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How many cues are sexy ? Evolution of mate preference towards multiple traits in sympatric species

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Abstract

While the impact of mate preference on adaptation and speciation has been extensively studied, the evolutionary factors determining which and how many traits are targeted by mate choice are largely unknown. In sympatric species, trait distribution is shaped by similar selective pressure, promoting similar adaptive traits in the different species. When preference targets such adaptive traits, the similarity between species induce heterospecific matings and costs for the choosy partners. The evolution of preference for different traits thus likely depends on the ecological interactions between species. Using a mathematical model, we thus study the evolution of preference towards two evolving traits shared by sympatric species and we investigate how selective regimes on traits, opportunity costs and sensory trade-off shape the evolution of preference for multiple traits. As expected, the evolution of multiple traits preference is favored when females have access to a large number of mates and when there is limited sensory trade-off. More surprisingly, opportunity costs promote preference based on adaptive traits, rather than on traits relevant for species recognition. Since adaptation reduces trait variability in males, the evolution of preferences based on adaptive traits hardly suffers from opportunity costs. Our model thus highlights that the evolution of preferences for different traits in sympatric species depends on within-species mating opportunities but also on the niche overlap between species, tuning the heterospecific interactions.

Introduction

The evolution of mate preference plays a major role in the diversification of traits and species in the wild. Yet, little is known on the evolutionary factors determining the traits preferentially targeted by preferences, and especially the number of different cues used during mate choice.

Preferences are based on traits displayed by the parents, but their evolution usually depends on the indirect fitness benefit in the offspring (Neff and Pitcher, 2005). The fitness of the offspring depends not only on the intraspecific competition but also on the ecological interactions with sympatric species. When poorly-divergent species occur in sympatry, mate preferences targeting certain traits can be promoted because of the reduced fitness in the hybrids (Merrill et al., 2012), but also because of the reduction in costly sexual interactions with heterospecifics (Gröning and Hochkirch, 2008). The evolution of preferences may therefore strongly depend on the selection regimes acting on the targeted traits within species, but also on the distribution of these traits in other species living in sympatry. Such multifarious selection acting on the different traits displayed by males may then

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favor the evolution of female preferences targeting several traits. Using multiple cues may indeed improve some components of the fitness in the offspring and/or enhance recognition of conspecific males (Candolin, 2003).

Multiple traits preference may then be promoted when targeting traits associated with different components of the indirect fitness benefit (*e.g.* (Doucet and Montgomerie, 2003; Girard et al., 2015; Dale and Slagsvold, 1996)). Theoretical modeling show that preference towards multiple traits providing different indirect fitness benefit can evolve (Iwasa and Pomiankowski, 1994). The evolution of preference towards multiple non-adaptive cues can occur, when these cues provide greater reproductive success in the sons (*sexy sons hypothesis*) (Pomiankowski and Iwasa, 1993), suggesting that sexual selection can also promote the evolution of preference for multiple traits. Furthermore, selection promoting species recognition also promotes the evolution of preference for multiple traits that differentiate closely related species (Hohenlohe and Arnold, 2010; Vortman et al., 2013; Patten et al., 2004). While several sexual and natural selection have been suggested to favor the evolution of multiple traits preference, such evolution is likely to crucially depend on trait variations and covariation within and among sympatric species. By contrast with classical 'magic' traits (Servedio et al., 2011), similar traits may be promoted by natural selection in different sympatric species (*e.g.* in mimetic species, Boussens-Dumon and Llaurens (2021)), indirect fitness benefit may then induce selection on preference conflicting with species recognition(*e.g.* (Gumm and Gabor, 2005; Higgie and Blows, 2007)). For example, in the spadefoot toad, preference for mating call increases the number of eggs fertilized in choosy females but leads to reproductive interference, because of the similarity of call between sympatric species (Pfennig, 2000). Preferences targeting multiple traits may then allow to improve both offspring fitness through the transmission of adapted alleles and species recognition. For example, in field crickets of the genus *Teleogryllus*, female targets both (1) CHCs, providing fitness benefits to their offspring (Berson and Simmons, 2019), and (2) male calling song (Hill et al., 1972) that differentiate sympatric species (Moran et al., 2020).

While preference based on multiple traits may be promoted by natural and sexual selection, several constraints might limit the number of traits targeted by preference. Preferences are generally associated with fixed cost generated by mate searching, and these costs might be increased when preference targets multiple traits. Theoretical studies indeed show that the joint fixed costs of preference based on different trait indeed promotes preference based on single trait providing the greatest benefit (Schluter and Price, 1993), especially when the joint fixed costs quickly increases with the strength of preference for each trait (Pomiankowski and Iwasa, 1993; Iwasa and Pomiankowski, 1994). The evolution of preference for multiple traits may also be limited by the number of available partners displaying the preferred combination of traits. Opportunity costs associated with female rejection in choosy females may then increase when the number of targeted traits grows.

The evolution of multiple traits preference may also be limited by the complex cognitive processes involved, explaining the low number of traits used in mate choice in some clades (Candolin, 2003). Multiple traits-based mate choice may thus preferentially evolve in species where multiple sensory systems allow such cognitive integration. Evolutionary trade-off are often thought to limit the evolution of multiple sensory system: the development of sensory systems is frequently associated with the regression of others (Barton et al., 1995; Nummela et al., 2013). Moreover, physical constraints may generate sensory trade-offs: for example, visual system model of the surfperch reveals trade-off in the performance between luminance and chromatic detection, because of the limited numbers of the different types of cones in the eyes (Cummings, 2004). Neural integration of multiple information may also be limited, generating trade-offs in the use of multiple traits in decision. In the swordtail fish *Xiphophorus pygmaeus*, females express preference for a visual and

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an olfactory traits when there are exposed to the variation of only one trait within potential mate. However, when both traits vary within potential mates, females do not express preference (Crapon de Caprona and Ryan, 1990), suggesting that sensory trade-off limits the use of multiple traits in preference.

These contradictory developmental and ecological factors call for a general framework determining the evolution of preferences towards different traits shared between sympatric species, that may be either neutral or shaped by natural and sexual selection. Here, we thus use mathematical modeling to investigate the evolution of preference based on multiple traits. We study the evolution of preference towards two evolving traits (T_1 and T_2) shared by two sympatric species (A and B) aiming at identifying how selection regimes acting on the targeted traits, as well as reproductive interference between species favor preference targeting a single *vs.* multiple traits.

Method

Modelling the evolution of female preference targeting different traits

We consider two closely-related species (A & B) living in sympatry, and assume that individuals from both species display two main traits controlled by a single haploid locus (loci T_1 and T_2 respectively, with two possible alleles 0 or 1). We fix the genotypic distribution in species B and we study the evolution of traits and preference on those traits in the focal species species A.

Only females express mate preference towards the traits displayed by males, and their preference depends on their own phenotype (following the matching rule described in Kopp et al. (2018)): we assume assortative preference whereby preferentially mate with males displaying traits similar to their own traits (Figure 1). Female assortative preference can target either traits (1 and 2) displayed by the males. A preference modifier locus M controls the relative level of attention of females toward trait 1 *vs.* trait 2 during their choice expressed by males (referred to as the preference direction γ). We assume that only two alleles can occur at locus M with different values of γ modulating the level of attention on either traits. The set of different loci is given by $\mathcal{L} = \{T_1, T_2, M\}$ and each genotype is a vector in $\mathcal{G} = \{0, 1\}^3$. We study the invasion of the mutant allele 1 associated with the value γ_m in the species A, where the allele 0, associated with the value γ_{wt}, was initially fixed.

We assumed that females can encounter and have sexual interactions with heterospecifics. Heterospecific sexual interactions lead to fitness costs but do not produce any viable offspring. The evolutionary fate of the mutant at locus M in species A may thus depend on (1) reproductive interference promoting preferences that enhance species recognition and (2) the selection regime acting on traits T1 and T2, enhancing the offspring survival. We assume an infinite population and we track down the frequency of each genotype across generations in species A. We assume that a generation is composed of three steps: (1) natural selection, (2) reproduction and (3) mutation, as detailed below.

Selection regime acting on the displayed traits

We assume that the traits T_1 and T_2 displayed by the individuals can modify their survival. We define f_i and f_i' as the frequencies of genotype $i\{1, 2\}$ in the focal species before and after a step of natural selection acting on survival, respectively. The resulting frequency after selection, f_i' is then

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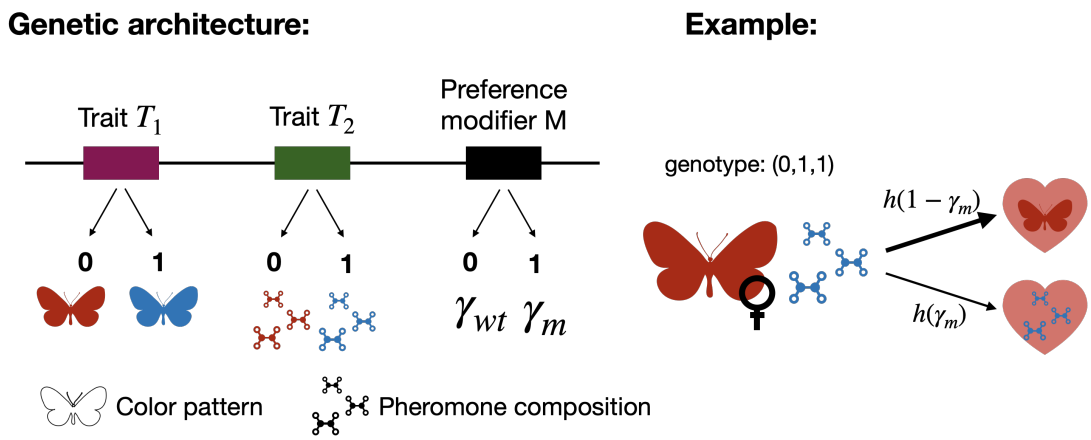

Figure 1: **Genetic architecture underlying trait and preference in species A**. As an illustrative example, here we show trait 1 as wing coloration and the trait 2 as a pheromonal composition. See also an illustration of the phenotype and behavior of a female of genotype vector $(1, 0, 1)$. We note γ as the parameter controlling the preference direction, and h as the function describing the cognitive trade-off regulating the amount of attention paid to both traits

given by

$$f_i' = \frac{w_i}{\overline{w}} f_i, \tag{1}$$

where w_i is the fitness component due to natural selection of an individual of genotype i, while $\overline{w}$ is the average fitness component due to natural selection averaged.

$$\overline{w} = \sum_{i \in \mathcal{G}} w_i f_i, \tag{2}$$

where $\mathcal{G}$ is the set of all genotypes.

