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# **Dispersal evolution alters**

# evolution-mediated priority effects

## in a metacommunity

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#### 1 Abstract

2 Biologists have long sought to predict the distribution of species across landscapes to understand 3 biodiversity patterns and dynamics. These efforts usually integrate ecological niche and dispersal 4 dynamics, but evolution also can mediate these ecological dynamics. Species that disperse well and 5 arrive early might adapt to local conditions, which creates an evolution-mediated priority effect that 6 alters biodiversity patterns. Yet, dispersal is also a trait that can evolve and affect evolution-mediated 7 priority effects. We developed an individual-based model where populations of competing species not only can adapt to local environments, but also can adapt different dispersal probabilities. We found 8 9 that lower regional species diversity selects for populations with higher dispersal probabilities and 10 stronger evolution-mediated priority effects. When all species evolved dispersal, they monopolized 11 fewer patches and did so at the same rates. When only one of the species evolved dispersal, it evolved 12 lower dispersal than highly dispersive species and monopolized habitats once freed from maladaptive 13 gene flow. Overall, we demonstrate that dispersal evolution can shape evolution-mediated priority 14 effects when provided with greater ecological opportunity in species-poor communities. Dispersal-15 and evolution-mediated priority effects likely play greater roles in species-poor regions like the upper 16 latitudes, isolated islands, and in changing environments.

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18 Keywords: adaptive evolution, metacommunity, dispersal evolution, priority effects, eco-evolution

#### 19 1. Introduction

20 Biologists have long sought to predict how species interact and assemble into communities across 21 landscapes to understand biodiversity patterns and dynamics [1-3]. These efforts have generally 22 focused on combining niche or neutral processes with dispersal dynamics [4-6], including competition-23 colonization tradeoffs [2, 7, 8]. However, these efforts almost always exclude the potential for 24 evolution [9-11]. However, adaptation can occur at fine spatial and temporal scales, which can interact 25 with a wide range of ecological processes to shape biodiversity patterns [12-16]. Ecological and 26 evolutionary processes often act analogously on species and genetic diversity (e.g., dispersal and gene 27 flow) and thus can interact at similar spatiotemporal scales to alter predictions generated by ecology 28 or evolution alone [17-24]. Therefore, a full understanding of biodiversity patterns across space will 29 often be insufficient without exploring the joint operation of ecological and evolutionary dynamics.

30 Ecological and evolutionary dynamics are especially likely to interact during community 31 assembly. Ecological priority effects can occur when the early arrival of a species alters its interactions 32 with late-arriving species, often affecting the potential for coexistence and the ultimate richness and 33 composition of the community [25-27]. If an early arriving species can evolve and increase its fitness 34 in the local habitat, it may enhance this priority effect [28]. These so-called evolution-mediated 35 priority effects, also called community monopolization [9], can occur when early arrival provides 36 sufficient time for local adaptation to proceed, and these adaptations then limit the effective 37 colonization or final abundances of late-arriving species [9, 19, 28, 29]. These adaptations usually 38 expand the species' original niche to become more generalist and able to occupy a greater range of 39 environments [30, 31]. Theory indicates that evolution-mediated priority effects can occur as long as 40 species with high local fitness do not arrive too fast to outcompete the early colonists and prevent 41 them from adapting [29, 30]. In addition, theory suggests that evolution-mediated priority effects are 42 robust to many realistic contexts and can occur when species disperse at the same rate such that 43 differences in arrival occur solely through stochasticity, with both sexual and asexual reproduction, 44 and in landscapes of different patch configurations [29, 30]. Empirical tests have confirmed the

45 operation of evolution-mediated priority effects under laboratory conditions [32, 33], and some 46 natural community and phylogenetic patterns across biogeographic scales are consistent with the 47 operation of evolution-mediated priority effects [34, 35]. However, if the diversity of species already 48 adapted to available environments is large and all species disperse well across the metacommunity, 49 then species sorting – the ecological matching of species niches to environments – dominates [30, 36, 50 37]. Thus, the diversity of the regional species pool and the degree of connectivity through dispersal 51 determine if and to what extent evolution-mediated priority effects might shape community 52 assembly.

