

LETTER

Evolution of mate choice and the so-called magic traits in ecological speciation

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Abstract

Non-random mating provides multiple evolutionary benefits and can result in speciation. Biological organisms are characterised by a myriad of different traits, many of which can serve as mating cues. We consider multiple mechanisms of non-random mating simultaneously within a unified modelling framework in an attempt to understand better which are more likely to evolve in natural populations going through the process of local adaptation and ecological speciation. We show that certain traits that are under direct natural selection are more likely to be co-opted as mating cues, leading to the appearance of magic traits (i.e. phenotypic traits involved in both local adaptation and mating decisions). Multiple mechanisms of non-random mating can interact so that trait co-evolution enables the evolution of non-random mating mechanisms that would not evolve alone. The presence of magic traits may suggest that ecological selection was acting during the origin of new species.

Keywords

Adaptation, evolution, ecological speciation, gene flow, magic traits, non-random mating, individual-based simulation.

Ecology Letters (2013) 16: 1004–1013

INTRODUCTION

There are multiple reasons for non-random mating. One is naturally occurring biases in the way potential mates are identified (e.g. if certain colours are more visible or attractive Boughman 2001; Seehausen *et al.* 2008). Such biases in one sex can be exploited by the other sex (Seehausen *et al.* 2008). Morphological or genetic incompatibilities can constraint the range of possible mates (Coyne & Orr 2004). Non-random mating can also increase the likelihood of receiving direct benefits (e.g. food or protection) and obtaining better genes from mates that would increase offspring viability, fertility or attractiveness (Jennions & Petrie 2000). Non-random mating can be mediated by reproduction place and/or time (Kirkpatrick & Ravigné 2002). For example, in many phytophagous insects mating occurs on the host, and evolving host preference results, as a by-product, in non-random mating (Hawthorne & Via 2001). In plants, the flowering time, which itself may be affected by the environment (e.g. soil type), directly controls the patterns of mating. Non-random mating can also be mediated by direct mate choice. A spectacular variety of visual (Andersson 1994; Boughman 2001; Puebla *et al.* 2007; Seehausen *et al.* 2008), chemical (Wyatt 2003), acoustic (Podos *et al.* 2004) and behavioural (Andersson 1994) signals and cues are used, in isolation or in combinations (Møller & Pomiankowski 1993), when mating pairs are formed in natural populations and also in humans (Mautz *et al.* 2013). Non-random mating can be costly (Jennions & Petrie 1997). For example, a female who is too choosy may not mate or a male exhibiting a conspicuous trait preferred by the females may expose himself to a higher predation risk.

Non-random mating contributes to a number of important evolutionary patterns and processes such as the origin of exaggerated traits (Andersson 1994), maintenance of genetic diversity (M'Gonigle *et al.* 2012), local adaptation (Thibert-Plante & Hendry 2009) and speciation (Dieckmann & Doebeli 1999; Servedio 2000; Boughman 2001; Kirkpatrick & Ravigné 2002; Gavrilets 2004; Seehausen *et al.* 2008). In particular, the evolution of non-random mating is crucial for the success of speciation driven by selection for local adaptation in the presence of a locally deleterious gene flow (Schluter 2000). The speciation process is promoted when both natural selection and non-random mating are strong, there is sufficient genetic variation, the number of underlying loci is small, the costs of non-random mating are low, and there is a close association of the traits controlling local adaptation and mating decisions (Gavrilets 2004, 2005). The latter requirement is helpful because of the power of recombination in destroying coadapted combinations of genes (Felsenstein 1981). It can be satisfied if the genes underlying the corresponding traits are tightly linked or have pleiotropic effects. In fact, it has been argued that non-allopatric speciation is most plausible when the phenotypic traits underlying local adaptation are also used in mating decisions – a situation dubbed *magic trait* speciation (Gavrilets 2004, see Maan & Seehausen 2011; Servedio *et al.* 2011; Smadja & Butlin 2011 for more recent discussions, critiques and extensions of this notion). At the same time, there is plenty of theory showing that biases in mating preferences can overcome natural selection and result in the evolution of maladaptive traits (Andersson 1994) and that speciation with gene flow is possible even if the genes underlying relevant traits are completely unlinked and the traits controlling local adaptation and mating pat-

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terns are completely independent (Dieckmann & Doebeli 1999; Kondrashov & Kondrashov 1999).

On the empirical side, a number of 'magic traits' have been known for some time including size in sticklebacks (Nagel & Schluter 1998), colour in *Heliconius* butterflies (Jiggins *et al.* 2006), colour in *Hypoplectrus* coral reef fishes (Puebla *et al.* 2007) and beak morphology in Darwin's finches (Podos *et al.* 2004). However, the common perception has been that magic traits are rare in nature (Møller & Jennions 2001; Gavrillets 2004). Surprisingly, a recent survey suggests that magic traits are quite common (Servedio *et al.* 2011).

Although a variety of different mechanisms of non-random mating have been studied theoretically (Dieckmann & Doebeli 1999; Servedio 2000; Kirkpatrick & Ravigné 2002; Gavrillets 2004; Otto *et al.* 2008; Proulx & Servedio 2009; van Doorn *et al.* 2009), there are still major gaps in our understanding of how different phenotypic traits become co-opted for mating decisions, how long it takes, and what are the resulting evolutionary patterns. One of the reasons is that the conclusions of different models are not easy to compare because of the differences in implementation and assumptions. Moreover, most models postulate a particular mechanism of non-random mating and then study its evolutionary consequences rather than look at how phenotypic traits become used in mating decision. Finally, existing models allow only for a single mechanism of non-random mating to be present, while in nature multiple traits, cues and factors are involved in mating decisions (Candolin 2003). It is unclear if single-trait results generalise to multiple traits because of the possibility of between-trait interactions. Our goal here is to consider multiple mechanisms of non-random mating simultaneously within a unified modelling framework in an attempt to understand better which are more likely to evolve and be observed in natural populations that have undergone, or are going through, the process of local adaptation and ecological speciation. We also seek to explain why 'magic traits' have proved to be more common than expected. To achieve our goals, we formulate a series of simple mathematical models which we study using intensive stochastic individual-based simulations.

