

MINI REVIEW

Character displacement: *in situ* evolution of novel phenotypes or sorting of pre-existing variation?

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Abstract

Character displacement – the divergence of traits between species in response to competition for resources or mates – has long been viewed as a major cause of adaptive diversification and species coexistence. Yet, we lack answers to basic questions concerning the causes and consequences of character displacement, not the least of which is why some species are more prone than others to undergo character displacement. Here, we address these questions by describing how character displacement can proceed through two nonexclusive routes that differ in the source of phenotypic variation, and, hence, in the ease with which character displacement may unfold. During *in situ* evolution of novel phenotypes, new traits that are divergent from a heterospecific competitor are generated and spread in sympatry. During sorting of pre-existing variation, such traits are initially favoured in allopatry before the two species encounter one another. Later, when they come into contact, character displacement transpires when these pre-existing divergent phenotypes increase in frequency in sympatry relative to allopatry. Because such sorting of pre-existing variation should unfold relatively rapidly, we suggest that species that express resource or mating polymorphism prior to interactions with heterospecifics may be more prone to undergo character displacement. We discuss the key differences between these two routes, review possible examples of each, and describe how the distinction between them provides unique insights into the evolutionary consequences of species interactions, the origins of diversity, and the factors that govern species coexistence.

Introduction

Character displacement (Brown & Wilson, 1956), or what Darwin (1859) called divergence of character, is a commonly observed pattern in plants and animals (reviewed in Howard, 1993; Schluter, 2000; Dayan & Simberloff, 2005). Populations of two closely related species are often different phenotypically where the species occur together ('sympatry') but are indistinguishable where each species occurs alone ('allopatry'; Fig. 1a).

Character displacement may take two distinct forms. First, when species compete for resources, selection may lead to 'ecological character displacement' (Slatkin, 1980; Schluter, 2001). Ecological character displacement arises when competition between similar heterospecific individuals imposes directional selection on each species' resource use and associated phenotypic characters, leading to divergence between species in these traits and a concomitant reduction in competition (reviewed in Robinson & Wilson, 1994; Schluter, 2000; Day & Young, 2004; Dayan & Simberloff, 2005). Secondly, when species interfere with each other's ability to identify conspecific mates, or when they risk costly mismatings with one another, selection may lead to 'reproductive character displacement' (Blair, 1955; Crozier, 1974). Reproductive character displacement arises when

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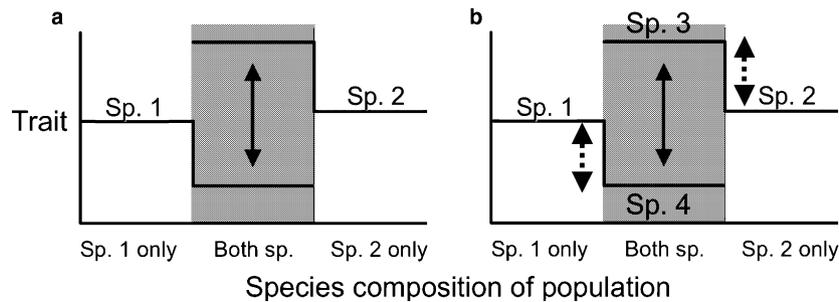


Fig. 1 Character displacement promotes diversity and coexistence between close competitors, and may even promote the origin of new species. (a) When two species compete and overlap in only part of their geographical range, they are often recognizably different where they occur together and indistinguishable where each occurs alone. The evolution of such exaggerated phenotypic differences in sympatry may reflect selection to minimize competition for shared resources (ecological character displacement) or to lessen the risk of hybridization or reproductive interference (reproductive character displacement). (b) Regardless of the precise cause of such divergence, because conspecific populations in sympatry and in allopatry with the competitor experience different selective regimes, character displacement may promote the origin of new species and, possibly, an adaptive radiation (indicated here by the formation of new species 3 and 4).

interactions between similar heterospecific individuals imposes directional selection on each species' mating signals or preferences, leading to divergence between species in these traits and a concomitant reduction in reproductive interference (reviewed in Howard, 1993; Coyne & Orr, 2004).

Although character displacement has long been viewed as a major factor in promoting species divergence, species coexistence, and adaptive radiation (Fig. 1; reviewed in Howard, 1993; Schluter, 2000; Coyne & Orr, 2004; Day & Young, 2004), we lack answers to basic questions such as: What factors determine whether species interactions result in character displacement as opposed to competitive exclusion (Hardin, 1960; Connell, 1961)? Is character displacement invariably a slow process? What role does character displacement play in the origin of novel phenotypes? Why does character displacement sometimes ignite speciation and adaptive radiation and sometimes not? And, perhaps most fundamentally, why are some species more prone than others to undergo character displacement?

In this paper, we provide potential answers to these questions by describing how character displacement can proceed through two nonexclusive routes. These routes differ in the geographical source of phenotypic variation (i.e. allopatry or sympatry with a heterospecific competitor), and hence, in the ease with which character displacement may occur. Under one route, divergent traits that lessen resource competition or signal interference arise and then spread in sympatry following contact with the heterospecific competitor. Under the other route, selection in allopatry may lead to the evolution of phenotypes that are pre-adapted for, and therefore differentially spread in response to, competition in sympatry. We suggest that this second route may make character displacement more likely to occur and may therefore be the more common route. We discuss the key differences between these two routes, review possible

examples of each, and describe how the distinction between them provides unique insights into the evolutionary consequences of species interactions, the origins of diversity, and the factors that govern species coexistence.

