Costly mate preferences can promote reproductive isolation along ecological gradients

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Abstract

Species often replace each-other spatially along ecological or environmental gradients. In models of parapatric speciation driven by assortative mating, delayed mating when females are too choosy about mates has so far been ignored. Yet, this generates a cost of choosiness, which should cause direct sexual selection against female choosiness. In our spatially-explicit individual-based model, disruptive viability selection leads to divergence of an ecological trait in a population distributed along an ecological gradient. Additionally, female choosiness (following a 'matching mating rule' based on the same ecological trait) can evolve at the risk of delaying mating, and can limit gene flow between diverging populations. We show that, along ecological gradients, a cost of choosiness associated with delayed mating modifies the genotypic frequencies on which viability selection acts. This cost can even remove much of the viability selection acting indirectly against choosiness at the ends of the gradient, thereby *favouring* the evolution of strong choosiness. A cost of choosiness can therefore promote reproductive isolation in parapatry, depending on the characteristics of the ecological gradient.

INTRODUCTION

Since the publication of *The Origin of Species* by Darwin in 1859, a large amount of research has been carried out on speciation (see Turelli et al., 2001; The Marie Curie Speciation Network, 2012, for a review). Traditionally, speciation events have been categorized according to their geographical context – allopatry (extrinsic barrier to genetic exchange during divergence), parapatry (partial extrinsic barrier) and sympatry (no extrinsic barrier). The allopatric mode of speciation had been viewed as the most plausible one for decades until mounting empirical evidence suggested that speciation with gene flow (i.e., in sympatry or parapatry) can occur in nature (Rice and Hostert, 1993; Via, 1999; Barluenga et al., 2006; Savolainen et al., 2006; Soria-Carrasco et al., 2014; Momigliano et al., 2017). Mathematical models have since been developed to dissect the factors involved in speciation with gene flow (see Gavrilets, 2003, 2014). From this point on, research on speciation has shifted from a focus on the geographical context of differentiation to a focus on the role of viability and sexual selection in reproductive isolation (Via, 2001; Kirkpatrick and Ravigné, 2002; Kopp et al., 2018). It is now widely accepted that geography is but one factor among others that can influence the progress toward speciation (The Marie Curie Speciation Network, 2012).

Viability and sexual selection can act on heritable traits if individuals differ in their survival rate and mating success, respectively. In particular, disruptive selection – when individuals with intermediate phenotypic traits have a low fitness – plays a key role for population divergence and speciation (Kirkpatrick and Ravigné, 2002). First, abiotic or biotic environmental factors can cause disruptive viability selection if individuals with intermediate phenotypes suffer viability costs (e.g., high predation risk, low efficiency in resource use, genetic incompatibilities). Second, under the right circumstances, mate preferences can cause disruptive sexual selection on traits used as phenotypic cues for mate choice. In particular, if individuals express a preference for mates of their own phenotype ('matching mating rule', described below), the mating success associated with a phenotype increases with its frequency (positive frequency-dependent sexual selection). Therefore, individuals with intermediate phenotypes may have a low mating success if they are rare; sexual selection may be disruptive (Kirkpatrick and Nuismer, 2004; Pennings et al., 2008; Otto et al., 2008). Such disruptive selection – either via reduced survival or via reduced mating success of individuals with intermediate phenotypes – strongly contributes to the divergence of populations with distinct adaptive phenotypes (Kirkpatrick and Ravigné, 2002).

Assortative mating – i.e., the tendency of individuals of similar phenotype to mate together more often than expected at random – contributes to premating isolation and also plays a key role in generating reproductive isolation. It can arise as a by-product of adaptive divergence via temporal or spatial isolation (e.g., mediated by the evolution of host choice or phenology; Servedio et al., 2011), or can be driven by various behavioural processes (Kirkpatrick and Ravigné, 2002; Cézilly, 2004). Of particular interest is the case of matching mating rules (Kopp et al., 2018), where individuals preferentially choose mates with which they share phenotypic traits

such as colours (Summers et al., 1999; Jiggins et al., 2001; Reynolds and Fitzpatrick, 2007; Bortolotti et al., 2008) or acoustic signals (Snowberg and Benkman, 2007). Disruptive selection can indirectly favour the evolution of choosiness (hereafter, choosiness refers to the strength of preferences for 'matching' mates) through linkage disequilibrium, thereby leading to premating isolation between diverging populations (Rundle and Nosil, 2005; Sobel et al., 2010). This process can be facilitated if phenotypic traits subject to disruptive selection are also used as bases of mate choice (so-called 'magic traits'; Servedio et al., 2011).

This recent focus on the role of viability and sexual selection in reproductive isolation actually put the geographical context aside, especially from a theoretical perspective. Gavrilets (2014) noted that parapatric speciation is the least theoretically studied geographical mode of speciation, whereas he argued that it should be "the most general" one (Gavrilets, 2003). Environmental heterogeneity taking the form of ecological gradients is pervasive in natural systems, and applies to both abiotic factors (e.g., temperature, humidity, altitude) and biotic factors (e.g., predation risk). While ecological gradients setting the stage for parapatric speciation are ubiquitous, most of the theoretical studies have focused on sympatric speciation (Dieckmann and Doebeli, 1999; Matessi et al., 2001; Bolnick, 2004; Bürger et al., 2006; Kopp and Hermisson, 2008; Otto et al., 2008; Thibert-Plante and Hendry, 2011; Rettelbach et al., 2011), maybe because speciation in parapatry seems more straightforward to understand than sympatric speciation. Limited dispersal and reduced survival of immigrants in foreign environments can be seen as just an additional isolating barrier (Nosil et al., 2005). Nevertheless, gradual spatial structure has been shown to facilitate speciation – potentially even more than complete spatial isolation –, and the ecological contact is actually the driving force leading to reproductive isolation in parapatry (Doebeli and Dieckmann, 2003).

Along ecological gradients, diverging populations replace each-other spatially. The relative proportions of phenotypes change and can be unbalanced as one moves away from the centre of the gradient. This property can strongly affect density- and frequency-dependent forces acting during speciation and can lead to outcomes that are specific to the parapatric context. In particular, positive frequency-dependent sexual selection caused by female choosiness can promote ecological divergence by favouring different phenotypic traits across the ecological gradient (Servedio, 2011). However, in such parapatric context, very strong female choosiness causes rare males to mate with rare (matching) females, resulting in the loss of sexual selection (i.e., in equal mating success among males). Such loss of sexual selection under strong choosiness weakens the positive genetic association between choosiness and locally favoured ecological alleles. This ultimately leads to the removal of alleles coding for strong choosiness by indirect viability and sexual selection. As a result, only intermediate choosiness can evolve in parapatry (Servedio, 2011; Cotto and Servedio, 2017).

