

LETTER

Biodiversity inhibits species' evolutionary responses to changing environments

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Abstract

Despite growing interplay between ecological and evolutionary studies, the question of how biodiversity influences evolutionary dynamics within species remains understudied. Here, using a classical model of phenotypic evolution in species occupying a patchy environment, but introducing global change affecting patch conditions, we show that biodiversity can inhibit species' evolution during global change. The presence of several species increases the chance that one or more species are pre-adapted to new conditions, which restricts the ecological opportunity for evolutionary responses in all the species. Consequently, environmental change tends to select for changes in species abundances rather than for changing phenotypes within each species. The buffering effects of species diversity that we describe might be one important but neglected explanation for widely observed niche conservatism in natural systems. Furthermore, the results show that attempts to understand biotic responses to environmental change need to consider both ecological and evolutionary processes in a realistically diverse setting.

Keywords

Adaptation, climate, environmental change, evolution, global, model, niche conservatism, species diversity.

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INTRODUCTION

Understanding how ecosystems respond to environmental change is fundamental to explaining diversity patterns and to predicting future responses to anthropogenic global changes. Broadly, ecosystems can either respond by ecological changes in species abundance and composition, or by evolutionary changes in the constituent species. Despite growing recognition that ecological and evolutionary dynamics interact strongly (Yoshida *et al.* 2003; Bonsall *et al.* 2004; Pulido & Berthold 2004; Davis *et al.* 2005; Hairston *et al.* 2005), the question of how biodiversity affects the evolutionary responses of species to environmental change has been neglected. Evolutionary theory typically treats species in isolation, considering the population genetics of single populations or pairs of interacting species such as hosts and parasites. In principle, the presence of co-occurring species might stimulate evolution within species, for example by initiating co-evolutionary interactions (Stenseth & Maynard Smith 1984; Christensen *et al.* 2002; Thompson & Cunningham 2002; Otto & Nuismer 2004). Alternatively, interactions among co-occur-

ring species might inhibit evolution and promote stasis (Stenseth & Maynard Smith 1984; Ackerly 2003; Brockhurst *et al.* 2007). However, those few studies that have considered the effect of species richness on species evolution have focused on constant physical environments, rather than looking at the interaction between ecological and evolutionary responses to environmental change.

Here, we use a modified version of the Levene model, a classical model widely used at the interface between ecology and evolution (Levene 1953; de Meeus & Goudet 2000; Kisdi 2001), to show that biodiversity inhibits evolution within species during global change. The model considers coexisting and evolving species in a metacommunity (Leibold *et al.* 2004) consisting of patches linked by dispersal but differing in environmental conditions. In a stable environment the community comprises a guild of species each specialized on one of the patches (Levene 1953; Kisdi 2001). An individual's fitness is determined by the match between a single phenotypic trait, which can evolve, and the optimum phenotype in the patch where it lives (see Material and Methods). Given this starting point, we ask how does biodiversity affect the system's response to a period of

global change represented by an average increase in optimum phenotype across patches (Fig. 1). Possible biological examples are (i) an overall global warming affecting optimum trait values for plant species in a series of microclimates; each may become cooler or warmer, but the global trend is to become warmer, or (ii) the effect of globally increased nitrogen deposition or acidification that affects particular locations differently.

In our model, species richness is maintained by occupation of distinct patches in the environment by each species. Therefore, the effects of environmental heterogeneity and species richness are potentially confounded. To distinguish the effects of environmental heterogeneity and biodiversity, we consider amounts of evolution for each species under three treatments shown in Fig. 1. First, under treatment A, we simulated each

species in turn alone in an environment containing just one patch, i.e. a spatially uniform environment. Sixteen hundred runs with different initial and final optima of the patch were performed, such that the runs differed in the rate and magnitude of environmental change affecting the patch (Fig. 1, Treatment A). For treatments B and C, we grouped the 1600 runs of initial and final optima to obtain 800 systems with two patches, 400 systems with four patches and 100 systems with 16 patches. Under treatment B, we simulated each species in turn, alone in an environment containing all the patches (Fig. 1, Treatment B). Under treatment C, we simulated all species together in an environment containing all the patches (Fig. 1, Treatment C). Runs of these systems for a given number of patches differ both in rates of environmental change in each patch and in the similarity

