Dispersal evolution can only rescue a limited set of species from climate change

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LAY SUMMARY: Global biodiversity is under threat from climate change. A key process for understanding species' responses to climate change is dispersal: the movement of an individual to reproduce somewhere other than its birthplace. Dispersal allows species to shift their range to more suitable habitats when conditions change. In addition, dispersal can evolve rapidly, especially during such range shifts. Here, we explore whether rapid dispersal evolution can save species from climate change. We identify a small set of cases in which this is theoretically possible. Our results outline general characteristics of species and their environments that make such rescue possible and therefore aid both with our fundamental understanding and applied conservation measures.

Altered environmental conditions due to anthropogenic climate change, such as rising temperatures, threaten biodiversity on Earth. In response, species may adapt evolutionarily to the novel environments and/or shift their ranges via dispersal to colonize suitable habitats. However, dispersal itself can evolve on ecological timescales, which could impact biodiversity maintenance under global change. Here, we explore theoretically how dispersal evolution modulates the response of metacommunities to climate change. We find that this response is heavily contingent on the environmental conditions experienced by the metacommunity prior to climate change. In particular, highly variable environments harbour dispersive but species-sparse communities. Species from such environments are more likely to survive climate change, as they can rapidly shift their ranges with their evolved dispersal abilities. In contrast, more stable environments lead to the evolution of less dispersive but more diverse metacommunities. Species' survival during climate change in such environments is less likely and depends on the evolvability of dispersal, as historically stable environments may lead to robust dispersal traits. We identify a limited set of scenarios in which contemporary dispersal evolution can rescue species from climate change. In doing so, we stress the importance of species' evolutionary histories and evolutionary rates, as determined by their genotype-phenotype maps, for their responses to rapid environmental change.

One of the main drivers of current biodiversity loss is the rise in temperatures due to climate change [1, 2]. Understanding which species survive under increasing temperatures, and why, is crucial for forecasting and potentially preventing further species extinctions [3, 4]. Generally, organisms can survive changing conditions (i) via local adaptation, that is, evolutionarily adapt to new conditions by shifting their niches to track environmental change [5, 6] or (ii) via dispersal, that is, species shift or expand their range and disperse to habitats they are already adapted to, thereby tracking conditions in space [7, 8]. However, any species' response to environmental change is heavily modulated by biotic interactions such as competition [9, 10]: If suitable habitat is already occupied, dispersing into this habitat may not be an option.

Theoretical work on the evolutionary ecology of metacommunities under climate change has generated one relatively consistent prediction: Dispersal and local adaptation can be antagonistic for the maintenance of biodiversity [11–13]. In particular, the interplay of these two processes can produce monopolization effects in space: Early-arriving species may adapt to the local conditions and then prevent later-arriving species from colonizing [14–16]. As a consequence, these evolution-mediated priority effects can contribute to biodiversity loss [12, 17].

This theoretical work has generally assumed invariant dispersal rates. However, dispersal is genetically determined [18, 19] and can evolve on ecological timescales, particularly during range expansions [20, 21]. Single-species models have presented proof-of-concept that rapid dispersal evolution can rescue populations during climate change [22, 23]. Multi-species models have, so far, only studied dispersal evolution during metacommunity assembly but show important interaction effects with local adaptation and the abiotic and biotic environment [24, 25]. To better forecast biodiversity loss, it is crucial that we understand how these interactions impact the potential of dispersal evolution to rescue species during climate change.

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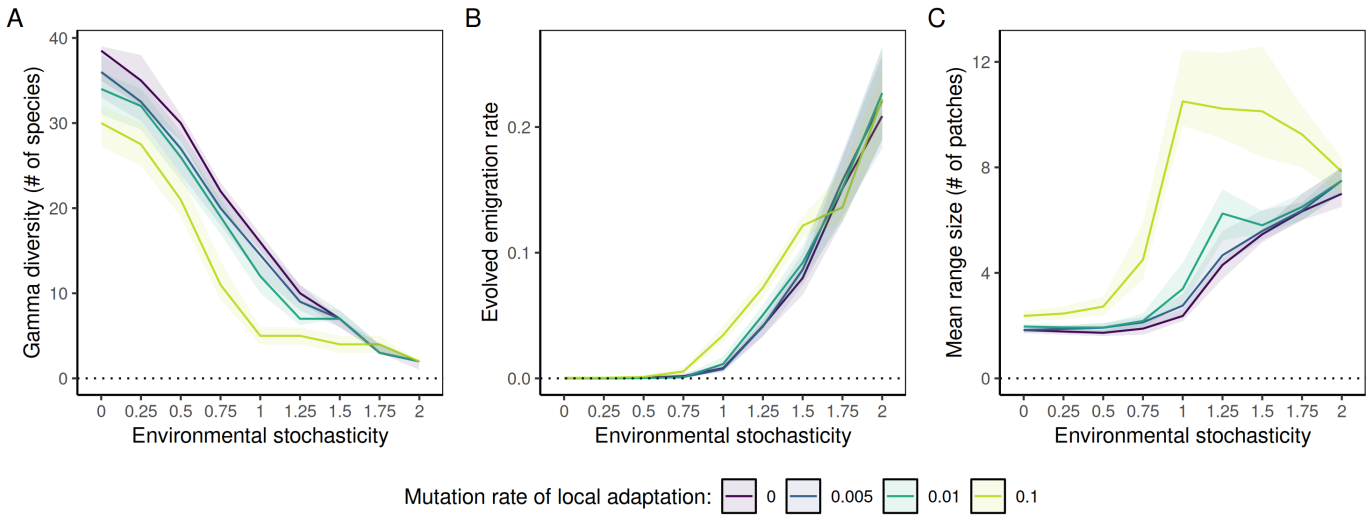