53 Despite its importance in eco-evolutionary community models, dispersal is usually treated as 54 a static trait that cannot evolve. Yet, dispersal is a trait like any other that can undergo adaptive 55 evolution depending on the relative fitness costs and benefits of dispersing [38-41]. Higher dispersal 56 evolves when dispersal costs are low or under high local intraspecific (also kin) competition, habitat 57 fragmentation, frequent habitat destruction, or the availability of new, low-competition patches [42-58 46]. Dispersal polymorphisms can evolve in response to disruptive selection originating from spatial 59 and temporal environmental heterogeneity, population fluctuations under different population 60 regulation, patch size variation, and random patch extinctions [47-49]. The contemporary evolution 61 of dispersal abilities has been documented for a growing list of species, including insects, plants, and 62 amphibians [50-54]. Given this capacity, the question emerges: to what extent might dispersal evolve 63 to promote evolution-mediated priority effects, niche expansion, and the monopolization of new 64 environments? We might expect that the evolution of increased dispersal of one species will decrease 65 priority effects and thus increase local diversity, whereas the evolution of increased dispersal in all 66 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 71 species and genotypes, and with and without dispersal costs and periodic patch extinction. We expect 72 that as the number of competing species increases, the opportunities will diminish for adaptation 73 before another species adapted to that patch arrives. We predict that increasing immigration from a 74 diverse mainland population will also decrease evolution-mediated priority effects and alter dispersal 75 evolution through maladaptive gene flow. We also expected that dispersal costs and no patch 76 extinction would lead to the evolution of lower dispersal. We were also interested in how variation in 77 genetic variation for dispersal could generate divergent dispersal abilities among competing species 78 and thereby alter the potential for evolution-mediated priority effects. We therefore contrast 79 scenarios where no, all, or one species can evolve dispersal probabilities to understand what happens 80 when the genetic variation needed to evolve dispersal is available to varying degrees in a species pool.

81

### 82 2. Material and methods

#### 83 2.1 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  $\epsilon$  of 0.20, 0.35, 0.50, 0.65 and 0.80 for patches one to five, 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 artifacts. 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 98 25-patch scenario), depending on the assumed number of species in the regional species pool. All 99 species have an identical genetic architecture. Like Leibold et al. [31], we use an explicit multi-locus 100 genotype featuring 50 biallelic (0/1) loci related to their environmental phenotype and 50 biallelic 101 (0/1) loci related to their dispersal phenotype, arranged in a diploid fashion (i.e., 2 x 50 loci for the 102 environmental and dispersal phenotypes). The environmental and dispersal phenotypes, e and d, 103 respectively, are calculated as the average of the binary allele values of the environmental and 104 dispersal loci respectively.

105 The environmental phenotype of each species inhabiting the mainland exactly matches the 106 environmental value of one of the five island patches (e.g., the environmental phenotype of species 1 107 matches the environment of patch 1), while the dispersal phenotype of all species that can evolve 108 dispersal matches an initial dispersal probability,  $\delta_{init}$ . This scenario simulates the realistic scenario 109 where a long-term equilibrium has been reached on the mainland where patches are full, competition 110 is widespread, and dispersal is low. To control standing genetic variation within each species on the 111 mainland, all genotypes of a species are derived from a single, randomly generated, ancestral 112 haplotype, with an appropriate ratio of binary alleles to match the prescribed phenotype of that 113 species. Genetic variation is introduced by randomly reshuffling a fraction  $\gamma$  of loci of the ancestral 114 haplotype, without affecting its overall phenotypic value (e.g., '00110' becomes '10010'). In total, 100 115 reshuffled environmental and dispersal haplotypes per species are created this way. A catalogue of 116 10,000 diploid genotypes per species is subsequently created by randomly sampling and pairing 117 available environmental and dispersal haplotypes. At each generation and for each patch, a draw from a Poisson distribution with expected value,  $\lambda$ , dictates how many individuals are seeded from the 118 119 mainland by sampling them from the catalogue of genotypes with replacement. Species inhabiting the 120 mainland are static and do not evolve over the course of the simulation. Hence, dispersal from 121 mainland is independent from the dispersal phenotype of individuals, which only dictates inter-island 122 dispersal.