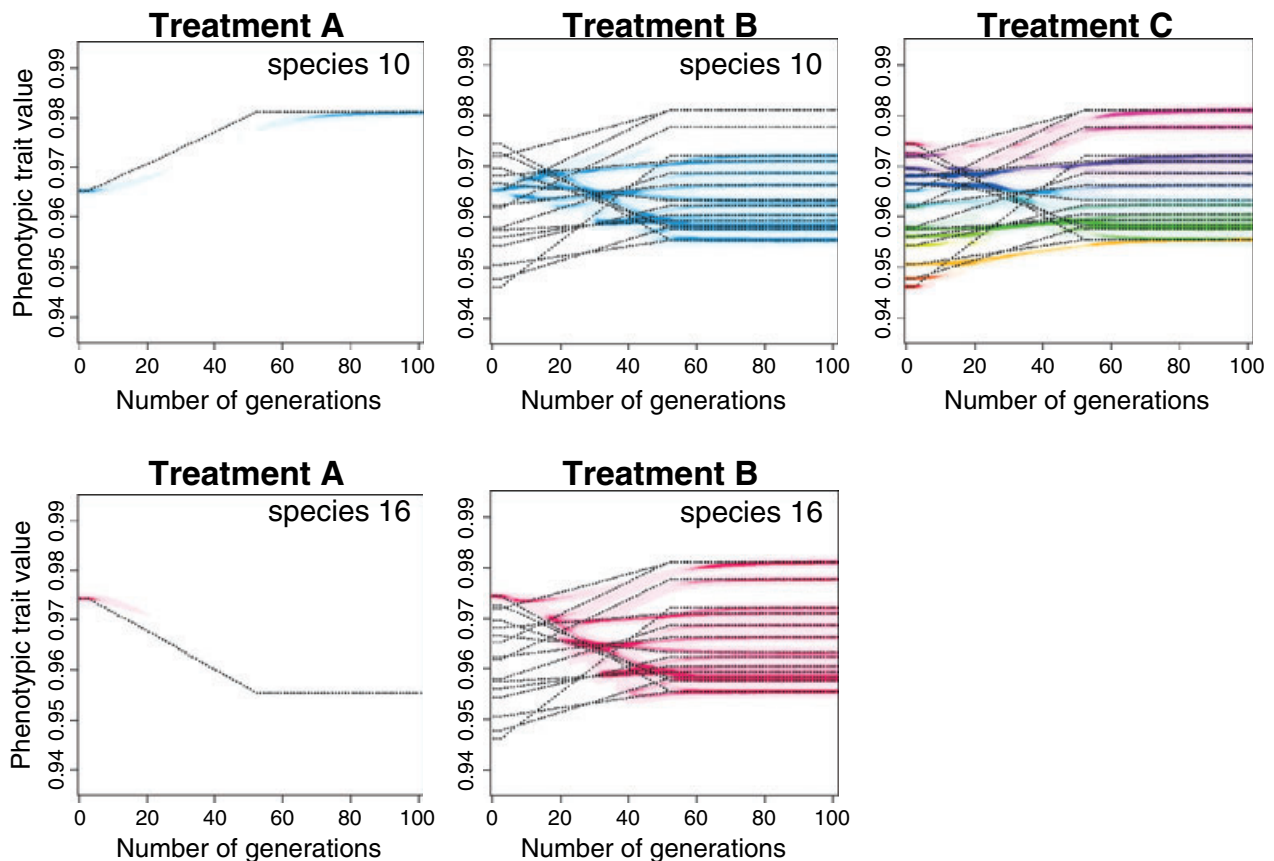


Figure 1 A typical simulation run showing the effects of environmental change on a sixteen species system. Treatment A: Two examples showing the one species run with presence of just the patch that it originally was adapted to: species 10 (blue) and species 16 (purple). Treatment B: The same two example species with all other patches present but unoccupied. Treatment C: All species and patches present. The simulation starts at equilibrium with each species adapted to one of the patches. The optimum phenotype in each patch changes for 50 generations towards a new stable value (black dots). Species phenotypes are represented by different colours and intensity represents the density of individuals with each trait value. In their own patch in isolation (Treatment A), species can adapt to change (species 10), or go extinct (species 16); in a heterogeneous but unoccupied environment (Treatment B), species can diversify to occupy several patches; but in a heterogeneous but occupied environment (Treatment C), species see their evolutionary range restricted by competition with other species.

