Five questions on ecological speciation addressed with individual-based simulations

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Abstract

We use an individual-based simulation model to investigate factors influencing progress toward ecological speciation. We find that environmental differences can quickly lead to the evolution of substantial reproductive barriers between a population colonizing a new environment and the ancestral population in the old environment. Natural selection against immigrants and hybrids was a major contributor to this isolation, but the evolution of sexual preference was also important. Increasing dispersal had both positive and negative effects on population size in the new environment and had positive effects on natural selection against immigrants and hybrids. Genetic divergence at unlinked, neutral genetic markers was low, except when environmental differences were large and sexual preference was present. Our results highlight the importance of divergent selection and adaptive divergence for ecological speciation. At the same time, they reveal several interesting nonlinearities in interactions between environmental differences, sexual preference, dispersal and population size.

Introduction

Ecological speciation occurs when barriers to gene flow evolve as a result of ecologically based divergent selection. This process is now well supported by data from natural systems (Schluter, 2000; Rundle & Nosil, 2005; Barluenga *et al.*, 2006; Savolainen *et al.*, 2006), laboratory experiments (Rice & Hostert, 1997, review) and theoretical models (Dieckmann & Doebeli, 1999; Doebeli & Dieckmann, 2003; Gavrilets & Vose, 2007; Gavrilets *et al.*, 2007). Despite this growing body of work, some fundamental aspects of ecological speciation have rarely been formally investigated in theoretical models, leaving some outstanding basic questions. We address five of these questions through individual-based simulations of a scenario where dispersers from one environment colonize a new environment and then evolve in the presence of ongoing gene flow (i.e. 'divergence with gene flow', Rice & Hostert, 1997).

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Our first question relates to the length of time required for a population to completely occupy a new niche, because this event will be critical for progress toward ecological speciation. Several factors may come into play. First, the number of initial colonizers will often be small, thus increasing stochastic extirpation and Allee effects, as well as restricting the genetic variation available for adaptation (Kinnison & Hairston, 2007). However, these negative effects can be circumvented by an increased number of colonizers or ameliorated by reduced density dependence owing to small initial population sizes. Second, if the new environment is too different from the original environment, colonizers may be so poorly adapted that they cannot achieve a positive rate of increase (Gomulkiewicz *et al.*, 1999). In this case, the new population may never adapt and become self-sustaining (Holt & Gomulkiewicz, 1997). To address these possibilities, we measured the time to full occupation of a new environment as a function of dispersal rates (influencing the number of colonizers) and the magnitude of environmental differences (influencing the degree of initial maladaptation).

Our second question concerns how ecological speciation is influenced by natural selection against immigrants

(Hendry, 2004; Nosil, 2004; Nosil *et al.*, 2005). This potential barrier to gene flow occurs when individuals that move between environments are less likely to survive owing to maladaptation. Some likely examples include increased predation owing to compromised crypsis (Nosil, 2004) and reduced feeding efficiency owing to trait–food mismatches (Schluter, 1995). Selection against immigrants may be particularly potent during ecological speciation because it acts before other reproductive barriers; i.e. an immigrant must survive if mate choice or hybrid inviability are to be important. Empirical studies support this suggestion (Via *et al.*, 2000; Nosil, 2004; Nosil *et al.*, 2005; Nosil, 2007), but no model has examined the importance of selection against immigrants in comparison with other potential reproductive barriers. We address this question by considering the relative contributions of both natural and sexual selection against immigrants and any resulting hybrids.

Our third question involves the role of mate choice (sexual selection) in ecological speciation. This particular reproductive barrier is thought to be very important, as revealed by empirical studies (Grant & Grant, 1997; Boughman, 2001; Nosil *et al.*, 2002; Huber *et al.*, 2007) and theoretical models (e.g. Dieckmann & Doebeli, 1999; Kondrashov & Kondrashov, 1999). One general conclusion from this previous work is that speciation occurs most easily when the same genes (or physically linked genes) determine both adaptation and mate choice (i.e. 'magic trait' models, Gavrilets, 2004). It is less clear how easily and rapidly ecological speciation will proceed when mate choice and adaptation are both based on multiple genes that are unlinked across traits. In this latter case, several models have shown that some reproductive isolation can accrue quickly when assortative mating is based on habitat choice (Fry, 2003; Gavrilets *et al.*, 2007), but we are here interested in the role of mate choice within a given habitat. To address this situation, we examine the contribution of mate choice to ecological speciation when traits and preferences are both based on multiple, unlinked genes.

Our fourth question focuses on the role of ongoing dispersal and any resulting gene flow between environments. In principle, gene flow can either enhance or constrain adaptive divergence (review: Garant *et al.*, 2007) and therefore positively or negatively influence ecological speciation. On the positive side, dispersal can increase the genetic variation necessary for adaptation (Swindell & Bouzat, 2006), reduce inbreeding (Ingvarsson & Whitlock, 2000), alleviate Allee effects (Holt *et al.*, 2005), reduce demographic stochasticity (Alleaume-Benharira *et al.*, 2006), promote 'reinforcement' (Servedio & Kirkpatrick, 1997) and contribute to competition-driven diversification (Dieckmann & Doebeli, 1999; Doebeli & Dieckmann, 2003; Gavrilets & Vose, 2005; Gavrilets *et al.*, 2007). On the negative side, dispersal can prevent the independent responses of populations to different selec-

tive regimes (Slatkin, 1987; Hendry *et al.*, 2001; Lenormand, 2002) and can increase recombination between genes for adaptation and genes for mate choice (Felsenstein, 1981; Fry, 2003). We attempt to narrow down these possibilities by examining how different levels of dispersal influence adaptive divergence and reproductive isolation at different levels of natural and sexual selection.

Our fifth question examines one potential method for inferring ecological speciation. Specifically, some authors use neutral genetic markers to test whether gene flow is lower between populations in different environments than between populations in similar environments (e.g. Lu & Bernatchez, 1999; Ogden & Thorpe, 2002; Crispo *et al.*, 2006). This method of inference has recently been brought into question by the realization that alleles at neutral markers unlinked to selected loci might flow almost freely between populations in different environments (Emelianov *et al.*, 2004; Gavrilets & Vose, 2005). But ambiguity remains because a generalized barrier to gene flow (Gavrilets, 2004; Grahame *et al.*, 2006; Nosil *et al.*, 2007, 2008) might arise if selection acts against the whole genome of migrants and first-generation hybrids (i.e. before recombination between parental genomes). We inform this topic by examining how differentiation at unlinked, neutral markers is related to rates of dispersal and to the magnitude of ecological differences between environments.

Ecological speciation involves a complex interplay among natural and sexual selection, gene flow, adaptive divergence and reproductive isolation. Our overall goal is to examine the factors that influence these interactions and thus gain insight into the conditions that promote or constrain ecological speciation. The present paper introduces the modelling framework that we have developed to work in this broad area, and then uses this framework to address the above five questions on ecological speciation.

Modelling framework

For this individual-based model, we first describe the individuals, then their environment, and lastly their interactions. This description also provides a framework to outline the basic assumptions we make in this modelling exercise.

Individuals are diploid with two possible allelic states (0 and 1) at each locus, and each locus may be coding or noncoding with respect to phenotypic traits. A specific set of loci contributes additively to a given phenotypic trait. Random noise can also affect the transcription between alleles and traits, thus leading to heritabilities that are less than unity. We generate this noise around an individual's expected phenotype by drawing from a normal distribution with a variance of σ_N^2. We here consider two phenotypic traits: one that determines the resources an individual can use (the 'foraging trait', F) and another

that determines female mating preferences for individuals with different foraging trait values (the 'target of sexual preference', T). This situation, where mate choice directly targets the phenotypic trait that influences foraging, does occur in the context of ecological speciation. Examples include beak size in Darwin's finches (Grant & Grant, 2008; Huber *et al.*, 2007) and colour in aggressive mimics (Puebla *et al.*, 2007). Although the traits under selection thus influence mate choice, this is not a 'magic trait' model, because adaptation and mate choice are based on different, and unlinked sets of loci. The foraging trait was influenced by 256 diploid loci located to an equivalent of 20 cM apart (recombination rate 0.2 with crossover points determined randomly). The target trait had a similar genetic structure but was located on a different chromosome, and so was unlinked to the foraging trait. We also tracked eight neutral unlinked diploid loci, each located on its own chromosome.