97

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  $\epsilon_{patc}$  (i) of the individual's patch, by means of a squared exponential kernel with scale s, acting as the environmental selective pressure (with lower values corresponding to stronger selection):

129 
$$m_i = \exp\left(-\frac{\left(e_i - \epsilon_{patc}\right)^2}{s}\right).$$

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:

133 
$$r_{i} = \begin{cases} m_{i} \cdot \left( r_{max} \cdot \left( 1 - \frac{N}{K} \right) + \frac{N}{K} \right) & \text{if } N \leq K \\ m_{i} \cdot \frac{K}{N} & \text{if } N > K \end{cases}$$

134 We assume inter- and intraspecific competition to be equal. Hence, the local density of individuals Nand the carrying capacity K pertains to the density of all species combined. The effective reproductive 135 136 output of each individual, i, is obtained by drawing from a Poisson distribution with expected value  $r_i$ . 137 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 138 139 that they have been assigned a non-zero reproductive output as well to prevent individuals with a 140 poor environmental match being selected as mates. No restrictions on self-mating are imposed. During recombination of both parent's genotypes, independent assortment of all loci is assumed. Each 141 142 locus is prone to mutation to the alternative binary allele with probability  $\mu$ . Offspring individuals 143 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 144 higher dispersal probabilities did not usually evolve. Constraining the extent of dispersal probabilities 145 146 to a sensible range increases the phenotypical resolution for selection without affecting model

147 outcomes because dispersal probabilities > 0.1 do not evolve in any of the scenarios. Dispersing 148 individuals are randomly displaced to any of the island patches (including their natal patch). In 149 scenarios assuming a cost of dispersal, individuals die with a probability equal to the product of the 150 cost of dispersal parameter  $\chi$  and their dispersal phenotype d (i.e.  $\chi \cdot d$ ). As such, this cost of dispersal 151 solely depends on an individual's phenotype, reflecting a trade-off between survival and the 152 development of dispersal-related traits. This phenotype-dependent cost of dispersal complements the 153 implicit cost of dispersing to unsuitable patches, leading to a strongly lowered reproductive output 154 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.

161 In scenarios assuming random patch extinctions, all individuals inhabiting a patch die, 162 including offspring, with a probability  $\psi$ . Each simulation spans 2500 generations, at which point 163 metrics remained stable. At each generation, an inventory of individuals, including their patch 164 location, species identity as well as their environmental and dispersal phenotype is stored. To ease 165 memory usage, data on 1% of randomly selected individuals is stored, which is still highly 166 representative of the composition of individuals across space and time. A graphic overview of the 167 individual-based model and key life cycle characteristics is displayed in Figure 1.

168

169 *2.2 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 (Table 1 and 2). For each scenario, we ran a total of 25 replicate simulations.

173 We consider 13 different scenarios, that vary with respect to the number of species, whether the 174 species can evolve dispersal, and the fixed dispersal probability of species that cannot evolve dispersal. 175 Scenarios 1-6 pertain to a setting where none of the species can evolve dispersal (and have a fixed low 176 or high dispersal probability), scenarios 7-9 pertain to a setting where all species can evolve dispersal, 177 and scenarios 10-13 pertain to a setting where only one species can evolve dispersal while the other 178 species have a fixed (low or high) dispersal probability (Table 2). This last case reflects what might 179 happen if not all species can evolve because of limited genetic variation for this trait. This scenario 180 also allows us to explore the potential for stronger evolution-mediated priority effects if, for example, 181 one species evolves higher dispersal and can prevent colonization by the other species. Additionally, 182 we evaluate if the evolving species' location on the environmental gradient (whether at the boundary, 183 scenarios 10 and 12, or the center, scenarios 11 and 13) affects evolution-mediated priority effects 184 (Table 2).