in optima between patches. Matched runs of treatment B and C allow comparison of the same species evolving in the same heterogeneous environment but with or without the presence of other species. Matched runs of treatment A and B allow comparison of the same species experiencing the same conditions of environmental change in a given patch but depending on whether other ecologically distinct patches are present or not. We explore results for a range of dispersal rates and a range of species environmental tolerances.

MATERIAL AND METHODS

Population dynamics

The model assumes an environment of 1, 2, 4 or 16 patches, each characterized by a different optimum phenotype, X_i . The model was programmed in R (R Development Core Team 2003). Dynamics of each species were followed by keeping track of the abundances, phenotypes and locations of their descendents. Population dynamics followed this sequence:

(i) *Dispersal*. A fraction of propagules produced in a patch (see step *iv*) disperse globally to all patches while the rest remain in their parental patch. Different patches thus contribute different numbers of individuals to the next generation. We ran the model for dispersal rates equal to 10^{-4} , 10^{-3} , 0.1, 0.2, 0.5, 0.8 and 1.

(ii) *Recruitment*. Patches recruit individuals from the pool of propagules up to a carrying capacity of $K = 10,000$. Individuals thus compete for recruitment sites as in a lottery, and phenotypes have a probability of being recruited proportional to their frequency in the pool.

(iii) *Growth*. At the end of the season, recruited individuals have a biomass that depends on the similarity between their phenotypic trait, x and the optimum phenotype X_i of the patch they find themselves in:

$$\text{biomass} = 95 \times \exp\left(-\frac{(x - X_i)^2}{2 \times \omega^2}\right),$$

where ω determines the growth range of individuals, with ω^2 inversely proportional to the strength of stabilizing selection. ω is thus the parameter that controls the environmental tolerance of phenotypes; we ran the model for $\omega = 10^{-4}$, 5×10^{-4} , 10^{-3} , 2×10^{-3} and 10^{-2} .

(iv) *Reproduction*. Sexual reproduction occurs within a patch among individuals of the same species. The number of propagules produced locally by species is their local biomass times their fecundity, where the fecundity is assumed to be the same for all the species. The offspring phenotypes are drawn from a normal distribution with mean and variance equal to the mean and variance of the phenotype distribution of the parental local population (weighted by biomass; Lande 1976). Simulations assuming

clonal reproduction, in which offspring inherit a phenotype drawn from a Gaussian distribution around their parent's phenotype, yielded the same conclusions as those we present here (Fig. S1).

The model is intermediate between a soft and hard selection model (Christiansen 1975; Wallace 1975), with local density regulation in patches (soft selection) but a variable contribution of each patch to the next generation (hard selection). Under stable conditions, distinct phenotypic species each specialized on the environment of a single patch can coexist assuming that patches are distinct relative to the environmental tolerance of individuals and that dispersal is not too high (otherwise generalist phenotypes evolve; de Meeus & Goudet 2000; Kisdi 2001).

Environmental change

We modeled climate change as a linear change in optimum trait values in each patch from initial values drawn at random between limits (0.945–0.975) to final values drawn at random between higher limits (0.955 and 0.985). We ran the model under constant conditions for 400 generations to obtain steady state before climate change began, starting with each species assigned an initial phenotype matching the optimum for one of the patches. Climate change occurred over 50 generations from their initial values to final values. After climate change, we ran the model for a further 50 generations to let the communities recover from the climate change. We then calculated the final amount of phenotypic evolution for each species as the 'standard deviation' of final trait values from the ancestral phenotype:

$$\sqrt{\frac{\sum_{\text{individuals}} (\text{FinalPhenotype}_{\text{individual}} - \text{AncestralPhenotype})^2}{n_{\text{individuals}}}}$$

We chose this measure because a simpler measure such as the change in mean phenotype would be inaccurate in cases in which a species diversifies to occupy patches with both higher and lower optimal phenotypes than its ancestral patch, i.e. it could yield an amount of evolution of zero when in fact considerable evolutionary change had occurred. Extinct species were excluded from calculations of amounts of evolution. By choosing different random and final patch values, our simulations incorporate variation in both the similarity of optima between patches and the relative rate of environmental change vs. evolution, the key parameters affecting species' responses.