Some parameters are common to all individuals and are fixed in all simulations (Table 1). One of these parameters is mutation rate: the probability of an allele mutating from one allelic state to the other. Note that in our model each locus has only two possible allelic states and mutation occurs between them. We here allow mutation rates to be higher for noncoding loci than for coding loci, as often seems to be the case when using biologically realistic values (Gavrilets & Vose, 2005). Another fixed parameter is the energy cost of offspring production: i.e. individuals accumulate resources prior to reproduction and then use those resources to produce offspring. We specify this energy cost as the amount of accumulated resources needed to produce one individual offspring.

The 'environment' determines the distribution of resources available to individuals having particular

foraging trait values. We here assume two spatially discrete environments, the 'old' environment being the source of colonists for the 'new' environment (see below). Within each environment, the total amount of resources is limited in a given generation but is renewed each generation so that the preforaging resource distribution remains constant over time. This distribution is a Gaussian function and is defined by three parameters: the position of the resource peak with respect to foraging trait values (Υ), the width of the resource distribution with respect to trait values (Ω) and the total amount of resources (R_{tot}):

$$R(x) = \frac{R_{tot}}{\sqrt{2\pi}\Omega} \exp\left[\frac{-(x - \Upsilon)^2}{2\Omega^2}\right]. \qquad (1)$$

An individual's acquisition of resources (energy) depends on the initial distribution of resources with respect to different foraging trait values and the degree of competition from other individuals according to their foraging trait values. The range and efficiency of resource use as defined by an individual's foraging trait are specified by a Gaussian distribution as in (Ackermann & Doebeli, 2004):

$$f(x) = \frac{1}{\sqrt{2\pi}\sigma} \exp\left[\frac{-(x - F)^2}{2\sigma^2}\right]. \qquad (2)$$

Each range of resources x is then split among all the individuals with $f(x) > 0.01$ present in the environment. This $f(x)$ is a modified Gaussian function that is truncated when it falls below 0.01. In particular, each individual receives an amount p_i of the resources x proportional to its $f(x)$. The total amount of resources acquired by an individual is the integral across the resource range:

$$p_i = \int R(x) \frac{f_i(x)}{\sum_j f_j(x)} \, dx. \qquad (3)$$

For the main simulations, we did not assume any maximum limit on the number of offspring that an individual could produce as a female. This decision meant that, in some colonization situations, individuals could acquire a large amount of resources and produce many offspring, which might not be realistic. We therefore evaluated the effect of this simplification by running some additional simulations after specifying that females could produce a maximum of only five offspring. All results were similar to the model without this restriction, except that colonization of a new environment became slightly more difficult with the restriction (results not shown).

After resource acquisition according to the above procedure, foraging stops and reproduction begins. Every individual is a hermaphrodite (for simplicity and simulation efficiency, Gavrilets & Vose, 2005), but self-fertilization is not possible. Individuals can reproduce as males irrespective of their energy stores (resources

Table 1 Parameter space explored in the simulations.

Parameters	Symbol (if any)	Values
Mutation rate coding		10^{-5}
Mutation rate noncoding		10^{-3}
Quantity of resource in each environment	R_{tot}	40
Cost to produce an offspring		0.1
Width of the resource distribution	Ω	10
Width of the resource acquisition function	σ	5
Number of immigrants	Nm	{10,20,30,40,50,60}
Strength of sexual selection	a	{0,0.001,0.005,0.01,0.05,0.1}
Noise in gene transcription	σ_N	{0,2,4,6}
Heredity (measure)	h^2	{1.00 ± 0.06,0.97 ± 0.06,0.87 ± 0.06,0.72 ± 0.08}

The heredity was measured on the simulation with only one environment and without sexual preferences, the measure reported are the mean ± SE. Each heredity measure (h^2) corresponds to the amount of noise in gene transcription (σ_N).

acquired) but can reproduce as females only when they have more resources than the minimum required to produce a single offspring. If an individual can thus act as a female, it will choose another individual from the population to act as its male mate and will then produce a single offspring, with energy resources decreasing accordingly. The specific individual that a given female selected as a mate was based on a probability distribution (across all individuals in the entire population) that depended on the difference between the target preference of the 'female' and the foraging trait of each possible 'male' (see below). After mating as a female and producing one offspring, an individual would again act as a female, according to the above procedure, only if she had enough resource to produce another individual offspring. This procedure continued until none of the individuals in the population had enough resources to reproduce as a female. Note that resources are depleted only during offspring production, and only when an individual acts as a female. After reproduction ceased, all parents died (i.e. semelparity with nonoverlapping generations).

As noted above, mating probabilities depend on the difference between the female target preference (T) and the male foraging trait (F), as well as the importance of that difference (a). This idea is similar to the Bush (1975) approach described in Fry (2003), except that the preference is not directed toward an environment, but rather toward a phenotypic trait. Our specific preference function follows Bürger *et al.* (2006):

$$\Pi_{u}(T - F) = e^{-a(T-F)^2}, \qquad (4)$$

where Π_{u} is the unweighted mating probability. This probability is then weighted according to the distribution of unweighted mating probabilities across all 'males' in the population:

$$\Pi(T - F) = \frac{\Pi_{u}(T - F)}{\sum_{i} \Pi_{u}(T - F_i)}. \qquad (5)$$

At $a = 0$, sexual selection is absent because the mating probability is independent of the foraging trait. As a increases, the unweighted probability of mating decreases as shown in Fig. 1.

The range of possible trait values can be normalized to range from zero to one. Under such normalization, $\{F, T, \sigma, \sigma_N, \Omega, \Upsilon\}$ are divided by 512, and a is multiplied by 512^2.

Simulations, data collection and presentation

Each simulation starts with a base population in the 'old' environment, initially established by individuals with a uniform distribution of trait values across the 99% range of available resources. The population then evolves in this environment for 1000 generations, which was sufficient for stabilization. We define stabilization as occurring when selection on the traits remains constant
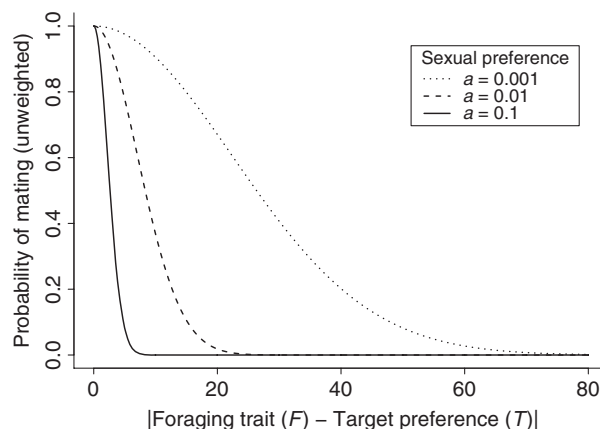
Fig. 1 Unweighted probability of mating as a function of the difference between the foraging trait F and the target of sexual preference T for different strengths of sexual preference (a).

across generations, which becomes essentially zero in the absence of immigration. After this initialization phase, we add a 'new environment' without any resident individuals. The two environments have identical resource distributions except for the position of the peak (Υ). In short, the same amount of resource is available in each environment but the resources are of different types, accessible to individuals with different foraging trait values. An example might be two islands with different distributions of seed sizes, which are therefore most accessible to birds with different beak sizes (e.g. Schluter & Grant, 1984). To continue this analogy, we simulate the situation thought to be important in the evolution of this group (Lack, 1947; Grant & Grant, 2008), where individuals adapted to conditions on one island colonize another island. Each generation, a certain number of individuals, Nm, disperses from the old environment to the new environment. This is a one-way dispersal only – there is no dispersal back from the new environment to the old environment. This number of dispersers then remains constant for the rest of the simulation (1000 generations). The corresponding immigration rate (proportion of the new population composed of immigrants) will decrease until the resident population achieves its final size and then remains constant thereafter (and at a level that was virtually the same across all the simulations). One thousand generations following the appearance of the new environment was chosen because it was a sufficient length of time for stabilization of population and evolutionary dynamics. Simulations were run eight times for each range of parameter values shown in Table 1.

