LETTER

The evolution of species recognition in competitive and mating contexts: the relative efficacy of alternative mechanisms of character displacement

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Abstract

Sympatric divergence in traits affecting species recognition can result from selection against cross-species mating (reproductive character displacement, RCD) or interspecific aggression (agonistic character displacement, ACD). When the same traits are used for species recognition in both contexts, empirically disentangling the relative contributions of RCD and ACD to observed character shifts may be impossible. Here, we develop a theoretical framework for partitioning the effects of these processes. We show that when both mate and competitor recognition depend on the same trait, RCD sets the pace of character shifts. Moreover, RCD can cause divergence in competitor recognition, but ACD cannot cause divergence in mate recognition. This asymmetry arises because males with divergent recognition traits may avoid needless interspecific conflicts, but suffer reduced attractiveness to conspecific females. Therefore, the key empirical issue is whether the same or different traits are used for mate recognition and competitor recognition.

INTRODUCTION

When closely related, formerly allopatric species become sympatric during secondary contact, individuals that fail to distinguish between heterospecifics and conspecifics can incur strong fitness costs (Gröning & Hochkirch 2008). The fitness costs associated with interspecific courtship and mating have been well documented as effective drivers of sympatric divergence in traits affecting mate recognition (the process of reinforcement and reproductive character displacement, or RCD; reviewed by, e.g., Howard 1993; Noor 1999; Servedio & Noor 2003; Coyne & Orr 2004; Pfennig *et al.* 2007). In addition, individuals can incur a fitness cost when they engage in aggressive behaviour toward individuals of another species (reviewed by Ord & Stamps 2009; Grether *et al.* 2009; Peiman & Robinson 2010; Ord *et al.* 2011). When the benefits of securing a scarce, common resource outweigh such costs, aggression toward heterospecifics can be adaptive (Orians & Willson 1964; Cody 1969; Cody 1973; Peiman & Robinson 2007; Tobias & Seddon 2009). However, when two species do not share a common resource, individuals that avoid aggressive interactions with heterospecifics can evade the costs of such behaviour without compromising access to a resource. Divergence in traits involved in competitor recognition can therefore result from selection against such costly recognition errors (Lorenz 1962; Kral *et al.* 1988; Alatalo *et al.* 1994; Tynkkynen *et al.* 2004; Tynkkynen *et al.* 2005; Tynkkynen *et al.* 2006; Kirschel *et al.* 2009; Grether *et al.* 2009; Anderson & Grether 2009, Anderson & Grether 2010).

Divergence in competitor recognition traits is one of several possible consequences of agonistic character displacement (ACD), which can be defined simply as phenotypic evolution caused by interspecific interference competition (Grether *et al.* 2009). Other possible consequences of ACD include temporal or spatial shifts in activity that reduce the frequency of interspecific encounters and improvements in interspecific fighting ability (reviewed in Grether *et al.* 2009). In many respects, ACD and RCD can both be expected to influence traits affecting species recognition in ways that ecological character displacement (ECD) cannot. This is because ECD is driven by indirect competition (i.e. resource depletion; Brown & Wilson 1956) and often results in shifts in morphology or habitat use that reduce resource overlap between sympatric species, while RCD and ACD are driven by direct interactions (i.e. aggression and sexual behaviour) and usually result in shifts in traits that affect the rate or outcome of such direct interactions (Grether *et al.* 2009; for an alternative view, see Pfennig & Pfennig 2012). Although the relationship between RCD and ECD has received some formal theoretical attention (e.g. Goldberg & Lande 2006; Aguilè *et al.* 2011), the relationship between ACD and the other two processes has not.

Here, we seek to partition the contributions of ACD and RCD in driving divergence in traits affecting species recognition. These processes have only rarely been investigated in the same systems (Grether *et al.* 2009), and their relative importance has not been formally evaluated. In particular, when the same traits are potentially used for both competitor and mate recognition, elucidating the interplay between these mechanisms, and how they can give rise to different observed patterns of divergence between closely related species, remains an important challenge (Honkavaara *et al.* 2011). For example, patterns of divergence in male wing colouration between sympatric species of territorial damselflies (Calopterygidae) have recently been attributed to ACD (Tynkkynen *et al.* 2004; Tynkkynen *et al.* 2005; Tynkkynen *et al.* 2006; Anderson & Grether 2009). Males of these species use wing colouration to identify conspecific competitors. Thus, divergence in wing colouration reduces the rate of costly, and unnecessary, interspecific fights (Tynkkynen *et al.* 2004; Tynkkynen *et al.* 2006; Anderson & Grether 2011). However, RCD is a plausible alternative explanation for the same geographic patterns, especially in *Calopteryx* because maladaptive interspecific mate selection still occurs (Tynkkynen *et al.* 2008) and females appear to choose males on the basis of wing colouration (Siva-Jothy 1999; Cordoba-Aguilar 2002; Svensson *et al.* 2007; Honkavaara *et al.* 2011).

The difficulty in distinguishing ACD from RCD applies to any species in which the same cues are potentially used for recognising both mates and competitors. Such dual-use traits are extremely common in intraspecific interactions (Berglund *et al.* 1996). Berglund *et al.* (1996) gave 48 specific examples of male traits that appear to be used as signals in both male–male competition and female mate choice. The examples span a wide range of taxonomic groups (insects, arachnids, crustaceans, fish, amphibians, reptiles, birds, mammals) and sensory modalities (visual, acoustic, chemical, electric). Although there are perhaps fewer known examples of traits being used for species recognition in both contexts (Table 1 and Supplement S1), mate recognition has been studied more intensively than competitor recognition, and it is rare for species recognition to be studied in both contexts in the same systems (Ord *et al.* 2011). Although RCD has been reported far more often than has ACD, this might only reflect research effort. Indeed, until recently, ACD was not recognised as a distinct form of character displacement, and thus some purported cases of RCD may in fact be cases of ACD. On the other hand, RCD has been explicitly ruled out in only 1 of 15 putative cases of divergent ACD (Grether *et al.* 2009). The patterns generated by the two processes can be indistinguishable, and no practical method has yet been identified for distinguishing between them empirically. Indeed, some character displacement patterns have been presented as evidence for both ACD and RCD (reviewed in Grether *et al.* 2009). Could the two processes have acted together and perhaps synergistically in such cases? Or does the operation of one of the two processes preclude the other?

