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

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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 demonstrate how dispersal and adaptation to environmental change independently and interactively contribute to biodiversity maintenance. Dispersal provides spatial insurance, whereby species persist on the landscape by shifting their distributions to track favourable conditions. In contrast, adaptation allows species to persist by allowing for evolutionary rescue. But, when species both adapt and disperse, these processes do not combine positively to affect biodiversity maintenance, even if they do increase the persistence of individual species. This occurs because faster adapting species evolve to hold onto their initial ranges (i.e. monopolization effects), 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. By demonstrating how dispersal and adaptation each independently and interactively contribute to the maintenance of biodiversity, we provide a framework that links the theories of spatial insurance, evolutionary rescue, and monopolization. This highlights the expectation that the maintenance of biodiversity in changing environments depends jointly on rates of dispersal and adaptation, and critically, the interaction between these processes.

Significance Statement

Species can persist when the environment changes by shifting their ranges through dispersal or by adapting to the new conditions that they experience. Thus, we might expect that dispersal and adaptation in combination would increase persistence. Using a simulation model, we show that this may not be the case. Instead, competition between species causes dispersal and adaptation to have conflicting contributions to biodiversity maintenance. Dispersal and adaptation each independently increase biodiversity maintenance under environmental change. But when species both disperse and evolve, faster evolving species persist in their current ranges, preventing slower adapting species from shifting their ranges to track environmental change. These findings highlight the need to consider ecological and evolutionary processes together, or we risk underestimating how global change will impact biodiversity.

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 (1) because of the unprecedented magnitude of environmental change resulting from human activities (2). 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 (3). 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 (4-6). 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 (7). 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 (8-10). In reality, both ecological and evolutionary processes are operating in concert, and are likely interacting, when ecological communities are faced with environmental change (11). We know that dispersal can affect the likelihood of evolutionary rescue. Evolutionary rescue can be promoted by dispersal across an environmental gradient (12) 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 (13, 14). 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
(15). This is a special case of evolutionary meditated priority effects, which have been termed monopolization effects (16-18), 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. (19) 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. (11) found that evolution, but not dispersal, minimized extinction risks. Surprisingly, 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 (7) and another simulation study that tested the role of dispersal in maintaining biodiversity in the absence of evolution (20). Thus, we currently lack a single theoretical framework that encompasses the theories of evolutionary rescue, spatial insurance, and monopolization and how they relate to one another.

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 (21). In contrast, evolutionary rescue should be possible under both analogue and non-analogue conditions (11). Monopolization effects should occur whenever evolution and dispersal combine (18).

Results and Discussion

Overall, we find that dispersal and adaptation both independently allow species to persist during environmental change (Fig. 1a, b), consistent with the spatial insurance and evolutionary rescue hypotheses and recent findings (7, 8, 20, 22). 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 (7), 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. Evolution, with no dispersal, also results in an increased proportion of species that persist, by allowing for evolutionary rescue (8) 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 adaptive potential 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 adaptive potential (≥1.08e-4), dispersal generally reduces the probability of evolutionary rescue, and so reduces the proportion of species that persist (Fig. S1a, upper-left quadrant). In contrast, adaptation 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 levels of adaptive potential reduce species persistence when dispersal rates are intermediate (Fig. S1a, lower-left quadrant). For example, when dispersal is 0.01, increasing adaptive potential from 0 to 1.08e-04 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 levels of adaptive potential in preserving species; with an adaptive potential of 1.08e-04, 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 adaptive potential (3.6e-05 or 1.08e-04) that persistence is greater when evolution and dispersal combine, compared to what is possible with either process in isolation (Fig. S1a, upper-right quadrant).

This antagonistic interaction between dispersal and adaptive potential occurs as the result of monopolization effects (18), 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 adaptive potential 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 (23, 24). 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 adaptive potential 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 adaptation 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 adaptive potential results 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 adaptation scenarios when adaptive potential and dispersal rates are intermediate (Fig. 3b). This corresponds to the region of parameter space where dispersal and adaptation potential have the greatest conflict in the contribution to species persistence (Fig. S1a).

An additional signature of the monopolization effect is that we see leading range boundaries shifting faster than trailing range boundaries, with intermediate adaptive potential 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 (25-27) (but see 28).