We begin by describing a possible bias in the occurrence of character displacement. This bias suggests that character displacement is more likely to occur when selection in allopatry leads to the evolution of divergent phenotypes that are predisposed to succeed in sympatry with heterospecific competitors.

A possible bias in character displacement

Although taxonomically widespread (Schluter, 2000), character displacement tends to be especially prevalent among species that are phenotypically variable (Milligan, 1985), particularly those that express resource or mating polymorphism (Pfennig & Murphy, 2002). For example, such polymorphism occurs in giant rhinoceros beetles (*Chalcosoma atlas* and *C. caucasus* Kawano, 2002), three-spine stickleback fish (*Gasterosteus aculeatus*: Day *et al.*, 1994), sunfish (*Lepomis gibbosus* and *L. macrochirus*: Robinson *et al.*, 1993; Robinson & Wilson, 1996), spadefoot toads (*Spea bombifrons* and *S. multiplicata*: Pomeroy, 1981; Pfennig, 1992), red-backed salamanders (*Plethodon cinereus*: Maerz *et al.*, 2006), and, potentially, numerous species of *Anolis* lizards (Losos *et al.*, 2000) and northern post-glacial fish (Robinson & Wilson, 1994). When these species co-occur with closely related heterospecific competitors, they typically undergo character displacement by shifting from producing two morphs to producing primarily the single morph that is less like the competing species [in *C. atlas* and *C. caucasus* (Kawano, 2002); *G. aculeatus* (Schluter & McPhail, 1992); *L. gibbosus* and *L. macrochirus* (Werner & Hall, 1976); *S. bombifrons* and *S. multiplicata* (Pfennig & Murphy, 2000); *P. cinereus* (Adams & Rohlf, 2000); *Anolis*

(Losos *et al.*, 2001); and northern post-glacial fish (Robinson & Wilson, 1994)].

We suggest that the greater prevalence of character displacement in species that express resource or mating polymorphism reflects a greater ease with which character displacement occurs in such species. Specifically, the presence of a resource or mating polymorphism may render species more prone to character displacement for three reasons.

First, character displacement may proceed more quickly in populations with resource or mating polymorphism because divergent phenotypes already exist in such systems. Models suggest that character displacement can be a slow process, particularly in populations that initially lack phenotypic variation (Slatkin, 1980; Milligan, 1985; Taper & Case, 1985). Thus, adaptation to competitors is often limited by the rate at which new variants are created by mutation and/or recombination. If the rate at which new variants are created is low, and competition intense, competitive exclusion, rather than character displacement, will likely result (Milligan, 1985; Pfennig *et al.*, 2006). If, however, divergent phenotypes pre-exist in allopatry (e.g. as might be the case if the competing species already express resource or mating polymorphism), then character displacement may get a 'jump-start' (Milligan, 1985; Schluter, 2000, p. 128) and proceed more quickly once a heterospecific competitor is encountered.

Secondly, populations that express resource or mating polymorphism have already undergone a sort of 'intra-specific character displacement' (*sensu* West-Eberhard, 2003). Many of the mechanisms and conditions that produce and maintain resource or mating polymorphism are the same as those that underlie character displacement. In both cases, divergent phenotypes are produced in response to competitively-mediated selection (Robinson & Wilson, 1994; Schluter, 2000; Day & Young, 2004). Thus, populations that express resource or mating polymorphism are poised to respond rapidly when they encounter a heterospecific competitor because they have already been 'tested' in competition.

Finally, alternative phenotypes that arise through phenotypic plasticity may be especially likely to undergo character displacement, because phenotypic plasticity facilitates character displacement. In many species, divergence between heterospecific competitors is mediated, at least in part, by competitively-mediated plasticity (e.g. Werner & Hall, 1976; Robinson & Wilson, 1994; Pfennig & Murphy, 2000; Losos *et al.*, 2001). Although some contend that competitively-mediated plasticity is not 'true' character displacement (Grant, 1972; Endler, 1986; Schluter & McPhail, 1992; Schluter, 2000) – because one of the six widely accepted criteria for character displacement is that phenotypic differences between populations and species should have a genetic basis (Grant, 1972; Arthur, 1982) – the magnitude and direction of a plastic response to the environment (the

'norm of reaction') is often genetically variable (Schlichting & Pigliucci, 1998) and subject to adaptive evolution (West-Eberhard, 1989).

More importantly, phenotypic plasticity may promote character displacement by facilitating 'valley crossing' (Pfennig *et al.*, 2006). Consider a population that occupies one of two possible peaks on an adaptive landscape (the two peaks might correspond to two morphs). If a superior competitor invades and begins to utilize the same limiting resource, the population would have to cross a fitness valley of maladaptive intermediate forms to climb the alternative peak (and use an alternative resource), a process normally prevented by natural selection. With phenotypic plasticity, however, populations can shift rapidly from one peak to the other without having to pass through the intervening selective valley (Kirkpatrick, 1982; Schlichting & Pigliucci, 1998; Pál & Miklos, 1999). Such populations can express an alternative, selectively favoured phenotype that is unlike the competitor's without having to wait many generations for such adaptive phenotypes to arise through mutation or recombination (Pfennig & Murphy, 2000, 2002). Without plasticity, a superior competitor may drive the focal species locally extinct before it has time to evolve new canalized traits that lessen competition.

