



CHARACTER DISPLACEMENT: ECOLOGICAL AND REPRODUCTIVE RESPONSES TO A COMMON EVOLUTIONARY PROBLEM

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ABSTRACT

Character displacement is the process by which traits evolve in response to selection to lessen resource competition or reproductive interactions between species. Although character displacement has long been viewed as an important mechanism for enabling closely related species to coexist, the causes and consequences of character displacement have not been fully explored. Moreover, character displacement in traits associated with resource use (ecological character displacement) has been largely studied independently of that in traits associated with reproduction (reproductive character displacement). In this review, we underscore the commonalities of these two forms of character displacement and discuss how they interact. We focus on the causes of character displacement and explore how character displacement can have downstream effects ranging from speciation to extinction. In short, understanding how organisms respond to competitive and reproductive interactions with heterospecifics offers key insights into the evolutionary causes and consequences of species coexistence and diversification.

INTRODUCTION

HOW can closely related species coexist in the same habitat? Why are even closely related species often phenotypically different from one another? What role do interactions between species play in the

process of diversification? In this review, we describe how the answers to these kinds of questions can emerge from a knowledge of how organisms respond to a common evolutionary problem: organisms often face reduced fitness stemming from interac-

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tions with other species that reduce access to resources or successful reproduction. Here, we show how selection minimizes competitive or reproductive interactions between species by favoring the evolution of divergent resource-use or reproductive phenotypes. This process, termed “character displacement” (Brown and Wilson 1956), is a potential leading cause of adaptive diversification (Schluter 2000). In particular, character displacement favors the evolution of novel resource-use or reproductive traits, drives divergence between sympatric and allopatric conspecific populations, and both initiates as well as finalizes the process of speciation.

Despite the significance of character displacement, previous research has focused largely on whether or not it occurs (Servedio and Noor 2003; Coyne and Orr 2004; Dayan and Simberloff 2005). The need exists, however, to move beyond establishing the existence of character displacement in order to discover its full implications. Moreover, research has tended to focus separately on ecological character displacement—character displacement in traits associated with resource use—and reproductive character displacement—character displacement in traits associated with reproduction (for notable exceptions, see research on stickleback fish [reviewed in Rundle and Schluter 2004] and Darwin’s finches [reviewed in Grant and Grant 2008]). Consequently, there has been relatively little cross-fertilization of ideas between researchers who study these two forms of character displacement.

Rather than comprehensively review the evidence for character displacement, as has been done previously by others (e.g., Howard 1993; Schluter 2000; Servedio and Noor 2003; Coyne and Orr 2004; Dayan and Simberloff 2005; Gröning and Hochkirch 2008), we highlight future directions for character displacement research, and our specific goals are threefold. First, we seek to unite ecological and reproductive character displacement under the same conceptual framework. Second, we underscore the value of exploring more fully the ecological and evolutionary causes and

consequences of character displacement. In particular, we describe why some species may be especially prone to undergoing character displacement, and we also discuss some of the downstream effects that may occur as a result of character displacement. Third, we evaluate how reproductive and ecological character displacement interact and thereby affect the likelihood that either process will unfold.

UNIFYING ECOLOGICAL AND REPRODUCTIVE CHARACTER DISPLACEMENT

We begin by presenting a unified framework for making the fields of ecological and reproductive character displacement parallel in focus. In doing so, we first discuss what constitutes character displacement and review, albeit briefly, the problems with definitions that have plagued both ecological and reproductive character displacement. We suggest that applying the conceptual framework developed for ecological character displacement to reproductive character displacement will alleviate confusion and place both fields on equal footing.

WHAT IS CHARACTER DISPLACEMENT?

