The conflict between adaptation and dispersal for maintaining biodiversity in changing environments

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Short title – Diversity in evolving metacommunities

Key words: metacommunity, evolution, local adaptation, spatial insurance, evolutionary rescue, monopolization, extinction, range shift, climate change, competition

Abstract – 149 words
Main text – 4805 words
References – 46
Figures – 4
Tables – 0
Boxes – 0

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Statement of authorship
PLT conceived of the study. EF and PLT wrote the model and performed the analysis. PLT wrote the first draft of the manuscript and EF contributed substantially to revisions.

Data accessibility statement
The simulation code produced for and used in this study is available on github. Zenodo DOI: 10.5281/zenodo.2019881

Abstract

Dispersal and adaptation represent two ways that allow species to persist in changing environments. Yet, we lack an understanding of how these processes interact to affect species persistence, especially in communities where biotic interactions greatly complicate responses to environmental change. Here we use a stochastic metacommunity model to show that dispersal and adaptation to environmental change can have conflicting contributions to biodiversity maintenance. Both dispersal and adaptation to environmental change independently contribute to the maintenance of biodiversity. But, when species both adapt and disperse, faster adapting species evolve to hold onto their initial ranges, thus impeding slower adapting species from shifting their ranges and thereby causing extinctions. Importantly, these differences in adaptation speed emerge as the result of competition, which alters population sizes and colonization success. Thus, the maintenance of biodiversity in changing environments depends jointly on rates of dispersal and adaptation, and critically, the interaction between these processes.

Introduction

When environmental conditions change, what determines whether biodiversity will be maintained? This question remains one of the greatest and most pressing challenges facing ecologists and evolutionary biologists (Urban *et al.* 2016) because of the unprecedented magnitude of environmental change resulting from human activities (IPCC 2013). When the environment changes, populations must adapt evolutionarily to those new conditions, shift their ranges via dispersal, persist in the new conditions, or go extinct (O'Connor *et al.* 2011). To date, these processes—adaptation to changing environments and dispersal—and

how they contribute to persistence have been largely studied independently, and rarely in a community context. Yet, there is great potential for these processes to interact, and to be mediated by the complex networks of biotic interactions that are an integral property of ecological communities (Gilman *et al.* 2010; Brown & Vellend 2014; Alexander *et al.* 2015). Therefore, there is pressing need for theory that integrates the three processes of dispersal, evolutionary change, and biotic interactions, if we wish to understand how biodiversity can be maintained in a changing world.

Our current understanding of the processes that maintain biodiversity in changing environments is based on two major theories, one from ecology and one from evolutionary biology. In ecology, metacommunity theory has established that dispersal can provide spatial insurance, which preserves biodiversity by allowing species to track favourable conditions by shifting their ranges (Loreau *et al.* 2003). In contrast, from an evolutionary biology perspective, evolutionary rescue occurs when advantageous genetic changes allow populations to persist in stressful environmental conditions, which would otherwise cause extinction (Gomulkiewicz & Holt 1995; Gonzalez *et al.* 2012; Bell 2017). In reality, both ecological and evolutionary processes are operating in concert, and are likely interacting, when ecological communities are faced with environmental change (Norberg *et al.* 2012). We know that dispersal can affect the likelihood of evolutionary rescue. Evolutionary rescue can be promoted by dispersal across an environmental gradient (Bell & Gonzalez 2011) due to the influx of preadapted individuals, but dispersal can also hinder local adaptation if dispersal rates are sufficiently high to cause maladaptation through gene swamping (Lenormand 2002; Uecker *et al.* 2014). Still, the major focus of this body of

research has been to understand how dispersal affects the likelihood of evolutionary rescue in isolated, single species. Extending this theory to the question of how ecological and evolutionary processes combine to contribute to the persistence of entire communities of interacting species remains a major gap in our knowledge.

Although evolution can help individual species persist in changing conditions, it is possible that it may actually be detrimental to the maintenance of community diversity because it may reduce the potential for spatial insurance. Differences in the rate at which species adapt to changing conditions may lead to differences in how much they need to shift their ranges to keep pace with environmental change. If fast adapting species remain in place, they may prevent their slower adapting competitors from successfully shifting their ranges (Urban *et al.* 2008). This is a special case of evolutionary meditated priority effects, which have been termed monopolization effects (De Meester *et al.* 2002; Urban *et al.* 2011; De Meester *et al.* 2016), whereby a species that is initially maladapted to the environmental conditions can exclude a better adapted competitor if it arrives first and is then able to adapt quickly enough. Yet, whether monopolization is likely to lead to extinctions and to the loss of biodiversity in changing conditions is unclear.

Theory suggests that dispersal and evolution do have conflicting effects on community responses to change. de Mazancourt et al. (2008) showed how dispersal could reduce rates of adaptation by offering an alternative strategy for dealing with environmental change. In simulating eco-evolutionary contributions to biodiversity maintenance under climate change, Norberg et al. (2012) found that evolution, but not dispersal, minimized extinction

risks. Furthermore, they found that dispersal did not reduce extinctions, because it allowed competitively superior species to expand their ranges to the detriment of other species. This result contrasts with the predictions of the spatial insurance hypothesis (Loreau *et al.* 2003) and another simulation study that tested the role of dispersal in maintaining biodiversity in the absence of evolution (Thompson & Gonzalez 2017). It is likely that this discrepancy is due to monopolization effects, resulting from interactions between dispersal and evolution of environmental optima. Yet, without a single theoretical framework that links the theories of evolutionary rescue, spatial insurance, and monopolization, how dispersal, evolution, and biotic interactions combine to affect the maintenance of biodiversity in changing environments remains unclear.