MATERIAL AND METHODS

We model a finite population of diploid individuals with separate sexes. Generations are discrete and non-overlapping. The population is subdivided into two parts (demes) subject to different selection regimes specifying two different ecological habitats (niches). Viability selection is density dependent and acts on a single ecological trait; the optimum trait values differ between the niches. The carrying capacity of the demes is the same and given by parameter K . In each generation, a small fixed proportion π of individuals has an opportunity to disperse to the other deme. The probability of actual dispersal to one or the other deme is controlled by an independent habitat preference trait which can evolve. We separately consider dispersal of offspring and dispersal of adults.

We study the evolution of six different genetically controlled behavioural mechanisms that can lead to non-random mating. These mechanisms are specified by male- and female-expressed traits which evolve as a result of different factors.

(1) With the *ecology-based preference*, there is an ecological trait subject to selection for local adaptation (e.g. size) and females prefer

males with ecological trait values similar to their own ecological trait. Such ecology-based preference was used in a number of studies, for example, (Dieckmann & Doebeli 1999; Thibert-Plante & Hendry 2011a, b)

(2) With *target preference*, female choice is based on the male's ecological trait (e.g. colour) which is under natural selection; females differ in their preferences which are not subject to direct selection. Target preference is commonly used in models of sexual selection (Andersson 1994; Thibert-Plante & Hendry 2009).

(3) With *similarity-based neutral marker trait preference*, there is an additional marker trait expressed in both sexes; the trait is neutral with respect to natural selection; females prefer males with the trait values similar to their own value of the trait (Shaw *et al.* 2011). This mechanism is similar to the ecology-based preference, but involves a neutral rather than selected trait.

(4) With *matching-based neutral marker trait preference*, there are two additional neutral marker traits one of which is expressed in females and another in males; females prefer males with the male-expressed trait values matching their own value of the female-expressed trait. This mechanism is similar to the target preference, but involves a neutral rather than selected trait. The two mechanisms based on neutral marker traits have been previously used in a number of mathematical models (Dieckmann & Doebeli 1999; Kondrashov & Kondrashov 1999; Gavrillets 2004; Gavrillets *et al.* 2007) showing that speciation is possible if strong linkage disequilibrium evolves between selected and neutral loci.

(5) With the *condition-based preference*, males directly express their fitness through a honest indicator. Females prefer males that express indicators of high fitness (van Doorn *et al.* 2009). Note that a male expressing such indicators may still carry locally maladaptive genes if the male is an immigrant.

(6) With *habitat-based preference*, individuals exhibit preferences for different ecological niches but once they enter a particular niche, they mate randomly there (Edelaar & Bolnick 2012). That reproductive isolation can emerge as a result of evolution of habitat preferences is well established both theoretically (Ravigné *et al.* 2009) and empirically (Rice & Hostert 1997).

Note that we do not aim to perform an exhaustive study of non-random mating mechanisms or to offer a comprehensive classification of such mechanisms (Kirkpatrick & Ravigné 2002; Coyne & Orr 2004; Gavrillets 2004; Maan & Seehausen 2011; Servedio *et al.* 2011; Smadja & Butlin 2011). Rather, we look at a subset of related models that can be relatively easily compared and that have been used within the context of ecological speciation, where mate choice is thought to evolve to reduce the deleterious gene flow between populations experiencing divergent ecological adaptation. Other more complex mechanisms of non-random mating have been discussed or could be envisioned which would include learning, plasticity, density dependence, imperfect indicator of fitness or other types of habitat choice (Servedio *et al.* 2009; Edelaar & Bolnick 2012; Webster *et al.* 2012).

We assume that different non-random mating mechanisms are controlled by different evolvable traits, and each trait is controlled by L (between 4 and 8) independent unlinked additive diallelic loci. Mutation is symmetrical and its probability is the same for all loci. For simplicity, we did not include any costs of non-random mating.

We consider three different scenarios of parapatric speciation driven by ecological selection:

(1) In the *secondary contact scenario*, two niches are initially occupied by two locally adapted populations that come into secondary contact via dispersal.

(2) In the *niche invasion scenario*, only one niche is occupied initially by locally adapted individuals when the second niche becomes available for invasion.

(3) In the *adaptive radiation scenario*, both niches are subject to simultaneous invasion of individuals who are not adapted to either of them.

We are interested in whether and what type of non-random mating evolves if mating is random initially (i.e. prior to speciation), how long it takes, what are the effects of different factors and parameters, and, with multiple traits present, what is the typical order of changes in different traits. To determine if non-random mating has evolved, we compare female preferences for a typical immigrant male and a typical native male. For more details on our models and numerical simulations, see Model and Supplementary Information (SI).

MODEL

Individuals differ with respect to an ecological trait x controlling survival in a local environment, a habitat preference trait b controlling dispersal, and several additional traits controlling mating preferences. The traits are scaled to be between 0 and 1 so that changing the number of loci per trait (L) does not change the range of possible phenotypes or the phenotypic distance between two locally adapted phenotypes. However, the mutation effect size decreases with increasing L . Since our focus is on the differences between species rather than, say, on the within-population genetic variation, our scaling is preferential to alternative scalings which would keep the mutation effect size or within-population genetic variation independent of the number of loci.

Selection

Natural selection is density-dependent and spatially heterogeneous. The 'condition' ω of an individual with an ecological trait x in a given environment is defined as

$$\omega = \exp\left(-\frac{(x - \theta)^2}{2\sigma_s^2}\right), \quad (1)$$

where θ is an optimum trait value and parameter σ_s characterises the strength of selection. The optimum θ is equal to 0 in deme 0 and to 1 in deme 1. The condition ω of an individual defines its viability (i.e. the probability to survive to reproduction stage):

$$v = \frac{1}{1 + \left(\frac{b}{2} - 1\right) \frac{N}{\omega K}}, \quad (2)$$

where b is the average number of offspring per female, K is the carrying capacity of the population, and N is the population size. The above equation represents an analogue of the Beverton–Holt model.