RESULTS

Increasing the number of species in the system reduces the amount of evolution in those species that survive

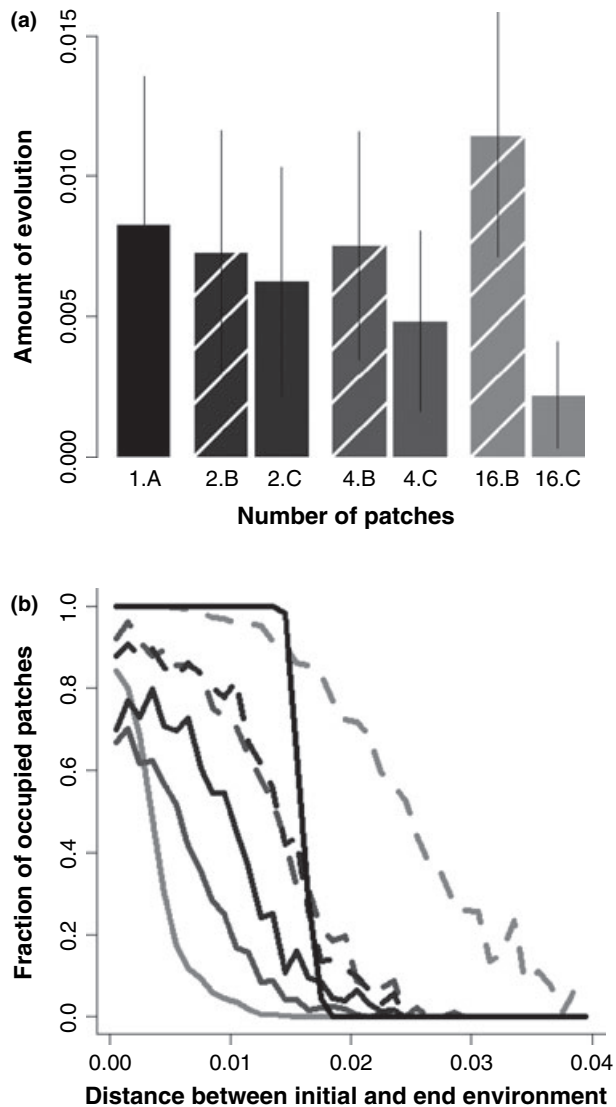


Figure 2 (a) The amount of evolution per species decreases with diversity. The numbers below each column indicate the number of patches present. The letters indicate the treatment: treatment B with just one species present (also indicated by hatched shading), or treatment C with all species present (also indicated by full shading). The effects of diversity can be compared between treatments B and C in environments with the same numbers of patches (matched by degree of shading) or the same treatment across environments with different numbers of patches. (b) The fraction of final patches that are occupied by a species in relation to the distance between the optimal phenotype of the final patch and of the species' initial patch. The greater the phenotypic distance, the more a species has had to evolve to occupy the patch. When diversity increases, species become more restricted to patches that are similar in optimum phenotype to their initial patch. Shading denotes the numbers of patches: with 1 (black), 2 (dark intermediate grey), 4 (light intermediate grey) and 16 (lightest grey). Dashed lines indicate results from runs with only one species (Treatment B), solid lines indicate results from runs with all species present (Treatment C).

environmental change (Fig. 2a). Increased heterogeneity on its own, in terms of the presence of additional empty patches (Treatment B, indicated by hatched bars and dashed lines in Figs 2 and 3), can increase or decrease the amount of evolution compared to a single species in a uniform environment (Treatment A), depending on exact conditions (discussed further below). However, when other species are present (Treatment C, indicated by solid bars and lines in Figs 2 and 3), the amount of evolution in species that survive climate change is reduced on average, compared to the same species on its own in either a uniform (Treatment A) or a heterogeneous (Treatment B) environment. For example, with 16 species present, the average amount of evolution per species is 73% less than when the same species is on its own in a uniform environment (Treatment C vs. Treatment A) and 81% less than the same species with all 16 patches present but empty (Treatment C vs. Treatment B, for medium values of dispersal and environmental tolerance as in Fig. 2).

