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Coevolution of male and female mate choice can destabilize reproductive isolation

Thomas G. Aubier[1,2,*], Hanna Kokko[3] & Mathieu Joron[1,*]

1. Centre d'Ecologie Fonctionnelle et Evolutive, CEFE - UMR 5175 - CNRS, Université de Montpellier, EPHE, Université Paul Valéry, 1919 route de Mende, F-34293, Montpellier 5, France

2. Institut de Systématique, Evolution, Biodiversité, ISYEB - UMR 7205 - CNRS, MNHN, UPMC, EPHE, Muséum National d'Histoire Naturelle, Sorbonne Universités, 57 rue Cuvier, CP50, F-75005, Paris, France

3. Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057, Zurich, Switzerland

∗ Corresponding authors; e-mail: thomas.aubier@normalesup.org; mathieu.joron@cefe.cnrs.fr

Abstract

Sexual interactions play an important role in generating reproductive isolation with clear consequences for speciation. Despite increasing empirical evidence of premating isolation caused by mutual mate choice, theoretical developments have focused on the evolution of mate preferences in each sex separately. Here, using a population genetics model, we investigate the joint evolution of female and male mate choice (phenotype matching rule) under polygyny in a context of emerging reproductive isolation. We show that the evolution of female preferences increases the mating success of males with reciprocal preferences. Consequently, selection favouring mutual mate choice may be common. However, in turn, the evolution of male preferences weakens indirect selection favouring female preferences. Therefore, with weak genetic drift, the coevolution of female and male mate choice leads to periodic episodes of random mating with increased hybridization rate. Thus, counterintuitively, the process of establishing premating isolation proves very fragile if both sexes can contribute to assortative mating. Our predictions sheds new light on the evolutionary dynamics of reproductive isolation and encourages further research on the lability of isolating barriers. (<250 words)

INTRODUCTION

Whenever hybridization occurs, it can have profound consequences for species evolution (e.g. speciation[1], transgressive segregation[2], adaptive introgression[3], genetic swamping[4]). Reproductive isolation among taxa can be caused by many different isolating barriers, such as ecological divergence, premating isolation, hybrid sterility and microspatial partitioning[5,6]. While those different isolating barriers contributing to reproductive isolation have been well described, their temporal stability is little studied theoretically and empirically.

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Assortative mating – the tendency of individuals of similar phenotype to mate together more often than expected at random – is widespread in animals[7]. It associates with premating isolation and therefore plays a key role in generating reproductive isolation[8]. Assortative mating can arise as a by-product of adaptive divergence via temporal or spatial isolation[9], or can be driven by various behavioural processes[10,11]. Of particular interest is the case of homotypic mate preferences ('matching mating rule'[12]), where individuals preferentially choose mates with which they share phenotypic traits such as colours[13–16], acoustic signals[17,18] or pheromones[19,20]. When mate choice is based on traits that are diverging in the population, indirect selection favouring strong choosiness (hereafter "choosiness" refers to strength of homotypic preferences) can theoretically lead to premating isolation between diverging populations[12,21–26]. In particular, choosiness induces positive frequency-dependent sexual selection that favours the most common phenotype; unless assortment is perfect, individuals matching the most common phenotype have the highest mating success. If the population is already differentiated, choosiness therefore induces additional disruptive selection on the phenotypic trait used as the basis of mate choice; this can drive further evolution of choosiness in sympatry[27–29] (but note that this sexual selection pressure can also inhibit the evolution of strong choosiness in sympatry[28–30] or parapatry[31–33]). Overall, traits subject to disruptive selection and used as a basis for mate choice are often associated with reproductive isolation during speciation[31,34,35]. Here, we are interested in whether this common premating isolating barrier is stable or not.

In most mathematical models of speciation involving homotypic preferences[21–26], female mate choice causes premating isolation. The assumption that males are not choosy about mates rests on so-called Darwinian sex roles in courtship[36]; in many animal species, males are typically eager to copulate (even with heterospecific females), whereas females are choosy about mates[37–42]. In accordance with Bateman's principle[43], a greater variability in mating success is often observed in males than in females[44], probably reflecting females' mating success being limited by gamete and offspring production rather than by mate acquisition. Mate choice ensuring offspring quality should therefore be under stronger selection in females than in males.

Males and females do not always follow Darwinian sex roles[45]. In particular, interspecific sexual interactions in which males are the choosy sex are observed[41,46–49]. Under strict polygyny, males can be thought of as an unlimited resource for females, while females are a limited one for males. This has profound implications for the evolutionary pressures acting on female and male preferences. If all females have equal mating success, female mate preferences do not directly affect fitness through mating success[50]. The situation is drastically different for males, for whom male-male competition for access to females generates differences in mating success; consequently, having a preference directly affects how much competition a male faces in gaining a mate. Typically, males place themselves in a disadvantageous competitive setting if they preferentially court "popular" females – which can be phrased as sexual selection directly acting against male preferences[51–53]. Male preferences can nevertheless evolve if direct or indirect benefits (e.g. increased probability to mate[51,54], fertility[51,55], or offspring quality[52,56]) outweighs this competitive cost.

The extent of courtship effort (resources[57,58] or time[59,60]) allocated towards preferred females is a key factor for male mate choice evolution. Male choosiness can evolve if choosy males improve their chance to mate with preferred females by overlooking unpreferred females. Yet, such reallocation of courtship effort may be incomplete in many species. In extremes cases, males should not reject mating opportunities with unpreferred females if this does not improve their chance of finding and courting preferred females afterwards. The economics of partial reallocation of courtship effort is therefore an important component of any male choice modelling. Therefore, while we know that male mate choice

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can evolve by reinforcement[52] or that strategic male courtship allocation can generate polymorphic male preferences[61], ultimately causing complete reproductive isolation within the population, the theory remains incomplete unless we relax the assumption of these models that males are able to perfectly reallocate courtship effort towards preferred females.

In some interspecific sexual interactions, both males and females discriminate against heterospecifics, and therefore engage in mutual mate choice at the level of species identity[41,42,62,63]. In cichlid fishes[64–66] and *Heliconius* butterflies[6,14,67–72], which are text-book examples of taxa where premating isolation may lead to speciation, both males and females can display homotypic preferences based on colour. However, the consequences of mutual mate preferences for reproductive isolation remain to be explored. Preferences have been shown to evolve independently if female and male choices are based on distinct traits[51]. However, females and males with mutual homotypic preferences often use the same trait to evaluate potential mates; through genetic linkage disequilibrium, mate preferences in one sex could therefore influence the evolution of preferences in the other[51,73–76]. For instance, female choosiness may affect the evolution of male choosiness by favouring males matching the most common phenotype. Additionally, choosy females may often reject nonchoosy males that have not focused their courtship effort on females that match their own phenotype. This may greatly favour the evolution of male choosiness.