185 To ensure the generality of our findings, we performed sensitivity analyses. In a first sensitivity 186 analysis, we consider a reduced mutation rate of 10E-5, rather than 10E-4, enabling us to discriminate 187 between the importance of mutations and standing genetic variation in fueling evolution in the 188 modeled system. In a second sensitivity analysis, we consider 25 patches with environmental values 189 equidistantly spread over the [0.20, 0.80] interval, and 25 mainland species with an environmental 190 phenotype that exactly matched one of the patches. In this alternative setting, environmental 191 distances between patches are reduced and species correspondingly face a reduced environmental 192 mismatch and therefore a smaller fitness difference when colonizing other environments compared 193 to scenarios with five patches colonized by one to five species. Both sensitivity analyses are conducted 194 factorially with the parameters mentioned in Table 1 and in conjunction with scenarios 1-9 (Table 2).

195

#### 196 2.3 Summarizing metrics

To investigate how varying parameters shape the evolution of dispersal, we computed the averagedispersal phenotype across all species and individuals populating the final 250 generations of each

199 simulation. Additionally, we compute a monopolization index for the second half of each simulation, 200 measuring the degree to which evolution-mediated priority effects lead to the monopolization of non-201 natal patch environments. Specifically, this index is calculated as the fraction of individuals residing in 202 a patch to which they were not initially adapted, weighted by each individual's degree of adaptation 203 (equation presented in SI1). As such, individuals less adapted to non-natal patches contribute less to 204 the monopolization index. The monopolization index ranges from 0 (when all individuals reside in the 205 patch to which they were originally adapted) to 1 (when all individuals reside in a patch to which they 206 were not originally adapted, while simultaneously matching the environment perfectly). We also 207 computed the average population size per generation across all patches per species to assess the 208 demographic benefits of dispersal evolution.

209

## 210 2.4 Implementation

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

214

#### 215 3. Results

216 3.1 Evolution of Dispersal

217 In the scenarios where all species can evolve dispersal, we observed that greater dispersal evolved 218 when (1) regional species richness was low, (2) mainland immigration rates were low, (3) dispersal 219 costs were absent, and (4) patches did not undergo periodic stochastic extinctions (Fig. 2). Each of 220 these factors interacted. For instance, the negative influence of regional species richness on dispersal 221 evolution was most pronounced when mainland immigration was high (Fig. 2). The variation in 222 dispersal that arises within a single scenario is also governed by multiple factors. Specifically, the 223 variation and hence unpredictability in dispersal probability across time and space was lowest with 224 high regional species richness combined with high mainland immigration, whereas scenarios featuring

periodic patch extinctions and low mainland immigration produced considerably more variation indispersal evolution (Fig. 2).

227 Simulations performed under reduced mutation rates lead to qualitatively similar results, 228 though the evolution of dispersal is slowed as it relies more on available standing genetic variation, 229 yielding lower evolved dispersal after an equal number of generations (Fig. S1). We also observed 230 consistent patterns when extending the simulations from five species and patches to 25 species and 231 patches (Fig. S2). Communities with 25 species and environments were characterized by an additional, 232 but modest, decrease in evolved dispersal in most scenarios, along with a decreased variability (Fig. 233 S2). Being faced with periodic patch extinctions and low to moderate mainland immigration, these 234 more speciose communities evolved higher dispersal compared to communities consisting of five 235 species inhabiting five patches (Fig. S2).

236

## 237 3.2 Evolution-mediated priority effects

238 Long-lasting evolution-mediated priority effects occur when a colonizing species is allowed sufficient 239 time before a better-adapted species reaches the patch. Notably, these effects can already develop 240 after fewer than 20 generations (Fig. S3). Evolution-mediated priority effects (and adaptive radiation 241 for one species) were most prevalent for scenarios with low regional species richness (Fig. 3). 242 Scenarios with only a single species invariably led to complete monopolization of all patches and acted 243 as an upper boundary to what was expected with more species. For two species, the monopolization 244 index was almost as high as for one species. Although evolution-mediated priority effects were rarer 245 in a niche-saturated, 5-species community, they still occurred to a limited extent (Fig. 3). Low mainland 246 dispersal resulted in greater monopolization of other environmental patches as well as more variation 247 among species and unpredictability. This pattern was likely because of the additional time before a 248 well-adapted species arrived from the mainland, thus affording more time for adaptation and more 249 historical contingency in the evolutionary and demographic trajectories for each species (Fig. 3).