The distribution of diverging populations along ecological gradients may generate variations in mating success among females. In particular, variations in female mating success can take the form of a cost of

choosiness – i.e., a fitness cost to females that are choosy during mate choice –, thereby generating direct sexual selection inhibiting choosiness. Choosy females that refuse to mate with unpreferred males are more likely to delay mating than nonchoosy ones, possibly generating variations in mating success among females. When females may encounter a limited number of males in their lifetime [because of limited energetic reserves (Byers et al., 2005), high predation risk (Bonachea and Ryan, 2011), or low population density], delaying mating may even cause choosy females to remain unmated (Reynolds and Gross, 1990; Milinski et al., 1992; Heubel et al., 2008; Scott et al., 2020). Such direct sexual selection against choosiness can inhibit the evolution of choosiness in sympatry (Bolnick, 2004; Schneider and Bürger, 2006; Bürger et al., 2006; Kopp and Hermisson, 2008). In many theoretical models, however, female mating probabilities are normalized, so that all females eventually find a mate (Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2000, 2003; Servedio, 2011; Thibert-Plante and Gavrilets, 2013). Notably, this sexual selection pressure acting on choosiness depends on the local distribution of the phenotypes used as bases of mate choice. If the frequencies of the diverging populations are balanced, females often, if not always, end up mating with one of the males they prefer as long as they encounter enough males in their lifetime. Thus, when modelling speciation in sympatry, theoreticians can assume that all females eventually find a mate without loss of generality. Along ecological gradients, however, females with uncommon phenotypes (i.e., immigrant females) strongly delay mating, and risk to remain unmated if they are too choosy, even if they can encounter many males in their lifetime. Yet, so far, this risk has been ignored when modelling speciation along ecological gradients (Doebeli and Dieckmann, 2003; Kawata et al., 2007; Leimar et al., 2008; Ispolatov and Doebeli, 2009; Thibert-Plante and Gavrilets, 2013; Cotto and Servedio, 2017). Whether such direct sexual selection against choosiness inhibits the build-up of reproductive isolation in parapatry remains to be investigated.

With stochastic individual-based simulations, we here test if the risk of remaining unmated incurred by choosy females (hereafter called 'cost of choosiness' because only choosy females reject potential mates at the risk of remaining unmated) inhibits the evolution of choosiness in parapatry. We consider that two ecotypes are favoured in distinct habitats (i.e., with distinct abiotic or biotic environment) along an ecological gradient. We implement two 'main demes' where viability selection is convergent (only one ecotype is favoured), and a 'transition deme' where viability selection is disruptive (both ecotypes are favoured and hybrid individuals suffer viability costs). Such spatial discretization allows us to infer the global selection gradient from local selection gradients (using a method derived from Wickman et al., 2017). The ecological trait under disruptive viability selection can be used as the basis of mate choice by choosy females (matching mating rule), and the evolution of female choosiness can therefore lead to assortative mating and reproductive isolation between ecotypes. By assuming females may only encounter a limited number of males in their lifetime, we account for the possibility that choosy females may risk to remain unmated, in particular if matching males are locally rare,

thereby generating variations in mating successes in females. We show that such cost of choosiness generates additional sexual selection pressure against choosiness. However, interestingly, a cost of choosiness can favour the evolution of choosiness by removing viability selection, which indirectly inhibits choosiness in main demes. As a result, our model predicts that the effects of the cost of choosiness on reproductive isolation in parapatry greatly depend on the steepness of the ecological gradient and on the strength of viability selection.

METHODS

Individual characteristics and spatial context

Individuals are characterized by their sex, their ecological trait $x \in [0, 1]$ controlling survival in a local environment, and their choosiness trait $c \in \mathbb{R}$ controlling the strength of female preference during mate choice. The genetic architecture and inheritance rules are based on Claessen et al. (2008). The traits x and c are respectively determined by L_x and L_c diploid, additive loci on autosomal chromosomes. Each allele can take any real value in the range of the trait it is coding for – i.e., in $[0, 1]$ and $\mathbb{R}$ for the alleles coding for traits x and c, respectively. Trait x and c are calculated as the mean values of their alleles. In addition, individuals carry L_n diploid unlinked neutral loci with a large number ($= 50$) of possible alleles.

Individuals are distributed in two main demes with distinct convergent viability selection pressures (subscript 1 and 2) and in a transition deme with disruptive viability selection pressure (subscript T), with carrying capacities K_1, K_2 and K_T respectively (see the flowchart of the model, Fig. 1). The overall carrying capacity K is set to be constant ($K = K_1 + K_2 + K_\mathrm{T}$) and we assume that demes 1 and 2 have the same carrying capacity ($K_1 = K_2$). The carrying capacity of each deme depends on the relative size of the transition deme, called α_T ($\alpha_\mathrm{T} \in [0, 1]$). In particular, the carrying capacity of the transition deme is calculated as: $K_\mathrm{T} = \alpha_\mathrm{T}.K$.

During their lifetime, individuals may experience three processes in this given order: survival to adult state, dispersion and reproduction. We assume that generations do not overlap.

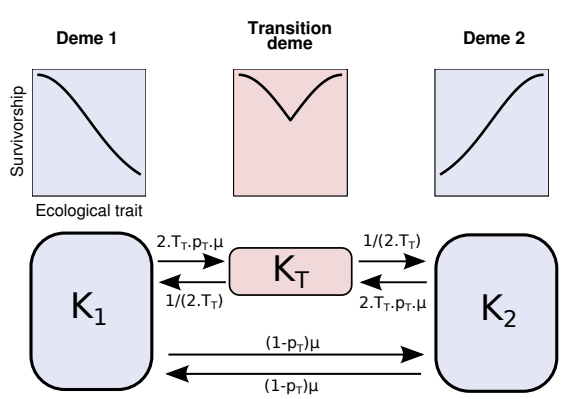

Figure 1: Flowchart of the model: individual survivorship, carrying capacities and migration rates. The main demes and the transition deme are coloured in blue and pink, respectively.

Survival to adult state

Viability costs, which affect survival to adult state, are heterogeneous in space. Through differential survivorship among individuals, viability selection acts on the ecological trait (Fig. 1). In main demes, viability selection is convergent. The 'condition' ω_i of one individual in a main deme $i \in \{1, 2\}$ depends on its ecological trait x. In particular, if $x \simeq \theta_i$, then the individual does not incur viability costs:

$$\omega_i = \exp\left(\frac{-(x-\theta_i)^2}{2{\sigma_\mathrm{s}}^2}\right) \tag{1}$$

Where θ_i is the local optimal trait value and σ_s is inversely proportional to the strength of viability selection, which is the same in both demes. We implement $\theta_1 = 0$ and $\theta_2 = 1$. Therefore, individuals with high viability in deme 1 suffer from low viability in deme 2, and vice versa.

In the transition deme, viability selection is disruptive in a way that individuals exhibiting ecological traits matching the optimal trait values θ_1 or θ_2 do not incur viability costs. On the contrary, individuals with an intermediate ecological trait suffer from high viability costs:

$$\omega_\mathrm{T} = \max\left[\omega_1,\ \omega_2\right] \tag{2}$$

Thus, we assume that σ_s is the same in the three demes.

In addition to individuals' condition, competition for resources will define individuals' survival to adult state. To do so, we derived the Beverton-Holt equation – i.e., the discrete version of the logistic growth – to calculate the survival probability v to adult state in deme $i \in \{1, 2, \mathrm{T}\}$:

$$v = \frac{1}{1 + (\frac{b}{2} - 1)\frac{N_i}{\omega_i K_i}} \tag{3}$$

With b the mean number of offspring per female, N_i the number of individuals in deme i and K_i the carrying capacity of the population in deme i.

Dispersal

Once individuals reach their adult state, they can migrate to other demes, before the reproduction stage.

We implement μ as the overall migration rate between the two main demes. This parameter affects all migration flows, and therefore represents the dispersal ability. Depending on the size of the transition deme, a fraction p_T of these migrants will experience the transition deme during a number of generations T_T before migrating again – i.e., a portion $1/T_\mathrm{T}$ of individuals from the transition deme are migrating at each generation.