By analyzing a population genetics model, we characterize the coevolutionary dynamics of female and male mate choice based on the same phenotypic trait under disruptive selection. We then assess its effects on the stability of reproductive isolation. We show that female choosiness favours the evolution of male choosiness and that selection for mutual mate choice should be common. In turn, because female and male preferences are based on the same phenotypic trait, male choosiness weakens indirect selection favouring female choosiness. Consequently, despite selection favouring mutual mate choice, the coevolution of male and female mate choice can destabilize reproductive isolation and may strongly increase hybridization rate among ecotypes in stochastic simulations.

MODEL OVERVIEW

We model the evolution of assortative mating in sympatry with a three-locus diploid population genetics model. Disruptive viability selection acts on an ecological locus A, but ecological divergence is hampered under random mating that brings divergent ecotypes (AA and aa) together to hybridize. Additionally, we implement two distinct choosiness loci F and M that are independently expressed in females and in males, respectively. Both sexes can therefore use the trait under disruptive viability selection as a basis for mate choice ('one-allele mechanism'[77] using a matching rule). In our model, female and male choosiness are therefore ecologically neutral and can evolve only if there is polymorphism at the trait loci (via indirect selection). Hybridization rates between ecotypes may decline due to assortative mating caused either by female, male or mutual preferences. We assume that the alleles coding for choosiness are recessive (only FF females and MM males are choosy), but we note that changing this to dominance does not change our results qualitatively.

At each generation, disruptive viability selection first occurs with strength s, such that heterozygotes at the ecological locus (Aa) suffer viability costs. Males then court females and are 'visible' to females (i.e. available as potential mates) proportionally to the courtship effort that they invest. Choosy males (MM) prefer females that match their own ecological trait. In case of a mismatch, choosy males reduce their courtship effort to a very small fraction $\epsilon_{\mathrm{m}} << 1$ of what nonchoosy males would invest. The courtship effort thus saved can be reallocated towards courtship of preferred females. The extent

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of this reallocation of courtship effort is described by the parameter α. In particular, if choosy males reallocate all saved courtship effort towards preferred females ($\alpha = 1$), they enjoy a strong mating advantage over nonchoosy males with these particular females. Females also express different propensities to accept 'visible' males. Choosy females (FF) prefer males that match their own ecological trait. We assume that, in case of a mismatch, choosy females reduce the probability of mating to a very small value $\epsilon_{\mathrm{f}} << 1$. High ϵ_{f} and ϵ_{m} therefore reflect weak choosiness (i.e. erroneously expressed preferences). Unlike males, all females have the same mating success (polygyny). Based on the resulting fractions of mating among genotypes and assuming Mendelian inheritance of all loci with no linkage, we obtain the theoretical genotype frequencies at the next generation.

This three-locus diploid model involving mutual mate choice is too complex to produce analytical solutions[51]. The behaviour of the model can be assessed, however, by numerical analyses and computer simulations. We first analyze the deterministic behaviour of the model. We then perform stochastic simulations to account for drift affecting traits under weak selection. At each generation, K offspring individuals are randomly picked following the theoretical genotype frequencies. We additionally assume that loci can mutate in offspring. Therefore, the genotype frequencies in this offspring population are subject to sampling errors (just like in the Wright-Fisher model of genetic drift) and mutations. The deterministic dynamic described above is applied on these stochastic offspring frequencies at each generation.

DETAILED METHODS

Genotypes

In a population genetics model, we consider three autosomal diploid loci. Alternative alleles at each locus are represented by small and capital letters. An ecological locus, A, is subject to disruptive selection and can be used as a basis for mate choice (homotypic preferences involving phenotypic matching). A female choosiness locus, F, alters female choosiness (i.e. the strength of female homotypic preference). A male choosiness locus, M, alters male choosiness (i.e. the strength of female homotypic preference) during courtship. We assume that choosiness alleles either code for no choosiness or for strong choosiness, i.e. preferences vary from indiscriminate to full assortative. Since there are three genotypes per locus (e.g. AA, Aa and aa for the A locus), we track the frequencies of $3^3 = 27$ genotypes in the population.

Deterministic simulations

Assuming discrete generations, we follow the evolution of genotype frequencies $\mathbf{p}(t)$ within an infinite population over time. $\mathbf{p} = \{p_i\}$ is a vector consisting of 27 elements $\{p_1, p_2, ..., p_{27}\}$ and refers to the frequencies of the 27 genotypes present in newborn offspring. The life cycle is as follow:

(1) Disruptive viability selection on the ecological locus

Environmental/ecological pressures act on an adaptive ecological trait and cause ecological divergence in two distinct ecological niches in sympatry. We assume that heterozygotes Aa suffer viability costs with parameter s representing the strength of disruptive viability selection on locus A. Through parameter $s' > 0$, the two homozygotes AA and aa occupy niches that are assumed to occur equally abundantly in the environment, such that neither allele will outcompete the

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other based on ecological competition. Following these assumptions, the genotype frequencies after disruptive viability selection before normalization are:

$$p_i^{\mathrm{S}} = \begin{cases} p_i \left(1 + s' \left(0.5 - \frac{\sum_{k \in \mathrm{aa}} p_k}{\sum_{k \in \mathrm{aa} \cup \mathrm{AA}} p_k}\right)\right), & \text{if } i \in \mathrm{aa} \\ p_i \left(1 + s' \left(0.5 - \frac{\sum_{k \in \mathrm{AA}} p_k}{\sum_{k \in \mathrm{aa} \cup \mathrm{AA}} p_k}\right)\right), & \text{if } i \in \mathrm{AA} \\ p_i \left(1 - s\right), & \text{if } i \in \mathrm{Aa} \end{cases} \tag{1}$$

We normalize the elements of $\mathbf{p}^{\mathrm{S}} = \{p_i^{\mathrm{S}}\}$, such that the sum of the vector equals unity. If $s' = 0$, one ecological allele can outcompete the other ('gene swamping'[78]); positive frequency-dependent sexual selection induced by female choosiness can lead to the fixation of the universally common trait (either AA or aa), hampering divergence[27,79,80]. We therefore implement $s' > 0$ to maintain polymorphism at the ecological locus A ($p_{AA}^{\mathrm{S}} \approx p_{aa}^{\mathrm{S}}$).