Competitively-mediated plasticity might eventually lead to the evolution of 'true' character displacement if divergent phenotypes become canalized under strong and persistent selection. Such canalization may occur, possibly through genetic assimilation (Waddington, 1956) or genetic accommodation (West-Eberhard, 2003), for two reasons. First, selection should become increasingly effective at producing a particular phenotype (as opposed to the alternative phenotype/s) as that phenotype becomes increasingly common in the population (West-Eberhard, 1989). Secondly, as one phenotype is expressed continuously in a population, and as the alternative phenotype is never expressed, alleles that regulate expression of this 'hidden' phenotype would not be exposed to selection, and thus are at risk of chance loss (e.g. through drift or gradual mutation accumulation).

For example, tadpoles of spadefoot toads (*S. multiplicata*) develop into two environmentally-triggered morphs: an omnivore morph that feeds on detritus at the pond bottom and a carnivore morph that feeds on anostracan fairy shrimp in open water (Pfennig & Murphy, 2002). When these tadpoles encounter another species, *S. bombifrons*, that produces a competitively superior carnivore morph, they facultatively switch to producing mostly omnivores (Pfennig & Murphy, 2002). Interestingly, *S. multiplicata* tadpoles from populations that historically have had more contact with *S. bombifrons* are canalized to produce all omnivores. Thus, competitively-mediated plasticity might often promote the rapid evolution of canalized character displacement.

In sum, character displacement tends to be especially prevalent among species that express resource or mating

polymorphism, possibly because: (i) divergent phenotypes already exist in such systems; (ii) these divergent phenotypes typically evolve in response to intraspecific competition and have therefore already been 'tested' in competition; and (iii) such alternative phenotypes often arise through phenotypic plasticity, and phenotypic plasticity may promote character displacement by facilitating 'valley crossing.' When such species encounter a closely related heterospecific competitor, they typically undergo character displacement by shifting (through phenotypic plasticity, canalization, or both) from producing two morphs to producing primarily the single morph that is less like the competing species.

Two routes to character displacement

As the above discussion suggests, character displacement may evolve through two nonexclusive routes (Fig. 2). First, traits that differ from the competitor's and that thereby lessen competition or reproductive interference may arise (through mutation, recombination, and/or hybridization) and then spread (through the action of competitively-mediated natural selection) in sympatry following contact with the competitor. This route, which we term '*in situ* evolution of novel phenotypes' (hereafter 'ISE'), generates new phenotypes in sympatry that are not initially present in either species in allopatry. Secondly, divergent traits may be selectively favoured in allopatry before interspecific competition takes place. As with ISE, such traits might spread through the action of competitively-mediated natural selection, albeit within species. Later, when the two species come into contact, character displacement occurs when these pre-existing divergent phenotypes increase in frequency in sympatry relative to allopatry. This second route, which we term 'sorting of pre-existing variation' (hereafter 'sorting'), selectively filters divergent phenotypes in sympatry that were already present in allopatry (as might be the case in populations that express resource or mating polymorphism).

As we describe below (see 'Case studies'), ISE and sorting are not mutually exclusive and may occur simultaneously or sequentially (Schluter & Grant, 1984; Schluter, 2000; Marko, 2005). Sorting may operate first, with ISE following and magnifying the pre-existing differences between species (Schluter, 2000, p. 128).

Most researchers do not consider sorting an alternative route to the evolution of character displacement (e.g. Slatkin, 1980; Arthur, 1982; Taper & Case, 1985; Doebeli, 1996; but see Endler, 1986, p. 62; Thompson, 1994, p. 248; Pfennig & Murphy, 2003; Marko, 2005). Although sorting between species has been widely discussed as a mechanism for community-wide character displacement (reviewed in Dayan & Simberloff, 2005), the possibility that sorting might function within species to promote character displacement is seldom considered.

Because selection must initially act on standing variation, it might be contended that all cases of character displacement begin as sorting (e.g. in Fig. 2b, individuals of the focal species that are in the left tail of the distribution will be selectively favoured through a process similar to sorting). However, ISE goes beyond this initial sorting process and favours novel and increasingly divergent phenotypes in sympatry (Fig. 2c). When resource or mating polymorphism is present in allopatry, character displacement due to the sorting of pre-existing variation *alone* may be sufficient to avoid interspecific competition (Fig. 2f).

In the next section, we explain how the distinction between ISE and sorting has important implications for the evolution of novel phenotypes and the likelihood that character displacement may promote ecological speciation and adaptive radiations. Indeed, as we will show, the distinction between these two routes is critical for predicting whether character displacement will occur in the first place.

Evolutionary implications of the two routes to character displacement

Although both sorting and ISE promote character divergence in the face of competition, the two processes differ in how and under what circumstances they promote character displacement (Table 1). These differences have important evolutionary implications for understanding: (i) why character displacement occurs in some situations but not in others; (ii) the speed with which character displacement evolves; (iii) the ultimate factors that generate divergent phenotypes; and (iv) the likelihood that character displacement will ignite ecological speciation or adaptive radiation.