Here we use a stochastic individual-based metacommunity model to provide such a framework and to test the hypotheses that 1) when species disperse, but do not evolve their environmental optimum, biodiversity is preserved through spatial insurance, 2) when species evolve their environmental optimum, but do not disperse, biodiversity is preserved through evolutionary rescue, and 3) when species both evolve their environmental optimum and disperse, biodiversity is preserved through a combination of spatial insurance and evolutionary rescue, but that monopolization effects lead to the loss of biodiversity. Thus, we expect that fast adapting species will monopolize local habitats and impede species sorting, and thus persistence of slower adapting species. Furthermore, we expect that dispersal will only provide spatial insurance in regions of the metacommunity that contain analogue environments—that is, post change conditions that fall within the initial range of environmental conditions present in the metacommunity (Williams &

Jackson 2007). In contrast, evolutionary rescue should be possible under both analogue and non-analogue conditions (Norberg *et al.* 2012). Monopolization effects should occur whenever evolution and dispersal combine (De Meester *et al.* 2016).

Model description

Model overview

The evolving metacommunity dynamics were simulated using an individual based model of discrete, non-overlapping generations. The model initially consists of S = 80 species in M = 30 patches, spanning an environmental gradient. Dispersal to neighbouring patches is natal and reproduction is sexual. Individuals inherit their environmental optimum from their parents. Thus, we consider only the role of evolution of the environmental niche, but not evolution of other traits such as dispersal or plasticity, which can also mediate persistence in changing conditions (Kubisch *et al.* 2013; Kingsolver & Buckley 2017).

After an initial period of constant environmental conditions to allow the communities to reach quasi ecological and evolutionary equilibrium, we gradually change the local environmental conditions in all patches equally, simulating directional environmental change (e.g., climate warming). This change is severe enough that species must disperse or adapt to persist on the landscape. We factorially contrast different rates of dispersal and mutation to ask how this affects the maintenance of biodiversity in the metacommunity.

Reproduction, inheritance and survival

The reproductive output of each individual is determined by a random draw from a poisson distribution, which simulates demographic stochasticity. After accounting for density regulation (following Beverton & Holt 1957) and environmental mismatch due to local adaptation, the expected value of this distribution λ_i for individual *i* of species *j* at time *t* in patch *l* is equal to:

$$1)\quad \lambda_{i,j,l}(t) = \frac{\lambda_0}{1+\sum_{k=1}^{S}\alpha_{j,k}N_{kl}(t)} e^{-\left(\frac{(x_l(t)-z_i}{2\sigma_{niche}}\right)^2},$$

where λ_0 is the fecundity, $\alpha_{j,k}$ is the per capita competitive effect of individuals of species *k* on individuals of species *j*, $N_{k,l}(t)$ is the abundance of species *k* in patch *l* at time *t*, x_l(t) - z_i represents the mismatch between the trait z_i and the environment x_l(t) experienced by individual *i*, and σ_{niche} is the niche width, with smaller values resulting in stronger selection. See Table S1 for a summary of parameters and tested values.

Species interaction parameters were generated such that most, but not all, species could co-exist locally, if they share the same environmental optimum. This was achieved by drawing the strength of intraspecific competition, $\alpha_{j,j}$ from a lognormal distribution with mean 0.002 and variance 0.1, and drawing the strength of interspecific competition, $\alpha_{j,k}$ from a lognormal distribution with mean 0.002 and variance 0.1.

We assume that reproduction is sexual and that the sex ratio is, on average, 0.5. As individuals are diploid, they inherit one randomly chosen allele from each parent. The phenotype z_i is the average across both alleles. Females choose a mating partner randomly

and produce 2 * λ_i offspring in order keep lambda interpretable at the population level. Offspring are randomly assigned as female or male with equal probability. During inheritance, new allele values are drawn at a certain rate *m* from a normal distribution with a mean value equal to that of the parent, and a standard deviation equal to a mutation width of σ_{mut}.

Dispersal and landscape

Dispersal is natal and occurs before reproduction. The probability that an individual disperses is governed by a Bernoulli distribution, with a probability equal to d_i. Dispersing individuals leave their natal patch and disperse to one of the adjacent patches (nearest-neighbour dispersal) with equal probability. Mortality during dispersal occurs with probability μ, which summarizes all possible costs of dispersal, be they risk, time or energy costs (Bonte *et al.* 2011).

Patches in the metacommunity are arranged in a ring, with each patch connected to its two adjacent patches. This ring arrangement allows us to avoid edge effects in our landscape. We assume that environmental values increase over the first half of the ring from 0 to $M/2 - 1$ in integer steps and decrease following the same rule in the second half. After a "burin-in" phase of 10,000 generations, environmental change occurs at a constant rate across the landscape such that $x_l(t+1) = x_l(t) + \Delta E$. The magnitude of environmental change was chosen so that 2/3 of the patches would have a pre-change analogue for their environmental conditions.

We initialized the landscape by adding individuals (half females, half males) from all species at their single-species equilibrium density $(\hat{N} = (\lambda_0 - 1)/\alpha_{j,j})$ to all patches. Individuals of one species always had the same local adaptation optimum at simulation start, randomly selected from a uniform distribution, that spanned the range of initial environmental conditions.

