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Dispersal evolution alters evolution-mediated priority effects in a metacommunity

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Biologists have long sought to predict the distribution of species across landscapes to understand biodiversity patterns and dynamics. These efforts usually integrate ecological niche and dispersal dynamics, but evolution can also mediate these ecological dynamics. Species that disperse well and arrive early might adapt to local conditions, which creates an evolution-mediated priority effect that alters biodiversity patterns. Yet, dispersal is also a trait that can evolve and affect evolution-mediated priority effects. We developed an individual-based model where populations of competing species can adapt not only to local environments but also to different dispersal probabilities. We found that lower regional species diversity selects for populations with higher dispersal probabilities and stronger evolution-mediated priority effects. When all species evolved dispersal, they monopolized fewer patches and did so at the same rates. When only one of the species evolved dispersal, it evolved lower dispersal than highly dispersive species and monopolized habitats once freed from maladaptive gene flow. Overall, we demonstrate that dispersal evolution can shape evolution-mediated priority effects when provided with a greater ecological opportunity in species-poor communities. Dispersal- and evolution-mediated priority effects probably play greater roles in species-poor regions like the upper latitudes, isolated islands and in changing environments.

This article is part of the theme issue 'Diversity-dependence of dispersal: interspecific interactions determine spatial dynamics'.

1. Introduction

Biologists have long sought to predict how species interact and assemble into communities across landscapes to understand biodiversity patterns and dynamics [1–3]. These efforts have generally focused on combining niche or neutral processes with dispersal dynamics [4–6], including competition–colonization trade-offs [2,7,8]. These efforts almost always exclude the potential for evolution [9–11]. However, adaptation can occur at fine spatial and temporal scales, which can interact with a wide range of ecological processes to shape biodiversity patterns [12–16]. Ecological and evolutionary processes often act analogously on species and genetic diversity (e.g. dispersal and gene flow) and thus can interact at similar spatio-temporal scales to alter predictions generated by ecology or evolution alone [9,17–23]. Therefore, a full understanding of biodiversity patterns across space will often be insufficient without exploring the joint operation of ecological and evolutionary dynamics.

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Ecological and evolutionary dynamics are especially likely to interact during community assembly. Ecological priority effects can occur when the early arrival of a species alters its interactions with late-arriving species, often affecting the potential for coexistence and the ultimate richness and composition of the community [24–26]. If an early-arriving species can evolve and increase its fitness in the local habitat, it may enhance this priority effect [27]. These so-called evolution-mediated priority effects, also called community monopolization [9], can occur when early arrival provides sufficient time for local adaptation to proceed, and these adaptations then limit the effective colonization or final abundances of late-arriving species [9,18,27,28]. These adaptations usually expand the species' original niche to become more generalist and able to occupy a greater range of environments [29,30]. Theory indicates that evolution-mediated priority effects can occur as long as species with high local fitness do not arrive too fast to outcompete the early colonists and prevent them from adapting [28,29]. In addition, theory suggests that evolution-mediated priority effects are robust to many realistic contexts and can occur when species disperse at the same rate such that differences in arrival occur solely through stochasticity, with both sexual and asexual reproduction, and in landscapes of different patch configurations [28,29]. Empirical tests have confirmed the operation of evolution-mediated priority effects under laboratory conditions [31,32], and some natural community and phylogenetic patterns across biogeographic scales are consistent with the operation of evolution-mediated priority effects [33,34]. However, if the diversity of species already adapted to available environments is large and all species disperse well across the metacommunity, then species sorting—the ecological matching of species niches to environments—dominates [29,35,36]. Thus, the diversity of the regional species pool and the degree of connectivity through dispersal determine if and to what extent evolution-mediated priority effects might shape community assembly.

Despite its importance in eco-evolutionary community models, dispersal is usually treated as a static trait that cannot evolve. Yet, dispersal is a trait like any other that can undergo adaptive evolution depending on the relative fitness costs and benefits of dispersing [37–40]. Higher dispersal evolves when dispersal costs are low or under high local intraspecific (also kin) competition, habitat fragmentation, frequent habitat destruction or the availability of new, low-competition patches [41–45]. Dispersal polymorphisms can evolve in response to disruptive selection originating from spatial and temporal environmental heterogeneity, population fluctuations under different population regulations, patch size variation and random patch extinctions [46–48]. The contemporary evolution of dispersal abilities has been documented for a growing list of species, including insects, plants and amphibians [49–53]. Given this capacity, the question emerges: to what extent might dispersal evolve to promote evolution-mediated priority effects, niche expansion and the monopolization of new environments? We might expect that the evolution of increased dispersal of one species will decrease priority effects and thus increase local diversity, whereas the evolution of increased dispersal in all species will decrease priority effects by reducing the difference in timing between species arrivals.

To address this question, we develop an individual-based mainland-island model where populations of competing species not only adapt to local island environments but also can evolve different dispersal probabilities. We quantify the degree to which evolution-mediated priority effects emerge in scenarios with different numbers of competing species, different rates of immigration of species and genotypes and with and without dispersal costs and periodic patch extinction. We expect that as the number of competing species increases, the opportunities will diminish for adaptation before another species adapted to that patch arrives. We predict that increasing immigration from a diverse mainland population will also decrease evolution-mediated priority effects and alter dispersal evolution through maladaptive gene flow. We also expected that dispersal costs and no patch extinction would lead to the evolution of lower dispersal. We were also interested in how variation in genetic variation for dispersal could generate divergent dispersal abilities among competing species and thereby alter the potential for evolution-mediated priority effects. We therefore contrast scenarios where no, all, or one species can evolve dispersal probabilities to understand what happens when the genetic variation needed to evolve dispersal is available to varying degrees in a species pool.

2. Material and methods

(a) Individual-based model

We develop a classic mainland-island model and combine it with a finite island model in which islands freely exchange migrants. The mainland component was chosen to provide a rain of individuals that were variable in their niche, as might be expected for islands, and because this structure can supplement species and genetic diversity on islands while also reducing stochastic effects in small populations. We assume that the recipient islands can then exchange individuals, providing a spatial and environmental context for niche and dispersal evolution.

We consider five island patches along a unidimensional environmental gradient, with environmental values ϵ of 0.20, 0.35, 0.50, 0.65 and 0.80 for patches 1 to 5, respectively. We also model an alternative model with 25 patches arranged along this same gradient but with smaller environmental differences between patches. The full environmental gradient ranges from 0 to 1, but we restrict the patches' environmental values to the range [0.20, 0.80] to avoid boundary artefacts. The island patches do not have an explicit spatial structure and are separated by equal pairwise spatial distances. Each island patch is empty at the onset of simulations and has a carrying capacity, K.

Individuals originate from a mainland that hosts up to five distinct species (25 species in the 25-patch scenario), depending on the assumed number of species in the regional species pool. All species have an identical genetic architecture. Like Leibold *et al*. [30], we use an explicit multi-locus genotype featuring 50 bi-allelic (0/1) loci related to the environmental phenotype and 50 bi-allelic (0/1) loci related to the dispersal phenotype, arranged in a diploid fashion (i.e. 2 × 50 loci for the environmental and

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dispersal phenotypes). The environmental and dispersal phenotypes, e and d, respectively, are calculated as the average of the binary allele values of the environmental and dispersal loci, respectively.