We note s_1 and s_2 the selective advantages associated with allele 1 at locus T_1 and T_2, respectively. When natural selection favors individuals with allele 0 at locus T_i, s_i is negative for $i \in \{1, 2\}$.

The fitness component due to natural selection of an individual of genotype i is thus given by:

$$w_i = (1 + (T_1)_i s_1)\,(1 + (T_2)_i s_2)\,, \tag{3}$$

where $(T_j)_i$ is the value of trait T_j (0 or 1) of individuals of genotype i for $j \in \{1, 2\}$.

Reproductive success depending on female preference on traits displayed by males

Genotypic frequencies after reproduction in the focal species then depend on the contribution to the next generation of the different crosses between females and males of genotype j and k respectively, described by $m_{j,k}$, for all j and k in $\mathcal{G}$. We note $\overline{m}$ the mean value of this contribution across all

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mating pairs

$$\overline{m} = \sum_{j,k \in \mathcal{G}} f'_j f'_k m_{j,k}. \tag{4}$$

The frequency after reproduction of genotype i in species A is then given by

$$f''_i = \sum_{j,k \in \mathcal{G}} f'_j f'_k \frac{m_{j,k}}{\overline{m}} \beta(i,j,k), \tag{5}$$

where $\beta(i,j,k)$ describes the segregation of alleles during reproduction and provides the probability that a mating between a female of genotype j and a male of genotype k produces an offspring of genotype i. We assume recombination between female's and male's haplotypes, then the offspring inherits randomly from one of the two recombined haplotypes.

The contribution to the next generation of a mating of a pair then depends on the female preference towards the traits displayed by males, controlled by loci T_1 and T_2. Assortative preference is assumed and the relative attention given by a female of genotype j to trait 2 vs. trait 1 is controlled by the preference direction parameter γ_j, determined by the allele at locus M: allele 0 is associated with γ_{wt} and allele 1 is associated with the value γ_m. The attention provided on male trait in a female of genotype j is thus given by:

$$\gamma_j = (1 - (M)_j)\gamma_{wt} + (M)_j \gamma_m, \tag{6}$$

where $(M)_j$ is the allele (0 or 1) at locus M in genotype j. We assume that the relative attentions to the two traits, controlled by the parameter γ are submitted to a cognitive trade-off described by the function h: attention on trait 1 and 2 are respectively given by $h(1-\gamma)$ and $h(\gamma)$ with

$$\forall x \in [0,1], h(x) = x^a \quad \text{and} \quad a \in [0, +\infty).$$

h is a non-decreasing function, so that attention on one trait diminishes attention on the alternative one. Moreover, $h(0) = 0$ and $h(1) = 1$, so that in the two extreme cases, female choice relies on a single trait. The parameter a tunes the shape of the trade-off function h (see Figure A1):

- when $a = 1$, h is linear, leading to a **linear trade-off**, where the female attention on traits 1 (resp. 2) is proportional to $1 - \gamma$ (resp. γ) (see black curve in Figure A1).
- when $a < 1$, h is concave, leading to a **weak trade-off** between attention towards the two male traits. Females can thus use both traits for mate choice (see blue curve in Figure A1).
- when $a > 1$, h is convex leading to a **strong trade-off** in female attention between the two traits. Females focusing on one trait largely ignore the alternative trait, and intermediate values of γ lead to poor attention on both traits (see red curve in Figure A1).

Therefore, when a female of genotype j in species A encounters a male of genotype k, she accepts the male with probability

$$\phi(j,k) = \Big(1 - \mathbb{1}_{(T_1)_j \neq (T_1)_k} \rho h(1-\gamma_j)\Big)\Big(1 - \mathbb{1}_{(T_2)_j \neq (T_2)_k} \rho h(\gamma_j)\Big), \tag{7}$$

where $\mathbb{1}_{\{.\}}$ is the indicator function that returns 1 if the condition in subscript is realized and 0 otherwise. The parameter ρ quantifies the strength of assortative female preference.

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During an encounter between individuals from different sexes, the probability that a female of genotype j accepts a conspecific male is then given by (Otto et al., 2008):

$$T(j) = \sum_{k \in \mathcal{G}} \overbrace{\frac{N}{N+\tilde{N}} f'_k}^{\substack{\text{probability of encountering} \\ \text{a conspecific male} \\ \text{of genotype } k}} \overbrace{\phi(j,k)}^{\substack{\text{probability of accepting} \\ \text{a conspecific male} \\ \text{of genotype } k}} , \tag{8}$$

where N and $\tilde{N}$ are the densities of species A and B respectively.

A female of genotype j may also accept an heterospecific male with probability

$$T_{RI}(j) = \sum_{k \in \mathcal{G}} \overbrace{\frac{\tilde{N}}{N+\tilde{N}} \tilde{f}_k}^{\substack{\text{probability of encountering} \\ \text{an heterospecific male} \\ \text{of genotype } k}} \overbrace{c_{RI}\phi(j,k)}^{\substack{\text{probability of accepting} \\ \text{an heterospecific male} \\ \text{of genotype } k}} , \tag{9}$$

where $c_{RI} \in [0,1]$ captures the investment of females in interspecific mating. This cost of reproductive interference incurred to the females can be reduced when female preference is also based on alternative traits differing between species, or when individuals from both species do not encounter frequently. We assume that heterospecific crosses never produce any viable offspring, and that a female engaged in such a mating cannot recover the associated fitness loss.

Knowing that a female of genotype j has mated with a conspecific male, the probability that this male is of genotype k is given by

$$\Phi(j,k) = \frac{\phi(j,k) f'_k}{\sum_{l \in \mathcal{G}} \phi(j,l) f'_l}. \tag{10}$$

If females only encountered one male, the proportion of crosses between a female of genotype j and a conspecific male of genotype k would be

$$\mathcal{P}^1(j,k) = f'_j T(j) \Phi(j,k). \tag{11}$$

However, we assume that females refusing a mating opportunity can encounter another male with probability $1-c$. We interpret c as the cost of choosiness (similar to the coefficient c_r, referred to as relative cost of choosiness in (Otto et al., 2008)). The proportion of crosses between a female of genotype j and a conspecific male of genotype k is thus given by

$$\begin{aligned} \mathcal{P}(j,k) &= \sum_{n=0}^{+\infty} \left(\left(1 - T(j) - T_{RI}(j)\right)(1-c) \right)^n \mathcal{P}^1(j,k) \\ &= \frac{\mathcal{P}^1(j,k)}{c + (1-c)(T(j) + T_{RI}(j))}, \end{aligned} \tag{12}$$

where $\left(\left(1 - T(j) - T_{RI}(j)\right)(1-c) \right)^n$ is the probability that a female of genotype j rejects the n males she first encounters and then encounters an $(n+1)-th$ male.

The contribution to the next generation of a mating between a female of genotype j and a male of genotype k is thus given by

$$m_{j,k} = \frac{T(j)}{c + (1-c)(T(j) + T_{RI}(j))} \frac{\phi(j,k)}{\sum_l f'_l \phi(j,l)}. \tag{13}$$

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Mutation

We assume that mutations can occur at loci T_1, T_2 within offspring. We assume that with probability $u^{T_i}_{0\to 1}$ (resp. $u^{T_i}_{1\to 0}$) allele 0 (resp. 1) mutates into allele 1 (resp. 0) at locus $T_i, i \in \{1, 2\}$.

All variables and parameters used in the model are summed up in Table A1.

Model exploration

Using QLE analysis to determine the evolutionary stable preference direction

We perform a Quasi-Linkage Equilibrium (QLE) analysis allowing to estimate the change of allele frequency at each locus. QLE analysis assumes that selection is weak and that recombination is strong compared to selection. In line with this hypothesis, we assume that s_1, s_2, ρ, c_{RI}, c are of order ε with ε low and that the recombination rates are of order 1. We also assume that mutation rates are of order ε. The QLE analysis is performed using Wolfram Mathematica 12.0 and all the details of the analytical results are presented in Appendix A1.

The QLE analysis allows to numerically estimate the evolutionary stable value of γ. The mutant is introduced at frequency P^0_M. We assume that the mutations at locus M have a low effect *i.e.* the difference γ_{wt} and γ_m is small (but see Appendix 1 for mutations with high effect). We consider:

- Evolutionary stable γ: value of γ_{wt} preventing the invasion of any other mutation of small effect at locus M.
- Repulsor: value of γ_{wt} enabling the invasion of other mutations of small effect at locus M.

We assume that once a mutant increases in frequency after its introduction it replaces the wild type allele in the population. Then the preference direction γ in the population tends to one of the evolutionary stable value refer as equilibrium value γ^*.

In these QLE analyses, we generally assume that ancestral preference equally targets both traits ($\gamma_0 = 1/2$). However, the evolutionary stable direction of preference γ^* may depend on the ancestral value γ_0, we thus study the dependence to ancestral preference direction assuming the three different selective regimes detailed below, and summarized our findings in the Appendix (see Figures A2, A5 and A7).

In all these three cases, we also study the effects of the shape of the trade-off function h (trough the parameter a) and of opportunity costs (through the parameter c) on equilibrium preference direction.

Selection regimes promoting the evolution of multiple trait preference

We applied the QLE analysis method described above to specifically investigate three main selective regimes and to test their respective effects on the evolution of multiple traits preference in females.

(a) Preference enhancing offspring fitness

First, we consider that both trait provide an indirect fitness benefit due to natural selection ($s_1 > 0$ and $s_2 > 0$). To explicitly investigate whether preference would be based on multiple traits or on

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the trait providing the strongest indirect fitness benefit, we assume that natural selection acts more intensely on trait T_1 than on T_2 (*i.e.* $s_1 > s_2$). We assume no cost generated by heterospecific interactions ($c_{RI} = 0$), but still hypothesize complete inviability in the hybrids.