Another fraction $1-p_{\mathrm{T}}$ will migrate directly to the other main deme, without experiencing the transition deme. We can then calculate all migration flows from the parameters μ, p_{T} and T_{T} (see the flowchart of the model, Fig. 1).

The relative size of the transition deme (α_{T}) will influence the intensity of these migration flows. A relationship between p_{T}, T_{T}, μ and α_{T} can be calculated if we apply a reciprocity rule to the number of individuals migrating from one deme to another. If we consider that there is the same number of migrants transiting from one main deme (say deme 1) to the transition deme than vice-versa, we get:

$$\left(\frac{1}{2.T_{\mathrm{T}}}\right) \times K_{\mathrm{T}} = (2.T_{\mathrm{T}}.p_{\mathrm{T}}.\mu) \times K_1 \tag{4}$$

Together with the relationship $K_{\mathrm{T}} = \alpha_{\mathrm{T}}.K$, we can calculate:

$$(p_{\mathrm{T}}, T_{\mathrm{T}}) = \begin{cases} \left(1\ ,\ \sqrt{\frac{\alpha_{\mathrm{T}}}{2(1-\alpha_{\mathrm{T}})\mu}}\right), & \text{if } \alpha_{\mathrm{T}} > \frac{2\mu}{1-2\mu} \\ \left(\frac{\alpha_{\mathrm{T}}}{2(1-\alpha_{\mathrm{T}})\mu}\ ,1\right), & \text{otherwise} \end{cases} \tag{5}$$

Therefore, with a large transition deme (high α_{T}), lineages of migrants leaving the main demes ($p_{\mathrm{T}} = 1$) experiment on average $T_{\mathrm{T}} > 1$ generations in the transition deme. With a small transition deme (low α_{T}), only a fraction $p_{\mathrm{T}} < 1$ of those migrants experiments on average one generation in the transition deme ($T_{\mathrm{T}} = 1$).

Reproduction

During the reproduction phase, each female is courted by a series of N_{male} males randomly chosen in her deme. We assume that males can mate more than once, do not exhibit any preferences and try to court all the females they encounter. On the contrary, we consider that a female can only mate once during her lifetime. Therefore, at each encounter, she evaluates the male and she decides to mate or not accordingly. If a choosy female does not choose to mate with any of the N_{male} males encountered, she does not mate at all.

To evaluate a potential mate, a female is using the male ecological trait as the basis of choice. Depending on her choosiness trait c and on the difference between their ecological traits, the female will choose to mate with a probability Ψ following a 'matching rule' (Kopp et al., 2018). We use the preference function defined by Carvajal-Rodriguez and Rolán-Alvarez (2014) (Fig. S1). It satisfies basic properties – monotonicity, proportionality and symmetry –, which are necessary to avoid some modelling artifacts during the evolution of choosiness:

$$\psi(c, x_f, x_m) = \begin{cases} \exp\left(\frac{-c^2\left(x_f - x_m\right)^2}{\sigma_c^2}\right), & \text{if } c > 0 \\ \exp\left(\frac{-c^2\left(|x_f - x_m| - 1\right)^2}{\sigma_c^2}\right), & \text{otherwise} \end{cases} \tag{6}$$

With x_f and x_m the ecological traits of the female and the male respectively, c the female choosiness trait and σ_c the strength of the preference, which makes the mating probability more or less sensitive to c. Mating is random if $c = 0$, whereas it is positive assortative if $c > 0$. A female with choosiness $c > 0$ would mate preferentially with a male matching her own ecological trait – i.e., $c > 0$ indicates her readiness to reject males that do not match her ecological trait.

After mating, the number of offspring is chosen randomly and independently from a Poisson distribution with parameter b – i.e., the average number of offspring per female. The sex of each offspring is chosen randomly assuming a balanced sex ratio. At the genetic level, we assume independent segregation. At each locus, one maternal allele and one paternal allele are randomly chosen. Mutation can occur at each allele determining trait k ($k \in \{c, x\}$) with a probability m_k. The mutant allele value is drawn from a normal distribution centered on the parent allele value with deviation $s_k\sqrt{2L_k}$ with s_k^2 the mutational variance at the trait level and L_k the number of loci determining the trait k (Aguilée et al., 2013). Mutation on each neutral locus occurs with probability m_n, in which case a random allele is chosen from the 50 possible alleles.

As we assume non-overlapping generations, all adult individuals are dying after their reproduction phase, and the population is then entirely reconstituted from offspring.

Numerical simulations and summary statistics

Our initial conditions correspond to a secondary contact scenario, where all individuals are specialists within their environment. All individuals have an ecological trait $x = 0$ in deme 1 and $x = 1$ in deme 2. In the transition deme, half of the population have an ecological trait $x = 0$ while the other half have $x = 1$. All individuals have a choosiness trait $c = 0$ – i.e., mating is initially random. All unlinked neutral loci are randomly picked, therefore there is no genetic differentiation at neutral loci among differentiated populations.

Over the course of each simulation, we record the distribution of the ecological and choosiness traits, both in the main demes and in the transition deme. To assess the level of gene flow in our model, we measure the frequency of strong nonrandom mating and the genetic differentiation in neutral marker traits between ecotypes. We arbitarily define two ecotypes based on individuals' ecological traits x; one ecotype is characterized by all individuals with $x \leq 0.5$ and the other ecotype by all individuals with $x > 0.5$. Considering populations from the two main demes as different ecotypes leads to the same results (Fig. S2). To detect strong nonrandom mating caused by choosiness, we use a simple statistics $\Gamma = \frac{\psi_s - \psi_d}{\psi_s}$, where ψ_d and ψ_s are the mean preference scores ψ between two individuals from different and the same ecotype respectively (following Thibert-Plante and Gavrilets, 2013). Γ reflects the strength of reproductive isolation between ecotypes via nonrandom mating. Specifically, we consider that *strong nonrandom mating* has evolved if $\Gamma > 0.99$, so that the probability of mating between individuals from different ecotype is at least 100 times smaller than that between two individuals from

the same ecotype (irrespective of their localisation). To assess the level of reproductive isolation among ecotypes, we compute the genetic differentiation F_{ST} statistics at neutral loci: $F_{\mathrm{ST}} = \frac{\Pi_s - \Pi_d}{\Pi_s}$. Π_d and Π_s represent the average number of pairwise differences in neutral loci between two individuals sampled from different ecotypes (Π_d) or from the same ecotype (Π_s). Therefore, in our numerical simulations, the F_{ST} index between ecotypes reflects the strength of reproductive isolation between ecotypes.