For each simulation, we recorded several variables. Time to full occupation was the number of generations from the time when the new environment appears to when it is occupied by the same number of individuals as in the old environment. We judge this to have occurred

when population size in the new environment remains within 1 SE of that in the old environment for at least 10 subsequent and consecutive generations. The average number of offspring produced by immigrants, hybrids or residents in the new environment is akin to mean absolute fitness. This metric is calculated as the total number of offspring produced by all individuals in the group divided by the number of potential parents in that group. When two parents came from different groups (e.g. one resident and one immigrant), a contribution of 0.5 offspring was assigned to each parental group. Hybridization rate is the number of matings between immigrants and residents in the new environment relative to that expected under random mating and assuming equal resource acquisition. The random expectation was determined as:

$$\frac{2xy}{(x + y)(x + y + 1)}, \qquad (6)$$

where x is the number of residents and y is the number of immigrants. Hybridization rates estimated in this manner were averaged over the last 100 generations of the simulation (i.e. 900 generations after the new environment appeared). Neutral genetic divergence was indexed as F_{st} according to Weir & Cockerham (1984). We here present the median value across noncoding loci of the mean F_{st} values within a locus over the last 100 generations of the simulation.

Results

We first discuss general evolutionary patterns within a given simulation, then present results that address each of the five questions raised in the Introduction. Where relevant, the magnitude of environmental differences is given perspective by standardizing the distance between the two peaks by the width of the resource acquisition function of an individual:

$$\frac{\Upsilon_{new} - \Upsilon_{old}}{\sigma}. \qquad (7)$$

Time series of the distribution of foraging traits in the new environment typically showed a short initial phase when maladapted dispersers predominate (Fig. 2) and phenotypic divergence between environments is minimal. This was followed by a transition period when the distribution of phenotypes shifted rapidly toward that expected to be adaptive in the new environment (Fig. 2). During this period, we sometimes see signs of evolutionary branching into two different modes, perhaps as a result of competition (see Discussion). With increasing time, phenotypes slowly asymptote toward those expected for the new environment and also tend to converge from the bimodal distribution back into a single, broad distribution of phenotypes. This distribution roughly matches the distribution of available resources (Fig. 3). Time series of the evolution of female target
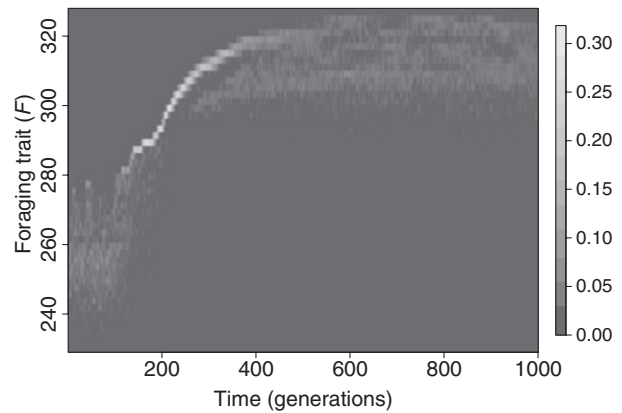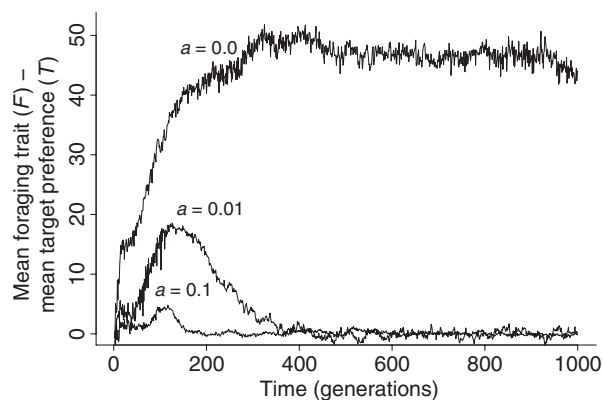

Fig. 2 Time series of the evolution of the distribution of the foraging trait (F) when there is no sexual preference. The grey scale represents the fraction of the population with a specific trait value at each iteration. Here, the position of the optimum in the old environment is 255 and the new is 310, i.e. a standardized environmental difference of 11. The number of immigrants is $Nm = 20$.
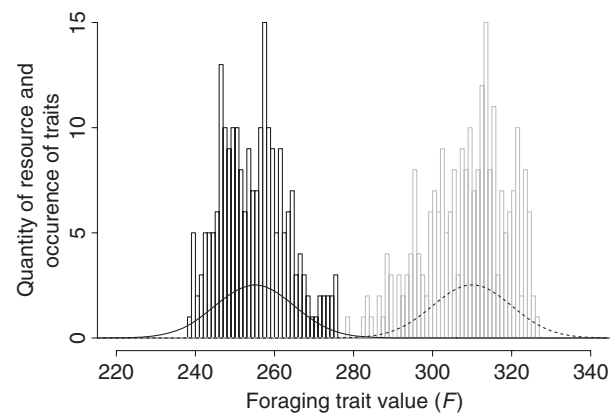
Fig. 3 Snapshot of the histograms of the foraging traits in the old (black) and new environment (grey) for the resident population only (no dispersers and no hybrids) at the last iteration. As can be seen in the distribution of the resource, the Gaussian distribution, the peak of the old (continuous line) and new (dashed line) environments are 255 and 310 respectively. There is no sexual preference ($a = 0$) and the number of immigrants is $Nm = 20$.

preferences in the new population initially lag those for the foraging trait (Fig. 4). As this mismatch increases, however, selection increasingly favours females who choose males with adaptive foraging traits in the new environment. For this reason, and because evolution of the foraging trait eventually slows down, female target preferences ultimately catch up and match the locally adapted foraging trait value.

Q1: *Time to full occupation*. In the absence of sexual preference ($a = 0$), the time required for the new population to become fully established depended on the

Fig. 4 Time series of the evolution of the difference between the foraging trait (F) and the target of sexual preference (T) for different strengths of sexual preference (a) for the population in the new environment. Here, the position of the optimum in the old environment is 255 and the new is 310, i.e. a standardized environmental difference of 11. The number of immigrants is $Nm = 60$.

difference in foraging trait optima between the old and new environments, and also on the number of dispersers (Fig. 5a). When the new environment was reasonably similar to the old environment (standardized environmental difference 0–10), full occupation was achieved in less than 100 generations, regardless of the level of dispersal ($10 \leq Nm \leq 60$, which corresponded roughly to a migration rate (m) between 3% and 20% at full occupation). For greater environmental differences, however, full occupation took considerably longer (Fig. 5a) and dispersal became important (see below). At large environmental differences (standardized difference > 13), colonization typically did not take place over the 1000 generation interval of our simulations. In these cases, dispersers were too poorly adapted to gain a foothold in the new environment. Adding sexual preference ($a > 0$) to the simulations (Fig. 5b) had little effect on time to full occupation when the new and old environments were similar (standardized environmental difference < 8). It did, however, decrease the threshold environmental difference at which full occupation became delayed. The reason was that females initially colonizing the new environment still preferred foraging trait values typical of the old environment (where their preference had evolved), and so maladapted immigrants were initially more likely than adapting residents to be chosen by both resident and immigrant females. This slows the process of adaptation until female target preferences (T) evolve substantially toward the locally adapted foraging trait values (see above).

Q2: *Selection against immigrants and hybrids*. We found strong natural selection against immigrants that was the direct result of adaptive divergence. This causal association was clearly seen as an increase in this component of reproductive isolation (difference in fitness between

residents and immigrants) with an increase in the environmental difference (Fig. 6a). In the absence of sexual preference, the average fitness (number of offspring produced per individual) of immigrants relative to residents had a lower limit of approximately 0.5. This particular limit arose because immigrants could still act as males (no energy required) even if maladaptation prevented them from acquiring enough energy to act as a female. If we had also assumed energy constraints on male reproduction, or if we had also included viability selection, then natural selection against immigrants would certainly have increased. The above patterns for selection against immigrants were largely mirrored when considering selection against hybrids (Fig. 6b). The latter was weaker, however, owing to the phenotypic (and therefore adaptive) intermediacy of hybrids relative to immigrants and residents (as a result of additive gene action). In the absence of environmental differences, populations drift in asynchrony around their resource peak, thus the dispersers can have a fitness advantage of being rare/slightly different. As dispersal increases so does competition for the resource, and this leads to a reduction in the average number of offspring per individual.