Scenarios

We contrasted 12 dispersal rates *d* spanning the range from 0 to 0.5. We combined this with a factorial comparison of five mutation rates spanning the range from 0 to 0.1. These ranges of dispersal and mutation rates were chosen to cover the range of full extinction, to full persistence in our model. These mutation rates are higher than what is typical in natural populations (but see Gingerich 2009), but were required to allow evolutionary rescue, given the small population sizes that were necessary to make the model computationally feasible. For each combination of dispersal and mutation rate, we ran 50 replicate simulations, each time drawing a new community matrix as described above. We additionally ran a sensitivity analysis for the most relevant parameter values (Fig. S1, S2).

Response variables

We calculated the proportion of species that were maintained over the course of environmental change at the regional metacommunity scale, separating patches based on whether their final environmental conditions had a pre-change analogue (here, environmental values below 15) or not. In all cases, we compared the communities at the final time step of the burn-in phase (t = 10, 000) with those at the end of the simulation,

after environmental change had occurred (t = 15, 000). The proportion of species maintained was calculated as the number of species that were present in the region (analogue or non-analogue) after environmental change, divided by the number of species that were present prior to environmental change.

We calculated the mean change in species range size as the number of habitat patches occupied by a species after change minus the number of habitat patches occupied by that species before change, at the end of the burn-in phase. We included both analogue and non-analogue patches in this calculation, but only included species that persisted over the course of environmental change.

We calculated the interspecific variation in range shift as the standard deviation in range size changes across all species that persisted during environmental change within each replicate run of the model.

We calculated the mean leading vs. trailing range edge expansion as:

2) $$\nu = \frac{\sum_{j=1}^{S_{post}} |\max(x_{j_{post}}) - \max(x_{j_{pre}})| - |\min(x_{j_{post}}) - \min(x_{j_{pre}})|}{S_{post}},$$

where $x_{j_{pre}}$ and $x_{j_{post}}$ are the environmental conditions in the habitats occupied by species j before and after environmental change, respectively. S_{post} is the regional diversity of the metacommunity, post environmental change. This measure calculates the degree to which

the range of each species shifts on its leading edge (min environmental conditions) vs. its trailing edge (max environmental conditions), on average.

Results and Discussion

Overall, we find that dispersal and evolution of environmental optima both independently allow species to persist during environmental change (Fig. 1a, b), consistent with the spatial insurance and evolutionary rescue hypotheses and recent findings (Gomulkiewicz & Holt 1995; Loreau *et al.* 2003; Low-Décarie *et al.* 2015; Thompson & Gonzalez 2017). However, in combination, dispersal and adaptive evolution can facilitate monopolization effects, which results in fewer species persisting than when either process operates on its own (Fig. 1c). Dispersal, in the absence of evolution (Fig. 1a), increases the proportion of species that persist (Fig. 2a), by providing spatial insurance (Loreau *et al.* 2003), whereby species track their environmental optimum through shifting their ranges. This is only possible when local conditions after environmental change fall within the range of initial conditions in the metacommunity (i.e., analogue environments). We see that the positive effect of dispersal on species persistence increases with dispersal rate, only decreasing slightly at the very highest dispersal rates, when source-sink dynamics become so strong as to detrimentally impact source population sizes. Mutations, with no dispersal, also results in an increased proportion of species that persist, by allowing for evolutionary rescue (Gomulkiewicz & Holt 1995) as species change their environmental optima through adaptation to new environmental conditions (Fig. 1b, 2).

When species both disperse and evolve their environmental optima, we find that these processes generally conflict in their contributions to the maintenance of biodiversity in changing conditions (Fig. 2). That is, we see that almost all combinations of dispersal and mutation result in a reduction in the proportion of species that persist, compared to the persistence that is possible with one of the two processes acting in isolation. First focusing on analogue environments, with high mutation rates (≥0.03), dispersal generally reduces the probability of evolutionary rescue, and so reduces the proportion of species that persist (Fig. S7a, upper-left quadrant). In contrast, mutations can either increase or decrease the proportion of species that persist with a given dispersal rate. In particular, we see that all but the very highest mutation rates reduce species persistence when dispersal rates are intermediate (Fig. S7a, lower-left quadrant). For example, when dispersal is 0.01, increasing mutation rates from 0 to 0.03 reduces the number of species that persist regionally from 0.74 to 0.59 (Fig. 2a). Likewise, intermediate dispersal rates reduce the effectiveness of intermediate mutation rates in preserving species; with a mutation rate of 0.03, the proportion of species that persist decreases from 0.75 when dispersal is 0 to 0.59 when dispersal is 0.01. It is only with extremely high rates of dispersal (≥0.01) and intermediate mutation rates (0.01 or 0.03) that persistence is greater when mutations and dispersal combine, compared to what is possible with either process in isolation (Fig. S7a, upper-right quadrant).

This antagonistic interaction between dispersal and mutations occurs as the result of monopolization effects (De Meester *et al.* 2016), whereby species that are able to adapt faster can remain in place as the environment changes, making it harder for slower

adapting species to persist by shifting their distributions. Differences in the speed of adaptation are an emergent property of our stochastic model: the first species in which an advantageous mutation arises, and spreads will increase in number, which increases the population scaled mutation rate and reduces genetic drift, leading to a positive feedback loop in terms of potential for adaptation. In contrast, species that by chance don't receive adaptive mutations early on will suffer from maladaptation and decrease in size which leads to a negative feedback loop (Bürger & Lynch 1995; Osmond & Klausmeier 2017). As species are lost from the landscape, dispersal allows the remaining species to expand their ranges (Fig. 3a) taking advantage of the reduced interspecific competition; thus, we see the greatest range expansions when dispersal rates are intermediate and low mutation rates result in low species persistence.

