relatively weak, but increased with the initial resource use of resource 1 by species C. There were two possible outcomes of this iterative evolution process: extinction of at least one species and co-existence of the remaining species on separate resources, or co-existence of all three species, requiring both convergence and divergence and co-existence of at least two species sharing the same resource. Each simulation encompassed 1000 generations, by which time all species had reached a steady state of both resource use and population abundance. At the steady state, the no-change variant in the evolutionary process consistently produced the highest population growth rate, resulting in no further evolutionary change.

In a second set of simulations, we also followed the evolution of more diverse communities. We varied the number of species in each community from two to eight species. We randomly determined the initial resource use of each species. We used an intermediate level of evolvability ($\delta = 0.025$) for 50 replicate simulations of the model for each level of species richness. In each run, we recorded the fate of each species after 1000 generations (extinction or co-existence via specialization on one of the two resources) and the overall number of surviving species.

RESULTS

With only one species competing for two resources in our model, populations quickly reached the carrying capacity, but resource use did not evolve through time (Fig. 1A). The lack of evolution reflects the fact that both resources were equally available and perfectly substitutable, such that all resource combinations produced the same growth rate and were thus equally valuable. Additional simulations that chose between equal-fitness variants at random resulted in random evolutionary walks in the single-species scenario, but revealed no qualitative differences in the results in multi-species scenarios.

When two species competed for two resources, each species always evolved to specialize on a different resource (Fig. 1B), eventually reaching their carrying capacities, although it took longer to reach the carrying capacity than in single-species simulations. Decreasing the evolvability (δ) led to longer divergence times and slower approaches to the steady state, but did not qualitatively change the results. Because species evolve to use completely different resources, the species no longer interact and the interaction coefficients in the community matrix go to zero, indicating a stable solution. The steady-state community could not be further invaded unless the invader had identical resource use to one of the other species, in which case the invader co-existed, but remained at the invasion density. Generalists did not evolve in any of our simulations, due to the structure of the model – the number of optima is directly related to the number of resources, as each resource represents a peak on a linear adaptive landscape, and species do not persist away from the peak.

In simulations with three species competing for two resources, each species evolved towards specialization on a single resource, but there were more species than resources. Two species either shared a single resource (Fig. 1C) or at least one species went extinct due to competitive exclusion. If two species successfully evolved to specialize on the same resource, those species co-existed because neither had a competitive advantage over the other since intra- and interspecific competition coefficients were identical. In such cases,