Brown and Wilson (1956) coined the term “character displacement,” but the catalyst for the idea can be traced to Gause (1934), who showed experimentally that two species cannot stably coexist if they overlap completely in resource requirements (Darwin [1859] had made a similar argument earlier but did not provide empirical support). In such situations, one species ultimately edges out the other. This hypothesis, termed the competitive exclusion principle (Hardin 1960), forms a cornerstone of ecology. The competitive exclusion principle has an important corollary—that species can stably coexist if they differ in their use of resources (Hardin 1960; Pianka 2000). Therefore, initially identical, interacting species will experience strong selection to evolve differences in resource use (Lack 1947; Grant 1972; Arthur 1982; Schluter 1994; Pfennig et al. 2007). Similarly, such

species may experience strong selection to evolve differences in reproductive traits (Butlin and Ritchie 1994; Servedio and Noor 2003; Coyne and Orr 2004); otherwise, one species could potentially drive the other to local extinction through “reproductive” exclusion (also referred to as “sexual exclusion”) (Hochkirch et al. 2007; Gröning and Hochkirch 2008).

Character displacement is likely a general phenomenon in that most species will, at some point in their evolutionary history, confront heterospecifics with which they will competitively or reproductively interact. In such situations, individuals most dissimilar from the average resource-use or reproductive traits of another species are expected to procure more resources or to be more reproductively successful than other members of their population (Slatkin 1980; Taper and Case 1985, 1992; Abrams 1986; Butlin and Ritchie 1994; Doebeli 1996; Servedio and Noor 2003; Coyne and Orr 2004). Consequently, these most divergent individuals should experience highest fitness. If heritable variation exists in these traits, each species will evolve to be less like the other; however, as we shall note briefly later, asymmetric character displacement can arise if the species differ in whether and how much they diverge (for a fuller discussion, see Schluter 2000; Cooley 2007). Such selection acts to lessen competitive or reproductive interactions between species, and it can promote evolutionary divergence in traits associated with resource use or reproduction (i.e., character displacement) (Figure 1) (for a review of the theory, see Schluter 2000; Coyne and Orr 2004). In the absence of character displacement, competitive or reproductive exclusion may ensue (Gause 1934; Liou and Price 1994; Gröning and Hochkirch 2008).

In this review, “character displacement” refers to the evolutionary accentuation of phenotypic differences between species, stemming from selection to lessen resource competition or reproductive interactions between them. Later, we will broaden this definition to include selection acting *within* species. Character displacement can assume two distinct forms that differ in the agent

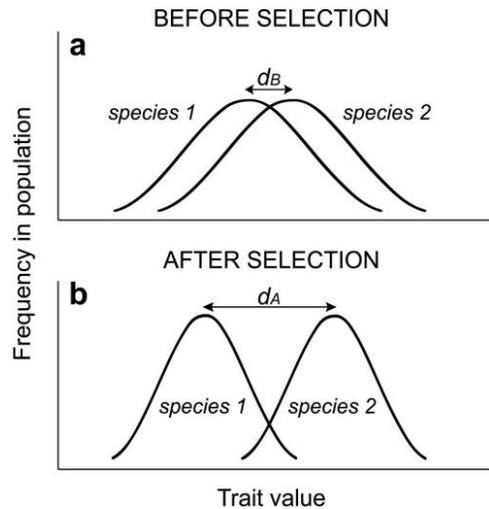


FIGURE 1. THE PROCESS OF CHARACTER DISPLACEMENT

(a) Initially, two species encounter each other and overlap in phenotypes associated with resource use or reproduction, indicated here by the two overlapping bell-shaped curves. Character displacement arises when individuals most dissimilar from the average resource-use or reproductive phenotypes of another species are more successful at acquiring resources or at reproducing than other members of their population. (b) Consequently, the most divergent individuals should experience the highest fitness, and the two species should evolve to be less similar to each other. Character displacement is indicated when the difference between species in mean trait value is greater after selection (d_A) than before selection (d_B).

and target of selection (Brown and Wilson 1956). “Ecological character displacement” refers to trait evolution stemming from selection to lessen resource competition between species and therefore acts on traits associated with resource use (e.g., morphological structures such as beaks and jaws) (Slatkin 1980; Schluter 2001). By contrast, “reproductive character displacement” refers to trait evolution stemming from selection to lessen sexual interactions between species and, accordingly, acts on traits associated with reproduction (e.g., sexual signals or female mate preferences) (Brown and Wilson 1956; Crozier 1974).