The environmental phenotype of each species inhabiting the mainland exactly matches the environmental value of one of the five island patches (e.g. the environmental phenotype of species 1 matches the environment of patch 1), while the dispersal phenotype of all species that can evolve dispersal matches an initial dispersal probability, δ_{init}. This scenario simulates the realistic scenario where a long-term equilibrium has been reached on the mainland where patches are full, competition is widespread and dispersal is low. To control standing genetic variation within each species on the mainland, all genotypes of a species are derived from a single, randomly generated, ancestral haplotype, with an appropriate ratio of binary alleles to match the prescribed phenotype of that species. Genetic variation is introduced by randomly reshuffling a fraction γ of loci of the ancestral haplotype, without affecting its overall phenotypic value (e.g. '00110' becomes '10010'). In total, 100 reshuffled environmental and dispersal haplotypes per species are created this way. A catalogue of 10 000 diploid genotypes per species is subsequently created by randomly sampling and pairing available environmental and dispersal haplotypes. At each generation and for each patch, a draw from a Poisson distribution with expected value, λ, dictates how many individuals are seeded from the mainland by sampling them from the catalogue of genotypes with replacement. Species inhabiting the mainland are static and do not evolve over the course of the simulation. Hence, dispersal from mainland is independent from the dispersal phenotype of individuals, which only dictates inter-island dispersal.

Whenever a patch hosts at least one individual, a series of local population dynamic steps are executed at each generation. First, the environmental match m_i of each individual i is assessed. The environmental match ranges from 0 to 1 and is solely determined by the match between the individual's environmental phenotype e_i and the environmental value $\epsilon_{\text{patch}(i)}$ of the individual's patch, by means of a squared exponential kernel with scale e_i, acting as the environmental selective pressure (with lower values corresponding to stronger selection),

$$m_i = \exp\left(-\frac{\left(e_i - \epsilon_{\text{patch}(i)}\right)^2}{s}\right).$$

The expected per capita reproductive output r_i depends on individual environmental match m_i, the maximum per capita reproductive potential $r_{\max}$, the local density of individuals N in the considered patch, and the carrying capacity K per patch,

$$r_i = \begin{cases} m_i \cdot \left(r_{\max} \cdot \left(1 - \frac{N}{K}\right) + \frac{N}{K}\right) & \text{if } N \le K \\ m_i \cdot \frac{K}{N} & \text{if } N > K \end{cases}.$$

We assume interspecific and intraspecific competition to be equal. Hence, the local density of individuals N and the carrying capacity K pertain to the density of all species combined. The effective reproductive output of each individual, i, is obtained by drawing from a Poisson distribution with expected value r_i .

We model sexual reproduction. For each individual offspring, a second parent is randomly assigned from the pool of conspecific individuals inhabiting the patch, with the additional condition that they have been assigned a non-zero reproductive output as well to prevent individuals with a poor environmental match being selected as mates. No restrictions on self-mating are imposed. During the recombination of both parent's genotypes, an independent assortment of all loci is assumed. Each locus is prone to mutation to the alternative binary allele with probability μ. Offspring individuals disperse with a probability equal to the dispersal phenotype multiplied by the maximum dispersal probability, $\delta_{\max} = 0.1$. The latter value was chosen since preliminary explorations revealed that higher dispersal probabilities did not usually evolve. Constraining the extent of dispersal probabilities to a sensible range increases the phenotypical resolution for selection without affecting model outcomes because dispersal probabilities greater than 0.1 do not evolve in any of the scenarios. Dispersing individuals are randomly displaced to any of the island patches (including their natal patch). In scenarios assuming a cost of dispersal, individuals die with a probability equal to the product of the cost of dispersal parameter χ and their dispersal phenotype d (i.e. $\chi \cdot d$). As such, this cost of dispersal solely depends on an individual's phenotype, reflecting a trade-off between survival and the development of dispersal-related traits. This phenotype-dependent cost of dispersal complements the implicit cost of dispersing to unsuitable patches, leading to a strongly lowered reproductive output across all scenarios.

Upon reproduction, all parent individuals die because we assume non-overlapping populations with a semelparous reproduction strategy, leaving only their offspring. Under these conditions, colonization depends only on dispersal to a patch and a non-zero reproductive rate provided by a sufficient match between the phenotype and the environment. However, an individual with a low environmental match is unlikely to produce many offspring relative to better-adapted residents.

In scenarios assuming random patch extinctions, all individuals inhabiting a patch die, including offspring, with a probability ψ. Each simulation spans 2500 generations, at which point metrics remained stable. At each generation, an inventory of individuals, including their patch location, species identity, as well as their environmental and dispersal phenotype, is stored. To ease memory usage, data on 1% of randomly selected individuals are stored, which is still highly representative of the composition of individuals across space and time. A graphic overview of the individual-based model and key life cycle characteristics is displayed in figure 1.

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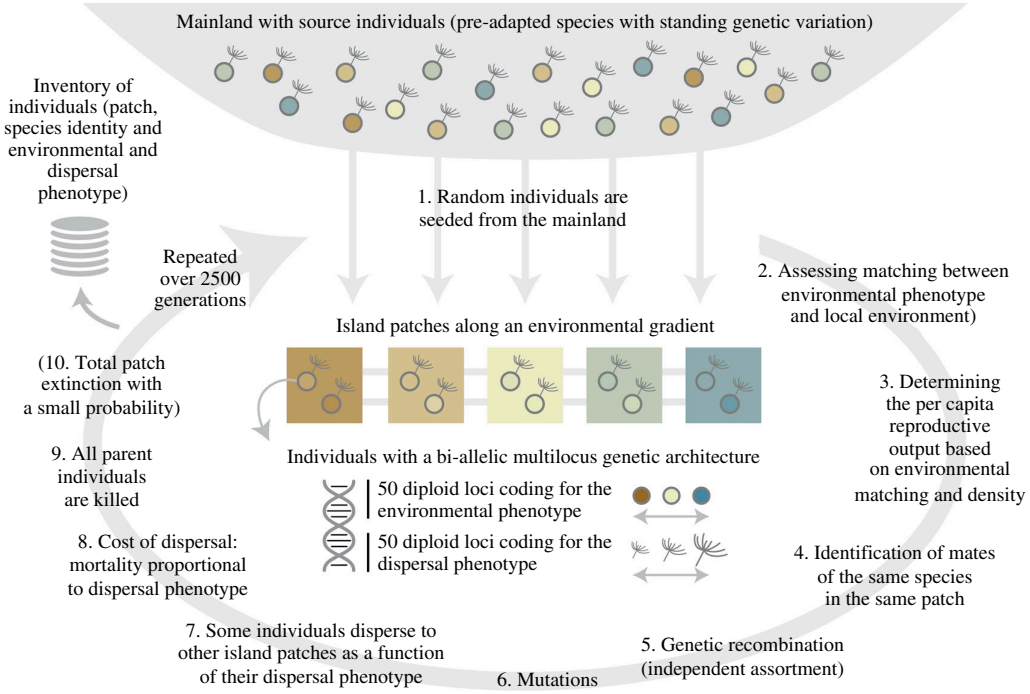


Figure 1. Schematic representation of the model structure, featuring important community and population dynamics steps. The colour of patches and individuals represents environmental and phenotypic values, while the size of the pappus (wind-dispersed seed structure) represents the dispersal phenotype, with bigger pappi corresponding to superior dispersal probabilities. Note that the five island patches are arranged linearly for ease of visualization, but that they are modelled in a spatially explicit way with equal pairwise distances among all of them.

(b) Scenarios

We perform a full factorial exploration of mainland immigration rate, cost of dispersal, probability of patch extinction and a set of scenarios, in conjunction with fixed model parameters, carefully chosen to yield realistic outcomes (tables 1 and 2). For each scenario, we ran a total of 25 replicate simulations. We consider 13 different scenarios that vary with respect to the number of species, whether the species can evolve dispersal and the fixed dispersal probability of species that cannot evolve dispersal. Scenarios 1–6 pertain to a setting where none of the species can evolve dispersal (and have a fixed low or high dispersal probability), scenarios 7–9 pertain to a setting where all species can evolve dispersal, and scenarios 10–13 pertain to a setting where only one species can evolve dispersal while the other species have a fixed (low or high) dispersal probability (table 2). This last case reflects what might happen if not all species can evolve because of limited genetic variation for this trait. This scenario also allows us to explore the potential for stronger evolution-mediated priority effects if, for example, one species evolves higher dispersal and can prevent colonization by the other species. Additionally, we evaluate if the evolving species' location on the environmental gradient (whether at the boundary, scenarios 10 and 12, or the centre, scenarios 11 and 13) affects evolution-mediated priority effects (table 2).