In non-analogue conditions, that is, regions where the final environmental conditions exceed those present in the initial metacommunity, adaptive potential is equally effective at preserving species diversity, but dispersal is far less effective (Fig. 2b). Furthermore, dispersal reduces the effectiveness of adaptive potential for preserving species diversity (Fig. 2b) because it reduces rates of adaptation through gene swamping (Fig. S2). The exception is when adaptive potential is zero. 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. (11), that biodiversity maintenance will depend most on evolutionary processes in regions of the planet where climate change creates non-analogue conditions (29), 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 (29), 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 (20). This effect of competition is evident when we compare our results with the case when species do not interact (Fig. S3); without interspecific interactions all species are able to persist, except in the limiting cases when dispersal or adaptive potential is 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 (8) and because they produce a greater number of dispersing individuals, making range shifts more likely (20). Second, competition alters the response of species to local environmental conditions and environmental

change (6, 30). 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. S3). 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. S4a), reducing the strength of intraspecific competition, which increases regional population size (Fig. S4a; 31) . 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 (20) 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, adaptation acts to 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 levels of adaptive potential are sufficient for maintaining all species as the environment changes (Fig. S3). With competition, higher levels are required (Fig. 2a). This occurs because competition reduces population sizes, increasing drift and resulting in fewer mutations for a given level of adaptive potential (32). Of course, it is possible that biotic interactions could also increase the potential for evolutionary rescue if these interactions select against maladapted individuals (32, 33). 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, adaptation, 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 adaptive potential 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 (16, 18, 34-36). However, Urban et al. (17) suggested that monopolization effects may impede species sorting under climate change, and our results support this prediction.

General discussion

Our findings allow us to link the concepts of spatial insurance, evolutionary rescue, and monopolization within a common theoretical framework (Fig. 4). These processes have each been demonstrated to independently mediate the persistence of species in changing environments (7, 8, 37), but how they relate and interact with each other has not been previously shown. Critically, our study explores a range of dispersal rates and levels of adaptive potential that covers the full range of species persistence outcomes: from full extinction to levels where further increases in dispersal or adaptive potential would not increase persistence. This distinguishes our study from that of Norberg et al. (11) who used a conceptually similar model to explore how

dispersal and evolution interactively affect community responses to climate change. Norberg et al. (11) demonstrated clear benefits of evolutionary responses to climate warming, but not spatial insurance. In fact, they found negative effects of dispersal on species persistence, thus precluding any potential for monopolization to reduce the effectiveness of spatial insurance. The lack of a positive effect of dispersal on species persistence is surprising, and contrasts with our findings and those of previous studies that have demonstrated spatial insurance effects (7, 20). However, it seems likely that the negative effect of dispersal in Norberg et al. (11) is due to the fact that environmental change appears to have had a relatively low impact on population performance relative to the effects of competition in their model. Without competition, all species persist and are present in all patches in the landscape, before and after environmental change. Thus, species do not need to shift their distributions in order to persist, but they can be driven extinct by competition with another species that does track its environmental optima through dispersal. Such competitive exclusion is likely in their model because of the assumption of equal inter- and intraspecific competition, which precludes stable coexistence at the local scale. Thus, the contrast between models highlights the fact that the outcome of dispersal is likely to depend on the balance in strength between the direct effects of environmental conditions and the density dependent effects of competition on the response of species to environmental change. Dispersal should have little benefit for species persistence if species distributions and the composition of species are predominantly structured by biotic interactions. But we predict that the contribution of dispersal to the maintenance of biodiversity should increase with the degree to which environmental change impacts population performance.

Although we find that high levels of either dispersal or adaptive potential 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 (12). Likewise, current evidence for evolutionary rescue in communities of interacting species suggests that both adaptation and dispersal play key roles (22).

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 adaptive potential 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. S6, S7). Of course, additional complexities that are not captured by our model may modify these effects. We suspect that interspecific variability in dispersal and adaptive potential should lead to stronger monopolization effects (11). However, if high variability in rates erodes equalizing coexistence mechanisms (38), 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 (39) as well as mutation rates (40) and this has the potential to also increase the likelihood of interactions between dispersal and the evolution of the abiotic niche. Specifically, dispersal is well known to

evolve during range shifts (39, 41). However, dispersal can also be highly plastic with respect to environmental gradients (42) and other species (43). While these complexities are beyond the scope of the present study, future theoretical and empirical work will have to account for the eco-evolutionary details of the dispersal process. 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 (44) and is already causing the reorganization of ecosystems globally (45). Whether species will keep pace and persist in this changing climate remains uncertain (46) but is expected to depend on both ecological and evolutionary processes (1, 11). 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.