(b) Preference enhancing species recognition

We then assume that heterospecific interactions generate costly reproductive interference between sympatric species ($c_{RI} = 0.01$) and investigate how selection promoting reproductive isolation impacts the evolution of multiple traits preference. When assuming reproductive interference costs, the advantage gained from a choice based on given trait crucially depends on the phenotypic distribution of this trait in the two sympatric species. We then consider that in species A, because of mutations, trait value 1 is common at both traits with the frequency of trait value 1 higher at trait T_1 than at trait T_2 ($u^{T_1}_{0\to1} = 0.003$, $u^{T_1}_{1\to0} = 0.001$, $u^{T_2}_{0\to1} = 0.002$ and $u^{T_2}_{1\to0} = 0.001$). We also explored the impact of different phenotypic distributions in species B in the evolution of preferences in species A. We focus only on the impact of reproductive interference on the evolution of preference and therefore assume that neither trait T_1 nor T_2 are submitted to natural selection ($s_1 = s_2 = 0$).

(c) Preference enhancing both offspring fitness and species recognition

Finally, we test whether multiple trait preference can be promoted when one trait is submitted to a natural selection in both sympatric species, therefore also promoting preference towards an alternative trait neutral from selection, that may enhance species recognition. We then assume a natural selection regime promoting the same trait value 1 at T_1 in both species. We thus assume that natural selection favors trait values 1 ($s_1 > 0$) in species A and that trait value 1 is fixed ($\tilde{P}_{T_1} = 1$) in species B. We then assume costs generated by reproductive interference ($c_{RI} > 0$), so that preferences based on T_1 are likely be costly. We then assume that both species are easily distinguishable based on trait T_2. We thus assume that the frequency of allele 0 at trait T_2, is higher in species A, whereas allele 1 is more common in species B ($\tilde{P}_{T_1} = 0.6$). We investigate several strengths of natural selection favoring allele 1 at trait T_1 (s_1), as well as several strengths of reproductive interference (c_{RI}). Because the proportion of maladapted trait value 0 at T_1 increases the advantage of choosing adapted trait value 1, we investigate the effect of different mutation rates at locus $T1$, assuming a symmetrical mutation rate ($u^{T_1}_{0\to1} = u^{T_1}_{1\to0}$).

Scripts availability

Scripts are available online at github.com/Ludovic-Maisonneuve/evolution$_of_multiple_traits_preference$.

Results

We investigate the evolution of multiple traits preference in females by studying the invasion of a mutant at a modifier locus M, determining the attention paid to either traits (T_1 and T_2) displayed in males. We applied a QLE approach to determine the equilibrium level of attention paid to either traits γ^*, depending on the shape a of the cognitive trade-off limiting the attention on both traits simultaneously (see methods).

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Which traits indicate 'good genes' ?

We first assume no costly heterospecific interaction and test the effect of natural selection acting on both traits (T_1 and T_2) on the evolution of female preference. Female preference towards the two traits can be promoted because of the positive effects generated on the fitness of their offspring when they carry the adapted alleles. Furthermore, preference may also be promoted by sexual selection, because females have an advantage to produce 'sexy offspring' (see Equation (A10)). By contrast with previous model (Pomiankowski and Iwasa, 1993), our model show that sexual selection alone can not promotes drive the evolution of multiple traits preference (see Appendix A2).

When assuming natural selection on the traits ($s_1 > 0$ and $s_2 > 0$), our model does predict the evolution of multiple trait preference. Assuming that ancestral preference equally target both traits ($\gamma^0 = 1/2$), the fitness benefit gained by the offspring displaying adapted alleles of females carrying a mutant allele at the preference at the modifier locus M promotes the evolution of multiple preference. To specifically study the evolution of preference towards several traits in this 'good genes' hypothesis, we consider that natural selection acts more intensely on T_1 ($s_1 > s_2$), and determine the condition favouring the evolution of preference on both traits. Assuming a weak cognitive trade-off (low a) and opportunity costs (low c), the evolutionary stable preference is based on both traits, with more attention on trait T_1 under stronger selection (see hatched area in Figure 2 (a)). This preference leads to the production of offspring with adapted alleles at both traits. However, stronger cognitive trade-off and opportunity costs prevent the evolution of such multiple traits preference (Figure 2 (a)). Interestingly, linear trade-off ($\log(a) = 0$) leads to preference uniquely based on the trait under stronger selection (Figure 2 (a)). A weaker trade-off than linear trade-off is thus a necessary condition for the evolution of multiple traits preference, when both traits are under natural selection.

When assuming a strong trade-off, the evolution of preference also tightly depends on the ancestral preference value (γ^0) (Figure A2). When the preference initially targets the trait T_2 ($\gamma^0 \simeq 1$), the evolution of female preference favours more attention towards the mildly selected trait T_2 (see Figure A3). This is probably due to the strong sexual selection initially promoting preference on T_2: when trait T_2 is ancestrally targeted by preference, it provides an indirect fitness benefit due to the production of 'sexy son'. This sexual selection promoting preference targeting T_2 conflicts with the natural selection, promoting preference targeting T_1. Moreover, when assuming a strong cognitive trade-off, preference based on both traits leads to poor attention towards both traits, thus creating a fitness valley limiting the switch of female attention from one trait toward the alternative ones. When female choice is ancestrally mainly based on trait T_2, therefore creating positive sexual selection favouring preference on T_2, the positive selection on T_1 is not powerful enough to cross this fitness valley, and the evolution towards attention to the trait T_1 is not observed. However, the cross of this fitness valley is facilitated when mutations have a larger effect size (see figure A4).

Which traits participate to reinforcement ?

We then investigate whether reinforcement of species barriers promoted by reproductive interference may promote the evolution of multiple traits preference. We assume costly reproductive interference ($c_{RI} = 0.01$), and that both traits are not under natural selection ($s_1 = s_2 = 0$). We assume that trait value 1 is common at both traits in species A, whereas trait value 0 is common at both traits in species B, so that both traits are relevant cues for species recognition. Similarly to the natural selection regime explored above (hypothesis (a)), we assumed a higher frequency of trait value 1 in trait T_1 than at trait T_2, making T_1 the best cue for species recognition. Similarly to the results

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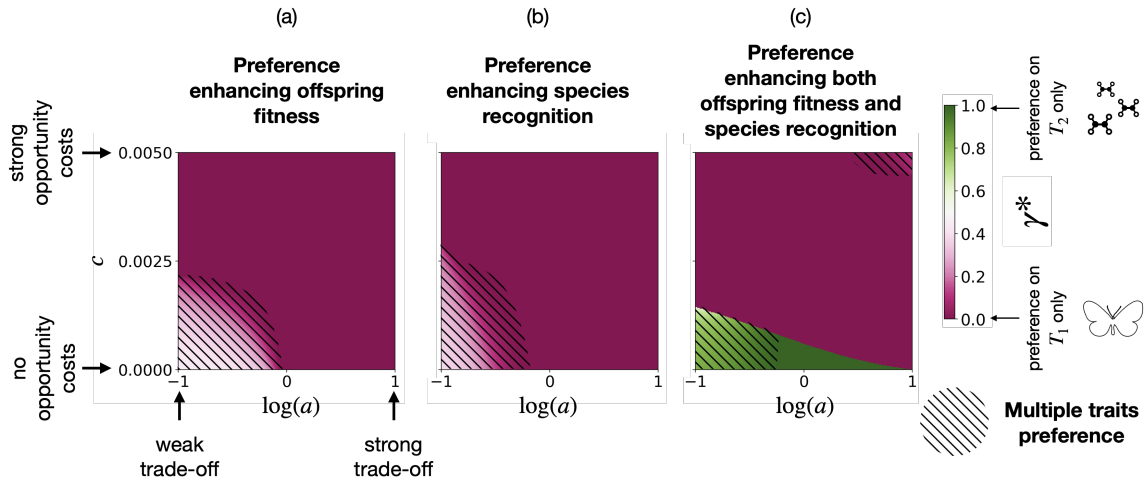

Figure 2: **Evolution of female preferences, depending on three different selection regime**. The three plot investigates the effect of the cognitive trade-off function a and on cost of choosiness c on the equilibrium preference direction γ^*, for these 3 selective regimes. Hatched area indicates parameter combinations where multiple traits preference is observed at equilibrium ($0 < \gamma^* < 1$). In species A, mutation and natural selection promotes trait value 1 at both traits ($u^{T_1}_{0\to1} = 0.003$, $u^{T_1}_{1\to0} = 0.001$, $u^{T_2}_{0\to1} = 0.002$, $u^{T_2}_{1\to0} = 0.001$, $s_1 \geq 0$ and $s_2 \geq 0$). We assume: (a) that both traits are under natural selection, with stronger selection on T_1 than T_2 ($s_1 = 0.02$ and $s_2 = 0.01$), (b) reproductive interference ($c_{RI} = 0.05$) and that both trait may allow species recognition ($\tilde{P}_{T_1} = \tilde{P}_{T_2} = 0$) (c) reproductive interference ($c_{RI} = 0.05$), that trait T_1 is under natural selection ($s_1 = 0.02$) and that trait T_2 may allow species recognition ($\tilde{P}_{T_2} = 0.4$). Ancestrally preference equally targets both trait ($\gamma_0 = 1/2$). By default we assume: $P^0_{T_1} = P^0_{T_2} = 0.5$, $P^0_M = 0.01$, $\tilde{P}_{T_1} = \tilde{P}_{T_2} = 1$, $s_1 = s_2 = 0$, $\rho = 0.01$, $c_{RI} = 0$, $N = \tilde{N} = 10$. Note that the dependence of these results to the ancestral value γ_0 is detailed in Figure A2.

obtained for hypothesis (a), multiple traits preference can evolve when the cognitive trade-off and the opportunity costs are weak (Figure 2 (b)).

When assuming that heterospecific mating attempts may happen, the advantage gained from a choice based on a given trait crucially depends on the phenotypic distribution of this trait in the two sympatric species (see Equation (A6)). We then explored different phenotypic distributions in species B, to investigate the effect of heterospecific mating on the evolution of the targeting of the trait by females.

When species differ in the distribution of both traits preferences based on both traits then become advantageous, leading to multiple traits preference (Figure 3). Else single trait preference based on the trait that differentiate the most conspecific and heterospecific evolve. The parameter space where females choose only on trait T_1 is wider because this trait is more likely to differentiate species as the frequency of trait value 1 is higher at trait T_1 than at trait T_2.