To ensure the generality of our findings, we performed sensitivity analyses. In a first sensitivity analysis, we consider a reduced mutation rate of 10E−5, rather than 10E−4, enabling us to discriminate between the importance of mutations and standing genetic variation in fuelling evolution in the modelled system. In a second sensitivity analysis, we consider 25 patches with environmental values equidistantly spread over the (0.20, 0.80) interval and 25 mainland species with an environmental phenotype that exactly matched one of the patches. In this alternative setting, environmental distances between patches are reduced and species correspondingly face a reduced environmental mismatch and therefore a smaller fitness difference when colonizing other environments compared with scenarios with five patches colonized by one to five species. Both sensitivity analyses are conducted factorially with the parameters mentioned in table 1 and in conjunction with scenarios 1–9 (table 2).

(c) Summarizing metrics

To investigate how varying parameters shape the evolution of dispersal, we computed the average dispersal phenotype across all species and individuals populating the final 250 generations of each simulation. Additionally, we compute a monopolization index for the second half of each simulation, measuring the degree to which evolution-mediated priority effects lead to the monopolization of non-natal patch environments. Specifically, this index is calculated as the fraction of individuals residing in a patch to which they were not initially adapted, weighted by each individual's degree of adaptation (electronic supplementary material, equation presented in SI1). As such, individuals less adapted to non-natal patches contribute less to the monopolization index. The monopolization index ranges from 0 (when all individuals reside in the patch to which they were originally adapted) to 1 (when all individuals reside in a patch to which they were not originally adapted, while simultaneously matching

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Table 1. Overview of model parameters and considered parameter values. Values separated by semicolons refer to different scenarios.

parameter	description	value(s)
K	carrying capacity per patch	250
r_{max}	per capita reproductive potential	10
s	environmental selective pressure	0.01
γ	genetic diversity in the mainland population	0.1
μ	mutation rate	0.001
δ_{init}	initial dispersal probability (when dispersal evolves)	0.002
λ	seeding rate from mainland per patch	0.1;1;10
χ	cost of dispersal	0;0.1
ψ	probability of complete patch extinction	0;0.01

Table 2. Scenarios investigated. Simulations vary along the number of species of the regional species pool (immigrating from the mainland) and to which environmental value each of these species is adapted, whether or not the species can evolve dispersal, and the fixed dispersal probability of species that cannot evolve dispersal. The terms 'centre patch' or 'centre species', and 'outer patch' or 'outer species', pertain to where a patch or a species' pre-adapted phenotypic value is located along the environmental gradient.

scenario	number of species	species pre-adapted to	able to evolve dispersal?	fixed dispersal probability
1	1	centre patch	no	0.001
2	2	outer patches	no	0.001
3	5	each patch	no	0.001
4	1	centre patch	no	0.1
5	2	outer patches	no	0.1
6	5	each patch	no	0.1
7	1	centre patch	yes	—
8	2	outer patches	yes	—
9	5	each patch	yes	—
10	5	each patch	only one outer species	0.001
11	5	each patch	only the centre species	0.001
12	5	each patch	only one outer species	0.1
13	5	each patch	only the centre species	0.1

the environment perfectly). We also computed the average population size per generation across all patches per species to assess the demographic benefits of dispersal evolution.

(d) Implementation

We implemented the individual-based model and performed all subsequent analyses in R v. 4.3.1 [54]. All code required to replicate our analysis is available through the following GitHub repository: https://github.com/mfajgenblat/ibm-dispersal-evolution [55].

3. Results

(a) Evolution of dispersal

In the scenarios where all species can evolve dispersal, we observed that greater dispersal evolved when (i) regional species richness was low, (ii) mainland immigration rates were low, (iii) dispersal costs were absent, and (iv) patches did not undergo periodic stochastic extinctions (figure 2). Each of these factors interacted. For instance, the negative influence of regional species richness on dispersal evolution was most pronounced when mainland immigration was high (figure 2). The variation in dispersal that arises within a single scenario is also governed by multiple factors. Specifically, the variation and hence unpredictability in dispersal probability across time and space were lowest with high regional species richness combined with high mainland immigration, whereas scenarios featuring periodic patch extinctions and low mainland immigration produced considerably more variation in dispersal evolution (figure 2).

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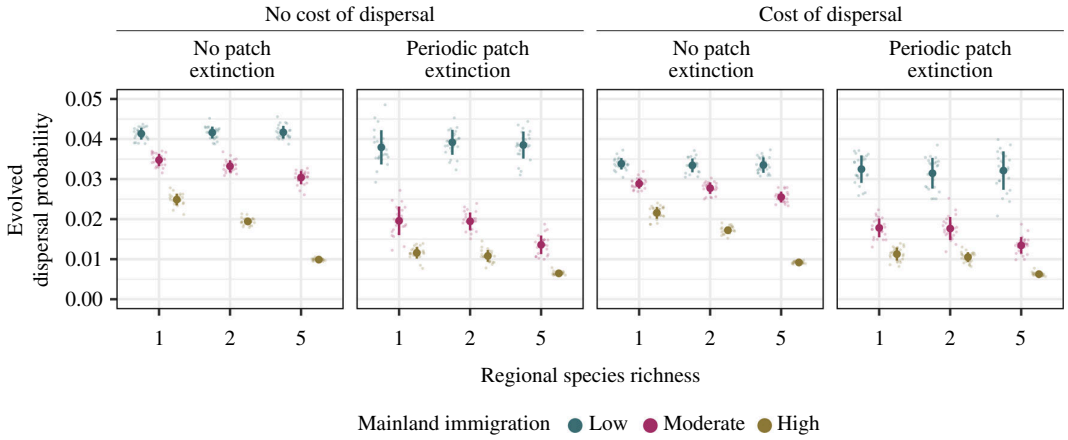


Figure 2. Average evolved dispersal probabilities across all species per simulation during final (2251–2500) generations for each of the scenarios where species can evolve dispersal (scenarios 7–9; table 2). Average dispersal probabilities for each simulation are represented by small, horizontally jittered dots. The mean dispersal phenotypes and corresponding standard deviations (mean ± 1 s.d.) for each scenario are represented by circles and vertical bars. Mainland immigration for low, moderate and high scenarios (offset to the left, middle and right, respectively) results in 0.1, 1 and 10 migrants per patch on average, respectively.

Simulations performed under reduced mutation rates lead to qualitatively similar results, though the evolution of dispersal is slowed as it relies more on available standing genetic variation, yielding lower evolved dispersal after an equal number of generations (electronic supplementary material, figure S1). We also observed consistent patterns when extending the simulations from five species and patches to 25 species and patches (electronic supplementary material, figure S2). Communities with 25 species and environments were characterized by an additional, but modest, decrease in evolved dispersal in most scenarios, along with a decreased variability (electronic supplementary material, figure S2). Being faced with periodic patch extinctions and low-to-moderate mainland immigration, these more speciose communities evolved higher dispersal compared with communities consisting of five species inhabiting five patches (electronic supplementary material, figure S2).

(b) Evolution-mediated priority effects

Long-lasting evolution-mediated priority effects occur when a colonizing species is allowed sufficient time before a better-adapted species reaches the patch. Notably, these effects can already develop after fewer than 20 generations (electronic supplementary material, figure S3). Evolution-mediated priority effects (and adaptive radiation for one species) were most prevalent for scenarios with low regional species richness (figure 3). Scenarios with only a single species invariably led to complete monopolization of all patches and acted as an upper boundary to what was expected with more species. For two species, the monopolization index was almost as high as for one species. Although evolution-mediated priority effects were rarer in a niche-saturated, five-species community, they still occurred to a limited extent (figure 3). Low mainland dispersal resulted in greater monopolization of other environmental patches as well as more variation among species and unpredictability. This pattern was probably because of the additional time before a well-adapted species arrived from the mainland, thus affording more time for adaptation and more historical contingency in the evolutionary and demographic trajectories for each species (figure 3).

