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The degree of spatial variation relative to temporal variation influences evolution of dispersal

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In the face of ongoing global climate and land use change, organisms have multiple possibilities to cope with the modification of their environment. The two main possibilities are to either adapt locally or disperse to a more suitable habitat. The evolution of both local adaptation and dispersal interacts and can be influenced by the spatial and temporal variation (of e.g. temperature or precipitation). In an individual based model (IBM), we explore evolution of phenotypes in landscapes with varying degree of spatial relative to global temporal variation in order to examine its influence on the evolution of dispersal, niche optimum and niche width. The relationship between temporal and spatial variation did neither influence the evolution of local adaptation in the niche optimum nor of niche widths. Dispersal probability is highly influenced by the spatio-temporal relationship: with increasing spatial variation, dispersal probability decreases. Additionally, the shape of the distribution of the trait values over patch attributes switches from hump- to U-shaped. At low spatial variance more individuals emigrate from average habitats, at high spatial variance more from extreme habitats. The comparatively high dispersal probability in extreme patches of landscapes with a high spatial variation can be explained by evolutionary succession of two kinds of adaptive response. Early in the simulations, extreme patches in landscapes with a high spatial variability act as sink habitats, where population persistence depends on highly dispersive individuals with a wide niche. With ongoing evolution, local adaptation of the remaining individuals takes over, but simultaneously a possible bet-hedging strategy promotes higher dispersal probabilities in those habitats. Here, in generations that experience extreme shifts from the temporal mean of the patch attribute, the expected fitness becomes higher for dispersing individuals than for philopatric individuals. This means that under certain circumstances, both local adaptation and high dispersal probability can be selected for for coping with the projected environmental changes in the future.

Synthesis

In landscapes characterised by temporal environmental variability, spatial heterogeneity may impose opposite selection on individuals adapted to abundant average or to rare extreme habitats. For the former, increasing spatial heterogeneity expectedly selects against dispersal, but for the latter the opposite is true. We explain this as result of bet-hedging benefits that allow dispersing individuals from extreme habitats to potentially achieve large fitness benefits in extreme years.

Introduction

In the face of ongoing global climate and land use change, organisms have multiple possibilities to cope with the modification of their environment. The two main possibilities are to either adapt locally or disperse from their original, increasingly unsuitable habitat to more suitable habitats (Bowler and Benton 2005, Fournier-Level et al. 2011, Hoffmann and Sgró 2011, Schiffers et al. 2014, Barnes et al. 2015, Hillaert et al. 2015, Romero-Mujalli et al. 2018). Both strategies however, have their own set of constraints and evolutionary patterns.

Given a large enough intraspecific variation (Hoffmann and Sgró 2011, Vincenzi 2014, Sieger et al. 2019), high mutation rates or large mutation amplitudes (Schiffers et al. 2014) organisms can adapt rather quickly to a changing habitat by adjusting their niche optimum. Survival depends, however, also on the ability to cope with short-term temporal fluctuations of the environment and thus the innate specialist–generalist tradeoff (Vasseur et al. 2014, Vincenzi 2014, Nguyen et al. 2019, Sieger et al. 2019). Together this leads to two general strategies, often described in the literature: specialists and generalists (Huey and Hertz 1984, Jacob et al. 2018). Specialists are described as organisms with a high fitness (e.g. reproductive success) at optimum conditions but a pronounced sensitivity towards deviations from that ideal environment, i.e. specialists have a narrow niche. Generalists have a broader niche and are therefore less susceptible to fluctuations in environmental conditions that deviate from their niche optimum, but at the same time, have a lower fitness at said optimum. The existence of such a tradeoff was shown not only to be true when comparing different species (MacDonald et al. 2018), but also as part of intra-specific variation (Fournier-Level et al. 2011, Scheepens et al. 2018). Tolerance to environmental conditions can also result from phenotypic plasticity, where organisms can change their own phenotype according to environment condition without loss of maximum fitness (DeWitt et al. 1998, Charmantier et al. 2008, Gunderson et al. 2017). In modeling contexts, both niche width and change of phenotype have been used to account for habitat tolerance. Both characteristics of a niche (position of the niche optimum and niche width) can evolve and help organisms to adapt to changing conditions if mutations in either are beneficial (Bennett et al. 2019, Sieger et al. 2019). However, evolution of the niche width is presumably constrained by the strength of a specialist–generalist tradeoff: if evolution of a broader niche is costly, organisms might ultimately not be able to evolve a broad enough niche to cope with the existing environmental variation (Sieger et al. 2019), and thus have to choose different strategies to survive changes, e.g. by following a bet-hedging reproductive strategy of having offspring with distinct properties to spread mortality risk or by distribute offspring over different habitats.

Most organisms are able to either disperse by themselves or via propagules, e.g. seeds. The evolution of dispersal is influenced by a number of circumstances such as intense local competition – especially among kin – inbreeding avoidance, and the exploitation of spatio–temporally variance in fitness expectations (Bowler and Benton 2005, Clobert et al. 2009, Kubisch et al. 2014, Kaemingk et al. 2019, Mayer et al. 2019, Schwarzmueller et al. 2019). Obviously, dispersal implies the ability of organisms, even under stable (average) conditions, to spread to new habitats, exchange genes between patches, and increase inclusive fitness (Bowler and Benton 2005, Mortier et al. 2018). However, it can affect the survival of metapopulations both positively and negatively (Fobert et al. 2019, Jacob et al. 2019, Kisdi et al. 2020, Masier and Bonte 2020, Cronin et al. 2020). Due to the spread of genes between patches, maladaptations can spread as well as beneficial adaptations. Overall, high dispersal can lead to synchronized population dynamics due to the exchange of many individuals and thus increase the probability of parallel extinction events. Then again, if maladapted populations go extinct, dispersal helps repopulate empty habitat patches and again promote metapopulation persistence (Bowler and Benton 2005). These metapopulation dynamics can influence the advantages and penalties of dispersal itself, forming and eco-evolutionary feedback loop (Bowler and Benton 2005, Kubisch et al. 2014), possibly leading to an evolution of dispersal propensity over time (Clobert et al. 2009, Kubisch et al. 2013, 2014). Currently, most research deems dispersal a factor promoting ecological generalisation, because it counteracts local adaptation as genotypes are rapidly exposed to different habitat conditions (Kisdi 2002, Stevens et al. 2014, Mortier et al. 2018). In the face of ongoing habitat variability and change, leaving the natal habitat and moving to a new one is also a possible strategy for overcoming the challenges of a changing environment (Ronce et al. 2005), in particular if temporal variability in habitat conditions occurs at a different scale than spatial variation. How the latter aspect might influence the evolution of dispersal and the niche seems to be understudied, especially with regard to the relationship between the magnitude of spatial and temporal environmental variation.