Non-random mating

The probability of mating depends on one or more mating trait 'suites'. Each suite of mating traits includes one male trait m and

one or two female traits c and f . In the case of a single suite, the probability of mating is proportional to

$$\psi = \begin{cases} \exp(-(2c - 1)^2 \frac{(f-m)^2}{2\sigma_a^2}) & \text{if } c > 0.5 \\ 1 & \text{if } c = 0.5 \\ 2 - \exp(-(2c - 1)^2 \frac{(f-m)^2}{2\sigma_a^2}) & \text{if } c < 0.5 \end{cases} \quad (3)$$

Mating is positive assortative, random, or negative assortative if $c > 0.5$, $c = 0$, and $c < 0.5$ respectively. The absolute value of c controls the strength of female preferences; parameter σ_a specifies the maximum strength of preferences. Function (3) is a symmetrised version of that used in earlier publications (Dieckmann & Doebeli 1999; Gavrilets *et al.* 2007); for $c \geq 0.5$ (which is the case mostly observed in our simulations), it is qualitatively similar to a preference function introduced recently in Débarre (2012).

The traits m and f have different meaning depending on the non-random mating mechanism:

- With *ecology-based preference*, both m and f are the ecological trait x , so that each female prefers males with a matching value of their ecological trait.
- With *target preference*, m is the ecological trait x but f is a selectively neutral trait so that each female has its own preferred male trait value.
- With *matching-based neutral marker trait preference*, both f and m are independent selectively neutral traits.
- With *similarity-based neutral marker trait preference*, f and m are the same selectively neutral trait.
- With *condition-based preference*, m is the male condition ω and f is set to 1, so that all females with $c > 1/2$ prefer males with $\omega = 1$ but vary in the extent of their preference specified by their c trait.

When we allow for more than one mechanism of non-random mating to be present, the probability of mating is given by the product of the corresponding ψ 's, all with the same σ_a . Each female evaluates a subset of 10 randomly chosen males and mates with one of them with probabilities proportional to the corresponding ψ values. The evaluation is limited to a subset of males both because of computational simplicity and because in natural populations females do not necessarily observe and evaluate every male in the population. The number of offspring is chosen randomly and independently from a Poisson distribution with parameter b . There are no costs of being choosy since all surviving females mate and produce, on average, the same number of offspring. Sex is assigned randomly. Mutation occurs with a small probability μ per gene per generation.

Dispersal and habitat-based preference

Habitat choice is also a mechanism of non-random mating, even if it does not involve a direct male–female preference (Kirkpatrick & Ravigné 2002). In our model, dispersal occurs via a migrant pool. Individuals enter the migrant pool with probability π . An individual in the migrant pool with habitat preference trait b goes to demes 0 or 1 with probabilities b and $1 - b$ respectively.

Detection of strong non-random mating

In deciding whether a particular mechanism of non-random mating has evolved in our simulations we used a simple statistic

$\Gamma = \frac{\psi_d}{\psi_d + \psi_s}$, where ψ_d and ψ_s are the ψ between two average individuals from different and the same deme respectively. Specifically, we say that *strong overall non-random mating* has evolved if $\Gamma < 0.1$, so that the probability of mating between a native individual and an immigrant is at least 10 times smaller than that between two native individuals. We say that a *particular mechanism of non-random mating* has evolved if the Γ value computed on the basis of the corresponding ψ was smaller than 0.1. In the case of habitat preference, statistic Γ was set to b and $1 - b$ in the first and second demes, respectively. Note that simply using c as a measure of the strength of reproductive isolation may lead to erroneous conclusions. For example, if c evolves, say by drift, to high values but there is no divergence in the ecological trait x between the two demes, there will not be much reproductive isolation in spite of the preferential mating. Using the cut-off values of Γ and computing it for average individuals was done for computational simplicity. We note that the distribution of Γ in our simulations is bimodal with very low and very high values being most common (Fig. S1). This implies that the exact value of the cut-off is not too important.

Initial conditions

Initial conditions differ between three ecological scenarios considered. In the secondary contact scenario, each population was locally adapted so that all individuals in deme 0 have $x = 0$ and those in deme 1 have $x = 1$. In the adaptive radiation scenario, all individuals are generalists with $x = 0.5$. In the niche invasion scenario, only deme 0 is populated initially with all individuals being locally adapted with $x = 0$. All mating preference traits and the habitat preference trait are set to $1/2$ for all individuals. This implies that mating is random initially (i.e. speciation has not happen yet). Initially, all individuals in the same population have the same genotype and are homozygote for all loci.

Parameters

In numerical simulations, we varied the number of loci ($L = 4, 8$), the deme carrying capacity ($K = 512, 4096$), the fraction of the population going to the migrant pool ($\pi = 0.005, 0.05, 0.2$), and the timing of dispersal (before or after selection). The following parameters did not change: $\mu = 10^{-5}$, $b = 4$, $\sigma_a = 0.1$, $\sigma_s = 0.8$. The last value corresponds to the average strength of disruptive selection as estimated in Hereford (2009). Specifically, Hereford (2009) estimated that the relative difference R in fitness between local and foreign individuals in local adaptation studies was about 45%. Of course, this is not a universal constant but rather a representative value corresponding to weak selection. In terms of our model, $R = \frac{v_1 - v_2}{\bar{v}}$, where v_i is the average survival (and not the condition ω_i) in niche i and $\bar{v} = (v_1 + v_2)/2$. Assuming that both populations are at carrying capacity ($N_i = K$), that $b = 4$, and using eqns 1 and 2 with $\theta = 0$, $x_1 = 0$, $x_2 = 1$, allows us to express σ_s as

$$\sigma_s = \sqrt{\frac{-1}{2 \ln\left(\frac{1-R/2}{1+3R/2}\right)}} \quad (4)$$

leading to our choice of $\sigma_s = 0.8$. The simulations ran for 150 000 generations and 20 replicates were done for each parameter combination.