The reason why diversity decreases the amount of evolution is that, as diversity increases, species are increasingly restricted to only those patches with final optima close to the species' initial optimum phenotype, despite being able to evolve to occupy more dissimilar patches when other species are absent (Fig. 2b). In other words, competitive interactions among co-occurring species promote stabilizing selection and niche conservatism (Holt & Gaines 1992; Ackerly 2003, 2004): species migrate to occupy new patches with conditions closely matching their initial phenotype, rather than adapting to change in their original patch. We now discuss the mechanisms in more detail and the effects of varying key parameters of dispersal and environmental tolerance.

Effect of environmental heterogeneity on evolution with just one species present

In a single patch system, species either adapt to the change or go extinct, depending on the rate of environmental change relative to the species' environmental tolerance and potential evolutionary rate (Burger & Lynch 1995). If we increase the number of patches, but still with only one species present, the species can either occupy all, some or none of the patches at the end (contrast species 10 and 16, Treatment B, Fig. 1). Increasing the number of patches increases the chance of species surviving, except at very high dispersal rates, in which case species are maladapted to all patches (Fig. 3d–f, dashed lines).

Environmental heterogeneity can either increase or reduce the amount of evolution for the following reasons. Additional patches can have optima during or after the period of change that are similar to those in the species' initial patch. This is especially likely with a large number of