Methods

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. This optimum determines the conditions under which reproduction is maximized in the absence of competition, and this growth rate decreases following a gaussian response curve as the mismatch between the optimum and the local environment increases. 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 (39, 47).

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 levels of adaptive potential to ask how this affects the maintenance of biodiversity in the metacommunity over this period of environmental change. The formal specification of the model, and further details of the simulations are given in SI Appendix.

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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 adaptive potential is zero; 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 adaptive potential is intermediate (1.08e-04); 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 adaptive potential (1.08e-04) 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 adaptive potential 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 adaptive potential (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 S5.

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 adaptive potential (colour). 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 adaptive potential = 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

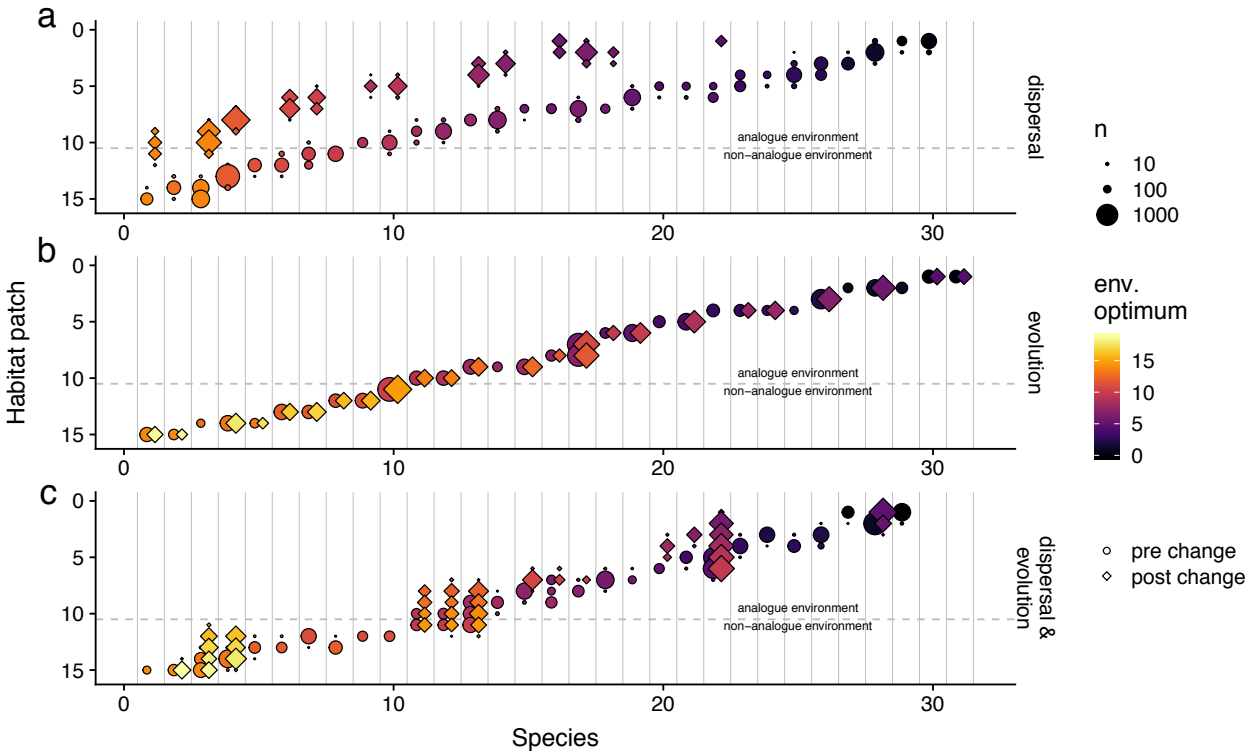

a
b
c
Habitat patch
Species
0
5
10
15
0
10
20
30
analogue environment
non−analogue environment
dispersal
evolution
dispersal &
evolution
n
10
100
1000
env.
optimum
15
10
5
0
pre change
post change

