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Research

Habitat choice stabilizes metapopulation dynamics by enabling ecological specialization

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Dispersal is a key trait responsible for the spread of individuals and genes among local populations, thereby generating eco-evolutionary interactions. Especially in heterogeneous metapopulations, a tight coupling between dispersal, population dynamics and the evolution of local adaptation is expected. In this respect, dispersal should counteract ecological specialization by redistributing locally selected phenotypes (i.e. migration load). Habitat choice following an informed dispersal decision, however, can facilitate the evolution of ecological specialization. How such informed decisions influence metapopulation size and variability is yet to be determined.

By means of individual-based modelling, we demonstrate that informed decisions about both departure and settlement decouple the evolution of dispersal and that of generalism, selecting for highly dispersive specialists. Choice at settlement is based on information from the entire dispersal range, and therefore decouples dispersal from ecological specialization more effectively than choice at departure, which is only based on local information. Additionally, habitat choice at departure and settlement reduces local and metapopulation variability because of the maintenance of ecological specialization at all levels of dispersal propensity. Our study illustrates the important role of habitat choice for dynamics of spatially structured populations and thus emphasizes the importance of considering that dispersal is often informed.

Keywords: dispersal, eco-evolutionary dynamics, local adaptation, spatial ecology

Introduction

Most populations are spatially structured and organized in metapopulations. Local populations are connected by dispersal, the movement of individuals or propagules that potentially generates gene flow across space (Ronce 2007). Dispersal thus acts as a glue that links local gene pools, local population dynamics and metapopulation dynamics (Hanski 2012). Dispersal is known to evolve in response to spatiotemporal variability in environmental conditions for instance as a bet-hedging strategy in variable environments (Olivieri et al. 1990, McPeek and Holt 1992, Bowler and Benton

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2005, Ronce 2007). Dispersal is also a strategy to escape kin competition and inbreeding depression (Bowler and Benton 2005, Ronce 2007). Dispersal is thus an essential attribute for fitness maximisation (Bonte and Dahirel 2017). Ultimately, these benefits are balanced against dispersal costs to determine the optimal dispersal strategy (in terms of frequency and distance).

In metapopulations, habitat heterogeneity introduces additional costs to dispersal. Divergent selection pressures among local habitats can result in local adaptation (Kawecki and Ebert 2004). This local adaptation can come at a cost of being less adapted in other environments (i.e. ecological specialization, Poisot et al. 2011). Across a heterogeneous landscape, dispersal redistributes locally adapted genotypes and may thus result in maladaptation (Farkas et al. 2015). Therefore, dispersal is expected to select against ecological specialization and vice versa (Kisdi 2002, Lenormand 2002, Bolnick and Nosil 2007, Nurmi and Parvinen 2011, Nagelkerke and Menken 2013, Berdahl et al. 2015, Dahirel et al. 2015).

However, if dispersal involves habitat choice, then dispersal and ecological specialization may be reconcilable (theory: Holt and Barfield 2008, Armsworth 2009, Ravigné et al. 2009, Bolnick and Otto 2013, Scheiner 2016; empirical: Rice and Salt 1990, Jacob et al. 2017, 2018). Habitat choice implies a non-random subset of the local population dispersing and/or dispersers redistributing themselves in a non-random way across a heterogeneous landscape (Holt 1987, Rice and Salt 1990, Edelaar et al. 2008, Edelaar and Bolnick 2012). Organisms can gather and use information before and during movement (Gillis 1982, Ahnesjö and Forsman 2006, Jacob et al. 2015a). Subsequently, depending on their phenotype and the environment encountered, they can decide whether to disperse (departure decision) and where to go (settlement decision; Bowler and Benton 2005, Clobert et al. 2009, Jacob et al. 2015b, 2017, Cote et al. 2017). A departure decision involves estimating how well an individual's phenotype matches the local habitat, while a settlement decision involves comparing how well the phenotype matches any of a possibly large selection of potential settlement habitats (Jacob et al. 2015b). Therefore, a choice at settlement seems the most adaptive. However, departure choices are expected to be more prevalent in nature since local information is more freely available and less costly compared to information from multiple potential settlement locations (Bowler and Benton 2005, Clobert et al. 2009).

Habitat choice, affecting the evolution of dispersal and specialization in a heterogeneous landscape, is expected to affect ecological dynamics in the same, short time frame at both the local and metapopulation level (Hendry 2016, Bonte et al. 2018). First, local adaptation should increase population growth rate by increasing individual fitness. This can increase population size accordingly (Farkas et al. 2013, but see Reed et al. 2013, Hendry 2016). Moreover, it increases population recovery speed after collapse, which decreases local population size variability (α variability, sensu Wang and Loreau 2014). Second, dispersal can also stabilize local population dynamics if immigration rescues small local populations from extinction (Abbott 2011, Wang et al. 2015). However, dispersal also affects metapopulation size variability and synchrony of the local population fluctuations (γ and β variability resp. sensu Wang and Loreau 2014). By synchronising local population dynamics, high levels of dispersal can cause local populations to decline simultaneously, decreasing stability at the landscape scale (Blasius et al. 1999) and threatening (meta)population extinction (Heino et al. 1997, Inchausti and Halley 2003). Ecological specialization and dispersal thus exert a strong influence on spatial population dynamics and the functioning of metapopulations. Nevertheless, we lack an understanding of how rapid evolution of either specialization or dispersal alter emerging ecological dynamics.