Here, we developed an individual based mechanistic model of a metapopulation with evolving dispersal probability, niche optimum and niche width, to account for all the aspects called for by Romero-Mujalli et al. (2018) and partly combining the approaches of Schiffers et al (2014) and Hillaert et al. (2015). The metapopulations inhabit a landscape with an approximately normal frequency distribution of habitat attributes in space that undergo global temporal environmental variability to include the effect of both spatial and temporal variability on local adaptation and dispersal. Our scenario thus implies that temporal variation like climatic variation takes place at a much larger spatial scale than spatial heterogeneity at the landscape scale. In particular, we

want to examine the influence of habitat frequency on local adaptation and dispersal, contrast the effect of spatial and temporal variance on such adaptation and consider the role of a tradeoff between maximum fitness and habitat tolerance. We hypothesize that 1) local adaptation in the niche optimum increases when spatial variation is larger than temporal variation, 2) local adaptation in the niche width is constant over landscapes and depends mostly on the imposed specialist–generalist tradeoff and the temporal variation and 3) higher dispersal emerges jointly with wider niches.

Material and methods

Overview

For this study, we expanded the model of an isolated population of annual, haploid individuals already described in Sieger et al. (2019) to a metapopulation model using the programming language Julia (Bezanson et al. 2012). Each patch (grid-cell) is characterized by a certain average habitat attribute such that the landscape exhibits spatial variability in habitat features. These attributes can be interpreted as reflecting certain environmental conditions like temperature, but every other continuous environmental variable is just as likely (e.g. precipitation, soil nitrogen content, water oxygen content, pH or salinity). However, temperature or precipitation would fit the pattern of larger scale temporal variation and smaller scale spatial heterogeneity best. Habitat attributes also vary in time. The temporal variation is synchronized over the whole landscape. We performed three time series of five landscapes for two specialist–generalist tradeoff strengths. This will be explained in more detail below. Each habitat patch in the metapopulation houses one populations as described in the above mentioned paper but individuals can also disperse to other patches by global dispersal. We use fertility (expected number of offspring) as a proxy for density-independent

fitness: For each individual, fertility depends on the fit between an individual's niche optimum and current environment condition as well as the individual's niche width. The dispersal trait and both niche traits are heritable and can mutate during inheritance thus allowing for adaptation to simulated conditions.

Landscapes

The metapopulation covers a spatially heterogeneous landscape of 64 by 64 habitat patches wrapped into a torus. We created five distinct landscapes using an algorithm for autocorrelated (fractal) landscapes with a Hurst-index of 0.3, developed by Chipperfield et al. (2011). This algorithm generates an approximately normal distribution of habitat attributes. We standardized each generated landscapes to a mean of 0 by calculating the mean of the landscape and subtracting this mean from each patch's value. Because of the global dispersal assumed the arrangement of habitat patches is not relevant but only the frequency distribution of mean patch attributes. Figure 1 exemplary shows one of the landscapes and the respective histogram for the distribution of environmental values. All five landscapes and their histograms can be found in the Supplementary material Appendix 1. The original landscapes had an average standard deviation of $\sigma_s = 0.32$ in the patches' mean habitat attribute.

In the simulation runs each landscape additionally experiences global temporal environmental variation: in every time step t a random value, drawn from a normal distribution with mean $= 0$ and $\sigma_T = 1$, is added to any patch's mean environmental value to form the current environmental value of each patch. For repeatability and to avoid unaccounted variance we created three different time series of environmental variation, that are utilized in all of the simulation experiments described below. All following scenarios will thus be based on 5×3 replicated simulation runs.
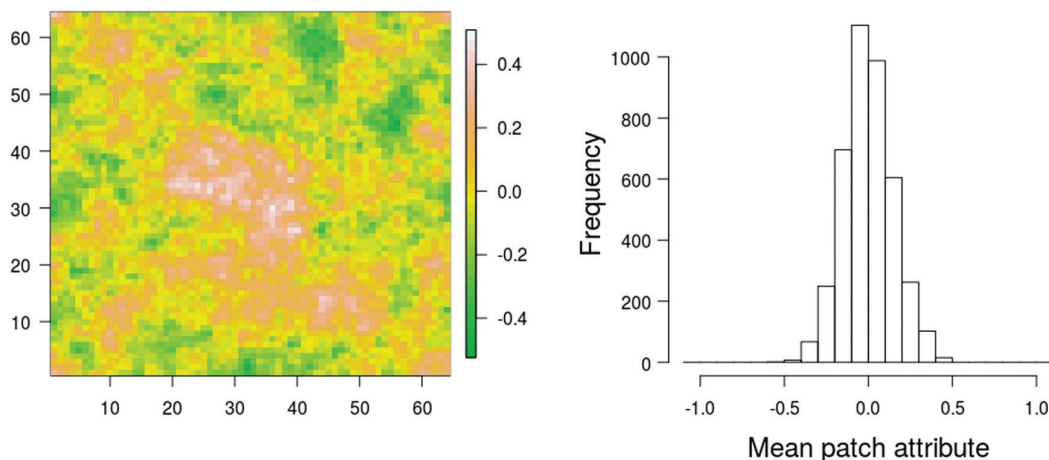

Figure 1. Example for landscape used in simulation experiments (for more details see text) with a standard deviation of 0.32. Because of the global dispersal assumed the arrangement of habitat patches is not relevant but only the frequency distribution of mean habitat attributes shown in the histogram.

Life-cycle and population dynamics

Newborn adult individuals first disperse. Each individual has a heritable and mutable trait d that codes for the probability to leave its natal patch. An individual leaves the natal habitat, when a random number drawn from a uniform distribution $U[0..1]$ is lower than the individual's dispersal trait value. After this decision, an emigrating individual either dies with a given dispersal mortality ($m = 0.1$) or immigrates into a randomly selected new patch. Here, we only implemented global dispersal, since it is a common simplification in metapopulation models (Kisdi et al. 2020) to assume each individual can reach each patch in the metapopulation. After dispersal, density-independent but habitat dependent reproduction of the N_j adults i in each patch j takes place. The fit between environmental conditions and the individual i's niche, determines its reproductive success. If the niche optimum is not identical to the environmental value, the expected fertility is consequently lower then the maximum fertility under optimal conditions. As mentioned above, the individual's niche is defined by two heritable traits, the position of the niche optimum h_i in the environmental space and the niche width (tolerance) g_i. Combined, the two traits define a normal distribution for the expected fertility around the niche optimum. The number of offspring for each adult i is calculated, with inclusion of a generalist–specialist tradeoff term (Eq. 1), following Chaianunporn and Hovestadt 2015).

$$T_i = e^{\frac{-g_i^2}{2\alpha^2}}$$

Note that larger values of α imply lower tradeoff costs. The resulting, environment dependent expected number of offspring for adult i with traits h_i and g_i in patch j, $L(H_{j,t}, g_i)$ at time t is calculated as:

$$L\left(H_{j,t}, h_i, g_i\right) = R_0 \times T_i \times \frac{e^{-(H_{j,t} - h_i)^2}}{g_i^2}$$

with R_0 the maximum possible offspring number. The actual number of offspring (larvae) born by each adult i in patch j is then generated by drawing from a Poisson-distribution with mean $L(H_{j,t}, h_i, g_i)$. When the difference between h_i and $H_{j,t}$ is low or the value of g_i is high, $L(H_{j,t}, g_i)$ is also high. The offspring inherit the three trait values from their parent, changed by a mutation event. After the birth of all offspring, the adult population dies.