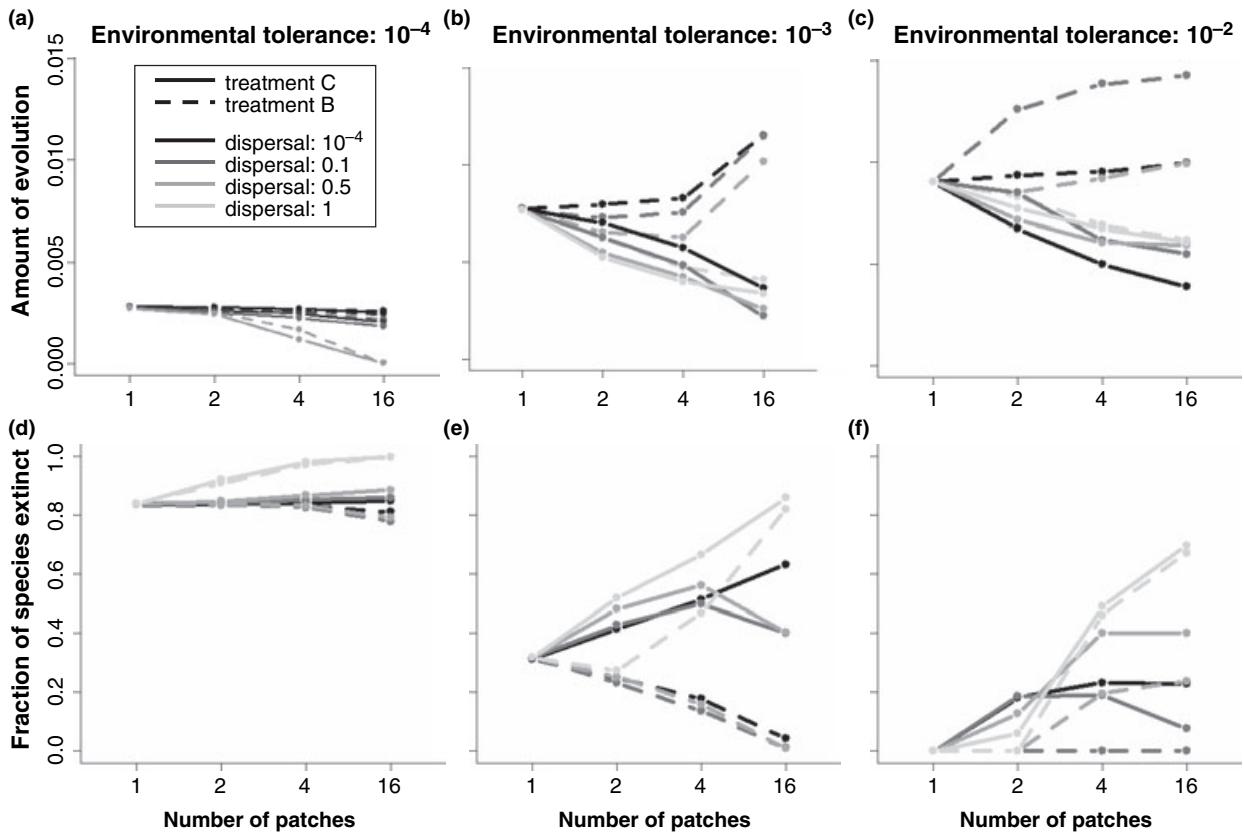


Figure 3 The average amount of evolution per species (a–c) and fraction of species going extinct (d–f) across environments containing 1, 2, 4 and 16 patches with only one species (dashed lines, Treatments B), or with all species present (solid lines, Treatment C), across a range of dispersal and environmental tolerances. Line shading represent dispersal rates of 10^{-4} (black), 0.1 (dark intermediate grey), 0.5 (light intermediate grey) and 1 (lightest grey). Panels (a and d), environmental tolerance 10^{-4} ; (b and e) environmental tolerance 10^{-3} ; (c and f) environmental tolerance 10^{-2} . Differences between treatments B and C for 2, 4 and 16 species are not significant in panel (a) except for the two intermediate values of dispersal with 16 species; they are all significant in panels (b) and (c) except for the highest dispersal rate with 4 and 16 species in the latter panel.

patches. In some cases, this prevents a species adapting to change in its own patch, even if it could do so with no other patches present (Fig. 1, compare Treatments A and B for species 10). This scenario reflects niche conservatism: the species tracks its optimal environment by migrating to new patches rather than by adapting to changes in its initial patch. The amount of evolution is reduced. In other cases, additional patches with similar optima provide ‘stepping stones’ for the species to survive and adapt to the changes in its own patch, when it would not have been able to with no other patch present (Fig. 1, compare Treatments A and B for species 16). This can lead to an increase in the amount of evolution with increasing heterogeneity. Which outcome occurs in a given simulation depends on the similarity of patch optima and their trajectories during environmental change.

The frequency of those two cases, and hence the average effect of patch heterogeneity on evolution, varies with the

number of patches, the rate of environmental change, the dispersal rate, and the environmental tolerance of species (Fig. 3a–c, dashed lines). At intermediate values of dispersal and environmental tolerance, the amount of evolution decreases with two or four patches compared to a single patch, because species migrate into patches with final optima similar to initial conditions in their original patch (Fig. 1 – Treatment B, species 10; Fig. 2b, mid and dark grey dashed lines). However, with 16 patches present, the amount of evolution is greatly increased, because patches tend to have more similar optima and provide ‘stepping-stones’ for species to adapt to conditions farther removed from their original phenotype (Fig. 1 – Treatment B, species 16; Fig. 2b, light grey dashed lines). With very high dispersal rates and very low environmental tolerances, the amount of evolution decreases monotonically with patch number: very high dispersal rates prevent local adaptation because of remixing of the population, whereas low environmental

tolerance leads to high mortality in patches with optima divergent from the species' phenotype. With high environmental tolerances and low dispersal rates, the amount of evolution increases monotonically with the number of patches: high environmental tolerance enables the species to colonize new patches and survive under changing conditions, and low dispersal allows local adaptation to take place (Fig. 3a–c, dashed lines). To summarize, there are no simple predictions concerning the effects of patch heterogeneity on amounts of evolution when only a single species is present.