A signature of the monopolization effect is interspecific variation in the degree to which species expand their ranges (Fig. 1c, 3b). When dispersal or mutations occur in isolation, we see relatively little variation in the number of patches that the remaining species occupy. This variation increases with increasing rates of dispersal (Fig. 3b), but intermediate mutation rates result in even greater variation in range size change at any given dispersal rate because they facilitate monopolization. Monopolization occurs when faster evolving species expand their distributions as conditions change (Fig. 1c), with adaptation allowing them to remain in place on their trailing (e.g., warm) edge, and dispersal allowing them to expand their ranges on their leading (e.g., cold) edge (Fig. 3c). This monopolization of the landscape by a few species causes the other species to go extinct or to be restricted to only a few patches. Consequently, we see the greatest

difference in interspecific variation in range size compared to the no mutation scenarios when mutation and dispersal rates are intermediate (Fig. 3b). This corresponds to the region of parameter space where dispersal and mutations have the greatest conflict in the contribution to species persistence (Fig. S7a).

An additional signature of the monopolization effect is that we see leading range boundaries shifting faster than trailing range boundaries, with intermediate mutations and dispersal (Fig. 1c, 4c). Species hold onto their trailing edge (i.e., warm boundary) by adapting as the environment changes, but the range expands on the leading edge (i.e., cold boundary) through dispersal. This pattern corresponds with the observation that species ranges tend to shift faster at leading edges compared to trailing edges in response to climate change (Sunday *et al.* 2012; Ordonez & Williams 2013; Poloczanska *et al.* 2013) (but see Robinson *et al.* 2015).

In non-analogue conditions, that is, regions where the final environmental conditions exceed those present in the initial metacommunity, mutations are equally effective at preserving species diversity, but dispersal is far less effective (Fig. 2b). Furthermore, dispersal reduces the effectiveness of mutations for preserving species diversity (Fig. 2b) because it reduces rates of adaptation through gene swamping (Fig. S4). The exception is when mutations do not occur. In this case, persistence in non-analogue environments increases with dispersal, but this is simply due to the fact that high dispersal facilitates source sink dynamics so that species are able to persist in non-analogue patches that are in close proximity to analogue patches, where population growth rates are positive. This

follows the conclusions of Norberg et al. (2012), that biodiversity maintenance will depend most on evolutionary processes in regions of the planet where climate change creates non-analogue conditions (Mahony *et al.* 2017), and that dispersal has the potential to reduce evolutionary rescue in these regions. Maintaining biodiversity in regions that have no current climate analogue will likely be a major challenge. However, as non-analogue climatic regions are expected to cover a minority of the globe (Mahony *et al.* 2017), we have elected to focus mostly on analogue regions here.

Biotic interactions and persistence under change

We find that diversity losses result from asymmetric responses of the species to environmental change that are driven by competition between species. Previous work has shown that these asymmetries can also arise from trophic interactions (Thompson & Gonzalez 2017). This effect of competition is evident when we compare our results with the case when species do not interact (Fig. S5); without interspecific interactions all species are able to persist, except in the limiting cases when dispersal or mutation rates are so low that persistence is not possible. Competition results in asymmetric responses to environmental change through two mechanisms. First, it causes unequal reductions in equilibrium abundances so that some species have larger population sizes than others, and so that all species have smaller population sizes than they would in isolation. Species with larger populations are more likely to persist under environmental change because they tend to contain more genetic variation, making adaptation faster (Gomulkiewicz & Holt 1995) and because they produce a greater number of dispersing individuals, making range shifts more likely (Thompson & Gonzalez 2017). Second, competition alters the response of species to

local environmental conditions and environmental change (Ives & Cardinale 2004; Alexander *et al.* 2015). This leads to interspecific differences in the ability of species to colonize new habitats in order to track environmental change through species sorting. This is because the ability of a species to successfully colonize a habitat patch that has suitable abiotic environmental conditions also depends on the resident species that are already present. This resident community acts as a filter, allowing some species to colonize, while repelling others, even if both colonizing species are equally adapted to the local environment.

The interaction between dispersal and biotic interactions

Dispersal acts to maintain biodiversity as the environment changes by providing spatial insurance, whereby species shift their distributions to ensure that they are locally adapted. Without interspecific competition, relatively low rates of dispersal (dispersal ≥ 0.001) are sufficient to allow almost all species to persist as the environment changes (Fig. S5). However, with interspecific competition, higher rates of dispersal are required for maintaining biodiversity (Fig. 2a). This occurs because high rates of dispersal generate source-sink dynamics, which counteract the effects of biotic interactions in two ways. First, dispersal spreads populations out across more patches (Fig. S6a), reducing the strength of intraspecific competition, which increases regional population sizes (Fig. S6b; Holt 1985). These larger regional population sizes make the species less prone to extinction as conditions change. Second, dispersal allows species to maintain sink populations in marginal conditions. These marginal conditions are generally on the edge of a species' range, where abiotic conditions are suboptimal, but persistence would be possible without

competition. Dispersal overcomes this resistance of the biotic community by providing a constant flow of immigrants. Then, if the environment changes, these populations are already in place and pre-adapted to the new conditions which makes them new potential source populations. We see that the positive effect of dispersal on regional species diversity increases with dispersal, only decreasing slightly at the very highest dispersal rates, when source-sink dynamics become so strong as to detrimentally impact source population sizes. These results are entirely consistent with Thompson and Gonzalez (2017) where high rates of dispersal reduced the degree to which biotic interactions resulted in biodiversity loss and food web reorganization in changing environmental conditions. Still, this beneficial effect of source sink dynamics is somewhat unexpected, as we tend to consider sink populations to be a drain on the overall metapopulation. However, our results suggest that source sink dynamics may play a key role in providing spatial insurance in changing environments.