The total number of larvae $L(j,t)$ produced in patch j at time t then undergo density-dependent survival, with survival probability calculated according to the Beverton–Holt-model:

$$s_{i,j,t} = \frac{1}{1 + a \times L\left(H_{j,t}, g_i\right)}$$

with $a = \frac{R_0 - 1}{K \times R_0}$ and K the carrying capacity. This survival probability is used to allocate a random binomial factor to each individual offspring indicating whether it survives or not; the surviving larvae constitute the new adult population of the next generation. One time step t therefore equals one generation.

All three trait values of an individual are inherited from the parent and evolve by mutation and selection. Evolution of the niche optimum and dispersal trait are not penalized, but according to Eq. 1 enlarging niche width underlies a tradeoff of different strength (parameter α), depending on scenarios: it is either weak (i.e. evolution of a higher tolerance diminishes maximum fitness at the optimum only slightly) or strong, leading to a bigger drop in maximum fitness when tolerance increases. The traits of each individual mutate separately and in each generation according to the following rules. In principle, the niche optimum is not bound to a certain range. Therefore a value drawn from a normal distribution with mean 0 and standard deviation 0.03 is added to the niche optimum inherited from the parent. The tolerance trait value however needs to stay a positive number. Therefore a similar additive mutation (that might lead to adding negative values) is prohibited. Additionally, it seems sensible to scale the mutation amplitude to the parent values, to prevent too drastic changes. Therefore, the tolerance trait value inherited from the parent is multiplied with a value drawn from a uniform distribution between 0.97 and 1.03. The dispersal probability d is also changed additively by adding a value drawn from a normal distribution with mean 0 and standard deviation 0.001. Values for d can thus also take values outside the range $[0..1]$ but this is not problematic, since the dispersal routine implemented treats dispersal with $d < 0$ as $d = 0$ and values of $d > 1$ as $d = 1$.

Initialization and scenarios

All patches were initialized with 100 individuals each. Individuals were initialized with a niche optimum drawn from a normal distribution with mean 0 and standard deviation 1. The optimum is drawn from a normal distribution to start with a certain amount of variation, similar to the temporal variation. Since the optimum trait value and the environmental attribute can both have positive and negative values, drawing from both sides of zero seems sensible. The tolerance value however needs to be a positive value, to give the niche its shape. Therefore, the niche width (tolerance) was drawn from a Log-normal distribution with =1 and =0. This avoids the emergence of negative values. The starting dispersal probability for each individual is 0.2. The single dispersal value was chosen to see the directional evolution of dispersal better. However, this does not limit the evolutionary potential of this trait, since we start with 409 600 individuals in the very first generation, whose offspring all mutate in this trait. Therefore large genetic variance rapidly builds due to ongoing mutation. The carrying capacity K of each patch is 1000 individuals, while the maximum number R_0 of offspring per

individual is 10 (only when perfectly adapted to the environment). To contrast the effect of spatial versus temporal variation, we further created variations of the 5 landscapes by modulating the magnitude of spatial variation. In the original set of landscapes, the temporal and the spatial variation had standard deviations of $\sigma_T = 1$ and $\sigma_s = 0.32$ respectively. To achieve different relationships, we kept the temporal variation the same and multiplied each patch attribute in the landscapes with either 4 (spatial variation higher than temporal variation, $\sigma_s = 1.28$), 2 or 0.5 (spatial variation smaller than temporal variation, $\sigma_s = 0.64$ and 0.16). This leads to 20 distinct landscapes. A single simulation run was carried out over 200 time steps (= generations). For each landscape and each scenario simulations were replicated three times, using three different vectors of global temporal variation. To look into the effect the dispersal mortality has on the evolution of the ecological niche and the dispersal probability, we performed one replication of one landscape for each degree of spatial heterogeneity and just the weak tradeoff with dispersal mortality $m = 0.0$ and $m = 0.2$.

Analysis

Graphical presentations of results were created using R (<www.r-project.org>) with the 'tidyverse' package (Wickham et al. 2019). No statistical significance tests on the results were performed, since this is not meaningful in modeling approaches. For each patch in each landscape scenario the means of all trait values were calculated, as well as the mean population size and fertility (as a proxy for fitness) every fifth generation. A smooth curve was fitted to the data using the 'gam' method of the geom_smooth function, which uses a generalized additive model for fitting. In each landscape, exemplary patches of the environmental average and extreme were examined to highlight the trait evolution over time. Here, the smooth curve was accomplished with the 'loess' method of the plotting function. Additionally, the evolved individual trait values were recorded for a single patch with the same, arbitrarily chosen coordinates in each landscape for each simulation in the last generation. Out of those patches, the ones with patch attributes close to the landscape mean ('average') or far from the landscape mean ('extreme') were selected. Results from these patches were used as examples for the individuals' trait spaces in the respective patches. The resulting data is not shown here.

Results

Overall, the results did not differ qualitatively between tradeoff strengths, therefore we only show the results for the weaker tradeoff. The corresponding results for the stronger tradeoff can be found in the Supplementary material Appendix 1. The outcome was also principally similar for the different dispersal mortalities min(0.0,0.2) and are also not shown here but can be found in the Supplementary material Appendix 1.

Local adaptation in the environmental niche

The average niche optimum value of individuals in the last generation approximates the corresponding patch's mean environment (Fig. 2a), showing a close relationship between the trait means and the patches' mean attribute values. This is consistent for both tradeoff strengths. However, in particular with the weaker tradeoff and when spatial variance is smaller or equal to the temporal variance, a tendency of a 'regression towards the mean' can be noticed with individuals in extreme habitat patches not exactly adapted to local conditions. The evolving mean niche width trait values in the last generation are only influenced by tradeoff strength. In the scenarios with a stronger tradeoff, niche width expectedly becomes narrower than in the scenarios with a weaker tradeoff. In generation 200 (final time step) populations in all patches have established about similar mean niche widths independent of the patches' habitat attributes (Supplementary material Appendix 2). However, the evolution of the niche width trait value over time differs with degree of spatial variation. With increasing spatial variation, the difference in temporal progression of niche width between central and extreme patches becomes more pronounced. In particular, with $\sigma_s : \sigma_T = 1.28:1$, in early generations, the average niche width trait values in extreme patches are much bigger than the average niche width trait values in average patches. The values for niche width also show much more variance in the extreme habitats. Over time, however, the niche width trait values in extreme patches approach the values in average patches (Fig. 3a), leading to the homogeneous trait distribution over patch mean attribute described above.