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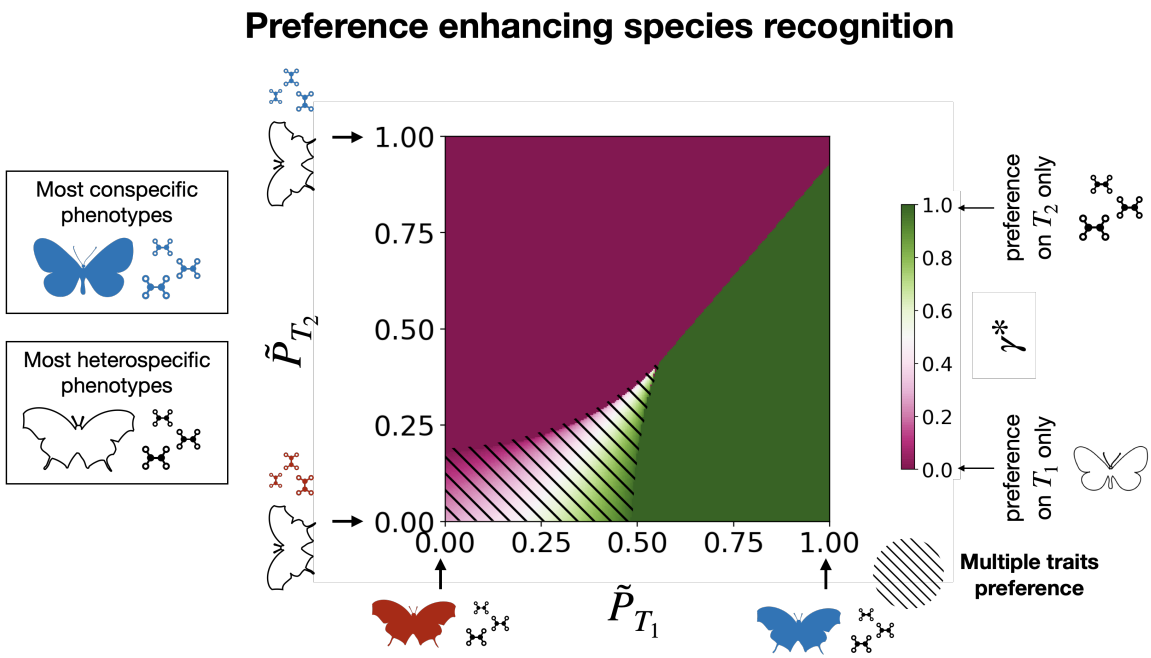

Figure 3: **Equilibrium preference direction γ^* depending on the phenotypic distributions in species B ($\tilde{P}_{T_1}$ and $\tilde{P}_{T_2}$).** Hatched area indicates parameter combinations where multiple traits preference is observed at equilibrium ($0 < \gamma^* < 1$). In species A, mutations promote trait value 1 at both traits ($u^{T_1}_{0\to1} = 0.003$, $u^{T_1}_{1\to0} = 0.001$, $u^{T_2}_{0\to1} = 0.002$, $u^{T_2}_{1\to0} = 0.001$. Ancestrally, preference equally targets both trait ($\gamma_0 = 1/2$). We assume: $P^0_{T_1} = P^0_{T_2} = 0.5$, $P^0_M = 0.01$, $s_1 = s_2 = 0$, $\rho = 0.01$, $c = 0.001$, $c_{RI} = 0.05$, $a = e^{-1}$, $N = \tilde{N} = 10$. Note that the dependence of these results to the ancestral value γ_0 is detailed in Figure A5.

Connecting 'good genes' and reinforcement theory

We explore the evolution of multiple traits preference that may allow producing fitted offspring, while enhancing species recognition. We thus assume that the trait T_1 is under natural selection, leading to resemblance to species B (*e.g.* modeling sympatric species where the same trait allow local adaptation in both species): we assume that natural selection favors trait values 1 ($s_1 > 0$) in species A and that trait value 1 is fixed ($\tilde{P}_{T_1} = 1$) in species B. In contrast, the trait T_2 is not submitted to natural selection, but is a relevant cue for species recognition: we assume that the frequency of allele 1 is higher in species A, whereas allele 0 is more common in species B ($\tilde{P}_{T_1} = 0.4$).

Weak trade-off and opportunity costs allow the evolution of multiple traits preference mainly based on the neutral trait allowing species recognition (T_2) (Figure 2 (c)). Opportunity costs then promote preference based on trait under natural selection T_1 (Figure 2 (c)). Indeed natural selection acting on trait T_1 reduces phenotypic diversity in the focal species and therefore also reduces opportunity costs associated with preference based on the trait T_1 in this species (see Equation (A9)). Thus high mutation rate at trait T_1, leading to high phenotypic diversity, limits

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preference based on trait under natural selection T_1 (Figure A6). Increasing values of the cognitive trade-off promotes choice on the the trait T_2 (Figure 2 (c)), because it provides a better fitness benefit (Note that this fitness benefit depends on our assumptions on the relative levels of strength of natural selection on T_1 and of reproductive interference, see below). However, when opportunity costs increases, an increase of trade-off then leads preference to target only targeting the trait under natural selection (T_1) (Figure 2 (c)). Trade-off promotes preference mainly based on one trait, however preference mainly based on neutral trait leads to stronger opportunity cost because of the higher phenotypic diversity in the neutral trait (T_2), while natural selection on the trait T_1 strongly limit intra-specific diversity. Then strong trade-off, in interaction with opportunity costs, promotes preference targeting only the naturally selected trait T_1.

Very strong trade-off and opportunity costs surprisingly promote multiple traits preference (Figure 2 (c)). Due to the important trade-off, this preference leads to poor attention on both traits, resulting in almost random mating, that limits opportunity costs.

We then investigate the impact of the strength of natural selection favoring allele 1 at trait T_1 (s_1) and the strength of reproductive interference (c_{RI}) on the evolutionary stable preference direction. As expected natural selection (resp. reproductive interference) promotes preference based on the naturally selected trait T_1 (reps. the trait allowing species recognition T_2) (Figure 4). Without opportunity costs ($c = 0$), natural selection promotes multiple traits preference, whereas reproductive interference leads to preference targeting T_2 only. Because we assume complete inviability in the hybrids, with strong reproductive interference, females prioritize species recognition.

Opportunity costs ($c = 0.001$) allow only the evolution of multiple traits preferences that mainly target the neutral trait. Multiple traits preferences mainly targeting the naturally selected trait would reduce the phenotypic diversity at trait T_1, *via* sexual selection. Thus such preferences would, by reducing opportunity costs, strongly advantage preference targeting T_1 and then promotes the single trait preference targeting the trait T_1.

Altogether our results show how natural and sexual selection, sensory trade-off and ancestral preference shape the evolution of female preference toward different traits displayed by males.

Discussion

Mate preferences have been extensively studied in the light of the 'good genes' hypothesis (Puurtinen et al., 2009) or in the context on reinforcement (Servedio and Noor, 2003). By jointly considering (1) the selection regimes acting on the targeted traits within species, as well as (2) interactions with other species living in sympatry, our theoretical study provides a general framework reconciling these research fields.

We thus focused on natural selection regime shared between sympatric species promoting species similarity, increasing risks of reproductive interference. Our approach thus drastically differ from classical studies on reinforcement, focusing on 'magic traits', submitted to disruptive selection between species (Servedio et al., 2011). Because 'magic traits' are honest signals of both local adaptation and of species identity, there is no antagonistic selection regimes that may promote the evolution of multiple trait preferences in this case.

Our results show that opportunity costs play a key role in the evolution of multiple trait preference. In our model, the opportunity costs promotes preference based on naturally selected traits rather than on traits allowing species recognition. As natural selection erodes phenotypic diversity, preference based on traits allowing species recognition leads to stronger opportunity cost, promoting preference targeting the naturally selected traits. However, the low level of variations are usually

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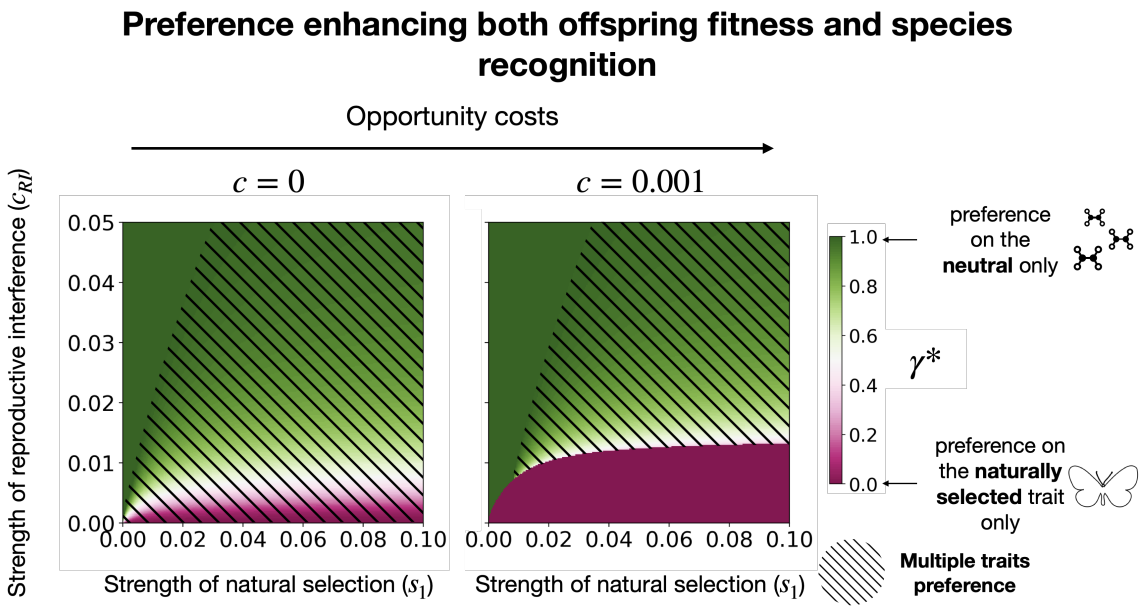

Figure 4: **Evolution of preference direction γ^*, depending on the strength natural selection acting on trait T_1 (s_1) and the strength of reproductive interference (c_{RI}), for different cost of choosiness (c).** We assume (a) $c = 0$ and (b) $c = 0.001$. Hatched area indicates parameter combinations where multiple traits preference is observed at equilibrium ($0 < \gamma^* < 1$). Ancestrally, preference equally targets both trait ($\gamma_0 = 1/2$). We assume: $P^0_{T_1} = P^0_{T_2} = 0.5$, $P^0_M = 0.01$, $\tilde{P}_{T_1} = 1$, $\tilde{P}_{T_2} = 0.4$, $s_2 = 0$, $\rho = 0.01$, $a = e^{-1}$, $N = \tilde{N} = 10$, $u^{T_1}_{0\to1} = 0.003$, $u^{T_1}_{1\to0} = 0.001$, $u^{T_2}_{0\to1} = 0.002$, $u^{T_2}_{1\to0} = 0.001$. Note that the dependence to γ_0 is detailed in Figure A7.

observed in locally adapted traits prevent positive selection on these traits: because there is hardly any 'maladapted' variants, there is no longer selection to avoid it. Our model highlights that female preference may then preferentially target traits that differ from other species (Figure A6). For example in *Heliconius* butterflies, wing pattern is under selection because predators associated locally abundant wing patterns with unpalatability, leading to the fixation of a local wing pattern within and between species. In some of these mimetic species, female preference targets chemical cues differentiating sympatric species. (González-Rojas et al., 2020).