Figure 2

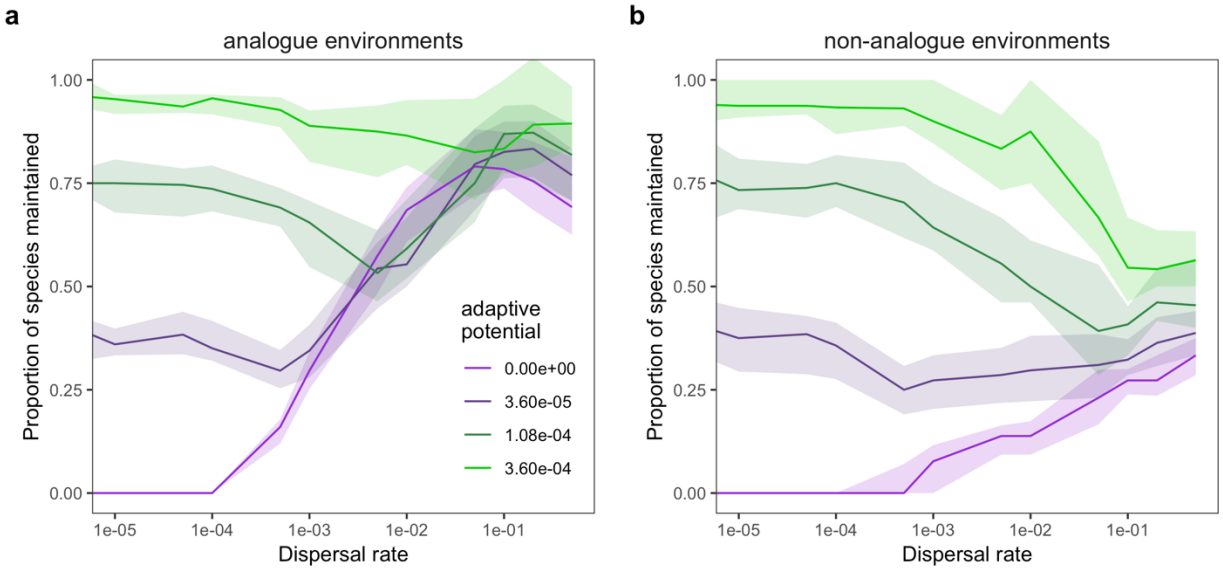

a
analogue environments
Proportion of species maintained
1.00
0.75
0.50
0.25
0.00
1e-05
1e-04
1e-03
1e-02
1e-01
Dispersal rate
adaptive potential
0.00e+00
3.60e-05
1.08e-04
3.60e-04
b
non-analogue environments
Proportion of species maintained
1.00
0.75
0.50
0.25
0.00
1e-05
1e-04
1e-03
1e-02
1e-01
Dispersal rate