250

#### 251 3.3 Evolution of dispersal and evolution-mediated priority effects

When dispersal could evolve for all species, the species underwent intermediate levels of monopolization (Fig. 3), because their evolved dispersal probabilities fell between the fixed values of high and low dispersal probabilities for the non-evolving dispersal scenarios. Compared against 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 (Fig. 3).

258 In a second approach, we allowed for only one species to evolve dispersal while others 259 remained fixed (non-evolving). When the other, non-evolving species had a high fixed dispersal, the 260 one species evolved low dispersal, and this species usually monopolized all the patches, especially 261 with moderate mainland immigration and no patch extinction (Figs. 4-5, Fig. S4). However, when other 262 species had a low fixed dispersal probability, the one with evolved dispersal did not undergo more 263 monopolization than the others. In general, high mainland immigration, low fixed dispersal 264 propensities, and periodic patch extinctions reduced the opportunities for monopolization by the 265 dispersal-evolving species in these simulations (Fig. 5). The position of the evolving species on the 266 environmental gradient (middle vs. edge) had little effect on dispersal evolution or monopolization effects. 267

268

## 269 4. Discussion

#### 270 *4.1 Dispersal evolution and species diversity*

271 Many species have adapted different dispersal probabilities, distances, or habitat selection in nature, 272 suggesting that this trait commonly evolves under varying landscape contexts [50-54]. Understanding 273 the evolution of dispersal requires a view that extends beyond the typical limits of the local population 274 and embraces a multi-patch perspective that includes the availability of high-fitness habitats external 275 to the population and considers the costs accrued during transit to these habitats [17, 56, 57]. 276 Dispersal evolution can thus be intricately tied to changes in habitat quality across landscapes and the ability to move across unsuitable habitat [51, 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.

284 Our simulations demonstrated that populations evolve lower dispersal probabilities when 285 species diversity is higher in the metacommunity (Fig. 2). This outcome likely reflects the higher 286 probability that dispersal into a new patch is maladaptive because that patch is dominated by a 287 competitor already adapted to the local environment. When fewer species exist, the potential fitness 288 advantages of colonization and exploitation of new niches increase. We could not find any models in 289 the literature that evaluated both niche and dispersal evolution in metacommunities of varying 290 species richness. Laroche et al. [59] allowed dispersal to evolve in a metacommunity without niche 291 evolution and assumed point speciation. They found that large communities become dominated by 292 low-dispersing endemic species and small communities become dominated by good dispersers that 293 are not strong competitors. Although difficult to compare to our model, this model indicates the 294 degree to which colonization-competition tradeoffs, habitat size, and dispersal evolution can interact 295 to determine species richness patterns. Outcomes from our model also correspond to the results of 296 several models that evaluate what happens on range edges, where populations become freed from 297 intraspecific competition. These models find that dispersal probability often evolves to higher levels 298 to take advantage of open, competition-free patches [38, 60]. Other models that evaluate the impact 299 of patch extinctions on dispersal evolution also find that the availability of open, competition-free 300 patches selects for the evolution of higher dispersal [51, 56-58]. In general, we can expect that lower 301 competition in both single-species metapopulations and multi-species metacommunities can select 302 for the evolution of higher dispersal. However, our model assumes that the competition-free

environment is a different environment, which could prevent colonization if the fitness of the colonistin the new habitat is too low.

305 We expected that higher dispersal would evolve when patches underwent periodic 306 extirpations and created more open environments to colonization [38, 60]. Instead, we observed 307 evolution towards lowered dispersal with periodic patch extinctions. This result occurred because we 308 modeled a constant rain of immigrants from the mainland pool in our model, all with the same low, 309 initial dispersal probability. These immigrating mainland individuals drove down the dispersal 310 probability in the new patches through gene flow (see Fig. S5), even though the first colonizers from 311 other patches were generally characterized by greater dispersal. This effect decreased in models with 312 a lower mainland immigration rate (Fig. 2). Interestingly, periodic extirpations combined with low to 313 moderate mainland immigration favored higher dispersal evolution in systems with more species and 314 closer niche optima (Fig. S2), indicating an interactive effect of diversity, niche differences, and patch 315 extirpation.