RESULTS

Evolution under random mating

Without immigration and assuming no extinction, each population would perfectly adapt to local conditions. Immigration however brings locally maladaptive genes and as a result can significantly change evolutionary dynamics. In the models of spatially heterogeneous density-dependent selection of the type studied here, if mating is random, then generically there are three possible evolutionary regimes (Ronce & Kirkpatrick 2001; Gavrilets *et al.* 2007; Ravigné *et al.* 2009; Birand *et al.* 2012). (1) If selection for local adaptation is relatively weak and migration is relatively high, then the population evolves to a state where individuals are generalists (i.e. have intermediate values of the ecological trait, $x \approx 0.5$). (2) If selection is relatively strong and migration is relatively low, then each deme is occupied by locally adapted specialist genotypes with $x \approx 0$ in one deme and $x \approx 1$ in another deme. Because of the continuous immigration of locally deleterious alleles, the average level of adaptation will however be somewhat reduced and the average within-deme trait values will be shifted towards 0.5. (3) It is also possible that the population is adapted only to one niche. In this case, the locally adapted deme will be at the carrying capacity while in the other deme will have a significantly reduced population size. Of course, stochasticity due to random genetic drift can blur the distinction between these regimes. In our simulations, the strength of selection was fixed while the fraction π of the population going to the migrant pool varied. The first regime was observed for $\pi = 0.2$, while the second regime was observed for $\pi = 0.005$ and 0.05 . The third regime has been observed in less than 1% of runs (see Table S1); these runs have been excluded from analysis. Complete extinction has never happened.

A single mechanism of non-random mating

If we allow only for a single mechanism of non-random mating, only the ecology-based preference and the condition-based preference evolve frequently (Fig. 1a) with the former observed less often than the latter. Evolution in neutral marker traits and habitat choice, which was observed in other models (Dieckmann & Doebeli 1999; Gavrilets *et al.* 2007), does not occur in our simulations because we used weaker strength of selection, lower levels of initial genetic variation, smaller rates of mutation and smaller size of dispersal pool. When non-random mating does evolve, both the degree of local adaptation (Fig. 2) and population densities increase (see Fig. S2).

The lack of the evolution of habitat choice was particularly unexpected. Therefore, we repeated our simulations with stronger selection and did observe the evolution of habitat preference in almost all cases when dispersal was high (Fig. S3). The difference between the likelihood of evolving the habitat-based preference vs. the ecology-based preference and condition-based preference in our models can be explained in terms of one-allele vs. two-allele mechanisms (Felsenstein 1981; Otto *et al.* 2008). Evolution of habitat-based preference requires divergence in the habitat preference trait between two demes (which is a quantitative trait equivalent of ‘two-allele mechanism’). In contrast, the ecology-based preference and condition-based preference can be established if females in both demes share a low tolerance (which is a quantitative trait equivalent of ‘one-allele mechanism’) for males deviating from their most pre-