Evolution of dispersal

The patch-wise mean dispersal probability in the last generation decreases with increasing spatial variation for both implemented tradeoff strengths; the strength of the tradeoff itself has little effect on dispersal evolution. We also recognize a larger across patch variability in the mean dispersal trait with larger spatial variance (Fig. 4). Furthermore, the distribution of the mean trait values over the patches' environmental mean value changes from hump shaped when $\sigma_s < \sigma_T$ (spatial variation lower than temporal variation) to U-shaped when $\sigma_s > \sigma_T$ the same pattern shows when plotting the patch-wise mean dispersal trait values of individuals over their mean evolved local niche optimum (Fig. 2b). Indeed, the largest mean dispersal traits across all scenarios are observed in extreme habitat patches in scenarios with the largest spatial variance, despite the fact the we also see evolution of the lowest mean dispersal in average patches for those same scenarios. Following initialization dispersal probability decreases over time in all scenarios but a stable difference establishes between the average and the extreme
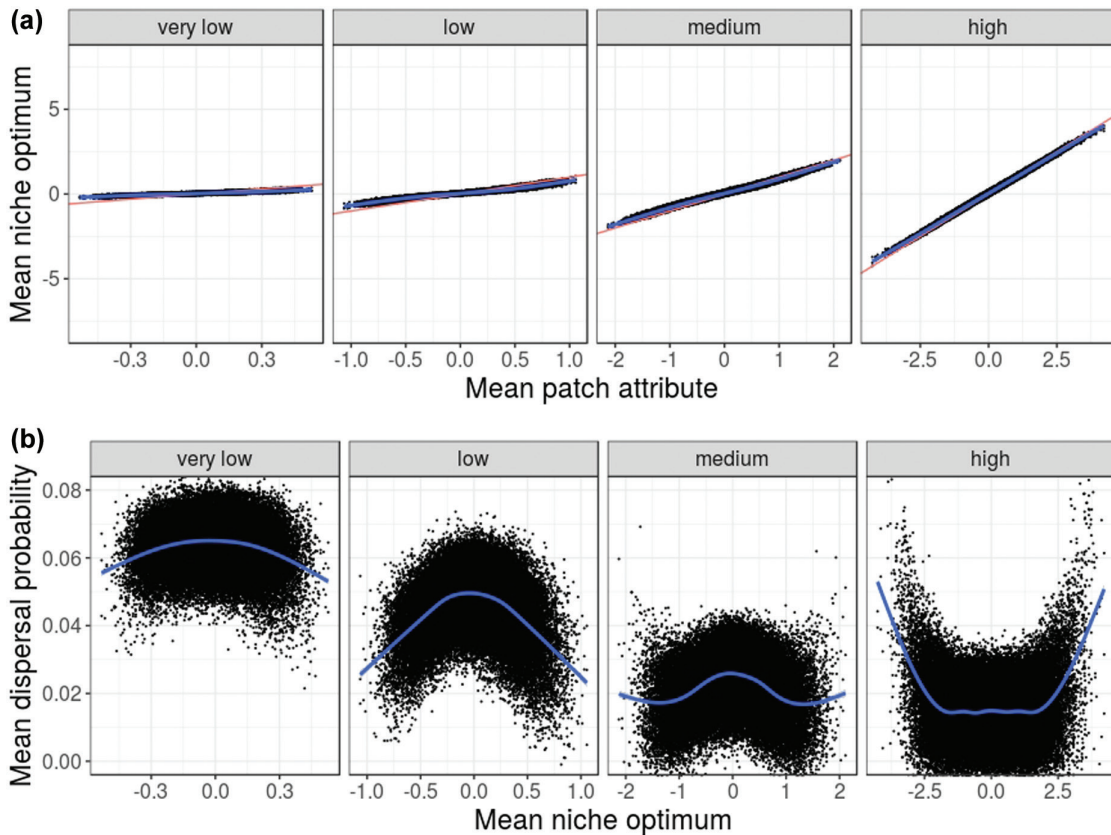
Figure 2. (a) Mean niche optimum trait value calculated in the last generation for each patch plotted over the patches' mean environmental attribute H_j. Panels show values for four degrees of spatial variation, which increases from left to right and is labeled relative to the temporal variation of $\sigma_T = 1$. Mean niche optimum trait values (fitted blue line) approximate the patches' mean environmental attribute (red line) indicating local adaptation. (b) Mean dispersal trait value of each patch plotted over the mean niche optimum trait value of the respective patch evolving by the end of the simulation. Data points from pooled data from the 15 replicate simulation runs for each scenario. Arrangement and classification of panels as in panel (a).

habitat patches in the landscapes with the highest spatial variation (Fig. 3b).

Population size and fitness

To better understand the reasons underlying the larger dispersal probability evolving in more extreme habitats we analyzed the fitness (expectation) of the individuals in each patch by calculating the geometric mean of the expected fertility (as a proxy for fitness) of each patch over the whole simulation run. In landscapes with a spatial variation smaller than the temporal variation, the geometric mean of expected fertility of the patches stays constant over the whole spectrum of the patch environmental attributes. A stronger tradeoff leads to an lower overall fitness. In landscapes with a spatial variation with SD 1.28, the geometric mean fertility becomes hump-shaped over the environmental spectrum. In more extreme patches the geometric mean of the expected fertility is smaller than in patches with an environmental attribute close to the landscapes mean (Fig. 2b). This hump-shape is found for both tradeoff strengths. Additionally, only in the geometric mean of the expected fertility there is a visible effect of the three

different time-series used for the global temporal variance. The lowest fitness corresponds to the iteration, where the vector of values for temporal variation has the biggest range of values (= higher temporal variation, Supplementary material Appendix 1). This influence of the different time runs of temporal variation is consistent for all tradeoff strengths. It is not found in the trait values, which are similar across all iterations and therefore similar across all time runs of temporal variation.