The interaction between evolution of environmental optima and biotic interactions

In contrast, mutations maintain biodiversity by facilitating evolutionary rescue, whereby environmental optima shift through mutation and selection to ensure that species are locally adapted. Without interspecific competition, moderate mutation rates are sufficient for maintaining all species as the environment changes (Fig. S5). With competition, higher rates are required (Fig. 2a). This occurs because competition reduces population sizes, increasing drift and resulting in fewer mutations for a given mutation rate (Osmond & de Mazancourt 2012). Of course, it is possible that biotic interactions could also increase the potential for evolutionary rescue if these interactions select against maladapted individuals

(Osmond & de Mazancourt 2012; Osmond *et al.* 2017). However, in our case this selective boost does not occur. Rather, competition acts to slow down rates of evolutionary rescue by reducing population sizes.

Dispersal, evolution of environmental optima, and biotic interactions

When dispersal, mutations, and competition are combined, monopolization effects are possible, which reduce the ability of spatial insurance and evolutionary rescue to preserve regional biodiversity. This occurs when mutation and dispersal rates are intermediate (Fig. 2a) and is only possible because of interspecific competition. Competition leads to interspecific differences in population sizes. Species with larger population sizes are more likely to adapt to the changing conditions and they have a higher probability of colonizing new habitats because they produce more dispersers. These species begin to occupy more space on the landscape, to the detriment of their competitors, which can lead to extinctions and the loss of diversity (Fig. 2a). Previous consideration of the monopolization hypothesis has mostly focused on static or fluctuating environments, with studies highlighting the potential for early colonizers of a habitat to become locally adapted and then repel later arriving colonists (De Meester *et al.* 2002; Loeuille & Leibold 2008; Vanoverbeke *et al.* 2015; De Meester *et al.* 2016; Leibold *et al.* n.d.). However, Urban et al. (2011) suggested that monopolization effects may impede species sorting under climate change, and our results support this prediction.

General discussion

Our finding that intermediate to high dispersal rates in evolving species assemblages can preserve biodiversity under environmental change contrasts with the conclusions of Norberg et al. (2012). They used an eco-evolutionary model to investigate how dispersal and evolution of environmental optima could jointly impact the maintenance of biodiversity in a warming world and found that dispersal generally did not act to preserve biodiversity. Rather, it resulted in reduced rates of adaptation. This difference from our findings may be due to the fact that the highest dispersal rate explored by Norberg et al. (2012) was 0.01, which is relatively low and corresponds to the region of parameter space in our model when dispersal is limiting or where strong monopolization effects occur (Fig. 2a). Indeed, over the range of dispersal rates explored by Norberg et al. (2012), our findings agree, that with intermediate mutation rates, dispersal reduces the number of species that persist.

Although we find that high rates of either dispersal or mutation are sufficient to preserve almost all species in analogue environments (Fig. 2a), we believe that this is unlikely to occur in many natural communities. Instead, we expect that rates will be limiting enough so that dispersal and evolution interactively determine whether species are able to persist under environmental change. This is especially likely for organisms with long generation times, small populations, and limited dispersal ability, or in fragmented landscapes. Even in bacterial monocultures, where we expect rapid adaptation to occur, evolutionary rescue is facilitated by dispersal (Bell & Gonzalez 2011). Likewise, current evidence for evolutionary rescue in communities of interacting species suggests that both adaptation and dispersal play key roles (Low-Décarie *et al.* 2015).

We expect that monopolization effects, resulting from the interaction between dispersal, evolutionary change, and biotic interactions should be a fairly general phenomenon in changing environments. The degree to which dispersal and mutation rates have conflicting contributions to the maintenance of biodiversity under environmental change depends on the specific parameters in our model but is pervasive across all the combinations of parameter strengths in our sensitivity analyses (Fig. S1, S2). Of course, additional complexities that are not captured by our model may modify these effects. We suspect that interspecific variability in dispersal and mutation rates should lead to stronger monopolization effects (Norberg *et al.* 2012). However, if high variability in rates erodes equalizing coexistence mechanisms (Chesson 2000), pre-change diversity may be reduced, thus precluding strong monopolization effects. Furthermore, we also know that dispersal rates and distance are under selection in changing environments (Kubisch *et al.* 2013) as well as mutation rates (Cobben *et al.* 2017) and this has the potential to also increase the likelihood of interactions between dispersal and the evolution of the abiotic niche. Despite these open questions, our findings clearly highlight the fact that dispersal and evolution of environmental optima can interact to produce monopolization effects in the community context, and that ignoring this interaction may lead us to overpredict species persistence under future environments.

Conclusions

Climate change poses a major risk for biodiversity (Urban 2015) and is already causing the reorganization of ecosystems globally (Walther 2010). Whether species will keep pace and

persist in this changing climate remains uncertain (Loarie *et al.* 2009) but is expected to depend on both ecological and evolutionary processes (Norberg *et al.* 2012; Urban *et al.* 2016). To date, ecological and evolutionary contributions to the maintenance of biodiversity have largely been studied independently. Indeed, our results clearly highlight how evolutionary rescue and spatial insurance can each independently allow species to persist in changing conditions. However, in combination these processes interact, creating the potential for monopolization effects, which can result in the loss of biodiversity. Together, our findings provide a more general understanding of the processes that act to maintaining diversity in a changing world (Fig. 4). This understanding highlights the need for more focus and study on the interactions between ecological and evolutionary processes and how they jointly determine how species and communities will respond to future environmental conditions.