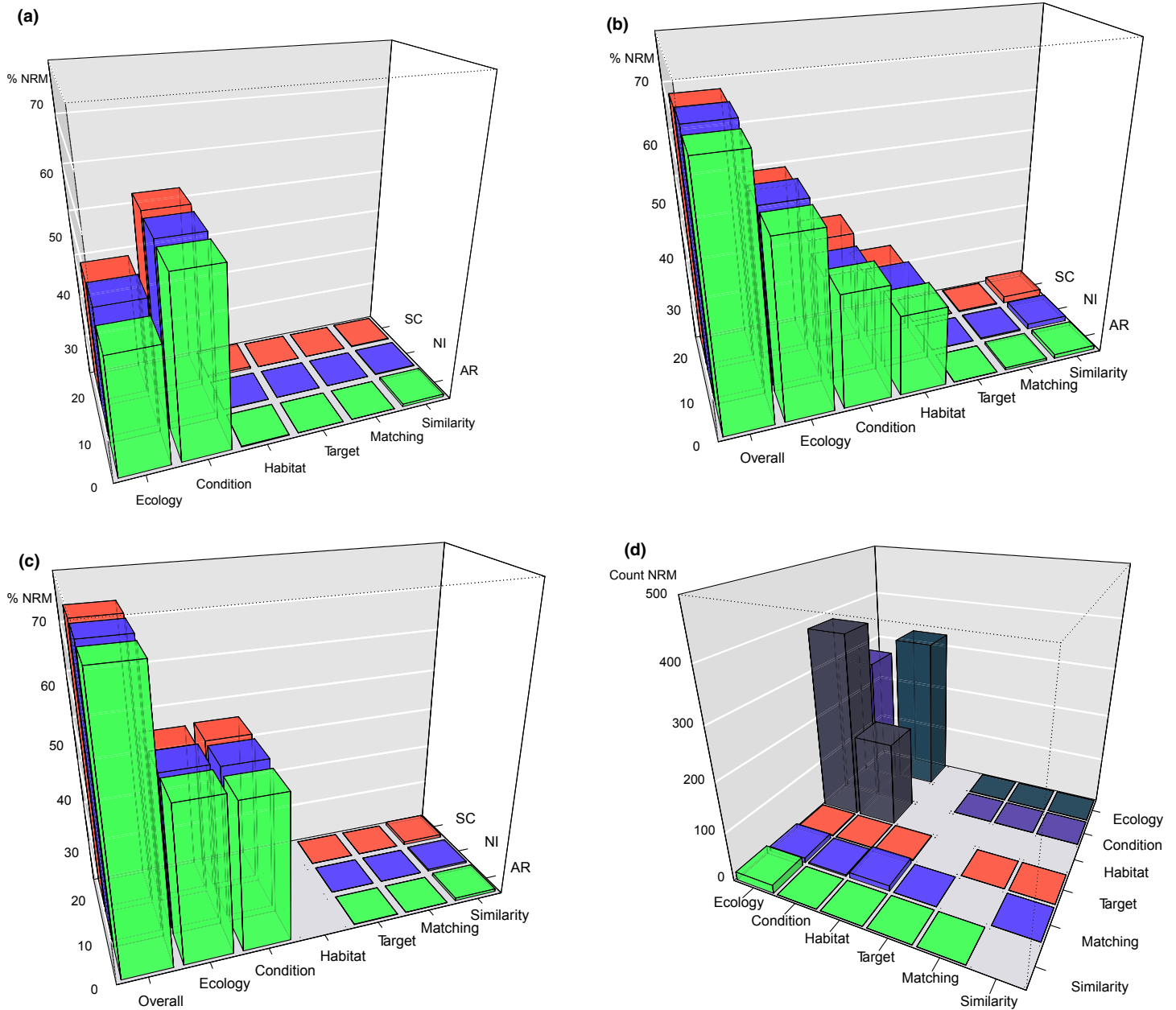


Fig. 1. (a) Percentage of demes with strong non-random mating (NRM) when only one mechanism can occur for adaptive radiation (AR), niche invasion (NI) and secondary contact (SC) scenario. (b) same as (a), but when all mechanisms can occur. 'Overall' shows cases when several mechanisms have evolved simultaneously as well as those where each particular mechanism was weak but, their cumulative strength was strong. (c) same as (b) but evolution of habitat preference is not allowed. (d) The number of times specific pairs of the mechanisms coevolve. The left part of the graph: all the mechanisms can evolve. The right part of the graph: all mechanisms except for habitat preference can evolve. All graphs use combined data for the whole set of different parameters values.

ferred males. Our results appear consistent across a range of the strength of stabilising selection (Fig. S4).

Multiple mechanisms of non-random mating

If we allow for multiple mechanisms to be present simultaneously, the overall probability of non-random mating increases. For example, in the adaptive radiation scenario when only condition-based preference is allowed, strong non-random mating evolves with probability 41%. When multiple mechanisms are allowed, strong

non-random mating is observed with probability 57% (Fig. 1b, the row marked 'overall'). Fig. 1b also shows the frequencies at which different mechanisms are observed. Now it is ecology-based preference that is most often observed; this happens because it often coevolves with habitat preference. If habitat preference is not allowed, the ecology-based and condition-based preferences evolve equally frequently (Fig. 1c).

In approximately 22% of all cases, there are two mechanisms coevolving. In particular, the habitat-based preference coevolves frequently with the ecology-based and condition-based preferences (Fig.

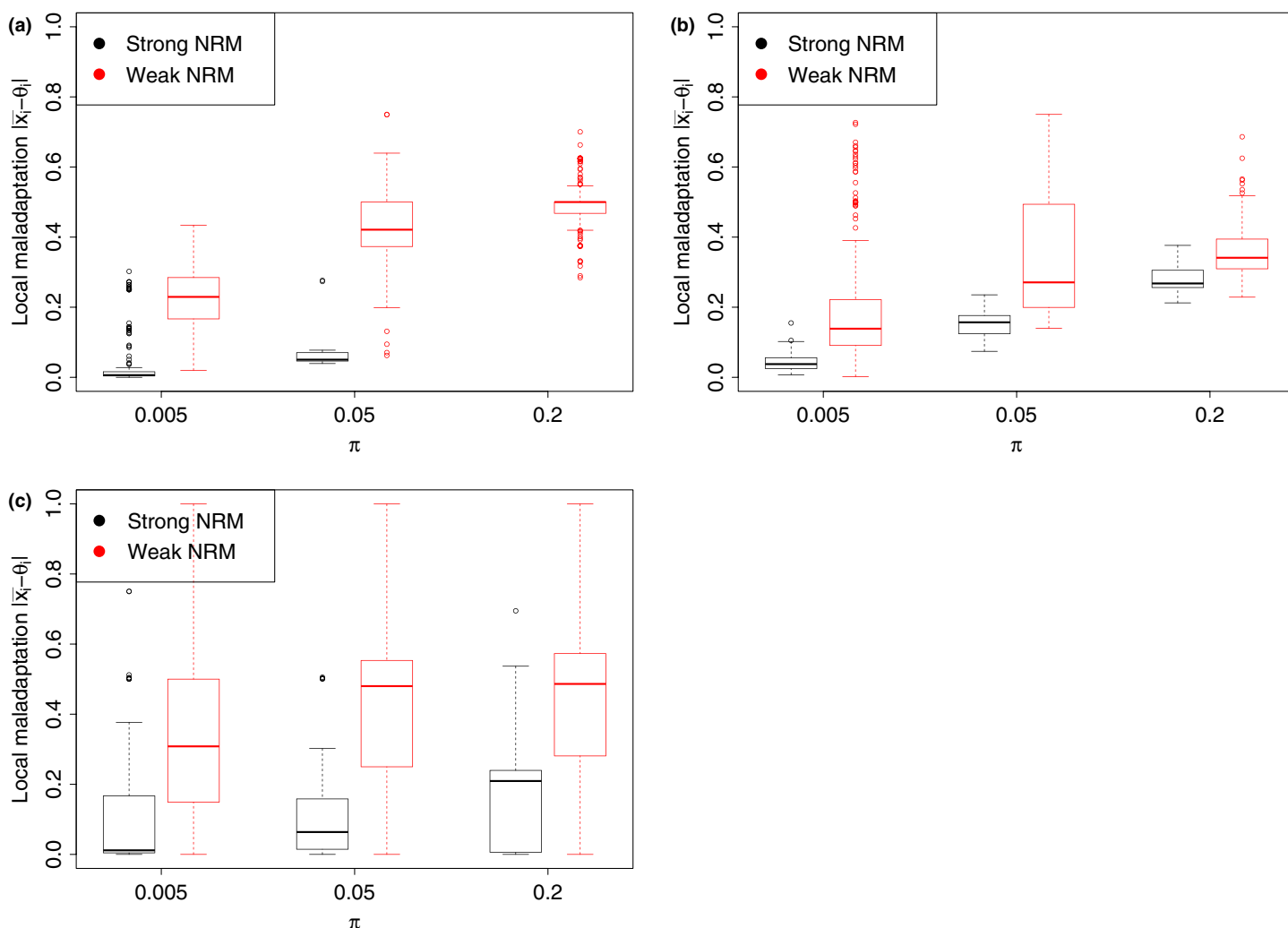


Fig. 2. Ecological differentiation and non-random mating (NRM) in the secondary contact scenario. Each set of three boxplots illustrates the distribution of the extent of local adaptation (measured by the deviation of the ecological trait x from the local optimum θ) for runs with strong (in black) and weak (in red) non-random mating. Three different dispersal rates. (a) Ecology-based preference in isolation for the secondary contact scenario. Strong non-random mating was not observed for $\pi = 0.2$. (b) same as (a), but for condition-based preference. (c) same as (a), but all mechanisms can evolve.