Discussion

Overview

Our simulations produce some expected results but also some unforeseen results that can be traced to the particular assumptions we make in our approach. We believe that our assumption of synchronized global temporal variance affecting a spatially structured landscape reflects a plausible scenario for some real world situations (Travis 2001, Poethke et al. 2003) – in particular for the effects of climatic
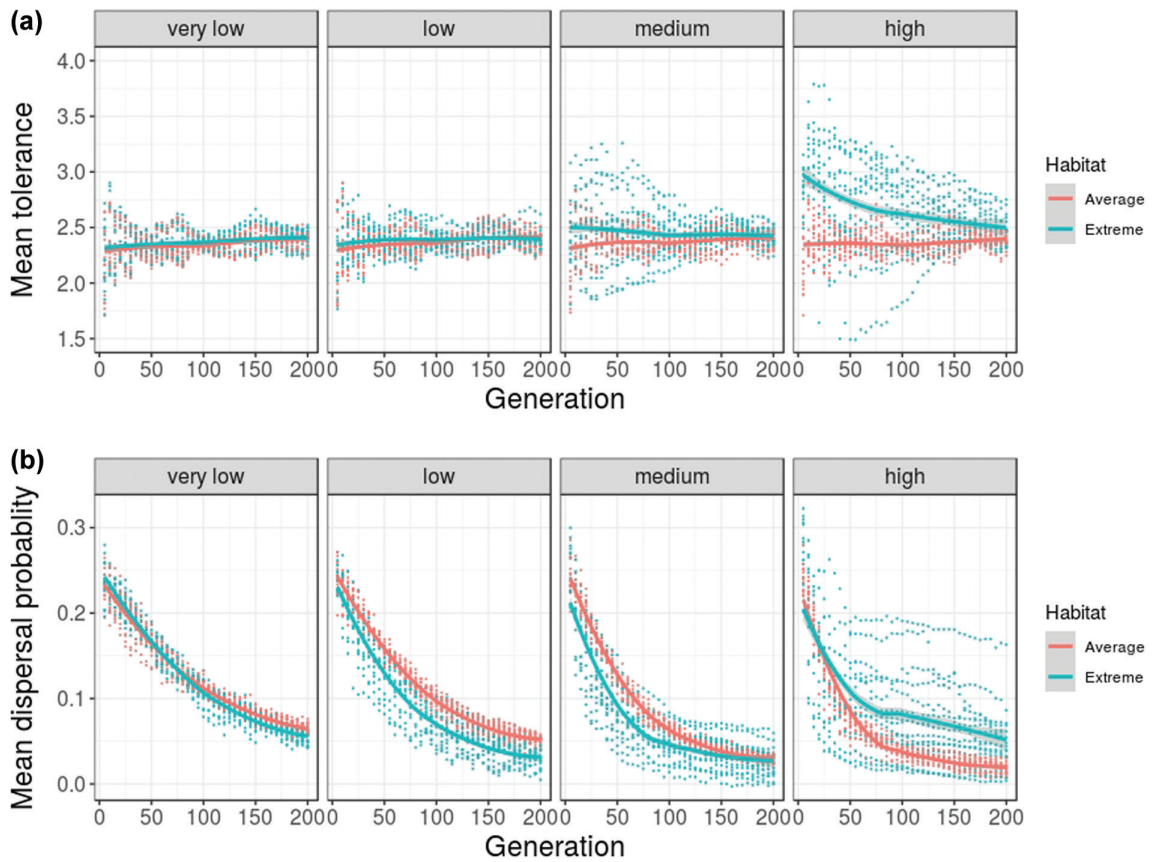
Figure 3. (a) Evolution of patch-wise mean tolerance values over time, starting in the fifth generation for two patches per landscape. For each of the 15 replicate simulation runs (5 landscapes × 3 time series) the patch with the most extreme habitat (the patch with the highest absolute value for the habitat attribute; blue dots and line) and the patch closest to average conditions (the patch with the lowest absolute value for the habitat attribute; red dots and line) are shown. (b) Change in patch-wise mean dispersal probability trait values over time, starting in the fifth generation for average (blue dots and lines) and extreme habitats (red dots and lines). Arrangement and classification of panels as in Fig. 2.

variation. The spatial variation experienced by any type of organism depends on the size of its 'daily activity range' and spatial demands on the one hand and its dispersal abilities on the other. For many organisms the former may only cover a few square meters and the latter distances of a few meters to a few kilometers – both scales, at which natural environments may show (strong) spatial variation in critical habitat attributes including temperature or soil humidity. However, climatic conditions and year-to-year variance in such conditions tend to correlate over much larger distances so that even
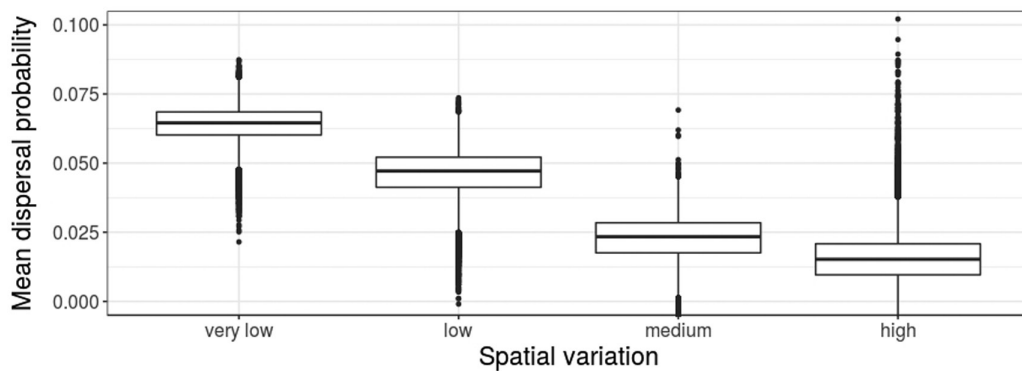

Figure 4. Box-plot of mean evolved dispersal traits values (averaged over 15 replicate scenarios) for the different degrees of spatial variation. Spatial variation increases to the right and is labeled relative to the temporal variation of 1.

moving and dispersing individuals are not likely to experience different climate than those that do not disperse. Most interestingly, we observe an inversion in evolving emigration probability with increasing spatial habitat heterogeneity: at low spatial variance individuals were more likely to emigrate from abundant average habitats, whereas with high variance they emigrated with larger probability from rare but extreme habitats. Nonetheless, local populations were mostly adapted to the attributes of the patch of residence with equal habitat niche width evolving in average and extreme habitats. In the following, we will provide a more detailed discussion of these results.

Local adaptation

Spatial heterogeneity will generally select for local adaptation and for lower dispersal as heterogeneity implies the cost of immigrating into non-suitable habitat (Mortier et al. 2018) and because dispersal has the tendency to generate a net-flow from large to small populations resulting in a net fitness-loss for dispersers (Hastings 1983, Venable and Brown 1993). In our simulation individuals' traits indeed tend to match, on average, the attribute of the patch of residence. In the scenarios with larger spatial than temporal variance mean niche optimum matched the patches' attributes so closely that individuals need to be considered perfectly locally adapted. However, for the scenarios with low spatial variance populations in extreme patches showed a relatively large degree of local maladaptation; this can certainly be traced to the net-gene flow from the abundant average habitats to the rare extreme habitats creating a 'regression towards the mean' effect. We must recognize, however, that this maladaption (gap) is small in absolute terms and has little fitness consequences; due to the selection imposed by the temporal variance on niche width (tolerance) individuals can easily cope with the much smaller spatial variance.

These results correspond with many empirical findings. A large proportion of natural populations show local adaptation (Hereford 2009, Schiffers et al. 2014), but it was also found that gene swamping – immigration of locally less adapted individuals – can hinder complete local adaptation (Kawecki 2008, Bridle et al. 2019, Bachmann et al. 2020, Weiss-Lehman and Shaw 2020). In case of steep environmental gradients even small populations can undergo rapid evolution and adapt to local conditions (Cropp and Norbury 2019). Ants, for example, were reported to show local adaptation, even in marginal habitats at their northern range edge (Nguyen et al. 2019). Fire salamanders could also adapt to environmentally extreme habitats which were connected to core zones and did show a high genetic diversity (Sinai et al. 2019); similar results were found by Schiffers et al. (2014).

Tolerance

Contrary to our expectation the tolerance levels ultimately evolving were only influenced by the tradeoff parameter α but did not depend on the amount of spatial variation. The mean tolerance values evolving were in fact close to the optimal tolerance values reported in our previous study for scenarios with only a single population; the unavoidable temporal variance in environmental conditions imposes selection for a specific tolerance value that maximizes the geometric mean fitness (Sieger et al. 2019), thus preventing an extreme 'narrowing' of the habitat niche on local average habitat conditions. Further, tolerance did not evolve to different values in average as compared to extreme habitat patches. Together, our findings suggest that evolution of dispersal probability and tolerance can be decoupled, especially when looking at the evolution of tolerance trait values in landscapes with low spatial variation over time.