An important prediction of character displacement is that species should differ in traits associated with resource use or repro-

duction if they occur together (Brown and Wilson 1956; Grant 1972; Schluter 2000). Moreover, selection to lessen resource competition or reproductive interactions should act only where species do indeed co-occur (Lack 1947; Brown and Wilson 1956). Consequently, character displacement should also produce a distinctive pattern in which species are more dissimilar where they occur together than in areas where each occurs alone (Figure 2a, b) (Lack 1947; Brown and Wilson 1956). Thus, within each species, populations in sympatry with the heterospecific should differ from those in allopatry (Figure 2b) (Lack 1947). Character displacement therefore consists of two hallmark features: (1) the *process* of phenotypic evolution, which stems from selection to lessen resource competition or reproductive interactions between species (Figure 1), and (2) the resulting *pattern* of geographical variation in which sympatric species show exaggerated divergence, and in which conspecific populations in sympatry with a heterospecific differ from those in allopatry (Figure 2b).

CONFLATION OF PROCESS AND PATTERN

Character displacement has often been conflated with the pattern that is predicted to arise from it (Grant 1972; Endler 1986; Schluter 2000; Goldberg and Lande 2006). Defining character displacement as a pattern, however, is problematic, because patterns of divergence between species and populations can be generated via processes other than selection to avoid interactions with heterospecifics (Grant 1972; Strong et al. 1979; Simberloff and Boecklen 1981; Arthur 1982; Endler 1986; Diamond et al. 1989). In the case of ecological character displacement, the conflation of process and pattern provoked a lengthy and spirited debate over what constituted "true" character displacement (Schluter 2001). In response to this debate, researchers generally agreed to define ecological character displacement as the process described above (i.e., defining ecological character displacement as trait evolution stemming from selection to lessen resource competition between species is widely accepted) (e.g., see Schluter 2001, 2002). By defining

