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LETTER

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The ecological stage maintains preference differentiation and promotes speciation

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Abstract

Influential models of speciation by sexual selection posit either a single shared preference for a universal display, expressed only when males are locally adapted and hence in high condition, or that shared loci evolve population-specific alleles for displays and preferences. However, many closely related species instead show substantial differences across categorically different traits. We present a model of secondary contact whereby females maintain preferences for distinct displays that indicate both male condition and their match to distinct environments, fostering reproductive isolation among diverging species. This occurs even with search costs and with independent preference loci targeting independent displays. Such preferences can also evolve from standing variation. Divergence occurs because condition-dependent display and female preference depend on local ecology, and females obtain different benefits of choice. Given the ubiquity of ecological differences among environments, our model could help explain the evolution of striking radiations of displays seen in nature.

KEYWORDS
condition-dependent, environmental-match, female preference, search costs, secondary contact, sexual selection, speciation

INTRODUCTION

A common hallmark of closely related species is that they often differ markedly in sexual display traits. This causes females to choose their own males over those of other species, reducing genetic exchange and suggesting that sexual selection can promote speciation and help maintain differentiation after secondary contact of populations that diverged in allopatry. However, theoretical models reveal that differentiated preferences along a single trait axis such as coloration are hard to maintain under gene flow, and can instead homogenise and impede speciation (Servedio & Bürger, 2014; Weissing et al., 2011). This raises dual questions of how population-specific preferences could arise and persist, and whether speciation is facilitated or instead hindered by sexual selection. Secondary contact of populations that undergo hybridisation is of particular interest both because of the widespread nature of allopatric differentiation, and the increasing frequency of secondary contact due to anthropogenic change (Chunco, 2014; Mooney & Cleland, 2001; Sánchez-Guillén et al., 2015).

Despite assuming a single trait axis, other theoretical studies find that sexual selection enhances speciation when females prefer a male display that is condition-dependent (i.e. strongly expressed only by high-condition males) and populations inhabit different environments (Proulx, 1999, 2001; van Doorn et al., 2009). In these models, only local males are adapted to the local environment; they thus have high condition and can strongly express the condition-dependent indicator trait. In contrast, migrant males, who are in the 'wrong' environment and thus in low condition, have low display trait values. Even though females in these models possess a

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single, universal preference for the universal condition-dependent display, this single preference favours local males in each environment, therefore fostering assortative mating and speciation without preference divergence, bypassing the most theoretically difficult part of the speciation process.

Yet, females of closely related species can prefer different displays, which these models cannot explain. Critically, these are not only different values of the same display but can be categorically different displays altogether, especially in cases where species inhabit distinct environments (Chaine & Lyon, 2008; Endler & Houde, 1995; Hebets et al., 2013; Kodric-Brown & West, 2014; Lindholm et al., 2014; Rosenthal & Ryan, 2011). For example in some cases, females prefer males with bright colours while in a closely related species females prefer males with large body size (Boughman et al., 2005; Kozak et al., 2009). So, how do these preference differences arise? If they arise in allopatry, can they be maintained if taxa come into secondary contact? Do they foster assortative mating and promote the speciation process? We focus on these questions here, presenting a mechanism that we term 'the ecological stage', and exploring it with a population genetic model of secondary contact.

Under the ecological stage mechanism, the presence of categorically different, ecologically relevant selection pressures among populations promotes the evolution of distinct preferences for categorically distinct indicator traits, furthering reproductive isolation. The speciation models cited above (Proulx, 1999, 2001; van Doorn et al., 2009) invoke condition dependence and highlight that the action of sexual selection depends on local ecological conditions, but there are important differences between those models and the ecological stage mechanism. Specifically, the ecological stage mechanism has three components (Figure 1).

First, categorically different selective regimes among environments underlie local adaptation. Ecological conditions often vary among populations; in turn causing primary selective agents to differ between environments (Hereford, 2009; Schluter & McPhail, 1992). In Figure 1, in the first environment, parasitism may be intense so that individuals with high resistance to parasitism have high fitness (shown by low parasite load; Karvonen & Seehausen, 2012). In the second environment, high density enhances resource competition, so that individuals with high foraging ability have enough food and high fitness (shown by large size; Grant & Grant, 2006). Because ecological traits that confer high fitness in the local environment differ across populations with different selective regimes, the targets of selection also differ (parasite resistance vs. foraging ability in Environments 1 vs. 2). The loci underlying these traits would thus show conditional neutrality, where an allele affects fitness in one environment but is neutral or nearly neutral in another, which genomic studies have shown to be fairly common (Anderson et al., 2013; Mitchell-Olds et al., 2007; Savolainen et al., 2013). Importantly, there are not just different magnitudes or directions of selection from a single source, but different primary selective agents altogether.

Second, in populations with different selective drivers, categorically different male displays indicate local adaptation and environmental-match in each environment, thus signalling an individual's genetic quality in that environment. For example indicators in Figure 1 are bright colour, indicating parasite resistance in the first environment, and size, indicating foraging ability in the second. We stress that each indicator is relevant only in its local environment. These distinct displays serve two indicator functions. First, they indicate male condition (here, the extent of local adaptation). Second, they indicate the specific type of benefit females can obtain (here, whether the male matches the local environment, e.g. parasite resistance vs. good foraging). That displays serve as honest indicators of environmental-match is key to the ecological stage mechanism (e.g. in Environment 1 only males with high parasite resistance have low parasite load and display red, whereas with few parasites in Environment 2 all males have low parasite load and could display red if they have the proper display allele, consistent with conditional neutrality). This differs from standard condition dependence of former models, where universal displays indicate general condition and level of adaptation, versus the ecological stage, where distinct displays indicate the specific nature of local adaptation and reason for high condition in the local environment.

Environmental-match indicators should be favoured because costs and benefits are environment specific. Male displays are likely to be sensitive to varying ecological conditions (Bussière et al., 2008; Proulx, 1999, 2001), and because of their high energetic and selective costs, indicator traits may trade-off against each other (Bussière et al., 2008; Miller & Svensson, 2014). Evolutionarily, this likely results in individuals expressing a high value of the single best indicator in their environment rather than lower values of multiple displays. Such trade-offs could contribute to differentiated displays in distinct environments that serve as honest indicators. Predicting categorically different displays and that these indicate environmental match also distinguishes the ecological stage mechanism from most models (Proulx, 1999, 2001; van Doorn et al., 2009), but see van Doorn (2004).