In our model, species recognition traits are neutral. However constraints act on trait display, depending notably on the detectability of the displayed trait . We assume that choosers perceived all trait values equally. However, increased trait detectability may induce costs: for example, the conspicuousness of a trait display increase parasitism and predation risks (Zuk and Kolluru, 1998). Increasing costs of sexual trait conspicuousness may theoretically promotes the light display of several traits (Johnstone, 1995), therefore promoting preference multiple towards multiple cryptic traits.

Our results highlight how indirect fitness benefit and/or reproductive interference can promotes

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female preference for multiple traits. Our model highlights that the evolution of multiple traits occur only when the cognitive trade-off is weak. The evolution of multiple trait preference is therefore probably more likely to emergence in species where complex neural processes do occur. Nevertheless, several alternative decision mechanisms may reduce this cognitive trade-off. For example sequential/hierarchical mate preference, whereby targeted traits are process in a hierarchical order, efficiently produce decision, even considering a large number of traits (Gigerenzer et al., 1999). Sequential mate preference is frequently observed (*e.g.* (Shine and Mason, 2001; Eddy et al., 2012; Gray, 2022)) and may allow the evolution of multiple traits preference. Sequential mate choice may emerge because some trait are visible at long-distance (such as color or calls), whereas others are perceived only at short distances (such as oviposition site guarded by males or male-emitted pheromones) (*e.g.* (Candolin and Reynolds, 2001; López and Martín, 2001; Mérot et al., 2015)).

The distance at which different traits are perceived may play a key role in reproductive isolation (Moran et al., 2020). Females deceived by short-distance trait of the heterospecific males may have already spent time and energy or may need to deploy substantial efforts to avoid heterospecific mating. Therefore, females may still suffer from increased costs associated to reproductive interference, even if they eventually manage to avoid mating with heterospecific males (Gröning and Hochkirch, 2008). Therefore reproductive interfere may promote preference targeting long-distance trait that may reduce efficiently heterospecific interactions.

Reproductive isolation between species also depends on the niche of individuals of both species. Mating occurs between individuals sharing the same niche leading to niche-based assortative mating. Niche segregation may play a key role in the evolution of reproductive isolation. In two teafrogs species, differing by there mating call (Park et al., 2013), different spatial and temporal segregation in calling and resting places during breeding period increases reproductive isolation (Borzée et al., 2016). As well as sequential mate preference, niche segregation may efficiently participate to reproductive isolation without generating trade-off with preference for other traits. Niche segregation limit opportunity costs because there is no need to sample a species recognition trait, whereas sequential mate preference increase sampling time.

Our study shows how natural and sexual selection may promote multiple traits preference in sympatric species. Our study highlights the importance of understanding trade-off between preference targeting different trait whereas opportunity costs to understand what trait are targeted by preference.

Conclusion

We study the direction of preference towards two evolving traits shared by sympatric species. We consider selection regimes acting on traits that increase similarity with heterospecific individuals, leading to costly sexual interactions. We study how selective regimes on traits, heterospecific interactions, opportunity costs and sensory trade-off shape the evolution of preference for multiple traits. Weak opportunity costs and sensory trade-off allow the evolution of multiple traits preference enhancing offspring fitness and/or species recognition. Our main result is that that opportunity costs promote preference based on adaptive traits rather than on traits relevant for species recognition. Because adaptation reduces the number of trait values, preference based on adaptive traits hardly suffer from opportunity costs. Then opportunity costs may limit multiple traits preference enhancing both offspring fitness and species recognition.

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Appendix

A1 QLE analysis

Evolution of mating traits under natural and sexual selection

First, we explored the relative effects of natural and sexual selections on the evolution of traits in species A. Following the QLE approach, the change of allele 1 frequency at T_i, for $i \in \{1, 2\}$, after one generation in this species is given by:

$$\Delta P_{T_i} = G_{T_i} \overbrace{\left(s_i + \overline{\rho}_i \left(P_{T_i} - \frac{1}{2}\right)\right)}^{\text{natural and sexual selections}} + \overbrace{(1 - P_{T_i}) u_{0\to1}^{T_i} - P_{T_i} u_{1\to0}^{T_i}}^{\text{action of mutations}} + O(\varepsilon^2), \tag{A1}$$

where G_I is the genetic diversity at locus $I \in \{T_1, T_2, M\}$ given by

$$G_I = P_I(1 - P_I), \tag{A2}$$

and $\overline{\rho}_1$ and $\overline{\rho}_2$ are the average strengths of preference on traits T_1 and T_2 respectively in the population

$$\overline{\rho}_1 = \rho\left((1 - P_M)h(1 - \gamma_{wt}) + P_M h(1 - \gamma_m)\right), \tag{A3}$$

$$\overline{\rho}_2 = \rho\left((1 - P_M)h(\gamma_{wt}) + P_M h(\gamma_m)\right). \tag{A4}$$

While the action of natural selection simply depends on the advantage of trait value 1 due to natural selection s_i, the effect of sexual selection is modulated by the average strength of preference on trait T_1 in the population $\overline{\rho}_i$. Sexual selection promotes (resp. disfavors) allele 1 when this allele is the most common (resp. rare) in the population *i.e.* when $P_{T_1} > 1/2$ (resp. $P_{T_1} < 1/2$) generating a positive frequency-dependent selection. The assortative mate preference assumed implies that most females display the most common trait and seek for males exhibiting this trait. The most frequently displayed trait allele is therefore associated with an enhanced reproductive success. An enhanced attention of females towards one out of the two male traits then results in a reduction of the polymorphism for this trait more targeted by sexual selection.

Evolution of mutants modifying the trait used by females for mate choice

The traits targeted by preference in species A can be shared with species B. This is even more likely when these traits are submitted to similar natural selection pressures in both sympatric species, enhancing a similar frequencies of traits. The natural selection exerted on the traits in both species might therefore strongly affect the risk of heterospecific mate choice. We thus investigate the evolution of the focus of female preference on either trait in species A, depending on the natural selection exerted on either trait. We thus study the invasion of a mutant at locus M associated with the value γ_m, differing from the value γ_{wt} associated with the ancestral allele. Under the QLE approximation, the allele frequency variation at the preference locus can be divided into three terms, denoted $\Delta^{\text{dir-RI}}, \Delta^{\text{dir-c}}$ and $\Delta^{\text{ind}} P_M$, reflecting the effect of direct selection due to reproductive interference and opportunity costs and indirect selection, on the change of the mutant frequency ΔP_M respectively.

$$\Delta P_M = \Delta^{\text{dir-RI}} P_M + \Delta^{\text{dir-c}} P_M + \Delta^{\text{ind}} P_M + O(\varepsilon^3). \tag{A5}$$

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Reproductive interference promotes preference targeting the trait leading to strongest species recognition.

The effect of reproductive interference on the change of mutant frequency is given by

$$\Delta^{\text{dir-RI}} P_M = G_M c_{RI} \frac{\tilde{N}}{N} \Bigg(\delta\rho_1 \left(P_{T_1} - \frac{1}{2} \right) \left(P_{T_1} - \tilde{P}_{T_1} \right) + \delta\rho_2 \left(P_{T_2} - \frac{1}{2} \right) \left(P_{T_2} - \tilde{P}_{T_2} \right) \Bigg), \tag{A6}$$

where $\tilde{P}_{T_1}$ and $\tilde{P}_{T_2}$ are the frequencies of allele 1 at loci T_1 and T_2 respectively in heterospecific. $\delta\rho_1$ and $\delta\rho_2$ quantify the effect of the mutant allele on the preference on trait T_1 and T_2 respectively compared to the wild type allele

$$\delta\rho_1 = \rho \left(h(1-\gamma_m) - h(1-\gamma_{wt}) \right), \tag{A7}$$

$$\delta\rho_2 = \rho \left(h(\gamma_m) - h(\gamma_{wt}) \right). \tag{A8}$$

For instance when $\delta\rho_2 > 0$ the mutant allele leads to more attention on trait T_2 than the wild type allele. Note that h is an increasing function: $\delta\rho_1$ and $\delta\rho_2$ thus have opposite signs, *i.e.* when mutant allele increases female attention on one trait, it also decreases female attention on the other trait.

As expected, the effect of reproductive interference mainly depends on density ratio between species A and B, $\tilde{N}/N$: the probability that a female encounters an heterospecific male increases with $\tilde{N}/N$. Selection caused by reproductive interference also increases with the strength of preference ρ, because the stronger preferences are, the more females with preference leading to heterospecific rejection avoid heterospecific mates. This leads to a greater fitness difference between females with different preferences intensifying selection, due to reproductive interference.