Q3: *Sexual preference*. The addition of sexual preference considerably increased reproductive isolation over that achieved solely by natural selection against immigrants. This can be shown most clearly by examining the number of hybrids produced relative to the random expectation (Fig. 7). Without sexual preference ($a = 0$), an increase in the environmental difference decreases hybrid production to a minimum of 0.5 (for the reasons explained above). Increasing levels of sexual preference ($a > 0$) then further decreased hybrid production for a given environmental difference (Fig. 7). This result is driven by adaptive divergence because it increased with increasing environmental differences. Indeed, essentially no hybrids were produced when environmental differences were large and when sexual preference was present. In short, adaptive divergence dramatically reduced hybrid production through the joint effects of natural and sexual selection against immigrants (Fig. 7).

Q4: *Dispersal rate*. All of the above conclusions are robust to the level of dispersal, which nevertheless caused some interesting nuances. First, when colonization is slowed by large environmental differences, increasing dispersal reduces this delay (Fig. 5), probably by providing more variation on which selection can act. Second, increasing dispersal reduces the average relative fitness (number of offspring produced) of immigrants and hybrids (Fig. 6) and the number of hybrids produced (Fig. 7). The reason is that dispersers (and hybrids) compete amongst themselves for an already scarce resource in the new environment (one tail of the resource distribution) and so more dispersers (and hybrids) reduce the amount of energy available to each. Third, dispersal influences final population sizes depend-
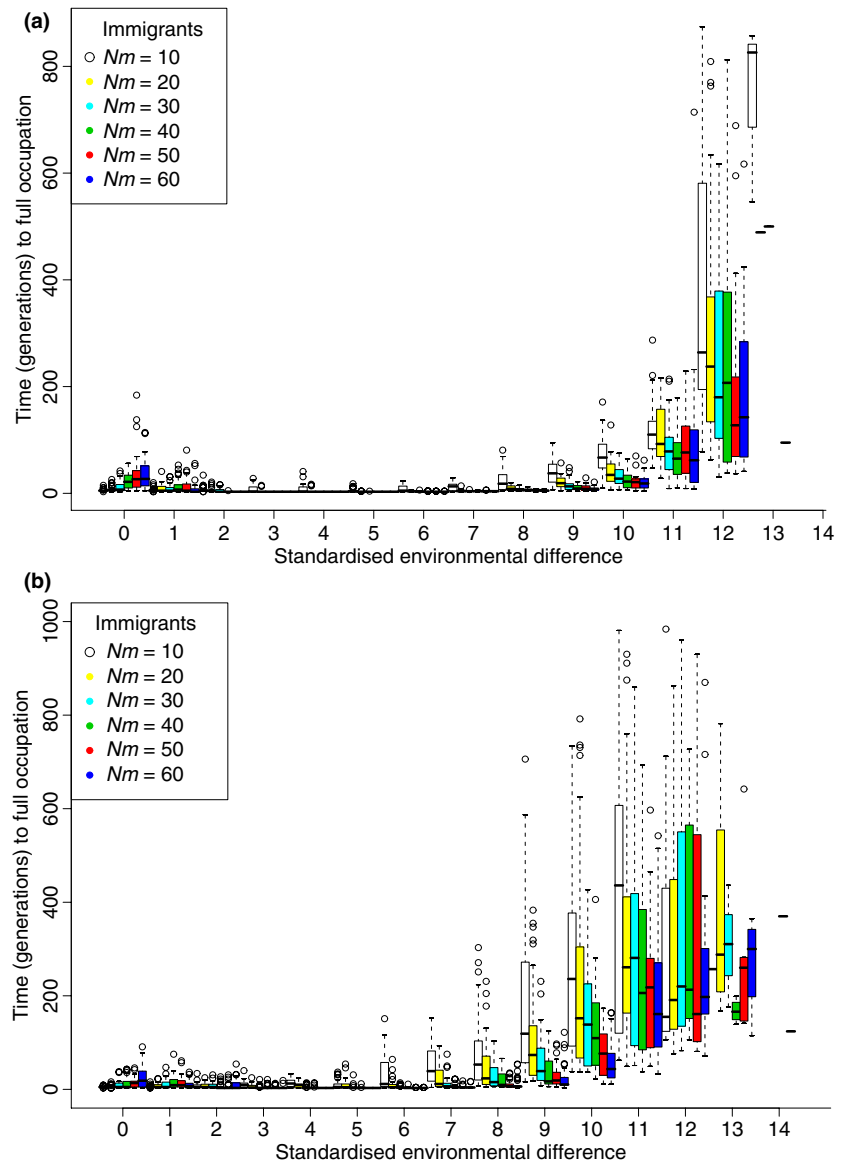
Fig. 5 Time to full occupation in number of generations as a function of the standardized environmental difference for different levels of immigration (Nm) increasing from left to right for each environmental difference. Without sexual preference ($a = 0$) (panel a) and with sexual preference ($a = 0.1$) (panel b). The box is bounded by the first and third quartiles. The line inside the box is the second quartile (median). The whisker extends to 1.5 times the interquartile range (third quartile minus first quartile) above the third quartile or to the maximum value, whichever is the smallest. The same rule applies for the lower part, but considering the minimum values between the 1.5 times the interquartile range below the first quartile and the minimum value. All data outside the whisker range are considered outliers and are represented by open circles. [Colour version of figure available online.]

ing on the environmental difference and sexual preference. In the first scenario (new and old environments are reasonably similar), increasing dispersal reduces resident population sizes (Fig. 8), because increasing competition reduces the number of individuals that obtain enough energy for reproduction. In the second scenario (new and old environments are quite different and sexual preference is absent), increasing dispersal increases resident population sizes (Fig. 8). This occurs because more residents mate with immigrants and produce maladapted offspring that obtain few resources. The remaining residents can therefore obtain more resources, thus increasing their offspring production. In the third scenario (new and old environments are quite different and sexual preference is present), immigrants do not contrib-

ute as females (not enough resources) or as males (resident females disfavour them), and so they have no measurable effect on resident population size.

Q5: *Neutral genetic divergence*. When sexual preference was absent, average genetic differentiation (F_{st}) at neutral, unlinked loci was very low – although the number of simulations with outlying large F_{st} values increased somewhat at the highest environmental differences (Fig. 9a). When sexual preference was present, F_{st} was low for small environmental differences, increased over the range of moderate environmental differences and decreased again for the very highest environmental differences (Fig. 9b). The main reason for the increase in mean F_{st} over part of this range was that large environmental differences, coupled with sexual preference,

(a)