Third, alternate populations maintain categorically different female preferences for distinct displays. Their evolution is affected by both environmental-match and condition-dependent indicator functions. Within populations, preferences are expected to evolve for male displays that honestly indicate benefits to females, whether for direct or indirect benefits (Houle & Kondrashov, 2002; Price et al., 1993). Additionally, empirical studies demonstrate that benefits of mate choice may depend on ecological context (Chaine & Lyon, 2008; Hale & St Mary, 2007; Pfennig, 2007;

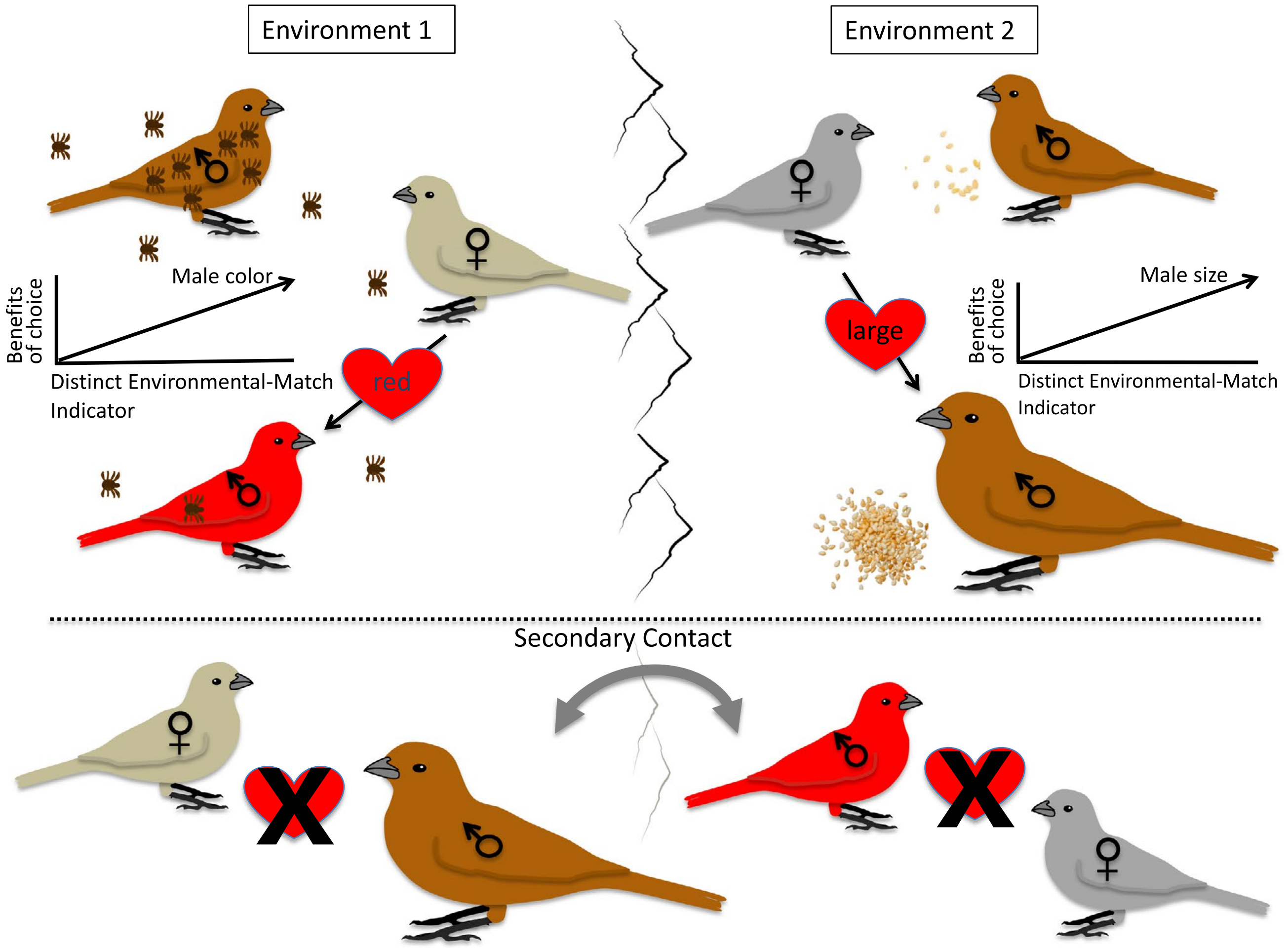

FIGURE 1 Conceptual framework for the ecological stage mechanism. Allopatric populations experience two distinct environments subject to distinctly different primary selective drivers targeting distinct traits. In Environment 1 the primary selective driver is parasitism targeting parasite resistance (E_{M1}; refer to The Model section for more detail), while in Environment 2 food availability targets foraging efficiency (E_{N2}). Distinctly different male displays function to indicate environmental match in each population; red colour (M_1) indicates low parasite load, requiring parasite resistance when in Environment 1, while large body size (N_2) indicates high food intake, requiring good foraging ability when in Environment 2. Male displays also depend on individual condition in both populations. Displays thus function to honestly indicate local adaptation, for the environment in which the selection pressure related to that particular display is acting. Female preferences evolve for the display that honestly indicates a match to that environment and high condition; preference for the red colour that indicates low parasite load in Environment 1 (P_{R2}) and preference for the large body size that indicates high food intake in Environment 2 (P_{L2}). Mating with males expressing high values of distinct displays confers both direct fecundity benefits and indirect benefits for females' offspring of high survival due to parasite resistance (Environment 1) versus foraging ability (Environment 2). Upon secondary contact due to the onset of migration, females generally reject foreign males because they do not display the correct distinct indicator. This occurs because males generally lack locally adapted alleles and are thus in low condition or lack alleles for the local display; in both cases, they express low values of the distinct local indicator. Most importantly, females do not prefer the foreign display, as the foreign indicator is not relevant in the local environment. (Artwork by Marcella Willett)

Rodríguez & Greenfield, 2003; Schmoll, 2011; Welch, 2003). Given these points, the ecological stage mechanism posits that females should evolve to prefer the particular display that indicates local adaptation, because it indicates specific benefits that match their local environment (Ingleby et al., 2010; Proulx & Servedio, 2009; Reinhold, 2004; Servedio, 2004). In Figure 1, this would be preference for colour indicating the specific benefit of parasite resistance in Environment 1 versus preference for large size indicating the benefit of good foraging in Environment 2. Because the ecological stage hypothesis assumes categorically distinct indicator traits, there would likely be different loci for the two displays as well the two preferences (i.e. preference for colour and for size would be controlled by two different loci). Similarly, van Doorn (2004) considered the evolution of separate preferences for revealing indicator traits. However, predicting categorically different preferences for displays that match the local environment, and are controlled by separate loci, also distinguishes the ecological stage mechanism from almost all earlier models.