Understanding these changes in metapopulation dynamics should enable us to understand and predict metapopulation persistence in a spatially structured and heterogeneous environment. Here, we present an individual-based model to study how evolutionary processes resulting from habitat choice influence metapopulation dynamics. We separately analyse 1) the ecological consequences of dispersal, habitat choice and the evolving levels of ecological specialization; and 2) the ecological consequences of ecological specialization, habitat choice and the evolution of dispersal. We allow either dispersal or specialization to evolve in order to disentangle their respective effects on metapopulation dynamics. According to previous studies, random dispersal can have diverging effects across spatial scales. While random dispersal stabilizes populations at the local scale, it synchronizes local dynamics across the landscape which result in variable net effects on metapopulation stability (Taylor 1990, Abbott 2011, Wang et al. 2015). However, we also expect ecological specialization to influence the amount of patch heterogeneity with respect to fitness expectations. Thus, if dispersal causes individuals to be less locally adapted, less specialism will evolve and we expect local populations to be less stabilised. In consequence, we predict that local fitness maximisation by habitat choice should increase metapopulation size, stability and eventually, persistence. Furthermore, the consequences of habitat choice for ecological dynamics are expected to differ depending on whether informed decisions occur at departure (whether to leave a patch or stay), settlement (where to go) or both (Jacob et al. 2015b). We thus modelled four dispersal modes: random dispersal, habitat choice at departure, habitat choice at settlement, and habitat choice at both departure and settlement.

Model

Landscape

We model a finite landscape: a toroidal lattice of 32 × 32 grid cells. Each patch (i.e. grid cell) has a random environmental value $v_{x,y} \in [0, 1]$ at coordinates x, y, without any spatial autocorrelation. This environmental value is the local selective pressure. Its values are randomly distributed in space and constant in time creating a heterogeneous environment. Additionally, each patch contains a certain amount of resources ($G_{x,y}$) that regulate local consumer population densities.

Population

For simplicity, we model an asexually reproducing organism with discrete generations. During every generation and in a random sequence, all individuals of that generation perform a schedule of life-history events. Each individual potentially disperses prior to reproduction, after which population regulation occurs. This closely resembles soft selection in a semelparous species with a single dispersal phase (Massol and Débarre 2015). These life-history events are explained below and assumed parameters are summarized in Table 1. As in other theory, we simplify life histories as much as possible to facilitate understanding of the emerging dynamics. Although the parameterization does not resemble a specific system, it is inspired by grassland arthropod herbivore biology. Additionally we performed a sensitivity analysis of the parameters in Table 1 (Supplementary material Appendix 1).

Resource gathering

We model two evolving traits that determine an individual's ability to gather resources, which subsequently determines habitat choice and reproduction.

The optimal habitat trait (muT) indicates the optimal environmental value ($v_{x,y}$) for an individual to have its highest possible fitness ($muT \in [0, 1]$).

The niche width ($varT$) determines the extent of ecological specialization, by determining an individual's fitness for values of the environment ($v_{x,y}$) a certain distance away from the individual's optimal habitat (muT). A wide niche results in fitness far away from the optimal habitat that is higher compared to that of a narrow niche at the same distance from the optimum (Eq. 2; derived from Chaianunporn and Hovestadt 2012, but decreases fitness in the optimal habitat (Eq. 3, Fig. 1). The match of an individual's optimal habitat (muT) with the local environmental value ($v_{x,y}$) combined with its $varT$ determines the individual's efficiency in this particular habitat (α_i, Eq. 2). The amount of gathered resources (F_i) combines the individual's efficiency (α_i) with the local resource density ($G_{x,y}$) and is proportional to the individual's expected reproductive success (Eq. 1).

Table 1. Assumed model parameters.

R_G	optimal resource growth rate	0.25
K_G	resource carrying capacity	1
h	handling time	0.2
$a_{\max}$	maximum resource gathering rate	0.05
ct	cost of generalism	1
	mutation rate	0.01 generation^{-1}
$r_{\max}$	maximum dispersal distance	2
σ	resource conversion factor	300

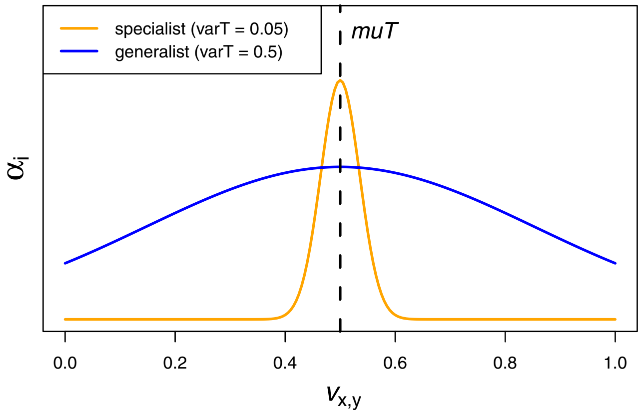

Figure 1. Relation of local environmental value ($v_{x,y}$) to individual efficiency in that location for a specialist (orange) and a generalist (blue) with optimal environment (muT) = 0.5.