Figure 1: Community assembly dependent on environmental stochasticity. Lines represent medians and shaded areas interquartile ranges across 50 replicate simulations at the end of community assembly (t=10,000). Outcome variables are: (A) γ-diversity i.e., total number of species in the metacommunity; (B) the average emigration rate in the metacommunity; (C) the average range size of a species in number of patches. Dispersal mortality is set to an intermediate $\mu_0 = 10\%$. For all other parameters see Table S1.

Here, we use a stochastic, spatially explicit, individual-based model to explore how the joint evolution of local adaptation to an environmental gradient and dispersal modulates the response of a metacommunity to climate change. We ask the following questions: (1) How do dispersal evolution and its drivers shape community assembly? (2) How do species respond to climate change when both dispersal and local adaptation can evolve? (3) Can contemporary dispersal evolution rescue species from climate change, and if so, under which conditions? By answering these questions, we refine our mechanistic understanding of the processes governing biodiversity maintenance - which is urgently needed for both fundamental and applied purposes [4].

Results & Discussion

In our metacommunity model, the landscape is characterized by a temperature gradient, to which individuals can locally adapt. We allow the community to assemble until it reaches quasi-equilibrium, and then gradually increase temperatures uniformly across the landscape to simulate climate change. Individuals can disperse between patches. In our model, dispersal evolution is mainly driven by dispersal mortality (which selects against dispersal, [26]) and by environmental stochasticity (which selects for increased dispersal, [19, 27]). We do not vary dispersal mortality in the results presented in the main text, but the Supplementary Material contains sensitivity analyses in which this parameter is varied for all results.

To understand a metacommunity's response to climate change, we must first understand the processes and outcomes of community assembly, as it sets the scene for any adaptation to climate change. Therefore, we first analyze the metacommunity pre-climate change depending on different levels of environmental stochasticity. Then, we explore the response to climate change and the drivers of this response for two representative environmental scenarios: invariable (low environmental stochasticity) and variable (high environmental stochasticity). The Supplementary Material contains sensitivity analyses for alternative values of environmental stochasticity for all results.

Environmental stochasticity shapes metacommunity assembly via dispersal evolution

During community assembly, total biodiversity in the metacommunity is lower in more variable environments (Figure 1A). The species that survive in such environments evolve higher dispersal abilities (Figure 1B) and occupy larger ranges (Figure 1C). They thus hedge their bets in space, which is a widely known result [19, 27]. The higher the environmental stochasticity, the less species coexist (Figure S4A) and the more similar local communities are to each other (Figure S4B). Changes in dispersal mortality do not qualitatively change the results (Figure S5).

The loss of diversity at higher evolved dispersal rates is consistent with previous findings: Loreau et al. [28] find that at such high levels of dispersal, spatial insurance is not effective anymore in conserving regional biodiversity. Similarly, Amarasekare & Nisbet [29] find that dispersal rates above certain thresholds can inhibit coexistence between asymmetric competitors. In our model, priority effects might further compound these effects. We ran additional simulations, in which the environmental stochasticity was replaced by random patch extinctions, an extreme version of environmental noise [19]. The results are qualitatively similar, but a large amount of biodiversity is lost even when the rate of patch extinctions is very low (Figure S6). After such extinctions, the empty patches represent colonization opportunities, and therefore possible first-mover advantages. If dispersal rates are intermediate, local adaptation by the first movers might additionally reinforce these