Here, we develop a common theoretical framework to compare how the fitness costs associated with cross-species mate selection, on the one hand, and interspecific aggression, on the other, could affect the evolution of species recognition. We analyse how a single trait that is used for recognising conspecific mates, conspecific competitors, or both mates and competitors, evolves when species with similar values of the trait come into secondary contact.

MATERIALS AND METHODS

The model

We modelled secondary contact between two closely related species in which males compete for mating territories and females are the

choosy sex. Males are assumed to distinguish territory competitors from non-competitors using a single male-specific trait and the same trait may or may not be used for mate recognition by females. Competition among males for mating territories is extremely common (Maher & Lott 2000), and in diverse taxonomic groups, males have been shown to respond aggressively to heterospecific territorial signals during the reproductive season (Grether *et al.* 2009; Peiman & Robinson 2010; Ord *et al.* 2011). As mates are a species-specific resource, there is little apparent benefit to securing mating territories against heterospecific males. Divergence in territorial signals between sympatric species therefore provides a mechanism by which such interspecific encounters could be avoided. However, the same traits that are used as territorial signals are often also targets of female mate choice (Berglund *et al.* 1996) and are thus likely used by females for discriminating between males of different species (Table 1 and Ord *et al.* 2011). Hence, the potential for ACD and RCD to operate simultaneously applies to several taxa. To enhance biological realism, we parameterise the model for a particular system, *Hetaerina* damselflies (Supplement S2), but the theoretical framework itself is quite general and could be adapted to other systems.

The model was implemented as an individual-based model (e.g. DeAngelis & Mooij 2005) integrating local behavioural interactions, genetics, population dynamics and environmental stochasticity. The ecological component of the model describes the individual's interactions with its environment. We explicitly characterise the behaviour and life history of individuals for the duration of their adult lives. Differential fitness emerges from the interactions between individuals and their environment. The key processes modelled are as follows: (1) male–male competition and territory acquisition, (2) mating, (3) reproduction and recruitment and (4) mortality. The model's dynamics occur on a daily time step. In each time step, the model cycles through all individuals to determine their fates. The genetic component of the model characterises the genetic distributions of traits affecting individual behaviour, and how these distributions change between generations.

In our model, every individual male *i* (of either species) either holds a territory or does not, and territories can be vacant, occupied by a single male, or occupied by multiple males. Males recognise competitors based on a single sex-specific trait (e.g. wing colouration); if two males occupy the same territory and either male recognises the other as a competitor, a fight ensues. Males expend energy reserves fighting, which reduces their ability to acquire and hold territories in subsequent fights. If neither male recognises the other as a competitor, they share the territory. We model the fitness consequences of sharing a territory as depending only on whether the males compete for the same females, which in turn depends on female mate recognition.

A male's fitness costs associated with male–male competition and ACD in this system depend strongly on local interactions – whether he shares a territory with other males, and the species identity and phenotypes of the other males with which he may share a specific territory. Moreover, a male's ability to occupy a territory also depends critically on the feedback between his propensity to engage in interspecific territorial fights and his dynamic energy reserves, as well as the energy reserves of other males he encounters. Such processes are difficult to integrate in analytical models. Our individual-based model captures the localised, frequency-dependent relative fitness observed in the field by explicitly accounting for the

Table 1. Examples of dual-use traits in species recognition, that is, traits used for both mate recognition and competitor recognition. See Table S1 for supporting references

Taxon	Trait description
Calopteryx damselflies	Wing coloration
Dendrobatid frogs	Call
Ficedula flycatchers	Plumage
Gasterosteus sticklebacks	Body coloration
Geospiza finches	Song
Haplochromine cichlids	Body coloration
Hyla frogs	Call
Hypocnemis antbirds	Song
Laupala crickets	Song
Passerina buntings	Song
Pogoniulus tinkerbirds	Song
Rana frogs	Call
Serinus finches	Song
Streptopelia doves	Vocalization

acquisition and loss of specific territories by males with specific phenotypes (Supplement S2).

Furthermore, accounting for the different selective pressures on males and females is necessary to characterise the interplay between ACD and RCD. Male competitor recognition only affects male fitness, whereas female mate recognition affects both male and female fitness. In our model, males are indiscriminate about mates, but females have control over whether they come into physical contact with males by discriminating among potential mates either using the same male trait that males use to discriminate among potential competitors (e.g. song, wing colouration) or a different trait. As a first step, we examine the effects of reproductive interference without the complications of hybridisation (e.g. introgression and different degrees of hybrid vigor), and assume that interspecific mating attempts do not proceed to the insemination stage. For simplicity, we assume an equal sex ratio at birth, and the parameters governing female availability were kept constant during the analysis (see Supplement S2 for details). Varying female availability did not affect our qualitative results. If a female selects a heterospecific male (i.e. allows a heterospecific male to come into physical contact with her), she must pay an energetic penalty h_C to extricate herself from the heterospecific pairing, which reduces her clutch size. Our characterisation of the mechanism of RCD can approximate the situation where cross-species matings result in inviable or infertile hybrids by assuming that females lose their entire clutch as a result of mistaken mate recognition (i.e. $h_c = 1$).