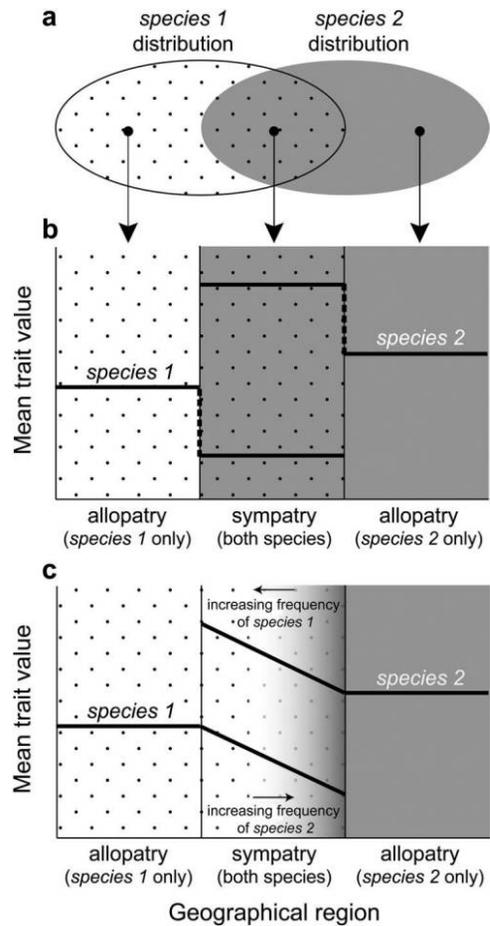


FIGURE 2. PATTERNS OF CHARACTER DISPLACEMENT (a) For two species that occur in sympatry with each other as well as in allopatry, character displacement should produce a distinctive pattern of divergence (b) in which the two species are more dissimilar to each other in sympatry, where there is selection for divergence, than in allopatry, where there is no such selection. Moreover, within such species, populations in sympatry with the heterospecific are expected to diverge from conspecific populations in allopatry. (c) Because the likelihood of encountering heterospecifics may increase along a spatial gradient (for instance, as one moves from the edge to the center of a species' geographical range), character displacement may produce a pattern within each species in which the magnitude of divergence increases along a gradient with increasing likelihood of encountering heterospecifics.

character displacement in terms of process rather than pattern, researchers can thereby focus strictly on the ecological and evolutionary implications of resource competition between species (Grant 1972; Schluter 2000).

UNIFYING THE CONCEPTUAL FRAMEWORK
OF ECOLOGICAL AND REPRODUCTIVE
CHARACTER DISPLACEMENT

Although the field of ecological character displacement is largely reconciled as to what constitutes character displacement, the field of reproductive character displacement has achieved no such resolution. Consequently, conflation of pattern and process is widespread when dealing with reproductive character displacement (for additional discussion, see Butlin and Ritchie 1994; Servedio and Noor 2003; Coyne and Orr 2004). However, as the literature on ecological character displacement clearly illustrates, patterns of trait divergence can be generated via processes other than selection to avoid interactions with heterospecifics (e.g., founder effects) (Marko 2005; reviewed in Grant 1972; Schluter 2000). Defining reproductive character displacement as a process rather than as a pattern has the same benefit as defining ecological character displacement as a process, as it enables researchers to focus specifically on the ecological and evolutionary implications of the interactions between species that drive reproductive trait divergence. Moreover, taking a parallel process-oriented approach to both ecological and reproductive character displacement allows for a more complete understanding of how they interact. If the two fields continue to define character displacement differently, then the ability to adequately delineate, let alone address, questions regarding how and why ecological and reproductive character displacement interact will be hampered.

Defining reproductive character displacement as a process is not new. Indeed, Butlin and Ritchie (1994) defined reproductive character displacement as “the *process* of divergence in mating signal systems between reproductively isolated species” (p. 62, emphasis ours). The definition of

reproductive character displacement that we use here is a more general form than that of Butlin and Ritchie (1994). Yet, this more general definition serves to clarify the relationship of reproductive character displacement to reinforcement—the evolution of traits that minimize hybridization between species (Dobzhansky 1940; Servedio and Noor 2003; Coyne and Orr 2004). By the general definition we use here, reinforcement constitutes a special case of reproductive character displacement. This approach is also not new. Indeed, Blair (1974)—who is credited with coining the term “reinforcement” (Coyne and Orr 2004)—refers to reinforcement as “a rather restricted form of character displacement” (p. 1119).

Defining reproductive character displacement broadly as the selective process by which reproductive traits diverge in order to minimize costly reproductive interactions with heterospecifics, and including reinforcement as a form of character displacement, emphasizes the general importance of selection as the driving force behind reproductive trait divergence. The definition we use here thereby minimizes confusion about what does, and does not, constitute reproductive character displacement versus reinforcement, and it also overcomes the issues associated with confounding pattern and process when describing reproductive character displacement (e.g., those who study reinforcement typically consider reproductive character displacement to be a signature pattern resulting from reinforcement) (see Howard 1993; Servedio and Noor 2003 and references therein).

Butlin and Ritchie (1994) argued that reproductive character displacement and reinforcement should be considered separate processes based, in part, on the nature of interactions between species (see also Butlin 1987). Reinforcement was defined as arising from interactions where species could actually exchange genes during mating, whereas reproductive character displacement was deemed to arise from all other mating interactions (Butlin 1987; Butlin and Ritchie 1994). Yet, in the same

way that competition for resources can take different forms (i.e., exploitative or indirect competition, and interference or direct competition) but still generate ecological character displacement (Schluter 2000), different types of reproductive interactions between species can promote reproductive character displacement. In particular, reproductive interactions between species can take two general forms: direct interactions, in which the two species actually risk hybridizing with one another, and indirect interactions, in which the two species utilize similar aspects of their habitat (e.g., signaling space or pollinators) to seek and attract mates.