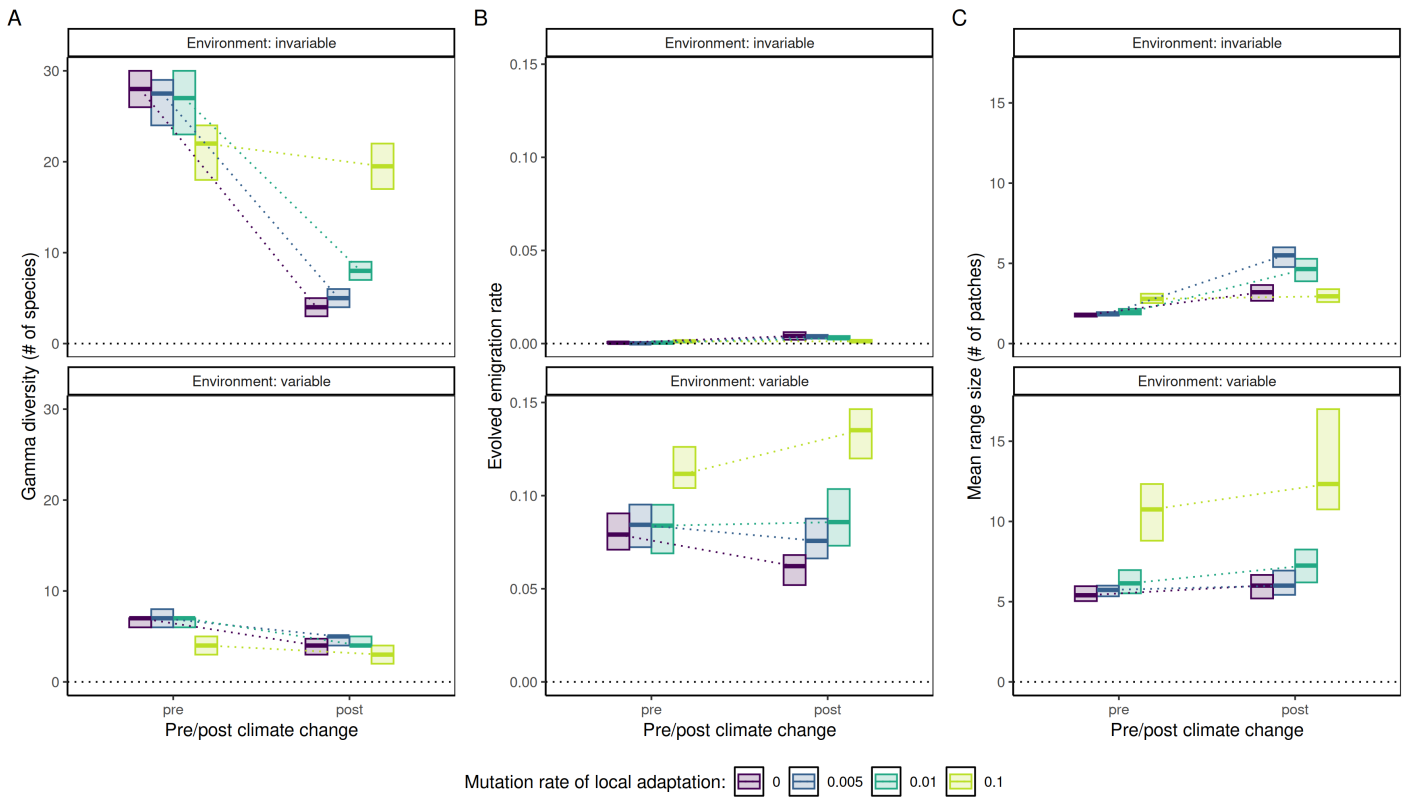

Figure 2: Response of the metacommunity to climate change. Thick lines represent medians and shaded boxes interquartile ranges across 50 replicate simulations pre (t=10,000) and post (t=15,000) climate change. Dispersal mortality is set to $\mu_0 = 10\%$ and the mutation rate of dispersal during climate change is set to $m_d = 0.0005$. In invariable environments, environmental stochasticity is set to $\sigma = 0.5$. In variable environments, environmental stochasticity is set to $\sigma = 1.5$. Outcome variables are: (A) γ-diversity i.e., total number of species in the metacommunity; (B) the average emigration rate in the metacommunity; (C) the average range size of a species in number of patches.

priority effects evolutionarily [15]. This reasoning might also explain the peak in range sizes at intermediate levels of stochasticity and high potential for local adaptation (Figure 1C). Our interpretation of the results matches natural and experimental observations from floodplains [30] and temporary ponds [31], typical instances of highly variable environments. In these systems, local communities were shown to become more similar across space and less diverse overall if given repeated and stochastic chances to recolonize habitat.

In concordance with previous research, our results demonstrate that environmental stochasticity is not only an important driver of dispersal evolution [27] but also of community assembly in heterogeneous environments [24, 25]. Different levels of stochasticity select for different dispersal rates and can subsequently produce a continuum of metacommunity dynamics from species sorting to mass effects [17, 32, 33]: Species sorting occurs in invariable environments that select strongly against dispersal and describes a case with many species occupying small, overlapping ranges. Mass effects occur in highly variable environments that select for dispersal, and describe a scenario with a few species that occupy large ranges and competitively exclude each other. These different dynamics in the community assembly process will prove crucial to understanding the response of the metacommunity to climate change.