In numerical simulations, we vary the relative size of the transition deme ($\alpha_{\mathrm{T}} = \{0, 0.1, 0.2\}$), the strength of selection ($\sigma_{\mathrm{s}} = \{0.2, 0.3, 0.4, 0.5\}$) and the maximum number of males encountered per female ($N_{\mathrm{male}} = \{1, 2, 4, 8, 16, 32, 64, \infty\}$). We constrain the range of α_{T} and σ_{s} analyzed to prevent the loss of polymorphism at the ecological locus (by genetic swamping; Lenormand, 2002) or the formation of a monomorphic transition deme at equilibrium (Fig. S3). The other parameters are fixed: $K = 10,000$, $\mu = 0.01$, $\sigma_{\mathrm{c}} = 0.2$, $b = 5$, $L_x = 4$, $L_c = 1$, $m_x = m_c = 5.10^{-2}$, $s_x = s_c = 0.002$, $L_n = 20$, $m_n = 10^{-4}$. Note that we do not aim to perform an exhaustive study of the factors affecting the evolution of choosiness in parapatry (see more complete sensitivity analyses in Thibert-Plante and Gavrilets, 2013; Cotto and Servedio, 2017). We intentionally choose optimal values of parameters for choosiness to evolve without loss of polymorphism (secondary contact scenario, single locus coding for the choosiness trait, few loci coding the ecological trait, high carrying capacity, high mutation rate) and we test the effects of weak (if N_{male} is intermediate) or strong (e.g., if $N_{\mathrm{male}} = 1$) costs of choosiness on the evolution of choosiness. The high mutation rate implemented ($m_x = m_c = 5.10^{-2}$) is offset by a small expected phenotypic variance at those traits ($s_x = s_c = 0.002$). This allows us to speed up the evolution of choosiness, while assessing the choosiness state reached at equilibrium. Simulations end after 100,000 generations and 30 replicates are done for each combination of parameters.

Selection gradient

To characterize the direction of selection on choosiness in each deme, we numerically determine local selection gradients, defined by Geritz et al. (1997) as:

$$D_\lambda(c) = \left.\frac{\partial \lambda\left(c, \tilde{c}\right)}{\partial \tilde{c}}\right|_{\tilde{c}=c} \tag{7}$$

With $\lambda\left(c, \tilde{c}\right)$ the invasion fitness – i.e., the reproductive success – of a mutant with a choosiness trait $\tilde{c}$ in a population with choosiness trait c. D_λ describes how, in the vicinity of the resident mating strategy, a rare mutant's strategy influences its (invasion) fitness. Choosiness (c) increases if D_λ is positive, and decreases if D_λ is negative. A convergence-stable intermediate equilibrium is achieved if $D_\lambda = 0$ and $\frac{\partial D_\lambda}{\partial c} < 0$.

To determine numerically $D_\lambda(c)$, we consider a population with choosiness trait c at its ecological equilibrium. We implement 10% of mutants with a choosiness trait $\tilde{c} = c + 0.1$, such that the alleles coding for $\tilde{c}$ are in

linkage disequilibrium with the ecological trait (this linkage typically arises after 3 generations and is assessed preliminary). After viability selection and reproduction, we measure the local frequencies of the allele coding for $\tilde{c}$ in the population and use them as a proxy of the invasion fitness $\lambda(c, \tilde{c})$. With analog simulations, we estimate $\lambda(c, c)$. We then calculate the local selection gradient as:

$$\hat{D}_{\lambda}(c) = \frac{\lambda(c, \tilde{c}) - \lambda(c, c)}{\tilde{c} - c} \tag{8}$$

To characterize the direction of selection on choosiness in the entire population, we estimate the global selection gradient as a weighted average of local selection gradients (calculated in the three demes). Following Wickman et al. (2017), the weights are the square of the local population densities. Indeed, the intuitive approach of averaging selection across all members of the populations is wrong. Under weak selection, the resulting selection gradient takes the form of a weighted sum of selective effects, where the weights are the class frequencies and the reproductive values calculated in the resident population (Taylor and Frank, 1996). The reproductive value in a given class is the long-term contribution of individuals in this class to the future of the population relative to the contribution of other individuals in the population (Fisher, 1930). The reproductive value of individuals in a locality with high density is higher than in locality with low density. Therefore, selection gradients at points in space where the population is abundant are disproportionately stronger than where it is rare. If the global selection gradient for choosiness is positive (resp. negative), stronger (resp. weaker) choosiness should evolve in the population. Additionally, we also decompose local selection gradients to infer how the frequency of the choosier allele change as a result of viability selection (via viability costs) and sexual selection (via differential mating) in each deme.

Note that implementing a smaller initial fraction of mutant individuals and a smaller mutation size considerably increases the number of replicates (more than billions) and the computer runtime necessary to detect local selection in the main demes. Likewise, in simulations, different choosiness alleles can be present in the population at a given time step and the method computed here may look unrealistic in this regard. Nonetheless, the evolutionary dynamics of choosiness predicted by the global selection gradient predicts well the choosiness state reached at equilibrium in our numerical simulations. We can then confidently use these statistics to dissect the selective forces acting on choosiness.

RESULTS

A cost of choosiness can favour the evolution of choosiness in parapatry

In the simulations, the initial population splits into two ecologically-specialized subpopulations, hereafter called ecotypes, distributed along the ecological gradient. Over a large range of parameters α_{T} and N_{male} (relative size of the transition deme and maximum number of males encountered per female, respectively), populations evolve a positive choosiness trait – i.e., females mate preferentially with ecologically-similar males – (Fig. 2a), which favours the ecological differentiation between ecotypes (Fig. 2b). Therefore, strong nonrandom mating between ecotypes can evolve (Fig. 2c), reducing gene flow and leading to genetic differentiation at neutral loci ($F_{\mathrm{ST}} > 0$, Fig. 2d). Since reproductive isolation reduces gene flow between ecotypes, the F_{ST} index reflects the strength of reproductive isolation between ecotypes.

In simulations with intermediate N_{male} values, choosy females risk to remain unmated, but despite this weak cost of choosiness, assortative mating evolves and reduces gene flow between ecotypes (high F_{ST}, Fig. 2d). Interestingly, with such weak cost of choosiness, stronger choosiness evolve (Fig. 2a), leading to stronger assortative mating (Fig. 2c), than in simulations with no cost of choosiness ($N_{\mathrm{male}} = \infty$; when all females eventually find a mate). However, if the cost of choosiness is extremely strong ($N_{\mathrm{male}} = 1$), choosiness does not evolve and gene flow is unrestricted.

The effects of a cost of choosiness depend on the strength of disruptive viability selection (inversely proportional to σ_{s}). If viability selection is very strong (resp. very weak), choosiness is strongly (resp. weakly) favoured, so a weak cost of choosiness have no effect on the evolution of choosiness (for $\sigma_{\mathrm{s}} \leq 0.2$ and $\sigma_{\mathrm{s}} \geq 0.5$, Fig. S4). The extent of the effects of the cost of choosiness also depends on the relative size of the transition deme (α_{T}). Under weak viability selection, a cost of choosiness strongly favours the evolution of choosiness along shallow ecological gradients (for $\alpha_{\mathrm{T}} > 0$ if $\sigma_{\mathrm{s}} \geq 0.4$, Fig. S4). Under strong viability selection, a cost of choosiness strongly favours the evolution of choosiness along steep ecological gradients (for $\alpha_{\mathrm{T}} = 0$ if $\sigma_{\mathrm{s}} \leq 0.3$, Fig. S4). Consequently, if choosiness is costly, strong choosiness may evolve along steep ecological gradients (with a small transition deme) and not along shallow ecological gradients (with a large transition deme) (e.g., for $N_{\mathrm{male}} = 2$ in Figs. 2 and S4).

Note that we get similar results if we vary the absolute size of the transition deme, instead of its relative size (Fig. S5).