Distinguishing between ISE and sorting may help explain why character displacement occurs in some situations but not others. Contrary to sorting, with ISE, new phenotypes that differ from those of ancestral predisplacement populations (allopatry) are selectively favoured in sympatry. Exploitable resources (or, in the case of reproductive character displacement, signal space) beyond those in allopatry must therefore be available for this process to occur, i.e. a superior competitor should not already utilize these resources. In the absence of such exploitable resources, competitive exclusion, rather than ISE-mediated character displacement, may result (Pfennig *et al.*, 2006). If a population already utilizes an alternative resource, even at low frequencies, it may be better poised to take advantage of that resource when faced with competition for its primary resource (Fig. 2d–f). Sorting may therefore be a more likely mechanism for character displacement in 'saturated' communities, i.e. species-rich communities that contain relatively few underexploited niches. In such communities, novel phenotypes arising through ISE may be unsuccessful because of a dearth of available, underutilized resources.

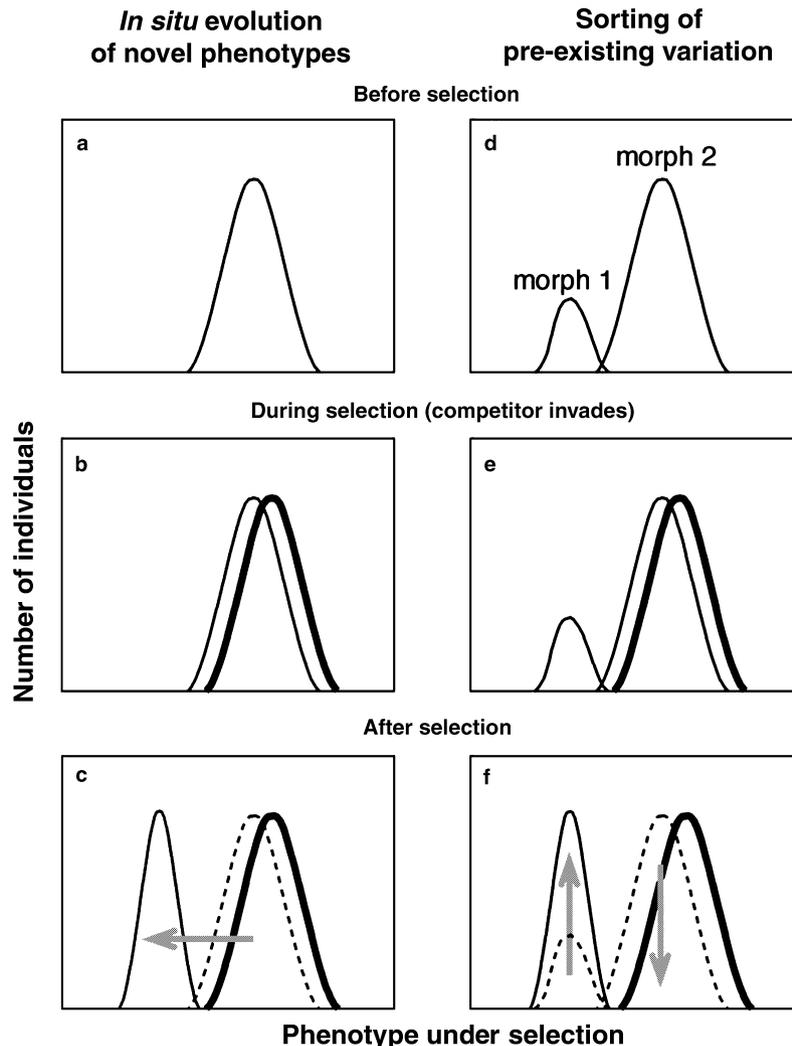


Fig. 2 Two routes to character displacement: (a–c) *in situ* evolution of novel phenotypes, and (d–f) sorting of pre-existing variation. Initially (a, d), a focal species (species 1) occurs alone in allopatry, either as a monomorphic species (a) or as a polymorphic species (d) consisting of alternative resource use or mating tactic morphs (morphs 1, 2), one of which is initially rarer than the other(s). Later (b, e), a superior competitor, species 2 (heavy line), comes into sympatry with species 1 (either because species 2 invades the habitat of species 1 or vice versa). Finally (c, f), because of selection imposed by species 2, species 1 undergoes an evolutionary shift in resource use and associated phenotypic features (ecological character displacement) or in mating signals/preferences (reproductive character displacement; in both cases, the distributions of species 1 before selection are shown in dashed lines). With *in situ* evolution of novel phenotypes (c), character displacement unfolds when novel phenotypes that are more dissimilar to the competitor spread in sympatry following the invasion of species 2. Because they are associated with reduced competition, these new phenotypes are selectively favoured. As a result, the entire distribution of species 1 shifts to the left; i.e. away from the competitor. By contrast, with sorting of pre-existing variation (f), character displacement unfolds when the morph that is more dissimilar to the competitor (here, morph 1) is selectively favoured and thereby increases in frequency at the expense of the alternative morph. As a result, the entire distribution of species 1 again shifts to the left. Although we have illustrated sorting of pre-existing phenotypes as involving discrete morphs, it could also occur in populations expressing continuously distributed phenotypes. In both cases (c, f), the outcome of character displacement is identical, even though the two populations undertook two different routes.

By contrast, novel phenotypes arising through ISE may be more successful when there are a wide variety of resources to exploit with few competitors, as may be the case, for example, following mass extinctions or the colonization of new habitats. In such settings, few competitors would be present, and underutilized

resources would therefore be available to permit the evolution of new resource-use phenotypes that are required for ISE to unfold (Fig. 2c).

Differentiating ISE from sorting may also help explain the speed of character displacement (Fenchel, 1975; Diamond *et al.*, 1989; Pfennig & Murphy, 2002, 2003).

Table 1. Summary of differences between the two routes to character displacement.