(b)
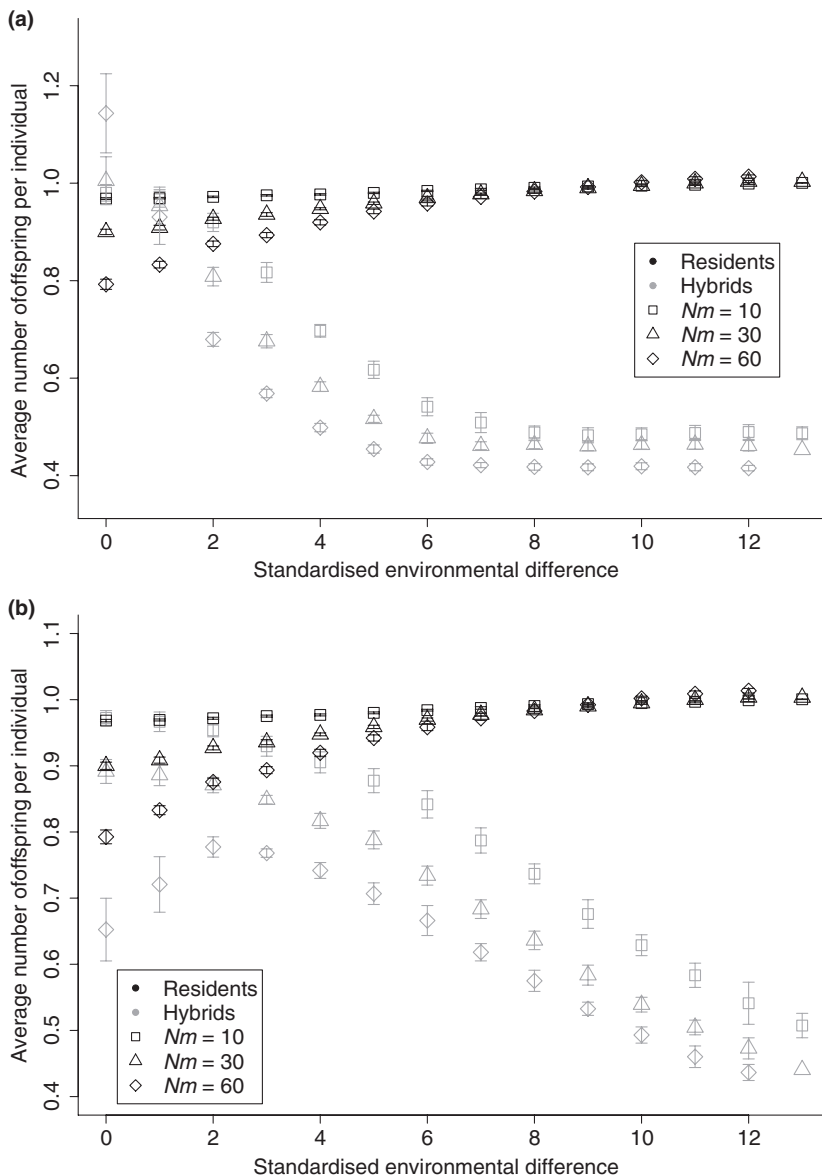
Fig. 6 Average number of offspring per individual in the new environment as a function of the standardized environmental difference and the number of immigrants (Nm). For each simulation we group the pedigree for the last 100 iterations. The vertical bars are the standard errors among the simulations with the same parameters. The immigrants (top panel) and hybrids (bottom panel) are compared with the residents.

can lead to very few hybrids (Fig. 7). Gene flow thus becomes very low and drift can cause substantial neutral divergence. The minor decreases for large environmental differences can be explained by time to full occupation: as it takes longer to adapt, the populations drift for a smaller amount of time. In short, divergent selection can dramatically reduce gene flow at unlinked, neutral markers, but perhaps only under some conditions and for some populations. Dispersal had relatively little effect on F_{st}, except perhaps that increasing dispersal decreased genetic divergence when sexual preference was absent (Fig. 9b). The reason was that the numbers of hybrids produced was affected much more strongly by variation in environmental differences and sexual preference than it was by variation in dispersal.

Discussion

Our model complements previous theoretical work on ecological speciation. First, it was an individual-based simulation that can tackle complex systems where analytical solutions cannot yet be found (Grimm & Railsback, 2005). Second, it was specifically designed to address the importance of particular reproductive barriers (natural selection against immigrants, natural selection against hybrids, sexual preference) across a range of conditions (environmental differences, dispersal). Third, it allowed us to directly evaluate one of the common empirical methods for inferring ecological speciation (neutral genetic differentiation). In the following paragraphs, we discuss how our results inform each of the

(a)

(b)
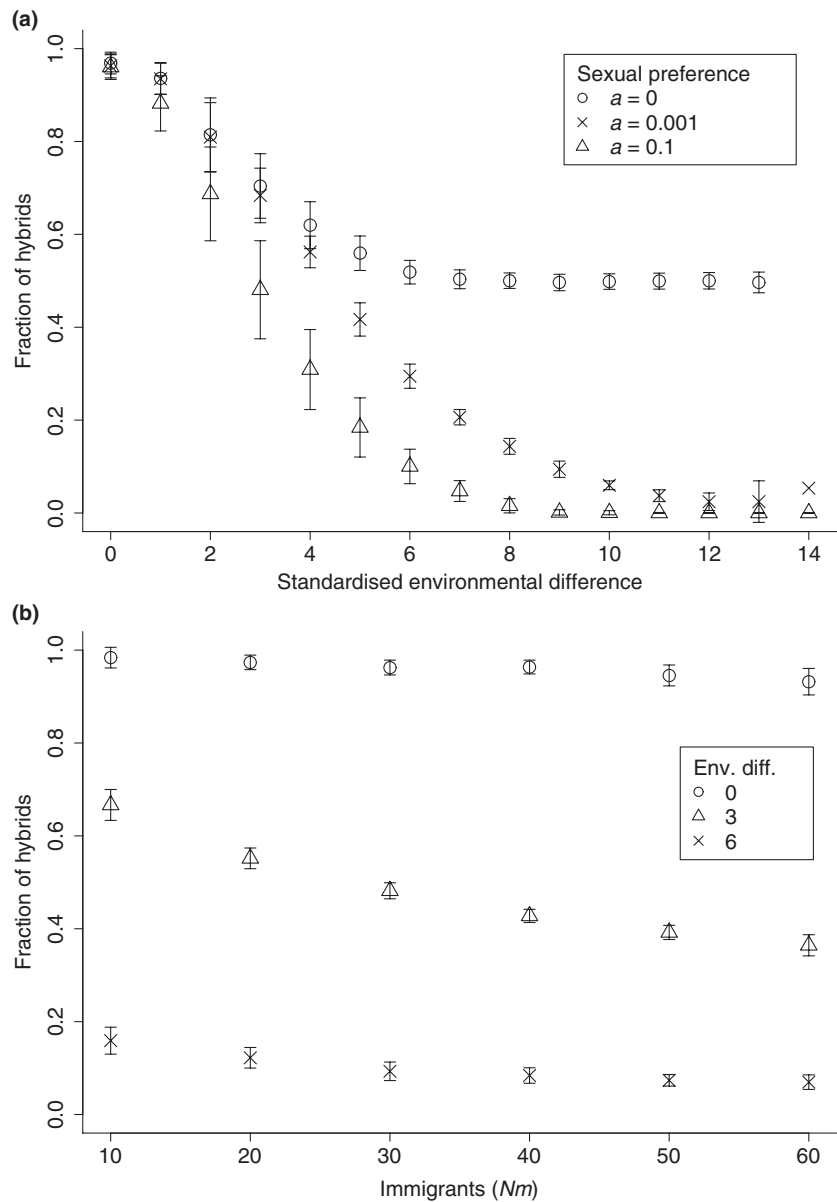
Fig. 7 Fraction of hybrids (number of hybrids produced relative to random mating expectation) as a function of the standardized environmental difference and the strength of sexual preference (*a*) for all levels of immigration (*N*m) grouped (top panel). Fraction of hybrids as a function of the number of immigrants for different environmental differences for simulation with sexual preference (*a* = 0.1) (bottom panel). In both cases, vertical bars represent the standard error among the fraction of hybrids for last 100 iterations.

questions about ecological speciation that were raised in the Introduction. We place these findings in the context of previous work, and we discuss implications for the understanding and study of ecological speciation.

Q1: *Time to full occupation.* Environmental differences are a prerequisite for ecological speciation (Schluter, 2000; Rundle & Nosil, 2005), but we here formally demonstrate that environmental differences can be a double-edged sword. On the one hand, increasing environmental differences increase adaptive divergence, and thereby promote ecological speciation. On the other hand, particularly large environmental differences can constrain colonization and adaptation, thereby also constraining ecological speciation (Fig. 2). This result is

obvious if one looks at adaptive radiations in nature. Darwin's finches of the Galápagos, for example, have radiated into a diverse array of different feeding niches (Lack, 1947; Grant & Grant, 2008), but none are scavengers, or cave dwelling, or marine, despite the continued availability of these and many other niches.