1d). With relatively low dispersal ($\pi = 0.005$), evolution of habitat choice requires stronger selection for local adaptation than used in our simulations (Figs. S3 and S4), and evolving ecology- or condition-based preference first, effectively increases selection against immigrants making subsequent evolution of habitat choice possible. Ecology- and condition-based preference can coevolve if habitat-preference is not allowed. There is also occasional co-evolution of ecology-based and similarity-based neutral preferences (Fig. 1d).

Only very rarely (<5%) do we observe some other preferences evolving (Table S2). In 5% of runs more than two mechanisms have evolved. Evolution of multiple mechanisms happens rarely because the effects of the deleterious gene flow are already substantially reduced by the first two mechanisms to evolve. In 2% of runs, the overall degree of reproductive isolation was strong but each particular preference was not. When non-random mating evolves, both the degree of local adaptation (Fig. 2) and population densities increase (see Fig. S2).

The order of evolutionary events and time-scales

It has been argued that different traits controlling local adaptation, habitat choice and preferential mating are expected to evolve at different rates so that particular sequences of evolutionary events are more likely than others (Gavrilets 2004; Gavrilets *et al.* 2007; Ravigné *et al.* 2009; The Marie Curie SPECIATION Network 2012). In our simulations, the ecological trait was the first to evolve, typically on the time scale of 1000 generations. Then, ecology-based preference or condition-based preference evolve (the latter typically faster than the former) before habitat preference in the vast majority of the cases (Fig. 3). In some runs, ecology-based or condition-based preferences weaken once strong habitat-based preference gets established (SI). The time scale to evolve the first non-random mating mechanisms is on the order of 10 000 generations. When more than one mechanism evolve, there is on the order of 10 000 generations delay between the evolution of the first and second mechanism (see Fig. S5). Evolution of non-random mating would bring

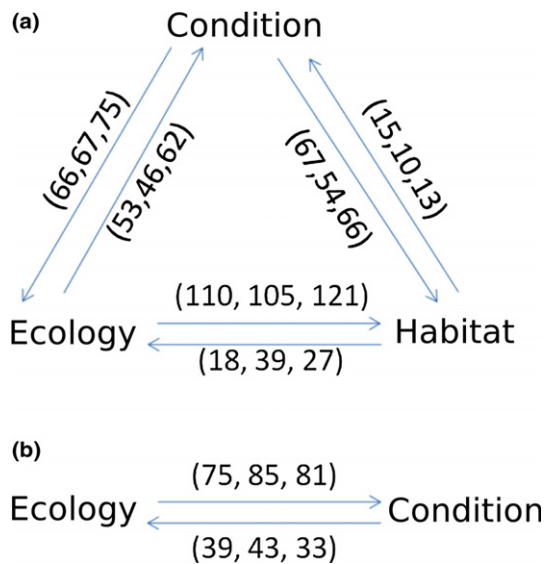


Fig. 3. Number of times the mechanism at the tail of the arrow evolves before the mechanism at the head of the arrow within a single population. (a) All mechanisms can evolve. (b) Habitat preference cannot evolve. The triplets of numbers correspond to the different initial conditions: secondary contact, niche invasion and adaptive radiation respectively. Only simulations where at least both mechanisms evolved are reported.

additional changes in the ecological trait and an increase in local adaptation and population densities.

Effects of parameters

To understand better these results, we need to look at the effects of parameters on the evolutionary dynamics (illustrated in Fig. 4; see also Figs. S6–S9, S11–S14 and S16–S19). Increasing the population size increases the probability to evolve non-random mating as

selection becomes more important relative to drift and the number of advantageous mutations grows (Gavrilets *et al.* 2007). This effect is most apparent for habitat and ecology-based preferences, when all mechanisms are competing. Decreasing the number of loci L typically has a similar effect (see SI for an additional discussion of the effects of L). This happens because with decreasing L , but constant strength of selection on phenotype, the strength of selection on each individual locus increases while recombination and dispersal become less powerful in destroying co-adapted combinations of genes (Gavrilets *et al.* 2007; Thibert-Plante & Hendry 2011a, b). The effects of dispersal are convoluted because increasing π both increases homogenisation and simultaneously makes selection against hybridisation more effective (which decreases homogenisation). As a result, intermediate dispersal rates result in the strongest preferences. Condition-based preferences can evolve for larger migration rates than ecology-based preferences. This happens because the evolution of the latter requires substantial divergence in the ecological trait between the demes, which however will not be maintained at large migration rates. In contrast, the evolution of condition-based preference requires variation in the ecological trait has been reduced. Habitat preference is most often observed at high dispersal (Figs. S7, S12 and S17) because of stronger selection pressure induced by gene flow. The timing of dispersal has the largest impact on the condition-based mating choice as it evolved less often when dispersal was after natural selection. In the latter case, individuals may look fit in the wrong environment if they just immigrated, which would provide a false cue for mating. Simultaneous evolution of habitat preference and condition-based preference or ecology-based preference allows for the evolution of strong reproductive isolation for parameter values that are typically unfavourable for speciation (e.g. high dispersal rates and large number of loci). That is, different mechanisms of non-random mating interact synergistically.