(2) Male choice and courtship

$P_{m,f}^{♂}$ denotes the courtship effort of a male with genotype m towards females with genotype f (m and $f \in \{1, 2, .., 27\}$). Males with genotype mm or Mm at the locus M are nonchoosy and court all females with the same intensity ($P_{m,f}^{♂} = 1$ towards all females). Homozygous MM males are choosy (i.e. they express homotypic preferences). They exhibit courtship that depends on the match between the ecological trait (locus A) of the female and their own. In case of a mismatch (e.g. between a male with genotype AA and a female with genotype Aa or aa), choosy males reduce their courtship effort to a small fraction $P_{m,f}^{♂} = \epsilon_{\mathrm{m}} << 1$ of what nonchoosy males would invest (high ϵ_{m} reflects weak choosiness and therefore erroneously expressed preferences). In other words, choosy males reduce resources (e.g. time or energy) they spend on courting unpreferred females. Saved courtship effort can be reallocated (partially, totally, or not at all) towards courtship of preferred females matching their ecological trait. The extent of this reallocation of courtship effort is described by parameter α. Overall, of all possible courtship that could happen in the population, a fraction $C_{m,f}$ will occur between males of genotype m and females of genotype f:

$$C_{m,f} = p_m^{\mathrm{S}}\, p_f^{\mathrm{S}} \overbrace{\left(\underbrace{P_{m,f}^{♂}}_{\substack{\text{Baseline courtship effort of} \\ \text{a male of genotype } m \text{ towards} \\ \text{a female of genotype } f}} + \overbrace{\alpha \left(1 - \sum_{f'=1}^{27} p_{f'}^{\mathrm{S}} P_{m,f'}^{♂}\right)}^{\substack{\text{Courtship effort that} \\ \text{a male of genotype } m \\ \text{reallocates}}} \times \overbrace{\frac{P_{m,f}^{♂}}{\sum_{f'=1}^{27} p_{f'}^{\mathrm{S}} P_{m,f'}^{♂}}}^{\substack{\text{Proportion of courtship effort that} \\ \text{a male of genotype } m \text{ reallocates} \\ \text{towards a female of genotype } f}} \right)}^{\text{Total courtship effort of a male of genotype } m \text{ towards a female of genotype } f} \tag{2}$$

where p_m^{S} and p_f^{S} are the frequencies of males of genotype m and females of genotype f after viability selection has occurred. If $\alpha = 0$, choosy males do not reallocate saved courtship effort towards preferred (matching) females. If $\alpha = 1$, choosy males reallocate all saved courtship effort towards preferred females and therefore enjoy a strong mating advantage over their competitors with these particular females. This is modulated by the propensity of females to accept these matings (see below). Contrary to previous population-genetics models of male courtship[51,52,54,81], male preferences can

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induce lost courtship opportunities. If $\alpha < 1$, all possible courtship effort is not necessarily allocated ($\sum_m \sum_f C_{m,f} < 1$) and males do not have equal overall courtship effort ($\sum_f C_{m,f} \neq p_m^{\mathrm{S}}$). Equation (2) therefore differs from those previous models and is instead analog to a model of mating involving female preferences and opportunity costs[29]. As expected, without female choosiness and with all ecological genotypes present at the same frequency, implementing male choosiness in linkage equilibrium do not generate sexual selection on the ecological locus (even when $\alpha < 1$).

(3) Female choice and mating

We assume that males are 'visible' to females (i.e. available as potential mates) proportionally to the courtship effort that they invest. The baseline mating rate with males is therefore proportional to their courtship effort but can then be adjusted downwards or upwards by female choice. $P_{f,m}^{♀}$ denotes the willingness of a female with genotype f to mate with males with genotype m. Females with genotype ff or Ff at the locus F mate indiscriminately ($P_{f,m}^{♀} = 1$ with all males), leading to mating rates that are directly proportional to courtship. Homozygous FF females are choosy (i.e. they express homotypic preferences). Their decision to mate depends on the match between the ecological trait of the male and their own. In case of a mismatch, choosy females reduce the occurrence of mating to a small fraction $P_{f,m}^{♀} = \epsilon_{\mathrm{f}} << 1$ of the baseline (high ϵ_{f} reflects weak choosiness and therefore erroneously expressed preferences). Thus, the overall fractions of matings $F_{m,f}$ between males of genotype m and females of genotype f are:

$$F_{m,f} = \frac{C_{m,f} P_{f,m}^{♀}}{\sum_{m'=1}^{27} C_{m',f} P_{f,m'}^{♀}} \times p_f^{\mathrm{S}} \tag{3}$$

This equation is analog to previous population-genetics models of mating with female preferences[31,50–52,54,81]. This equation ensures that all females, even the ones that are less preferred by males, have the same mating success. That is why, unlike female choosiness, male choosiness does not induce positive frequency-dependent sexual selection on the ecological locus. Likewise, the mating success of females with and without a preference is equal ($\sum_m F_{m,f} = p_f^{\mathrm{S}}$). These assumptions are realistic for a polygynous mating system; relaxing this assumption by implementing a cost of female choosiness ($\sum_m F_{m,f} < p_f^{\mathrm{S}}$ for $f \in$ FF) does not change our conclusions (Appendix A).

(4) Recombination

From the overall fractions of mating $F_{m,f}$, we can calculate the theoretical genotype frequencies $\mathbf{p}(t+1)$ in the next generation, assuming Mendelian inheritance of all loci with no linkage. Zygote production follows recombination by summing the appropriate elements of the matrix $\mathbf{F}$, determining the frequencies of all possible progeny genotypes after recombination and segregation.

Stochastic simulations

Based on the above deterministic system, we also perform stochastic simulations to account for drift on loci that are under weak selection. At each generation, we pick randomly K offspring individuals from the theoretical genotype frequencies $\mathbf{p}(t)$, to form a new vector $\mathbf{p}(t)$ for which deterministic dynamics (Eq. 1 to 3) is then applied. Additionally, we assume

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that each allele of each offspring mutates to the alternative allele with probability μ.

Parameters and initialization

Unless stated otherwise, we perform simulations with strong choosiness associated to genotypes FF and MM ($\epsilon_{\mathrm{f}} = 0.01$, $\epsilon_{\mathrm{m}} = 0.01$). We also implement $s' = 0.5$ to ensure that polymorphism at the ecological locus A is maintained. Once ecological equilibrium is reached, 1% of alleles M and F are introduced in linkage equilibrium with alleles at locus A. When choosy alleles are introduced, heterozygotes Aa are always in lower frequencies than homozygotes AA and aa (because of disruptive viability selection) and are never favoured by positive frequency-dependent sexual selection. Thus, we do not consider the case where sexual selection induced by female preferences is stabilizing and hampers ecological divergence[27–29].

Deterministic equilibrium is typically reached in less than 1,000 generations. In stochastic simulations, we model populations of appreciable size $K = 500$ with a probability of mutation $\mu = 10^{-3}$ per individual and per locus. For each combination of parameters tested, 40 stochastic simulations are run for 100,000 generations.