Climate change causes biodiversity loss and range expansions

During climate change, biodiversity in the metacommunity declines in both invariable and variable environments (Figure 2A). The only exception occurs when species have such high potential for local adaptation that they can perfectly track the changing conditions by rapidly adapting their niche (Figure 2A, green; Figure S7A). During climate change, dispersal rates tend to increase in invariable environments and stay mostly constant in variable environments (Figure 2B). We observe an increase in range size, particularly in invariable environments (Figure 2C), and these range expansions are directed towards the poles (Figure S7B). Changes to dispersal mortality or the environmental variables do not qualitatively change the outcomes, except in highly chaotic environments (Figure S8).

We identify two major determinants of species survival during climate change: First, species occupying ranges closer to the poles are more likely to go extinct during climate change (Figure 3A). Compared to more equatorial species, their capacity for poleward shifts is reduced. This effect is particularly pronounced in variable environments, where poleward range contractions reduce the capacity for bet-hedging. This result is rather unsurprising and matches a widely accepted finding from the literature [34].

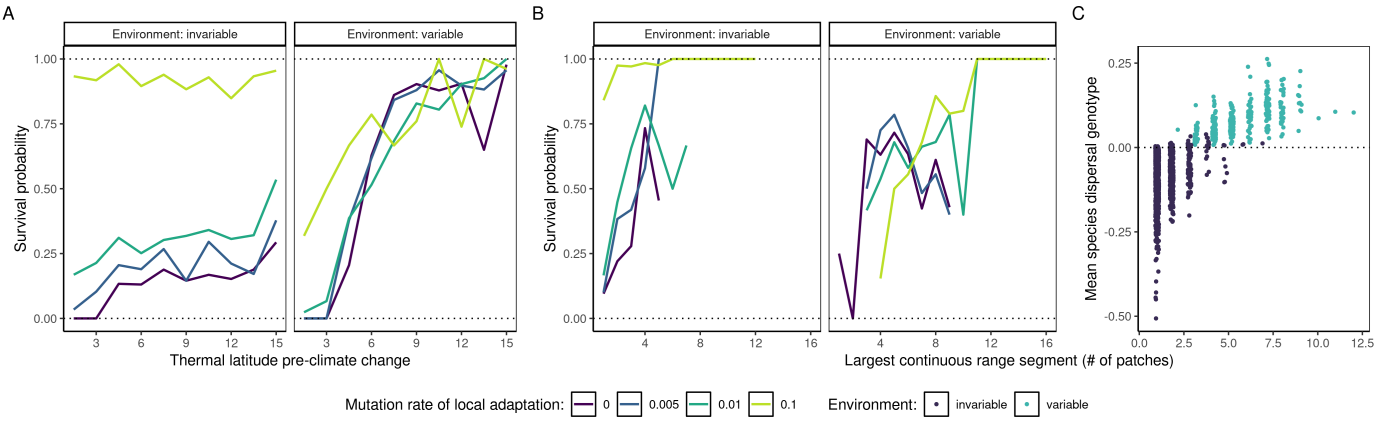

Figure 3: Determinants of species survival. (A) Survival probability of a species depending on the temperature in its range centroid pre-climate change. (B) Survival probability of a species depending on the size of the largest continuous segment of its range. (C) The genotypic mean of the dispersal trait of a species against its largest continuous range segment just before climate change (t=10,000) with a mutation rate of local adaptation of $m_{la} = 0.005$. For all graphs, data comes from 50 replicate simulations. Probabilities are calculated for values of the independent variables with a sample size greater than two. Dispersal mortality is set to $\mu_0 = 10\%$ and the mutation rate of dispersal during climate change is set to $m_d = 0.0005$. In invariable environments, environmental stochasticity is set to $\sigma = 0.5$. In variable environments, environmental stochasticity is set to $\sigma = 1.5$.

The size and fragmentation of a species' range pre-climate change is the second important determinant of its survival. Generally, species with smaller and more fragmented ranges are more likely to go extinct during climate change (Figure 3B), matching field observations [for a meta-analysis, see 35]. In our model, the reason likely lies in the selection pressures on dispersal and the sexual nature of reproduction: Species with isolated ranges could face mate-finding Allee effects during range expansions, which would select further against dispersal [36]. This dynamic mirrors observations of island and mountaintop populations experiencing strong dispersal reduction over time [37]. Once the climate starts changing, such species would neither have the dispersal abilities nor the neighboring populations to complete successful poleward range shifts. Our results do not depend on changes in dispersal mortality and environmental stochasticity, barring extremely chaotic environments (Figure S9).