We model mate recognition and competitor recognition as Gaussian functions of a conspicuous male trait Z (e.g. colour patch). The Gaussian recognition functions are specified by two parameters, the central location μ_Z and width σ_Z (e.g. Grether *et al.* 2009). When encounters occur, the probability of two males responding aggressively to each other depends on their respective values of Z, μ_{Z_1} and σ_Z. The probability of a territory resident attacking an intruder peaks when the intruder's value of Z equals the resident's value of μ_{Z_1}, and vice versa. Likewise, the probability of a female selecting a male as a mate peaks when the male's value of Z matches the female's value of μ_{Z_2} with width ς_Z. For further details, see Supplement S2.

The male recognition cue Z and the four recognition function parameters (μ_{Z_1}, μ_{Z_2}, σ_Z, ς_Z) are all evolvable traits in the model. To follow changes in the genotypic distributions of these traits over time, and to examine the pleiotropic effect of a single trait being used for both competitor and mate recognition, we track the underlying alleles and loci explicitly (Supplement S2). All traits are modelled as quantitative traits with genetic values determined additively and subject to stochastic mutational, environmental and developmental noise. Reproduction is sexual, and the loci were modelled as autosomal, diploid and freely recombining.

Model analysis

We sought to characterise the rate at which traits affecting mate and competitor recognition diverge following secondary contact between formerly allopatric populations of two species. At the onset of secondary contact, the mean phenotypes for trait Z and the recognition function parameters μ_{Z_1}, μ_{Z_2} were set to differ between species by a quantity δ. We varied δ from 0 to 1 standard deviation units and found that the initial level of divergence had no qualitative effect on the outcome. Hence, for brevity, we only present detailed results for when $\delta = 0$.

We investigated three basic scenarios:

(1) Trait Z is only used for competitor recognition. In this case, we assume that females discriminate between conspecific and heterospecific males using some other, unspecified trait that differs between species.
(2) Trait Z is used for both competitor recognition and mate recognition.
(3) Trait Z is only used for mate recognition. In this case, we assume that males distinguish between conspecific and heterospecific males using some other, unspecified trait that differs between species.

We characterised divergence in the recognition cue Z in each generation as $\dfrac{|E[Z_1] - E[Z_2]|}{(\sqrt{(\mathrm{var}(Z_1))} + \sqrt{(\mathrm{var}(Z_2))})/2}$, where the average ($E[\cdot]$) and variance $\mathrm{var}(\cdot)$ were calculated across all individuals in each species.

When territories are scarce, competition for territories is more intense, and males that deplete their energy reserves fighting with heterospecifics (see Supplement S2) are at a greater disadvantage, compared to when territories are abundant. Moreover, both theoretical and empirical studies across a wide range of taxa have repeatedly demonstrated how the evolution of territorial defense in both heterospecific and conspecific contexts depends crucially on territory abundance (e.g. Peiman & Robinson 2010). Thus, in scenarios 1 and 2, we examined how the intensity of competition among males affects the rate of ACD by varying the number N_T of territories available. In scenarios 2 and 3, we varied the relative strength of RCD by varying the reduction h_C in the female's clutch size caused by mistaken mate recognition.

Further details on the equations for the processes in the model and the corresponding parameter values are justified and formulated in full in Supplement S2. Supplement S2 also highlights some approaches to modifying our model to accommodate alternative biological assumptions, including taxa with monogamous females, systems where territory possession or past mating experiences affect additional components of male fitness, and taxa where either male or female offspring are produced by parthenogenesis. In each simulation, we ran the model for 10 000 generations following secondary contact, after a 1000-generation allopatric burn-in period. We ran 20 replicates of our model for different parameter combinations under each scenario to assess how different strengths of ACD and RCD governed the evolutionary trajectories of the recognition cue Z and the recognition functions.

RESULTS

We confirmed that either ACD alone or RCD alone could drive rapid divergence in the recognition cue Z (Fig. 1). Indeed, varying the availability of territories had a strong effect on divergence in Z under ACD (Fig. 1a), as did varying the female's penalty for mistaken mate recognition under RCD (Fig. 1b). However, for the parameter ranges used, a large fitness cost (e.g. $h_C \geq 0.5$) for females selecting heterospecific males resulted in stochastically driven competitive exclusion upon secondary contact. The populations of the two species were subject to stochastic fluctuations, and females of the rarer species were unable to diverge in their recognition traits rapidly enough to offset frequent mating attempts by males of the more abundant species. Rarer females suffered large losses to their clutches and the species that gained numerical
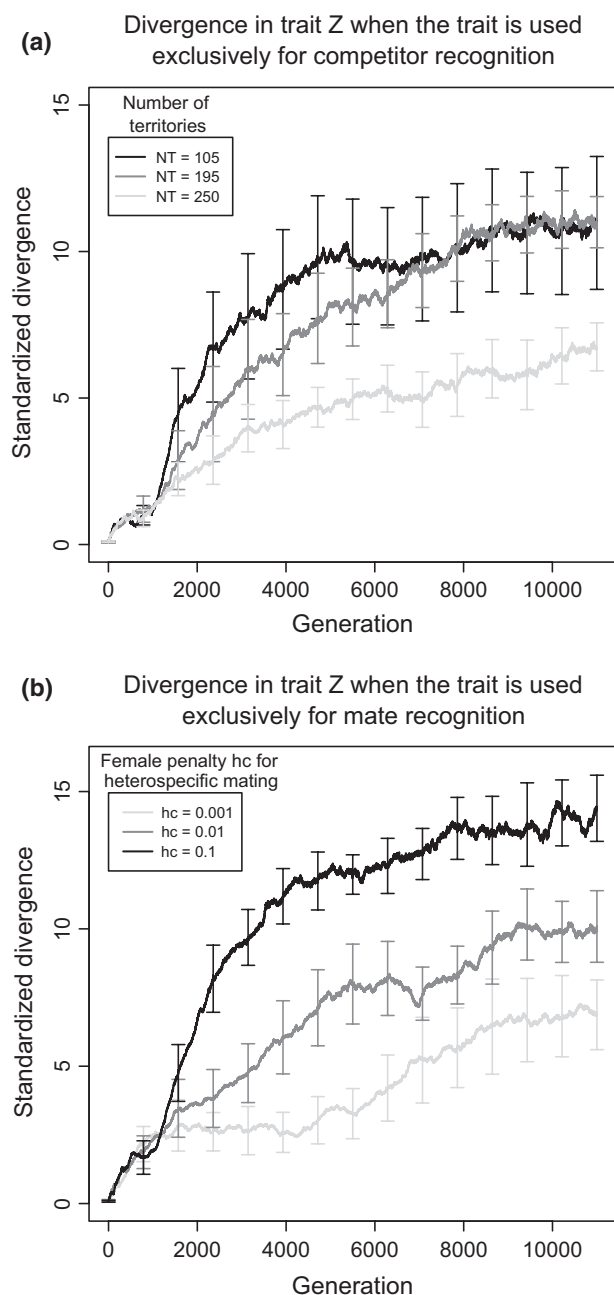
(a)