(c) Evolution of dispersal and evolution-mediated priority effects

When dispersal could evolve for all species, the species underwent intermediate levels of monopolization (figure 3), because their evolved dispersal probabilities fell between the fixed values of high and low dispersal probabilities for the non-evolving dispersal scenarios. Compared with a scenario with a low fixed dispersal probability, dispersal evolved to a higher probability across species, which supported more evolution-mediated priority effects. However, the converse is true when comparing against a scenario with a high fixed dispersal probability (figure 3).

In a second approach, we allowed for only one species to evolve dispersal while others remained fixed (non-evolving). When the other, non-evolving species had a high fixed dispersal, the one species evolved low dispersal, and this species usually monopolized all the patches, especially with moderate mainland immigration and no patch extinction (figures 4 and 5 and electronic supplementary material, figure S4). However, when other species had a low fixed dispersal probability, the one with evolved dispersal did not undergo more monopolization than the others. In general, high mainland immigration, low fixed dispersal propensities and periodic patch extinctions reduced the opportunities for monopolization by the dispersal-evolving species in these simulations (figure 5). The position of the evolving species on the environmental gradient (middle versus edge) had little effect on dispersal evolution or monopolization effects.

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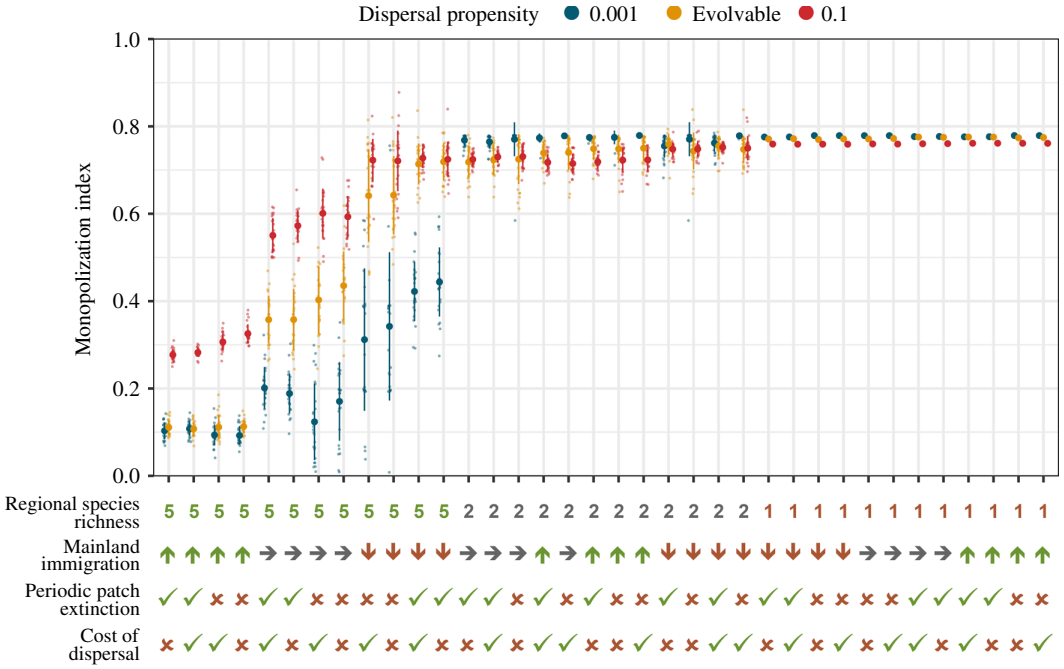


Figure 3. Monopolization indices for each of the scenarios where all species have a fixed low dispersal probability of 0.001 (blue; offset to the left; scenarios 1–3; table 2), where all species are able to evolve dispersal (yellow; no offset; scenarios 7–9; table 2) and where all species have a fixed high dispersal probability of 0.1 (red; offset to the right; scenarios 4–6; table 2). The monopolization index measures the degree to which species occur in habitats that they were not initially adapted to but now are, where 0 indicates no evolution-mediated priority effects and 1 indicates that all individuals have perfectly adapted to all other habitats. Monopolization indices for each simulation are represented by small, horizontally jittered dots. The mean monopolization index and corresponding standard deviations (mean ± 1 s.d.) for each scenario are represented by circles and vertical bars. Scenarios are ordered by the mean monopolization index, with scenarios at the right corresponding to the highest monopolization indices. The four bottom rows graphically depict the parameter setting for each scenario, with the regional species richness represented by actual numbers, the level of mainland immigration by arrows (upwards, sidewards and downwards for high, moderate and low, respectively), whether periodic patch extinction occurs by symbols (check mark and cross for yes and no, respectively) and whether there is a cost of dispersal by symbols (check mark and cross for yes and no, respectively).

4. Discussion

(a) Dispersal evolution and species diversity

Many species have adapted different dispersal probabilities, distances or habitat selection in nature, suggesting that this trait commonly evolves under varying landscape contexts [49–53]. Understanding the evolution of dispersal requires a view that extends beyond the typical limits of the local population and embraces a multi-patch perspective that includes the availability of high-fitness habitats external to the population and considers the costs accrued during transit to these habitats [17,56,57]. Dispersal evolution can thus be intricately tied to changes in habitat quality across landscapes and the ability to move across unsuitable habitats [50,56–58]. As a result, dispersal can be considered a metapopulation adaptation that responds to selection at landscape scales. Because species interactions are likely to be important aspects of potential fitness in other patches, dispersal could also often evolve in response to the diversity and distribution of other species in the metacommunity. Our simulations indeed demonstrate that the evolution of dispersal depends on regional species richness and thus metacommunity context, landscape features such as patch extinction and species' characteristics such as the cost of dispersal.

Our simulations demonstrated that populations evolve lower dispersal probabilities when species diversity is higher in the metacommunity (figure 2). This outcome probably reflects the higher probability that dispersal into a new patch is maladaptive because that patch is dominated by a competitor already adapted to the local environment. When fewer species exist, the potential fitness advantages of colonization and exploitation of new niches increase. We could not find any models in the literature that evaluated both niche and dispersal evolution in metacommunities of varying species richness. Laroche *et al.* [59] allowed dispersal to evolve in a metacommunity without niche evolution and assumed point speciation. They found that large communities become dominated by low-dispersing endemic species, and small communities become dominated by good dispersers that are not strong competitors. Although difficult to compare with our model, this model indicates the degree to which colonization–competition trade-offs, habitat size and dispersal evolution can interact to determine species richness patterns. Outcomes from our model also correspond to the results of several models that evaluate what happens on range edges, where populations become freed from intraspecific competition. These models find that dispersal probability often evolves to higher levels to take advantage of open, competition-free patches [37,60]. Other models that evaluate the impact of patch extinctions on dispersal evolution also find that the availability of open, competition-free patches selects for the evolution of higher dispersal [50,56–58]. In general, we can expect that lower competition in both single-species metapopulations and multi-species metacommunities can select for the evolution of higher dispersal. However, our model assumes that the competi-