The historical environment in which species have evolved is crucial for understanding the survival of species during climate change (Figure 3B,C): Variable environments exclusively produce dispersive species with larger and more connected ranges that can respond relatively well to climate change. In invariable environments, interspecific differences in range isolation and dispersal abilities make survival more conditional on historical range formation and stochastic processes during community assembly (see Figure S10 for an illustration).

More globally, biodiversity post-climate change converges to similar levels almost regardless of the level of environmental stochasticity or evolutionary potential of local adaptation, even though diversity pre-climate change differs wildly between scenarios (Figure 2A). In the absence of complete evolutionary rescue (Figure 2A, green), both the absolute and the relative impact of climate change is strongest for those metacommunities that experienced the least environmental stochasticity pre-climate change. This result is reminiscent of the findings of Bell & Gonzalez [38, 39] who show experimentally that evolutionary rescue is most likely to occur in metapopulations with a history of environmental stress. The analog in our model is that only those species who have evolved to survive high levels of environmental stochasticity also survive climate change.

Overall, our results demonstrate that climate change causes biodiversity loss and forces range expansions. Importantly, we have also shown that the impact of climate change depends heavily on the environmental history and subsequent evolution of dispersal in the metacommunity. The metacommunity's history will also determine the extent to which contemporary dispersal evolution can rescue species from climate change.

Dispersal evolution can rescue some, but not all species

Dispersal evolution has some capacity to rescue species during climate change, but it depends on the evolutionary potential of both traits, local adaptation and dispersal. When species can track their niche via local adaptation, increasing the mutation rate of dispersal has no effect (Figure 4A, green lines). When the evolutionary potential for local adaptation is relatively low, biodiversity maintained during climate change increases with the mutation rate of dispersal in invariable environments (Figure 4A, left panel). There is no such effect in variable environments (Figure 4A, right panel). However, the amount of species lost to climate change dwarfs the amount of species rescued by dispersal evolution (Figure 4B, left panel). The results do not depend on changes in dispersal mortality and environmental stochasticity as long as the environment does not become intolerably chaotic (Figure S11). The results are also insensitive to changes in the speed and volume of climate change (Figure S12) but suggest an interaction with local adaptation.

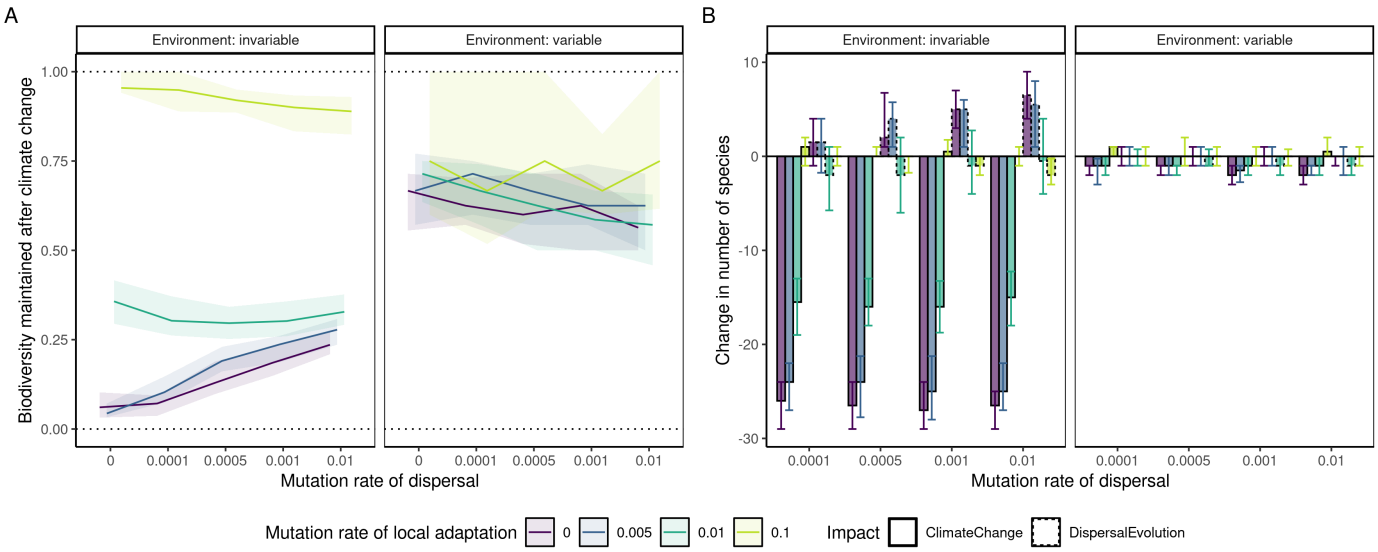

Figure 4: The impact of dispersal evolution under climate change. Lines/bars represent medians and shaded areas/error bars interquartile ranges across 50 replicate simulations. Dispersal mortality is set to $\mu_0 = 10\%$. In invariable environments, environmental stochasticity is set to $\sigma = 0.5$. In variable environments, environmental stochasticity is set to $\sigma = 1.5$. (A) The proportion of γ-diversity maintained after climate change (t=15,000) compared to before (t=10,000). (B) The change in γ-diversity during climate change due to the ecological effects of climate change, compared to the change due to dispersal evolution. We disentangle the species lost due to climate change and the species rescued due to dispersal evolution using a benchmark scenario, in which we do not allow for dispersal evolution during climate change (see Supplementary Methods).