RESULTS

Viability and sexual selection on female and male choosiness

Viability and sexual selection acts directly on choosiness loci (through differential viability and differential male mating success among genotypes, respectively; see Fig. S1), but also generates linkage disequilibrium between loci by favouring specific combinations of alleles at different loci – i.e. genotypes at each locus are not independent from genotypes at other loci (despite free recombination between loci) (Fig. S2). In particular, choosy females and choosy males are mostly homozygous at the ecological locus. Additionally, choosy males often carry alleles coding for female choosiness (which are neutral during courtship); this linkage disequilibrium between choosiness loci arises because choosy females and choosy males both use a 'matching rule' when evaluating potential mates. Therefore, selection on each locus also indirectly act on other loci – i.e. change in frequencies at a given locus changes frequencies at other loci via linkage disequilibrium.

We first consider the cases where choosiness can only evolve in one sex. Disruptive viability selection directly acts on the ecological locus (black arrow, Fig. 1) with homozygotes having high viability (hereafter, 'homozygous' and 'heterozygous' refer to the genotype at the ecological locus). Female choosiness also induces positive frequency-dependent sexual selection on the ecological locus (green arrow, Fig. 1) with more frequent homozygous males having a high chance to mate. Consequently, in the case where only female choosiness can evolve, female choosiness is favoured by indirect viability and sexual selection via linkage disequilibrium (Fig. 1a and S3).

Male choosiness does not induce positive frequency-dependent sexual selection on the ecological locus because all females, even the ones that are less preferred by males, have the same mating success (polygyny scenario). However, male choosiness distorts male-male competition and induces sexual selection on the male choosiness locus (pink arrow, Fig. 1). Indeed, because choosy males are mostly homozygous at the ecological locus (linkage disequilibrium), males courting 'popular' homozygous females face strong male-male competition (Fig. S1). Choosy homozygous males therefore place themselves in a disadvantageous competitive setting and have a low mating success. Additionally, if reallocation of

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courtship effort is partial ($\alpha < 1$), male choosiness associates with lost courtship opportunities, which also lower mating success (blue arrow, Fig. 1). Consequently, in the case where only male choosiness can evolve, male choosiness is favoured if viability selection can oppose sexual selection (Fig. 1b and S3).

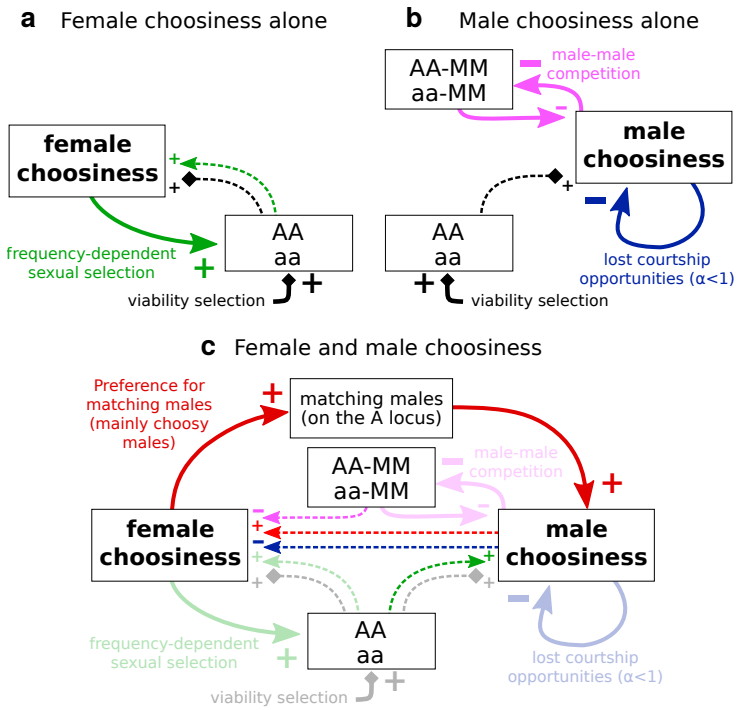

Figure 1: Selective forces acting on female and male choosiness if choosiness can only evolve in one sex (a, b) or if choosiness can evolve in both sexes (c). Diamond arrows and classic arrows represent viability and sexual selection, respectively. Viability selection acts through differential survival (i.e. change in frequencies during the disruptive viability selection process), whereas sexual selection acts through differential male mating success (detailled in Fig. S1). Bold and dashed arrows represent direct and indirect selection, respectively. AA and aa refer to the genotype of homozygotes at the ecological locus and MM refers to the genotype of choosy males. Selective forces represented with a low opacity in subfigure c are the ones that are already shown in subfigures b and c .

We now consider the case where choosiness can evolve in both sexes. Along with the selective forces acting on female and male choosiness separately (Fig. 1a-b), choosiness in each sex induces additional selective forces on choosiness in the opposite sex. First, because choosy females mainly reject nonchoosy (nonmatching) males, female choosiness directly increases the mating success of choosy males (red arrow, Fig. 1c). Second, sexual selection induced by female choosiness on the ecological locus also indirectly favours male choosiness (dashed green arrow, Fig. 1c). Finally, via linkage disequilibrium between choosiness loci, all selective forces acting on male choosiness indirectly affect the evolution of female choosiness (dashed pink, red and blue arrows in Fig. 1c). To characterize the resulting coevolutionary dynamics of female and male choosiness, we measure the change in frequencies of choosy females and choosy males resulting from viability and sexual selection over one generation (Fig 2a-e). Interestingly, the evolution of female choosiness changes the direction of sexual selection acting on male choosiness (sex. + on male choosiness, Fig. 2b-e) and can even favour the evolution of male

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choosiness (Fig. 2b and S3). Likewise, male choosiness changes the direction of sexual selection acting on female choosiness (sex. - on female choosiness, Fig. 2a-e) and can even inhibit the evolution of female choosiness if viability selection is weak (Fig. 2d-e and S3). Besides, if males are choosy, the female choosiness locus forms a weak linkage disequilibrium with the ecological locus (Fig. S2). This greatly weakens viability and sexual selection indirectly favouring female choosiness (cf. selection gradients in Fig 4), so female choosiness may easily drift.