Acknowledgements

We would like to thank Matthew Osmond, Luc De Meester, Sally Otto, Mary O'Connor and Nathaniel Sharp for valuable discussions and feedback. PLT is supported by Killam and NSERC Postdoctoral fellowships. This is publication ISEM-YYYY-XXX of the Institut des Sciences de l'Evolution - Montpellier.

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Figure Legends

Figure 1. Illustration of how dispersal and evolution of environmental optimum, in isolation (a,b, respectively) and in combination (c), affect how species respond to environmental change. Circles and diamonds are paired for each species and indicate position and size of each population prior to and after environmental change, respectively. Species with circles but not diamonds failed to persist. The colour shows the mean environmental optimum in each population. Panel a shows a scenario where dispersal is intermediate (0.01) and the mutation rate is 0; here, species respond to environmental change by shifting their distributions to maintain the match between their phenotype and their local environmental conditions. Panel b shows a scenario where dispersal is 0 and mutation rates are intermediate (0.03); here species respond to environmental change through adaptation (change in colour), with no change in their distribution. Panel c shows a scenario where dispersal (0.01) and mutation (0.03) rates are both intermediate; here species respond through a combination of shifting their distributions and through adaptation. Results shown are from one representative simulation run with standard parameter values (Table S1). To explore additional combinations of dispersal and mutations in a Shiny app visit - https://shiney.zoology.ubc.ca/pthompson/Meta_eco_evo_shiny/.

Figure 2. The proportion of species that are maintained following environmental change depending on dispersal and mutation rates (colour). The proportion of species maintained was calculated as the number of species that were present in the region (a - analogue or b - non-analogue) after environmental change, divided by the number of species that were

present before. Therefore, species that were only present in analogue patches would not be included in the non-analogue diversity. The lines show the median value across 50 replicate simulations with standard parameter values (Table S1) and the bands show the interquartile range. This figure shows patterns for regional scale diversity. Local scale patterns are shown in Figure S3.

Figure 3. Change in the average number of habitat patches occupied (range size) by the species that persist during environmental change (a), the interspecific variation in range size change, excluding species that go extinct (b), and the leading vs. trailing edge asymmetry of the range expansion (c), depending on dispersal and mutation (colour) rates. Positive (negative) values of range change asymmetry indicate that the centroid of the range shifted towards warmer (colder) conditions, relative to the mean environmental optima of the species. The lines show the median value across 50 replicate simulations with standard parameter values (Table S1) and the bands show the interquartile range. Analogue and non-analogue regions are included together in these estimates. The lines for mutation = 0 do not extend to the lowest dispersal rates because all species went extinct during environmental change.

Figure 4. Conceptual illustration of how dispersal and the evolution of environmental optima independently and interactively act to maintain biodiversity in changing environmental conditions. Panel a shows the distribution and abundance of three species spanning a climate gradient (e.g., warm to cold). Mean position shown by vertical dashed lines. Each species is locally adapted to a different part of this gradient as indicated by the

warmth of the color of the curves. Panels b, c, and d show hypothetical scenarios after the environment has changed. In panel b, with dispersal but no evolution of environmental optima, the species persist by shifting upwards (spatial insurance). In panel c, with evolution of environmental optima but no dispersal, the species persist by adapting to the changed conditions (change in color - evolutionary rescue), but do not shift their ranges. In panel d, with both dispersal and evolution, the two outer species evolve faster than the middle species, holding onto their initial trailing edge through adaptation but expanding on their leading edge through dispersal (monopolization). By monopolizing the landscape, they drive the middle species extinct (dashed curve). Panel e shows how dispersal and the evolution of environmental optima each allow for species persistence via spatial insurance and evolutionary rescue, respectively. But together they can lead to monopolization effects, which can reduce biodiversity in changing environments.