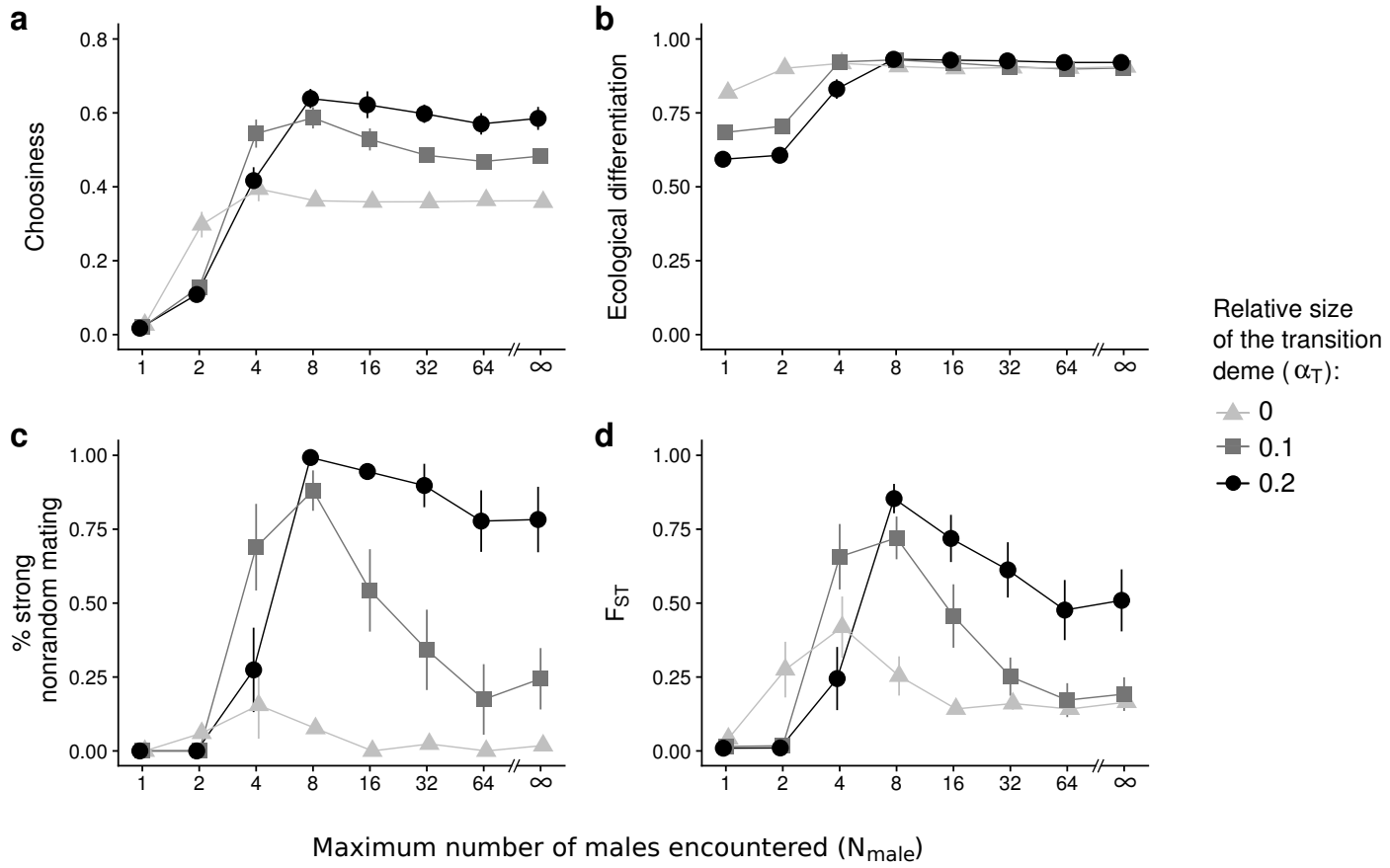

Figure 2: Ecological differentiation, nonrandom mating caused by choosiness and genetic differentiation with different geographical contexts and maximum numbers of males encountered per female. Statistics are measured from the traits and loci of individuals belonging to the two ecotypes (with ecological traits $x \leq 0.5$ or $x > 0.5$). After equilibrium has been reached (after $100,000$ generations), we record the choosiness in the population (a) and differences in ecological traits between ecotypes (b). To evaluate the strength of reproductive isolation, we measure both the percentage of runtime with strong nonrandom mating (c) and the genetic differentiation at neutral loci (F_{ST}) (d). For each combination of parameters ($\alpha_{\mathrm{T}}, N_{\mathrm{male}}$), the point and the error bars respectively represent the mean value of the statistic and its 95% confidence intervals. The x-axis is plotted on a logarithmic scale. $\sigma_{\mathrm{s}} = 0.4$.

Selection on choosiness

We aim at understanding how the cost of choosiness affects selection acting on choosiness. We here dissect in each deme the different selective forces (viability and sexual selection) acting on choosier alleles (for $\alpha_{\mathrm{T}} = 0.1$, Fig. 3). Note that we can draw the same conclusions from the selection gradients obtained in ecological settings with a different relative size of the transition deme ($\alpha_{\mathrm{T}} = 0$ or 0.2; see Figs. S6 and S7).

With no cost of choosiness ($\mathbf{N}_{male} = \infty$). – We first consider the situation where all females eventually find a mate (black points in Figs. 3 and 4). In the transition deme, alleles coding for strong choosiness are

associated with locally favoured alleles at the ecological trait loci (i.e., with alleles coding for extreme ecological phenotypes x close to 0 or 1) (linkage disequilibrium caused by selection, Fig. 4a,c). Therefore, selection on the ecological trait indirectly acts on choosiness via this linkage disequilibrium. Positive frequency-dependent sexual selection – i.e., high mating success of males whose ecological phenotype is in high frequency locally – weakly inhibits or favours the evolution of choosiness in the transition deme, depending on the distribution of ecological phenotypes (Fig. 3a). More importantly, disruptive viability selection – i.e., low survival of males with intermediate ecological phenotypes – strongly favours the evolution of choosiness in the transition deme (Fig. 3c). In the transition deme, selection therefore favours the evolution of strong choosiness (Fig. 3e).

In the main demes, alleles coding for strong choosiness are associated with locally favoured alleles at the ecological trait loci (here, with alleles coding for the extreme ecological phenotype that is locally favoured) (Fig. 4i). Just like in the transition deme, positive frequency-dependent sexual selection weakly inhibits or favours the evolution of choosiness, depending on the distribution of ecological phenotypes (Fig. 3b). More importantly, alleles coding for strong choosiness are strongly associated not only with with locally *favoured* alleles but also with locally *unfavoured* alleles at the ecological trait loci (i.e., leading to a very weak association with alleles coding for an intermediate ecological trait, Fig. 4g-i). Indeed, females with a rare ecological phenotype mostly mate assortatively if they are very choosy (whereas they mostly mate with locally adapted males, because they are common, if they are only weakly choosy). This linkage leads to the removal of alleles coding for strong choosiness by viability selection (Fig. 4j). In other words, viability selection indirectly inhibits the evolution of strong choosiness (Fig. 3d). In main demes, selection therefore favours the evolution of partial choosiness (Fig. 3f).

In the absence of cost of choosiness, strong choosiness is favoured in the transition deme (Fig. 3e) but not in the main demes (via indirect viability selection; Fig. 3f). Overall, the global selection gradient predicts that for $\alpha = 0.1$, only partial choosiness can evolve (Fig. 3g). This explains why in our numerical simulations, partial choosiness evolves if the transition deme is small, whereas strong choosiness evolves if the transition deme is large (Fig. 2). These results without a cost of choosiness are consistent with the results of Cotto and Servedio (2017).

