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How mechanisms of habitat preference evolve and promote divergence with gene flow

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Abstract

Habitat preference may promote adaptive divergence and speciation, yet the conditions under which this is likely are insufficiently explored. We use individual-based simulations to study the evolution and consequence of habitat preference during divergence with gene flow, considering four different underlying genetically based behavioural mechanisms: natal habitat imprinting, phenotype-dependent, competition-dependent and direct genetic habitat preference. We find that the evolution of habitat preference generally requires initially high dispersal, is facilitated by asymmetry in population sizes between habitats, and is hindered by an increasing number of underlying genetic loci. Moreover, the probability of habitat preference to emerge and promote divergence differs greatly among the underlying mechanisms. Natal habitat imprinting evolves most easily and can allow full divergence in parameter ranges where no divergence is possible in the absence of habitat preference. The reason is that imprinting represents a one-allele mechanism of assortative mating linking dispersal behaviour very effectively to local selection. At the other extreme, direct genetic habitat preference, a two-allele mechanism, evolves under restricted conditions only, and even then facilitates divergence weakly. Overall, our results indicate that habitat preference can be a strong reproductive barrier promoting divergence with gene flow, but that this is highly contingent on the underlying preference mechanism.

Introduction

Understanding the origin of species in sexually reproducing organisms equates to understanding the nature of the reproductive barriers constraining gene flow between diverging groups of organisms (Rice & Hostert, 1993; Kirkpatrick & Ravigné, 2002; Coyne & Orr, 2004; Gavrilets, 2004; Sobel *et al.*, 2010). Studying these barriers is most informative in populations in their early stages of divergence when the barriers initiating divergence are not yet confounded by barriers emerging after reproductive isolation has become complete. In these early stages, reproductive isolation will often be driven by divergent natural selection, with reproductive barriers emerging as a by-product of local adaptation to ecologically distinct habitats (Endler, 1977; Rice & Hostert, 1993; Gavrilets *et al.*, 2000; Schilthuizen, 2000; Schluter, 2000; Wu, 2001; Kirkpatrick & Ravigné, 2002; Coyne & Orr, 2004; Rundle & Nosil, 2005; Sobel *et al.*, 2010).

Empirical studies of ecologically based reproductive isolation typically focus on performance trade-offs between different habitats, and on sexual isolation. In the former, divergent selection results in the reduced fitness of migrants and hybrids (Barton & Hewitt, 1989; Schluter, 2000; Coyne & Orr, 2004; Hendry, 2004; Nosil *et al.*, 2005). The latter occurs when traits targeted by divergent selection also mediate sexual interactions, and adaptive divergence consequently disrupts reproductive compatibility (Ritchie, 2007; Bonduriansky, 2011; Maan & Seehausen, 2011). A source of reproductive isolation that has received much less empirical attention, despite

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some theoretical foundation, is habitat preference (Thorpe, 1945; Jones, 1980; Rice, 1987; Diehl & Bush, 1989; Kirkpatrick & Ravigné, 2002; Barton, 2010; Sobel *et al.*, 2010; Edelaar & Bolnick, 2012; Webster *et al.*, 2012). We here define habitat preference broadly as the evolution of any modification of dispersal causing a bias with respect to the habitat of reproduction. Although our study focuses primarily on animal speciation, this definition applies to any organism able to disperse. For example, the evolutionary loss of a trait promoting seed dispersal in a plant is a form of habitat preference, because it biases individuals to stay in the habitat where their zygotes were formed.

Habitat preference can reinforce the exposure of populations to specific selective habitats and drive assortative mating by reducing reproductive interactions among populations in different habitats. Promoting adaptive divergence and restricting gene flow in this way, habitat preference has the potential to act as a major reproductive barrier, or at least set the stage for divergence in other traits that will further strengthen reproductive isolation (Immelmann, 1975; Rice, 1987; Rice & Hostert, 1993; Sobel *et al.*, 2010). Consequently, 'classical' isolating mechanisms such as ecologically based immigrant and hybrid inferiority or divergent mate preference might sometimes *appear* as important reproductive barriers when measured in isolation (e.g. through field transplant and laboratory experiments), but the role of these barriers in *initiating* speciation might be overestimated. They may not have emerged without habitat preference initially reducing gene flow, or they may not have the opportunity to operate in nature at all if habitat preference is strong (Sobel *et al.*, 2010).

Accordingly, theoretical analyses indicate that habitat preference, coupled with divergent selection on ecologically important traits, can facilitate speciation in the face of gene flow (Maynard Smith, 1962 1966; Balkau & Feldman, 1973; Karlin & McGregor, 1974; Rice, 1984; Garcia-Dorado, 1986; Diehl & Bush, 1989; Hedrick, 1990; De Meeus *et al.*, 1993; Kawecki, 1996; Kisdi, 2002; Fry, 2003; Ravigné *et al.*, 2004; Beltman & Haccou, 2005; Beltman & Metz, 2005; Gavrilets & Vose, 2005; Thibert-Plante & Gavrilets, 2013). This theory, however, suffers two important shortcomings. First, habitat preference can have very different underlying mechanistic causes. For instance, an individual might display a preference for a specific habitat because that habitat resembles the habitat the individual experienced during its early ontogeny (Immelmann, 1975; Davis & Stamps, 2004). As a possible alternative, an individual might have inherited alleles encoding a direct and stable preference for a specific habitat feature (Diehl & Bush, 1989). Diversity in causation, however, is rarely taken into account in theoretical investigations; how specific habitat preference mechanisms evolve and/or contribute to speciation has generally been studied piecemeal (but see Kawecki, 1996; Fry, 2003; Beltman & Metz, 2005). The second shortcoming is that available theory has too rarely attempted to explore the role of habitat preference in divergence within a biologically realistic framework (Fry, 2003). For example, the genetic basis of habitat preference has generally been modelled as a single locus (e.g. Maynard Smith, 1962; Balkau & Feldman, 1973; Karlin & McGregor, 1974; Diehl & Bush, 1989; Hedrick, 1990; Kisdi, 2002; Beltman & Haccou, 2005). Although information on the genetic basis of habitat preference is still scarce and largely restricted to host preference in insects (Hawthorne & Via, 2001; Fox *et al.*, 2004; Jones, 2005; Tucić & Šešlija, 2007; Desjardins *et al.*, 2010; Caillaud & Via, 2012), there is little support for the assumption of such a simple genetic architecture. Overall, it is not evident how available theory applies to natural systems.

Empirical evidence of a role of habitat preference in speciation also exists, but is largely restricted to organisms tightly associated with a host species, that is, phytophagous insects and parasites [reviewed in Diehl & Bush (1989); Tauber & Tauber (1989); Jaenike & Holt (1991); ten Cate (2000); Berlocher & Feder (2002); Drès & Mallet (2002); for rare examples outside these groups, see MacCallum *et al.* (1998); Cruz *et al.* (2004); Grant & Grant (2008); Bolnick *et al.* (2009); Eroukhmanoff *et al.* (2011)]. However, even in these systems, identifying the precise cause(s) of habitat preference is challenging. Therefore, the relative importance of different habitat preference mechanisms remains largely unexplored empirically (Edelaar & Bolnick, 2012; Webster *et al.*, 2012; Duputié & Massol, 2013).