Evolution in time

Results revealed clear temporal evolutionary dynamics, in particular in scenarios with large spatial variation. The initial rise to very high tolerance values in extreme patches is a consequence of the initialization routine: individuals were randomly initialized with trait values for the niche optimum taken from the same distribution as the temporal variation. This means that in extreme patches in landscapes with a large spatial variation, the individuals' niche optimum initially matched local habitat conditions poorly in the extreme habitats resulting in low fertility and frequent population extinction. Therefore, individuals with a high tolerance and high dispersal probability were initially favored, similar to results by Hillaert et al. (2015). Indeed, in our previous publication (Sieger et al. 2019) we could already demonstrate that an initial evolutionary response to local maladaption as, for example, initiated by climate change, may also be niche widening beyond the optimum under static average conditions as such a response can also reduce the cost of maladaptation. Only when the niche optimum had adapted to new conditions did the tolerance values evolve back to the optimal values.

Dispersal

In our simulations, the implemented dispersal strategy was global dispersal, i.e. dispersing individuals reach any patches in the landscape with equal probability. This is usually considered an antagonist for local adaptation (Jacob et al. 2018, Ducros et al. 2020) and leads to selection against dispersal in spatially heterogeneous landscapes. But even if costly, a minimum of dispersal (and thus gene-flow) is nearly universally selected for driven by the emerging kin structure (Hamilton and May 1977, Poethke et al. 2007) and exploitation of emergent stochastic variability in population sizes (Comins et al. 1980, Poethke et al. 2003). Not surprisingly, in our simulations evolution of average (median) emigration probability was consequently determined by the degree of spatial variation. Emigration probability declined as spatial variation increased due to the enlarged risk of dispersing into non-suitable habitat. In contrast, the magnitude of the tradeoff had no noticeable effect on the mean evolving dispersal probabilities.

More interestingly, in landscapes with lower or equal spatial than temporal variation, populations in extreme patches evolved lower emigration probabilities than those in average habitats (hump-shaped pattern in Fig. 4) whereas the opposite was true in scenarios where spatial variance was larger than the temporal variance (U-shaped pattern). To understand this we have to realize that the landscape 'looks' different from the perspective of individuals adapted to average than from that of individuals adapted to more extreme habitats. With the normal distribution of habitat attributes implemented in our simulations the former individuals likely immigrate into habitats more or less similar to the one of origin whereas the latter are likely to immigrate into very different habitats. In fact, in the scenarios with small spatial versus temporal variance migrants surviving dispersal and adapted to average habitats can expect the same fertility than individuals that do not emigrate (cf. Fig. 5). This is not quite so for individuals adapted to extreme habitats explaining the evolution of reduced dispersal from such habitats. In any case, long-term geometric mean fitness is much more dominated by the temporal variance in these scenarios that cannot be avoided by dispersing.

However, with spatial variance getting larger the landscape offers an opportunity for bet-hedging on the effects of temporal variation. In particular, in extreme years with low fitness expectations in the (on average) optimal habitat, emigrants may have much higher fitness expectations than philopatric individuals (Fig. 5). Whereas this effect is about symmetric (with regard to the direction of temporal extremes) and rather weak for individuals adapted to average conditions it is highly asymmetric for individuals adapted to extreme habitats favoring dispersal in the latter group; in some extreme years such individuals may find favorable conditions in far more patches than in the average seasons. Conversely, for individuals adapted to average conditions only few patches will offer optimal conditions in extreme years. It is important to recognize that in our scenarios, and in contrast to other studies implementing spatio–temporal variance, the fitness expectations of emigrants do not fluctuate randomly as compared to that of philopatric individuals; emigrants can expect high rewards in particularly in years were conditions in the natal patch are very poor. For this reason the bet-hedging benefit is more important for individuals adapted to extreme habitats promoting evolution of higher emigration probabilities in these patches. By analyzing individual trait combinations recorded for single patches we could verify that this was not due to gene-swamping of more dispersive but poorly adapted individuals from other patches. In comparison to results from patches that had a mean closer to the landscape's mean, the trait for emigration probability took generally larger values in extreme habitats but was not correlated with the level of maladaptation.

Apart from this direct benefit of bet-hedging a second effect may add to the evolution of higher emigration probability in extreme habitats. Individuals adapted to extreme conditions have no chance of avoiding the drastic effects of temporal extremes in the 'wrong direction' (cf. Fig. 5) presumably leading to more frequent local lineage/population extinction. For example, a cold-adapted individual adapted to conditions 3 SD below the landscape average, will have very low fitness expectations in a very hot season wherever it is, whereas for individuals adapted to average conditions favorable conditions will occur in some habitat patches in every season. Lineages/populations adapted to extreme
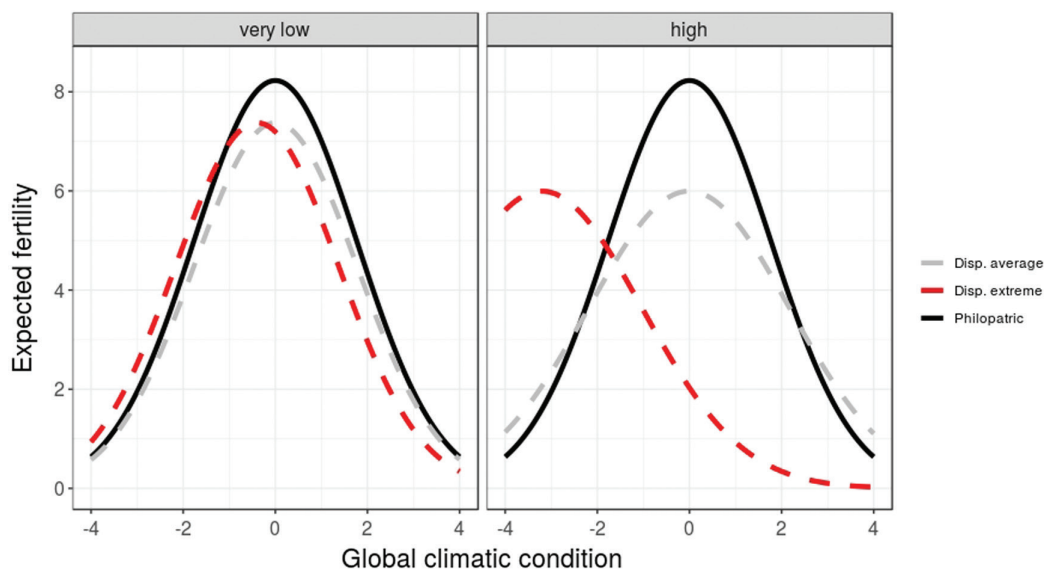

Figure 5. Expected mean fertility for individuals either remaining philopatric and adapted to the patch of origin ($h_j = H_j$) in dependence of actual climatic condition (black line) or randomly dispersing (accounting for 10% dispersal mortality). Grey hatched line for individuals adapted to and emigrating from an average patch ($H_j = 0$) and red hatched line for individuals adapted to conditions -2.5 spatial standard deviations below the spatial mean (cold adapted). Left panel shows values for the lowest spatial variation ($\sigma_s = 0.16$), the right column for the highest spatial variation ($\sigma_s = 1.28$).

conditions will thus suffer occasional local and even global population collapses increasing the likelihood of local extinction, the emergence of tighter kin-structure and the chance for recolonizing suitable habitats; all these effects are known to promote evolution of dispersal (Hamilton and May 1977, Ronce et al. 2000, Leturque and Rousset 2002, Poethke et al. 2003, 2007). We think that this is a likely added effect and it deserves further attention in future developments of our approach.