Thus, in the ecological stage mechanism, distinct environments generate consistently different selection pressures, which cause differentiation in both ecological traits and male displays. This results in entirely different types of displays serving as indicators of local adaptation in each environment, and correspondingly different benefits to females who thus prefer distinct displays in each environment (Tinghitella et al., 2020). We ask here whether this allows differentiated preferences to be maintained or even to evolve from standing variation, thereby increasing reproductive isolation among populations. Does it avoid homogenising preferences between populations as seen in prior models? Previous condition-dependent models predict that the same display and preference are found across populations (Proulx, 1999, 2001; van Doorn et al., 2009), which cannot fully explain the diversification of preference and display seen in nature. If the ecological stage hypothesis allows preference differentiation, it instead provides a mechanism whereby distinct condition-dependent and environmental-match indicators exist in different ecological contexts, predicting different preference-trait combinations in natural populations.

THE MODEL

We investigate a population genetic model of the evolution after secondary contact of two populations, each occupying a different environment and thus dominated by a different primary selective agent (we develop equations in full in Supplementary Material A: Methods, and in the code archived on Dryad https://doi.org/10.5061/dryad.44j0zpcfy). Supplementary Table A5 summarises all parameters. The majority of cases examined assume that populations in each environment have already undergone local adaptation and preference differentiation in allopatry, and consider evolutionary responses upon secondary contact; see the final section for divergence occurring after gene flow commences. Specifically, each population has fixed an allele at an ecological locus critical for adaptation to that environment (loci E_M and E_N in populations 1 and 2 respectively; these loci represent categorically different traits locally adapted in each environment, e.g. E_{M1} is an allele for parasite resistance allowing low parasite load when parasites are prevalent and E_{N2} is an allele for good foraging ability enabling high food intake under high competition, Figure 1). Prior to secondary contact, a different male display evolves as an honest indicator of local adaptation in each environment, at loci M and N in populations 1 and 2 respectively; for example allele M_1 allows the expression of red colour and allele N_2 allows the expression of large size (both depending on condition specific to the local selection pressure). For example in Environment 1 parasites are prevalent and an allele that increases parasite resistance, E_{M1}, has fixed at the ecological locus E_M. Red colour, controlled by allele M_1, serves as an honest indicator in Environment 1 of parasite resistance at the display locus M (e.g. M_1 allows carotenoid sequestration if the male has allele E_{M1} and is thus in good condition with low parasite load; the subscript 1 thus marks the most relevant alleles at the ecological and display loci in population 1). Key to the ecological stage mechanism is that in Environment 2, parasites are not the primary selective agent, and thus allelic variation at the E_M locus is nearly neutral (with allowable exceptions explained below) making these conditionally neutral alleles with fitness effects below the selection-drift threshold (Anderson et al., 2013; Wadgymar et al., 2017). In Environment 2, red can be expressed by rare M_1 individuals, as all individuals have low parasite load; red is thus not an honest indicator of condition in this environment. In Environment 2, a different trait (e.g. foraging ability, at locus E_N, coded for by allele E_{N2}) is ecologically important and marked by a different honest indicator, of foraging (e.g. large size, coded for by allele N_2 at locus N; the subscript 2 thus characterises the most relevant alleles in population 2); foraging ability is of little ecological importance in Environment 1. Assuming separate loci for environment-specific traits accords with studies showing, for example that pigmentation genes (e.g. MC1r, MITF) underlie colour, whereas growth genes (e.g. IGF2BP1) underlie size (e.g. Zhou et al., 2018). Variation at the ecological and display loci is generated in each population by the onset of migration upon secondary contact in this two-island model.

For most analyses, we assume that female preferences also differentiated in allopatry, but also consider cases when they evolve from a low starting frequency upon secondary contact. Female preferences are characterised by locus P_R in population 1 and P_L in population 2. The subscript R denotes a preference for red coloration (to continue our example in Figure 1). At both preference loci, allele 2 (P_{R2} and P_{L2}) denotes the preference is present (for red colour and large size respectively) and allele 1 (P_{R1} and P_{L1}) denotes no preference. Preferences are environmentally dependent such that a display is only preferred in the environment in which it is an honest indicator (e.g. P_{R2} females only prefer red in Environment 1). We use the subscript R to remind readers that preference is for the colour red, not merely the presence of the ‘correct’ allele at the M locus. Similarly, subscript L denotes preference for large size in population 2.

The life cycle assumed consists of unidirectional mutation against the beneficial alleles at the ecological and display loci, migration (at rate *mig*) between the two populations, viability selection, mating and fecundity selection. Offspring are produced after recombination (following standard equations for haploids) and segregation.

After migration, each ecological locus undergoes viability selection in both sexes, with selection coefficients s_{EM} and s_{EN} describing the benefits for the local allele at loci E_M and E_N. Male displays develop after migration and experience costs during viability selection, controlled by selection coefficients s_R, cost to red colour, or s_L, cost to large size. Displays are expressed fully by high-condition males in their local environment who possess alleles for local adaptation and local display, but can also be fully or partially expressed in other contexts (described after preferences, below). Additionally, we incorporate trade-offs, over and above other costs, when males attempt to express both displays (even partially); these have selection coefficient s_{TL} and s_{TH} for low and high-condition males respectively.

Viability selection is followed by mating and fecundity selection. During mating, females with allele $\mathrm{P}_{\mathrm{R}2}$ or $\mathrm{P}_{\mathrm{L}2}$ prefer red colour or large size, respectively, with a preference strength of α_R or α_L. Preferences are generally only expressed by females when in their local environment, but exceptions are described in the next paragraph. Preference strength affects the search costs females experience. Specifically, we use parameters s_{CR} and s_{CL} (for red and large preference respectively) to set frequency-dependent search costs that are higher when the preference is stronger or the preferred male is rarer (see Methods). High-condition males and females both have higher fecundity, with benefit f for local alleles at the ecological loci, although we also explore the case of no fecundity benefit. Females can thus gain both direct benefits via the fecundity advantage of mating with a well-adapted male, and indirect benefits via choosing high-condition males carrying locally adapted alleles. By including both direct and indirect benefits we can evaluate their effects on preference differentiation and reproductive isolation.

As presented in the Supplementary Methods, we also allow partial display expression (e.g. pink colour or medium size), partial costs and partial expression of female preferences, to explore the consequences of broad-sense condition dependence and environmental-match. We allow for low-condition males to partially express a display by multiplying the selection coefficient s_R or s_L for those genotypes by γ_{low} ($0 < \gamma_{low} < 1$), which induces condition-dependent costs of display; reduced costs are interpreted as reduced expression (see Methods for additional interpretations). We allow partial costs of display in the wrong environment similarly using modifier γ_{envt}, which induces environmentally specific costs of display. Additionally, modifiers σ_{low} or σ_{envt} modify preference strengths α_R and α_L. Parameter σ_{envt} causes females with the 'wrong' preference allele for an environment, (e.g. a $\mathrm{P}_{\mathrm{L}2}$ female in Environment 1) to express their preference only partially, or not at all if $\sigma_{envt} = 0$. Thus, female preference depends on ecological context as has been shown in several example studies (Chaine & Lyon, 2008; Moehring & Boughman, 2019; Pfennig, 2007; Rosenthal & Ryan, 2011; Tinghitella et al., 2013). Parameter σ_{low} can be interpreted as partial preference for low-condition males in the 'correct' environment or fully expressed preferences for a partial display. In most figures we allow moderate partial preferences and display costs, so that males in the 'wrong' environment or in low condition present a display that has, for example half the cost and is preferred half as much as a fully expressed display (i.e. $\gamma_{low} = \gamma_{envt} = \sigma_{envt} = \sigma_{low} = 0.5$); by doing so results shown are generally conservative regarding divergence.