Route	Source of divergent phenotypes	Ultimate selective agents favouring divergent phenotypes	Relative speed of character displacement	Situations where route may be most common	Likelihood of triggering ecological speciation or adaptive radiation
ISE	Sympatry	Interspecific resource competition or reproductive interference	Slow	Unsaturated communities with many open niches	High
Sorting	Allopatry	Often intraspecific competition for resources or mates	Fast	Either unsaturated or saturated communities	Low

Traditionally, character displacement was thought to be a slow process (Slatkin, 1980; Taper & Case, 1985), limited by the rate at which divergent traits arise and spread in sympatry. If species are initially similar phenotypically, and the rate at which divergent traits are introduced is low but competition intense, competitive exclusion may result (Milligan, 1985). If, however, divergent traits pre-exist in allopatry (as with sorting; Fig. 2), then character displacement will likely proceed more quickly than if it were driven entirely by ISE. Sorting may therefore 'buy' time and enable competing species to co-exist long enough for ISE to produce new variation in sympatry that amplifies differences between competitors. Thus, because sorting should transpire more rapidly, this route may be primarily responsible for character displacement in systems with recent sympatric contact. By contrast, ISE may operate primarily in systems with more ancient sympatry.

Sorting and ISE also differ in the ultimate agents of selection that generate competitively-mediated phenotypes. During ISE, the agent of selection that favours divergent phenotypes is interspecific competition. By contrast, during sorting, divergent phenotypes evolve in allopatry, prior to contact with the competitor. In this case, the agents of selection that favour divergent phenotypes are forces that act in allopatry. Intraspecific competition, for example, might initially select for alternative resource use or mating tactic morphs (Pfennig, 1992; Hori, 1993; Maret & Collins, 1997; reviewed in Gross, 1996; Smith & Skúlkason, 1996; West-Eberhard, 2003). Later, when two such polymorphic species come into contact, character displacement occurs when these pre-existing divergent phenotypes increase in frequency in sympatry relative to allopatry. Thus, in contrast to ISE, for sorting, divergent phenotypes that lessen competition between species are not initially favoured because of *interspecific* competition.

Finally, whether character displacement arises through ISE or sorting may dictate whether sympatric and allopatric populations within a species diverge to the point of triggering ecological speciation (Fig. 1b; for a general review of ecological speciation, see Rundle & Nosil, 2005). Character displacement can ignite ecological speciation if sympatric and allopatric populations diverge to such a degree that any offspring produced by matings between such populations have lower fitness than those produced within populations. If character

displacement arises via ISE, novel phenotypes in sympatry are much more likely to be incompatible with those in allopatry. Such incompatibility between sympatric and allopatric populations may favour the evolution of isolating mechanisms between these populations. Sorting, by contrast, results in sympatric phenotypes that are a subset of those already present in allopatry. Therefore, if character displacement arises through sorting, phenotypes in sympatry are much less likely to be incompatible with those in allopatry. As a result, sorting should be less likely than ISE to promote the evolution of reproductive isolation and speciation. Indeed, adaptive radiations, by definition, are unlikely to arise by sorting, because novel phenotypes are not generated.

Case studies

Below, we outline a series of case studies that potentially illustrate how character displacement can arise through ISE or sorting. For each example, we inferred the signature of each route by comparing the population mean phenotypes in sympatry with the range of phenotypes present in allopatry. We reasoned that if character displacement evolved through sorting, then phenotypes in sympatry would be within the range of those in allopatry (Pfennig & Murphy, 2003). Alternatively, we reasoned that ISE would account for character displacement if sympatric population phenotypic mean values were more extreme than allopatric population phenotypic ranges for a given example (see Fig. 2). When phenotypic range data were not available, we compared sympatric phenotypic mean values to allopatric standard deviations (SDs) (e.g. *Hydrobia* snails, Fenchel, 1975) or allopatric standard errors (SEs) (e.g. *Spea* toads, Pfennig & Murphy, 2003). Such a comparison is more likely to implicate ISE and less likely to implicate sorting than a comparison of sympatric mean values to allopatric ranges, because the allopatric phenotypic range would be broader than the allopatric mean ± 1 SD or SE.

Although we used a comparison of sympatric mean values to allopatric ranges to infer the signatures of sorting and ISE in the following examples, when raw data are available, a comparison of trait variances between populations in sympatry and allopatry may also be employed. When sorting involves a shift from producing two morphs in allopatry to producing primarily the

single morph that is less like the competing species, trait variance in sympatry should be reduced relative to the variance in allopatry (compare Fig. 2d with Fig. 2f). In contrast, with ISE, because new phenotypes are selectively favoured in sympatry, trait variance in sympatry may not be reduced relative to allopatry. The variance ratio test (Zar, 1999) can be used to determine whether the variance in sympatry is reduced relative to allopatry or not. This test may be preferable to a comparison of sympatric mean values to allopatric ranges because it may be used for multivariate data. However, like the comparison of mean values with ranges, the variance ratio test cannot conclusively distinguish between ISE and sorting for two reasons: first, although likely to be less drastic, ISE may also show a reduction in variance in sympatry due to the action of selection; and secondly, in some sorting situations (e.g. when both morphs from allopatry are present in sympatry, but have reversed frequencies, such as if morph 1 from Fig. 2d increased to the original morph 2 frequency after selection, and vice versa for morph 2), variance between allopatry and sympatry may not be reduced (e.g. Pfennig & Murphy, 2003). Because these scenarios are not likely to be common, the variance ratio test is still useful as an initial analysis. Along with a comparison of sympatric mean values with allopatric ranges, this preliminary test may then be followed with more rigorous testing (see 'Suggestions for future research'). Because the raw data in three of the following four examples were unavailable to us, we were only able to perform the variance ratio test on the *Spea* toads.