Divergence in trait Z when the trait is used exclusively for competitor recognition

(b)

Divergence in trait Z when the trait is used exclusively for mate recognition

Figure 1. Standardised divergence of the recognition cue (Z) when (a) ACD operates alone and (b) RCD operates alone. In panel A, when fewer territories are available (darker lines), encounters between males are more frequent, which accelerates divergence in Z. In panel B, when females pay a higher fitness cost for mistaken mate recognition (darker lines), divergence in Z is correspondingly accelerated. In this and subsequent figures, the first 1000 generations represent a burn-in period prior to secondary contact, error bars represent $\pm$ 2 SEM at the specified generation, and lines represent the mean of 20 simulation runs. Here, but not in subsequent figures, divergences are normalised by the trait variances.

dominance rapidly drove the rarer species to extinction. Thus, for the remainder of the results, we focus only on cases where the fitness costs to females for mistaken mate recognition was comparatively less severe (i.e. $h_C \leq 0.1$).

Because both RCD and ACD can cause divergence in recognition cues, the two processes operating together on the same trait might

be expected to result in more rapid divergence than under either process operating alone. This was not the case, however, in our model.

Instead, we found that divergence in the recognition cue Z was driven entirely by RCD (Fig. 2). Even during the transient stages, divergence in Z closely tracked divergence in the female mate recognition function (μ_{Z2}) and appeared unaffected by divergence in the male competitor recognition function (μ_{Z1}).

Strengthening ACD and weakening RCD allowed competitor recognition to diverge more rapidly than mate recognition, but divergence in trait Z proceeded at the same pace as when RCD operated alone (Fig. 2). This can be understood as a result of strong selection on males to be recognised as mates by conspecific females. Moreover, because males must continue to be able to identify conspecific male competitors, a low cost of mistaken mate recognition constrained divergence in male competitor recognition as well. With weak RCD constraining divergence in the recognition cue Z, males continued to mistake heterospecifics as competitors for much longer periods than when ACD operated alone (Fig. 3a). Indeed, simply modelling female mate recognition to depend on Z was sufficient to prevent ACD from driving divergence in Z, even if females paid no cost whatsoever for mate recognition errors (i.e. $h_C = 0$). In the latter case, divergence in Z was constrained by the rate at which the female mate recognition function (μ_{Z2}) evolved due to genetic drift (Fig. 3b).

When RCD was strong, the probability of errors in competitor recognition can decline at a slightly faster rate than when ACD operated alone (Fig. 3a), but this was because RCD drove divergence in trait Z instead of a synergistic interaction between ACD and RCD. Increasing the strength of RCD accelerated divergence in the central location of the male competitor recognition function (Fig. 2) because of selection on males to recognise conspecific male competitors, not because of increased selection against interspecific fighting (this remains clear because divergence in Z reduces interspecific fighting). Conversely, varying territory availability, and thus the strength of ACD, had no effect on the rate of divergence in female mate recognition (Figs 3c and 4a).

Even though divergence in trait Z was driven entirely by RCD, the availability of territories affected the rate of divergence between species in male competitor recognition (Fig. 4b–4d). The effect of territory availability on divergence in competitor recognition was particularly evident when the cost of mate recognition errors was low (Fig. 4b). In this region of parameter space, divergence in trait Z was driven by the rate of divergence in female mate recognition (Fig. 4c), but the availability of territories still affected the strength of selection on males to discriminate between conspecific and heterospecific males (Fig. 4d). Thus, when RCD is weak, ACD can still drive shifts in competitor recognition, but this should not be taken as evidence that ACD has caused divergence in the trait upon which competitor recognition is based (i.e. Z in our model).