Reproductive interference promotes preference on the trait allowing more accurate species recognition. Selection due to reproductive interference depends then on relative phenotypic frequencies in both species. Preference on a trait leads to increased intraspecific matings than expected under random mating, when the targeted trait is more common within the species A than within species B. The higher the difference in trait frequencies between species, the stronger species recognition is. However, natural selection favors resemblance on the selected trait between species A and B and thus leads to similar cost of reproductive interference than expected under random mating. By contrast, when traits are neutral, phenotypic distributions within the two species can be more different. Preference based on trait may either increase or decrease species recognition compared to random mating. Females are more attracted by heterospecifics when the most common preferred trait value is more common within heterospecifics. Therefore in some cases focusing on neutral traits may be worst for species recognition than naturally selected trait.

Sympatry with other species intensifies opportunity costs

Preference allows to reject heterospecific males but also leads to the rejection of conspecific males. After rejecting a male, a female has a probability c of not encountering another male leading to an opportunity cost. The effect of these opportunity costs on change of mutant frequency is given by

$$\Delta^{\text{dir-c}} P_M = - G_M c \frac{N + \tilde{N}}{N} \left(\delta\rho_1 G_{T_1} + \delta\rho_2 G_{T_2} \right). \tag{A9}$$

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The fate of a mutant depends on trait polymorphism and on its effect on the attention towards either male traits. Limited polymorphism in a male trait indeed reduces opportunity costs, associated with female choice based on that trait. Because we assume assortative mating, most females have and prefer the most abundant trait value leading to low opportunity cost. Since natural selection reduces polymorphism at the male adaptive trait, opportunity costs may promote female preference towards trait under stronger natural selection.

Surprisingly, selection due to opportunity costs increases with the proportion of heterospecifics. When a female rejects a conspecific male, she has to wait to encounter another conspecific male to produce offspring and avoid opportunity cost. However, the more there are heterospecifics, the more females will encounter heterospecific males before encountering a conspecific male, making the rejection of a conspecific more dramatic when conspecific males are rare. The effect of opportunity costs is thus proportional to the average number of males that females will encounter until she encounters a conspecific $(N + \tilde{N})/N$.

Indirect selection promotes preference on the trait providing the strongest indirect fitness benefit

The mutant at locus M does not only directly change the fitness because it modifies reproductive interference and opportunity costs, but also because it can be associated with different alleles at the traits loci T_1 and T_2 in the offspring, leading to contrasted indirect fitness benefits. Within offspring, the mutant allele at locus M becomes associated with the preferred alleles at trait T_1 or T_2. Therefore selection on the traits T_1 and T_2 can indirectly affect the frequency of the mutant at locus M. The term describing the effect of indirect selection on mutant alleles at locus M is given by

$$\begin{aligned}\Delta^{\text{ind}} P_M = & \overbrace{D^*_{T_1 M}}^{\substack{\text{genetic association}\\ \text{between } T_1 \text{ and } M}} \overbrace{\left(s_1 + \overline{\rho}_1 (P_{T_1} - \frac{1}{2})\right)}^{\text{direct selection on } T_1} \\ & + \underbrace{D^*_{T_2 M}}_{\substack{\text{genetic association}\\ \text{between } T_2 \text{ and } M}} \underbrace{\left(s_2 + \overline{\rho}_2 (P_{T_2} - \frac{1}{2})\right)}_{\text{direct selection on } T_2},\end{aligned} \tag{A10}$$

where $D^*_{T_1 M}$ (resp. $D^*_{T_2 M}$) is the genetic association between the mutant allele at locus M and allele 1 at locus T_1 (resp. T_2), see (A11). When the mutant is associated with a trait value, direct selection on this trait indirectly affects change of mutant frequency.

The genetic association between the mutant at locus M and the trait T_i, for $i \in \{1, 2\}$, is given by

$$D^*_{T_i M} = G_{T_i} G_M \delta\rho_i \left(P_{T_i} - \frac{1}{2}\right) + O(\varepsilon^2). \tag{A11}$$

When the mutant leads to more attention on T_i ($\delta\rho_i > 0$), the mutant becomes associated with the most common allele at T_i. Because of assortative female preference, when one trait value is common, females mostly prefer this trait. This generates a tighter association between preference and trait alleles. Accordingly, when the mutant leads to less attention on T_i ($\delta\rho_i < 0$), it is associated with the rarest allele. As trait alleles promoted by natural selection are more common, indirect selection promotes preference towards the trait under stronger selection. This selection includes natural and

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sexual selections, highlighting the importance of the ancestral value of γ in the population which determines the strength of sexual selection acting on each trait.

A2 Preference enhancing offspring 'sexinesss'

We consider the case where the indirect fitness benefit provided by each trait is exclusively due to production of 'sexy son'. We then assume no natural selection and no reproductive interference ($s_1 = s_2 = c_{RI} = 0$). Because opportunity costs may depends on the distribution of trait values at each trait we assume that mutations promote a more balanced proportion of trait values on T_2 ($u^{T_2}_{0\to1} = 0.002$ and $u^{T_2}_{1\to0} = 0.001$) than on T_1 ($u^{T_1}_{0\to1} = 0.003$ and $u^{T_1}_{1\to0} = 0.001$).

Without opportunity costs ($c = 0$), multiple traits preference evolve only for very weak trade-off ($\log(a) \simeq -1$) (Figure A2.1). With subsequent opportunity costs, the evolution of preference depends on the shape of the trade-off:

- With strong trade-off ($\log(a) > 0$), the opportunity costs surprisingly promote preference based on both traits. This preference leads to poor attention on both traits, leading to an almost random mating that limits opportunity costs. This result is observed because we assume fixed strength of level preference (ρ). Considering an evolving strength of level preference, the high opportunity costs would promote no preference ($\rho = 0$).

- By contrast, with weak trade-off ($\log(a) < 0$), opportunity costs favor attention only on trait T_1. Females with preference on both traits suffer from high opportunity costs, because they are likely to refuse a large number of males and may therefore have a decreased reproductive success. Females then choose on the trait with the lower phenotypic diversity limiting opportunity costs.

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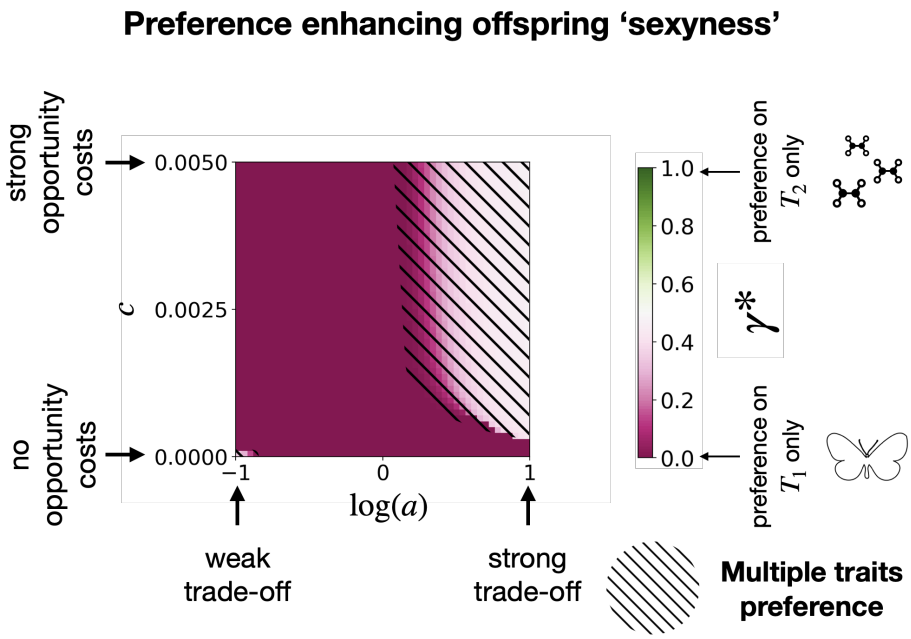

Figure A2.1: **Equilibrium preference direction γ^* depending on $\log(a)$ where a tunes the shape of the trade-off function and on cost of choosiness (c).** Hatched area indicates parameter combinations where multiple traits preference is observed at equilibrium ($0 < \gamma^* < 1$). In species A mutations promotes higher phenotypic diversity at trait T_2 ($u^{T_1}_{0\to1} = 0.003$, $u^{T_1}_{1\to0} = 0.001$, $u^{T_2}_{0\to1} = 0.002$, $u^{T_2}_{1\to0} = 0.001$). Ancestrally preference equally targets both trait ($\gamma_0 = 1/2$). We assume: $P^0_{T_1} = P^0_{T_2} = 0.5$, $P^0_M = 0.01$, $\tilde{P}_{T_1} = \tilde{P}_{T_2} = 1$, $s_1 = s_2 = 0$, $\rho = 0.01$, $c_{RI} = 0$, $N = \tilde{N} = 10$, .

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A3 Table and Figures

Abbreviation	Description
$\mathcal{L}$	Set of different loci for the *matching rule* model: $\mathcal{L} = \{T_1, T_2, M\}$ and for the *preference/trait* model $\mathcal{L} = \{T_1, P_1, T_2, P_2, M\}$.
$\mathcal{G}$	Set of different genotypes for the *matching rule* model: $\mathcal{G} = \{0,1\}^3$ and for the *preference/trait* model $\mathcal{G} = \{0,1\}^5$.
$f_i/\tilde{f}_i$	Frequency of genotype i in species A or B.
$P_I/\tilde{P}_I$	Frequency of allele 1 at locus I, for $I \in \mathcal{L}$, in species A or B.
$N/\tilde{N}$	Density of species A/B.
G_I	Genetic diversity at locus I in species A, $G_I = P_I(1-P_I)$ for $I \in \mathcal{L}$.
$(I)_i$	Allele at locus I of the genotype i for $(I,i) \in \mathcal{L} \times \mathcal{G}$.
$D_{\mathcal{I}}$	Genetic association between alleles at loci in $\mathcal{I}$: $D_{\mathcal{I}} = \sum_{i \in \mathcal{G}} f_i \prod_{I \in \mathcal{I}} (P_I - (I)_i)$ for $\mathcal{I} \subset \mathcal{L}$.
$f_i'/f_i''/f_i'''$	Frequency of genotype i in species a after natural selection/reproduction/mutation.
s_n	Selective advantage of allele 1 at locus T_n, $n \in \{0,1\}$.
γ_i	Preference direction.
h	Trade-off function determining the relative focus of females on either trait displayed by males.
a	Trade-off parameter tuning the shape of the function h
ρ	Strength of female preference.
c_{RI}	Strength of reproductive interference.
c	Cost of choosiness.
$u^I_{0\to1}/u^I_{1\to0}$	Mutation rate of allele 0/1 towards 1/0 at locus $I \in \mathcal{L}$.