In this study, we attempt to address these conceptual gaps through a series of models simulating adaptive divergence with habitat preference. We consider four different mechanisms of habitat preference. The first mechanism is *habitat imprinting* (or natal habitat preference induction) (Immelmann, 1975; Beltman *et al.*, 2004; Davis & Stamps, 2004; Beltman & Haccou, 2005; Beltman & Metz, 2005). Here, a feature of the natal habitat is imprinted (i.e. learned irreversibly) during an individual's early ontogeny and forms a dispersal target. The second mechanism is *phenotype-dependent habitat preference* (or matching habitat preference) (De Meeus *et al.*, 1993; Ravigné *et al.*, 2004; Armsworth & Roughgarden, 2008; Edelaar *et al.*, 2008; Clobert *et al.*, 2009). Here, we assume that an individual's dispersal behaviour is influenced by how well its phenotype matches a habitat. The third mechanism is *competition-dependent habitat preference*. Here, an individual bases its dispersal decision on the strength of competition in a habitat. The fourth mechanism, finally, is *direct genetic habitat preference* (Rice, 1984; Diehl & Bush, 1989; Hedrick, 1990; Jaenike & Holt, 1991; Fry, 2003; Gavrilets & Vose, 2005; Ravigné *et al.*, 2009; Thibert-Plante & Gavrilets, 2013). Here, individuals can accumulate alleles causing a straight genetic preference for a specific habitat type. We ask how likely each of these habitat preference mechanisms is to evolve under divergent selection, and to what extent they promote progress towards speciation.

Materials and Methods

We use individual-based simulations to model a niche invasion scenario in which a source population adapted to an ancestral habitat colonizes and adapts to a novel, contiguous, selectively different habitat. We study the likelihood of habitat preference to evolve through different underlying mechanisms when dispersal between the habitats is initially random, and explore to what extent evolved habitat preferences facilitate adaptive divergence between the habitats as compared to random dispersal.

The initial population p_0, occurring in the first habitat H_0, consists of diploid individuals with separate sexes (an overview of the notation used in our simulations is provided in Table 1). The carrying capacity K_0 of this habitat is 8192 individuals. At the onset of the simulations, the novel habitat H_1 becomes available for colonization. This habitat has either the same carrying capacity K_1 as the first (symmetry in population sizes) or only half that carrying capacity (i.e. 4096; asymmetry). Generations are discrete and nonoverlapping, and the life cycle of an individual includes potential juvenile dispersal, viability selection, reproduction and death, in this order. Specifically, in the beginning of each generation, a fixed proportion π of individuals selected at random, referred to as the dispersal pool, is given the opportunity to disperse from one habitat to the other. The probability of an individual in the dispersal pool to *actually disperse* is called P and is either 0.5 (random dispersal, no habitat preference) or controlled by one of the four distinct habitat preference mechanisms described below. The dispersal pool is used to give individuals the opportunity to express a preference for a specific habitat even when they are already in that habitat. Biologically, the dispersal pool can be understood as the proportion of a habitat in which dispersal to the alternative habitat is possible. For instance, if π is small, this mimics a situation where the two habitats are mostly isolated from each other, and only few individuals residing in a small contact zone have the potential to disperse into the alternative habitat at all. Conversely, as π increases, the contact zone between the habitats increases.

Individuals exhibit a single ecological trait called x encoded by L unlinked, additive loci with two alleles (0, 1):

$$x = \frac{1}{2L}\sum_{i=1}^{2L} X_i, \qquad (1)$$

where X_i is a focal locus. We note that x can be imagined to combine *multiple* independent ecological traits encoded by a subset of the loci, although the fitness effects of the loci in our model are not additive, see eqn 2 defining ecological performance. The optimum trait value for x, termed θ, differs between the habitats, causing divergent selection. That is, θ is 0 in habitat H_0 and 1 in H_1. Because initially only H_0 is occupied and the corresponding population p_0 is perfectly adapted, the simulations start with $x = 0$ for all individuals. All loci encoding x are thus initially fixed for the 0 allele. Variation in x arises from mutation, which represents the transition from one allelic state to the other and occurs with the same, fixed probability $\mu = 10^{-5}$ at all loci. Because the optimum trait values in the two habitats coincide with the endpoints of the range of x, mutation becomes one-sided once a population is perfectly locally adapted (i.e. mutation cannot displace x beyond θ).

Table 1. Variables and symbols used in the study, listed in the order in which they appear in the text

Name	Symbol	Description
Population	p_i	Population with its name as subscript
Habitat	H_i	Habitat with its name as subscript
Carrying capacity	K_i	Carrying capacity of the habitat with its name as subscript
Dispersal pool	π	Proportion of the individuals in a population with the opportunity to disperse
Dispersal probability	P	Probability of individuals in the dispersal pool to disperse
Ecological trait	x	Trait under divergent natural selection
Number of loci	L	Number of loci encoding the ecological trait and the habitat preference traits
Ecological optimum	θ	Optimal trait value for the ecological trait
Mutation	μ	Probability of an allele to mutate to the alternative state
Performance	ω	Individual performance
Selection strength	σ	Strength of divergent selection between the habitats
Viability	v	Probability of an individual to survive to reproduction
Population size	N	Current number of individuals in a habitat
Imprinted information	i_{imp}	Information imprinted in the natal habitat
Imprinting-based habitat preference trait	a_{imp}	Strength of imprinting-based habitat preference
Phenotype-dependent habitat preference trait	a_{pheno}	Strength of phenotype-dependent habitat preference
Competition-dependent habitat preference trait	a_{comp}	Strength of competition-dependent habitat preference
Direct habitat preference trait	a_{hab}	Strength of direct genetic habitat preference

To quantify to what extent progress towards speciation is promoted by habitat preference, we will compare the magnitude of divergence in the ecological trait between the habitats ($\bar{x_1} - \bar{x_0}$) achieved with each habitat preference mechanisms to the magnitude of divergence observed under random dispersal. Our study thus explicitly equates ecological divergence with progress towards speciation, analogous to Kirkpatrick & Ravigné (2002). The rationale is that the emergence of substantial adaptive divergence despite initially high gene flow represents the pivotal fission of mating pools promoting the subsequent accumulation of further reproductive barriers (e.g. sexual isolation, intrinsic incompatibilities) (Rice & Hostert, 1993; Schilthuizen, 2000; Sobel *et al.*, 2010).

An individual's performance ω in a given habitat is a function of the deviation of the individual's trait value x from the optimum θ:

$$\omega = \exp\left(\frac{-(x-\theta)^2}{2\sigma^2}\right), \tag{2}$$

where σ specifies the strength of selection. The performance ω, in turn, defines an individual's viability v, that is, the probability to survive to reproductive stage:

$$v = \frac{1}{1 + (N/(\omega K))}, \tag{3}$$

where N is the current population size in the focal habitat and K is the habitat's carrying capacity. We thus model a density-dependent selection scheme allowing for logistic growth, representing an analogue of the Beverton–Holt model (Kot, 2001) (see also Gavrilets & Vose, 2005; Thibert-Plante & Gavrilets, 2013). A feature of this selection scheme is that as long as a population is not perfectly adapted ($\omega < 1$), N will remain below K. This is biologically reasonable; our carrying capacity can be viewed to reflect the amount of resources provided by a habitat, and a well-adapted population will use these resources more effectively and will thus reach a higher density than a maladapted population. Mating pairs are formed at random within each habitat by monogamous females and potentially polygamous males surviving to reproductive stage, and produce a number of offspring drawn from a Poisson distribution with an average of four. Offspring sex is assigned at random.