DISCUSSION

Sympatric divergence in traits that affect species recognition is usually interpreted as evidence for RCD, but ACD offers an alternative explanation for the same patterns, and in certain cases, ACD is viewed as the preferred explanation (reviewed in Grether *et al.* 2009). If the displaced traits are known to affect both mate and competitor recognition, the relative contributions of the two processes to observed character shifts is controversial and no empirical method has yet been devised for resolving this issue (Grether *et al.* 2009; Honkavaara *et al.*
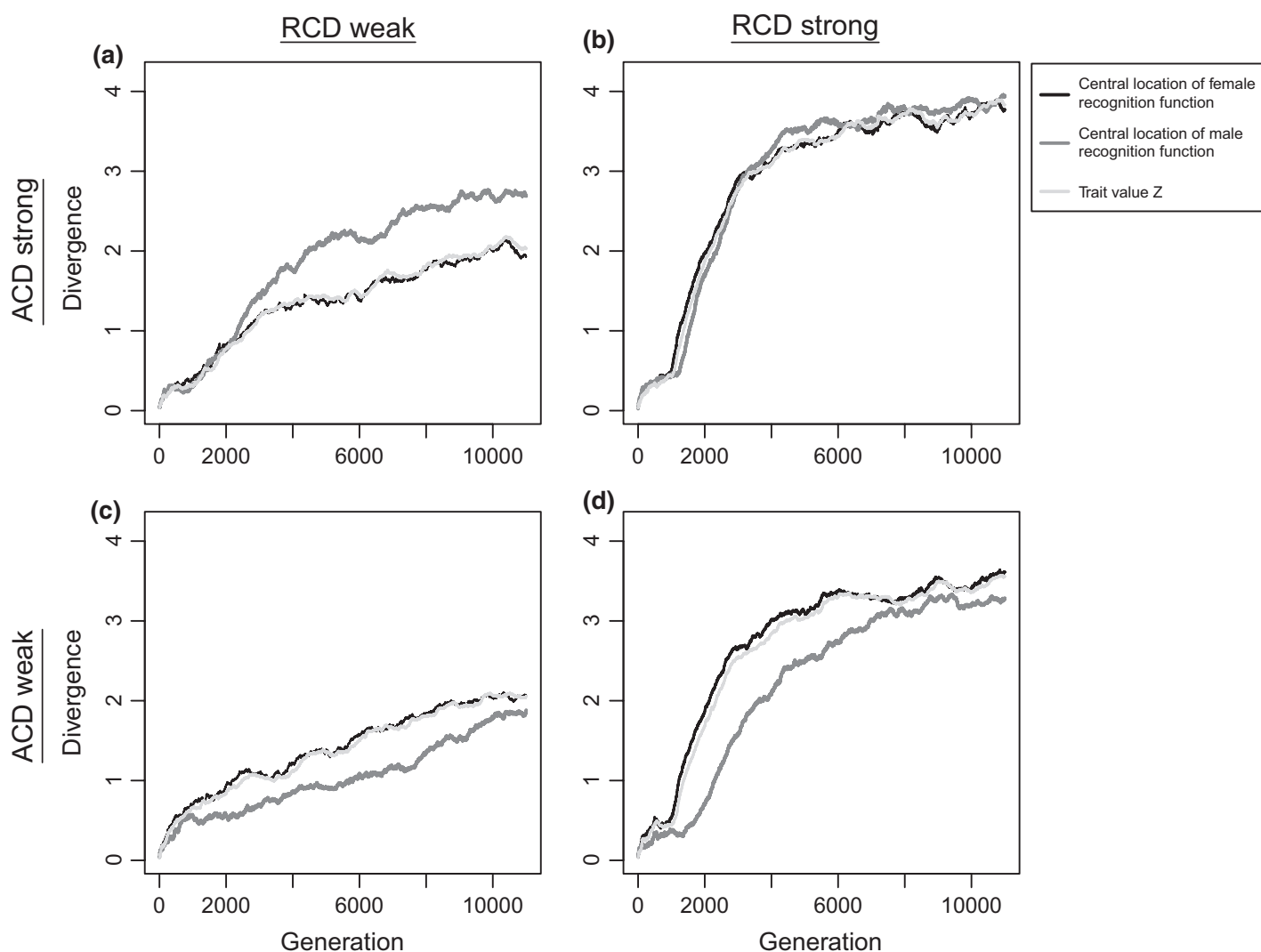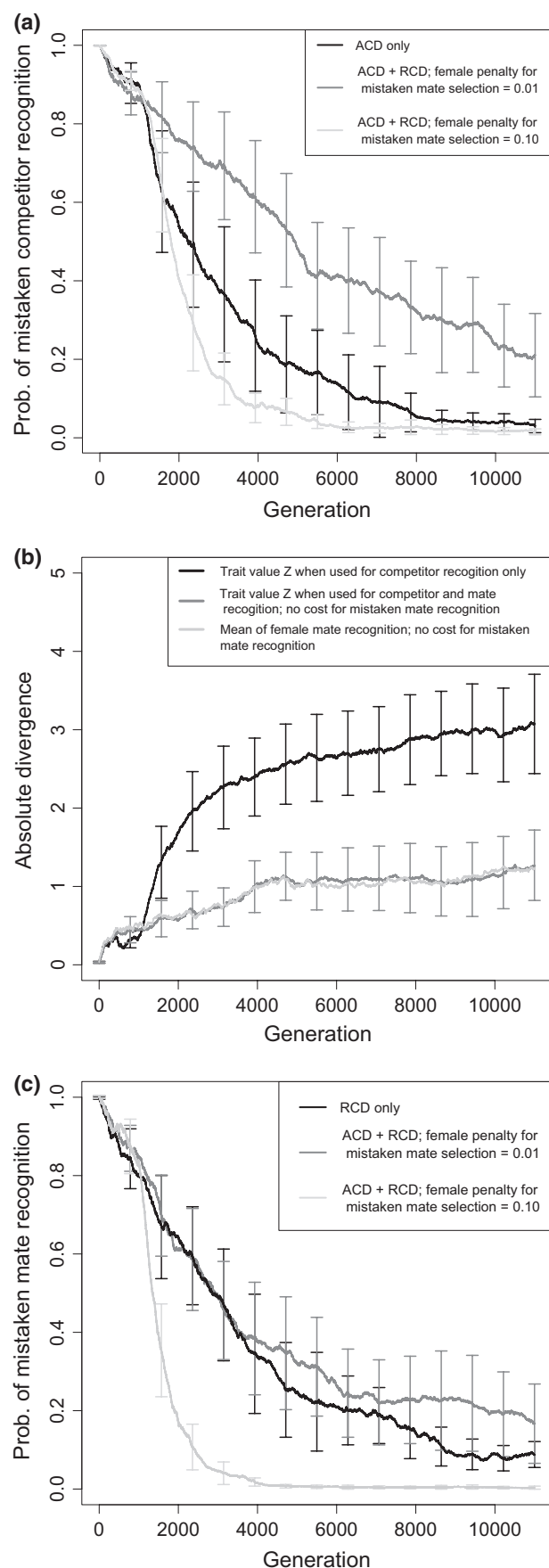
Figure 2. Divergence in the recognition cue Z (light grey line), the central location μ_{Z_1} of the male competitor recognition function (dark grey line) and the central location μ_{Z_2} of the female mate recognition function (black line), when (a) ACD is strong (number of territories $N_T = 86$) and RCD is weak (female penalty b_C for mistaken mate recognition = 0.005); (b) ACD and RCD are both strong ($N_T = 86$ and $b_C = 0.1$); (c) ACD and RCD are both weak ($N_T = 230$ and $b_C = 0.005$); and (d) ACD is weak and RCD is strong $N_T = 230$ and $b_C = 0.1$). Z always closely tracks μ_{Z_2}.