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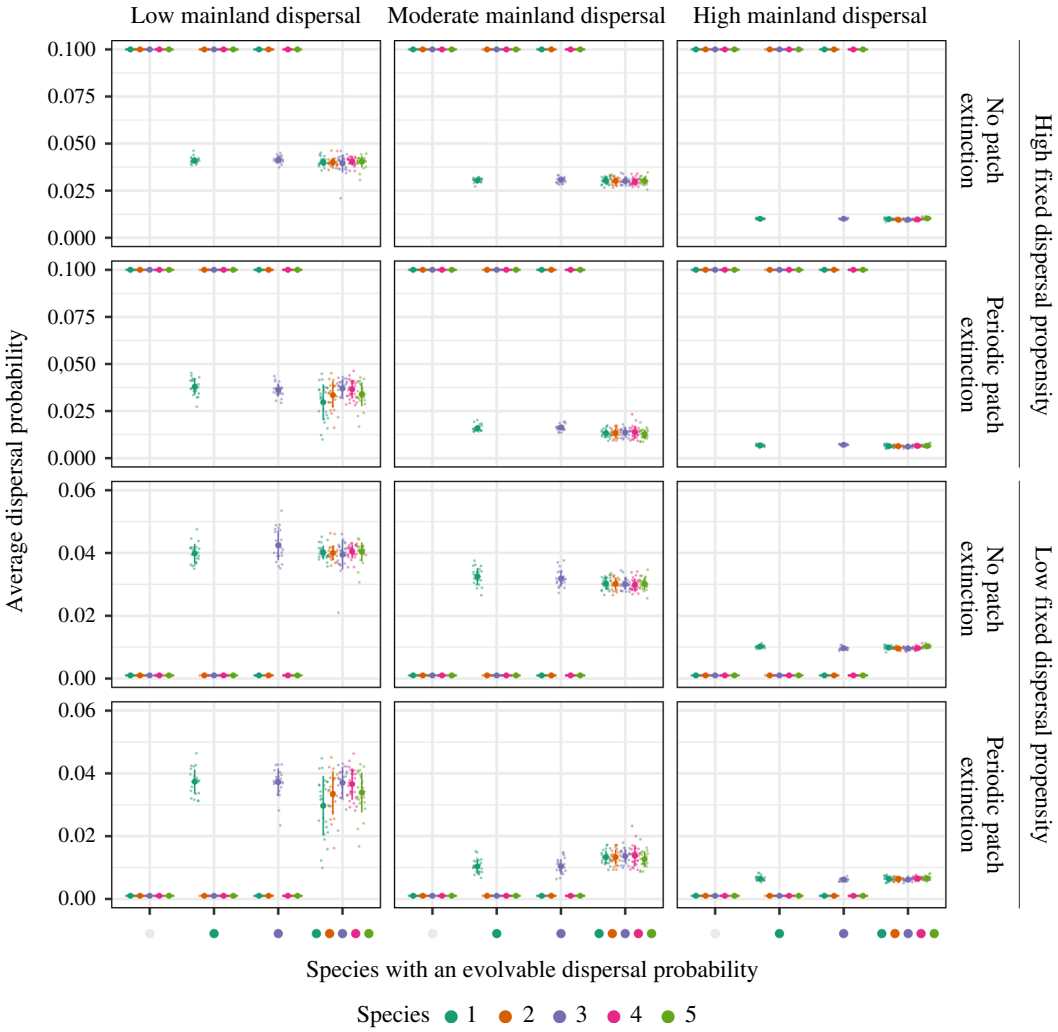


Figure 4. Evolved dispersal probabilities as a function of different dispersal evolution scenarios averaged over the second half of the simulations (generations 1251–2500). The four scenarios of dispersal evolution are arranged along the *x*-axis (from left to right: no, only an outer species, only the middle species and all species that can evolve dispersal). The evolved dispersal probabilities of individual simulations are represented by small, horizontally jittered dots. The mean evolved dispersal probability and corresponding standard deviations (mean ± 1 s.d.) for each scenario are represented by circles and vertical bars.

tion-free environment is a different environment, which could prevent colonization if the fitness of the colonist in the new habitat is too low.

We expected that higher dispersal would evolve when patches underwent periodic extirpations and created more open environments for colonization [37,60]. Instead, we observed evolution towards lowered dispersal with periodic patch extinctions. This result occurred because we modelled a constant rain of immigrants from the mainland pool in our model, all with the same low, initial dispersal probability. These immigrating mainland individuals drove down the dispersal probability in the new patches through gene flow (see electronic supplementary material, figure S5), even though the first colonizers from other patches were generally characterized by greater dispersal. This effect decreased in models with a lower mainland immigration rate (figure 2). Interestingly, periodic extirpations combined with low-to-moderate mainland immigration favoured higher dispersal evolution in systems with more species and closer niche optima (electronic supplementary material, figure S2), indicating an interactive effect of diversity, niche differences and patch extirpation.

(b) Effects on evolution-mediated priority effects

Reduced regional species diversity was strongly associated with higher rates of monopolization and, accordingly, reduced rates of pure ecological species sorting (figure 3). Fewer species in the metacommunity generated more open niches and fewer chances that a species already adapted to that patch could arrive quickly and dominate. Under these circumstances, the existing species could colonize new habitats, adapt to them and reduce the establishment success of subsequent immigrants, leading to evolution-mediated priority effects. Previous models that included niche adaptation but not dispersal adaptation similarly found that as species diversity increased, adaptation to broader niches was strongly curtailed [35,36]. When environments changed, these species quickly re-sorted into high-fitness patches if they had sufficient dispersal rates, and the impact of evolution on community dynamics was limited [36]. Thus, species richness generally determines ecological opportunity and therefore the potential for evolution-mediated priority effects [36].

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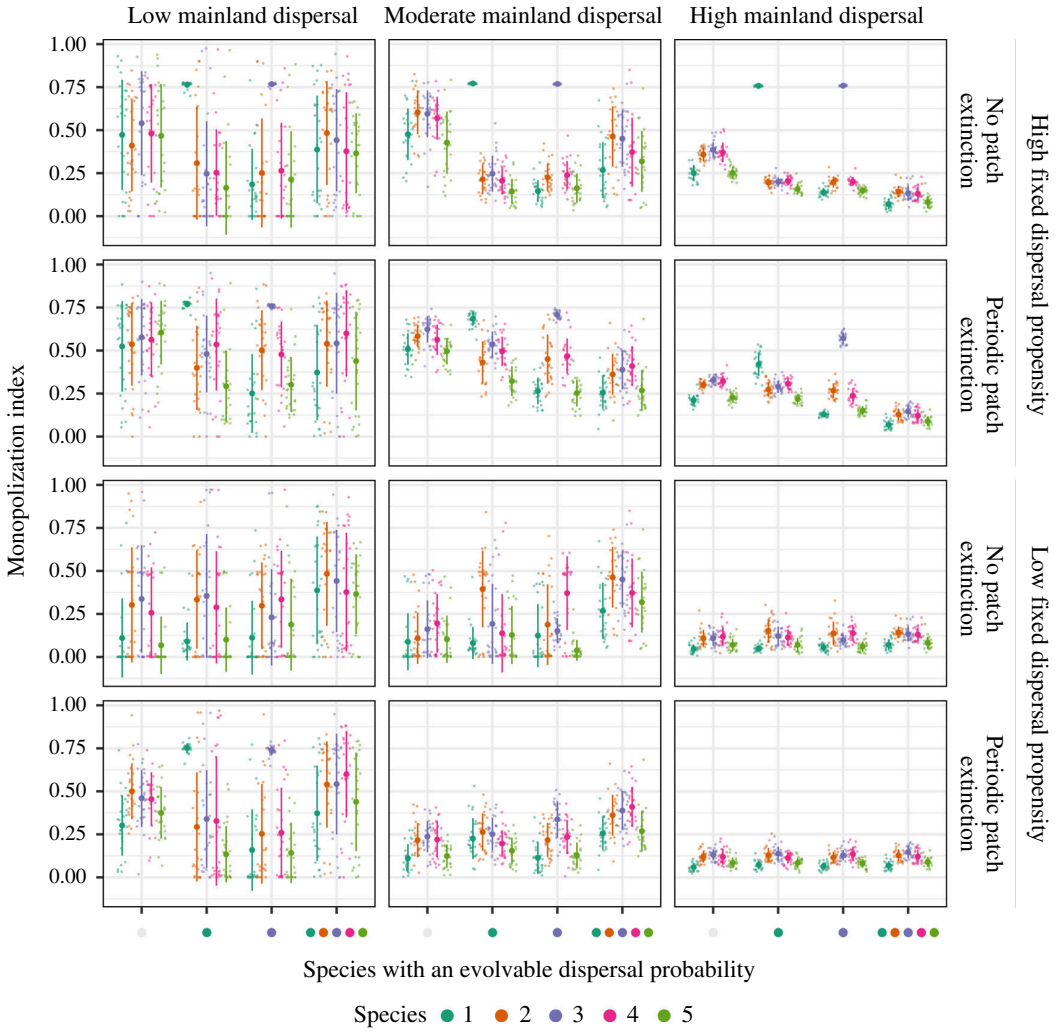


Figure 5. Monopolization indices as a function of different dispersal evolution scenarios averaged over the second half of the simulations (generations 1251–2500). The four scenarios of dispersal evolution are arranged along the *x*-axis (from left to right: no, only an outer species, only the middle species and all species that can evolve dispersal). The evolved monopolization indices of individual simulations are represented by small, horizontally jittered dots. The mean monopolization index and corresponding standard deviations (mean ± 1 s.d.) for each scenario are represented by circles and vertical bars.