Habitat preference

We consider four distinct mechanisms causing habitat preference, each modelled as a genetically based trait encoded by L unlinked, additive, diallelic loci (depending on the trait, the alleles are either -1 and 1 or 0 and 1, see below). These traits can evolve, although in the beginning of the simulations, p_0 exhibits no habitat preference. Genetic variation in the preference traits arises from mutation, as described for the ecological trait.

In the first mechanism, natal habitat imprinting, individuals acquire a dispersal target through learning of a feature specific to the habitat in which they are born. This learned habitat information is defined as $i_{\text{imp}} = \theta_{\text{natal habitat}}$ (i.e. for computational convenience, we use the local optimum value of the ecological trait as a proxy for some habitat-specific feature that can be imprinted). A trait called a_{imp} governs habitat preference based on the imprinted habitat information (Beltman & Metz, 2005). An increase in a_{imp} towards one implies an increasing preference for the natal habitat. Conversely, as a_{imp} decreases towards minus one, natal habitat aversion builds up. Habitat imprinting thus qualifies as a one-allele mechanism of assortative mating (*sensu* Felsenstein, 1981) – an allele strengthening the habitat preference trait will reduce gene flow between the habitats *irrespective* of the habitat type in which it occurs. (This also holds for the two habitat preference mechanisms that follow below.) The dispersal probability P for an individual in the dispersal pool is thus a function of the imprinted information i_{imp} and the value of the preference trait a_{imp} (Fig. 1, 'Imprinting'):

$$P = \frac{1}{2} \pm a_{\text{imp}}\left(i_{\text{imp}} - \frac{1}{2}\right). \tag{4}$$

Note that in this equation, and in the equations of the three other preference mechanisms that follow, the sign of ± varies according to the habitat from which an individual is originating: + for H_0 where $\theta = 0$, and − for H_1 where $\theta = 1$. For example, if a_{imp} is one, P is zero in *each* habitat.

In the second mechanism, phenotype-dependent habitat preference, an individual possesses information about its own ecological phenotype x, acquired indirectly through the performance within the current habitat, as performance is determined by x. The dispersal probability of an individual in the dispersal pool is a function of the match between x and the optimum for x within the habitat on the one hand and the value of the habitat preference trait a_{pheno} on the other hand (Fig. 1, 'Phenotype') (De Meeus *et al.*, 1993; Armsworth & Roughgarden, 2008):

$$P = \frac{1}{2} \pm a_{\text{pheno}}\left(x - \frac{1}{2}\right). \tag{5}$$

Note that given our scaling of the habitat-specific optima for x, θ is implicit but does not appear in this notation. For a_{pheno} increasing towards one, individuals will display an increasing preference for the habitat where their phenotype is favoured and performance is high, whereas a_{pheno} decreasing towards minus one represents an increasingly strong aversion to this habitat. Although we consider this habitat preference mechanism biologically plausible, an alternative could involve individuals actively choosing the habitat where their

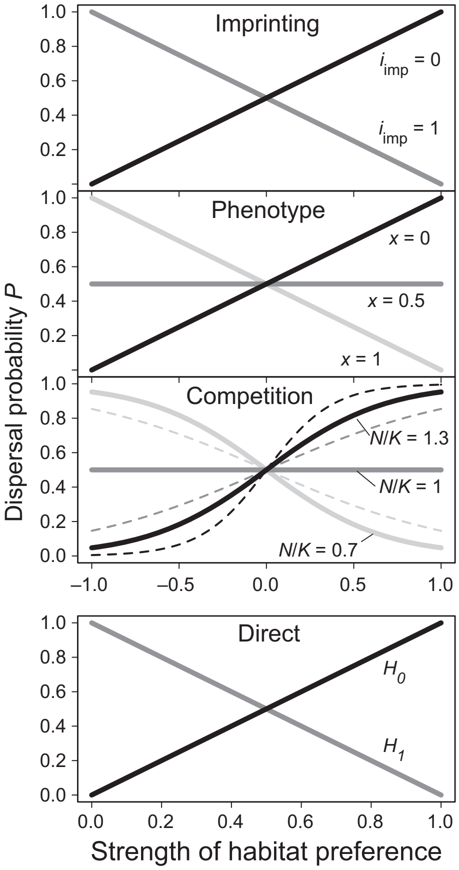

Fig. 1 Dispersal probability of individuals in the dispersal pool as a function of the strength of imprinting-based, phenotype-dependent, competition-dependent and direct genetic habitat preference. The *x*-axes thus represent, from top to bottom, the traits a_{imp}, a_{pheno}, a_{comp} and a_{hab}. For imprinting-based, phenotype-dependent and direct habitat preference, dispersal probabilities refer specifically to the habitat H_1; in H_0, the probabilities would be reversed. For phenotype dependence, the dispersal probability is displayed for three values of the ecological trait *x*, including complete maladaptation (0), and intermediate (0.5) and perfect adaptation (1). For competition dependence, the probability is visualized for three densities (population size well below, equal to and well above carrying capacity in light grey, dark grey and black), and for two performance levels. The first performance ($\omega = 1$, thick solid lines) corresponds to perfect adaptation and hence reflects the special case of a purely density-dependent response. The second performance ($\omega = 0.85$, thin dashed lines) corresponds to a deviation in *x* of about 0.5 from the local optimum at intermediate selection strength, or complete phenotypic maladaptation when selection is very weak.

performance is highest (De Meeus *et al.*, 1993; Ravigné *et al.*, 2004; Edelaar *et al.*, 2008). This would imply, however, that individuals can disperse back and forth between habitats to evaluate which habitat they match better phenotypically. As our models allow only for a single bout of dispersal within the life cycle, this alternative mechanism is not considered.

In the third mechanism, competition-dependent habitat preference, an individual in the dispersal pool bases its dispersal decision on how crowded the natal habitat is, and hence how intense competition is (Travis *et al.*, 1999; Poethke & Hovestadt, 2002):

$$P = 1 - \frac{1}{1 + \exp(10a_{\mathrm{comp}}(N/(K\omega) - 1))}, \qquad (6)$$

where a_{comp} is the trait governing habitat preference (Fig. 1, 'Competition'), and *N* is the size of the juvenile population (*N* in this formula is thus not identical to the post-dispersal population size influencing viability, see above). For a_{comp} increasing towards one, the probability to disperse increases as the population size in the natal habitat increases. A decrease of a_{comp} towards minus one, in turn, implies an increasing tendency to disperse from habitats with small population size. In addition, an individual's response to the density of competitors is conditioned on its own performance, as expressed by ω (this mechanism and the previous one are therefore not functionally orthogonal). That is, for a given population density, an individual is more likely to attempt to avoid competition through dispersal when being relatively poorly adapted. In a separate, complete set of simulations, however, we relax this latter condition by setting the performance term ω in the above formula to one (reflecting maximal performance – ω drops out). This special case of competition dependence thus reduces to a purely *density-dependent* habitat preference mechanism:

$$P = 1 - \frac{1}{1 + \exp(10a_{\mathrm{dens}}((N/K) - 1))} \qquad (7)$$

(Gadgil, 1971; Travis *et al.*, 1999; Poethke & Hovestadt, 2002), and is referred to as such. Note that the factor 10 in the formula was chosen to make the mutation effect size and the potential range of dispersal probabilities as comparable as possible to those in the other habitat preference mechanisms (given the difficulty that this function is nonlinear). However, representative simulations were performed with higher and lower factors within a biologically reasonable range, which produced qualitatively similar results.