Direct interactions can produce wasted mating effort (e.g., in terms of lost gametes or costs of searching for a mate) if no viable offspring are produced (for discussion of hybrid fitness see Barton and Hewitt 1989; Arnold 1997; Coyne and Orr 2004). Even if hybrid offspring are viable, hybridization may still result in low fitness if hybrids have lower survivorship or reduced fertility and fecundity (reviewed in Barton and Hewitt 1989; Arnold 1997; Coyne and Orr 2004). Consequently, selection should generally minimize the risks of hybridization by favoring divergence in reproductive traits between species (i.e., reproductive character displacement). In other words, direct interactions that contribute to gene flow between species can lead to reinforcement, which we consider to be a special case of reproductive character displacement (see also Blair 1974).

By contrast, indirect interactions can generate interference between species that makes mate localization difficult and costly in terms of increasing signaling effort or increasing search times and their associated costs (Butlin and Ritchie 1994; Gerhardt and Huber 2002). For example, species that use acoustic signals can mask, jam, or attenuate aspects of one another's signal properties, making it difficult to discern either signal (Gerhardt and Huber 2002). Similarly, plants that compete for pollinators may cope with pollen limitation and pollen interference (Levin 1985; Caruso 2000; Smith and Rausher 2008). As

with the direct reproductive interactions described above, selection should generally minimize indirect reproductive interference by favoring divergence between species in reproductive traits (i.e., reproductive character displacement).

This dichotomy of direct and indirect interactions should not be taken as mutually exclusive; species can interact in both ways, and how they interact may change spatially and temporally. The key point is that, for direct and indirect reproductive interactions, both the agent and the target of selection are the same. Consequently, both types of interactions can promote divergence in reproductive traits as a means of minimizing costly reproductive interactions between species. In other words, both can promote reproductive character displacement (according to the definition we use here).

Now that we have described the framework for defining ecological and reproductive character displacement in a similar way, we turn to evaluating the causes of character displacement. In particular, we seek to examine what factors facilitate character displacement and thereby make it more likely to occur than the alternative outcomes of competitive or reproductive exclusion.

CAUSES OF CHARACTER DISPLACEMENT

The consensus that has emerged from decades of research is that character displacement is taxonomically widespread (Schluter 2000; Servedio and Noor 2003; Coyne and Orr 2004; Dayan and Simberloff 2005); however, the reasons why character displacement appears to be more likely to transpire in some circumstances and taxa than in others remains relatively unexplored (Schluter 2000; Rice and Pfennig 2007). Understanding when and why character displacement is more likely to proceed is important, because differences in the occurrence of character displacement could explain ecological and evolutionary patterns of diversity. For example, communities or taxa that are more prone to experiencing character displacement will likely be more diverse than those com-

munities or taxa where character displacement does not occur, for at least two reasons. First, species that undergo character displacement are less likely to go extinct through competitive or reproductive exclusion (see above). Second, as we will describe later, character displacement may promote speciation. Hence, as part of a more general theory for why some communities or taxa are more diverse than others (Schluter 2000), it is important to determine which factors facilitate character displacement.

FACTORS THAT FACILITATE CHARACTER DISPLACEMENT

Four nonexclusive factors appear to facilitate character displacement, making it more likely to occur. Two are evolutionary factors: strong selection disfavoring interactions with heterospecifics and ecological opportunity. The remaining two are proximate factors: initial trait differences between species and abundant standing variation. Although these factors facilitate adaptive evolution in general and are therefore not unique to character displacement, studies are needed to examine how they affect character displacement specifically. Below, we describe each factor and its potential effect on character displacement.