316

## 317 4.2 Effects on evolution-mediated priority effects

318 Reduced regional species diversity was strongly associated with higher rates of monopolization and, 319 accordingly, reduced rates of pure ecological species sorting (Fig. 3). Fewer species in the 320 metacommunity generated more open niches and fewer chances that a species already adapted to 321 that patch could arrive quickly and dominate. Under these circumstances, the existing species could 322 colonize new habitats, adapt to them, and reduce the establishment success of subsequent 323 immigrants, leading to evolution-mediated priority effects. Previous models that included niche 324 adaptation but not dispersal adaptation, similarly found that as species diversity increased, adaptation 325 to broader niches was strongly curtailed [36, 37]. When environments changed, these species quickly 326 re-sorted into high-fitness patches if they had sufficient dispersal rates, and the impact of evolution 327 on community dynamics was limited [37]. Thus, species richness generally determines ecological 328 opportunity and therefore the potential for evolution-mediated priority effects [37].

329 In our simulations, species evolved an intermediate dispersal rate relative to assumed fixed 330 rates based on the relative costs and benefits of dispersing under model conditions. Evolving this 331 intermediate dispersal rate led to a higher impact of evolution-mediated priority effects in multi-332 species simulations relative to low fixed dispersal probabilities in immigrants from the mainland but a 333 lower occurrence of evolution-mediated priority effects relative to simulations with high fixed 334 dispersal probabilities in immigrants from the mainland (Fig. 3). This result implies that models that 335 do not account for the evolution of dispersal might be over- or under-estimating the importance of 336 evolution-mediated priority effects in real communities where dispersal might evolve naturally to 337 different levels. Dispersal evolution in the high-diversity setting led to a metacommunity dominated 338 by low dispersal and species sorting, where each species is matched to a particular environment, even 339 though all species could adapt and spread to all other environments. In contrast, dispersal ability 340 evolves higher in metacommunities with low species richness, and the resulting greater dispersal 341 probabilities combined with more ecological opportunities promote niche expansion and habitat 342 monopolization, which could prevent additional species from colonizing. Thus, the evolution of 343 dispersal can operate to reinforce existing metacommunity dynamics and regional diversities, either 344 by reinforcing species sorting or monopolization of habitats (Fig. 3). For regions with high species 345 extinction rates, this dynamic could lead to the evolution of more dispersal and the continued 346 maintenance of low diversity.

347 We assumed that all species could adapt their dispersal probability, but this also meant that all 348 species converged on the same dispersal levels. These similar dispersal abilities reduced the potential 349 advantages of higher dispersal for colonizing competition-free patches. Therefore, we also evaluated 350 scenarios where only one species could evolve dispersal and the others could not, because the others 351 lacked sufficient genetic variation for this trait. In these simulations, the species evolved a dispersal 352 probability ranging from approximately 0.5% to 5%, increasing as mainland immigrant dispersal 353 decreased (Fig. 4). These evolved dispersal probabilities did not depend on the fixed dispersal 354 probabilities of the other non-evolving species. However, the degree to which they could monopolize

355 habitats depended strongly on the fixed dispersal abilities of the other species (Fig. 5). When the non-356 evolving species had a high, fixed dispersal, the single evolving species evolved relatively lower 357 dispersal probabilities, strongly monopolized habitats, and reached high abundances as a result (Figs. 358 4-5, Fig. S4). In contrast, when non-evolving species had a low, fixed dispersal, the single evolving 359 species evolved relatively higher dispersal probabilities and did not differ in monopolization extent 360 and even monopolized less under some scenarios (Figs. 4-5, Fig. S4). These results indicate an 361 underappreciated effect of maladaptive gene flow in determining evolution-mediated priority effects. 362 When species dispersed often and did not evolve a lower rate, they also could not adapt to local 363 habitats effectively because of the disruptive maladaptive gene flow from other habitats [61, 62]. The 364 evolving species adapted lower dispersal probabilities, however, and could adapt and monopolize 365 additional environments. Although we often consider strong dispersal as a prerequisite for a species 366 to undergo evolution-mediated priority effects, too much dispersal can reduce this ability, suggesting 367 an optimum dispersal probability for monopolization. In fact, the best monopolizers will be the species 368 that disperse well into other habitats, but then gene flow is very quickly reduced from other habitats 369 to allow rapid local adaptation through mechanisms such as selection against migrants [28, 63]. This 370 strategy constitutes a type of Darwinian Demon that disperses well, resists gene flow, and adapts 371 quickly. The evolution of reduced dispersal adds to these mechanisms that can reduce gene flow and 372 facilitate more rapid adaptation to new habitats amid a reduced threat of maladaptive gene flow.