In the fourth mechanism, direct genetic habitat preference, individuals can accumulate alleles causing a genetically hard-wired preference for one or the other habitat type (Garcia-Dorado, 1986; Diehl & Bush, 1989; Hedrick 1990; Kawecki, 1996; Fry, 2003; Gavrilets & Vose, 2005; Thibert-Plante & Gavrilets, 2013). Note that the three previous habitat preference mechanisms also have a genetic basis, but additionally incorporate non-heritable information about the habitat. The probability for individuals in the dispersal pool to move is given by

$$P = \frac{1}{2} \pm \left(a_{\mathrm{hab}} - \frac{1}{2}\right), \qquad (8)$$

where a_{hab} is the habitat preference trait (Fig. 1, 'Direct'). If a_{hab} decreases towards zero, individuals evolve an increasing preference for H_0, whereas values approaching one represent a preference for H_1. The alleles strengthening the habitat preference trait are thus habitat-specific so that direct genetic habitat preference represents a two-allele mechanism of assortative mating, contrary to all the habitat preference mechanisms introduced above.

As the simulations start without habitat preference, a_{imp}, a_{pheno} and a_{comp} are initially zero in p_0. That is, for these traits, one half of the loci is fixed for the -1 allele, whereas the other half is fixed for the 1 allele. Similarly, a_{hab} is initially 0.5, with the loci being fixed for either the 0 or the 1 allele. The three former habitat preference traits are thus scaled from -1 to 1, whereas a_{hab} is scaled from 0 to 1, like the ecological trait x (eqn 1). This differential scaling ensures that changing the number of loci (L) does not change the range of possible phenotypes. Each of the preference mechanisms is simulated independently; that is, the mechanisms cannot compete. Costs to habitat preference and dispersal are not modelled. However, assuming that the selectively different habitats are contiguous, cost arising from dispersal *per se*, and hence not captured by our modelled habitat-related performance trade-offs, is expected to be marginal.

Parameter values

We explore a wide range of combinations of number of loci L per trait, intrinsic dispersal propensity (specified by the proportion π of individuals recruited to the dispersal pool) and divergent selection strength σ. For L, we use 2, 4, 10, and 20. We thus do not consider the single-locus scenario. The reason is that we want habitat preference to be initially absent. With a single locus, this would require modelling each individual as heterozygous for the two opposed habitat preference alleles, causing the habitat preference traits to exhibit genetic variation right after the first generation of random mating. This is inconsistent with the scenarios involving two or more loci, where trait variation has to arise from mutation. For π, we consider $5 \times 10^{-5}, 10^{-4}$, $5 \times 10^{-4}, 10^{-3}$, $5 \times 10^{-3}, 10^{-2}$, $5 \times 10^{-2}, 10^{-1}$, 5×10^{-1} and 1. Accordingly, with symmetric carrying capacities and in the absence of habitat preference ($P = 0.5$), the expected number of dispersers from one habitat to the other ranges from 0.2 to 4096 per generation (the latter can be viewed as sympatry). Note that all values of $\pi \leq 1$ imply some level of philopatry, that is, a tendency to stay in the current habitat. However, this is distinct from habitat preference; according to our definition (see Introduction), habitat preference is an *evolved* modification of dispersal relative to some uniform baseline condition. For σ, we use 2.2629, 1.6177, 1.1661, 0.96757, 0.84932, 0.76819, 0.70763, 0.66698, 0.62034, and 0.58667. This translates to a difference in relative fitness between the habitats at carrying capacity of 0.05, 0.10, 0.20, 0.30, 0.40, 0.50, 0.60, 0.70, 0.80, and 0.90 for an individual completely adapted to one habitat. Each parameter combination is replicated 10 times. The evolution of the ecological trait and the habitat preference traits is tracked over 150 000 generations.

Because of the large scale of our modelling and the space restrictions on graphing within the study, we have created a Web browser visualizing the complete results across the *entire* parameter space considered (both as simulation endpoints and as time series). This Web browser is accessible on the Dryad repository (http://dx.doi.org/10.5061/dryad.nn77p). The reader is invited to explore this tool complementing the presentation of our key results in the article.

Results

Under random dispersal, the scenario where no form of habitat preference can evolve, the colonization of the novel habitat H_1 is almost always successful (colonization failed in only 0.3% of the simulations, all of them concerning asymmetry in population sizes and the strongest divergent selection). The magnitude of divergence in the ecological trait x is then determined by migration–selection balance and drift. As expected (García-Ramos & Kirkpatrick, 1997; Hendry *et al.*, 2001), migration–selection balance allows substantial adaptive divergence when divergent selection is strong (low σ), and when the intrinsic propensity for dispersal between the habitats (π) is low (Fig. 2; for full details, explore our supporting Web browser). To evaluate how this situation is altered when habitat preference is allowed to evolve, we treat the magnitude of ecological divergence between the habitats under random dispersal, averaged across the replicate simulations (i.e. $\overline{\bar{x}_1 - \bar{x}_0}$), as a benchmark for every parameter combination, and quantify the *deviation* from it caused by a given habitat preference mechanism. We start by considering symmetric population sizes ($K_0 = K_1$) and a modest number of large effect loci ($L = 4$), that is, a relatively simple genetic architecture facilitating ecological divergence (Gavrilets, 2004; Gavrilets & Vose, 2005), and then relax these assumptions.

Habitat preference through imprinting

Across a relatively wide range of parameter combinations, the trait a_{imp} evolves consistently to its maximal positive value (or just one mutation away from it), implying the emergence of a strong preference for the natal habitat (i.e. philopatry or dispersal avoidance) (Fig. 3, 'Imprinting', upper row). Specifically, this includes combinations of moderate-to-strong divergent selection (difference in relative fitness $\Delta\omega \geq 0.2$) and a relatively high dispersal propensity

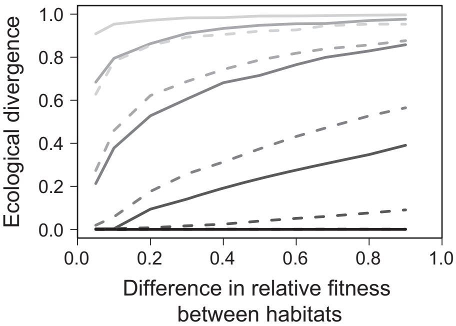

Fig. 2 Mean magnitude of divergence in the ecological trait ($\overline{x_1 - x_0}$) between the two populations achieved at migration–selection balance in the absence of habitat preference (i.e. with random dispersal). This divergence represents the benchmark against which the magnitude of divergence with habitat preference is evaluated. The strength of divergent selection between the habitats is indicated on the *x*-axis, and variation in intrinsic dispersal propensity (i.e. the proportion of each population recruited to the dispersal pool) is visualized by grey shades, ranging from 10^{-4} (light grey) to 10^{-3}, 10^{-2}, 10^{-1} and 1 (black). Data are shown for a low number (4; solid lines) and a high number (20; dashed lines) of loci encoding the ecological trait (for the highest dispersal, the latter are hidden by the former). Habitat carrying capacities are symmetric. For the ease of presentation, only the mean divergence across the replicate simulations for each parameter combination is shown. Note that divergence is facilitated by strong selection, low dispersal propensity and a low number of loci.