Community rescue in invariable environments depends on high mutation rates (Figure 4A, left panel) because robust dispersal traits emerge in these environments. A trait is robust when genotypic changes due to mutation or recombination do not incur significant phenotypic changes [40, 41]. Whether a trait can evolve robustness depends on the genotype-to-phenotype map [42]. In our model, we assume that the dispersal trait is not bounded at the genotypic level. However at the phenotypic level, the dispersal trait - a probability - necessarily takes values between 0 and 1. This genotype-phenotype map implies that, under conditions that select very strongly and consistently against dispersal (such as invariable environments, Figure 1B), robustness can emerge: The genotype can take values below zero, implying that a phenotypic change away from zero is more difficult (Figure 3C). In our model, robustness occurs only in those species that have faced very strong selection pressures against dispersal in their evolutionary history (see Figure S10 for a comparison of genotypic trajectories between invariable and variable environments). This is representative of cases in which robustness should occur in natural populations, as it has been shown to evolve rather rapidly in the presence of strong selection pressures [43].

Previous work on robustness and evolvability has demonstrated that the genotype-to-phenotype map and its consequences for mutational effects can have eco-evolutionary implications up to the landscape scale [44, 45]. While lacking in sophistication, our genotype-to-phenotype map gives us the intuition that certain environmental and range characteristics might select so strongly against dispersal that it becomes difficult to regain these abilities once lost. In natural populations, for example, there is broad empirical support for loss of flight ability in many insects and birds that are isolated on islands or in habitat fragments [for a review, see 37]. Re-evolution of wings on the other hand is very rare - which may suggest robustness, but this remains of course speculative [37, 46]. Similarly, there is evidence for reduced and robust dispersal abilities at higher elevations, co-occuring with isolated populations in mountaintop habitats [47]. Our results suggest that such robustness of dispersal due to species' environmental and evolutionary histories could severely constrain their potential of rescue via dispersal evolution during climate change.

More generally, rescue effects via dispersal evolution have been shown in other theoretical work [22, 48], as has the rapid evolution of dispersal at range edges in natural populations [49, 50]. The evidence for the capacity of natural populations to track climate change with their niches on the other hand is ambiguous [34, 51], but such evolutionary rescue via local adaptation has been documented in freshwater fish [52], *Drosophila* flies [53], and marine phytoplankton [54]. Depending on species' life- and environmental histories, rescue via contemporary dispersal evolution is likely a salient but limited factor in predicting biodiversity loss due to climate change.

When is contemporary dispersal evolution relevant?

The ultimate goal of this article is to delineate the space in which contemporary dispersal evolution is relevant for biodiversity maintenance under climate change. To be relevant, it is necessary that rapid dispersal evolution enables range shifts that would not have been possible otherwise. In the absence of complete evolutionary rescue via local adaptation, there are thus three general cases to distinguish: (i) Range shifts are possible with the historically evolved dispersal abilities, (ii) range shifts are impossible, and (iii) range shifts become possible with rapid dispersal

evolution. Figure 5 conceptualizes these three cases and their eco-evolutionary origins.