The parameters γ and σ also allow the model to capture important concepts in other sexual selection models. They allow display expression to correspond to three traditionally recognised types of good genes models (condition-dependent, epistatic or revealing, see Methods; Andersson, 1994; Dhole et al., 2018). In addition, parameters for partial preference can correspond to different preference functions (e.g. linear or threshold; see Methods).

Some reproductive isolation occurs in our model when preferences are diverged, specifically when a different preference is common in each population but rare in the other population. For example at equilibrium the red preference allele at the P_R locus may be common in population 1, where red is an honest indicator of local adaptation, but the allele for random mating at this locus may be common in population 2; the opposite would be true at the P_L locus. Reproductive isolation is assessed by a measure of the hybridisation rate at the ecological and display trait loci. That reproductive isolation occurs by the spread of preference alleles at two different preference loci, one relevant in each environment, is a substantial departure from the assumptions of almost all prior speciation models. Those instead assume that opposing alleles at each of one or more loci control preferences across populations (e.g. Doebeli, 2005; Weissing et al., 2011; Servedio & Bürger, 2014). Different preference loci underlying categorically distinct preferences (e.g. for colour and size) most likely far better approximates the genetics of such preferences than assuming they are controlled by the same locus.

RESULTS AND DISCUSSION

Our first and primary finding is that the ecological stage mechanism effectively maintains preference and trait differentiation. Upon secondary contact, the locally adapted ecological traits of each population are initially diverged; male displays and female preferences are also differentiated. Despite the gene flow that constitutes contact, substantial preference differentiation is retained at the evolutionary equilibrium (Figure 2a: maximum preference differentiation is 0.74 across populations at the P_R and P_L loci). The strength of preference is critically important to this maintenance: below $\alpha \approx 4$ there is less preference differentiation, but above this value much of the original differentiation is maintained. Strong preferences cause the preference loci to become tightly correlated with the display loci M and N and hence the ecological loci E_M and E_N; this allows evolutionary divergence at the preference loci as the ecological loci respond to viability selection during local