The following examples highlight two key predictions outlined in the previous section. First, because sorting should precede ISE in the evolution of character displacement, sorting should be more common in species that have come into contact and undergone character displacement relatively recently. Secondly, species that express resource or mating polymorphism prior to interactions with heterospecifics should be more likely to undergo character displacement through sorting.

Galapagos finches

Two species of ground finch on the Galapagos Islands, *Geospiza fortis* and *G. fuliginosa*, exhibit divergence in beak depth on sympatric islands, but possess similar beak depths on allopatric islands (Lack, 1947). Beak depth has been linked to preferred seed size, and competition for resources (seeds) appears to be responsible for divergence of the beak depth phenotype in sympatry (Lack, 1947; Schluter & Grant, 1984). The first sympatric contact between these two species likely occurred in the last 80 000 years, sometime after the split between *G. fortis* and *G. fuliginosa* (Yang & Patton, 1981; Grant, 1994).

Sorting may be primarily responsible for the character displacement in *G. fuliginosa*, whereas ISE has likely been acting in *G. fortis*. In *G. fuliginosa*, data from Lack (1947) indicate that mean beak depths for eight of 10 sympatric

islands lie within the range of beak depths present on Los Hermanos, the allopatric island habitat of *G. fuliginosa*. However, in *G. fortis*, all 10 population beak depth mean values in sympatry lie outside the range of beak depths in allopatry (Isla Daphne), suggesting that ISE has been operating in this species.

This example therefore illustrates how ISE and sorting potentially operate to generate character displacement. More critically, this example underscores that ISE and sorting may operate independently within each interaction, i.e. one species in a competitive interaction can undergo character displacement through sorting, whereas the other can undergo character displacement through ISE.

Hydrobia snails

Shell lengths for two mud snail species in the Limfjorden, Denmark, *Hydrobia ulvae* and *H. ventrosa*, have diverged in sympatric populations, but not in allopatric populations (Fenchel, 1975). Food particle size corresponds to shell length (Fenchel, 1975; Fenchel & Kofoed, 1976), and these species exhibit interspecific competition and partition resources based on size (Fenchel & Kofoed, 1976; Gorbushin, 1996). In addition, this sympatric divergence in shell length has occurred within no more than 175 generations, as the presence of these species in this fjord, and hence their contact, post-dates 1825 (Fenchel, 1975).

Sorting appears to be primarily responsible for the evolution of character displacement in these two species, although there is evidence of ISE in some populations of *H. ulvae*. In *H. ventrosa*, shell length mean values for all sympatric locations fall within 1 SD of the mean for seven of eight allopatric locations. This pattern is not quite as strong for *H. ulvae*, in which eight of 15 sympatric population mean values lie within 1 SD of the allopatric mean values, suggesting sorting, whereas seven of 15 sympatric populations average shell lengths greater than 1 SD above the allopatric mean values, suggesting ISE.

As in the previous example, each species differs in whether ISE or sorting accounts for character displacement. Moreover, both sorting and ISE can contribute to trait evolution in the same population.

Giant rhinoceros beetles

Body size and genitalia length in two South-east Asian giant rhinoceros beetle species, *Chalcosoma caucasus* and *C. atlas*, exhibit divergence in sympatry relative to allopatry (Kawano, 2002). These species show male dimorphism, with a large-bodied, long-horned major morph, and a smaller-bodied, short-horned minor morph, which likely reflects alternative behaviours for finding mates (Kawano, 2002 and references therein). Moreover, body size is highly variable within populations, whereas genitalia length is not (Kawano, 2004). Whether morphs are analysed separately or together,

divergence between sympatry and allopatry in body size and genitalia length remains significant (Kawano, 2002). Sympatric differentiation in overall body size may reflect selection to avoid interspecific combat, whereas divergence in genitalia length likely reflects selection to avoid hybridization (Kawano, 2002). It is unknown how long these species have been sympatric.

Sorting may mediate divergence in body size, whereas ISE may mediate divergence in genitalia size. For *C. caucasus*, mean body size for all sympatric populations falls within the ranges of the three allopatric populations. Likewise, for *C. atlas*, all seven sympatric mean values fall within the ranges of eight of nine allopatric populations, suggesting sorting. In contrast, for genitalia length, all sympatric population mean values for *C. caucasus* lie outside two of the three allopatric ranges, whereas all *C. atlas* sympatric population mean values fall outside the ranges of four of nine allopatric locations (data from Kawano, 2002). This pattern suggests that ISE has acted on genitalia length.

This example indicates that ISE and sorting may operate independently on different traits within a single population. When one trait exhibits more variation within the population than another trait, such as body size in this example, sorting on the more variable trait may 'jump-start' character displacement, quickly reducing competition between species. This initial reduction in competition may allow coexistence long enough for variation to arise in another trait, which may subsequently diverge through ISE. Thus, not only can both ISE and sorting operate independently between species, as in the Galapagos finches and *Hydrobia* snails examples, but they can operate independently on different traits within species as well.