$$F_i = \frac{\alpha_i \times G_{x,y}}{1 + h\left(1 + \alpha_i \times G_{x,y}\right)} \tag{1}$$

$$\alpha_i = a_{\max} \times \gamma_i \times e^{-\frac{(muT_i - v_{x,y})^2}{varT_i^2}} \tag{2}$$

$$\gamma_i = e^{-ct \times varT_i} \tag{3}$$

F_i represents the gathered resources by individual i, determined by a resource–consumer model with h being handling time, $G_{x,y}$ the amount of resources present locally, $a_{\max}$ the maximum resource gathering rate, muT_i and $varT_i$ being the optimal habitat trait and niche width respectively for that individual and $v_{x,y}$ the local environmental value. γ_i implements the niche width-performance tradeoff with ct indicating the strength of the tradeoff.

Dispersal

The dispersal trait (d) represents the individual's inclination to disperse. Individuals disperse before selection occurs. We model two decision points in a dispersal event:

First, at departure, an individual disperses with a probability equal to its dispersal trait (d) if departure is random, meaning that a higher dispersal trait implies a higher tendency to disperse. With departure choice, the dispersal trait (d) represents the minimal reproductive output, expected based on the locally gathered resources, at which an individual chooses not to disperse. Below this threshold, the local conditions are considered too bad and the individual leaves. In parallel with random departure, a higher threshold implies a higher tendency to disperse.

At settlement, an individual i settles in a random patch within its dispersal range determined by a maximum dispersal distance ($r_{\max}$) if settlement is random (all patches $x_i', y_i' \mid x_i' \in [x_i - r_{\max}, x_i + r_{\max}]; y_i' \in [y_i - r_{\max}, y_i + r_{\max}]$). Its current location is excluded from this range to force dispersing individuals to change location. With habitat choice at settlement, the dispersing individual settles in the location where the local environmental value ($v_{x,y}$) best matches its own optimal habitat trait (*muT*) within its dispersal range.

Note that habitat choice at both decision points involves evaluating how well the individual's optimal habitat (*muT*) trait matches an environmental value ($v_{x,y}$; Edelaar et al. 2008).

Reproduction

Reproducing individuals have an expected number of offspring (λ_i) proportional to their gathered resources (F_i) in the patch after the dispersal phase.

$$\lambda_i = \sigma \times F_i$$

σ indicates how many offspring each unit of resources results in. The actual reproductive output of an individual is sampled from a Poisson distribution with mean λ_i.

Local population regulation

Local consumer populations are regulated through local resource availability ($G_{x,y}$). These resources restock each generation according to a logistic growth function,

$$\delta G_{x,y} = R_G \times \left(1 - \frac{G_{x,y}}{K_G}\right)$$

where the local resource increase $\delta G_{x,y}$ depends on $G_{x,y}$, the amount of resources already present locally. Furthermore, R_G and K_G represent the optimal growth rate and carrying capacity of the resources respectively. Within each generation, every individual depletes resources in sequence (Eq. 1) proportionally to the number of offspring. A consumer's offspring without the required amount of resources remaining in their local patch, will die (depleting any leftover resources). The local amount of resources ($G_{x,y}$) also regulates local populations by determining the amount of gathered resources (Eq. 1). Population regulation depends on resource availability and, consequently, is density-dependent, while habitat choice is decoupled from local population densities for simplicity. Hereby, we avoid including density-dependent habitat choice (Berner and Thibert-Plante 2015 for a comparison of different types of habitat choice).

Mutation

Non-fixed traits mutate at a rate of 0.01 generation^{-1}. The optimal habitat trait (*muT*), dispersal trait (*d*) and niche width (*varT*) mutate by randomly sampling a new trait value from a normal distribution with the initial trait value as mean and standard deviation 0.1. New values of *d* are limited to [0, 1] using reflecting borders. This possibly accumulates dispersal trait (*d*) values very close to the border by mutation, but this effect should be largely overwhelmed by the selective pressure on the dispersal trait.

Simulations

We analyse four dispersal modes that represent all combinations of either random dispersal or habitat choice at departure or at settlement. First, we analyse how niche width (*varT*) evolves for different fixed values of the dispersal trait (*d*) and for different dispersal modes. Second, we analyse how dispersal evolves for different fixed values of niche width for different dispersal modes. Fixed traits are varied over 20 values with equal increments within a range (random departure *d*: (0, 1], informed departure *d*: (0, 5], *varT*: (0, 0.5]). The range of the dispersal trait (*d*) with informed departure differs from the random dispersal since it represents the minimal acceptable reproductive output of an individual instead of its dispersal propensity. This range of *d* with informed departure, however, results in actual dispersal propensities that cover the range (0, 1]. We replicate each scenario of a fixed trait value with a certain dispersal mode ten times with each replicate simulated for 500 generations. We analyse average niche width of the last generation in scenarios with evolving niche width, and the proportion of individuals that dispersed in the last generation in scenarios with the dispersal trait evolving. Additionally, we analyse the metapopulation size (i.e. total number of individuals) in the last generation and temporal variability in local population sizes, temporal variability in metapopulation size and asynchrony (α-, γ- and β-variability respectively; Wang and Loreau 2014) over the last 250 generations for each replicate when evolution and dynamics had stabilised.