Table A1: Description of variables and parameters used in the model.

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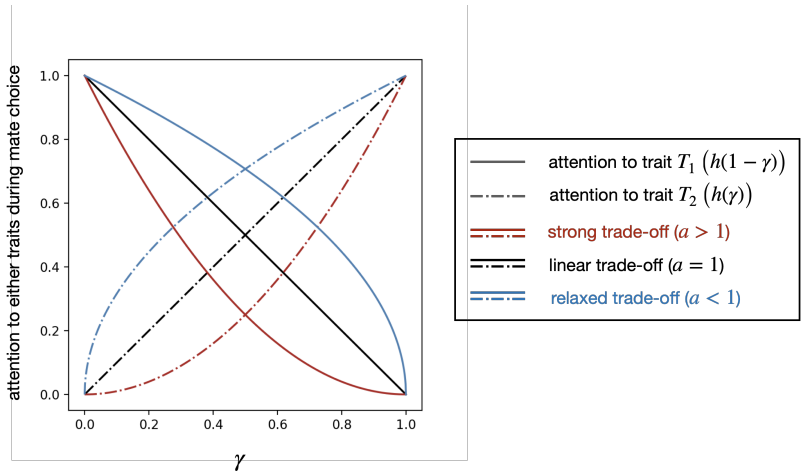

Figure A1: **Attention paid by females to either traits displayed by males during assortative mate choice, depending on the preference direction parameter γ controlled by the locus M, for different shapes of the trade-off function h. Blue, red and black lines indicate concave, convex and linear trade-off functions respectively.**

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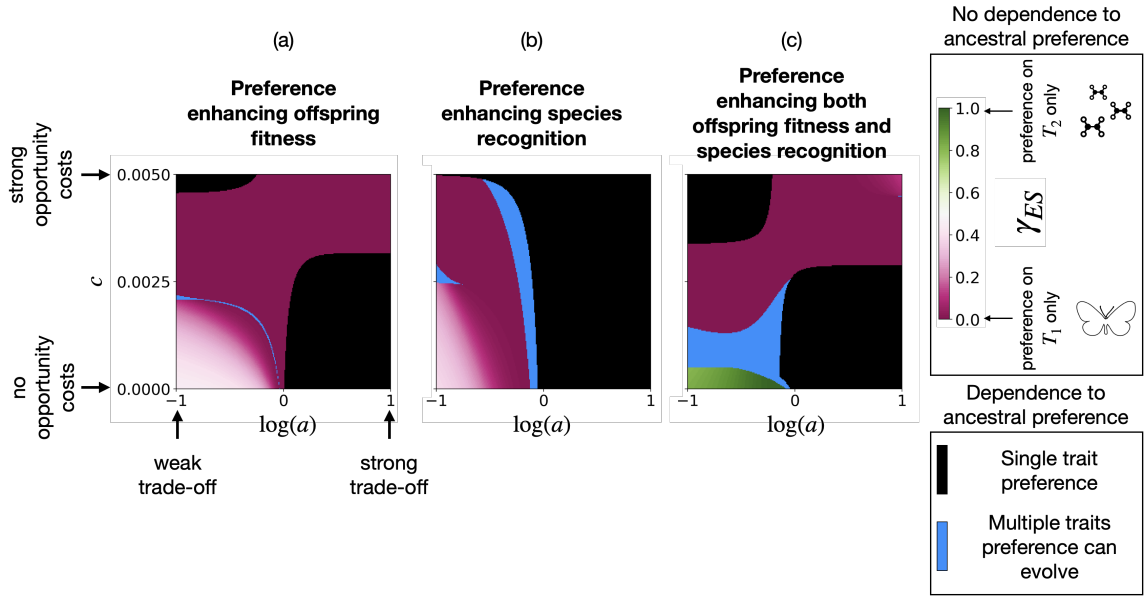

Figure A2: **Evolutionary stable preference, depending on three different selection regime**. The three plot investigates the effect of the cognitive trade-off function a and on cost of choosiness c on the evolutionary stable preference, for these 3 selective regimes. Shades of color indicates the unique value γ_{ES}. Black and blue area indicates parameter spaces with several values γ_{ES}. In black area only single trait preferences are evolutionary stable. In blue area at least one γ_{ES} value corresponds to multiple trait preference. In species A mutations and natural selection promotes trait value 1 at both traits in species A ($u^{T_1}_{0\to1} = 0.003$, $u^{T_1}_{1\to0} = 0.001$, $u^{T_2}_{0\to1} = 0.002$, $u^{T_2}_{1\to0} = 0.001$, $s_1 \geq 0$ and $s_2 \geq 0$). We assume: (a) that both traits are under natural selection ($s_1 = 0.02$ and $s_2 = 0.01$), (b) reproductive interference ($c_{RI} = 0.05$) and that both trait may allow species recognition ($\tilde{P}_{T_1} = \tilde{P}_{T_2} = 0$) (c) reproductive interference ($c_{RI} = 0.05$), that trait T_1 is under natural selection ($s_1 = 0.02$) and that trait T_2 allowing species recognition ($\tilde{P}_{T_2} = 0.4$). By default we assume: $P^0_{T_1} = P^0_{T_2} = 0.5$, $P^0_M = 0.01$, $\tilde{P}_{T_1} = \tilde{P}_{T_2} = 1$, $s_1 = s_2 = 0$, $\rho = 0.01$, $c_{RI} = 0$, $N = \tilde{N} = 10$, .

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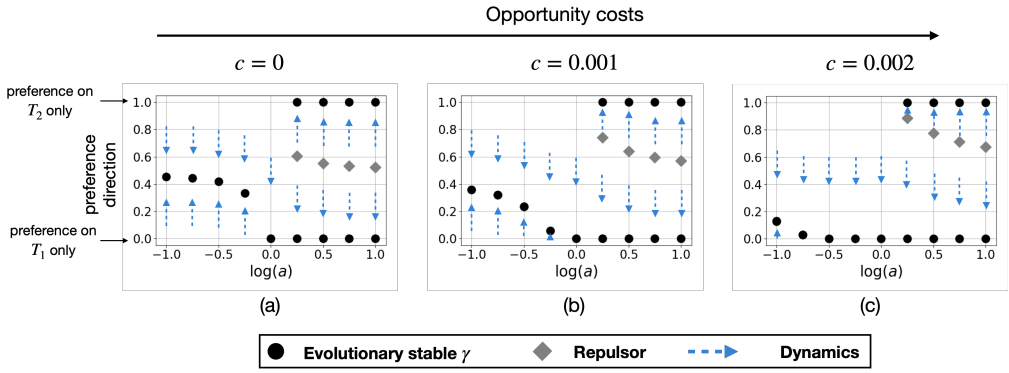

Figure A3: **Evolutionary stable value of γ depending on $\log(a)$ where a tunes the shape of the trade-off function for different values of cost of choosiness (c).** Black dots represent evolutionary stable γ, grey squares represent repulsors and blue arrows represent dynamics (see Method part). We assume (a) $c = 0$, (b) $c = 0.001$ and (c) $c = 0.002$. We also assume: $P^0_{T_1} = P^0_{T_2} = 0.5$, $P^0_M = 0.01$, $\tilde{P}_{T_1} = 1 = \tilde{P}_{T_2} = 0$, $s_1 = 0.02$, $= s_2 = 0.01$, $\rho = 0.01$, $c_{RI} = 0$, $N = \tilde{N} = 10$, $u^{T_1}_{0\to1} = 0.003$, $u^{T_1}_{1\to0} = 0.001$, $u^{T_2}_{0\to1} = 0.002$, $u^{T_2}_{1\to0} = 0.001$.

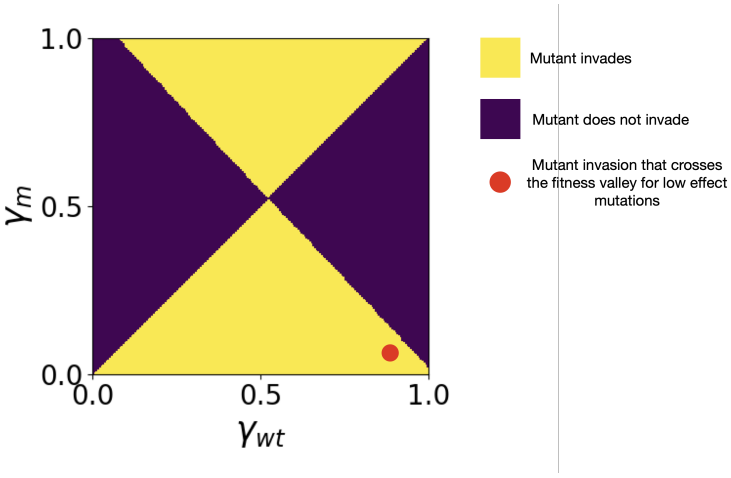

Figure A4: **Invasion graph.** Red dot shows the invasion of the mutant with high effect mutation. We assume: $\log(a) = 1$, $P^0_{T_1} = P^0_{T_2} = 0.5$, $\tilde{P}_{T_1} = \tilde{P}_{T_2} = 1$, $s_1 = 0.02$, $s_2 = 0.01$, $\rho = 0.01$, $c = 0$, $c_{RI} = 0$, $N = \tilde{N} = 10$, $u^{T_1}_{0\to1} = 0.003$, $u^{T_1}_{1\to0} = 0.001$, $u^{T_2}_{0\to1} = 0.002$, $u^{T_2}_{1\to0} = 0.001$.