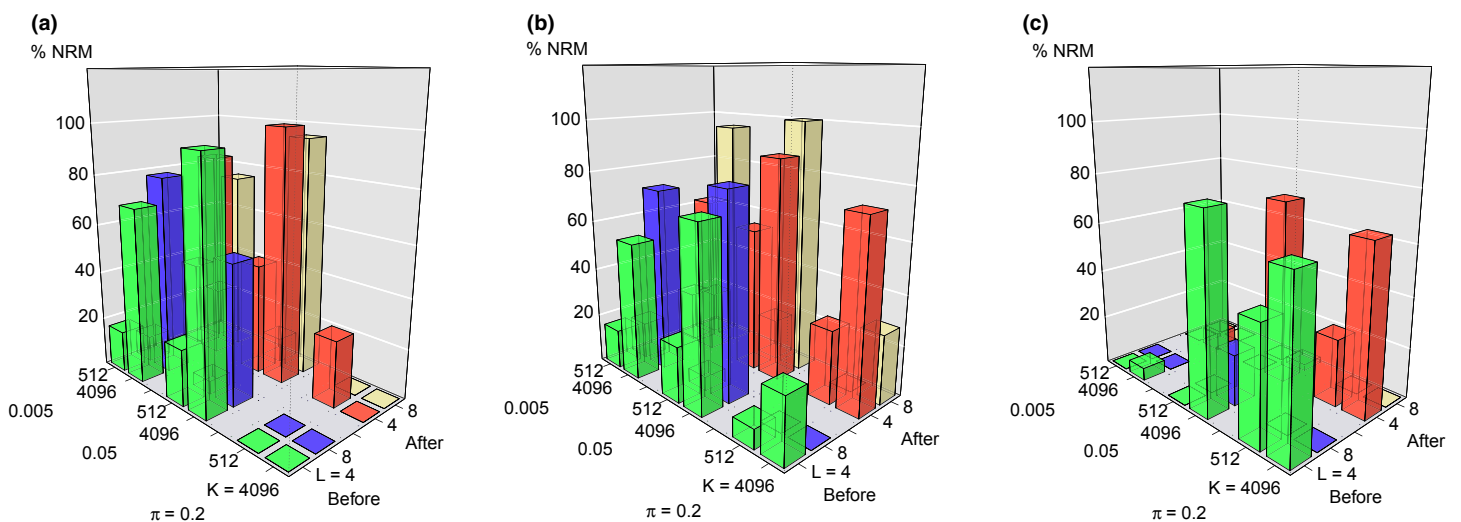


Fig. 4. The effects of parameters. Each cluster of four bars corresponds to one particular combination of dispersal rate π and life cycle type ('Before': dispersal occurs before selection, 'After': dispersal occurs after selection). Within each cluster, the bars correspond to different combinations of the carrying capacity K and the number of loci L . (a) The percentage of runs with strong ecology-based preferences when habitat preference cannot evolve. (b) Same as (a) but when habitat choice can evolve. (c) The percentage of runs with strong habitat preferences. The results shown are for the secondary contact scenario, but the results are similar for the other two scenarios (see Figs. S6–S9, S11–S14 and S16–S19).

Evolution of generalists and specialists

In principle, strong non-random mating can evolve just by random genetic drift without any ecological divergence (Gavrilets 2004). However in our simulations, strong non-random mating was always coupled with ecological divergence, local adaptation, and the emergence of specialists (Fig. 2). Generalists were only observed when mating remained random (cf. Birand *et al.* 2012).

DISCUSSION

Non-random mating can provide multiple evolutionary benefits (Andersson 1994). Biological organisms are characterised by a myriad of different phenotypic characters many of which can, at least in principle, serve as mating cues. Here, we used a series of mathematical models in an attempt to shed light on the questions about which phenotypic traits are more likely to be used in mating decisions and about the characteristics of the process of co-option of phenotypic traits as mating cues. Our focus has been on local adaptation in a spatially heterogeneous system where evolving non-random mating is a way to reduce the deleterious gene flow and increase fitness and population density. A by-product of this process is ecological parapatric speciation. We have studied six different mechanisms of non-random mating evolving separately or jointly under three different scenarios: niche invasion, adaptive radiation and secondary contact. To analyse our models we used stochastic individual-based simulations.

Our results show that there are striking differences between different mechanisms in their ability to evolve strong non-random mating. Specifically, only ecology-based and condition-based preferences evolved often. A characteristic time scale for their evolution is on the order of 10 000 generations. Habitat preference evolved mostly in conjunction with ecology-based or condition-based preference and with a significant delay (on the order of 10 000 generations after the evolution of one of these preferences). Target-based preference and two neutral marker trait-based preferences almost never evolved. Our results are not compatible with the examples of the fastest speciation events (Hendry *et al.* 2007, some of which are controversial), since we were conservative with our choice of parameter values. As already well established in theoretical literature, certain conditions (e.g. stronger selection, particular genetic architecture, higher mutation rates, high initial genetic variation) would make speciation much faster (Gavrilets 2004, 2005).

Our results demonstrate that different mechanisms of non-random mating may interact in a complicated way. In particular, we have shown that trait co-evolution can enable the evolution of non-random mating mechanisms that would not evolve when alone. This implies that one has to be cautious in interpolating the predictions of simple models focusing on a single mechanism to biologically more realistic (and complex) situations of joint evolution of multiple traits. Earlier work has already demonstrated complex interactions between local adaptation and a single mechanism of non-random mating (Ravigné *et al.* 2009; Thibert-Plante & Hendry 2009, 2011b).

Of the six mechanisms of non-random mating studied, four involve 'magic traits', that is, traits that simultaneously affect fitness and mating, but only two of these evolved consistently. This shows that not all 'magic traits' are equal in their ability to lead to strong non-random mating as already argued by (Servedio *et al.* 2011).

The two mechanisms based on neutral preferences evolved very rarely. Evolution of neutral preference mechanisms requires the establishment of strong correlations between traits and strong linkage disequilibrium between the loci involved, which are vulnerable to the homogenising effects of gene flow, recombination and segregation (Felsenstein 1981). The difference between our results and earlier models in which the evolution of matching-based neutral preferences was observed (Dieckmann & Doebeli 1999; Kondrashov & Kondrashov 1999; Gavrilets *et al.* 2007) is that the latter assumed much stronger selection than is typically observed in natural populations (Hereford 2009) and that was used here. Note that in earlier studies (Gavrilets *et al.* 2007) where both habitat choice and neutral marker trait-based preference were allowed to evolve, the latter evolved tens of thousands of generations after the former.