Several factors influenced the transition between the above promoting and constraining effects of environmental differences. First, when adaptation to the new environment was difficult because of large environmental differences, increasing dispersal made it easier. This result is not particularly novel given that several models have already argued for positive effects of dispersal on adaptive potential, particularly in the presence of Allee
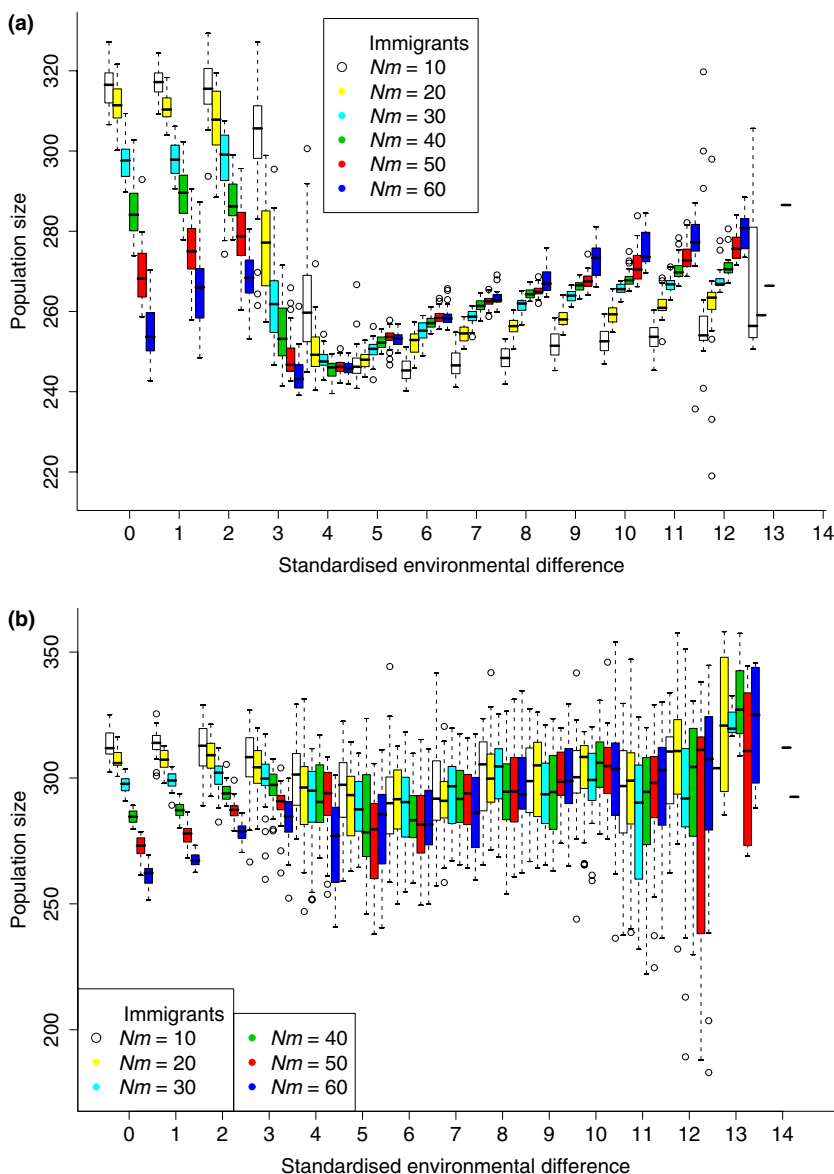
Fig. 8 Population size as a function of the standardized environmental difference and the number of immigrants. Panel (a) represents simulations without sexual preference ($a = 0$) and panel (b) represents simulations with sexual preference ($a = 0.1$). See Fig. 5 caption for explanation of the boxplot. [Colour version of figure available online.]

effects (e.g. Holt *et al.*, 2004), inbreeding (e.g. Ingvarsson & Whitlock, 2000) or low genetic variation (e.g. Gomulkiewicz *et al.*, 1999). Of these effects, the last was most relevant to our model. The reason is that adaptation to a dramatically different environment requires that colonizers include at least some individuals capable of reproducing in the new environment. These individuals with extreme phenotypes would be rare in the old environment. The chance of their inclusion with colonists therefore increases with the number of dispersers, although this effect might be less important if emigration was phenotype dependent (not considered here). It is also likely that the initially low level of competition in the new environment facilitates resource acquisition by these otherwise marginal individuals. Indeed, the success

of immigrants dramatically decreased as the new population became increasingly adapted to its environment (Fig. 6).

A second factor influencing the transition between the promoting and constraining effects of environmental differences was sexual preference. In particular, we found that when environmental differences were so large that they hamper colonization, stronger sexual preferences exacerbated this problem (Fig. 5). The reason was that evolution of the female target preference lagged behind evolution of the male trait (Fig. 4), because colonizing females carry mate preferences that were adaptive in the old, but not new, environment. That is, females in the new population initially prefer trait values typical of the old population, and thus tend to mate with

(a)

(b)
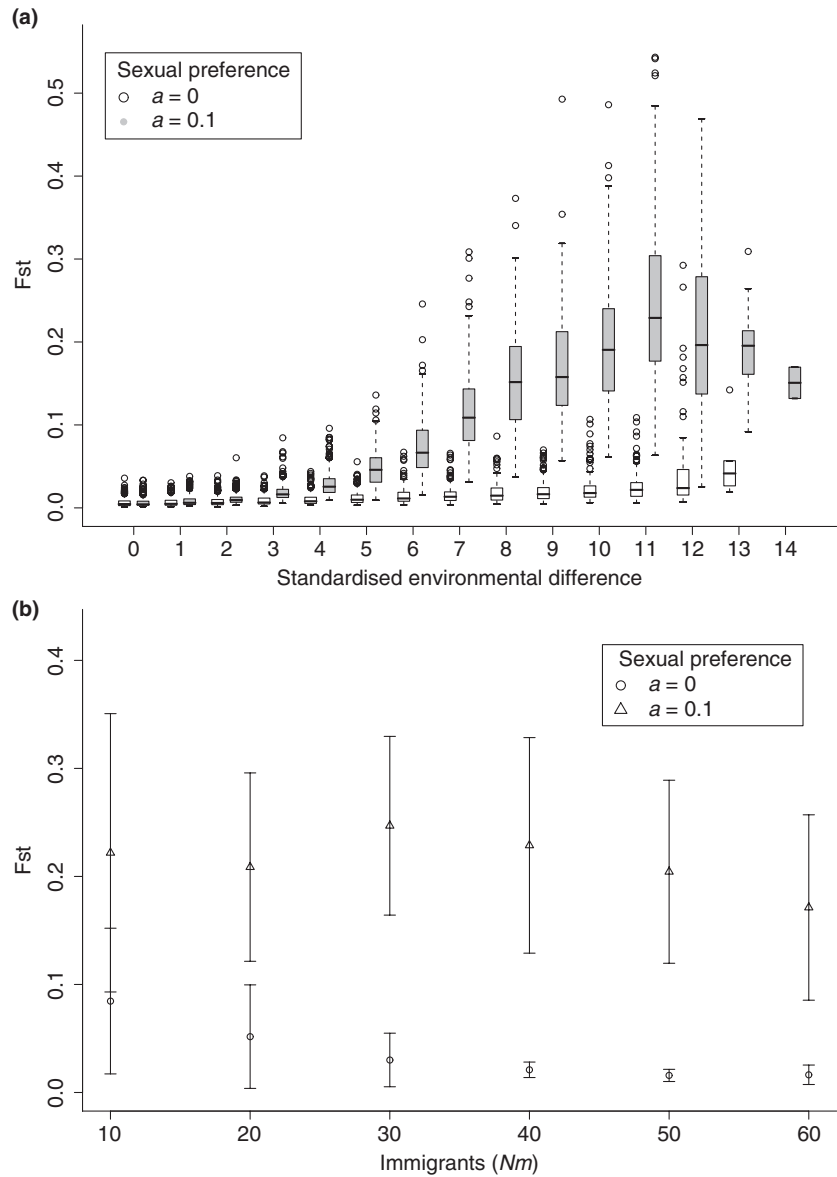
Fig. 9 Boxplot of the F_{st} as a function of environmental difference with and without sexual preferences (panel a). F_{st} as a function of the number of immigrants (Nm) for a standardized environmental difference of 12 with and without sexual preference (panel b). See Fig. 5 caption for explanation of the boxplot.

maladapted immigrant males rather than adapting resident males. This initial trait–preference mismatch slows adaptation in the new environment, and thus limits population growth. Eventually, however, partial adaptation of the male trait leads to selection on females to prefer adapted trait values (offspring survival is thereby higher), and the female target preference begins to shift in the appropriate direction. This 'reinforcement' of mating preferences (Servedio & Kirkpatrick, 1997; Servedio, 2004) then allows local adaptation to accelerate.