With a cost of choosiness ($\mathbf{N}_{male} \neq \infty$). – A cost of choosiness (when choosy females risk to remain unmated) induces sexual selection inhibiting choosiness via differential *female* mating success (Fig. 3a-b). This additional sexual selection pressure is therefore distinct from positive frequency-dependent sexual selection caused by differential *male* mating success.

In the transition deme, a strong cost of choosiness induces very strong sexual selection inhibiting the evolution of choosiness (e.g., for $N_{\text{male}} = 2$), whereas a weak cost of choosiness induces weak sexual selection compared to the strength of viability selection (e.g., for $N_{\text{male}} = 8$) (Fig. 3a). Additionally, indirect viability

selection strongly favours the evolution of choosiness in the transition deme (Fig. 3c). Therefore, only a strong cost of choosiness can inhibit the evolution of choosiness in the transition deme (Fig. 3e).

In the main demes, a cost of choosiness induces sexual selection inhibiting the evolution of choosiness (Fig. 3b). A strong cost of choosiness (e.g., for $N_{\text{male}} = 2$) does not induce particularly strong sexual selection because locally adapted females often find a matching mate at the first encounter (Fig. 3b). Interestingly, a cost of choosiness also modifies the local population assembly on which viability selection acts. In particular, choosy females with a rare ecological phenotype have little chance to find preferred (matching) males and often remain unmated. Consequently, a cost of choosiness weakens the association between alleles coding for strong choosiness and locally *unfavoured* alleles (in low frequency) at the ecological trait loci (Fig. 4g) and remove viability selection, which indirectly inhibits strong choosiness in main demes (as explained in the previous section) (Figs. 3d and 4j). Therefore, in main demes, a cost of choosiness induces additional sexual selection and removes viability selection, both of which inhibit choosiness. Overall, in the main demes, a strong cost of choosiness inhibits the evolution of choosiness (for $N_{\text{male}} = 2$, Fig. 3f). A weak cost of choosiness, however, inhibits the evolution of intermediate choosiness (via additional sexual selection) but favours the evolution of strong choosiness (via the removal of indirect viability selection) (for $N_{\text{male}} = 8$, Fig. 3f).

With a strong cost of choosiness, choosiness is deleterious along the ecological gradient (for $N_{\text{male}} = 2$, Fig. 3e-f). With a weak cost of choosiness, however, choosiness is favoured in the transition deme (via indirect viability selection which overcome sexual selection caused by the cost of choosiness across the selection gradient) and indirect viability selection no longer inhibits the evolution of strong choosiness (for $N_{\text{male}} = 8$, Fig. 3e-f). This explains why a weak cost of choosiness can favour the evolution of strong choosiness in our simulations (Fig. 2).

Moreover, unlike in main demes, a strong cost of choosiness induces strong sexual selection against choosiness in the transition deme (for $N_{\text{male}} = 2$, Fig. 3b). This explains why, if choosiness is very costly, strong choosiness can evolve along steep ecological gradients (with a small transition deme) but not along shallow ecological gradients (with a large transition deme) (Fig. 2).

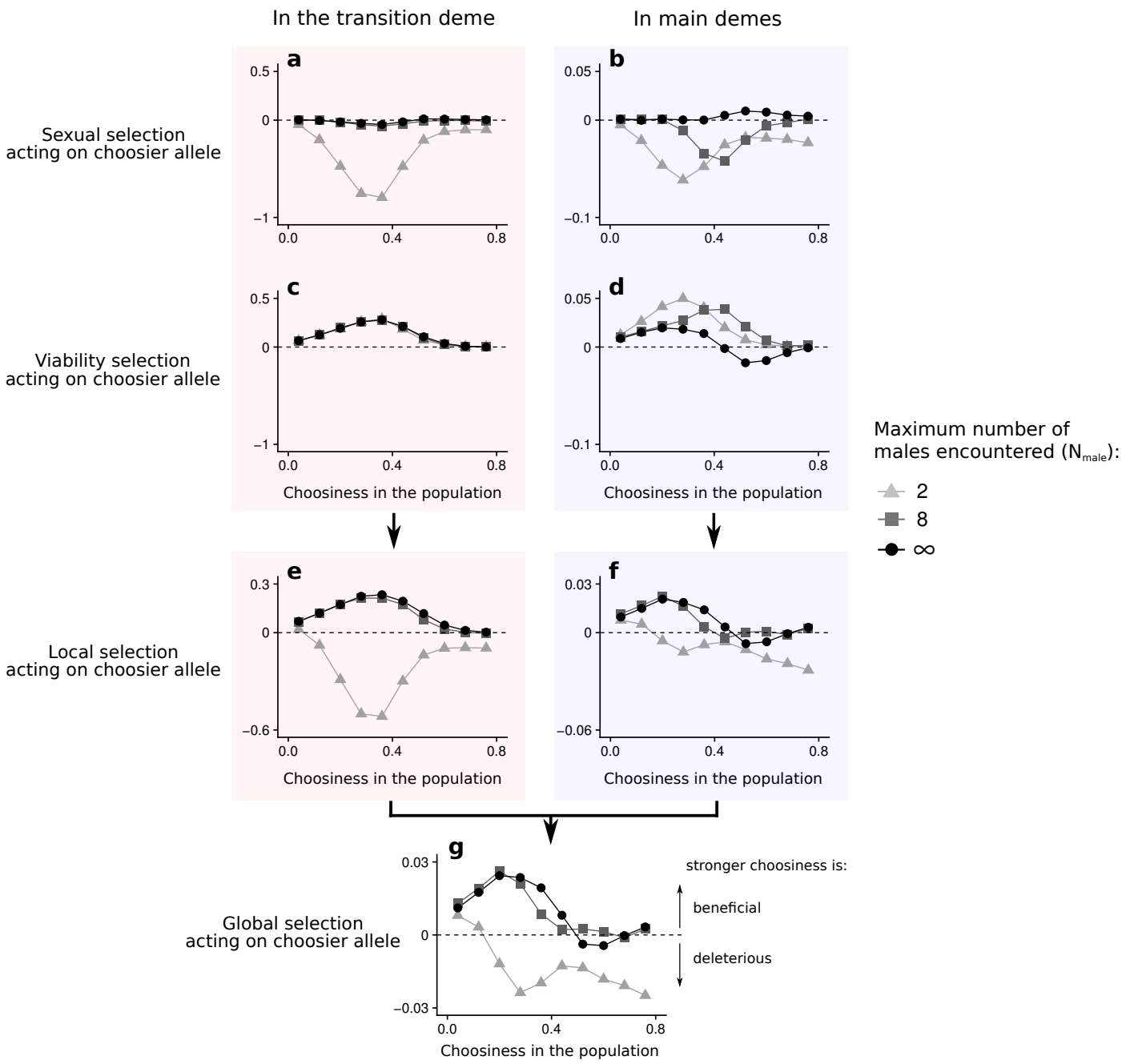

Figure 3: Local selective forces acting on choosiness in the transition deme (a, c, e) and in main demes (b, d, f), and global selection acting on choosiness (g). After the introduction of 10% of mutants with a choosier allele, local selection gradients are measured as changes in frequencies of these choosier alleles over one generation (e-f). Sexual selection (resp. viability selection) acting on alleles coding for stronger choosiness is measured as their change in frequencies during the reproduction phase (resp. viability selection phase) (a-d). Following Wickman et al. (2017), we estimate the global selection gradient as a weighted average of local selection gradients (g). $\sigma_s = 0.4$, $\alpha_T = 0.1$.