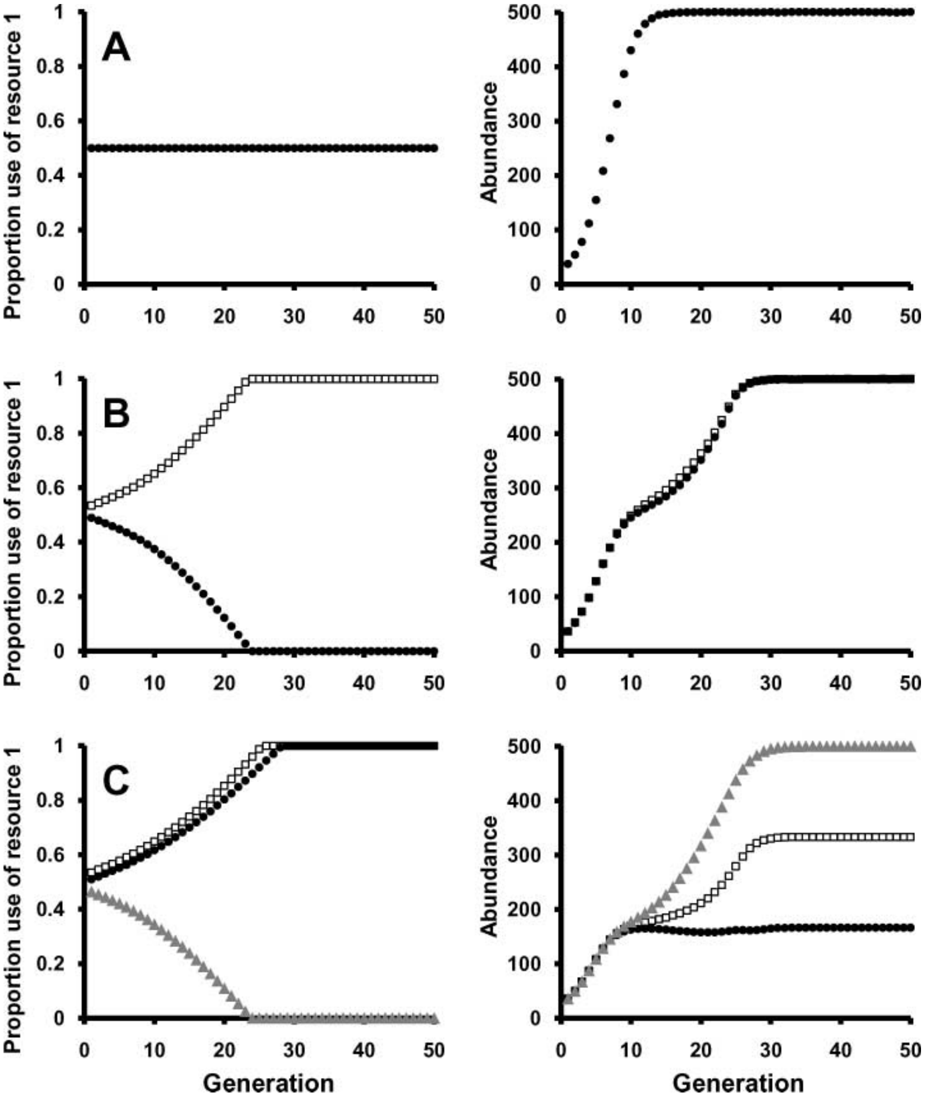

Fig. 1. Resource use (left) and species abundances (right) for simulations run with one species (A), two species (B), and three species (C) competing for two resources. Resource use values of 1 indicate specialization on resource 1; values of 0 indicate specialization on resource 2. When one species uses two resources, there is no selection to specialize on either resource and the species quickly reaches its carrying capacity. When two species compete for two resources, each species evolves to specialize on a unique resource, and both species reach their carrying capacity. When three species compete for two resources, two species must converge on one resource or at least one must go extinct, while the third species evolves to utilize the alternate resource; the two species sharing a resource co-exist, but at a reduced realized carrying capacity.

the interaction coefficients of species sharing a resource evolved to 1.0, while the interaction coefficients with the species using the other resource evolved to 0. Populations took longer to reach the carrying capacity than in two-species simulations and the final species

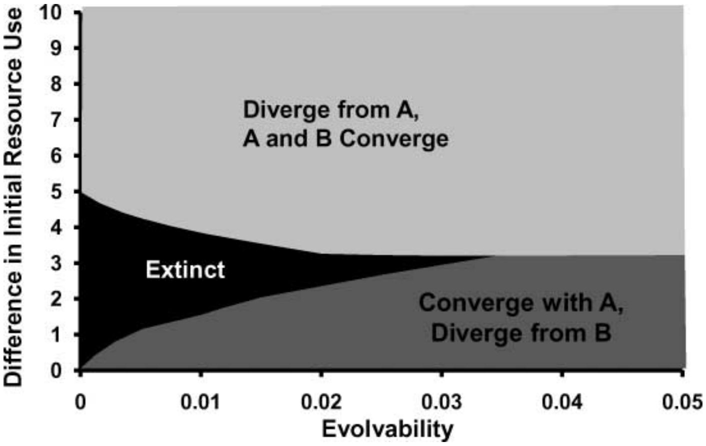

Fig. 2. The fate of species C in three-species communities. Simulations varied the evolvability (the amount by which a species can change its resource use each generation) and the initial difference in resource use between species. The initial difference in resource use between A and B was fixed at 2, but resource use by C was varied (*y*-axis reflects difference between A and C). Scenarios in which all three species co-exist require both convergence and divergence among species. Extinction occurs via competitive exclusion when species are initially too similar and evolve too slowly to successfully converge or diverge.

abundances decreased in proportion to the number of species sharing each resource (Fig. 1C).

The extinction and co-existence of species were affected by an interaction between evolvability and the initial strength of competition (Fig. 2). In our simulations, the initial similarity of any pair of species determined both the direction of evolution (convergence or divergence in resource use) and the probability of competitive exclusion. Species that initially converged experienced reduced, sometimes negative, growth rates due to strong competition, often leading to the extinction of the initially less specialized species. However, the frequency of extinction decreased as evolvability increased (Fig. 2).