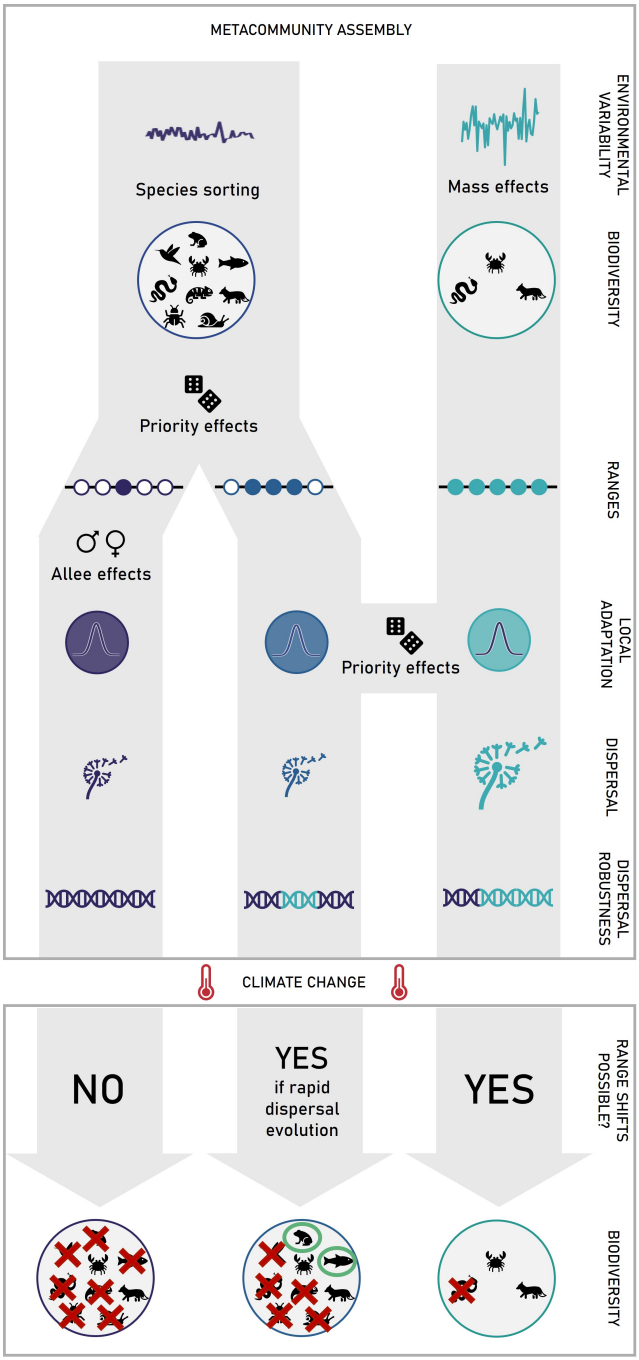

Figure 5: Conceptual framework of metacommunity dynamics during assembly from the landscape to the gene level, and the subsequent implications under climate change. At the bottom, red crosses signify species extinctions, green circles signify species rescue via rapid dispersal evolution.

The first case (range shifts are possible with historically evolved dispersal abilities, right side of Figure 5) appears mostly in historically variable environments. Community assembly is driven by spatial bet-hedging [19, 27] and species evolve relatively high dispersal rates and large ranges. Thus, mass effects occur during assembly [17, 32, 33], and communities are quite similar across space and not diverse overall. In this case, range shifts are likely possible with the evolved dispersal abilities. If any standing genetic variation is left in the population, those range shifts could be sped up via rapid evolution. However, our model predicts that the evolved dispersal abilities should be sufficient for species to track their environmental niche in space and biodiversity losses due to climate change should be rather small. Typical examples of this case could be metacommunities of northern European butterflies: They are characterized by relatively strong extinction-colonization dynamics [55], and climate change-induced range expansions have been shown in multiple species [50].

The second case (range shifts are impossible, left side of Figure 5) is the most catastrophic for biodiversity. It most likely occurs in historically invariable environments, in which dispersal is selected against [27] and species sorting [17, 32, 33] occurs. Once climate change starts, species do not have the necessary dispersal abilities to shift their ranges, and even if some individuals were to disperse, they would have to expand their range facing mate-finding Allee effects - if reproduction is sexual as we assume here. This case most likely occurs in isolated species with concordant ancient and strong selection that has reduced genetic variation to a minimum. Even if mutations could occur quickly enough, this stabilizing selection would likely produce dispersal traits that are canalized, that is, robust to mutations [40]. Natural examples include island and mountain-top populations, characterized by high degrees of endemism and isolation over long periods of time ([56, 57], but see [58]).

The third case (range shifts are possible with rapid evolution of dispersal, center of Figure 5) is more nuanced. In relatively invariable environments with species sorting dynamics, stochastic and historical interspecific differences can produce variable range sizes (Figure S10). For the few species that occupy comparatively large ranges in such environments, it depends on their historical presence in the range and subsequent local adaptation. Species with ancient and well-adapted local populations experience strong selection against dispersal, while species with newer and less well-adapted populations are still dispersive across the range (Figure S13). The latter scenario resembles the first case, depicted on the right side of Figure 5: Range shifts are possible with the evolved dispersal abilities. The former scenario captures the distinct subset of species that can theoretically benefit from contemporary dispersal evolution during climate change: Species from invariable environments, with large ranges and well-adapted local populations. If dispersal evolution is rapid enough, individuals from these species can disperse into neighboring populations and thus shift their range. Examples of natural systems for this case may include species with strongly peaked fitness surfaces across their geographical range, as recently shown in *Drosophila* [59], but this remains speculative.