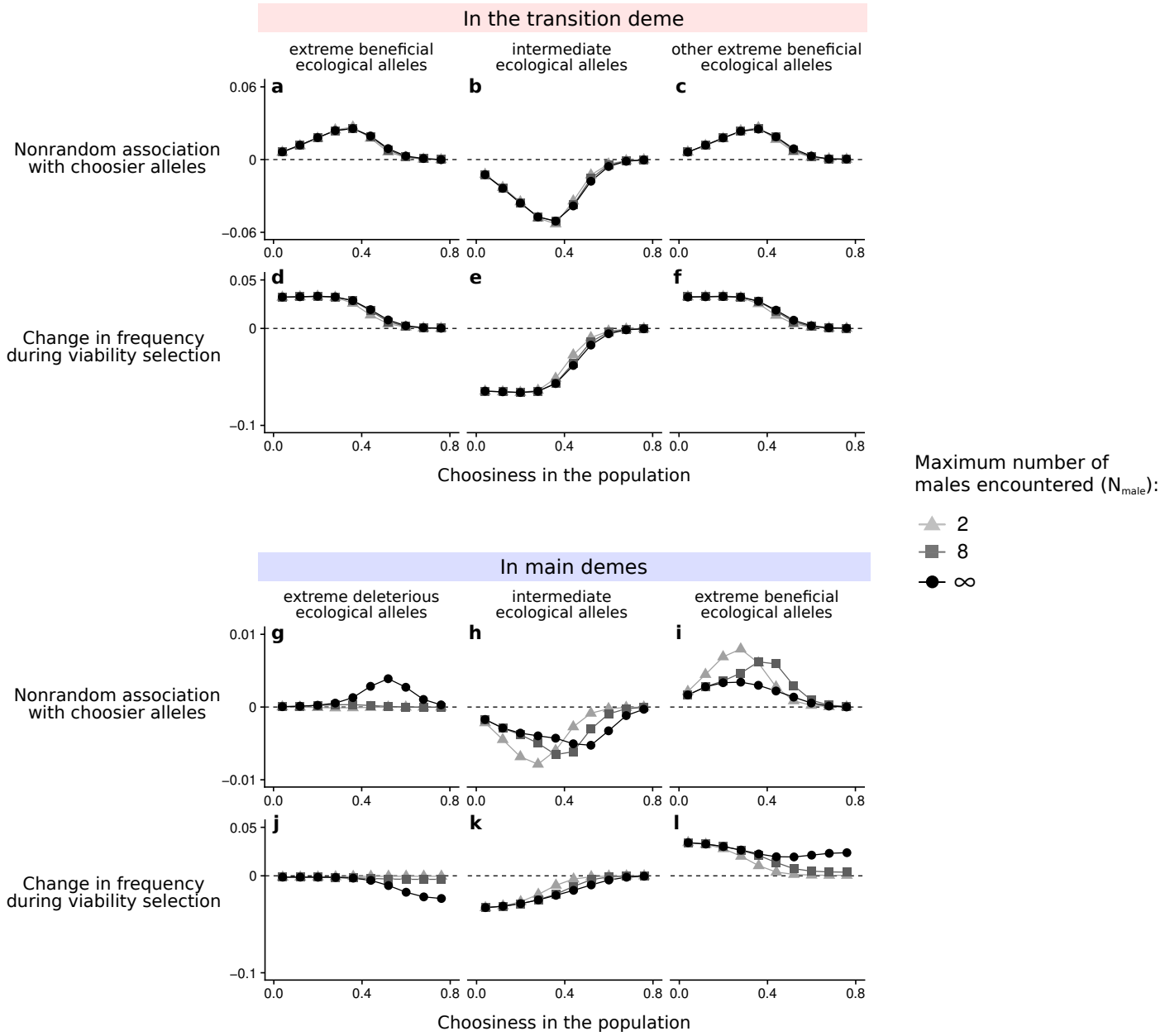

Figure 4: Linkage disequilibrium between choosiness and ecological loci after reproduction and change in frequency of ecological categories via direct viability selection in the transition deme (a-f) or in main demes (g-l). Individuals are categorized according to their ecological alleles (coding for: $x < 0.33$, $0.33 \leq x \leq 0.66$ or $x > 0.66$). Three generations after implementing mutant alleles at the choosiness locus, linkage disequilibrium between choosiness and ecological loci is measured as the nonrandom association of alleles coding for stronger choosiness with each ecological category after reproduction. We also measure the change in frequency of each ecological category during viability selection. Altogether, these graphs allow us to infer how viability selection indirectly acts on choosiness via linkage disequilibrium. In particular, for $N_{\text{male}} = \infty$, indirect viability selection inhibits the evolution of choosiness in main demes via a positive linkage between alleles coding for stronger choosiness and locally unfavoured alleles at the ecological locus. This positive linkage vanishes for $N_{\text{male}} \neq \infty$, and so does indirect viability selection inhibiting strong choosiness. $\sigma_{\text{s}} = 0.4$, $\alpha_{\text{T}} = 0.1$.

DISCUSSION

In a parapatric context of speciation, the evolution of assortative mate choice is driven by non-intuitive selective forces. We showed that along an ecological gradient, a cost of choosiness (i.e., associated with strong assortative mate preferences), which is mainly incurred by immigrants, can *favour* the evolution of choosiness in parapatry. This counterintuitive prediction relies on the effects of costs of choosiness on local sexual and viability selection acting in different localities along the gradient. Based on the predictions of our model, the width of the hybrid zone, the strength of fitness costs, and the ecology of mating all prove to be important when examining the likelihood of speciation along ecological gradients.

Previous models of parapatric speciation have not accounted for the possibility that females may suffer from delayed mating if they are are too choosy (Kawata et al., 2007; Leimar et al., 2008; Ispolatov and Doebeli, 2009; Servedio, 2011; Cotto and Servedio, 2017), while this 'cost of choosiness' should be high for female immigrants in foreign environments (as argued by Servedio and Hermisson, 2020). In our study, we model the deleterious effect of delayed mating as a risk of remaining unmated (a situation observed in nature; Reynolds and Gross, 1990; Milinski et al., 1992; Heubel et al., 2008; Scott et al., 2020). We show that in parapatry this cost of choosiness induces sexual selection which inhibits the evolution of choosiness just like in sympatry (Bolnick, 2004; Schneider and Bürger, 2006; Bürger et al., 2006; Kopp and Hermisson, 2008). Interestingly, this sexual selection pressure also removes viability selection, which inhibits the evolution of strong choosiness.

At the ends of the ecological gradient, ecotype frequencies are unbalanced so being choosy mostly delay mating of female immigrants, which also suffer viability costs. Sexual selection therefore weakens linkage disequilibrium between alleles coding for strong choosiness and locally *unfavoured* alleles at the ecological trait loci. Consequently, after a reproduction phase with choosy females (mostly immigrants) suffering a fitness cost, viability selection no longer removes alleles coding for strong choosiness via linkage disequilibrium. By removing the negative effect of viability selection on choosiness, a cost of choosiness can therefore favour the evolution of strong choosiness. At the ends of the ecological gradients, sexual selection therefore changes the frequencies on which viability selection acts (as shown without a cost of choosiness by Cotto and Servedio, 2017); this leads to this counterintuitive effect of the costs of choosiness on the evolution of choosiness.