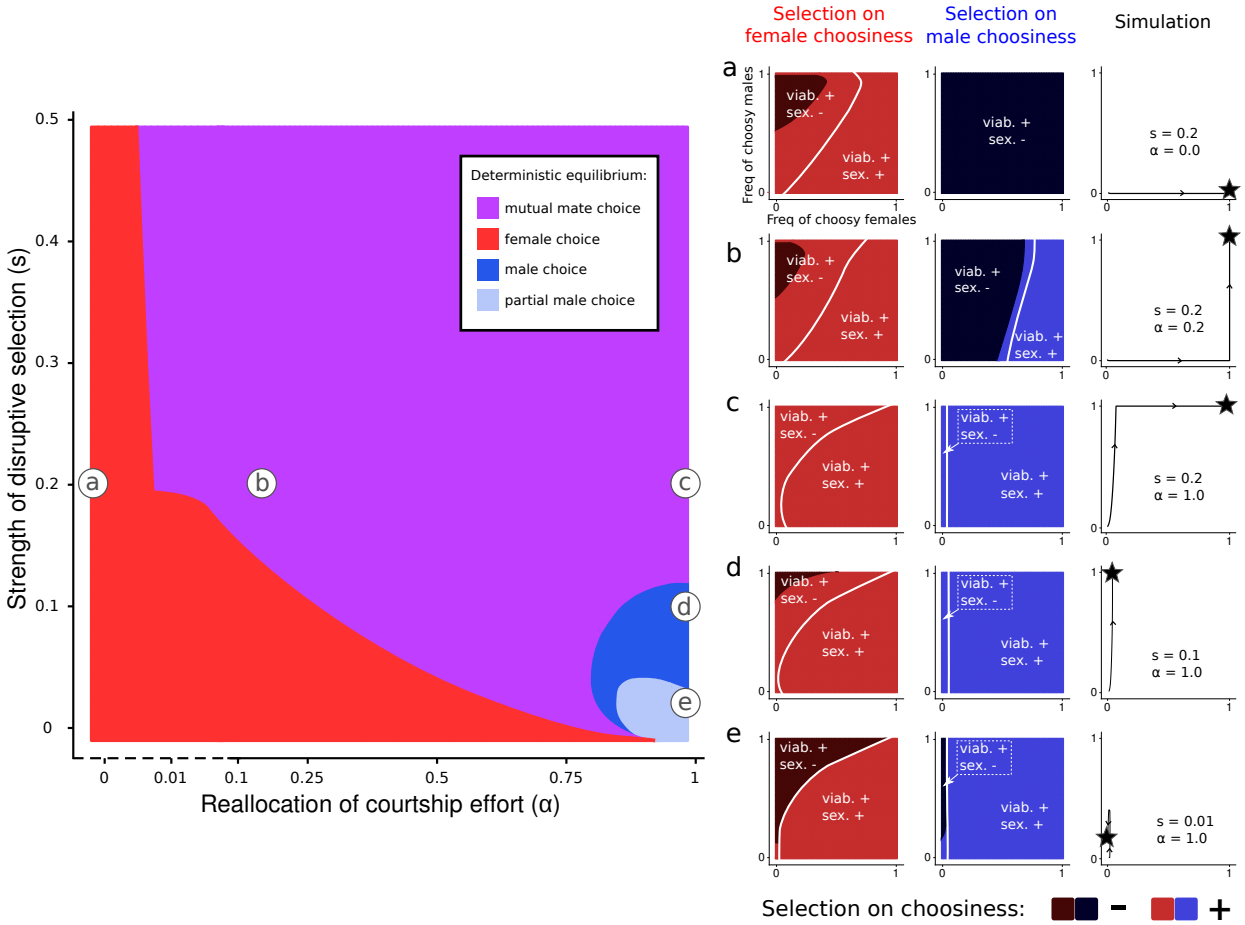

Figure 2: Deterministic equilibrium for different combinations of (α, s). Subfigures a-e refer to some combinations of (α, s) shown in the left figure. In those subfigures, we draw individual simulations leading to the deterministic equilibria (represented by black stars). To understand the direction of selection on female and male choosiness, we also measure the change in frequencies of choosy females and choosy males over one generation (in the red and blue plots, respectively). An increase or a decrease in frequency after mating is caused by sexual selection (via differential male mating success) (sex. + or sex. -). An increase in frequency after disruptive viability selection is caused by viability selection (viab. +). Sexual selection directly acts on male choosiness. Sexual and viability selection can also indirectly act on female and male choosiness via linkage disequilibrium between loci. Depending on (α, s), female mate choice, male mate choice or mutual mate choice can be stable deterministic equilibrium. In particular, under strong disruptive viability selection ($s \geq 0.2$), mutual mate choice evolves even if choosy males reallocate little courtship effort towards preferred females ($\alpha \geq 0.01$). In that case, the evolution of female choosiness favours the evolution of male choosiness by increasing the mating success of choosy males (sex. + in b).

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Deterministic outcome: selection favouring mutual mate choice is common

If viability selection is weak, all choosiness regimes can evolve at deterministic equilibrium depending on the extent of reallocation of courtship effort ($s < 0.15$, Fig. 2). In particular, without reallocation of courtship effort ($\alpha = 0$), only female choosiness evolves by indirect viability and sexual selection. On the contrary, with complete reallocate of courtship effort ($\alpha = 1$), sexual selection acting on male choosiness can indirectly inhibit the evolution of female choosiness (Fig. 2d-e); in that case, male choosiness alone causes assortative mating. Note that this deterministic outcome does not occur if females are initially choosy.

If viability selection is strong, mutual mate choice is a common deterministic equilibrium ($s > 0.15$, Fig. 2). It evolves even if choosy males reallocate little of their courtship effort towards preferred females (for $\alpha \geq 0.01$ if $s \geq 0.2$, Fig. 2). As explained above, female choosiness changes the direction of sexual selection acting on male choosiness (in particular because choosy females mainly reject nonchoosy males) and favours its evolution (Fig. 2b). Besides, female and male choosiness act in synergy to reduce hybridization rate between ecotypes (Fig. S4). Indeed, while choosy individuals avoid courting/mating across ecotype boundaries, we also assume this barrier is not perfect ($\epsilon_{\mathrm{m}} \neq 0$ and $\epsilon_{\mathrm{f}} \neq 0$). Overall, even if choosy males reallocate little courtship effort towards preferred females, mutual mate choice is often a stable equilibrium, associated with low hybridization rates.

Stochastic simulations: coevolution of male and female mate choice increases hybridization rate

Given that male choosiness weakens indirect selection favouring female choosiness (by weakening linkage disequilibrium), we next implement drift in populations of appreciable size ($K = 500$) to test the implication of such relaxed selection on the coevolutionary dynamics of male and female choosiness. Here we only consider scenarios with strong disruptive selection ($s = 0.2$). Otherwise, selection is too weak relative to genetic drift.

The regime of choosiness can evolve away from mutual mate choice. – To describe the evolutionary dynamics of female and male choosiness, we define a frequency threshold ($= 0.85$) above which female or male populations are considered to be mainly choosy. We thereby characterize four regimes of choosiness: female choice only ($\mathcal{F}$), male choice only ($\mathcal{M}$), mutual choice ($\mathcal{FM}$) and partial choice (i.e. both female and male populations are only partly choosy, $\mathcal{P}$) (Fig. 3a). For $\alpha > 0.01$, our deterministic analysis predicts mutual mate choice to be a stable equilibrium, yet when accounting for the effects of drift, preference traits can evolve away from this equilibrium (Fig. 3b). Over evolutionary time, assortative mating is often caused by male choosiness only (regime $\mathcal{M}$). Mating can also be partially or completely random when both female and male populations are partly choosy (regime $\mathcal{P}$).