($0.005 \leq \pi \leq 0.1$). The evolution of this type of habitat preference greatly promotes speciation, as strong divergence in x between the habitats is achieved across a much wider parameter range than with random dispersal only (Fig. 3, 'Imprinting', lower row). The domain where the gain in divergence is greatest and most consistent is moderate-to-strong divergent selection and a high dispersal propensity. If selection is strong enough, imprinting-based habitat preference can permit complete ecological divergence at dispersal propensities consistently precluding *any* divergence under random dispersal ($\pi \geq 0.5$). In this latter parameter range, however, the variance among the replicate simulations is substantial because either complete divergence between the habitats is achieved or no divergence at all. Note that with imprinting, the gain in divergence generally tends to decline with increasing selection strength across the selection range where strong habitat preference is observed to evolve. The reason is that across this range, imprinting drives maximal adaptive divergence between the habitats. But as the magnitude of divergence achieved under *random* dispersal increases with increasing selection strength (Fig. 2), the opportunity for habitat preference to boost divergence beyond this benchmark necessarily decreases.

Phenotype-dependent habitat preference

The evolution of a strong preference for the habitat matching an individual's phenotype (i.e. a_{pheno} rising to one, or just one mutation away from one) is observed across a slightly broader range than with imprinting-based habitat preference: intermediate-to-high dispersal propensities combined with almost any strength of divergent selection except the lowest (Fig. 3, 'Phenotype', upper row). The potential to promote divergence, however, is lower than with imprinting (Fig. 3, 'Phenotype', lower row). The domain where phenotype-dependent habitat preference confers the greatest benefit is moderate-to-strong divergent selection combined with high dispersal propensities. Across this parameter range, the magnitude of gained divergence tends to increase with increasing strength of divergent selection (e.g. $\pi = 0.1$ in Fig. 3). This is opposite to the situation with imprinting, and occurs because despite the evolution of full-blown phenotype-dependent habitat preference in this range, adaptive divergence remains incomplete. However, with stronger selection, the populations move closer to their local ecological optimum, which in turn makes phenotype-dependent habitat preference more effective (positive feedback).

Competition-dependent habitat preference

This type of habitat preference, governed by the trait a_{comp}, generally evolves towards positive values, corresponding to a preference for a low-competition habitat. Strong preference evolves consistently when selection is moderate to strong ($\Delta\omega \geq 0.2$) and dispersal propensity is high ($0.05 \leq \pi \leq 0.5$) (Fig. 3, 'Competition', upper row). Within the same parameter range, competition-dependent habitat preference also facilitates adaptive divergence (Fig. 3, 'Competition', lower row). However, compared to imprinting, the magnitude of gained divergence is rather low. The strongest benefit occurs under strong selection and very high dispersal propensities. In the special case of pure density-dependent habitat preference (i.e. performance ω omitted in eqn 7), the deterministic evolution of habitat preference is never observed; across the entire parameter range, a_{dens} just drifts and does not promote divergence (details presented on the supporting Web browser only). This indicates that the evolution of our competition-dependent habitat preference mechanism is driven primarily by individual performance, not by the density of competitors.

Direct genetic habitat preference

The consistent evolution of genetically hard-wired habitat preference (a_{hab}) occurs within a narrow parameter range only, where relatively strong dispersal propensities ($0.01 \leq \pi \leq 0.1$) coincide with strong

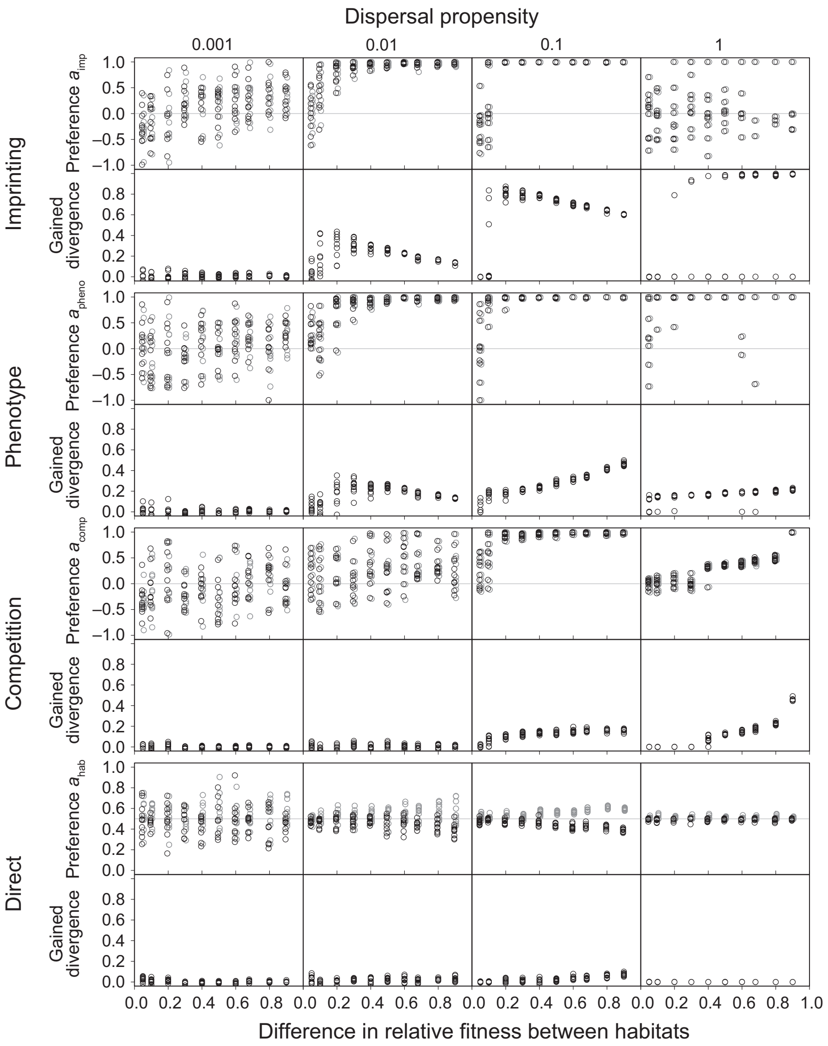

Fig. 3 Evolution of imprinting-based, phenotype-dependent, competition-dependent and direct genetically determined habitat preference, and the extent to which each of these mechanisms promotes ecological divergence, in relation to the strength of divergent selection and dispersal propensity. For each habitat preference mechanism, the upper row shows the evolution of the underlying preference trait in the population p_0 and p_1 (black and grey circles) at the end of each replicate simulation. The lower row shows the magnitude to which the evolved habitat preference enforces ecological divergence ('gained divergence'), expressed as the deviation in divergence from the benchmark (see Fig. 2). The number of loci underlying the ecological and the habitat preference trait is four, and habitat carrying capacities are symmetric. Note the general tendency of habitat preference to evolve at high dispersal, and the striking decline in the contribution of habitat preference to ecological divergence when moving from imprinting down to direct genetic preference.

selection (Fig. 3, 'Direct', upper row). In this range, a_{hab} evolves in opposed directions in the two populations, implying that p_0 and p_1 both develop a preference for their own habitat, although the magnitude of this preference is consistently weak. Stronger direct genetic habitat preference can arise – in the expected or opposed direction – at very low dispersal propensities only ($\pi \leq 0.001$), where a_{hab} evolves erratically by drift (similar stochastic evolution at minimal dispersal propensities is observed with all habitat preference mechanisms). Direct genetic habitat preference facilitates adaptive divergence measurably within the same narrow parameter range where its evolution is predictable, but the magnitude of this facilitation is marginal (Fig. 3, 'Direct', lower row).