Figure 3

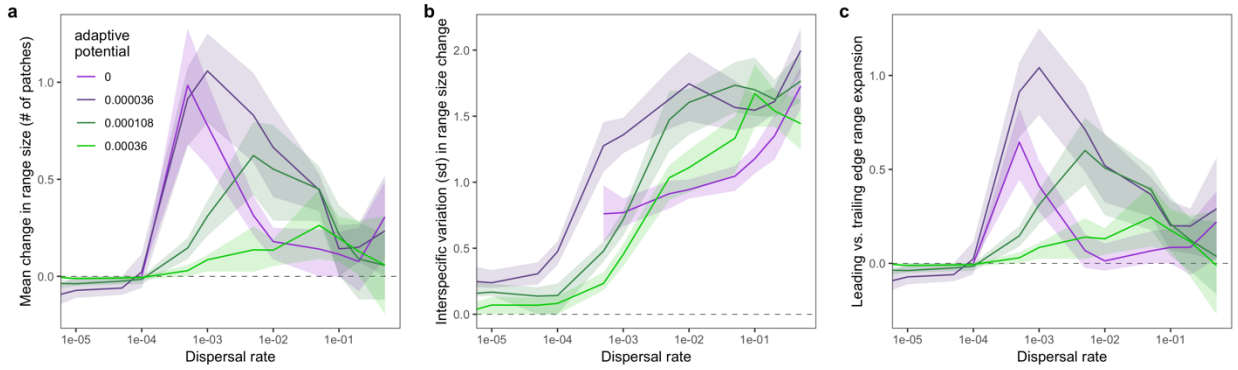
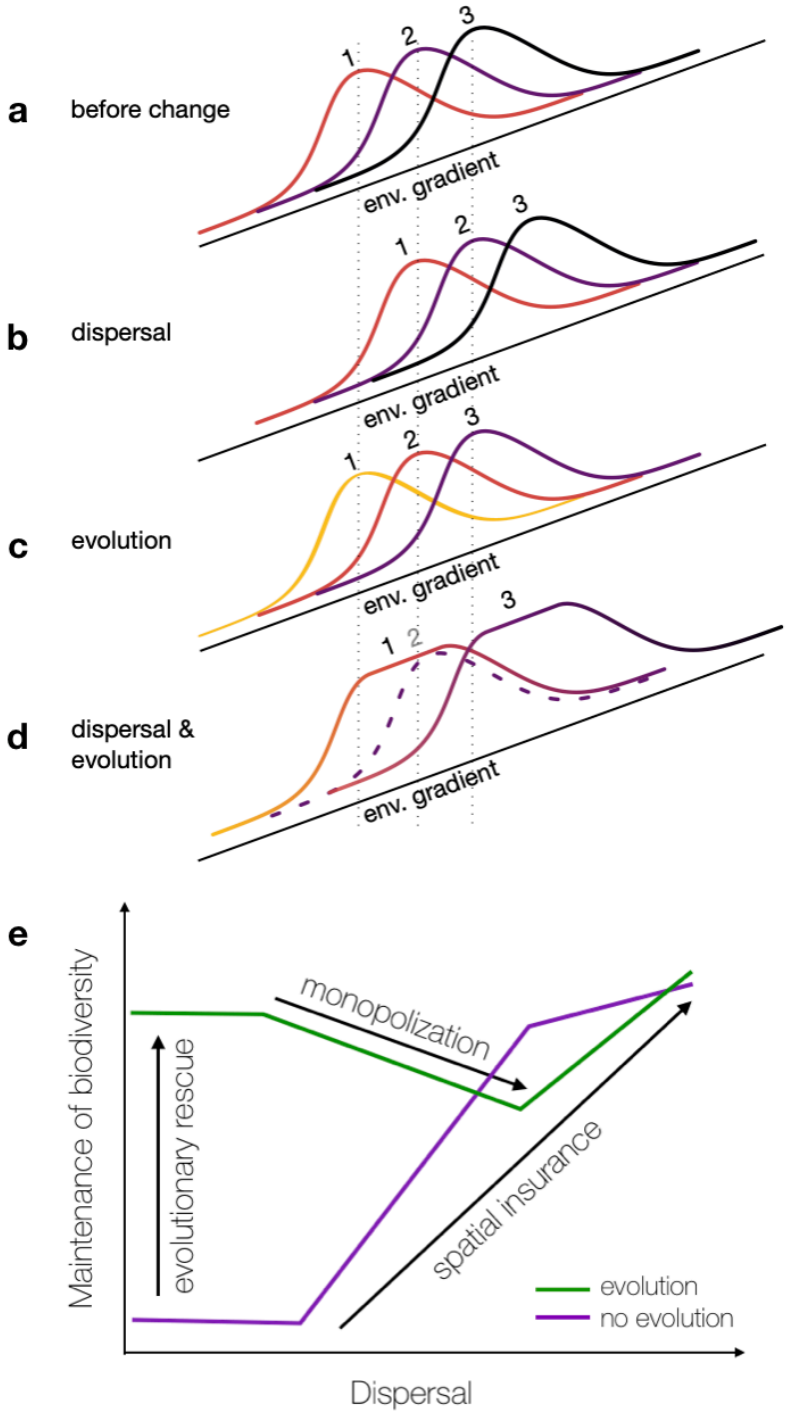

a
adaptive potential
0
0.000036
0.000108
0.00036
Mean change in range size (# of patches)
1.0
0.5
0.0
1e-05
1e-04
1e-03
1e-02
1e-01
Dispersal rate
b
Interspecific variation (sd) in range size change
2.0
1.5
1.0
0.5
0.0
1e-05
1e-04
1e-03
1e-02
1e-01
Dispersal rate
c
Leading vs. trailing edge range expansion
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