Despite selection favouring mutual mate choice, assortative mating is often caused by male choosiness only (regime $\mathcal{M}$, Fig. 3b). When females are choosy, male choosiness is strongly favoured with little influence of drift. However, when males are choosy, selection favouring female choosiness is weak; the frequency of choosy females may decrease by drift (Fig. 4). Nonchoosy females can persist for significant periods of time, during which assortative mating is caused by male choosiness only (regime $\mathcal{M}$).

Female and male populations are rarely simultaneously partly choosy (regime $\mathcal{P}$) for extreme values of α (Fig. 3b).

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When $\alpha < 0.01$, selection favouring female choosiness is strong enough to keep female choosiness at high frequency, and the same applies for male choosiness when $\alpha > 0.9$. The situation changes at intermediate α values, for which female and male populations are partly choosy (regime $\mathcal{P}$) for significant periods of time (5% of time). This is caused by the coevolutionary dynamics of female and male choosiness. Since male choosiness is favoured only when the frequency of choosy females is high, drift of female choosiness changes the direction of selection on male choosiness, which can then lead to a regime of partial choosiness (regime $\mathcal{P}$, Fig. 4b-d). Although selection predicts a return to mutual mate choice (i.e. regime $\mathcal{P}$ is only transient), the process takes time, and an observed outcome at a particular point in time features large fractions of both females and males being nonchoosy (regime $\mathcal{P}$). Hereafter, 'preference cycling' refers to this coevolutionary dynamics of female and male choosiness going through deterministic cycles triggered by stochasticity, involving departure from regime $\mathcal{FM}$ into regimes $\mathcal{M}$, $\mathcal{P}$ and sometimes $\mathcal{F}$ (before returning to regime $\mathcal{FM}$).

Preference cycling also occurs if we relax the hypothesis of polygyny (Appendix A) or if we implement continuous choosiness traits (Appendix B).

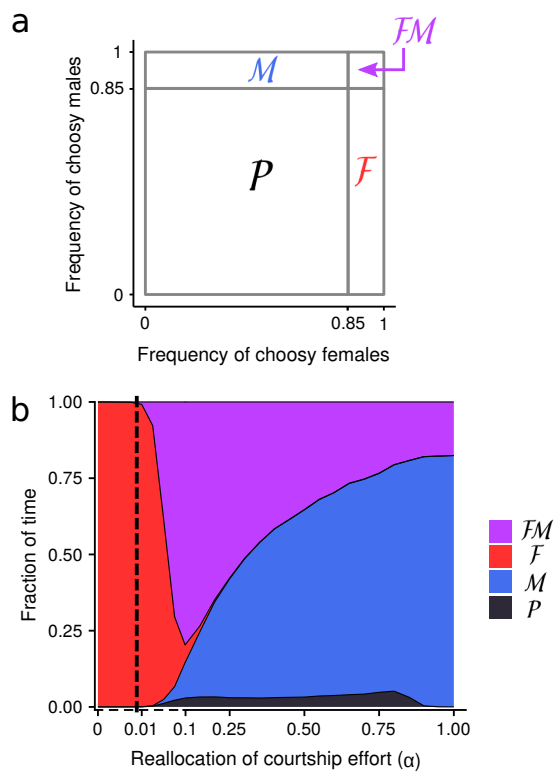

Figure 3: Four regimes of choosiness are defined to describe stochastic simulations (a): mutual mate choice ($\mathcal{FM}$), male mate choice ($\mathcal{M}$), female mate choice ($\mathcal{F}$) and partial mate choice (i.e. both female and male choosiness reach intermediate or low frequencies, $\mathcal{P}$). Fractions of time spent in each regime of choosiness in stochastic simulations are measured once the deterministic equilibrium is reached ($s = 0.2$, $K = 500$) (b). The vertical dashed line corresponds to the threshold above which mutual mate choice is the deterministic equilibrium ($\alpha > 0.01$, Fig. 2). Assortative mating is often caused by male choosiness only (regime $\mathcal{M}$) despite selection favouring mutual mate choice. Moreover, for partial reallocation of courtship effort ($\alpha \in [0.01, 0.9]$), female and male populations are partly choosy (regime $\mathcal{P}$) for significant time periods (5% of time).

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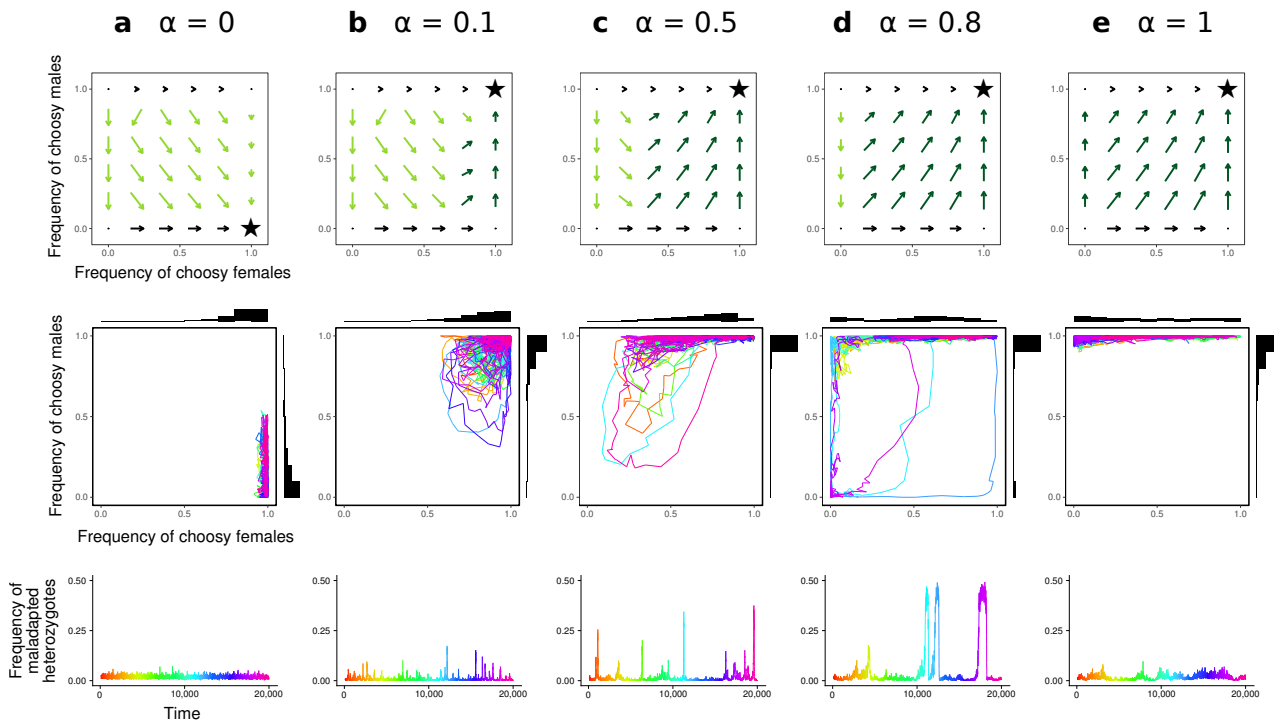