In our simulations, species evolved an intermediate dispersal rate relative to assumed fixed rates based on the relative costs and benefits of dispersing under model conditions. Evolving this intermediate dispersal rate led to a higher impact of evolution-mediated priority effects in multi-species simulations relative to low fixed dispersal probabilities in immigrants from the mainland but a lower occurrence of evolution-mediated priority effects relative to simulations with high fixed dispersal probabilities in immigrants from the mainland (figure 3). This result implies that models that do not account for the evolution of dispersal might be overestimating or underestimating the importance of evolution-mediated priority effects in real communities where dispersal might evolve naturally to different levels. Dispersal evolution in the high-diversity setting led to a metacommunity dominated by low dispersal and species sorting, where each species is matched to a particular environment, even though all species could adapt and spread to all other environments. In contrast, dispersal ability evolves higher in metacommunities with low species richness, and the resulting greater dispersal probabilities combined with more ecological opportunities promote niche expansion and habitat monopolization, which could prevent additional species from colonizing. Thus, the evolution of dispersal can operate to reinforce existing metacommunity dynamics and regional diversities, either by reinforcing species sorting or monopolization of habitats (figure 3). For regions with high species extinction rates, this dynamic could lead to the evolution of more dispersal and the continued maintenance of low diversity.

We assumed that all species could adapt their dispersal probability, but this also meant that all species converged on the same dispersal levels. These similar dispersal abilities reduced the potential advantages of higher dispersal for colonizing competition-free patches. Therefore, we also evaluated scenarios where only one species could evolve dispersal and the others could not because the others lacked sufficient genetic variation for this trait. In these simulations, the species evolved a dispersal probability ranging from approximately 0.5% to 5%, increasing as mainland immigrant dispersal decreased (figure 4). These evolved dispersal probabilities did not depend on the fixed dispersal probabilities of the other non-evolving species. However, the degree to which they could monopolize habitats depended strongly on the fixed dispersal abilities of the other species (figure 5). When the non-evolving species had a high, fixed dispersal, the single evolving species evolved relatively lower dispersal probabilities, strongly monopolized habitats, and reached high abundances as a result (figures 4 and 5 and electronic supplementary material, figure S4). In contrast, when non-evolving species had a low, fixed dispersal, the single evolving species evolved relatively higher dispersal probabilities and did not differ in monopolization extent and even monopolized less

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under some scenarios (figures 4 and 5 and electronic supplementary material, figure S4). These results indicate an underappreciated effect of maladaptive gene flow in determining evolution-mediated priority effects. When species dispersed often and did not evolve at a lower rate, they also could not adapt to local habitats effectively because of the disruptive maladaptive gene flow from other habitats [61,62]. The evolving species adapted lower dispersal probabilities, however, and could adapt and monopolize additional environments. Although we often consider strong dispersal as a prerequisite for a species to undergo evolution-mediated priority effects, too much dispersal can reduce this ability, suggesting an optimum dispersal probability for monopolization. In fact, the best monopolizers will be the species that disperse well into other habitats, but then gene flow is very quickly reduced from other habitats to allow rapid local adaptation through mechanisms such as selection against migrants [27,63]. This strategy constitutes a type of Darwinian demon that disperses well, resists gene flow and adapts quickly. The evolution of reduced dispersal adds to these mechanisms that can reduce gene flow and facilitate more rapid adaptation to new habitats amid a reduced threat of maladaptive gene flow.

(c) Ecological opportunity, dispersal evolution and priority effects

Ecological opportunity is defined as the potential to occupy a niche that is not exploited by competing species [64,65]. Ecological opportunity can potentially offer high fitness to the species that can colonize and adapt to it. Ecological opportunities arise either because no species exist in the regional pool that can occupy an empty niche, or species exist but were recently extirpated or have not yet colonized the habitat due to poor dispersal or poor connectivity among patches. For example, ecological opportunities often exist in the form of unexploited niches on isolated islands that make them particularly susceptible to invasions by long-distant dispersers and subsequent adaptive radiations [66]. As species diversity increases, the probability that a species is adapted to available niches also increases, thus limiting ecological opportunities. The ability to take advantage of open niches requires relatively strong initial dispersal (or luck) and a rapid rate of adaptation through existing standing genetic variation or high rates of recombination or mutation. Hence, we expect that ecological opportunity can select for higher dispersal when it provides access to competition-free habitats. As such, we can predict that evolution-mediated priority effects will play greater roles in species-poor regions like the upper latitudes, isolated islands and in changing and extreme environments. Under those conditions, one can view ecological opportunity as a form of natural selection for modified dispersal rates.

Given an ecological opportunity, the likelihood of evolution-mediated priority effects becomes a race between the arrival and adaptation of one species to an ecological opportunity before another species already adapted to that niche can colonize [29]. Absolute dispersal and the relative difference in dispersal among species are key traits that determine if and to what degree evolution-mediated priority effects can occur and the dynamics of metacommunities. With high dispersal rates across all species, evolution-mediated priority effects should disappear by reducing the time for adaptation between the arrival of different species. Then species sorting dominates, whereby each species arrives in an environment that matches its traits before other species that are less well adapted to that environment have the time to locally adapt; under those conditions, the impact of evolution on community assembly is generally low [36], and local and regional diversity should be higher. However, such high dispersal rates did not evolve in our simulations. To the extent that this observation can be generalized, it suggests that pure species sorting might be unlikely for species that have the capacity to evolve dispersal rates, especially in environments with high costs to dispersal. Instead, we observed the evolution of low dispersal probabilities in our simulations. At low–moderate rates of dispersal, some species can adapt to nearby similar environments and can prevent other species from colonizing or adapting to those habitats through the evolution of competitive exclusion [9,27–29]. At even lower rates of dispersal, the first species to arrive often has sufficient time to adapt to all or most environments and can fill niches before any other species arrive, mimicking a long-distance colonization of islands by one species or over longer time scales even an adaptive radiation into ecomorphs that fill all niches [33,66]. Because species diversity and dispersal strongly determine outcomes, the evolution of dispersal is likely to shift across these dynamics, depending on the direction it evolves and its relative heterogeneity among species.

Unfortunately, we know of no observations of natural systems that record both the evolution of niche-associated traits and dispersal. A few studies now indicate the potential for evolution-mediated priority effects. For instance, a laboratory study with *Haloferax* species demonstrated that a numerical advantage and adaptation of a weak competitor could reverse dominance by the stronger competitor that arrives later [31]. The reconstruction of niches and colonization times of *Tetragnatha* spiders on Hawaiian islands exemplifies what we might expect across varying degrees of connectivity [33]. At shorter distances, species sorting dominated, while at intermediate distances, island niches were filled by a combination of species sorting and adaptive radiation of first-arriving species. At long distances, only one species arrived and radiated into all available niches [33]. However, nothing is known about variation in dispersal among species or the possibility that it evolved during this colonization period. Yet, dispersal can evolve under many circumstances [49–53], such as when the ecological opportunity presents itself [49], as modelled here. Therefore, future experiments and empirical studies should not just track the evolution of niche-associated traits but also dispersal traits.