Q2: *Selection against immigrants (and hybrids)*. Many empirical studies provide evidence that natural selection against maladapted immigrants can dramatically reduce gene flow between populations adapted to different environments (e.g. Via *et al.*, 2000; Nosil, 2004; Nosil

et al., 2005, review). The only model (Hendry, 2004) to explicitly examine this phenomenon (separate from other reproductive barriers) found that it could evolve very quickly, but that model had rather restrictive assumptions. Nevertheless, our individual-based simulations were consistent with Hendry (2004) in finding that natural selection against immigrants can, by itself, substantially reduce hybrid production when environmental differences are large (Fig. 7). The maximum reduction in our model (one-half of the random expectation) was a product of our specific mechanism of selection: maladapted immigrants could not obtain enough energy to reproduce as females but could still reproduce as males. The effectiveness of selection against immigrants would thus have been greater had we also included other

selective factors, such as viability selection or energy constraints on male reproduction. It thus seems clear that selection against immigrants can sometimes be so strong as to render other potential reproductive barriers redundant, as suggested by others (Hendry, 2004; Nosil *et al.*, 2005).

Supporting empirical work (e.g. Schluter, 1995; Via *et al.*, 2000), selection against hybrids acted similarly to selection against immigrants, but was weaker. The main reason for this weaker effect was the assumption of additive gene action, which made hybrids phenotypically intermediate between residents and immigrants and therefore at a lower fitness disadvantage than immigrants. This formal confirmation of previous assertions (Hendry, 2004; Nosil *et al.*, 2005) further highlights the importance of directing more effort to the study of ecological selection against immigrants rather than hybrids. Of course, the relative importance of these two types of barriers in nature will depend on the type of selection (inviability, energy constraints on reproduction), nonadditive genetic effects and the life stage at which dispersal occurs. Finally, it is important to remember that ecologically based selection against immigrants and hybrids can be sensitive to environmental change (Grant & Grant, 1996; Taylor *et al.*, 2006), and so other reproductive barriers might be needed if speciation is to be irreversible.

Q3: *Sexual preference.* The importance of mate choice during ecological speciation is supported by many empirical studies (e.g. Seehausen & van Alphen, 1999; Boughman, 2001; Huber *et al.*, 2007) and theoretical models (e.g. Kondrashov & Shpak, 1998; Higashi *et al.*, 1999; Kondrashov & Kondrashov, 1999; Gourbiere, 2004). Many of these earlier analyses deal with one of the easiest situations for speciation with gene flow: i.e. 'magic trait' models, where the same trait determines both adaptation and assortative mating (Gavrilets, 2004). When these two phenomena are instead encoded by different genes, speciation becomes more difficult, although sometimes still possible (e.g. Kondrashov & Kondrashov, 1999; Fry, 2003). Many of these nonmagic trait models, however, dealt with a situation where assortative mating is based on habitat selection rather than mate preferences within a given habitat. Our model was designed to inform this latter situation, albeit in a spatial context.

We found that the addition of sexual preference leads to a strong decrease in the reproduction of immigrants, thus dramatically reducing the production of hybrids relative to random expectations. Indeed, the combined effects of natural and sexual selection essentially eliminated the production of hybrid offspring (Fig. 7) and allowed some divergence even at unlinked neutral genetic markers (see below). Note that these results really do reflect the interaction of natural and sexual selection because hybrid production was not reduced when environmental differences were absent but sexual preferences were present. We therefore agree with Arnegard & Kondrashov (2004) that speciation by sexual selection alone is difficult. We also agree with other authors (Kondrashov & Shpak, 1998; Higashi *et al.*, 1999; Gourbiere, 2004) that sexual selection can make a very important contribution to speciation that is initiated through divergent natural selection.

Q4: *Dispersal rate.* Numerous theoretical models, experiments and correlative analyses have argued that dispersal can have either positive or negative effects on adaptive divergence (see Introduction). We here illustrate how the balance between these effects depended on other parameters. When sexual preference was absent, increasing dispersal (1) decreased resident population size when environmental differences were small (because of increased competition with residents) but (2) increased resident population sizes when environmental differences were large (because interbreeding with residents reduced competition among resident offspring). The latter effect then disappeared when sexual preference was added, because immigrants did not acquire many resources and did not reproduce, thus becoming irrelevant to the resident population. Another interesting nonlinearity was that the time to full occupation of a new environment was not influenced by dispersal when environmental differences were small (because occupation was very fast) but decreased with increasing dispersal when environmental differences were large (because colonizers were more likely to include a few individuals capable of reproducing in the new environment). These results further highlight the multifarious effects of dispersal on adaptive divergence (Garant *et al.*, 2007).

We also examined how the above effects of dispersal on adaptive divergence might cascade to ecological speciation. Here, one might initially predict negative effects of dispersal because of increased recombination (Felsenstein, 1981; Coyne & Orr, 2004), but we instead found mainly positive effects. In particular, increasing dispersal enhanced several reproductive barriers, including selection against immigrants, hybrid production relative to random expectations and selection against hybrids. The reason for all of these positive effects of dispersal was competition. In particular, increasing dispersal meant that fewer immigrants were able to obtain sufficient resources for reproduction, which thus caused the reduction in hybrids relative to random expectations. Despite these effects, increasing dispersal nevertheless increased the absolute number of hybrids and their absolute effect on reproductive isolation (i.e. proportion of hybrids multiplied by their relative fitness; Fig. S1 in Supporting Information), which increased competition among them and thereby decreased their ability to acquire resources and therefore reproduce. Our results thus further highlight the need to consider both positive and negative effects of dispersal on ecological speciation, particularly in the case of competition for limited resources (Dieckmann & Doebeli, 1999; Day & Young, 2004).

Q5: *Neutral genetic divergence.* Divergence at neutral genetic makers has frequently been used to test for the onset of ecological speciation (e.g. Lu & Bernatchez, 1999; Ogden & Thorpe, 2002; Crispo *et al.*, 2006; Räsänen & Hendry, 2008). At present, however, the power and generality of this approach remain uncertain. The reason is that unlinked neutral genetic markers might flow almost freely between selective environments (Emelianov *et al.*, 2004; Gavrilets & Vose, 2005), although a generalized barrier to gene flow is also possible (Gavrilets, 2004; Grahame *et al.*, 2006; Nosil *et al.*, 2008). Our results suggest that neutral genetic markers might provide some indication of ecological speciation, but only under certain conditions. Specifically, environmental differences must be so strong that very few immigrants can successfully breed, which in our model required both large environmental differences and strong female preferences. In such cases, gene flow was very low and so neutral genetic divergence could proceed through genetic drift. It is therefore likely that greater neutral divergence would have been seen if we had simulated smaller populations (our populations usually attained sizes of more than 250 individuals).

Our results also provide a strong reminder of the stochastic effects of genetic drift. This random aspect of evolution lead to a large range in F_{st} values among independent simulations that used a common set of parameters (Fig. 9). This variation was evident across independent loci within a simulation (results not shown) and also across simulations when loci were averaged. The implications are that only a fraction of loci might show substantial differences between only a fraction of populations experiencing divergent selection. Indeed, this result fits well with recent empirical findings that only a few neutral, unlinked loci may differ between populations in different environments and that the specific loci showing this effect differ among different population comparison (Nosil *et al.*, 2007). We suggest that when investigators find the expected pattern (lower gene flow between than within environments), it probably does reflect ecological speciation. When they do not find this pattern, however, ecological speciation might still be occurring. For these reasons, neutral genetic markers are not a very reliable way to infer ecological speciation, or the lack thereof.