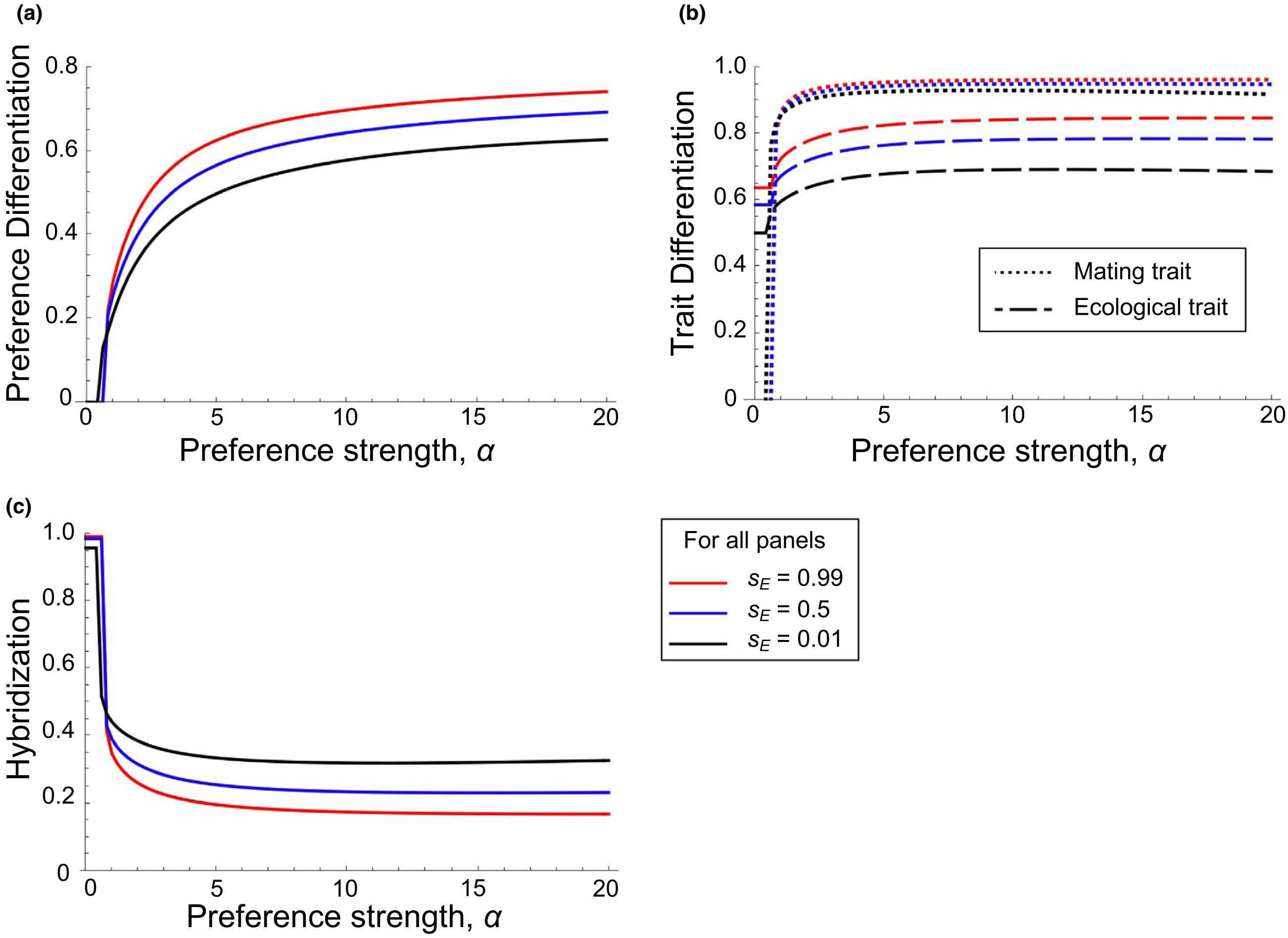

FIGURE 2 Differentiation and hybridisation between the two populations at equilibrium. Differentiation increases and hybridisation decreases with stronger ecological selection s_{EM} and s_{EN}. The populations were initiated with fully diverged preferences (where lower-case letters denote the frequency of the alleles in upper-case, the first subscript indicates which population the frequency is measured in and the second subscript indicates the allelic identity: $p_{R12} = 1.0$, $p_{R22} = 0$, $p_{L12} = 0$, $p_{L22} = 1.0$) and fully diverged ecological and mating traits ($e_{M12} = 0$, $m_{12} = 0$, $e_{\mathrm{N}12} = 0$, $n_{12} = 0$, $e_{\mathrm{M}22} = 1$, $m_{22} = 1$, $e_{\mathrm{N}22} = 1$, $n_{22} = 1$). This matches our assumption of secondary contact after divergence of preferences and traits in allopatry. Mutations rates $\mu_{EM} = \mu_{EN} = \mu_M = \mu_N = 0.01$ mimic the magnitude of mutation on several loci that might constitute a complex polygenic trait. Other parameters (see Methods) are $mig_1 = mig_2 = 0.01$, $\gamma_{low} = \gamma_{envt} = 0.5$, $\sigma_{low} = \sigma_{envt} = \sigma_T = 0.5$, $s_{CR} = s_{CL} = 0.015$, $s_R = s_L = 0.1$, $f_{fem,M} = f_{fem,N} = f_{male,M} = f_{male,N} = 0.1$, $s_{TH} = 0.5$, $s_{TL} = 0.9$. The x-axis represent preference strength α, defined as how much more likely a female is to mate with a male that she prefers versus a male that she does not, given equal encounters. (a) Preference differentiation between the populations, measured as the difference under varying ecological selection $s_E = s_{EM} = s_{EN}$ between the frequency of P_{R2} in population 1 (p_{R12}) and P_{R2} in population 2 (p_{R22}, yielding $p_{R12} - p_{R22}$; note that under symmetrical conditions this is equal to $p_{L22} - p_{L12}$). b) Mating trait (dotted) and ecological trait (dashed) differentiation. The former is measured as the difference between the frequency of M_2 in population 1 (m_{12}) and M_2 in population 2 (m_{22}, yielding $m_{12} - m_{22}$) and the latter is measured as the difference between the frequency of $\mathrm{E}_{\mathrm{M}2}$ in population 1 (e_{M12}) and $\mathrm{E}_{\mathrm{M}2}$ in population 2 (e_{M22}, yielding $e_{M12} - e_{M22}$). c) Proportion of the population that are hybrids, defined as containing a mismatch between the ecological and display loci for either loci specific to population 1 or loci specific to population 2 (e.g. all genotypes that are not $\mathrm{E}_{M1}\mathrm{M}_1\mathrm{E}_{N1}\mathrm{N}_1$, $\mathrm{E}_{M1}\mathrm{M}_1\mathrm{E}_{N2}\mathrm{N}_2$, $\mathrm{E}_{M2}\mathrm{M}_2\mathrm{E}_{N1}\mathrm{N}_1$, or $\mathrm{E}_{M2}\mathrm{M}_2\mathrm{E}_{N2}\mathrm{N}_2$)

adaptation. In addition, strong preferences generate more sexual selection on the display loci M and N, which also increases indirect selection on the P_R and P_L loci. Both the ecological traits and especially the male displays also maintain high levels of differentiation at equilibrium (Figure 2b). Similar to other secondary contact models, we find that population differentiation increases with decreasing migration rate, and is prohibited when migration is too high (with moderately strong preferences, $mig > {\sim}0.05$, Figure S1). These results confirm that preferences for distinct displays, and the displays themselves, can remain differentiated between populations, caused by distinct ecological contexts posited by the ecological stage mechanism.

Of special importance is our second major finding: that maintaining preference and trait divergence pushes hybridisation to low levels (Figure 2c). Low hybridisation can help maintain species boundaries over time, even in the face of gene flow (Barton & Hewitt, 1989; Harrison & Larson, 2014), with resulting patterns of high divergence for genomic regions containing loci underpinning reproductive isolation or differential adaptation even in an otherwise homogenised genome (e.g. in *Heliconius* butterflies: Arias et al., 2012; Martin et al., 2013). This demonstrates that the ecological stage mechanism can maintain a notable level of reproductive isolation, and thus contribute to speciation.

The evolutionary forces in the ecological stage mechanism are strong enough to drive preference differentiation even when divergent selection is entirely indirect. We find preference divergence with no direct fecundity benefit ($f = 0$, Figure 3), although strong benefits of mating with a more fecund locally adapted male ($f > 0$) further increase preference divergence. Moreover, ecological selection through local adaptation has only a moderate effect on preference divergence across fecundity values, as seen by the small differences between values of s_E (Figure 3), suggesting that differentiation is primarily due to sexual selection. When there is no fecundity selection, the net forces of direct and indirect selection in the system combine to provide disruptive selection; *direct* disruptive natural selection on any locus is absent, but still preference differentiation is maintained (Box 1, Supplementary Material B).

Distinct loci underlying ecologically relevant preferences remain divergent

One of the primary ways in which the ecological stage model departs notably from almost all previous theoretical work is that preferences for the male display characteristic of one population versus the other are controlled by entirely different loci (as are the population-specific ecological and display traits). While this may initially seem a technical distinction, it is actually of fundamental importance. Not only is it a more plausible match for the biology of categorically distinct preferences, but it has the property that the spread of one preference does not displace the other—instead both preferences can potentially co-exist at high frequency. One might therefore expect both preferences to spread across both populations upon secondary contact, as indeed they would if it were not for search costs, display trade-offs, and environmental matching (see next sections). In contrast, almost all previous models with separate preference and display loci assume a single preference locus (or each locus for a quantitative preference) has alternate alleles coding for each population's preference (Kopp et al., 2018). The single exception that we are aware of is a model by van Doorn (2004); in ‘Afterthoughts on Chapters 8 & 9’, pp. 286–289) that similarly considers different sets of loci to determine condition in two habitats. There, different displays are indicators of quality in each habitat (revealing indicators in their characteristic patch, but epistatic indicators in the other patch; Maynard-Smith, 1976, 1985), and females choose mates based on patch-specific preferences for each display. Neither partial expression of display, nor trade-offs between displays, nor direct versus indirect selection on preferences are assessed in that work; there is, however, a direct cost to expressing both preferences, which is not included in our model. We anticipate that including such a cost in our model would make it even less likely for preferences to reach high frequency in the ‘wrong’ population, further promoting preference divergence. Similar to our model (Figure S1), van Doorn finds that preference and display differentiation occur under a narrow range of migration rates. Thus, both models show that the increased biological realism of separate loci for categorically different preferences allow differentiation.