5. Conclusions and future work

The model we present in this study is a first exploration of how the evolution of dispersal interacts with metacommunity, landscape and species' traits to influence the likelihood that niche evolution shapes the trajectories of community assembly.

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We demonstrate that dispersal evolution affects the likelihood of niche evolution and evolution-mediated priority effects, and these outcomes are shaped by regional species diversity, habitat disturbance and background immigration and dispersal rates. Our results suggest that interactions among dispersal and niche evolution might be common and might significantly affect metacommunity structure and dynamics. Past studies usually evaluate dispersal evolution in a single species across landscapes [37,60] or multi-species niche evolution without dispersal evolution [29,30,35,36]. We hope that our initial model encourages additional theoretical explorations that allow species to adapt both traits tailored to specific environments and dispersal traits tailored to the landscape configuration. Some potential future directions include models that explicitly incorporate colonization–competition trade-offs among species in the presence and absence of dispersal evolution. Another suggestion is to explore these dynamics in spatially explicit landscapes, where environments or patchiness might vary randomly, with some spatial autocorrelation, and along clines. In our model, we only allowed dispersal probability to evolve, but the evolution of dispersal distance might also strongly affect the dynamics.

Exploring how these dynamics interact with environmental change (e.g. climate warming and invasive species) would be another fruitful area of research. Anthropogenic environmental change often causes extirpations on patches or creates new patches, such as when new habitats are made available by a shifting climate. In general, such new opportunities should support greater dispersal rates and therefore potentially alter the potential for evolution-mediated priority effects. In particular, if species are colonizing new habitats on the edge of their range, they could evolve greater dispersal to take advantage of new, competition-free habitats [43] as long as the new habitat is not too different. Species that can evolve the greatest dispersal ability or longest distance before other species might then monopolize habitats, preventing other species from tracking climate and decreasing their range and the diversity of species.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All code required to replicate our analysis is available from the GitHub repository [55].

Electronic supplementary material is available online [67].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. M.F.: conceptualization, methodology, writing—original draft, writing—review and editing; L.D.M.: conceptualization, writing—original draft, writing—review and editing; M.C.U.: conceptualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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References

1. Holyoak M, Leibold MA, Holt R. 2005 *Metacommunities: spatial dynamics and ecological communities*. Chicago, IL: University of Chicago Press.
2. Levins R, Culver D. 1971 Regional coexistence of species and competition between rare species. *Proc. Natl Acad. Sci. USA* **68**, 1246–1248. (doi:10.1073/pnas.68.6.1246)
3. MacArthur, RH. 1972 *Geographical ecology: patterns in the distribution of species*. New York, NY, Harper and Row.
4. Holyoak M, Leibold MA, Mouquet N, Holt RD, Hoopes MF. 2005 Metacommunities: a framework for large-scale community ecology. In *Metacommunities: spatial dynamics and ecological communities* (eds M Holyoak, MA Leibold, RD Holt), pp. 1–31. Chicago, IL: University of Chicago Press.
5. Leibold MA *et al*. 2004 The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett*. **7**, 601–613. (doi:10.1111/j.1461-0248.2004.00608.x)
6. Leibold MA, Chase JM. 2017 *Metacommunity ecology*. Princeton, NJ: Princeton University Press.
7. Cadotte MW, Mai DV, Jantz S, Collins MD, Keele M, Drake JA. 2006 On testing the competition-colonization trade-off in a multispecies assemblage. *Am. Nat.* **168**, 704–709. (doi:10.1086/508296)
8. Tilman D. 1994 Competition and biodiversity in spatially structured habitats. *Ecology* **75**, 2–16. (doi:10.2307/1939377)
9. Urban MC *et al*. 2008 The evolutionary ecology of metacommunities. *Trends Ecol. Evol.* **23**, 311–317. (doi:10.1016/j.tree.2008.02.007)
10. Thompson JN. 1999 The evolution of species interactions. *Science* **284**, 2116–2118. (doi:10.1126/science.284.5423.2116)
11. Vellend M, Geber MA. 2005 Connections between species diversity and genetic diversity. *Ecol. Lett*. **8**, 767–781. (doi:10.1111/j.1461-0248.2005.00775.x)
12. Hendry AP. 2016 *Eco-evolutionary dynamics*. Princeton, NJ: Princeton University Press.
13. Kinnison MT, Hendry AP. 2001 The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* **112**, 145–164. (doi:10.1023/A:1013375419520)
14. Urban MC *et al*. 2020 Evolutionary origins for ecological patterns in space. *Proc. Natl Acad. Sci. USA* **117**, 17 482–17 490. (doi:10.1073/pnas.1918960117)
15. Hairston NG, Ellner SP, Geber MA, Yoshida T, Fox JA. 2005 Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett*. **8**, 1114–1127. (doi:10.1111/j.1461-0248.2005.00812.x)
16. Post DM, Palkovacs EP. 2009 Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Phil. Trans. R. Soc. Lond. B* **364**, 1629–1640. (doi:10.1098/rstb.2009.0012)
17. Urban MC, Skelly DK. 2006 Evolving metacommunities: toward an evolutionary perspective on metacommunities. *Ecology* **87**, 1616–1626. (doi:10.1890/0012-9658(2006)87[1616:emtaep]2.0.co;2)
18. Leibold MA, Govaert L, Loeuille N, De Meester L, Urban MC. 2022 Evolution and community assembly across spatial scales. *Annu. Rev. Ecol. Evol. Syst.* **53**, 299–326. (doi:10.1146/annurev-ecolsys-102220-024934)