373

## 374 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 381 them particularly susceptible to invasions by long-distant dispersers and subsequent adaptive 382 radiations [66]. As species diversity increases, the probability that a species is adapted to available 383 niches also increases, thus limiting ecological opportunities. The ability to take advantage of open 384 niches requires relatively strong initial dispersal (or luck) and a rapid rate of adaptation through 385 existing standing genetic variation or high rates of recombination or mutation. Hence, we expect that 386 ecological opportunity can select for higher dispersal when it provides access to competition-free 387 habitats. As such, we can predict that evolution-mediated priority effects will play greater roles in 388 species-poor regions like the upper latitudes, isolated islands, and in changing and extreme 389 environments. Under those conditions one can view ecological opportunity as a form of natural 390 selection for modified dispersal rates.

391 Given an ecological opportunity, the likelihood of evolution-mediated priority effects becomes 392 a race between arrival and adaptation of one species to an ecological opportunity before another 393 species already adapted to that niche can colonize [30]. Absolute dispersal and the relative difference 394 in dispersal among species are key traits that determine if and to what degree evolution-mediated 395 priority effects can occur and the dynamics of metacommunities. With high dispersal rates across all 396 species, evolution-mediated priority effects should disappear by reducing the time for adaptation 397 between arrival of different species. Then species sorting dominates, whereby each species arrives in 398 an environment that matches its traits before other species that are less well adapted to that 399 environment have the time to locally adapt; under those conditions the impact of evolution on 400 community assembly is generally low [37] and local and regional diversity should be higher. However, 401 such high dispersal rates did not evolve in our simulations. To the extent that this observation can be 402 generalized, it suggests that pure species sorting might be unlikely for species that have the capacity 403 to evolve dispersal rates, especially in environments with high costs to dispersal. Instead, we observed 404 the evolution of low dispersal probabilities in our simulations. At low - moderate rates of dispersal, 405 some species can adapt to nearby similar environments and can prevent other species from colonizing 406 or adapting to those habitats through the evolution of competitive exclusion [9, 28-30]. At even lower

407 rates of dispersal, the first species to arrive often has sufficient time to adapt to all or most 408 environments and can fill niches before any other species arrive, mimicking a long-distance 409 colonization of islands by one species or over longer time scales even an adaptive radiation into 410 ecomorphs that fill all niches [34, 66]. Because species diversity and dispersal strongly determine 411 outcomes, the evolution of dispersal is likely to shift across these dynamics, depending on the 412 direction it evolves and its relative heterogeneity among species.

413 Unfortunately, we know of no observations of natural systems that record both the evolution 414 of niche-associated traits and dispersal. A few studies now indicate the potential for evolution-415 mediated priority effects. For instance, a laboratory study with Haloferax species demonstrated that 416 a numerical advantage and adaptation of a weak competitor could reverse dominance by the stronger 417 competitor that arrives later [32]. The reconstruction of niches and colonization times of *Tetragnatha* 418 spiders on Hawaiian islands exemplifies what we might expect across varying degrees of connectivity 419 [34]. At shorter distances, species sorting dominated, while at intermediate distances, island niches 420 were filled by a combination of species sorting and adaptive radiation of first-arriving species. At long 421 distances, only one species arrived and radiated into all available niches [34]. However, nothing is 422 known about variation in dispersal among species and the possibility that it evolved during this 423 colonization period. Yet, dispersal can evolve under many circumstances [50-54], such as when 424 ecological opportunity presents itself [50] as modeled here. Therefore, future experiments and 425 empirical studies should not just track the evolution of niche-associated traits, but also dispersal traits.