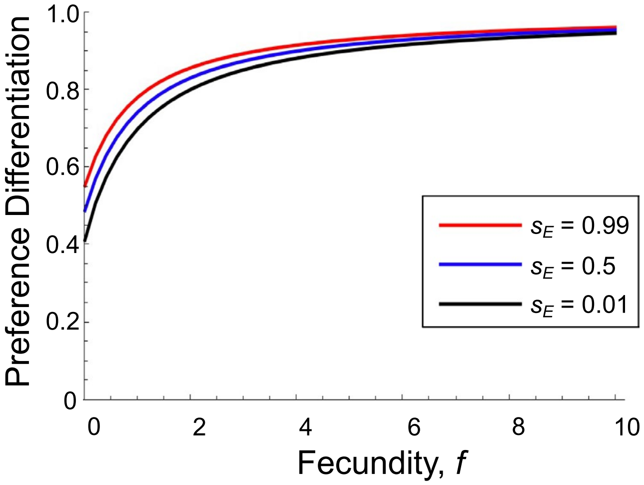

FIGURE 3 Effect on preference differentiation of direct benefits of the male's ecological trait through increased fecundity of the mated pair. Preference differentiation is measured as in Figure 2. Parameters are as in Figure 2 with $\alpha_R = \alpha_L = 4$. $f = f_{fem,M} = f_{fem,N} = f_{male,M} = f_{male,N}$

Environmental-match preferences and indicator displays are essential

A key element of the ecological stage mechanism is that indicators and preferences match selective pressures in the local environment, and we found that environmental matching is essential to maintain differentiation. High values of σ_{envt}, which reduce the environmental-matching of preferences, can erode differentiation (Figure 4a; effects of the three classical types of indicators are explored in Figures S3 and S4). Thus, when females prefer displays that do not honestly indicate benefits important in the local environment ($\sigma_{envt} > \sim 0.5$), both preferences tend to fix across both populations, removing preference differentiation (see also Figures S3 and S4). High costs to the foreign display, γ_{envt}, or very high trade-offs for high-condition males, s_{TH}, partly retard such fixation or even maintain preference differentiation.

The role of condition dependence can likewise be explored by increasing σ_{low}, which causes females to prefer low condition males. In contrast to the environmental-matching function of the indicators, it appears that while condition dependence is helpful it is not essential to differentiation, given the fairly small effects of σ_{low} and γ_{low}

BOX 1 Selective drivers of diversification

The interplay of direct and indirect selection on preference differentiation has intriguing effects. Fecundity benefits can play an important role in preference evolution by placing direct selection on each preference in its characteristic population. In our model, females that prefer the local display tend to mate with a more fecund locally adapted male, and therefore have more offspring. Because we find this can greatly increase preference divergence, we expect the ecological stage mechanism to be more important in natural systems where sexual selection yields direct benefits, such as parental care quality, (Candolin, 2000; Hale & St Mary, 2007); or avoiding parasite transmission, (Beltran-Bech & Richard, 2014; Paciência et al., 2019), especially when populations inhabit distinct environments. Local adaptation through viability selection, in contrast, exerts only indirect selection on preference through linkage disequilibrium between the preference and the favourable ecological alleles in each population; this is a weaker force, although local adaptation is widespread in natural populations (Hereford, 2009) and therefore could have a weak effect but be commonly observed.

It is interesting to examine these results further, in light of the fact that direct disruptive natural selection figures prominently in most models of speciation with gene flow, and is thought by many to be essential for speciation to proceed (e.g. Gavrilets, 2004; but see M'Gonigle et al., 2012). For cases of the ecological stage model without fecundity selection, direct disruptive viability or fecundity selection acting on any type of trait is absent; nonetheless, divergence is maintained in preference, male display, and ecological trait loci, and hybridisation is kept low. Instead, selection on these traits is a mix of direct viability selection in one population, with indirect viability selection or direct sexual selection acting in the opposite direction in the other population (see Supplementary Material B). The net effect of both these direct and indirect selective forces yields divergent selection among populations, a feature in common with ecological speciation (Rundle & Nosil, 2005; Schluter, 2000). Specifically, the ecological loci are directly favoured in one population but under no direct selection at all in the other population, where instead they decrease due to indirect selection via their association with the foreign display and preference alleles (both directly selected against—see next lines). Display loci increase in their local population due to sexual selection, and viability selection acts against the display in the foreign environment. The preference loci are directly selected against in both populations due to search costs, but increase in their focal population due to indirect selection so that preference differentiation is maintained even in the absence of direct fecundity selection. These forms of selection contrast with those in many other speciation models, which assume direct disruptive selection on ecological traits resulting from either local adaptation (e.g. Kirkpatrick, 2001; Servedio, 2004; Servedio & Bürger, 2014) or competition (e.g. Dieckmann & Doebeli, 1999; Bürger et al., 2006; Pennings et al., 2008; Rettelbach et al., 2013). Our finding that direct disruptive ecological selection is not necessary for the evolution of reproductive isolation in the ecological stage model highlights that researchers should be cautious about claiming that it is required for speciation; a combination of direct and indirect selection from multiple pathways, can instead suffice.

(Figure 4b). That condition dependence is not essential is surprising given its central role in former models (van Doorn et al., 2009). Our findings instead highlight a novel aspect of the ecological stage mechanism—the importance of distinct environments and having preferences and indicators in the proper ecological context to foster differentiation and speciation.

Display trade-offs are necessary

We explored whether trade-offs males experience from simultaneously expressing both distinct displays affect the maintenance of preference and display differentiation (Figure 4c). We find that fitness trade-offs tend to promote preference differentiation. In the case of a high-condition male (well adapted to his local environment), a threshold trade-off must be crossed (s_{TH} between 0.1 and 0.3) to allow any differentiation. After this point, increased trade-offs only slightly increase preference differentiation. Throughout this range, the strength of trade-offs faced by low condition males (s_{TL}) has a negligible effect, suggesting this aspect of condition dependence contributes little to differentiation likely because the affected males are at low frequency (Figures S3 and S4). We focus attention on cases where trade-offs faced by low-condition males are at least as strong as those faced by high-condition males ($s_{TL} \geq s_{TH}$), which accords with expectations from condition-dependent models (Grafen, 1990; Zahavi, 1975).

Search costs are critical

Search costs are critical to maintaining preference differentiation under the ecological stage mechanism.