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19. Govaert L, Altermatt F, De Meester L, Leibold MA, McPeek MA, Pantel JH, Urban MC. 2021 Integrating fundamental processes to understand eco-evolutionary community dynamics and patterns. *Funct. Ecol*. **35**, 2138–2155. (doi:10.1111/1365-2435.13880)
20. De Meester L *et al*. 2019 Analysing eco-evolutionary dynamics—the challenging complexity of the real world. *Funct. Ecol*. **33**, 43–59. (doi:10.1111/1365-2435.13261)
21. Thompson JN. 2005 *The geographic mosaic of coevolution*, p. 400. Chicago, IL: University of Chicago Press.
22. Vellend M. 2016 *The theory of ecological communities*. Princeton, NJ: Princeton University Press.
23. Holyoak M, Leibold MA, Holt RD. 2005 *Metacommunities: spatial dynamics and ecological communities*. Chicago, IL: University of Chicago Press.
24. Fukami T. 2015 Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annu. Rev. Ecol. Evol. Syst.* **46**, 1–23. (doi:10.1146/annurev-ecolsys-110411-160340)
25. Shorrocks B, Bingley M. 1994 Priority effects and species coexistence: experiments with fungal-breeding *Drosophila*. *J. Anim. Ecol.* **63**, 799–806. (doi:10.2307/5257)
26. Drake JA. 1991 Community-assembly mechanics and the structure of an experimental species ensemble. *Am. Nat*. **137**, 1–26. (doi:10.1086/285143)
27. De Meester L, Vanoverbeke J, Kilsdonk LJ, Urban MC. 2016 Evolving perspectives on monopolization and priority effects. *Trends Ecol. Evol.* **31**, 136–146, (doi:10.1016/j.tree.2015.12.009)
28. Urban MC, De Meester L. 2009 Community monopolization: local adaptation enhances priority effects in an evolving metacommunity. *Proc. R. Soc. Lond. B* **276**, 4129–4138. (doi:10.1098/rspb.2009.1382)
29. Vanoverbeke J, Urban MC, De Meester L. 2016 Community assembly is a race between immigration and adaptation: eco-evolutionary interactions across spatial scales. *Ecography* **39**, 858–870. (doi:10.1111/ecog.01394)
30. Leibold MA, Urban MC, De Meester L, Klausmeier CA, Vanoverbeke J. 2019 Regional neutrality evolves through local adaptive niche evolution. *Proc. Natl Acad. Sci. USA* **116**, 2612–2617. (doi:10.1073/pnas.1808615116)
31. Nadeau CP, Farkas TE, Makkay AM, Papke RT, Urban MC. 2021 Adaptation reduces competitive dominance and alters community assembly. *Proc. R. Soc. Lond. B* **288**, 20203133. (doi:10.1098/rspb.2020.3133)
32. Fukami T, Beaumont HJE, Zhang XX, Rainey PB. 2007 Immigration history controls diversification in experimental adaptive radiation. *Nature* **446**, 436–439. (doi:10.1038/nature05629)
33. Gillespie R. 2004 Community assembly through adaptive radiation in Hawaiian spiders. *Science* **303**, 356–359. (doi:10.1126/science.1091875)
34. Emerson BC, Gillespie RG. 2008 Phylogenetic analysis of community assembly and structure over space and time. *Trends Ecol. Evol.* **23**, 619–630. (doi:10.1016/j.tree.2008.07.005)
35. Loeuille N, Leibold MA. 2008 Evolution in metacommunities: on the relative importance of species sorting and monopolization in structuring communities. *Am. Nat*. **171**, 788–799. (doi:10.1086/587745)
36. de Mazancourt C, Johnson E, Barraclough TG. 2008 Biodiversity inhibits species' evolutionary responses to changing environments. *Ecol. Lett*. **11**, 380–388. (doi:10.1111/j.1461-0248.2008.01152.x)
37. Travis JMJ, Dytham C. 2002 Dispersal evolution during invasions. *Evol. Ecol. Res.* **4**, 1119–1129.
38. Duputié A, Massol F. 2013 An empiricist's guide to theoretical predictions on the evolution of dispersal. *Interface Focus* **3**, 20130028. (doi:10.1098/rsfs.2013.0028)
39. Kubisch A, Holt RD, Poethke HJ, Fronhofer EA. 2014 Where am I and why? Synthesizing range biology and the eco-evolutionary dynamics of dispersal. *Oikos* **123**, 5–22. (doi:10.1111/j.1600-0706.2013.00706.x)
40. Bohonak AJ, Jenkins DG. 2003 Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecol. Lett*. **6**, 783–796. (doi:10.1046/j.1461-0248.2003.00486.x)
41. Hanski I, Erälahti C, Kankare M, Ovaskainen O, Sirén H. 2004 Variation in migration propensity among individuals maintained by landscape structure. *Ecol. Lett*. **7**, 958–966. (doi:10.1111/j.1461-0248.2004.00654.x)
42. Henry RC, Bocedi G, Travis JMJ. 2013 Eco-evolutionary dynamics of range shifts: elastic margins and critical thresholds. *J. Theor. Biol*. **321**, 1–7, (doi:10.1016/j.jtbi.2012.12.004)
43. Shine R, Brown GP, Phillips BL. 2011 An evolutionary process that assembles phenotypes through space rather than through time. *Proc. Natl Acad. Sci. USA* **108**, 5708–5711. (doi:10.1073/pnas.1018989108)
44. McPeek MA, Holt RD. 1992 The evolution of dispersal in spatially and temporally varying environments. *Am. Nat*. **140**, 1010–1027. (doi:10.1086/285453)
45. Poethke HJ, Pfenning B, Hovestadt T. 2007 The relative contribution of individual and kin selection to the evolution of density-dependent dispersal rates. *Evol. Ecol. Res.* **9**, 41–50.
46. McPeek MA, Kalisz S. 1998 On the joint evolution of dispersal and dormancy in metapopulations. *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* **52**, 33–51.
47. Massol F, Duputié A, David P, Jarne P. 2011 Asymmetric patch size distribution leads to disruptive selection on dispersal. *Evolution*. **65**, 490–500. (doi:10.1111/j.1558-5646.2010.01143.x)
48. Kisdi E. 2002 Dispersal: risk spreading versus local adaptation. *Am. Nat*. **159**, 579–596. (doi:10.1086/339989)
49. Phillips BL, Brown GP, Webb JK, Shine R. 2006 Invasion and the evolution of speed in toads. *Nature* **439**, 803. (doi:10.1038/439803a)
50. Hanski I, Mononen T. 2011 Eco-evolutionary dynamics of dispersal in spatially heterogeneous environments. *Ecol. Lett*. **14**, 1025–1034. (doi:10.1111/j.1461-0248.2011.01671.x)
51. Cheptou PO, Carrue O, Rouifed S, Cantarel A. 2008 Rapid evolution of seed dispersal in an urban environment in the weed *Crepis sancta*. *Proc. Natl Acad. Sci. USA* **105**, 3796–3799. (doi:10.1073/pnas.0708446105)
52. Halverson MA, Skelly DK, Kiesecker JM, Freidenburg LK. 2003 Forest mediated light regime linked to amphibian distribution and performance. *Oecologia* **134**, 360–364. (doi:10.1007/s00442-002-1136-9)
53. Cody ML, Overton JM. 1996 Short-term evolution of reduced dispersal in island plant populations. *J. Ecol.* **84**, 53–61. (doi:10.2307/2261699)
54. R Core Team. 2023 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See https://www.R-project.org.
55. Fajgenblat M, De Meester L, Urban MC. *Dispersal evolution alters evolution-mediated priority effects in a metacommunity*. See https://github.com/MFajgenblat/ibm-dispersal-evolution.
56. Olivieri I, Michalakis Y, Gouyon PH. 1995 Metapopulation genetics and the evolution of dispersal. *Am. Nat*. **146**, 202–228. (doi:10.1086/285795)
57. Olivieri I, Gouyon PH. 1997 Evolution of migration rate and other traits: the metapopulation effect. In *Metapopulation biology* (eds I Hanski, ME Gilpin), pp. 293–324. San Diego, CA: Academic Press.
58. Heino M, Hanski I. 2001 Evolution of migration rate in a spatially realistic metapopulation model. *Am. Nat*. **157**, 495–511. (doi:10.1086/319927)
59. Laroche F, Jarne P, Perrot T, Massol F. 2016 The evolution of the competition–dispersal trade-off affects α- and β-diversity in a heterogeneous metacommunity. *Proc. R. Soc. Lond. B* **283**, 20160548. (doi:10.1098/rspb.2016.0548)
60. Phillips BL, Brown GP, Travis JMJ, Shine R. 2008 Reid's paradox revisited: the evolution of dispersal kernels during range expansion. *Am. Nat.* **172**, S34–S48. (doi:10.1086/588255)
61. Wright S. 1978 *Evolution and the genetics of populations, vol. 4: variability within and among natural populations*. Chicago, IL: University of Chicago Press.
62. Richardson JL, Urban MC, Bolnick DI, Skelly DK. 2014 Microgeographic adaptation and the spatial scale of evolution. *Trends Ecol. Evol.* **29**, 165–176. (doi:10.1016/j.tree.2014.01.002)

63. Ehrlich PR, Raven PH. 1969 Differentiation of populations. *Science* **165**, 1228–1232. (doi:10.1126/science.165.3899.1228)
64. Yoder JB *et al*. 2010 Ecological opportunity and the origin of adaptive radiations. *J. Evol. Biol*. **23**, 1581–1596. (doi:10.1111/j.1420-9101.2010.02029.x)
65. Wilson EO. 1961 The nature of the taxon cycle in the Melanesian ant fauna. *Am. Nat*. **95**, 169–193. (doi:10.1086/282174)
66. Losos JB, Ricklefs RE. 2009 Adaptation and diversification on islands. *Nature* **457**, 830–836. (doi:10.1038/nature07893)
67. Fajgenblat M, De Meester L, Urban MC. 2024 Supplementary text and figures from Dispersal evolution alters evolution-mediated priority effects in a metacommunity. Figshare. (doi:10.6084/m9.figshare.25887137)

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