2011). By modelling ACD and RCD in the same mathematical framework, we sought to theoretically assess the relative efficacies of the two processes under biologically plausible conditions. Our results are most directly applicable to relatively simple systems in which males compete for mating territories, females have control over mating, and interspecific pairings do not lead to the production of hybrid offspring (as is the case for, e.g. *Hetaerina* damselflies; see Methods).

We found that either ACD or RCD alone is sufficient to cause rapid and sustained divergence in species recognition traits (Fig. 1). This represents a significant advance in the theoretical foundation for ACD and should encourage further empirical research on this understudied evolutionary process. Our model shows that ACD is sufficiently potent to work in a relatively short time frame, given realistic genetic and life history processes, and thus may be more common in nature than generally appreciated. The only prior model of ACD (Grether *et al*. 2009) did not include explicit multilocus genetics, sexual reproduction or non-trivial population dynamics, nor was it constrained by parameter estimates from a real system

(as in the current model). Although it might seem intuitive that selection against interspecific fighting would generate divergence in species recognition traits, verbal reasoning alone is insufficient to establish the conditions under which this process would occur. Consider a case of secondary contact between two territorial species with similar mean values of a male trait that previously was used only for intraspecific competitor recognition. Territory holders could avoid initiating interspecific fights by tolerating intruders with trait values in the tail of the distribution closest to the mean of the other species, but this would also cause them to tolerate (i.e. fail to attack) some proportion of conspecific males. Would the benefit of avoiding unnecessary interspecific fights override the cost of sharing space with conspecifics, or vice versa? Indeed, it is not clear whether selection would readily favor divergence in competitor recognition. Nevertheless, our simulations demonstrate that even species that are initially identical in their competitor recognition systems can diverge through ACD, and that ACD proceeds more rapidly when competition for territories is more intense (Fig. 1a).

(a)

Legend:
- ACD only
- ACD + RCD; female penalty for mistaken mate selection = 0.01
- ACD + RCD; female penalty for mistaken mate selection = 0.10

(b)

Legend:
- Trait value Z when used for competitor recognition only
- Trait value Z when used for competitor and mate recognition; no cost for mistaken mate recognition
- Mean of female mate recognition; no cost for mistaken mate recognition

(c)

Legend:
- RCD only
- ACD + RCD; female penalty for mistaken mate selection = 0.01
- ACD + RCD; female penalty for mistaken mate selection = 0.10

Putting ACD and RCD into a common mathematical framework enabled us to directly examine the interplay between these processes. We had predicted that divergent ACD and RCD would be mutually reinforcing processes, and that traits used for both mate recognition and competitor recognition would diverge between species more rapidly than traits used for mate recognition or competitor recognition alone (Grether *et al.* 2009). We further expected that the relative importance of the two processes would depend on the relative strength of selection against interspecific mating for females and against interspecific fighting for males, which we varied by changing the fecundity cost of interspecific mating (i.e. the strength of RCD) and the scarcity of territories (i.e. the strength of ACD). Surprisingly, we found that when the same trait was used for recognising both competitors and mates, RCD thoroughly dominated the evolution of the species recognition trait (Figs 2 and 4). Even when the fecundity cost of interspecific mating was very low and competition for territories was intense, the evolutionary trajectory of the species recognition trait closely tracked the evolution of the female mate recognition function (Fig. 2a). In the presence of weak RCD, the species diverged more in their competitor recognition functions when ACD was strong than when ACD was weak (Figs 2a and 4d). Yet, such divergence in competitor recognition was ultimately constrained by the rate of evolution of the species recognition trait. Divergence in the recognition trait, in turn, was governed by the rate of divergence in female mate recognition (Figs 3b and 4c).