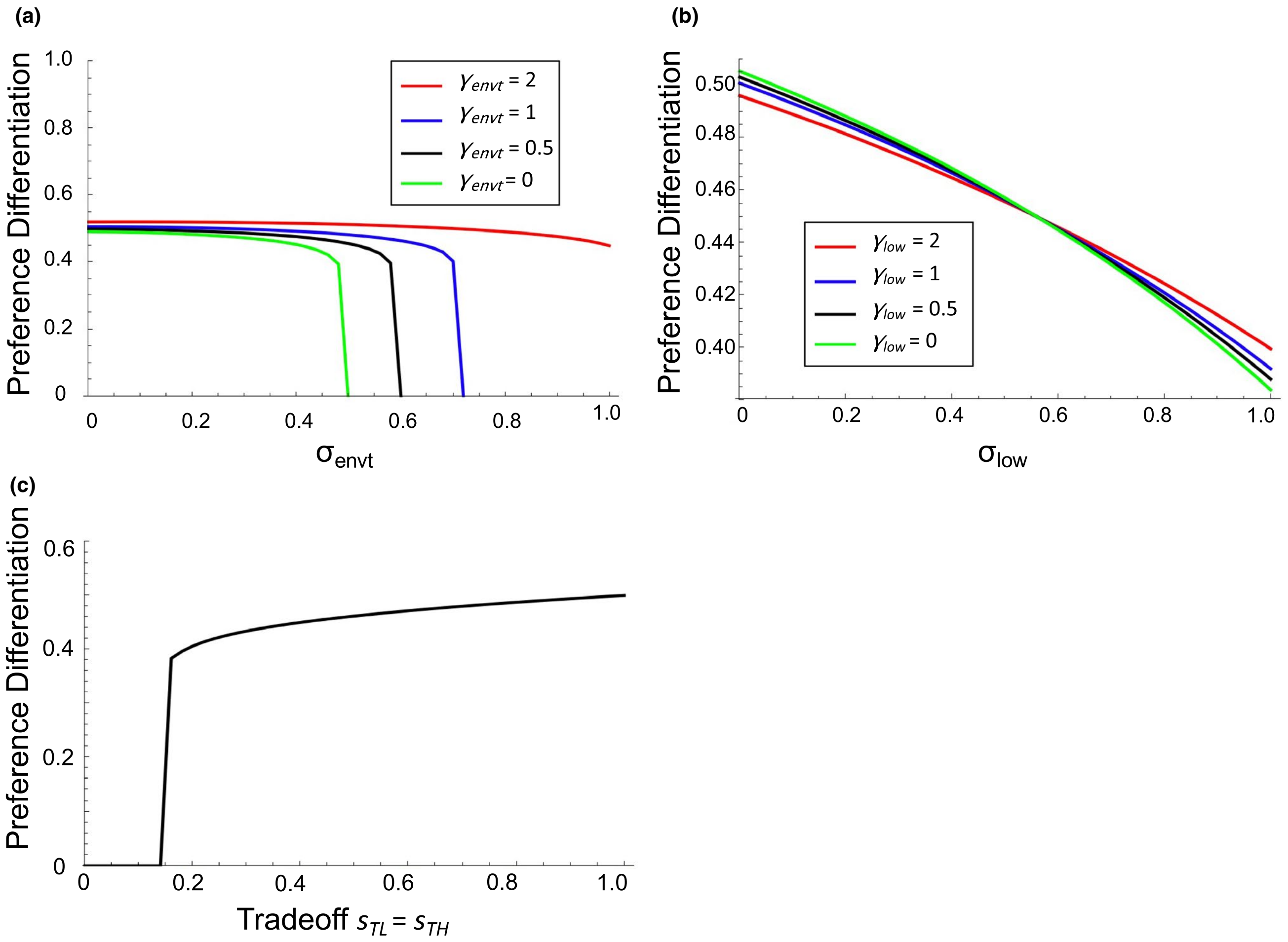

FIGURE 4 Effect on preference differentiation of environmental matching, condition dependence, and trade-offs. Preference differentiation is measured as in Figure 2. Parameters are as in Figure 2 (unless otherwise specified) with $\alpha_R = \alpha_L = 4$ and in panels (a) and (b) $s_{TH} = 0.1$, $s_{TL} = 0.9$. (a) When preferences are not environmentally specific preference differentiation is lowered. This occurs when females prefer the indicator trait regardless of it being in the wrong environment (higher γ_{envt} shows different costs that males are paying for expressing the trait in this 'wrong' environment). (b) Preference differentiation is also lowered, but very slightly (note *y*-axis) when females prefer males in low condition in addition to those in high condition (higher σ_{low}) in the 'right' environment. The lines for γ_{low} show different costs that males are paying for expressing the trait when they are in low condition. Condition-dependent costs of display (γ_{low}) have a minor slowing effect and show subtle changes in rank with high γ_{low} showing slightly less differentiation at $\sigma_{\text{low}} = 0$ and slightly more at $\sigma_{\text{low}} = 1$. (c) Preference differentiation is increased with trade-offs above a critical value. Trade-offs occur through selection on males when they express two display traits. The *x*-axis shows the trade-offs for dual trait expression from low male condition s_{TL} and high-condition males s_{TH} when these are equal. Additional analyses (Figures S3 and S4) indicate that when s_{TL} increases above s_{TH} there is a very slight increase in preference differentiation above values shown here

Specifically, having distinct female preferences (and displays) controlled by different loci risks losing preference differentiation; without search costs we expect both preferences to sweep across both populations, resulting in multiple shared preferences and displays, as follows. In its characteristic population, each preference is favoured directly by fecundity selection, because females with the local preference tend to pair with locally adapted and hence highly fecund males. Each preference is also favoured by indirect selection due to the linkage disequilibrium that the preference locus forms with the male display and ecological loci. When search costs are absent or very low (to the left of the curves in Figure 5a), there is essentially no force opposing these sources of selection. Because the populations are connected by migration, both preference alleles become universal; females in our example would prefer males that are both red and large provided $\sigma_{envt} > 0$, that is have multiple ornaments (Candolin, 2003; van Doorn et al., 2004). However, this homogenisation is countered when search costs increase. Specifically, preference differentiation occurs because high-condition displays are common in their characteristic population, making frequency-dependent search costs in that population weak (Figure 5b). In contrast, the preferred display is rare in the opposite population (when $\sigma_{envt} > 0$), making frequency-dependent search costs strong. Search costs thus generate strong direct selection against 'foreign' preferences, preventing them from spreading in the 'wrong' population and