Local selection on choosiness differs between the centre and the tails of the gradient because ecotypes coexist in the former and not in the latter. A weak cost of choosiness (for $N_{\text{male}} = 8$ in our simulations) does not change net selection on choosiness in the centre of the gradient, because sexual selection induced by this cost is always offset by strong indirect viability selection favouring choosiness. On the contrary, a weak cost of choosiness affects net selection acting on choosiness at the ends of the gradients. In particular, sexual selection induced by such cost removes indirect viability selection that inhibits choosiness. Consequently, the overall effect of a weak

cost of choosiness may change according to the relative importance of the transition zone and the main demes, where selection on choosiness may act in opposite directions depending on the strength of viability selection. In other words, the abruptness of the ecological gradient – i.e., the extent of range overlap between divergent ecotypes – and the fitness effects of ecological adaptation determine the evolution of choosiness when the cost of choosiness is weak.

Without a cost of choosiness, range overlap between ecotypes has been shown to affect the evolution of assortative mating in parapatry. In our model, high range overlap between ecotypes (i.e., shallow gradient) leads to the loss of polymorphism at the ecological trait because of positive frequency-dependent sexual selection (Kirkpatrick and Nuismer, 2004; Otto et al., 2008; Cotto and Servedio, 2017), while small range overlap gives scope for indirect viability selection inhibiting strong choosiness (Servedio, 2011; Cotto and Servedio, 2017). Without a cost of choosiness, reproductive isolation between divergent ecotypes is therefore the strongest for intermediate ecological gradients (as previously shown by Doebeli and Dieckmann, 2003; Cotto and Servedio, 2017). We here show that, if choosiness is costly in term of mating success, strong reproductive isolation does not necessarily evolve when the ecological gradient is of intermediate steepness. Unlike in the centre of the gradient, a strong cost of choosiness does not induce particularly strong sexual selection in the tails of the gradient because locally adapted females often find a matching mate at the first encounter. Therefore, if choosiness is very costly, strong levels of reproductive isolation can evolve when there is no range overlap (i.e., for very steep gradient). The ecology of mate finding and mating decision is therefore of prime importance to predict how range overlap would affect the evolution of assortative mating.

Hybrid zones are transition zones between the geographical ranges of closely related taxa where hybrids are produced (Hewitt, 1988). Hybrid zones are often represented as narrow strips separating much larger regions in which the two taxa reside, like in our model. When the gradient is environmental (adaptation to resources which are unevenly distributed for instance), the width of a hybrid zone depends on the change in environmental conditions. However, other hybrid zones are 'tension zones' maintained by a balance between dispersal and selection against hybrids (Slatkin, 1973; Mallet and Barton, 1989) and the width of such tension zones therefore results from this balance. Mallet et al. (1990) have used the width of multiple tension zone to estimate gene flow between races of *Heliconius erato* and those of *Heliconius melpomene*. Yet, in this study, gene flow was approximated by dispersal estimates, whereas actual gene flow also depends on pre- and post-zygotic reproductive barriers. We hope to stimulate similar empirical investigations on multiple hybrid zones, but this time precisely testing the link between hybrid zone width (or the steepness of the environmental gradient) and actual gene flow (that could be assessed from the F_{ST}). To our knowledge, only Seehausen et al. (2008) empirically showed such link between gradient steepness and gene flow (approximated by differentiation). Specifically, they showed that differentiation in cichlid fishes does not occur on very steep environmental light

gradients. In that case, our predictions suggest that cost of choosiness may be absent or weak. Otherwise, differentiation would have been favoured on very steep gradient. In the light of our theoretical predictions, similar empirical investigations would considerably strengthen our understanding of the role of the spatial dimension of ecological changes in parapatric speciation.

We acknowledge that our representation of space is still very simplified, since distributions of ecotypes along ecological gradients can form a diversity of patterns, from continuous gradations from one ecotype to another to patchy distributions of ecotypes called mosaic hybrid zones (Harrison and Larson, 2016). In a context of steep ecological gradient, our results should not depend on the ecotype distribution inside the transition region at a smaller scale. On the contrary, if the transition region is large, our predictions may not be robust to a context of mosaic hybrid zone. In that case, the relative proportion of the two taxa is always skewed in favour of one or the other taxon, even in the transition region. Therefore, local selection acting in each 'patch' of the mosaic may be similar to the one acting at the tails of the gradient where ecotype frequencies are unbalanced. The predictions of our model suggest that, under a context of mosaic hybrid zone, assortative mating should readily evolve if choosiness is costly. It may explain why reproductive isolation between *Timema cristinae* (stick insect) ecotypes – distributed in such mosaic hybrid zone – is incomplete in that complete speciation has not occured (assuming that the cost of choosiness is weak or absent) (Nosil, 2007).

In a recent theoretical study, Irwin (2020) explicitly considered a diverging population distributed along a 'tension zone' with all individuals having the same level of choosiness. He showed that costs of choosiness can prevent blending between incipient species, and can maintain a parapatric distribution. This adds support to the idea highlighted in our study that costs of choosiness can promote parapatric speciation, this time by maintaining the population distribution along the ecological gradient. We did not consider the feedback of the evolution of choosiness on the width of the hybrid zone; whether this effect is strong enough as choosiness evolves is an open question that warrants further theoretical investigation.

In the light of the predictions of our model, the maximum number of males that females can encounter in their lifetime is a key factor for the evolution of reproductive isolation along ecological gradients. Females have a limited time in which to mate, because of such factors as environmental constraints on the timing of reproduction and predation risks associated with searching, and usually cannot sample all males within a population (Morris, 1989; Wagner, 1998). However, it is difficult to estimate how many males females can evaluate in nature. The number of males evaluated by females prior to breeding has long been the best estimate available (Bolnick and Fitzpatrick, 2007). However, movement pattern has also been acknowledged to determine the potential for female mate choice to drive sexual selection (Dunn and Whittingham, 2007; Duval and Kapoor, 2015). Therefore, empirical data on how free-living females move among and select mates may therefore provide information on potential costs of choosiness. For instance, Kamath and Losos (2018)

managed to estimate encounters between potential mates from mark-recapture data of male and female *Anolis sagrei* lizards. Applying this method along ecological gradients on different ecotypes may provide good estimates of potential costs of choosiness. Indeed, from the estimation of encounter estimates within vs. between ecotypes, the risk of remaining unmated associated to choosiness may easily be assessed. In our model, females do not adjust their level of choosiness in response to the abundance of males from their own type (as shown by Willis et al., 2011). In this case, choosy immigrant females would keep mating with local common males and evolution of strong choosiness would not inhibit hybridization between ecotypes (as noted by Kopp and Hermisson, 2008). Such choosiness subject to adjustement may be best considered partial rather than strong.

Overall, our theoretical model sheds new light on the role of spatial dimension of ecological change in parapatric speciation. We show that, along ecological gradients, sexual selection pressures can have very counterintuitive effects on trait evolution by locally affecting the genotypic frequencies on which viability selection acts. Along ecological gradients, a cost of choosiness (when choosy females may risk to remain unmated) can even favour the evolution of choosiness and subsequent reproductive isolation. Consequently, the effect of spatial dimension of ecological change on speciation also depends on the strength of costs of choosiness. Our study should therefore stimulate further empirical research on the link between hybrid zone width, costs of choosiness and reproductive isolation.

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