Effect of biodiversity on evolution for a given environmental heterogeneity

The situation changes in diverse communities, i.e. when all the patches contain a separate species at the start of the run. The presence of other species increases the chance of extinction compared to a single species in a multi-patch system (Fig. 3d–f, contrast solid and dashed lines). This occurs because of strong lottery competition and the increased chance that other species are pre-adapted to the final environmental conditions. There are rare cases in which the amount of phenotypic evolution is increased for a given species, but the average amount of phenotypic evolution per species is decreased because diversification into multiple patches is inhibited (contrast Fig. 1, Treatment B and C for the two example species; Fig. 3a–c, contrast solid and dashed lines). The decrease is significant under nearly all scenarios when environmental tolerance is intermediate or high, but weak and not significant for most scenarios with low environmental tolerance (Fig. 3). This is because extinction in response to environment change is so high when environmental tolerance is low that species barely meet other species in treatment C. For example, in an environment with two species at the lowest environmental tolerance, a species alive at the end of a run has only between 1 and 8% chance of being in competition with the other species. To conclude, the presence of other species decreases phenotypic evolution per species because diversification into multiple patches is inhibited.

Combined effect of biodiversity and environmental heterogeneity on species evolution

Increasing both the number of different patches and the number of species decreases the amount of phenotypic evolution under all conditions (Fig. 3a–c, solid lines). Across all trials, species surviving in the 2, 4 and 16 species cases evolved on average between 6–36, 15–55 and 16–70% less than they did on their own with just their own initial patch present. This occurs because more species shift to different patches rather than adapting to change in their own patch

(Fig. 2b). The effect is strongest at intermediate values of both dispersal and environmental tolerance: if dispersal is too low, species adapt to local conditions; if environmental tolerance is too high, species can diversify to occupy most patches; high dispersal and low environmental tolerance lead to high extinction (Fig. 3a–c, solid lines).

Increasing both the number of different patches and the number of species affects the extinction rate in ways that depend on parameter values. At low and high dispersal rates, and at the lowest environmental tolerance, the chance of extinction increases with diversity (Fig. 3d–f, solid lines). At intermediate dispersal rates and intermediate or high environmental tolerances, extinction rate rises then falls with diversity (Fig. 3d–f, solid lines). To conclude, species diversity tends to promote stabilizing selection on ecological traits, inhibiting evolutionary responses within species and leading to niche conservatism. As a result, a greater proportion of the system's response to the change in environment occurs through changes in species abundances (Fig. 4), rather than evolutionary changes in species phenotypes.

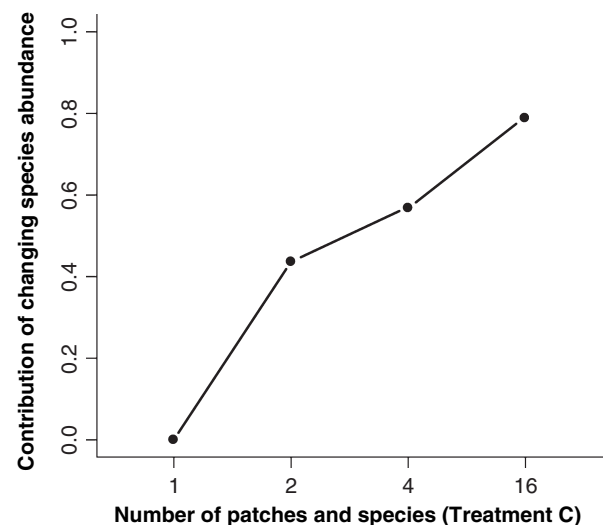


Figure 4 Relative contribution of changing species abundance to the overall response of the community to environmental change, depending on the number of patches and species (Treatment C). The community response was characterized broadly as the change in average phenotype from the start to the end of each simulation. From this the contribution of changes in species abundance were calculated as the sum of change in mean phenotype due to changing species abundances, defined as the change in relative abundance of the species multiplied by the initial patch value. Note that an equivalent measure to the standard deviation used for evolutionary responses within species cannot be calculated for ecological response (because there is no single starting phenotype around which to calculate a standard deviation), but the measure we use suffices to show the increase in importance of ecological changes. Dispersal = 0.1 and environmental tolerance = 0.001.