Initialisation

We initialize each replicate by allocating 70 000 individuals randomly across the 32×32-landscape grid. This initial metapopulation size close to the consumers' carrying capacity avoids drift effects. Each individual's optimal habitat trait value is sampled from a uniform distribution between 0 and 1. Unless it was fixed for that scenario, niche width and the dispersal trait are randomly sampled from a uniform distribution (with the same range as their fixed values for the fixed scenarios).

Imperfect habitat choice

In addition to the analyses presented in this manuscript, we tested whether imperfect rather than perfect choice (at departure and settlement) leads to different eco-evolutionary dynamics (Supplementary material Appendix 2). Perfect choice implies an individual consistently making an optimal decision, given the information available. We modelled imperfect choice as a probability at each decision point that the individual chooses randomly instead of in an informed way.

Cost of habitat choice

In addition to the analyses presented in this manuscript, we tested the effects of a fitness cost of habitat choice. Up to this point, we assume that individuals use information and make choices without any cost. However, in nature we expect habitat choice to come at a cost, either direct costs by investing time and energy in gathering information or genetic and developmental costs by developing specialized sensory and movement capacities.

All individuals in our habitat choice scenarios would pay such genetic and developmental costs, which would decrease each individual's fitness equally. This is already inherent in the sensitivity analysis of some of the parameters involved in determining resource gathering and fitness. We therefore additionally model a direct cost of prospecting all possible settlement locations in settlement choice scenarios, which is only incurred by dispersers in these scenarios (Supplementary material Appendix 3). We model scenarios with either a low or a high cost (resp. 0.01 or 0.1 of expected number of offspring, λ_i).

Scripts of the simulation model

We developed the model in Python 3.5 and we provide scripts to run the model at Github data repository: <https://github.com/fremorti/Habitat_choice_stabilizes_metapopulations> .

Results

Niche width evolution

With random dispersal (Fig. 2: orange crosses), we find a sudden increase of niche width (i.e. ecological generalism) when increasing dispersal propensity (inflexion point around 0.35). This means that, in accordance with classical predictions (Kisdi 2002, Nurmi and Parvinen 2011), a low dispersal propensity favours specialism while a high dispersal propensity leads to the evolution of generalists. Habitat choice, at either departure or settlement, enables specialism to evolve at a higher dispersal propensity. However, while generalism still evolves at high dispersal propensities with habitat choice at departure (Fig. 2: orange circles; inflexion point around 0.65), habitat choice at settlement selects for specialism in all scenarios regardless of dispersal propensity (Fig. 2: green crosses). This indicates a stronger effect of habitat choice at settlement than at departure. Moreover, adding a departure decision results in a trend of even stronger specialism than if only a settlement decision is made. A combination of departure and settlement decision shows specialism evolving in all scenarios but somewhat more strongly so at lower dispersal propensities (Fig. 2: green circles).

Regarding the emerging ecological dynamics, metapopulations exhibiting a low level of dispersal as well as those in which individuals have informed settlement achieve larger metapopulations (Fig. 3) with less variable local populations (α; Fig. 4, top left). The scenarios with a lower metapopulation size and higher local population variability (α) correspond with scenarios in which generalism evolved. However, if dispersers only choose at departure, the change towards lower metapopulation sizes follows a similar course as in a random dispersal scenario (Fig. 3: orange circles). Consequently, this decline precedes the change to a generalist strategy around a dispersal propensity of 0.65, at which point metapopulations are smallest (Fig. 3: orange circles). In the absence of a settlement choice, maladaptation and the evolution of generalism increase local population variability (α) despite the stabilising direct effect of increasing dispersal (Fig. 4, top left: orange). Settlement choice, which eliminates maladaptation, decreases local population variability independent of dispersal

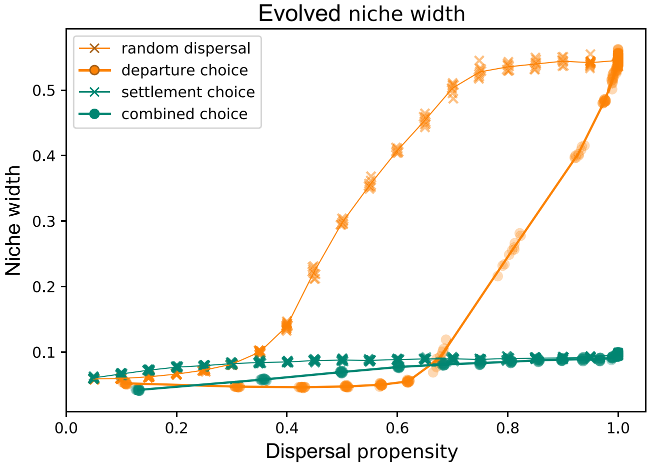

Figure 2. Niche width evolution in relation to effective dispersal propensity. Scenarios of random (×) and informed (○) departure combined with random (orange) or informed (green) settlement. Lines represent mean values for replicated scenarios. Because the fixed dispersal trait does not equate to the dispersal propensity in informed departure scenarios (○), their corresponding data points are not equally distributed across the dispersal propensity range.