Increasing the number of species competing for two resources showed that the basic pattern of divergence, convergence, and extinction continued in more diverse communities (Fig. 3). Suites of species converged on one resource, while simultaneously diverging from another suite of species that were converging on the other resource. The species did not always divide themselves evenly among resources; for example, in an eight-species community, two species specialized on one resource while six specialized on the other, with concomitant differences in population size. The probability of extinction increased with the number of species in the community (Fig. 3), due to increased competitive effects. Additional simulations demonstrated the same qualitative pattern with increased numbers of resources. When the number of species exceeded the number of resources, suites of species converged on different resources.

DISCUSSION

Classically, diversity in a community is thought to be limited by the number of resources, with each species thought to exist within its own niche, defined by its unique resource use

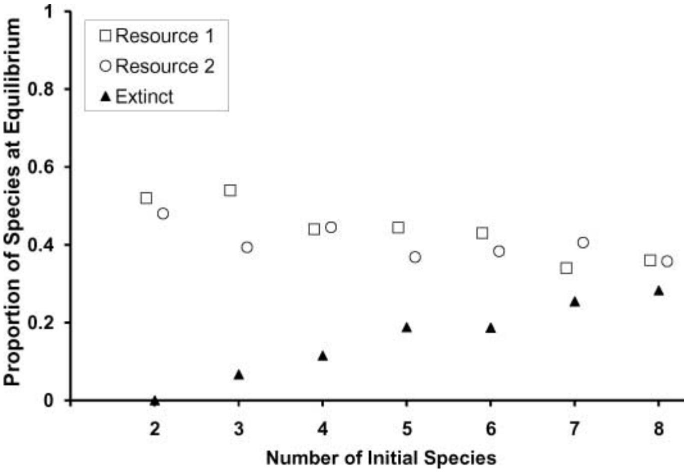

Fig. 3. The mean (± S.E.) number of species that specialize on each resource at equilibrium, or go extinct, as a function of the initial number of competing species in the community ($n = 50$ simulations at each level of species richness, with random initial resource use in each simulation). An intermediate level of evolvability ($\delta = 0.025$) was used in all simulations.

(e.g. Hutchinson, 1959; MacArthur, 1972; Chase and Leibold, 2003). However, more recent theory proposed that similar, or equivalent, species co-exist using the same niche for long periods of time because neither has sufficient competitive advantage to exclude the other (Bell, 2000; Hubbell, 2001). Debate has focused on the ecological importance of this idea (e.g. Gravel *et al.*, 2006; Leibold and McPeek, 2006; Adler *et al.*, 2007), but the evolutionary origin of these equivalent species has rarely been considered (Leibold and McPeek, 2006; but see Hubbell, 2006). Here we have demonstrated the conditions under which a suite of competitors could evolve to use identical niches. We conclude that: (1) convergence is a reasonable outcome of evolving competitors, but requires niche partitioning among multiple species (Fig. 1); (2) ecological and evolutionary outcomes will depend on initial similarity in resource use and the evolvability of resource use (Fig. 2); and (3) the number of functional groups is limited by the number of resources, but the number of co-existing species is not (Fig. 3).

Convergence may seem a poor evolutionary strategy, since it necessarily requires sharing a resource and a reduction in equilibrium population size. However, MacArthur and Levins (1967) recognized the possibility of convergence, and also concluded that species that are initially more similar are more likely to converge. We suggest that convergence is a viable strategy for two reasons. First, convergence reduces competitive differences between two species. A strong competitor quickly eliminates a poor competitor, but interactions between two strong competitors result in longer times to competitive exclusion (Aarssen, 1983; Abrams, 1998). Second, when the number of species exceeds the number of resources, any successful strategy must include convergence with some species, but divergence from others. In our model, convergence of two species only occurred when both diverged from a third species; that is, for multiple species to co-exist on the same resource, both niche convergence and niche divergence must occur (Fig. 1). In this multi-species context, although convergence with one or more species may negatively affect fitness, relative fitness is lowered further when diverging to share a resource with more, or more dominant, species. Thus, the evolution of neutral species in our model is ultimately driven by niche-based mechanisms (i.e. divergence). Considering evolution in this community context increases the accuracy of predicting evolution in nature, where species do not exist in isolation, but rather interact with many other species simultaneously (Strauss *et al.*, 2005; terHorst, 2010).