DISCUSSION

We conclude that species diversity can have profound effects on evolution. Because most ecological trait variation is among species rather than within them, at least in non-neutral, competitive communities, environmental changes tend to select for changes in relative species abundances rather than for changing phenotypes within each species. In addition, species in diverse communities tend to have, on average, lower effective population sizes than those on their own as a result of competitive interactions, which might slow down rates of adaptive evolution (Johansson *in press*) and increase the role of drift relative to selection. Other models have considered evolution in species rich systems. Stenseth & Maynard Smith (1984) used a general model of evolution in species assemblages occupying a constant physical environment. They concluded that ecosystems may occupy one of two evolutionary modes: a Red Queen scenario in which evolutionary change is perpetual vs. a mode of evolutionary stasis among species. They discussed the likely effects of physical environmental change, in terms of evolution in the 'stasis mode' being entirely dependent on external changes, but did not address the question of how species richness and ecological responses affect evolutionary responses to such changes. Other authors have used similar models to ours to explore the initial diversification of an ancestral population into multiple habitats or niches, but again none addressed the question of how diversity affects evolution within species (Dieckmann & Doebeli 1999; Kinzig *et al.* 1999; Tilman & Lehman 2001). Johansson (*in press*) has independently reached similar conclusions to ours in a model of resource competition among two and three species. Our model shows that the effects increase progressively with addition of more species, and reveals some circumstances in which effects are weaker, namely extremely high or extremely low dispersal rates or levels of environmental tolerance. Empirical evidence is even rarer: we know of only one recent study, which shows that adaptive radiation of *Pseudomonas fluorescens* in a laboratory mesocosm is inhibited by the presence of competing species (Brockhurst *et al.* 2007).

Our model assumes a simple mechanism for species coexistence and simple evolutionary mechanisms but the findings were robust across a range of parameters and we believe they would apply in a range of circumstances. The model considers a guild of competing species partitioning a patchy environment. Other formulations would be possible in which species partition use of a continuous range of resources (Lehman & Tilman 1997; Ackermann & Doebeli 2004). In addition, we assume that the aspect of the environment being partitioned by species is also the aspect experiencing environmental change. More complex multi-dimensional environments combining niche

axes and general aspects of physical environment could be considered (Ackerly *et al.* 2006). Allowing for additional interactions such as antagonism and mutualism might increase the frequency of scenarios in which diversity stimulates evolution (Fussmann *et al.* 2007; Johnson & Stinchcombe 2007), but we believe the tendency for high diversity of competing species to inhibit evolutionary responses to abiotic change would be robust to all of these alternatives.

Real ecosystems typically display much greater diversity than we can simulate in our models. So when and where does most evolution occur? Possible answers include: in marginal or unsaturated environments (Millien 2006); in response to small or very slow environmental changes; or when environmental change creates entirely new conditions outside the range of initial optimal trait values, or new combinations of optima for several traits, in which case large-scale turnover and diversification to fill new niches may occur (Tilman & Lehman 2001; Jackson & Erwin 2006; Carroll *et al.* 2007).

Our results have important implications for understanding evolution in the real world. Biologists long held the view that evolution occurred over longer timescales than ecological processes. Recently this has been challenged by theory and experiments showing that evolution can occur over short timescales (Agrawal 2003; Yoshida *et al.* 2003; Pulido & Berthold 2004; Davis *et al.* 2005; Hairston *et al.* 2005; Carroll *et al.* 2007). However, measures of evolutionary rates over longer timescales tend to be much slower than rates predicted from simple systems (Kinnison & Hendry 2001; Ackerly 2003, 2004), with many species displaying niche conservatism and tracking change by migration rather than evolution (Pease *et al.* 1989; Ackerly 2003). Numerous mechanisms have been proposed to explain such evolutionary stasis, but none seems fully satisfactory (Hansen & Houle 2004). The buffering effects of species diversity, a ubiquitous feature of natural systems, might be one important but neglected factor explaining why evolution appears to be 'too slow'. Attempts to understand how focal species or ecosystems respond to environmental change need to consider both ecological and evolutionary processes in realistically diverse assemblages.

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AUTHOR CONTRIBUTIONS

All authors contributed equally to this work. E. J. programmed the initial model and performed initial analyses. C. d. M. and T. G. B. contributed equally to devising the model, performing analyses and writing the manuscript.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Figure S1 Effect of diversity on species' evolutionary change in a model with asexual reproduction.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2008.01152.x>

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