Figure 4: Selection gradients for female and male choosiness and examples of stochastic simulations ($s = 0.2$, $K = 500$) with different courtship reallocation values (α). From top to bottom, we represent the deterministic selection gradients for female and male choosiness, the evolutionary dynamics of choosiness and the resulting frequencies of maladapted heterozygotes at the ecological locus before viability selection occurs (from the same simulations). The selection gradients for choosiness correspond to the relative change in frequencies of choosy vs. nonchoosy females and males over one generation (dark green arrows represent selection favouring male choosiness). Those representations of selection gradients are therefore simpler than in Fig. 2. To highlight weak selection on choosiness, we here use a logarithmic scale to draw arrow vectors. Stars corresponds to the regimes of choosiness at deterministic equilibrium. In the bottom graphs, starting from the choosiness regime predicted in the deterministic analysis, stochastic simulations are run, and rainbow colour gradients correspond to the passage of time. In stochastic simulations, we observe that the frequencies of choosy females and choosy males do not converge to the deterministic equilibrium.

Consequences for reproductive isolation. – When assortative mating is caused by male choosiness only (regime $\mathcal{M}$) because of drift on female choosiness, hybridization rate is higher than with mutual mate choice (blue area in Fig. 5d). If choosy males reallocate all courtship effort to court preferred females ($\alpha = 1$), there is no preference cycling (Fig. 5a); populations may drift into regime $\mathcal{M}$ for long periods of time, increasing hybridization rate (Fig. 5d).

If choosy males partially reallocate courtship effort (intermediate $\alpha \in [0.01, 0.9]$), preference cycling also increases hybridization rate (grey area in Fig. 5c-d). The coevolutionary dynamics underlying preference cycling greatly depends on how much courtship effort can be reallocated by choosy males (e.g. Fig. 4b vs. 4d). Overall, preference cycling strongly increases hybridization rate in simulations with $\alpha \simeq 0.8$ (Fig. 5d). For $\alpha \simeq 0.8$, preference cycling is rare (Fig. 5a), but it associates with long periods of time into regime $\mathcal{P}$ (Fig. 5b) during which hybridization rate is high (i.e. both female and male choosiness reach low frequencies, Fig. 5c). Overall, preference cycling leads to temporary peaks of hybridization

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(with up to 35% of hybridization, Fig. 5c), which periodically homogenize populations (e.g. fluctuation of the F_{ST}, Fig. S5).

Drift into regime $\mathcal{M}$ and preference cycling strongly increase hybridization rate in a context of weak disruptive viability selection (low s, Fig. S6) and in small populations (low K, Fig. S7) – i.e. if selection favouring female choosiness is too weak relative to genetic drift. Additionally, highly erroneously expressed choosiness are strongly favoured by selection and have the counterintuitive effect of decreasing hybridization rate (there is no preference cycling if ϵ_{m} and ϵ_{f} are high, Fig. S8).

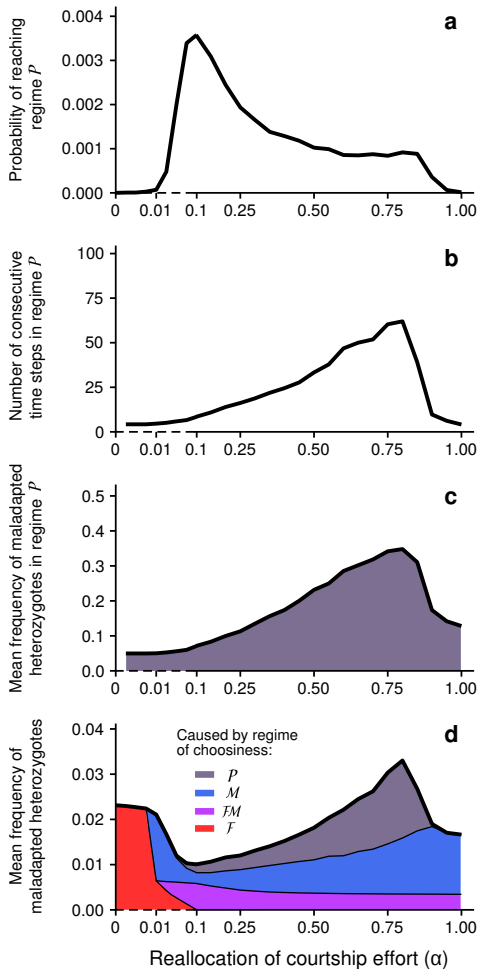

Figure 5: Coevolutionary dynamics of choosiness and resulting hybridization rate in stochastic simulations ($s = 0.2$, $K = 500$). To describe the coevolutionary dynamics of female and male choosiness, we record the probability of reaching regime $\mathcal{P}$ (a), the number of consecutive time steps in regime $\mathcal{P}$ (b) and the frequency of maladapted heterozygotes (Aa at locus A) in regime $\mathcal{P}$ before viability selection occurs (c). To assess the resulting hybridization rate, we record the mean frequency of maladapted heterozygotes over evolutionary time (d). In subfigure d, we also represent the mean contribution of each regime of choosiness to hybridization. In stochastic simulations, the coevolutionary dynamics of female and male choosiness increases hybridization rate despite selection favouring mutual mate choice ($\alpha > 0.01$) (d). In particular, the coevolution of female and male choosiness leads to periodic episodes of random mating, strongly increasing hybridization rate (with up to 35% of hybridization) (c).

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DISCUSSION

Surprising coevolutionary dynamics of male and female mate choice occur when the preferences of both sexes are based on the same phenotypic trait under disruptive selection. We showed that choosiness in one sex influences the evolution of choosiness in the other, a factor that has not been considered in previous models of mate choice in the context of reproductive isolation. Based on our model predictions, genetic drift, incomplete reallocation of courtship effort and errors in decision-making all prove to be important when understanding the outcome of this coevolutionary dynamics in term of reproductive isolation.