Our results suggest that both ecological (competitive exclusion) and evolutionary (convergence or divergence) rates are important for determining when species converge, diverge or go extinct. The effect of initial strength of competition on species co-existence depended on the rate of evolution (Fig. 2). Although evolution has traditionally been thought to occur over very long time scales, rates of evolution can, in many cases, be equivalent to or faster than some ecological processes (Thompson, 1998; Hairston *et al.*, 2005; Carroll *et al.*, 2007; terHorst *et al.*, 2010). Our results are consistent with other studies that have suggested that species may evolve quickly enough to prevent local extinction if selection is sufficiently intense (Gomulkiewicz and Holt, 1995). Evolutionary rates must match or exceed the rate of competitive exclusion for equivalent species to evolve and co-exist. However, as species become more similar to one another, the rate of competitive exclusion decreases because the net difference in competitive ability decreases (Aarssen, 1983; Abrams, 1998). In this eco-evolutionary feedback, evolutionary convergence slows the rate of competitive exclusion, allowing more time for species to evolve and adapt, which further slows rates of competitive exclusion and increases the likelihood of co-existence.

The results of our model are consistent with observations of functional groups in nature (Steneck and Dethier, 1994; Petchey and Gaston, 2002), whose existence has been considered by some to be paradoxical (Loreau, 2004). The insurance hypothesis predicts that diversity within a functional group and resultant ecological redundancy stabilizes communities (Hooper *et al.*, 2005), but the presence of similar species in a community should lead to instability due to species loss via competitive exclusion (Loreau, 2004). Our results suggest a resolution to this paradox, demonstrating that similar species may converge to become equivalent species in a single functional group (Fig. 3), and co-exist for long periods of time (Aarssen, 1983; Hubbell, 2001). This suggests two levels at which species diversity can be explained: niche differentiation and evolutionary divergence is more likely to drive diversity among functional groups, while neutral processes (e.g. stochastic death and recruitment, and evolutionary convergence) play a larger role in driving diversity within a functional group (Leibold and McPeek, 2006; Siepielski *et al.*, 2010).

We assume that evolvability (δ) increases with genetic diversity. Although the evolvabilities (and thus within-population genetic diversity) of all species in our model were equal, the evolvability of a species may be affected by many factors. Increased genetic diversity can increase the ability of a species to respond to selection from competition (Vellend, 2006), but genetic diversity is also likely to vary among species. Furthermore, in the absence of other evolutionary forces, such as gene flow, mutation or gene linkage, genetic diversity will decrease in species under strong selection. Thus, the evolvability of a species may change through time, which is likely to affect ecological outcomes (Fig. 2). Differences in generation times may also affect the rate of evolution and the ability of species to adapt to one another (terHorst *et al.*, 2010). Generating differences in the rates of evolution among species provides an interesting avenue for further investigation.

Although our model produces mathematically stable co-existence among suites of species, neutral dynamics (i.e. ecological drift) should make this an unstable equilibrium. Neutral species models predict that the probability of colonization of new niche space made available by stochastic deaths is based on the abundance of species in the community (Bell, 2000; Hubbell, 2001). Such ecological drift is predicted to result in the eventual extinction of all but one species within each niche, but extinction via ecological drift requires a very long time (Bell, 2000; Hubbell, 2001). Neutral species are likely to co-occur for time periods far exceeding most other ecological processes. Our model did not incorporate ecological drift, and thus only addresses how ecological equivalence may evolve, and does not predict the ultimate long-term ecological and evolutionary dynamics among equivalent species.

Niche and neutral theories are often considered opposing theories that may explain the ecology of species co-existence in communities, but recently there have been attempts to reconcile their differences (Gravel *et al.*, 2006; Leibold and McPeek, 2006; Adler *et al.*, 2007). We demonstrate that niche partitioning is indeed important in determining diversity among functional groups, while simultaneously confirming a key assumption of neutral theory – the evolution of equivalence is possible. Ecological equivalence not only can evolve, but also will be a derived outcome in communities composed of initially dissimilar species. Our model moves us beyond asking if equivalence evolves, to begin asking when it may evolve.

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