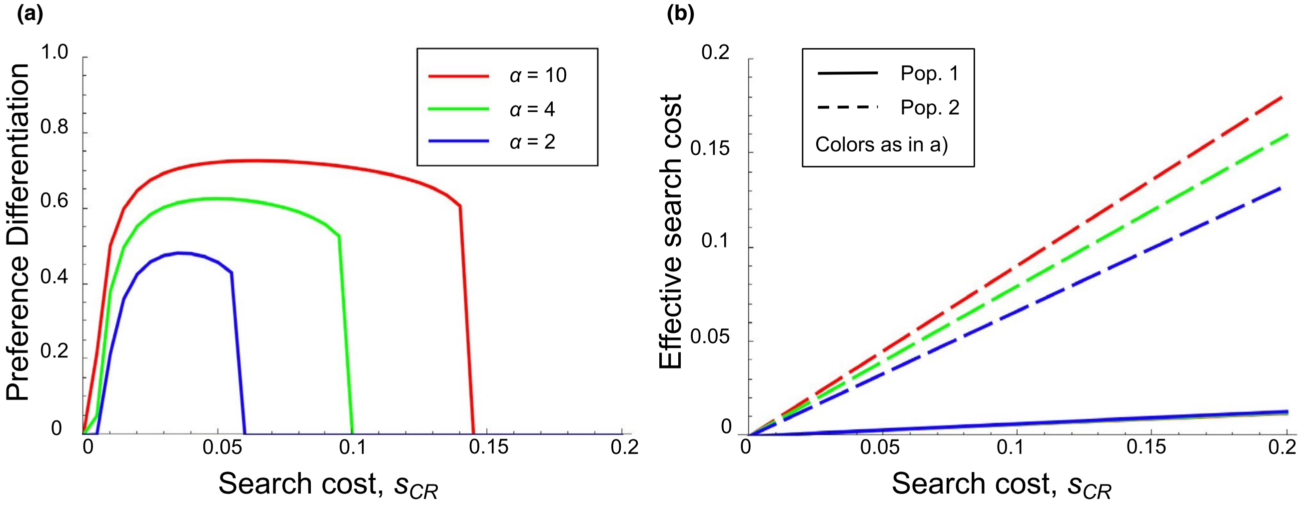

FIGURE 5 The effect of search costs on preference differentiation at equilibrium. (a) Preference differentiation, measured as in Figure 2, is maintained across a range of search costs. Stronger preferences broaden this range, and intermediate search costs are most effective at maintaining differentiation. (b) The effective search cost on the P_R locus (s^*_{cRk}) in population k, weighted by the preference strength and frequency of preferred male, is low in the 'local' versus 'foreign' population (where population 1 is 'local', solid: population 1, dashed: population 2, colours as in panel a). Specifically, the search cost is $s^*_{cRk} = s_{cR}\left(1 - z_{Rk}/(1+\alpha_R)\right)$, where z_{Rk} represents the sum of the frequencies of each type of male in population k times the strength of preference for that type of male (as in Otto et al., 2008). The frequency of the allele for the preferred trait (M_1) is very high in population 1 (between 0.95 and 0.98, with larger values at higher preference strengths) and is very low in population 2 (between 0.008 and 0.015, with lower values at higher preference strengths; see Figure S6). The solid lines in population 1 are visually indistinguishable at this scale, indicating there is very little change in the effective search cost as preference strength varies in the local population. Parameter values are set as in Figure 2 with $s_{EM} = s_{EN} = 0.1$, $s_{TL} = 0.5$, $\gamma_{low} = \gamma_{envt} = 0.5$ and $\sigma_{low} = \sigma_{envt} = \sigma_T = 0$

allowing preference differentiation to be maintained. When search costs are very strong, to the right of the curves in Figure 5a, they overwhelm all selection favouring the preference regardless of the population, so that no preference can be maintained; mating becomes random. Intermediate search costs are thus most conducive to preference differentiation.

Our inclusion of search costs fits with empirical expectations; female search costs are thought to be common and can affect fitness by increasing predation or the risk of going unmated, or losing foraging time (Etienne et al., 2014). A search cost of 0.1 would reduce female fitness by about 10%, and is in the range shown in some experiments (e.g. Lindström & Lehtonen, 2013). Search costs are also critically important for maintaining preference divergence in another model (M'Gonigle et al., 2012), which incorporates spatial differences in carrying capacity but no ecological divergence. However, in that model, different preference alleles compete at the same locus, preventing both preferences from spreading. This again highlights the importance of allowing different loci to control each preference; our model obtains preference differentiation despite the addition of this realistic feature. The need for search costs to maintain differentiation and reproductive isolation is in direct contrast to many models of sexual selection which suggest that costly mate choice undermines preference evolution (e.g. Bulmer, 1989).

Preferences can diverge from standing variation

Finally, we also assess conditions where preferences are initially rare, assuming either full divergence at both the male display and ecological loci, or initial divergence only in the ecological trait due to local adaptation, which is probably more realistic. These simulations directly address progress towards speciation with gene flow rather than maintaining divergence that has occurred in allopatry. We find that when preferences are strong, preference divergence can evolve when preferences start at a frequency above 0.05–0.07 (Figure S5), but no divergence occurs when preferences are notably rarer, e.g 0.01. Additionally, preferences differentiate more easily (with a slightly lower preference strength) when the preferred displays are also rare, suggesting that as male displays evolve, they drag the corresponding preferences along. Therefore, the ecological stage mechanism can promote divergence when preferences evolve from standing variation, but not via new mutation, which would introduce the preference at too low a frequency. In general, the ecological stage model is most applicable to secondary contact; however, the important finding that it can work from standing genetic variation in female preference and male display suggests that 'de novo' reproductive isolation could evolve via this mechanism. This broadens the contexts in which the ecological stage may contribute to the speciation process.

CONCLUSION

The ecological stage model emphasises that ecological conditions shape mating interactions and can significantly reduce hybridisation rate. We show that categorically distinct selection forces among populations can lead to divergence in male displays and female preferences that match the local environment. Differentiation persists in secondary contact, preventing hybridisation and furthering the speciation process. Differentiation can also occur with gene flow from low levels of standing variation. This all occurs because females choosing local males obtain distinctly different benefits that are especially favoured in that population's selective regime, and these benefits are indicated by the local male display; the foreign display indicates differing benefits that are not under notable selection in the local population. A recent empirical test supports our model by confirming several key predictions of distinct displays indicating distinct benefits that match the local environment (Tinghitella et al., 2020). The ecological stage model does not rely on differences in sensory environment or their effects on the evolution of communication, and is thus distinct from the sensory drive hypothesis and its contribution to speciation (Boughman, 2002; Endler, 1992). It could, however, work in conjunction with sensory drive and does share the feature that distinct environments lead to differentiation among populations in female preference and male display; however, the mechanisms causing this differ.

Under the ecological stage mechanism, search costs actually facilitate preference and display divergence and help prevent the universal fixation of preferences, in marked contrast to most earlier models of sexual selection in speciation. Divergence can persist even without direct disruptive ecological selection, in contrast to the widespread belief that it is a necessary ingredient for speciation in models emphasising ecological mechanisms (Box 1). Instead, our model shows that a combination of indirect and direct viability and sexual selection acting on preferences, which are environmentally dependent, in conjunction with trade-offs for males attempting to express both displays, is sufficient to maintain differentiation between populations and facilitate speciation. Our model adds important realism—allowing distinct loci to code for categorically different ecological traits, displays and preferences—and nevertheless reveals that preference homogenisation can be foiled and populations can maintain differentiation in all of these trait types. That this differentiation occurs both after secondary contact and from standing variation suggests that the ecological stage model may have broad relevance for the speciation process.

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AUTHORSHIP

JWB and MRS developed the model and wrote the manuscript. JWB also conceived the idea. MRS also wrote the code and ran the simulations.

DATA AVAILABILITY STATEMENT

The code for the manuscript is deposited on Dryad. DOI: https://doi.org/10.5061/dryad.44j0zpcfy.

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