The non-random mating mechanisms studied here also differ in the number of traits involved. There is one trait for ecology-based, condition-based and habitat preference mechanisms; two traits for target- and similarity-based preference; and three for matching-based preference. Our results show that the mechanisms based on a smaller number of traits are more likely to evolve (Smadja & Butlin 2011). At the same time, a larger number of mechanisms increases the probability to evolve non-random mating because of the increase in opportunity.

We have considered three different scenarios of ecological speciation (i.e. secondary contact, adaptive radiation and niche invasion) which differ in the initial levels of local adaptation. Since in our models local adaptation evolves much faster than non-random mating, the differences in ecological scenarios do not affect the dynamics of speciation and our results are similar for the three scenarios.

The model's complexity prevents directly testing the effects of some parameters and of violation of different assumptions. Besides the parameters studied here, the overall phenotypic architecture should be important. Specifically, the number of and variation in traits of different types can be of relevance. For example, the number of traits directly linked to ecological adaptation can be small, but almost any phenotypic trait can, at least in principle, serve as a marker trait. Then with many marker traits, the overall probability that mating is based on such a trait can be larger than that based on one or a few fitness-related traits. The validity of this argument depends on how many traits there are that can potentially be used in mating decisions are not subject to any selection. Some data (e.g. Brooks *et al.* 2005) suggest that mating cue traits are not neutral but are typically subject to stabilising selection.

Apart from the number of traits and their genetic architecture also the strength of selection associated with the various mechanisms is likely to be important. For example, if females cannot observe fitness directly but need to rely on a male signal-trait to infer the male's fitness, the selective advantage of condition-based preferences may be diluted by a factor that depends on how reliable the signal is. This problem may be less relevant for ecology-based preferences or habitat preferences, which might therefore be more likely to evolve when the signal is not reliable. At the same time, condition-based preference can evolve even if there is no gene flow or divergent selection, since it can help identify fit individuals within a population.

The strength of selection for local adaptation assumed in our simulations was relatively weak, so that individuals with intermediate trait values do relatively well. To parameterise our model, we used

data on the average strength of selection for local adaptation (Hereford 2009). Assuming stronger selection would decrease the fitness of intermediates and favour the evolution of non-random mating. Our results appear to be robust to changes in the strength of stabilising selection (Fig. S4), the only exception being the evolution of target preference at strong selection.

In our model, the ecological trait arises deterministically from genotype. Allowing for random micro-environmental effect would effectively decrease the strength of selection for local adaptation. The effects of adaptive phenotypic plasticity are expected to depend on the timing of dispersal. If plasticity is expressed after dispersal, selection is effectively weakened because plasticity allows immigrants to be better suited to their new environment. If plasticity is expressed before dispersal, selection can effectively be stronger (Thibert-Plante & Hendry 2011a).

Our model does not consider benefits of mate choice that are independent of the ecological trait under disruptive selection. (e.g. males may express an ornament that signals their resistance against parasites in both habitats, such that choosy females may avoid parasite infection or produce more resistant offspring.) How easily magic traits would evolve if they interfere with such other benefits of mate choice is an open question. This is particularly relevant if there are high costs of expressing multiple preferences (Møller & Pomiankowski 1993).

Our model does not consider costs of mate choice that are independent of the ecological trait under disruptive selection. For example, too choosy females do not mate and males with conspicuous traits preferred by the females may be exposed to higher predation risks. Such costs would inhibit the evolution of non-random mating.

There are also additional simplifying assumptions standard in theoretical research such as identical carrying capacities in both niches, simple additive genetic architectures, and no linkage or pleiotropy. We do not attempt to speculate on the effects of their violation as they are likely to depend on specific details.

Our conclusions are built on the assumption that at the time of colonisation of a new habitat, populations can in principle evolve a large number of different mechanisms for non-random mating. However, populations may be constrained in the number of options they have to evolve reproductive isolation. For example, some studies of reinforcement suggest that mating is non-random initially, and that whichever characters happen to be already used for mate choice, are the ones that are subject to reproductive character displacement (Saetre *et al.* 1997). Such constraints and historical contingencies can lead to interesting conflicts between local adaptation, mate choice and species recognition (Pfennig 1998).

Our results lead to some predictions relevant within the context of ecological speciation. Overall, we predict a large number of magic traits and a rarity of neutral preferences. Out of several possible types of magic traits, the most common will be those involved in ecology-based (at low dispersal) and condition-based mating (at higher dispersal). Some types of preferences will be found in combinations ('suites'), for example, habitat choice is expected to be coupled with other mechanisms. That our results are fairly similar across three different ecological scenarios (secondary contact, niche invasion and adaptive radiation) supports the generality of our conclusions.

We conjecture that mate choice is more often based on a few 'major traits' that have direct impact on fitness. Such traits (which are somewhat similar to 'major loci' in population genetics) might

be relatively easy to identify. We suggest that magic traits may represent an outcome of ecological speciation emerging as a result of co-option of locally adaptive traits for mating decisions. The trick behind the 'magic traits' is that such traits are not 'born', but rather evolve under a wide array of ecological conditions to become 'magic', that is, influencing simultaneously fitness and mating.

ACKNOWLEDGEMENTS

We thank B. M. Fitzpatrick, J. A. Fordyce, R. T. Gilman, D. Husley, B. O'Meara and numerous anonymous referees for comments on the manuscript. XTP was sponsored by Le Fonds québécois de la recherche sur la nature et les technologies (FQRNT) and Postdoctoral Fellow at the National Institute for Mathematical and Biological Synthesis, an Institute sponsored by the National Science Foundation, the US Department of Homeland Security, and the US Department of Agriculture through NSF Award #EF-0830858, with additional support from The University of Tennessee, Knoxville. SG was partially supported by the National Institutes of Health grant GM56693.

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Editor, Greg Grether

Manuscript received 4 December 2012

First decision made 7 January 2013

Second decision made 16 April 2013

Manuscript accepted 1 May 2013