Asymmetry in population sizes

Asymmetry in population sizes (carrying capacity $K_1 = K_0/2$) slightly reduces the magnitude of population divergence achieved in the absence of habitat preference (details presented in the supporting Web browser only). By contrast, this asymmetry generally extends substantially the parameter range in which habitat preference evolves. Specifically, all mechanisms except direct genetic habitat preference now evolve to great (often full) strength across a wider range of dispersal propensities including the highest, even when divergent selection is weak (e.g. Fig. 4, 'Imprinting', upper row). For imprinting-based habitat preference (but less so for phenotype- and competition dependence), asymmetry in population sizes similarly broadens the range across which ecological divergence is facilitated relative to random dispersal (Fig. 4, 'Imprinting', lower row). Imprinting-based habitat preference now permits full divergence across a wide domain where no divergence at all is possible in the absence of habitat preference.

The evolution of direct genetic habitat preference is also promoted by asymmetric population sizes. This preference now emerges consistently and reaches

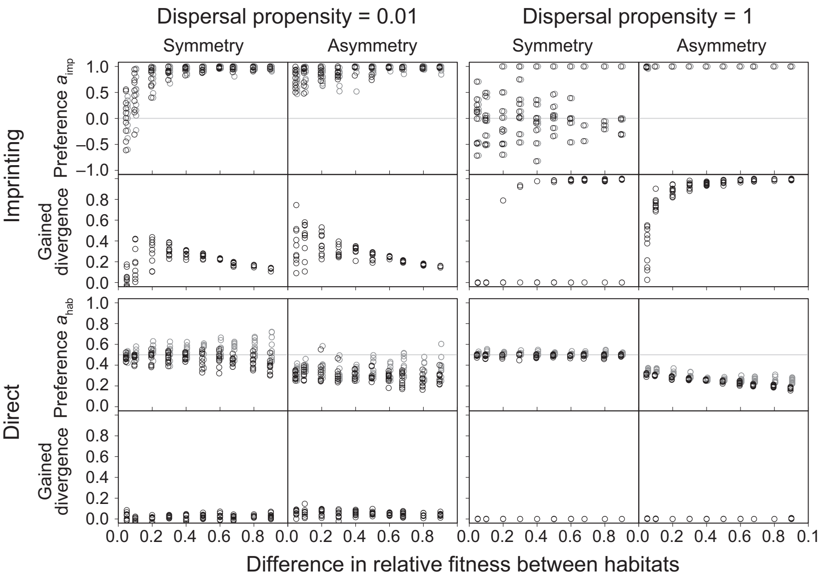

Fig. 4 Effect of symmetry vs. asymmetry ($K_1 = K_0/2$) in habitat carrying capacities on the evolution of habitat preference, and on the extent to which habitat preference promotes ecological divergence. Results are shown for imprinting-based and direct genetic habitat preference under low (10^{-2}) and maximal (1) intrinsic dispersal propensity. Phenotype- and competition-dependent habitat preferences are not shown, because for these mechanisms the effect of asymmetry is qualitatively similar to imprinting-based habitat preference. Note that with asymmetric carrying capacities, habitat preference generally evolves more easily and its contribution to ecological divergence is enhanced and that p_1 evolves maladaptive direct genetic habitat preference.

greater strength than with symmetric population sizes whenever dispersal propensity is not very low ($\pi \geq 0.005$) (Fig. 4, ‘Direct’, upper row). Interestingly, with asymmetry, a_{hab} evolves below 0.5 in *both* populations, implying the emergence of maladaptive habitat preference in the population with the smaller carrying capacity (here p_1). With asymmetry, the contribution of direct habitat preference to divergence is generally slightly enhanced, but still marginal in absolute terms (Fig. 4, ‘Direct’, lower row).

Number of loci

We here consider an increase in L, the number of loci influencing x and governing the habitat preference traits. As L increases, the magnitude of divergence among the populations under random dispersal decreases (Fig. 2). Similarly, increasing L consistently hinders the evolution of all habitat preference traits (Fig. 5, upper rows of all mechanisms). This effect is particularly pronounced under direct genetic habitat preference, where only the smallest number of loci simulated ($L = 2$) allows substantial progress towards habitat preference. However, for imprinting and competition dependence, we still observe the consistent evolution of maximal habitat preference for some combinations of strong selection and high dispersal propensity, even with the highest number of loci ($L = 20$). As the evolution of habitat preference becomes more difficult with increasing L, its facilitating influence on ecological divergence relative to random dispersal also diminishes (Fig. 5, lower rows of all mechanisms). With 10 and 20 loci, a_{imp} is the only habitat preference trait able to substantially enforce divergence beyond the magnitude observed under random dispersal. This occurs under relatively high dispersal propensity and strong selection. Conversely, direct genetic habitat preference confers a material gain in divergence only with the smallest number of loci.

Time scale of evolution

Under random dispersal, divergence reaches migration–selection balance rapidly, in the order of 1000 generations (details not presented). The evolution of habitat preference occurs only after migration–selection balance is achieved. In the parameter regions where preference evolves consistently and reaches its maximal value (or nearly so), this typically also happens within a few thousand generations after the initial ecological divergence, with the pace of evolution being highest under strong divergent selection (details presented in the supporting Web browser only). The emergence of strong habitat preference is thus rapid. Where strong preference evolves only occasionally, however, waiting time (and its variance) is generally much greater.