Moreover, this example confirms our prediction that species that express polymorphism prior to interactions with heterospecifics should undergo sorting. These beetles are dimorphic in body size in allopatry. Although both major and minor morphs are present in sympatry (likely reflecting intraspecific competition for mates), the combined body size range for both morphs of one species in sympatry approximately corresponds with the body size range for one morph in allopatry. This pattern suggests the divergence in body size has evolved by sorting, as predicted.

Spea toads

As noted above (see 'A possible bias in character displacement'), two species of spadefoot toad, *Spea multiplicata* and *S. bombifrons*, diverge in tadpole morph production in mixed-species ponds (sympatry) relative to pure-species ponds (allopatry) in the south-western United States (Pfennig & Murphy, 2000, 2003). In south-eastern Arizona (where much of the work on these two species has been conducted), sympatry has likely occurred within the last 150 years (D.W. Pfennig, A.M. Rice, G.R. Harper unpublished).

Morphological (Pfennig & Murphy, 2003; Pfennig *et al.*, 2006) and comparative population genetic (A.M. Rice and D.W. Pfennig, unpublished) data failed to provide evidence of sorting in this system. Using four trophic characters as an indication of morph production, Pfennig & Murphy (2003) found that all sympatric population mean values for three of the characters in *S. multiplicata* lie outside the SEs of the mean in at least 10 of 13 allopatric populations, which is consistent with ISE. Likewise, all sympatric population mean values (except one trait mean in one population) for three characters in *S. bombifrons* were outside the SEs for all of the allopatric populations (Pfennig & Murphy, 2003), again pointing to ISE. Moreover, for both species, no differences were found between syntopic and allopatric variances in pond mean values for a composite shape variable reflecting three trophic characters (*S. multiplicata*: $F_{16,6} = 1.34$, $P = 0.76$; *S. bombifrons*: $F_{7,4} = 1.48$, $P = 0.74$; data re-analysed from Pfennig *et al.*, 2006), providing further support for ISE. Reinforcing these morphological results, a comparative population genetic analysis of *S. multiplicata* employing a partial Mantel test indicated that the divergence in morph production between sympatric and allopatric populations cannot be accounted for by genetic distance between these populations (A.M. Rice and D.W. Pfennig, unpublished), as would be expected if sorting were important (see below).

Thus, at first glance, the lack of evidence for sorting would seem to run counter to our prediction that species (such as *Spea*) that express resource polymorphism prior to interactions with heterospecifics should undergo character displacement through sorting. Experiments reveal, however, that divergence between competitors in this system is mediated (at least in part) by phenotypic plasticity (Pfennig & Murphy, 2000, 2002). Such competitively-mediated phenotypic plasticity can be even faster than sorting in promoting phenotypic differences between species, thereby lessening the need for character displacement to evolve through sorting (Pfennig *et al.*, 2006).

Summary of case studies

The above case studies suggest that character displacement can evolve through either ISE or sorting. Indeed, different routes may promote character displacement among different species in the same competitive interaction (as in *Geospiza* finches) or even among different traits in the same species (as in *Chalcosoma* beetles).

These case studies also suggest that ISE and sorting differ in the speed with which they promote character displacement. Because sorting should precede ISE in the evolution of character displacement, we predicted that sorting may be responsible for the relatively rapid evolution of character displacement in systems with recent sympatric contact, whereas ISE may be important for magnifying interspecific divergence in systems with

more ancient sympatry. As predicted, in species that have come into contact recently (e.g. *Hydrobia* snails), character displacement appears to have evolved rapidly through sorting. By contrast, in species that have been in contact relatively long (e.g. *Geospiza* finches), ISE appears to have played a major role in at least one of the species. Thus, as predicted, sorting may be important in 'jump-starting' character displacement. Once enough time has passed for new variation to arise in sympatry, ISE may become more important as it further lessens competition or reproductive interference and magnifies the differences between species in sympatry.

Spea toads appear to run counter to the prediction that sorting promotes character displacement in systems with recent sympatric contact. Although competitors likely came into contact relatively recently, sorting does not appear to be important in driving character displacement. As noted above, there is no need for sorting, because phenotypic plasticity mediates the early divergence between sympatric competitors (Pfennig & Murphy, 2002). As with sorting, phenotypic plasticity may 'jump-start' the process of character displacement, preventing competitive exclusion before new variation has time to arise (Pfennig & Murphy, 2002; Pfennig *et al.*, 2006).

Our second prediction was that species that express resource or mating polymorphism prior to interactions with heterospecifics should be more likely to undergo character displacement through sorting. *Chalcosoma* beetles satisfy this prediction. In addition, because sorting of pre-existing variation should unfold relatively rapidly, we predicted that polymorphic species should be predisposed to undergo character displacement in the first place. Although a cursory review of the literature suggests that character displacement does indeed seem to occur more frequently among species that express alternative morphs (see 'A possible bias in character displacement'), additional studies are needed to evaluate this prediction more generally.

Finally, this overview demonstrates that alternative morphs are not necessary for sorting to occur, nor does the presence of alternative morphs ensure that character displacement will evolve via sorting. For instance, character displacement has likely evolved primarily through sorting in the finch *G. fuliginosa* and in both species of mud snail, *H. ulvae* and *H. ventrosa*. Yet, none of these species exhibits alternative phenotypes, suggesting that sorting may also occur in populations expressing continuously distributed phenotypes. Moreover, the presence of alternative morphs does not ensure that character displacement will evolve via sorting if, as in *Spea*, phenotypic plasticity mediates divergence.