426

427 Conclusions and future work

The model we present in this study is a first exploration on how evolution of dispersal interacts with metacommunity, landscape, and species' traits to influence the likelihood that niche evolution shapes the trajectories of community assembly. 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. 433 Our results suggest that interactions among dispersal and niche evolution might be common and 434 might significantly affect metacommunity structure and dynamics. Past studies usually evaluate 435 dispersal evolution in a single species across landscapes [38, 60] or multi-species niche evolution 436 without dispersal evolution [30, 31, 36, 37]. We hope that our initial model encourages additional 437 theoretical explorations that allow species to adapt both traits tailored to specific environments and 438 dispersal traits tailored to the landscape configuration. Some potential future directions include 439 models that explicitly incorporate colonization-competition tradeoffs among species in the presence 440 and absence of dispersal evolution. Another suggestion is to explore these dynamics in spatially 441 explicit landscapes, where environments or patchiness might vary randomly, with some spatial 442 autocorrelation, and along clines. In our model, we only allowed dispersal probability to evolve, but 443 the evolution of dispersal distance might also strongly affect the dynamics.

444 Exploring how these dynamics interact with environmental change (e.g., climate warming, 445 invasive species) would be another fruitful area of research. Anthropogenic environmental change 446 often causes extirpations on patches or creates new patches, such as happens when new habitats are 447 made available by a shifting climate. In general, such new opportunities should support greater 448 dispersal rates and therefore potentially alter the potential for evolution-mediated priority effects. In 449 particular, if species are colonizing new habitats on the edge of their range, they could evolve greater 450 dispersal to take advantage of new, competition-free habitats [44] as long as the new habitat is not 451 too different. Species that can evolve the greatest dispersal ability or longest distance before other 452 species might then monopolize habitats, preventing other species from tracking climate and 453 decreasing their range and the diversity of species.

454

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## 463 Tables

464

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

Parameter	Description	Value(s)	
K	Carrying capacity per patch	250	
r <sub>max</sub>	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	
$\delta_{init}$	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	
$\psi$	Probability of complete patch extinction	0; 0.01	

467

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 "center patch" or "center 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 pre-	Able to evolve dispersal?	Fixed dispersal
	species	adapted to		probability
1	1	Center patch	No	0.001
2	2	Outer patches	No	0.001
3	5	Each patch	No	0.001
4	1	Center patch	No	0.1
5	2	Outer patches	No	0.1
6	5	Each patch	No	0.1
7	1	Center 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 center species	0.001
12	5	Each patch	Only one outer species	0.1
13	5	Each patch	Only the center species	0.1

475 Figure captions

476

Figure 1. Schematic representation of the model structure, featuring important community and population dynamics steps. The color of patches and individuals represent 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.

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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 result in 0.1, 1, and 10 migrants per patch on average, respectively.

490

491 Figure 3. Monopolization indices for each of the scenarios where all species have a fixed low dispersal 492 probability of 0.001 (blue; scenarios 1-3; Table 2), where all species are able to evolve dispersal 493 (yellow; scenarios 7-9; Table 2), and where all species have a fixed high dispersal probability of 0.1 494 (red; scenarios 4-6; Table 2). The monopolization index measures the degree to which species occur 495 in habitats that they were not initially adapted to but now are, where 0 indicates no evolution-496 mediated priority effects and 1 indicates that all individuals have perfectly adapted to all other 497 habitats. Monopolization indices for each simulation are represented by small, horizontally jittered 498 dots. The mean monopolization index and corresponding standard deviations (mean ± 1 s.d.) for each 499 scenario are represented by circles and vertical bars. Scenarios are ordered by the mean 500 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).

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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, with dots representing species that can evolve dispersal. A grey dot under the x-axis indicates that none of the species 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.

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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, with dots representing species that can evolve dispersal. A grey dot under the x-axis indicates that none of the species 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.

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