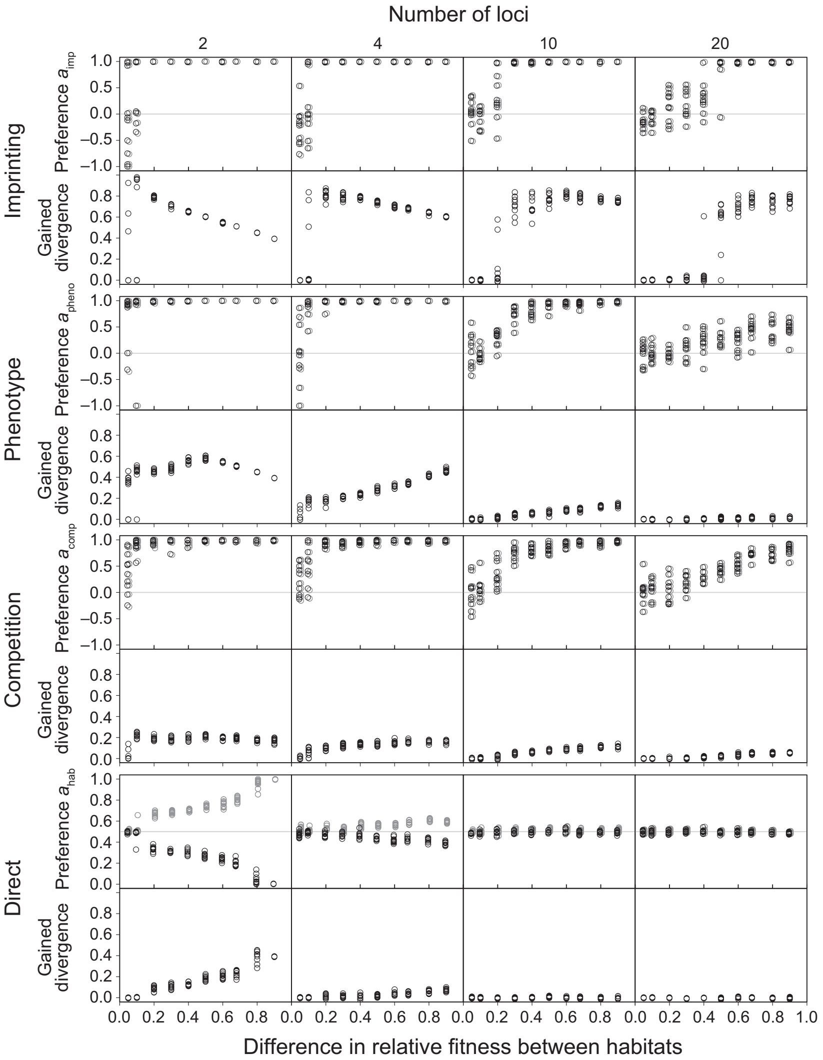

Fig. 5 Increasing the number of genetic loci generally impedes the evolution of habitat preference and reduces the contribution of habitat preference to ecological divergence. This effect, however, is least pronounced with imprinting-based habitat preference. Results are shown for a dispersal propensity of 10^{-1} and symmetric carrying capacities.

Discussion

We have used simulation models to explore (i) under what conditions populations diverging into selectively distinct habitats are likely to evolve habitat preference, (ii) whether some mechanisms underlying habitat preference are more likely to evolve than others and (iii) to what extent such mechanisms can promote progress towards speciation.

A first finding of our investigation is that across diverse habitat preference mechanism and a relatively broad parameter range, at least some degree of habitat preference will evolve deterministically during adaptive divergence. The result of this evolution is generally a reduction in the rate of dispersal. This result is in line with a family of theoretical investigations of dispersal modification under local adaptation (Balkau & Feldman, 1973; Karlin & McGregor, 1974; Gillespie, 1981; Asmussen, 1983; Kisdi, 2002; Billiard & Lenormand, 2005; note that these studies do not explicitly address habitat preference but fall within our broad definition of habitat preference: a modification of dispersal causing a bias with respect to the habitat of reproduction). This theory indicates that local adaptation generally causes indirect selection for a lower dispersal rate, provided the selective conditions in the habitats are relatively constant temporally. The reason is that alleles reducing dispersal will tend to find themselves associated disproportionally often with locally favourable alleles. Our models support this general result, but also refine it by showing that habitat preference emerges consistently only when the initial intrinsic dispersal propensity is substantial ($\pi \geq 0.005$). The reason for this condition is that given an intrinsically very low risk of dispersing to a habitat where ecological performance and associated fitness is reduced, selection for a further reduction in dispersal by habitat preference is necessarily weak. In this case, habitat preference can still arise fortuitously by drift but will not represent a material reproductive barrier because adaptive divergence is essentially unconstrained by gene flow in the first place.

In contrast to our finding that selection on dispersal rate occurs only at appreciable intrinsic dispersal propensities, Billiard & Lenormand (2005) showed that the selection can be strong under very low dispersal as well. Interestingly, in their model, selection favoured *higher* dispersal rates, an effect explained by the benefit of avoiding kin competition (Hamilton & May, 1977). Our models provide no indication of this mechanism. The likely reason is that very small population sizes and a large number of siblings are needed to make competition among close relatives a significant selective factor promoting dispersal (Poethke & Hovestadt, 2002; see also Fig. 2 in Billiard & Lenormand, 2005).

Contrasting the habitat preference mechanisms

A second finding of our investigation is that despite a general tendency for habitat preference to evolve deterministically during adaptive divergence, the magnitude of evolution differs dramatically among the underlying mechanisms: whereas habitat preference emerging through imprinting, phenotype dependence, and competition dependence is generally strong, genetically hard-wired habitat preference evolves to much lower levels. This observation agrees with and extends results from previous models comparing analogues of imprinting-based vs. direct genetic habitat preference under concurrent local adaptation (Kawecki, 1996; Beltman & Metz, 2005). These studies also found that the former habitat preference mechanism was more conducive to speciation than the latter, at least when the imprinting mechanism entailed no substantial direct cost. The reason for this difference lies in the distinction between one-allele and two-allele mechanisms of assortative mating (Felsenstein, 1981; Kirkpatrick & Ravigné, 2002; Fry, 2003; Coyne & Orr, 2004; Beltman & Metz, 2005; Webster *et al.*, 2012). With a one-allele mechanism, one and the same mutation promotes assortative mating in *all* habitats, whereas in the two-allele case, different alleles causing assortative mating have to establish separately within each habitat. As the latter process is counteracted by gene flow among habitats whereas the former is not, one-allele mechanisms are expected to be more conducive to speciation than two-allele mechanisms. Indeed, habitat preference based on imprinting, phenotype dependence and competition dependence represents one-allele mechanisms (even if they are based on more than one locus; Webster *et al.*, 2012). They differ, however, from *one-trait* mechanisms (Rice, 1984; Rice & Hostert, 1993; Fry, 2003) in that the habitat preference trait is not itself the direct target of divergent selection. By contrast, direct genetic habitat preference is a two-allele mechanism because habitat preference evolves and promotes ecological divergence only when separate alleles underlying a_{hab} become associated with the appropriate alleles driving x within each habitat. Without explicitly restricting recombination among loci (Beltman & Metz, 2005), this is difficult to achieve in the face of gene flow.

Although we readily observe the emergence of habitat preference through multiple one-allele mechanisms, the extent to which these mechanisms actually facilitate speciation is quite variable. Clearly, imprinting-based habitat preference increases the magnitude of ecological divergence most strongly and across the widest parameter range relative to a random dispersal situation. This mechanism is also the only one substantially promoting divergence when the number of loci encoding habitat preference is high (within the domain of high dispersal propensity and strong selection), and under imprinting, we observe the strongest facilitation of divergence when population sizes are asymmetric. Why is habitat preference based on imprinting such an effective reproductive barrier compared to phenotype- and competition-dependent habitat preference? The answer is that imprinting ties dispersal behaviour particularly reliably to selective conditions. To illustrate this point, imagine that the population p_1 has evolved substantial yet incomplete adaptation to its habitat H_1 (e.g. $x = 0.5$). Now even if phenotype-dependent habitat preference has evolved to full strength (i.e. $a_{\mathrm{pheno}} = 1$), a substantial proportion of p_1 will still disperse to H_0 because of the persisting mismatch between the actual phenotype and the phenotypic optimum within H_1 (right endpoint of the dark grey line in Fig. 1, 'Phenotype'). By contrast, for the same level of evolution in x, full-strength habitat preference based on imprinting (i.e. $a_{\mathrm{imp}} = 1$) will *completely* suppress maladaptive dispersal to H_0 because p_1 exhibits a perfect match between the imprinted dispersal target and the current habitat (right endpoint of the dark grey line in Fig. 1, 'Imprinting').