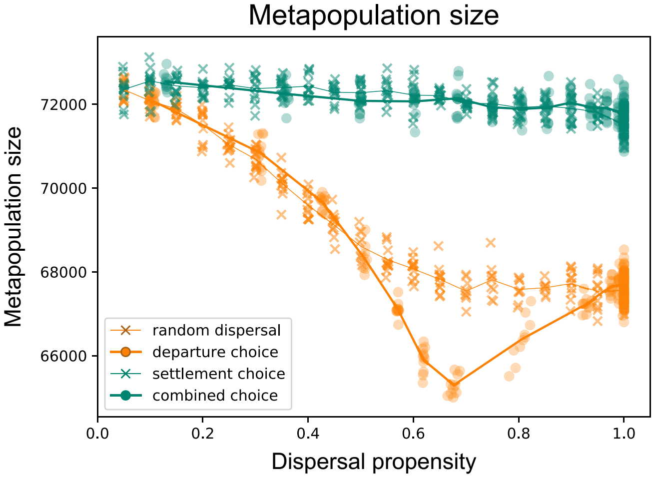

Figure 3. Metapopulation size for scenarios with fixed dispersal trait. Scenarios of random (×) and informed (○) departure combined with random (orange) or informed (green) settlement. Lines represent mean values for replicated scenarios.