Figure 1

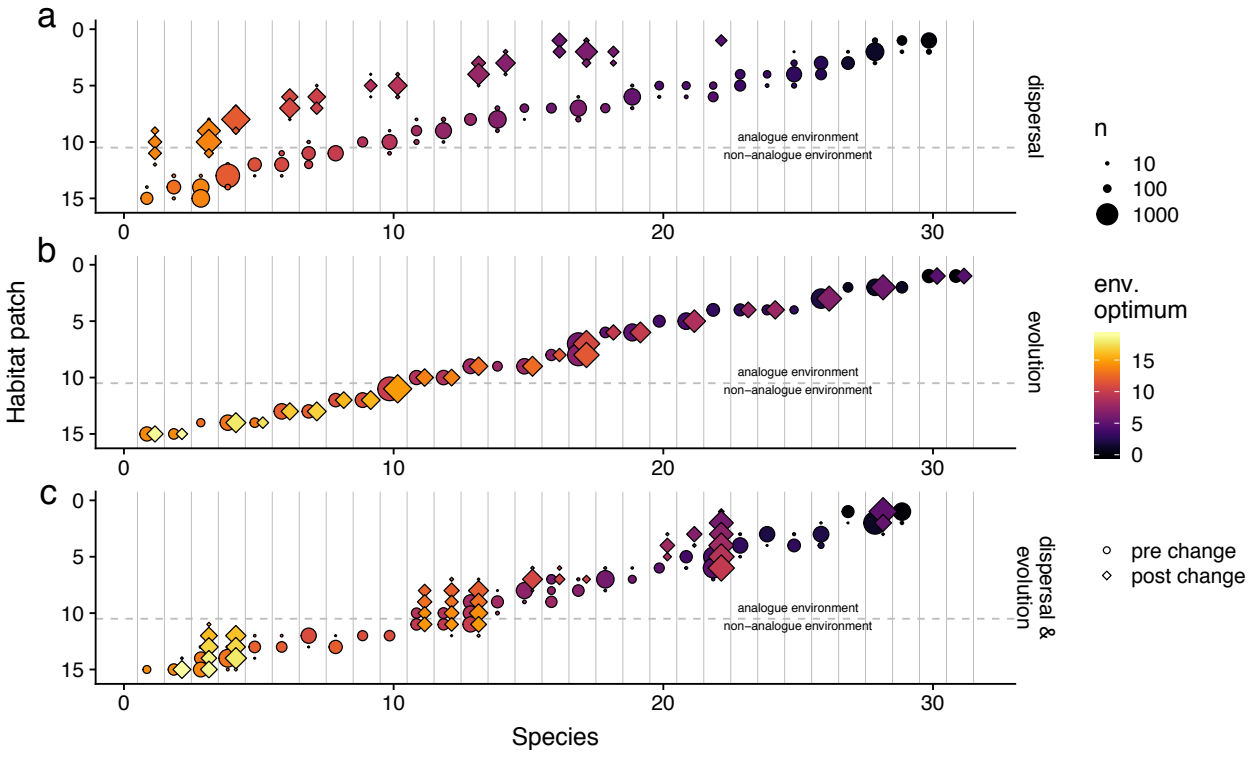

a
b
c
Habitat patch
Species
0
5
10
15
0
10
20
30
analogue environment
non−analogue environment
dispersal
evolution
dispersal & evolution
n
10
100
1000
env. optimum
15
10
5
0
pre change
post change

Figure 2

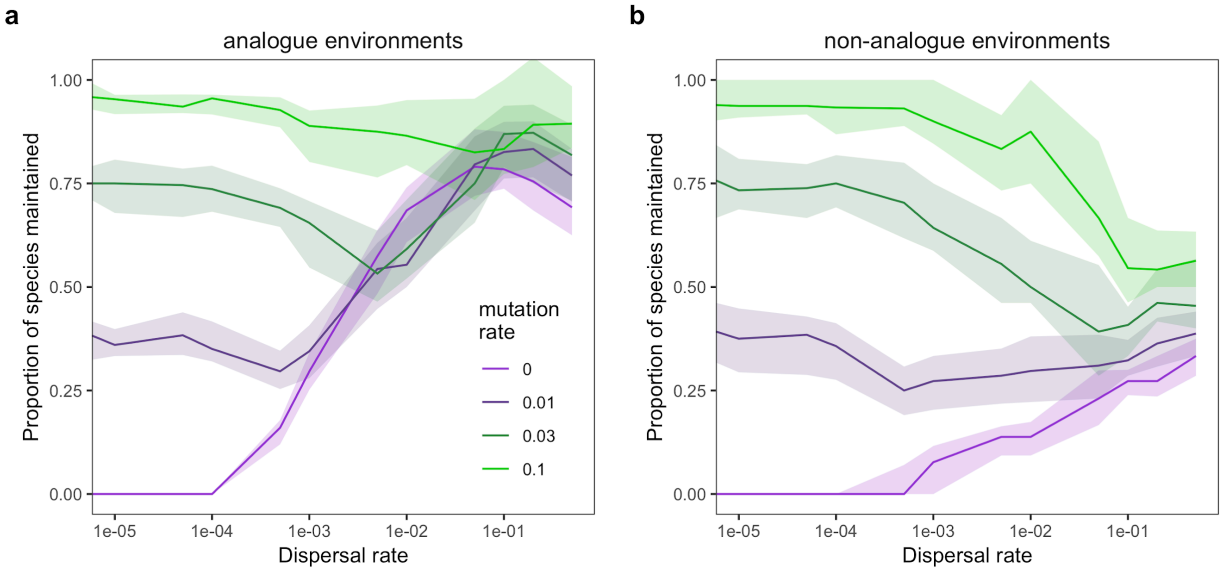

a
analogue environments
Proportion of species maintained
1.00
0.75
0.50
0.25
0.00
1e-05
1e-04
1e-03
1e-02
1e-01
Dispersal rate
mutation rate
0
0.01
0.03
0.1
b
non-analogue environments
Proportion of species maintained
1.00
0.75
0.50
0.25
0.00
1e-05
1e-04
1e-03
1e-02
1e-01
Dispersal rate