The predominance of RCD in driving divergence in male traits highlights two key predictions. First, weak RCD can actually slow down ACD. Second, when RCD is strong and ACD is weak, competitor recognition should readily evolve as an indirect effect of RCD (Fig. 3a). The latter outcome results because males must continue recognising conspecific males as the species recognition trait diverges between species. Thus, we found that divergence between species in competitor recognition can arise as a by-product of RCD but divergence in mate recognition cannot arise as a by-product of ACD. Perhaps, the least expected result was that ACD did not accelerate divergence in the species recognition trait even when females incurred no cost whatsoever for mistaken species recognition (and thus female mate recognition was selectively neutral; Fig. 3b). While this scenario may not plausibly occur in nature, it reveals that mate recognition, *per se*, prevents ACD from driving the evolution of the species recognition trait.

Why does mate recognition so thoroughly dominate the evolution of the species recognition trait in our model? This counterintuitive finding can be explained rather simply. If females recognised males of both species as potential mates at the time of secondary contact, males that tolerated heterospecifics on their territories would risk losing mating opportunities to heterospecifics, rendering

Figure 3. Divergence in species recognition under some illustrative scenarios. (a) Divergence in competitor recognition when ACD operates alone or in combination with weak or strong RCD. (b) Divergence in the recognition cue (Z) when Z only affects male competitor recognition (black line) or when Z also affects female mate recognition but females pay no penalty for mate recognition errors (dark gray line). In the latter case, divergence in Z closely tracks divergence in the female mate recognition function μ_{Z_2} (light grey line; error bars omitted for clarity). (c) Divergence in mate recognition when ACD operates in combination with RCD at two levels of h_C vs. weak RCD alone (black line).
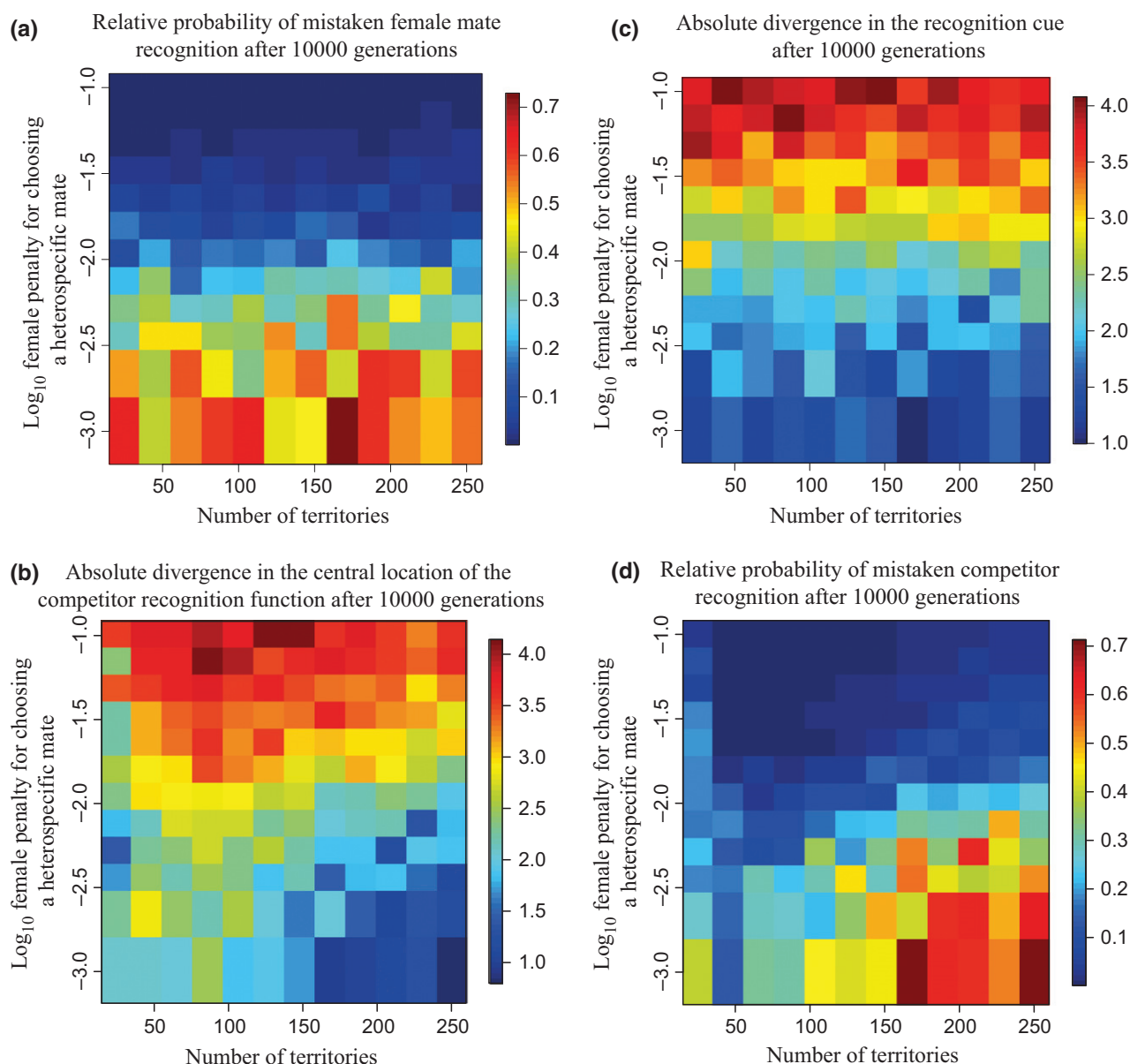
(a) Relative probability of mistaken female mate recognition after 10000 generations

(c) Absolute divergence in the recognition cue after 10000 generations

(b) Absolute divergence in the central location of the competitor recognition function after 10000 generations

(d) Relative probability of mistaken competitor recognition after 10000 generations