Limitations

The presented model makes some general (and common) assumptions for sake of simplicity and computational effectiveness. Some of these assumptions have the potential to influence our results on the evolution of dispersal and the environmental niche. First, the assumption of large-scale and random dispersal is not found as ubiquitous in nature and a high number of different and not mutually exclusive dispersal types and strategies can be found (Bowler and Benton 2005, Jacob et al. 2018, 2019, Fobert et al. 2019, Schwarzmueller et al. 2019, Ducros et al. 2020, Kisdi et al. 2020, Cronin et al. 2020). In particular in spatially autocorrelated landscapes more local dispersal may be a better strategy as it assures immigration into habitats more similar to the habitat of origin (cf. Hovestadt et al. 2001). In addition, habitat dependent emigration, habitat choice when settling and density dependent dispersal are all mechanisms worth of exploring with the particular scenario we have implemented here – we expect that with such 'smarter' dispersal strategies a greater diversity of niche and dispersal strategies may evolve in complex landscapes.

Sexual recombination can also play an important role in the evolution of dispersal (Leidinger and Cabral 2020, Weiss-Lehman and Shaw 2020) allowing for faster evolution and recombination. Nevertheless, the high standing variation in the founding population here ensured that inter-individual variability was high and sufficient phenotypic variability was present in the meta-population. Additionally, the 'time' and 'energetic' costs associated with dispersal, i.e. the costs associated with developing specialised dispersal organs and tissues or the time taken to disperse as described by Bonte et al. (2012), might also be of interest. It would be possible to include these e.g. by implementing a tradeoff between resource allocation to either reproduction and dispersal (as described in Saglam et al. 2008, Burton et al. 2010, Guerra 2011, Matsumura and Miyatake 2018, Renault 2020). However, certain dispersal costs are already included in our simulations via the penalization of dispersal by a mortality cost and especially the local maladaptedness of dispersers in the new habitat often enough resulting in the reduction of the number of offspring for dispersing individuals. Adding investment costs for dispersal would certainly result in selection for (even) lower emigration probabilities, but would, in our opinion, not change the general results we present here. This is corroborated by the small qualitative difference in evolution between scenarios with different degrees of dispersal mortality.

Conclusions

Our simulations document the importance of spatial and temporal variance in environmental attributes for the evolution of both the ecological niche and of dispersal. Importantly – and in difference to many previous studies – our scenarios assume that temporal variation occurs at a much larger scale than spatial variance which creates different selective pressures than under the assumption of uncorrelated temporal variance (Travis 2001, Poethke et al. 2003). Further, in our simulations we assume a normal distribution for the occurrence of habitat attributes in space resulting in a high frequency of average habitats and low frequency of extreme habitats. This has the consequence that in our simulations some patches may on average be the best suitable for an individual with a given niche, but that the identity of patches with optimal conditions nonetheless is dynamic in time. This allows and selects for the evolution of bet-hedging strategies in particular in lineages adapted to more extreme habitat conditions.

Notwithstanding the limitations of the presented work, our results thus suggest that the combination of spatial and large-scale temporal environmental variation may have specific effects on trait evolution. We conclude that the degree of spatial variation relative to the global temporal variation is highly relevant for the evolution of dispersal in habitats of different frequency but has only small effects on the evolution of niche attributes.

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.pg4f4qrm8> (Sieger and Hovestadt 2020).

References

Bachmann, J. C. et al. 2020. Gene flow limits adaptation along steep environmental gradients. – Am. Nat. 195: E67–E86.
Barnes, A. D. et al. 2015. Individual behaviour mediates effects of warming on movement across a fragmented landscape. – Funct. Ecol. 29: 1543–1552.
Bennett, S. et al. 2019. Integrating within-species variation in thermal physiology into climate change ecology. – Phil. Trans. R. Soc. B 374: 20180550.

Bezanson, J. et al. 2012. Julia: a fast dynamic language for technical computing. – <http://arxiv.org/abs/1209.5145>.

Bonte, D. et al. 2012. Costs of dispersal. – Biol. Rev. 87: 290–312.

Bowler, D. E. and Benton, T. G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. – Biol. Rev. 80: 205–225.

Bridle, J. R. et al. 2019. Local adaptation stops where ecological gradients steepen or are interrupted. – Evol. Appl. 12: 1449–1462.

Burton, O. J. et al. 2010. Tradeoffs and the evolution of life-histories during range expansion. – Ecol. Lett. 13: 1210–1220.

Chaianunporn, T. and Hovestadt, T. 2015. Evolutionary responses to climate change in parasitic systems. – Global Change Biol. 21: 2905–2916.

Charmantier, A. et al. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. – Science 320: 800–803.

Chipperfield, J. D. et al. 2011. An updated algorithm for the generation of neutral landscapes by spectral synthesis. – PLoS One 6: e17040.

Clobert, J. et al. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. – Ecol. Lett. 12: 197–209.

Comins, H. N. et al. 1980. Evolutionarily stable dispersal strategies. – J. Theor. Biol. 82: 205–230.

Cronin, J. T. et al. 2020. Modeling the effects of density dependent emigration, weak Allee effects and matrix hostility on patch-level population persistence. – Math. Biosci. Eng. 17: 1718–1742.

Cropp, R. and Norbury, J. 2019. An eco-evolutionary system with naturally bounded traits. – Theor. Ecol. 12: 401–412.

DeWitt, T. J. et al. 1998. Costs and limits of phenotypic plasticity. – Trends Ecol. Evol. 13: 77–81.

Ducros, D. et al. 2020. Beyond dispersal versus philopatry? Alternative behavioural tactics of juvenile roe deer in a heterogeneous landscape. – Oikos 129: 81–92.

Fobert, E. K. et al. 2019. Dispersal and population connectivity are phenotype dependent in a marine metapopulation. – Proc. R. Soc. B 286: 20191104.

Fournier-Level, A. et al. 2011. A map of local adaptation in *Arabidopsis thaliana*. – Science 334: 86–89.

Guerra, P. A. 2011. Evaluating the life-history tradeoff between dispersal capability and reproduction in wing dimorphic insects: a meta-analysis. – Biol. Rev. 86: 813–835.

Gunderson, A. R. et al. 2017. Estimating the benefits of plasticity in ectotherm heat tolerance under natural thermal variability. – Funct. Ecol. 31: 1529–1539.