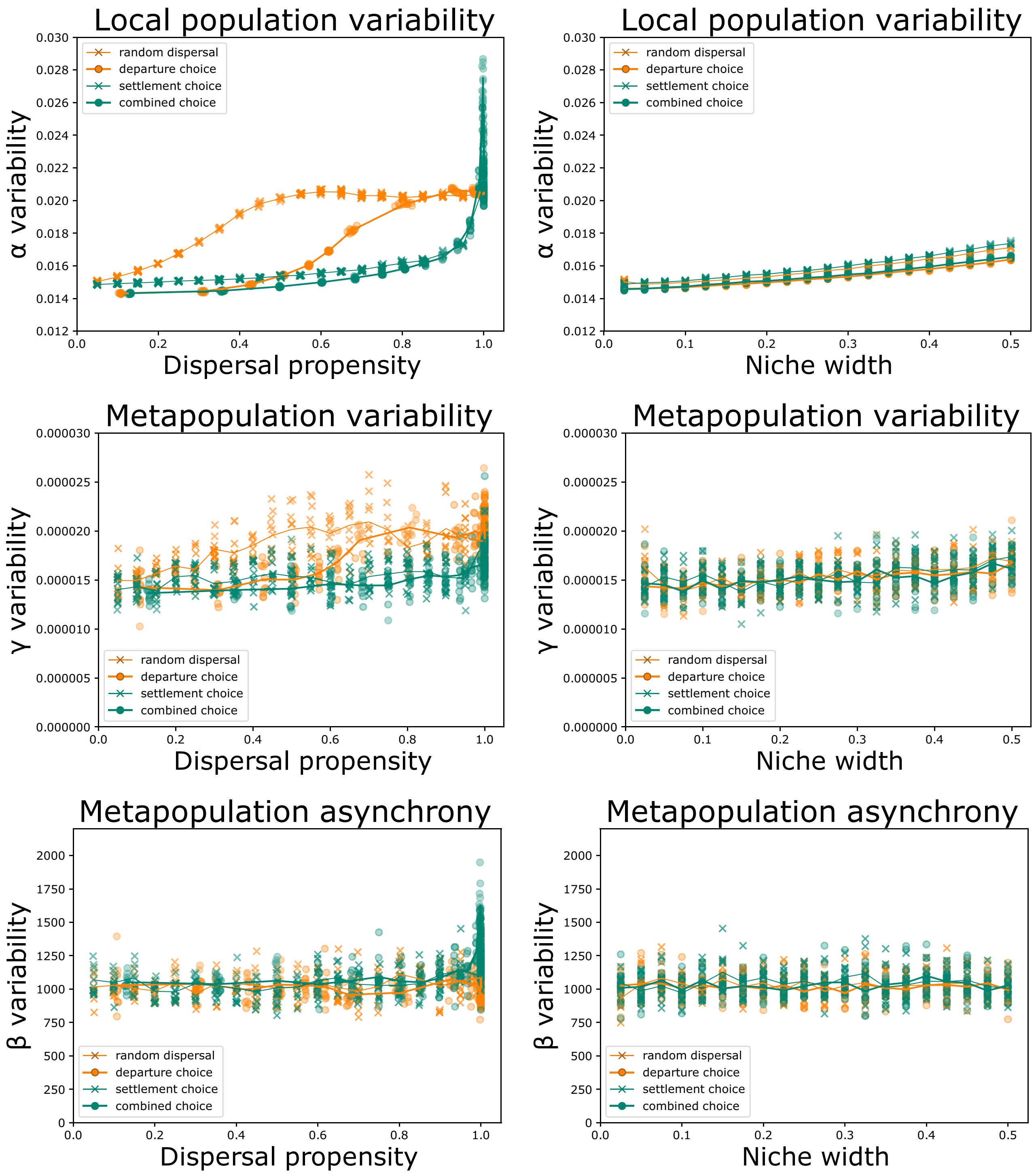

Figure 4. Local population variability (top), metapopulation variability (middle) and asynchrony (bottom) for scenarios with fixed dispersal trait (left) and scenarios with fixed niche width (right). Scenarios of random (×) and informed (○) departure combined with random (orange) or informed (green) settlement. Lines represent mean values for replicated scenarios.

propensity (α, Fig. 4: green). Only almost complete dispersal propensity results in increased local population variability (α). Metapopulation variability (γ) decreases with habitat choice (Fig. 4, middle left) following a pattern similar to, but less pronounced than, that of local population variability (α) and niche width evolution. Metapopulation asynchrony (β) is not affected by dispersal propensity, habitat choice at settlement or habitat choice at departure (Fig. 4, bottom left). Overall, the fitness-optimizing effect of habitat choice results in a stabilizing effect on local and metapopulation dynamics.

Dispersal evolution

With random dispersal, dispersal propensity increases with niche width as predicted, but overall levels of dispersal propensity are low (Fig. 5, left panel, orange crosses). A departure decision has a relatively small quantitative impact on dispersal propensity, mainly affecting specialists (Fig. 5, left panel, orange circles). This inverts the positive relationship between dispersal propensity and niche width to a negative relationship (Fig. 5, right panel, orange circles). In comparison, settlement choice increases dispersal propensity markedly, to around 0.35–0.40 (Fig. 5, green crosses). With a decision at both departure and settlement, dispersal propensity is even higher, but with a larger drop towards a higher level of specialization (Fig. 5, green circles).

With increasing niche width, metapopulation size decreases (Fig. 6) and local population variability increases (α; Fig. 4, top right). We find no noteworthy effect of the departure decision nor the settlement decision on metapopulation size. Local population variability (α) decreases with habitat choice at departure (Fig. 4, top right). The effect of habitat choice at settlement is quite small (Fig. 4, top right). Both metapopulation variability (γ; Fig. 4, middle right) and metapopulation asynchrony (β; Fig. 4, bottom right) are unaffected by niche width, settlement or habitat choice. When niche width is not able to evolve, habitat choice does not seem to affect dynamics at the metapopulation level.

Imperfect habitat choice

For imperfect habitat choice, we found patterns intermediate to those of random and perfectly informed scenarios (Supplementary material Appendix 2).

Habitat choice costs

Settlement choice costs do not change the evolved niche width (Supplementary material Appendix 3). In scenarios with evolving dispersal trait, settlement costs do change the resulting dispersal. Unsurprisingly, a fitness costs only paid by dispersers reduces the amount of dispersal that evolves. Moreover, metapopulation size in scenarios with settlement choice declines with an increasing cost of settlement choice in both scenarios of evolving niche width and scenarios of evolving dispersal. Metapopulation dynamics (α-, γ- and β-variability) are not affected in either scenario.

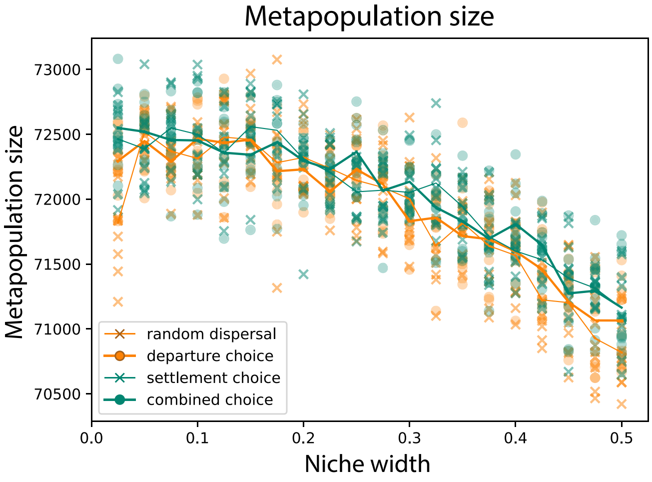

Figure 6. Metapopulation size for scenarios with fixed niche width. Scenarios of random (×) and informed (○) departure combined with random (orange) or informed (green) settlement. Lines represent mean values for replicated scenarios.