Figure 4. Diagrams summarising the joint effects of RCD and ACD after 10 000 generations. The colour scales show (a) the probability that females allow heterospecific males to come into physical contact with them, relative to the same probability at the onset of secondary contact; (b) divergence in the central location of the male competitor recognition function μ_{Z_i}; (c) divergence in the recognition cue Z; and (d) the probability that males mistake heterospecifics for competitors, relative to the same probability at the onset of secondary contact. When only 25 territories were available for 1600 males, divergence in male competitor recognition was weakened as even conspecific competitor recognition can be maladaptive. The values shown are the averages of the two species across 20 simulation runs.

interspecific territoriality adaptive. Some divergence in female mate recognition is therefore required to initiate divergent ACD. Hence, ACD does not occur when mate recognition is selectively neutral. If interspecific matings reduce female fitness (as would likely be the case in nature), the species recognition trait and female mate recognition will diverge through RCD. This causes male competitor recognition to initially evolve to track divergence in the species recognition trait. Once the rate of interspecific mating drops to a level where it is no longer advantageous for males to fight with heterospecifics, ACD can displace the mean of the competitor recognition function away from the mean of the species recognition trait. However, ACD cannot shift the species recognition trait itself because males that deviate from the mean are less attractive to conspecific females and suffer a

net decrease in expected fitness. Nor does weakening the mate recognition function in our model (by increasing the width parameter) allow ACD to drive divergence in the species recognition trait (see Supplement S3). The basic reason is that while weakening the mate recognition function reduces the cost to males of deviating from their species' mean value of the recognition trait, it simultaneously increases the rate of interspecific mating, thereby reducing the benefit to males of discriminating between conspecific and heterospecific males. Thus, it is not possible, at least in our model, for the benefit of reduced aggression from heterospecific males to exceed the cost of reduced attractiveness to conspecific females. We highlight that these mechanisms do not depend on the relative cost of interspecific fighting vs. interspecific mating.

Our model demonstrates that even shifts in competitor recognition, *per se*, could be a result of RCD rather than ACD, if competitor recognition and mate recognition are based on the same traits. Therefore, for taxa that meet the basic assumptions of our model, the key empirical question becomes whether mate recognition and competitor recognition are indeed based on the same traits, as would appear to be the case for *Calopteryx* damselflies (see Introduction). By contrast, for *Hetaerina* damselflies, it remains to be determined whether male competitor recognition and female mate recognition are based on the same traits in this group. Male competitor recognition is clearly based, at least in part, on wing colouration (Anderson & Grether 2010), but there is as yet no evidence that females discriminate among males based on wing colouration (Grether 1996; also see Contreras-Garduño *et al.* 2008; Guillermo-Ferreira & Del-Claro 2011). In light of the modelling results, determining whether females use the same cues for species recognition in sympatry is a priority for future research in systems such as *Hetaerina*.

While our model was parameterised for a specific system to maximise biological realism, we see no reason not to expect our findings to apply to other taxa in which males compete for mating territories (e.g. many insects, amphibians, reptiles, fishes, birds and mammals; Baker 1983; Clutton-Brock 1989; Davies 1991; Maher & Lott 2000). We expect that, in such taxa, RCD would dominate ACD if mate choice and competitor recognition were both based on the same male trait at the time of secondary contact. However, the qualification 'at the time of secondary contact' is key. In our model, species recognition evolves through the modification of an existing recognition system. In our ACD-only simulations, the trait used for competitor recognition is not a target of mate choice, and we do not model the de novo evolution of a mate recognition trait. Presumably, it would be possible to construct a model that allowed a trait that diverged first through ACD to later be co-opted for mate recognition. Whether this is likely to have happened in nature could be investigated by studying putative ancestral populations in allopatry. The ACD-first hypothesis predicts that traits used for species recognition in sympatry are only used for competitor recognition, not mate choice, in allopatry.

Our primary recommendation to empiricists is to be cautious in interpreting patterns of character divergence. RCD has been invoked far more often than ACD, and in some instances, patterns that have been interpreted as evidence for RCD may instead have been caused by ACD. By demonstrating the potential for ACD to drive divergence in species recognition cues, we hope to raise awareness of this alternative evolutionary process. The main contribution of this paper, however, is to show that RCD has priority over ACD in cases in which the same traits are targets of both competitor recognition and mate recognition. Thus, we emphasise that it is crucial to determine whether traits that have undergone character shifts are targets of mate recognition, competitor recognition, or both.

The modelling framework we developed could be extended in several directions. The dominance of mate recognition in our model stems from the fact that a change in a trait used for competitor recognition can only increase a male's fitness by increasing his mating rate. This might not be the case for species in which territory possession affects access to resources other than mates (e.g. food, refuges, nesting sites). Thus, it would be useful to extend the model to taxa that compete for all-purpose territories to determine whether, under these circumstances, ACD could contribute to the evolution of a trait also used for mate recognition (e.g. Ficedula flycatchers; Kral *et al.* 1988; Alatalo *et al.* 1994; Saetre *et al.* 1997; Saether *et al.* 2007). Alternatively, in species where males compete for access to females but do not compete for mating territories at all, the availability of females rather than of mating territories may affect the strength of ACD relative to RCD. Another priority for future modelling is to allow species recognition to be based on multiple, uncorrelated traits. Our ACD-only simulations mimicked a situation in which females already reliably distinguished between males of the two species at the time of secondary contact (based on some unspecified trait). This suggests that if multiple traits were available for species recognition, and mate recognition had not yet evolved, RCD could rapidly drive divergence in the traits that are most useful for mate recognition, allowing ACD to drive divergence in traits that are more useful for competitor recognition. Our modelling framework could also be used to explore the effects of gene flow between allopatric and sympatric populations. Finally, if future work on the genetic basis of the traits affecting species recognition reveals epistatic effects or differential linkage among the underlying loci, our framework could readily accommodate such developments.

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