Hamilton, W. D. and May, R. M. 1977. Dispersal in stable habitats. – Nature 269: 578–581.

Hastings, A. 1983. Can spatial variation alone lead to selection for dispersal? – Theor. Popul. Biol. 24: 244–251.

Hereford, J. 2009. A quantitative survey of local adaptation and fitness tradeoffs. – Am. Nat. 173: 579–588.

Hillaert, J. et al. 2015. The evolution of thermal performance can constrain dispersal during range shifting. – J. Biol. Dyn. 9: 317–335.

Hoffmann, A. A. and Sgró, C. M. 2011. Climate change and evolutionary adaptation. – Nature 470: 479–485.

Hovestadt, T. et al. 2001. Evolution of reduced dispersal mortality and 'fat-tailed' dispersal kernels in autocorrelated landscapes. – Proc. R. Soc. B 268: 385–391.

Huey, R. B. and Hertz, P. E. 1984. Is a jack-of-all-temperatures a master of none? – Evolution 38: 441–444.

Jacob, S. et al. 2018. Habitat choice meets thermal specialization: competition with specialists may drive suboptimal habitat preferences in generalists. – Proc. Natl Acad. Sci. USA 115: 11988–11993.

Jacob, S. et al. 2019. Variability in dispersal syndromes is a key driver of metapopulation dynamics in experimental microcosms. – Am. Nat. 194: 613–626.

Kaemingk, M. A. et al. 2019. Landscape edges shape dispersal and population structure of a migratory fish. – Oecologia 190: 579–588.

Kawecki, T. J. 2008. Adaptation to marginal habitats. – Annu. Rev. Ecol. Evol. Syst. 39: 321–342.

Kisdi, É. 2002. Dispersal: risk spreading versus local adaptation. – Am. Nat. 159: 579–596.

Kisdi, È. et al. 2020. The evolution of immigration strategies facilitates niche expansion by divergent adaptation in a structured metapopulation model. – Am. Nat. 195: 1–15.

Kubisch, A. et al. 2013. Predicting range shifts under global change: the balance between local adaptation and dispersal. – Ecography 36: 873–882.

Kubisch, A. et al. 2014. Where am I and why? Synthesizing range biology and the eco-evolutionary dynamics of dispersal. – Oikos 123: 5–22.

Leidinger, L. and Cabral, J. S. 2020. Temporal environmental variation imposes differential selection on genomic and ecological traits of virtual plant communities. – bioRxiv, p. 2020.03.24.005058.

Leturque, H. and Rousset, F. 2002. Dispersal, kin competition and the ideal free distribution in a spatially heterogeneous population. – Theor. Popul. Biol. 62: 169–180.

MacDonald, C. et al. 2018. Marginal sinks or potential refuges? Costs and benefits for coral-obligate reef fishes at deep range margins. – Proc. R. Soc. B 285: 20181545.

Masier, S. and Bonte, D. 2020. Spatial connectedness imposes local and metapopulation-level selection on life history through feedbacks on demography. – Ecol. Lett. 23: 242–253.

Matsumura, K. and Miyatake, T. 2018. Costs of walking: differences in egg size and starvation resistance of females between strains of the red flour beetle (*Tribolium castaneum*) artificially selected for walking ability. – J. Evol. Biol. 31: 1632–1637.

Mayer, M. et al. 2019. Seasonal effects of habitat structure and weather on the habitat selection and home range size of a mammal in agricultural landscapes. – Landscape Ecol. 34: 2279–2294.

Mortier, F. et al. 2018. Habitat choice stabilizes metapopulation dynamics through increased ecological specialisation. – bioRxiv, p. 267575.

Nguyen, A. D. et al. 2019. Tradeoffs in cold resistance at the northern range edge of the common woodland ant *Aphaenogaster picea* (Formicidae). – Am. Nat. 194: E151–E163.

Poethke, H. J. et al. 2003. Local extinction and the evolution of dispersal rates: causes and correlations. – Am. Nat. 161: 631–640.

Poethke, H. J. et al. 2007. The relative contribution of individual and kin selection to the evolution of density-dependent dispersal rates. – Evol. Ecol. Res. 9: 41–50.

Renault, D. 2020. A review of the phenotypic traits associated with insect dispersal polymorphism, and experimental designs for sorting out resident and disperser phenotypes. – Insects 11: 214.

Romero-Mujalli, D. et al. 2018. Individual-based modeling of eco-evolutionary dynamics: state of the art and future directions. – Regional Environ. Change 19: 1–12.

Ronce, O. et al. 2000. Kin selection and natal dispersal in an age-structured population. – Theor. Popul. Biol. 58: 143–159.

Ronce, O. et al. 2005. Plastic changes in seed dispersal along ecological succession: theoretical predictions from an evolutionary model. – J. Ecol. 93: 431–440.

Saglam, I. K. et al. 2008. Male sand crickets tradeoff flight capability for reproductive potential. – J. Evol. Biol. 21: 997–1004.

Scheepens, J. F. et al. 2018. Phenotypic plasticity in response to temperature fluctuations is genetically variable, and relates to climatic variability of origin, in *Arabidopsis thaliana*. – AoB Plants 10: ply043.

Schiffers, K. et al. 2014. Landscape structure and genetic architecture jointly impact rates of niche evolution. – Ecography 37: 1218–1229.

Schwarzmueller, F. et al. 2019. Resource landscapes and movement strategy shape Queensland fruit fly population dynamics. – Landscape Ecol. 34: 2807–2822.

Sieger, C. and Hovestadt, T. 2020. Data from: The degree of spatial variation relative to temporal variation influences evolution of dispersal. – Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.pg4f4qrm8.

Sieger, C. S. et al. 2019. Environmental change and variability influence niche evolution of isolated natural populations. – Regional Environ. Change 19: 1999–2011.

Sinai, I. et al. 2019. The role of landscape and history on the genetic structure of peripheral populations of the Near Eastern fire salamander, *Salamandra infraimmaculata*, in northern Israel. – Conserv. Genet. 20: 875–889.

Stevens, V. M. et al. 2014. A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animalsS. – Ecol. Lett. 17: 1039–1052.

Travis, J. M. J. 2001. The color of noise and the evolution of dispersal. – Ecol. Res. 16: 157–163.

Vasseur, D. A. et al. 2014. Increased temperature variation poses a greater risk to species than climate warming. – Proc. R. Soc. B 281: 20132612.

Venable, D. L. and Brown, J. S. 1993. The population-dynamic functions of seed dispersal. – Vegetatio 107: 31–55.

Vincenzi, S. 2014. Extinction risk and eco-evolutionary dynamics in a variable environment with increasing frequency of extreme events. – J. R. Soc. Interface 11: 20140441.

Weiss-Lehman, C. and Shaw, A. K. 2020. Spatial population structure determines extinction risk in climate-induced range shifts. – Am. Nat. 195: 31–42.

Wickham, H. et al. 2019. Welcome to the tidyverse. – J. Open Source Softw. 4: 1686.

Supplementary material (available online as Appendix oik-07567 at <www.oikosjournal.org/appendix/oik-07567>). Appendix 1.