Thus (i) character displacement can evolve through ISE, sorting, phenotypic plasticity, or some combination, (ii) both sorting and phenotypic plasticity may 'jump-start' character displacement, (iii) character displacement may proceed extremely rapidly if initiated by phenotypic

plasticity, and (iv) sorting is a general mechanism that applies to discrete or continuously distributed phenotypes.

Suggestions for future research

In the examples above, data on phenotypic mean values and ranges in sympatry vs. allopatry enabled us to determine if sympatric mean values lie within (consistent with sorting) or outside (consistent with ISE) allopatric ranges. Such data are typically available from studies of character displacement and so can generally be used to ascertain for a given system how character displacement arises. Additionally, if raw data are available, a comparison of trait variance between sympatric and allopatric populations can provide an additional test to distinguish between sorting and ISE (see 'Case studies'). Because ISE and sorting are not mutually exclusive, however, such analyses cannot establish which route is primarily responsible for the case of character displacement.

In combination with phenotypic data, genetic marker data can provide a powerful tool for evaluating which route leads to character displacement. Intraspecific independent contrasts (Felsenstein, 2002), partial Mantel tests (Thorpe *et al.*, 1995; Thorpe, 1996), and spatial autocorrelation (Edwards & Kot, 1995; Marko, 2005) utilize estimates of gene flow (intraspecific independent contrasts) or genetic distance (partial Mantel tests and spatial autocorrelation) to determine if population history can account for the observed phenotypic divergence between sympatry and allopatry (expected for sorting), or if most or all of the divergent phenotypes arose and spread after contact was established in sympatry (expected for ISE). These analyses are comparative, however, and therefore cannot establish a causal link between the presence of the competitor and phenotypic divergence. Moreover, the signatures of sorting and founder effects will be similar in these analyses. Evidence of interspecific competition (e.g. Fenchel & Kofoed, 1976; Gorbushin, 1996; Pfennig & Murphy, 2000, 2002) and/or selection for character displacement in sympatry (e.g. Pacala & Roughgarden, 1985; Schluter, 1994; Pritchard & Schluter, 2001; Gray & Robinson, 2002) is therefore necessary to establish that competition promotes divergence and that differences between sympatry and allopatry are not attributable to chance founder events.

If it is possible to link genetic or phenotypic markers to specific groups of populations, populations, families, or even individuals *and* also to a particular resource-use spectrum (*sensu* Day & Young, 2004) or signal-use spectrum, one could test whether certain markers, and therefore certain resource- or signal-use phenotypes, are overrepresented in sympatry compared with allopatry, an expected signature of sorting. If so, experiments in controlled conditions could be performed to determine if the over-represented groups tend to have a resource- or signal-use spectrum less like the competing species than

expected by chance. Such an outcome would support a major role for sorting in character displacement.

Additionally, if genetic markers and genes affecting phenotypes associated with resource use are physically linked, Tajima's *D* (Tajima, 1989) could be calculated for sympatry vs. allopatry in order to determine the relative importance of ISE vs. sorting. This analysis would gauge the relative strength of the signature of selective sweeps – very low levels of neutral variation linked to the trait under selection – in each region. If ISE has been more important, there should be no signature of a selective sweep in allopatry, while there should be a strong signature of a sweep in sympatry. Alternatively, if sorting has been important, there should be evidence of sweeps in both sympatry and allopatry. The signature in allopatry may be weaker, however, because selection for the divergent phenotype in allopatry should pre-date the selection in sympatry, allowing more time for the recovery of linked neutral variation. Moreover, if the sympatric contact is ancient, any evidence of a selective sweep in allopatry may have been erased by the subsequent build-up of linked neutral variation over time ('old' sorting). Such a genetic analysis should therefore be accompanied by either an analysis of whether or not the sympatric phenotypic mean values extend beyond the range of allopatric phenotypes or a variance ratio test comparing allopatric and sympatric phenotypic variance. Doing so should effectively differentiate between the two routes to character displacement.

Because sorting and ISE are not mutually exclusive, both may play a critical role in generating patterns of character displacement. Yet, the above analyses may help determine which route has been predominant in any given case of character displacement. Moreover, meta-analyses can be employed to determine whether ISE or sorting generates the general patterns that we have described above. For example, such analyses can be used to determine whether polymorphic species are more likely than monomorphic species to undergo character displacement and coexist with competitors. This information may ultimately help clarify why some species are more prone than others to undergo character displacement.

Finally, although we have focused on ecological character displacement (trait evolution resulting from selection to minimize resource competition between species), the same principles apply to reproductive character displacement (trait evolution resulting from selection to minimize reproductive interference between species). Future studies should test these predictions for reproductive character displacement.

Conclusion

Character displacement proceeds through two nonexclusive routes, which differ in the geographical source

of phenotypic variation (i.e. allopatry or sympatry with the competitor), and hence, in the ease with which character displacement may occur. During *in situ* evolution of novel phenotypes, newly divergent traits arise and are favoured in sympatry. During sorting of pre-existing variation, such traits initially arise and are favoured in allopatry. Later, when competitors come into contact, character displacement transpires rapidly when these pre-existing divergent phenotypes increase in frequency in sympatry relative to allopatry. Modern molecular tools and phylogenetic or population genetic approaches may help differentiate between these two routes in different examples of character displacement. Such studies promise to provide unique insights into the evolutionary consequences of species interactions, the origins of diversity, and the factors that govern species coexistence.

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