It is important to note that in our model, the capacity of the system to respond to climate change mainly depends on new variation introduced by mutations since existing variation is usually limited after community assembly. Some theoretical work predicts the rapid evolution of increased mutation rates during range expansions [44], but such *de*

novo mutations of dispersal may be too limited in their effect to fundamentally change a population's response on ecological timescales [37]. Rapid evolution of dispersal during range expansions, as documented in natural and experimental systems, likely acts on standing genetic variation [49, 60]. In natural systems, such genetic variation can be maintained through other environmental and genetic mechanisms such as dominance or epistasis [61, 62]. It is possible that selection on such genetic variation can lead to rescue effects via dispersal evolution in natural populations, and the same holds for phenotypic plasticity [63] or epigenetic mechanisms [64]. However, our work highlights that information on genotype-phenotype maps and trait robustness is a necessary complement to information on standing genetic variation and mutation rates if we want to predict how biodiversity responds to climate change. The lack of empirical data in this context is worrying and our work underlines the importance of such integration across scales, from genomes to species ranges.

Distinguishing the three cases above maps out a clear framework for understanding community responses to climate change: Knowledge of the environmental and evolutionary history of a given community is crucial, as is an understanding of the existing evolutionary potential, or conversely, the evolved robustness. Efforts to predict the capacity for range shifts should not just measure current dispersal abilities, but also the variation in the traits determining these abilities, species isolation, and extinction-colonization dynamics. Such a mechanistic understanding of the capacity for range shifts is particularly important for species in which the potential for sufficiently rapid local adaptation remains questionable [34].

Conclusion

Anthropogenic climate change is accelerating, and so are its impacts on global biodiversity [65]. Here, we show that dispersal evolution and its drivers are key factors in understanding both the history of ecological communities as well as their capacity to respond to climate change. Historically variable environments equip species with sufficiently large ranges and dispersal abilities for range shifts towards colder climates. Species from historically invariable environments depend on rapid evolution of dispersal for their survival during climate change. However, their rescue might be constrained by the evolution of robust dispersal traits. Conservation efforts such as assisted gene flow [66] may therefore be most necessary for species with smaller, more fragmented, or colder ranges with a history of relatively stable environments.

Materials & Methods

We use a stochastic, spatially explicit, individual-based metacommunity model that assumes non-overlapping, discrete generations. The model was first presented in [12] and featured only local adaptation as an evolving trait. Here, we add dispersal as a second evolving trait. The Supplementary Material contains a full model description including the explored parameter space.

In the model, we track 80 initial species through time and space. The world is a ring of 30 patches (so to avoid edge effects) with a gradient in local conditions that could, for example, represent temperature but also any other environmental factor. The ring shape of the gradient effectively creates geographic poles that can be approached from both sides (see Figure S1). One replicate simulation runs for a total of 15,000 generations. During the first 10,000 generations, temperatures are held constant to allow the system to obtain quasi-equilibrium. Climate change starts at generation 10,000: From then on, temperatures increase uniformly throughout the landscape until the end of the simulation.

Species interact through competition. Each replicate run uses a unique matrix of intra- and interspecific competition coefficients. These coefficients are drawn from lognormal distributions such that coexistence is possible on average due to stronger intra- than interspecific mean coefficients.

Individuals have two diploid loci, one coding for emigration probability, one for local adaptation to the environment. Individuals reproduce sexually under random local mating. The reproductive output of a female follows a Beverton-Holt model [67] and depends on environmental stochasticity, intra- and interspecific competition, as well as the match between the female's environmental phenotype (the arithmetic mean between its two alleles coding for local adaptation) and the environmental condition of the patch it resides in. Offspring inherit one random allele from each parent at both loci. During inheritance, mutations can occur.

Dispersal is natal and costly in the form of a mortality probability for the dispersing individual [26]. Individuals can only disperse to their two neighboring patches. The dispersal probability of an individual (its phenotype) is governed by the arithmetic mean across the two alleles coding for dispersal. The phenotypic values of dispersal probability are bounded between 0 and 1, but the genotypic allele values are not. We tested different boundary conditions for the genotypic values and found that the no-boundary case introduced the least amount of bias (Figure S2).

During community assembly, dispersal evolves with an intermediate mutation rate up to generation 2,500 to come close to its optimum. Between generation 2,500 and 5,000, we use a simple annealing process, by which the mutation rate declines linearly to 0 [68]. We implement this process to stop dispersal traits from drifting too far below 0, thereby making our results conservative in terms of robustness. Between generation 5,000 and 10,000 (the start of climate change), selection acts only on the remaining variance in the populations. Once climate change starts, we re-introduce mutations at varying rates. See Table S1 for details.

Data Availability

Computer code is available at GitHub and Zenodo (DOI: XXXX).

Use of AI

Artificial intelligence (DeepL Write) was used to correct errors in grammar, spelling, and sentence construction.

Author contributions

E.A.F., P.L.T and P.K. designed the research. P.K., N.L. and E.A.F. performed research. P.K. and N.L. analyzed data. P.K. wrote the paper and all authors commented on the manuscript.

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