In our model with polygyny, male and female preferences are based on the same phenotypic trait, but are themselves governed by different loci. Selection generates linkage disequilibria between preference and ecological loci (despite free recombination), and indirect viability and sexual selection resulting from this linkage has profound consequences on the evolution of female and male choosiness. Additionally, female or male mate choice can substitute each other as drivers of assortative mating. For instance, if males are choosy while females are not, this is enough to generate assortative mating. Consequently, male choosiness relaxes indirect selection on female choosiness; in particular, even nonchoosy females avoid getting unfit hybrids, as males focus their efforts on females of their own ecotype. In turn, female choosiness relaxes indirect selection on male choosiness in a similar manner, but also strongly favours the evolution of male choosiness. If females are not choosy, male choosiness is often a poor courtship strategy, as it brings about unnecessary competitive and opportunity costs that could have been avoided through indiscriminate courtship. On the contrary, if females are choosy, males with indiscriminate courtship waste courtship effort that could be used to court females likely to accept them. Female choosiness thereby favours the evolution of male choosiness even if little of the courtship effort saved (by refraining from courting unpreferred females) is reallocated to get a mating advantage with preferred females. As a whole, selection favouring mutual mate choice should therefore be common under disruptive viability selection.

Our model shows, however, that selection favouring mutual mate choice can make reproductive isolation unstable. The coevolutionary dynamics of female and male mate preferences may lead to transient break down of premating isolation, strongly increasing hybridization rate. The fact that either sex can cause assortative mating makes it difficult for mate choice to be maintained simultaneously in both sexes by selection; if male preferences are sufficiently strong to establish assortativeness, female choosiness has little effect on the mating outcome and is therefore free to drift. Reduced female choosiness eventually re-establishes selection inhibiting male choosiness, and the overall outcome is preference 'cycling'. Premating isolation is often considered to initiate the process of divergence among taxa and its stability is therefore a key component for other isolating barriers to evolve. For instance, only stable premating isolation leads to accumulation of genetic incompatibilities among taxa and to subsequent postzygotic isolation[82,83]. Overall, therefore, selection favouring mutual mate choice may even be considered to inhibit speciation because it leads to dynamic instability of premating isolation. This contrasts with the traditional view of speciation as a gradual process characterized by a constant accumulation of barriers to gene flow ('speciation continuum')[6,69,84,85]. Speciation can also be "undone"; barriers to gene flow can dissolve and genetic discontinuities may vanish, thereby merging two taxa into a single population by hybridization[86–89]. Our model predicts such cycles of divergence and gene flow may actually characterize the process of diversification in nature.

Empirical research often estimates isolating barriers between pairs of populations varying in their level of differentiation

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to track the so-called 'speciation continuum'[6,69,84,85]. Empirical measures of the strength of those barriers are only point measurements and do not inform on the stability of reproductive isolation among populations. In particular, given the coevolutionary dynamics of male and female mate preferences, premating isolation caused by mutual mate choice does not necessarily mean that gene flow is reduced over long periods of time. In the same vein, if a species is partially fragmented across its range, preference cycling could cause different evolutionary histories among populations. For instance, spatial variation in reproductive isolation in *Catostomus* fish species over a large geographic area has been documented[90,91]. Yet, variation in hybridization is rarely quantified across several natural populations and it could mislead conclusions about the overall dynamics of reproductive isolation among taxa. More studies characterizing the strength of isolating barriers at a broader spatial and temporal scale are therefore needed to assess the variability of reproductive isolation.

The coevolutionary dynamics of female and male mate preference (and resulting reproductive isolation) depends crucially on how much courtship effort males reallocate towards preferred females, as a result of foregoing courting unpreferred females. By considering the reallocation of courtship effort (α), our model encompasses the ecological diversity in courtship and mating systems in animals. Choosy males can reallocate resources, which are required to court females (e.g. resources-demanding spermatophores[57] or nourishment gifts[58]). They can also reallocate time into searching preferred females or into improving the quality of the courtship display (e.g. complex courtship display[59,60]) (except if courting males can broadcast their messages to all nearby females simultaneously). Of course, the reallocation of resources and time into the courtship of preferred females also depends on the risk of mortality associated with mate searching. Therefore, to better understand the process of divergence between diverging taxa, it may be informative to consider estimating how much resources or time (i.e. courtship effort) choosy males can reallocate to court preferred females. Based on the predictions of our model, selection should favour mutual mate choice as long as there is some reallocation of courtship effort; otherwise male choice should be deleterious. However, if reallocation is only partial, preference cycling is likely to occur, possibly hampering further differentiation between those taxa.

The extent of reproductive isolation also depends on how accurately preferences are expressed. Perhaps counterintuitively, our model suggests that erroneously expressed preferences lead to strong reproductive isolation as a whole by strengthening selection favouring choosiness. Likewise, in a context of local adaptation, error-prone female choice has been shown to be more strongly favoured by selection than error-free choice because it maintains a higher diversity of male types in the population[92]. In our context, this means that the genetic architecture of the preference traits expressed in females and males greatly affects the divergence process. For instance, female and male preference loci are not associated with the same colour pattern loci in *Heliconius melpomene* and *Heliconius cydno*[70]. Therefore, individuals may not completely stop courting/mating accross ecotype boundaries (error-prone choice) because each sex may rely on a given property of the trait under disruptive selection. Our model predicts this error-proneness could strengthen selection favouring mutual mate choice, which could in turn inhibit preference cycling and "favour" speciation. This provides new light to understand the genetic architecture of speciation, i.e. the number and linkage of traits and genes underlying preferences in one or the other sex. Likewise, many theoretical studies have found cases where partial choosiness is an equilibrium state (because of sexual selection)[28–31,33]. More thorough theoretical investigation is required to assess the occurence of preference cycling if choosiness is modelled as a quantitative trait. In particular, if strong choosiness does not evolve, preference cycling may not occur; counterintuitively, this may "favour" speciation.

Our predictions are not limited to the context of emerging reproductive isolation among diverging populations. We can

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expect similar coevolutionary dynamics of female and male preferences in more advanced stages of reproductive isolation. Indeed, low viability/fertility of hybrids caused by genetic incompatibilities among more distantly related taxa generates disruptive viability selection. In that context, preference cycling could also temporally increase hybridization rate. This dynamics of reproductive isolation could conceivably explain the formation of 'hybrid swarm' and subsequent genetic introgression[3] or hybrid speciation[93].

Overall, our theoretical model adds support to the idea that premating isolation may often be readily reversible[32,83,88]. Intriguingly, we show that premating isolation should be especially unstable when selection favours mutual mate choice. We highlighted some factors that could inhibit preference cycling (strong selection against hybrid, high carrying capacity, numerous erroneous mate choices). The geographical context of speciation and more detailed genetic architectures may also change the modalities of preference cycling and should therefore be investigated theoretically. On the empirical side, the occurence of preference cycling and its impact on reproductive isolation remains to be tested. More generally, our study should stimulate further research on the stability of barriers to gene flow.

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