In a similar vein, although our competition-dependent mechanism often makes at least a modest contribution to divergence, the special case of purely density-dependent habitat preference completely fails to evolve deterministically and to promote speciation. This difference arises because competition dependence considers individual performance, hence information about the match between ecologically important alleles and selective conditions. By contrast, the density of conspecifics is largely disconnected from local selection and hence cannot serve as a dispersal cue promoting local adaptation. Interestingly, models of dispersal modification *without* selectively different habitats have demonstrated a benefit of density-dependent dispersal across a broad range of conditions (Gadgil, 1971; Travis *et al.*, 1999; Poethke & Hovestadt, 2002). The opposite outcome in our density-dependent simulations with local adaptation indicates that divergent selection is a much stronger determinant of dispersal evolution than selection arising from demographic stochasticity.

Taken together, while recognizing that other types of habitat preference functions than those underlying our one-allele mechanisms could be imagined (see Methods), our comparative study makes the general point that a one-allele mechanism *per se* does not guarantee a significant facilitation of speciation. Instead, the potential of any such mechanism to promote speciation depends critically on how tightly the cue governing dispersal behaviour is connected to local selective conditions. This potential is maximal under imprinting, or analogous mechanisms directly increasing natal habitat fidelity, as indicated by previous theory (Maynard Smith, 1962 1966; Balkau & Feldman, 1973; Karlin & McGregor, 1974; Kawecki, 1996; Beltman & Haccou, 2005; Beltman & Metz, 2005). Striking examples of imprinting are indeed well known all across the animal kingdom (e.g. insects: Goulson & Cory, 1993; Schumann & Buschinger, 1995; crustaceans: De Bruyn *et al.*, 2011; fish: Arvedlund *et al.*, 1999; Quinn *et al.*, 2006; Verzijden & ten Cate, 2007; Kozak *et al.*, 2011; reptiles: Aubret & Shine, 2008; birds: Glück, 1984; Payne *et al.*, 2000; Slagsvold & Wiebe, 2007; mammals: Kendrick *et al.*, 1998; for reviews, see Immelmann, 1975; Dittman & Quinn, 1996; Irwin & Price, 1999; ten Cate, 2000; Davis & Stamps, 2004). Hence, neurosensory circuitry allowing the long-term storage of habitat information, and the corresponding modification of behaviour, is widespread. It is easy to imagine that such circuitry – perhaps evolved to improve foraging performance or to facilitate mate and species recognition – is recruited at little cost to optimize dispersal decisions during ecological divergence.

Asymmetry in population sizes

Another important finding emerging from our investigation is that the evolution of habitat preference is more likely when the carrying capacities of the habitats are asymmetric. At least with imprinting, this asymmetry also substantially extends the range where habitat preference promotes divergence. To understand these results, it is instructive to consider models of dispersal evolution in which habitats differ in carrying capacity only, that is, where divergent selection is absent (Hastings, 1983; McPeek & Holt, 1992). These models indicate that differences in population sizes alone will select against dispersal (see also Kisdi, 2002), which can be explained by competition: for a given initial random dispersal propensity, asymmetry increases the relative proportion of individuals dispersing in each generation to the habitat with the smaller carrying capacity. This intensifies competition within that habitat and thus increases the fitness benefit of any reduction in dispersal from the larger to the smaller habitat achieved by habitat preference. Of course, asymmetry in population sizes simultaneously *reduces* competition in the habitat with the larger carrying capacity, thus weakening selection against dispersal from the smaller to the larger population. Nevertheless, habitat preference will also establish in the smaller population as preference alleles accumulated in the larger population spread by gene flow. In our model with direct genetic habitat preference, this latter process is maladaptive in the smaller population: the generalized preference for the higher-capacity habitat emerging under asymmetry (Fig. 4) causes individuals from the smaller population to disperse to a habitat in which their ecological performance is relatively poor. The overall net effect of differences in population sizes is thus to reinforce ecologically based selection for habitat preference. Nevertheless, despite the ubiquity of differences in the sizes of diverging populations in nature, existing models of local adaptation with habitat preference of any type have almost exclusively considered symmetric (and often infinite) population sizes only (but see Kisdi, 2002).

Impact of the number of loci

Our models reveal that an increasing number of loci underlying both the ecological trait and habitat preference generally reduce the likelihood and magnitude of habitat preference evolution, and consequently its benefit to divergence. This finding is consistent with previous multilocus investigations of divergence with habitat preference (Fry, 2003; Beltman & Metz, 2005; Gavrilets & Vose, 2005). The reason is that with an increasing number of loci, the intensity of selection on each locus becomes weaker, leading to a slower fixation of beneficial alleles and a higher probability of their stochastic loss. Most previous theoretical treatments, however, have either assumed that habitat preference is already established initially (Maynard Smith, 1966; Beltman *et al.*, 2004; Beltman & Haccou, 2005) – telling little about the likelihood of such establishment – or that habitat preference evolves from a polymorphism at a *single* locus (Balkau & Feldman, 1973; Karlin & McGregor, 1974; Diehl & Bush, 1989; Hedrick, 1990; De Meeus *et al.*, 1993; Kawecki, 1996; Kisdi, 2002; Billiard & Lenormand, 2005). In the light of our results based on more realistic genetic architectures, previous arguments for the general ease of speciation with habitat preference, especially direct genetic preference, should be taken with caution.

Model limitations and potential extensions

An important feature of our models is that they consider a total of two habitat patches only, so that dispersing individuals necessarily encounter a habitat of the opposed type. Our results thus apply most naturally to situations where ecologically different habitats are contiguous and occur in large patches relative to an organism's dispersal range. To explore to what extent our findings generalize to more fine-grained habitat configurations, it would be valuable to extend our models to scenarios where each habitat is represented by multiple patches. Our expectation is that with a higher number of habitat patches, habitat preference should evolve less easily. The reason is that given an equal representation of each habitat type, an increase in the number of patches asymptotically reduces the probability of dispersing into a habitat with the opposed selective optimum from 1 with two total patches to 0.5. This reduces the benefit of a dispersal reduction imparted by habitat preference. Also, with habitat imprinting, models considering multiple habitat patches would offer the opportunity to distinguish the effect of a preference for the specific place of birth (i.e. philopatry in a strict sense) from the effect of a preference for a specific *habitat type* (i.e. irrespective of the place of birth); in our current models, these two preference types coincide, as the natal habitat is also the only habitat patch of its type. Our models further assume a single, irreversible bout of dispersal during life, and the absence of a cost to dispersal. In models with multiple patches, implying a high dispersal range relative to habitat patch size, it would appear valuable to allow dispersing individuals to choose actively among patches based on acquired information about the patches' quality, and to associate this information acquisition with a survival cost.

Conclusions

We have shown that at least under some biologically realistic conditions, habitat preference can greatly facilitate adaptive divergence. And yet, habitat preference is not sufficiently appreciated as a component of reproductive isolation outside herbivore insects and parasites. Because of its particular potential to restrict gene flow in the face of initially high dispersal, habitat preference should receive much greater attention in empirical speciation studies dealing with populations in their early stages of divergence. A major analytical challenge is that different mechanisms generating habitat preference can produce similar dispersal patterns in nature. This calls for incisive experiments to pin down the exact cause(s) of habitat preference and to evaluate their relative importance in speciation across taxa. Research along these lines might well reveal habitat preference to be a general and powerful engine of speciation.

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Supporting information

Supplementary materials are archived in Dryad: http://dx.doi.org/10.5061/dryad.nn77p

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