The speed of ecological speciation

The speed of ecological speciation has received little attention until only recently (Hendry, 2004). Indeed, Hendry *et al.* (2007) could find few relevant empirical studies, although those few did hint that substantial reproductive isolation can evolve on very short timescales (< 100 generations). This interpretation was, however, challenged by Gavrilets *et al.* (2007) and Gavrilets & Vose (2007), whose simulations were interpreted as showing the evolution of only limited reproductive isolation over such time frames. Indeed, their

simulations required on the order of 10 000 generations to complete speciation. We suggest that this apparent difference of opinion is illusory because the different studies examined different spatial contexts (essentially parapatry vs. sympatry) and different degrees of reproductive isolation (partial vs. nearly complete). Although the present study was not specifically designed to examine this question, the observed dynamics are nonetheless relevant. Our simulations showed that strong divergent natural selection (standardized environmental differences of 10–12), coupled with strong sexual preferences ($a = 0.1$) and high immigration rates ($Nm = 60$) often substantially reduced hybrid production and hybrid fitness (to less than 0.7) after only 50 generations. By 100 generations, essentially zero hybrids were formed and were able to reproduce. In short, ecologically based reproductive isolation can arise very rapidly, consistent with the deterministic simulations (Hendry, 2004) and existing empirical studies (Hendry *et al.*, 2007).

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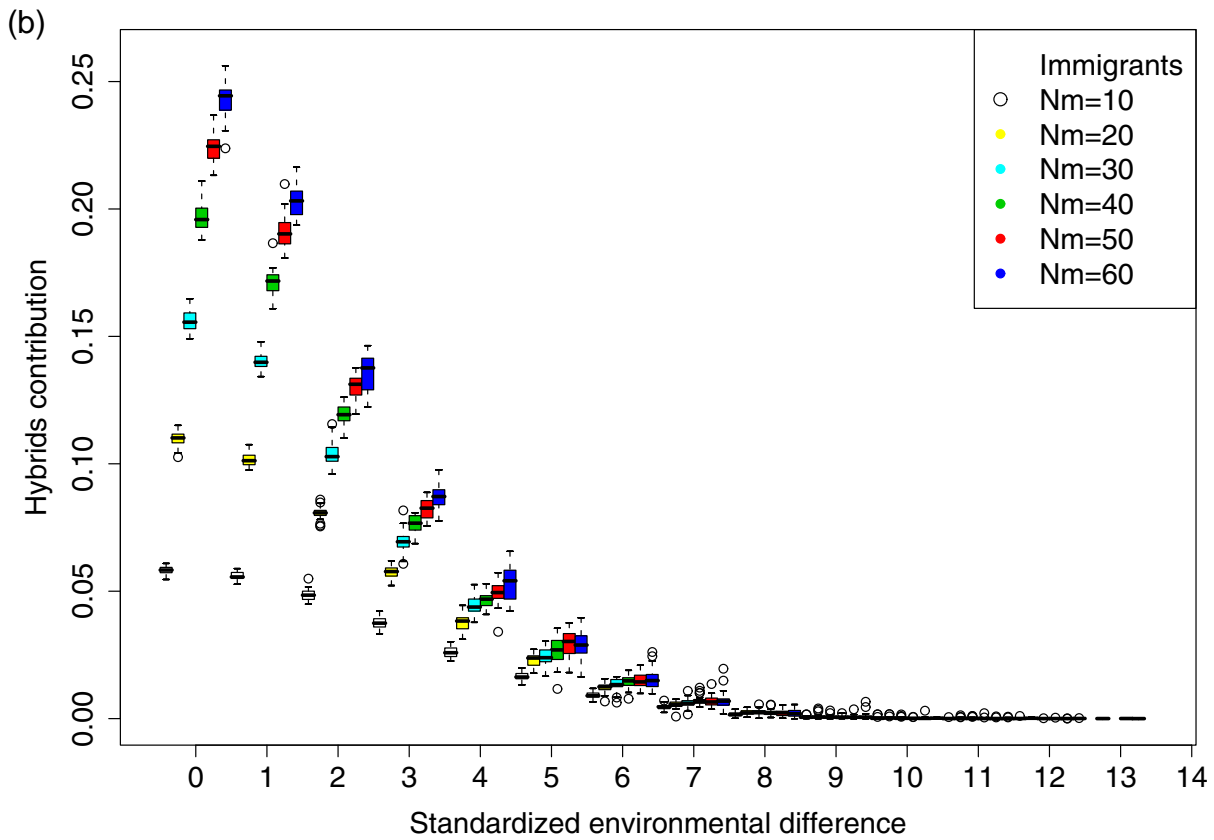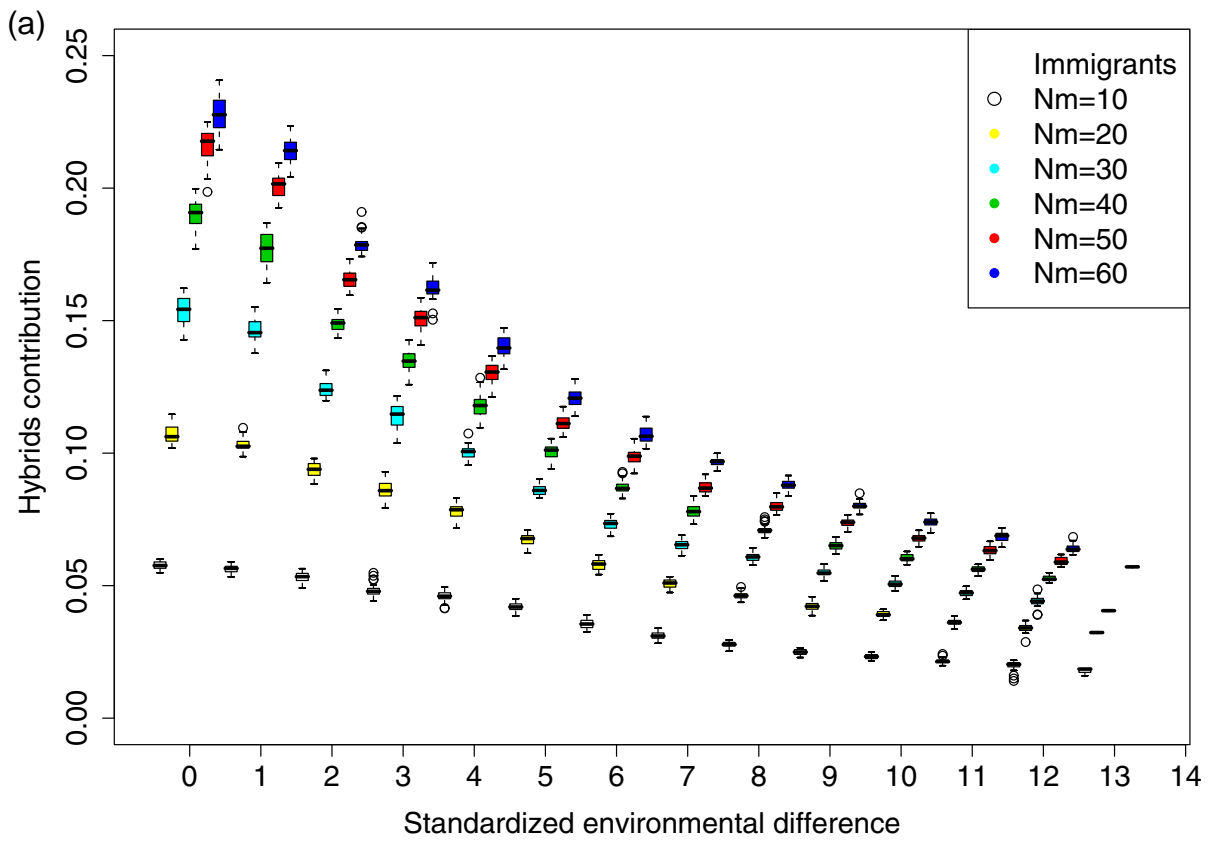
Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Hybrid contribution (proportion of hybrids multiplied by their relative fitness) as a function of the standardized environmental difference and the number of immigrants.

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Figure S1 Hybrid contribution (proportion of hybrids multiplied by their relative fitness) as a function of the standardized environmental difference and the number of immigrants. Panel (a) represents simulations without sexual preference ($a = 0$) and panel (b) represents simulations with sexual preference ($a = 0.1$). See Fig. 5 caption for explanation of the boxplot.