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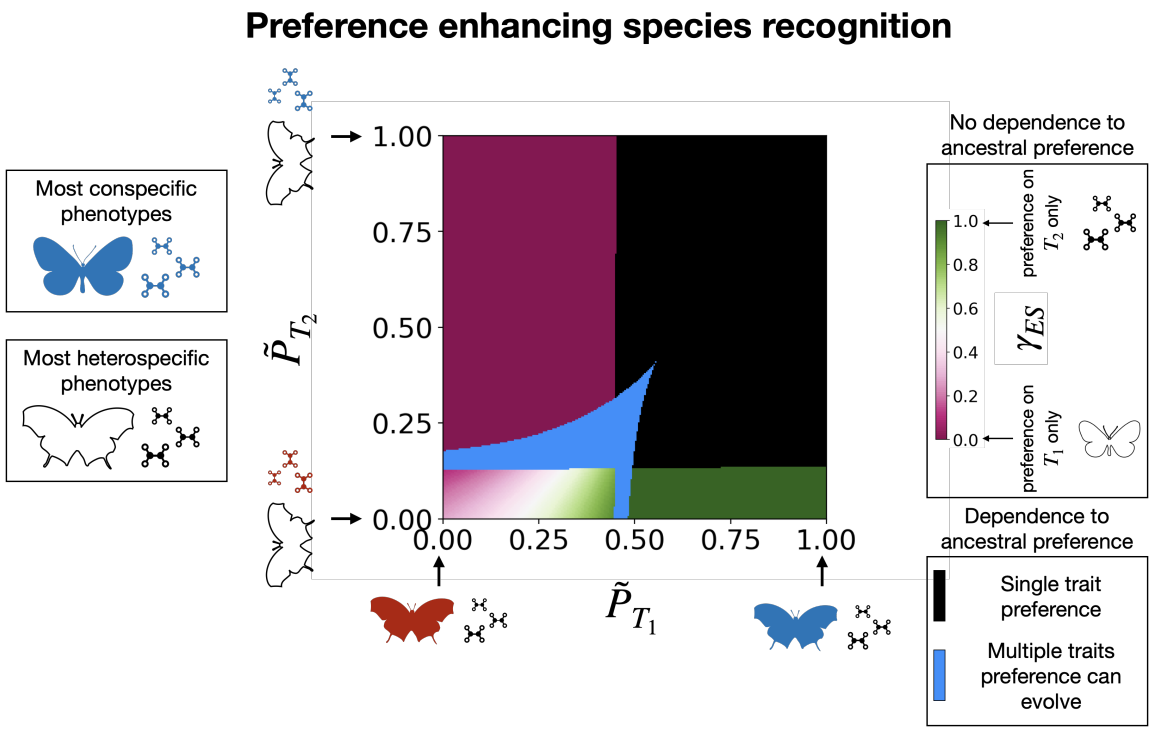

Figure A5: **Evolutionary stable preference direction γ_{ES} depending on the phenotypic distributions in species B ($\tilde{P}_{T_1}$ and $\tilde{P}_{T_2}$).** Shades of color indicates the unique value γ_{ES}. Black and blue area indicates parameter spaces with several values γ_{ES}. In black area only single trait preferences are evolutionary stable. In blue area at least one γ_{ES} value corresponds to multiple trait preference. In species A mutations promote trait value 1 at both traits in species A ($u^{T_1}_{0\to1} = 0.003$, $u^{T_1}_{1\to0} = 0.001$, $u^{T_2}_{0\to1} = 0.002$, $u^{T_2}_{1\to0} = 0.001$. We assume: $P^0_{T_1} = P^0_{T_2} = 0.5$, $P^0_M = 0.01$, $s_1 = s_2 = 0$, $\rho = 0.01$, $c = 0.001$, $c_{RI} = 0.05$, $a = e^{-1}$, $N = \tilde{N} = 10$.

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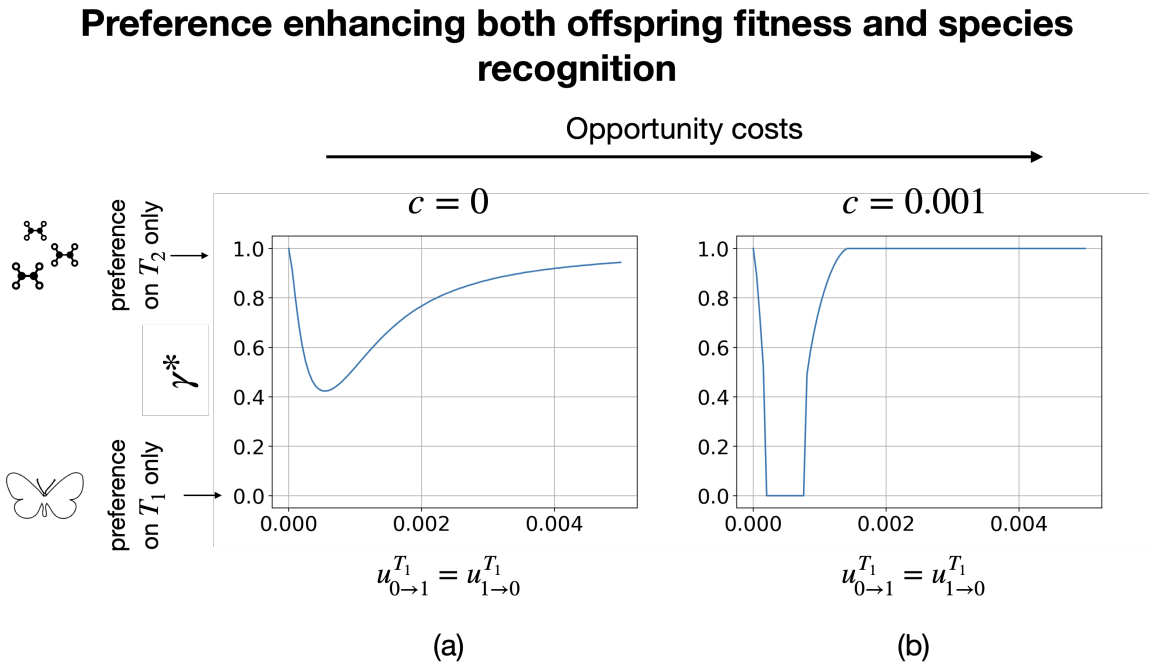

Figure A6: **Equilibrium preference direction γ^* depending on mutation rates at locus T_1 ($u^{T_1}_{0\to1} = u^{T_1}_{1\to0}$) for different cost of choosiness (c).** We assume (a) $c = 0$ and (b) $c = 0.001$. Ancestrally preference equally targets both trait ($\gamma_0 = 1/2$). We assume: $P^0_{T_1} = P^0_{T_2} = 0.5$, $P^0_M = 0.01$, $\tilde{P}_{T_1} = \tilde{P}_{T_2} = 1$, $s_1 = s_2 = 0$, $\rho = 0.01$, $a = e^{-1}$, $c_{RI} = 0$, $N = \tilde{N} = 10$, $u^{T_2}_{0\to1} = 0.002$, $u^{T_2}_{1\to0} = 0.001$.

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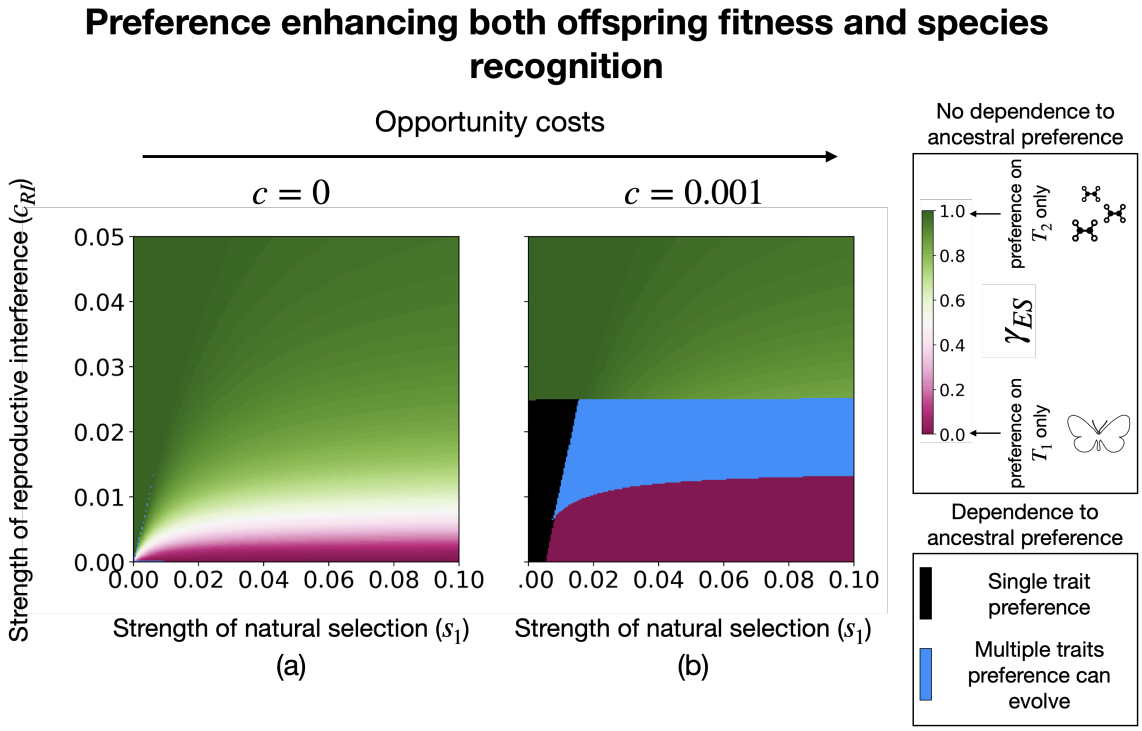

Figure A7: **Evolutionary stable preference direction γ_{ES} depending on natural selection acting on trait T_1 (s_1) and the strength of reproductive interference (c_{RI}) for different cost of choosiness (c).** We assume (a) $c = 0$ and (b) $c = 0.001$. Shades of color indicates the unique value γ_{ES}. Black and blue area indicates parameter spaces with several values γ_{ES}. In black area only single trait preferences are evolutionary stable. In blue area at least one γ_{ES} value corresponds to multiple trait preference. We assume: $P^0_{T_1} = P^0_{T_2} = 0.5$, $P^0_M = 0.01$, $\tilde{P}_{T_1} = 1$, $\tilde{P}_{T_2} = 0.4$, $s_2 = 0$, $\rho = 0.01$, $a = e^{-1}$, $N = \tilde{N} = 10$, $u^{T_1}_{0\to1} = 0.003$, $u^{T_1}_{1\to0} = 0.001$, $u^{T_2}_{0\to1} = 0.002$, $u^{T_2}_{1\to0} = 0.001$.