Discussion

We confirm that altering dispersal from a random process to one with habitat choice enables specialism and high levels of dispersal to evolve simultaneously (Holt 1987, Futuyma and Moreno 1988, Rice and Salt 1990, Holt and Barfield

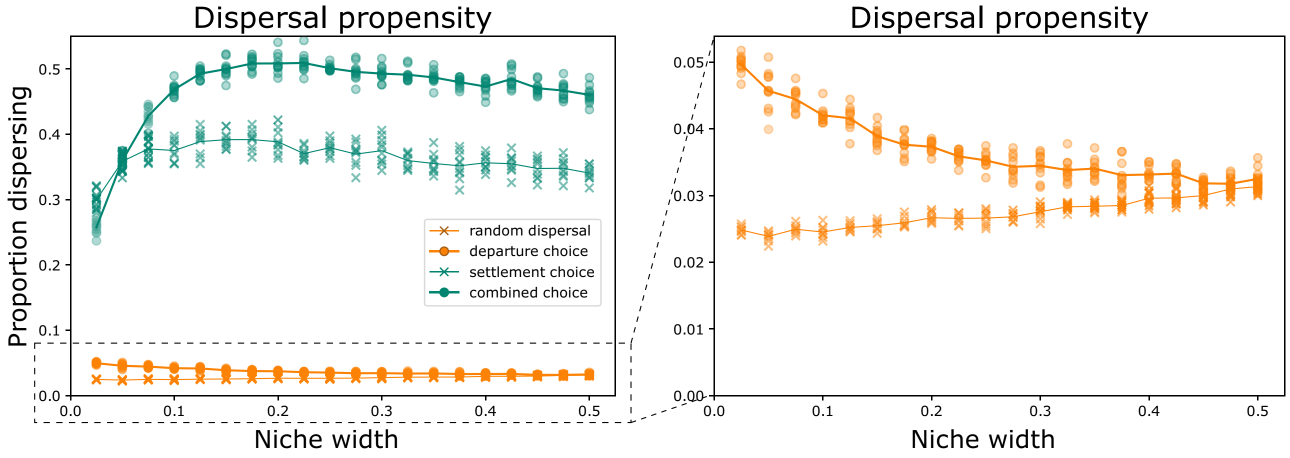

Figure 5. Effective dispersal propensity resulting from an evolving dispersal trait under fixed levels of niche width. Scenarios of random (×) and informed (○) departure combined with random (orange) or informed (green) settlement. Right panel zooms in on the scenarios of random settlement. Lines represent mean values for replicated scenarios.

2008, Armsworth 2009, Ravigné et al. 2009, Bolnick and Otto 2013, Scheiner 2016).

We demonstrate that choice mechanisms at settlement favour specialized strategies for even higher levels of dispersal than choice mechanisms at departure. This stronger effect of settlement decision follows from the fact that habitat choice at settlement inherently integrates information from all potential settlement locations, rather than only the natal location as in the case of informed departure. Consequently, the likely higher cost of information at settlement is offset by individual fitness benefits. The effect of departure choice on dispersal evolution is most apparent in metapopulations with a high level of specialization. Departure choice enables the large proportion of maladapted individuals to disperse in metapopulations with random settlement. It also prevents the large proportion of adapted individuals from dispersing in metapopulations with settlement choice.

Habitat choice, in enabling the evolution of dispersive specialists, causes altered metapopulation dynamics. Scenarios with fixed niche width show that metapopulation size is directly determined by the level of specialization and only indirectly by information use during departure or settlement. This also explains why the relationship between metapopulation size and dispersal is inverse to that between evolved niche width and dispersal in scenarios of fixed dispersal. When generalism is favoured (i.e. under high levels of random settlement), the optimal strategy results in smaller metapopulations despite the unaltered resource availability in our model. Individual interests do not necessarily line up with those of the metapopulation (Delgado et al. 2011). In addition, we show that metapopulations with more generalists are more variable at the local level and, with evolving niche width, the metapopulation level. Ecological dynamics do not completely follow the level of ecological specialization. In scenarios with departure choice, this is illustrated by the change to lower metapopulation sizes at a lower fixed dispersal rate than that at which generalism evolves. As niche width is the only evolving trait in these scenarios, departure choice shows an additional direct effect on metapopulation size. Because these changes in metapopulation dynamics seem to mainly follow the evolution of niche width, a settlement choice is more efficient at stabilising local and metapopulation dynamics compared to a choice at departure. In general, local and metapopulation stability are at most marginally affected by the realised dispersal propensity relative to niche width (Abbott 2011, Wang et al. 2015). Very high levels of dispersal do, however, decrease local population stability in settlement choosers because of asymmetric dispersal depleting resources at certain locations (Dey et al. 2014). Habitat choice has no effect on metapopulation synchrony. Small metapopulations, high local population variability (α) and low metapopulation asynchrony (β) increase the risk of extinction via demographic and genetic stochasticity (Lande 1993, 1994). The evolution of specialization is the key to bigger, more stable metapopulations. In a heterogeneous landscape, habitat choice enables specialization, and, as a consequence, can promote metapopulation persistence.