Figure 3

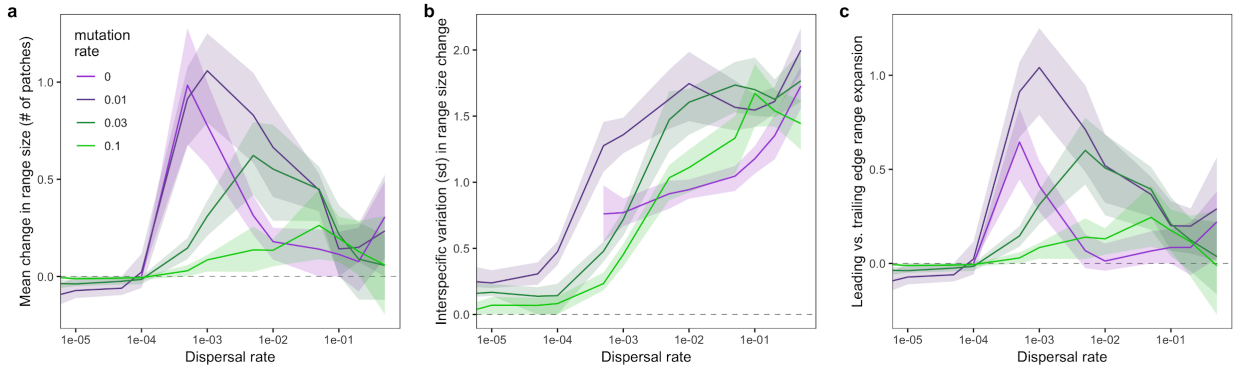
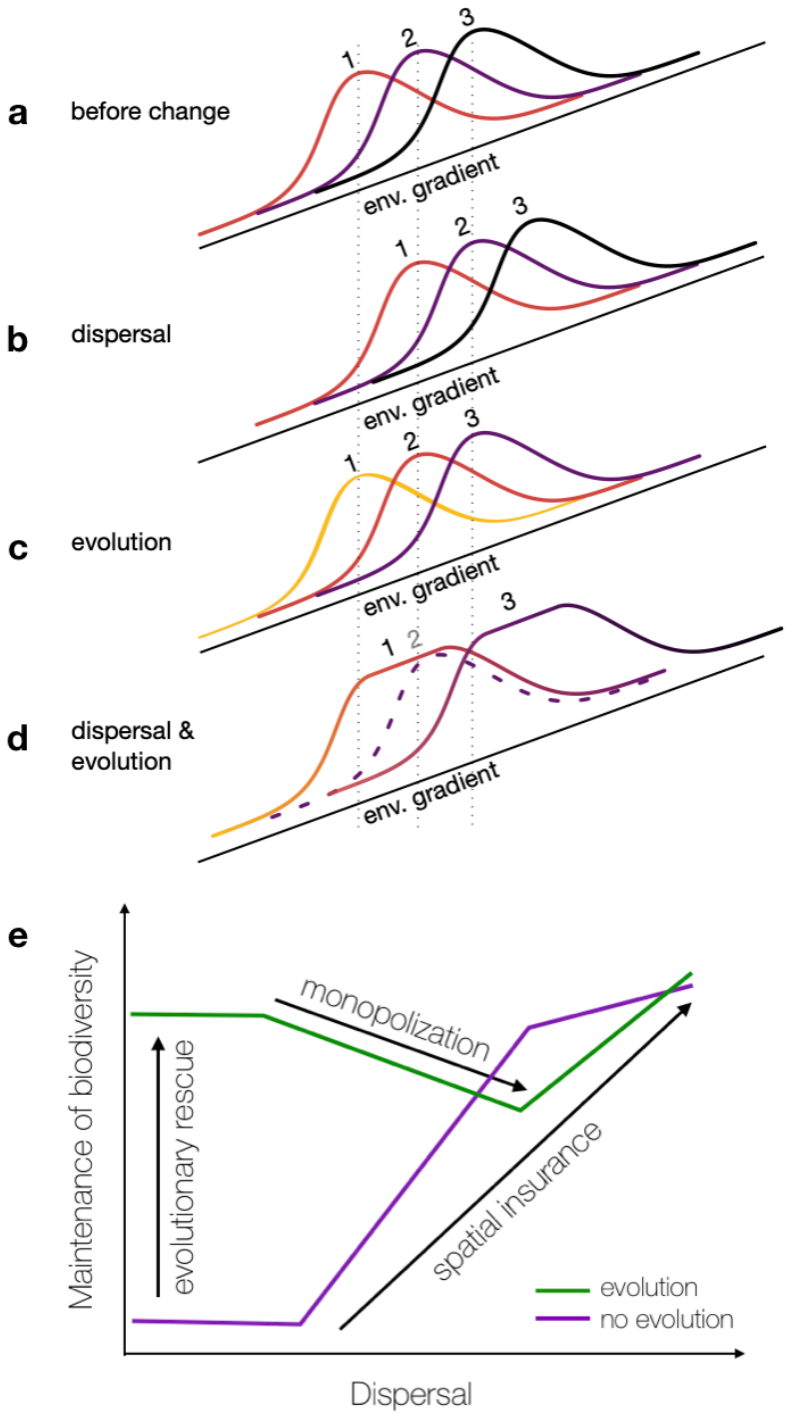

a
mutation rate
0
0.01
0.03
0.1
Mean change in range size (# of patches)
1.0
0.5
0.0
1e-05
1e-04
1e-03
1e-02
1e-01
Dispersal rate
b
Interspecific variation (sd) in range size change
2.0
1.5
1.0
0.5
0.0
1e-05
1e-04
1e-03
1e-02
1e-01
Dispersal rate
c
Leading vs. trailing edge range expansion
1.0
0.5
0.0
1e-05
1e-04
1e-03
1e-02
1e-01
Dispersal rate

Figure 4


a
before change
1
2
3
env. gradient
b
dispersal
1
2
3
env. gradient
c
evolution
1
2
3
env. gradient
d
dispersal &
evolution
1
2
3
env. gradient
e
Maintenance of biodiversity
evolutionary rescue
monopolization
spatial insurance
evolution
no evolution
Dispersal