The theoretical nature of our model results in assumptions that entail several important simplifications. First, information use during habitat choice is assumed perfect in our model. Very accurate information is costly (e.g. prospecting multiple locations or developing elaborate sensory organs; discussed in Bonte et al. 2012, Jacob et al. 2015b, Cote et al. 2017) and, as a consequence, accuracy of information can itself be a subject of selection. Organisms should rarely be able to acquire high-precision information because of its high cost while the ability to obtain a minimum of information is expected to be more adaptive compared to not using any information at all (Bocedi et al. 2012). We present results for scenarios of perfect information use, but even under imperfect habitat choice our general evolutionary and ecological results stand (Supplementary material Appendix 2). Second, analyses that include habitat choice costs show no effects except for the expected immediate effects on dispersal and fitness (Supplementary material Appendix 3). Third, we assume no spatial autocorrelation in habitat across the landscape, while most natural landscapes show autocorrelation to some extent, especially at shorter distances. Spatial autocorrelation inherently results in an increased match between habitat and specialized phenotypes. Therefore, only randomly distributed habitat enables us to isolate the effects of habitat choice from those of spatial autocorrelation. Moreover, our focus on the eco-evolutionary dynamics of dispersal renders our spatial scale of interest larger than that of e.g. foraging ecology. At this larger scale, spatial autocorrelation should be less prominent (Bell et al. 1993). Fourth, we do not model phenotypic plasticity. Phenotypic plasticity is another alternative mechanism that can match phenotypes to the local environment, in this case by altering the phenotype instead of altering where an individual disperses to. Evolutionary dynamics of habitat choice, phenotypic plasticity, their relative likelihood of evolution and their consequences have been studied before (Scheiner 2016, Edelaar et al. 2017, Nicolaus and Edelaar 2018). Fifth, while our model assumes asexual reproduction, habitat choice also occurs in many sexually reproducing species. We expect assumptions of sexual reproduction to affect our results little more than by an increase or decrease in the rate of adaptation. Recombination helps to buffer genetic variation (e.g. under harsh selection pressures) so that natural selection has more variation to act on (Holt and Barfield 2011, Kubisch et al. 2014). However, reproduction after maladaptive dispersal (i.e. maladaptive gene flow) is known to result in a higher level of maladaptation in uninformed dispersers (Kubisch et al. 2014).

By demonstrating the impact of habitat choice on eco-evolutionary dynamics, our results question the ecological insights derived from the numerous models assuming random dispersal (cf. Ravigné et al. 2009, Travis et al. 2012, Jacob et al. 2015b). Recently, Fronhofer et al. (2017) also showed that habitat choice in an expanding population slows down range expansion in an adverse ecological gradient. No control during any phase of dispersal likely applies to very few real systems such as wind-dispersed plants. Many organisms are capable of more selective ways of moving than just random dispersal, illustrated by obvious examples of habitat preference based on colour matching (Gillis 1982, Ahnesjö and Forsman 2006), the use of specific cues during movement (Prokopy 1968) and habitat choice (Jaenike and Holt 1991, Edelaar et al. 2008, Jacob et al. 2017, 2018). Selective movement is even found in organisms for which it seems less obvious, such as zoochorous plants that disperse their seeds to suitable habitat via animals (Spiegel and Nathan 2010) or plankton that drift on currents but are able to select where to settle (Bonte et al. 2012, Burgess et al. 2016). We show that habitat choice severely affects the level of ecological specialization, which in turn is the largest driver of the ecological dynamics. However, direct effects of habitat choice (e.g. because of extreme levels of asymmetric dispersal or on intermediately dispersive departure choosers) should not be neglected. Given this, we recommend considering habitat choice when predicting the dynamics of spatially structured populations, e.g. in species distribution models, meta-community models, or viability models (Ravigné et al. 2009, Edelaar and Bolnick 2012, Travis et al. 2012, Jacob et al. 2015b).

Different habitat-based choice behaviours that result in non-random dispersal may or may not differ in their eco-evolutionary consequences (Berner and Thibert-Plante 2015, Jacob et al. 2015b). Here, we show how the consequences of habitat choice at departure differ from those of habitat choice at settlement. Habitat choice may also vary in several other aspects, such as choice mechanisms and the reliability of information used (Jacob et al. 2015b, Akcali and Porter 2017). We expect such different variations in habitat choice to have additional influences of varying magnitude on evolutionary and ecological processes. Hence, disregarding these nuances might conceal some crucial insights or prevent us from generating detailed predictions. Unfortunately, we often lack information on the specifics of habitat choice in real-life populations. Our focus going forward should be on revealing the extent to which habitat choice varies along all these axes in nature, but also on evaluating their relative importance.

In summary, we demonstrate the profound effect of habitat choice on eco-evolutionary dynamics of metapopulations, including the dynamics of dispersal and ecological specialization. Moreover, habitat choice at settlement has a stronger impact on the model's outcome than choice at departure. Based on the difference between random dispersal and habitat choice, we encourage studies of real-world metapopulations to consider carefully whether habitat choice is applicable during the different phases of dispersal. Our results elucidate a potential impact of the often-erroneous assumption of random dispersal and may improve the accuracy of future predictions regarding spatially structured populations.

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Supplementary material (available online as Appendix oik-05885 at <www.oikosjournal.org/appendix/oik-05885>). Appendix 1–3.