First, character displacement is more likely to occur when selection against interactions with heterospecifics is strong. For example, reproductive character displacement is increasingly likely to occur as the costs of hybridization increase (Liou and Price 1994). Moreover, differences between species in the strength of selection to avoid interactions with the other species may explain asymmetric character displacement, in which one species diverges less than another (Cooley 2007). When one species suffers higher costs in the interaction, it may experience greater divergence than the other species (although asymmetric character displacement can occur for other reasons not described here; see Schluter 2000; Cooley 2007). Character displacement should also be more likely to occur when the encounter rate between species is high and, hence, when selection

disfavoring interactions with heterospecifics is strong (see Figure 2c) (for examples, see Pfennig and Murphy 2002; Tynkynen et al. 2004; Pfennig and Pfennig 2005).

Second, character displacement is facilitated by “ecological opportunity”—the availability of different resource types underutilized by other species (Simpson 1953; Schluter 2000). Although the concept of ecological opportunity has traditionally been applied to resources, a similar principle applies to available signal space in the case of reproductive character displacement. Character displacement often generates new resource-use or reproductive traits in sympatry that differ from pre-displacement traits in allopatry (Howard 1993; Schluter 2000; Servedio and Noor 2003; Coyne and Orr 2004; Dayan and Simberloff 2005; Gröning and Hochkirch 2008). Therefore, in order for character displacement to occur, exploitable resources or signal space that are not already being utilized by another species must be available; that is, there must be resources or signal space onto which a species can actually be displaced (Pfennig et al. 2006; Gröning and Hochkirch 2008). In the absence of exploitable resources or signal space, competitive or reproductive exclusion may result (Pfennig et al. 2006; Hochkirch et al. 2007; Gröning and Hochkirch 2008).

Third, character displacement occurs most readily if interacting species already differ in phenotypic traits under selection when they come into contact with one another (Slatkin 1980; Liou and Price 1994). Although character displacement can occur without such initial differences, it is often facilitated if other factors jump-start the divergence prior to interactions with heterospecifics (Slatkin 1980). Such factors may act in allopatry before the two species come into contact with one another, and they may include drift or spatially divergent natural or sexual selection (Schluter 2000). These differences may then be amplified in sympatry by selection acting to lessen interspecific interactions (Schluter 2000; Rice and Pfennig 2007). In the absence of initial differences between

species, one species will be more likely to drive the other locally extinct (e.g., through competitive or reproductive exclusion, as mentioned above). Thus, species that differ initially from heterospecifics should be more prone to undergoing character displacement (Slatkin 1980; Liou and Price 1994; Schluter 2000; Rice and Pfennig 2007).

Finally, character displacement may be more likely to occur when interacting species are phenotypically variable (Milligan 1985). Phenotypic variation is important, because it increases the chances that character displacement can evolve through the selective filtering of divergent phenotypes in sympatry that were already present in allopatry (Rice and Pfennig 2007; Barrett and Schluter 2008). Indeed, because this process should unfold relatively rapidly, abundant standing variation should facilitate character displacement as opposed to competitive or reproductive exclusion (Rice and Pfennig 2007). Therefore, species with abundant standing variation should be especially likely to undergo character displacement (Rice and Pfennig 2007).

Given that abundant standing variation might facilitate character displacement, what evolutionary and developmental mechanisms generate such variation? Answering this question could explain why some populations are predisposed to character displacement. In the next section, we discuss two such mechanisms: intraspecific competition and phenotypic plasticity.

INTRASPECIFIC CHARACTER DISPLACEMENT

As we have already noted, species with abundant standing variation should be especially prone to experiencing character displacement. Therefore, identifying the mechanisms that generate and maintain variation within natural populations is crucial for understanding the factors that facilitate character displacement. One such mechanism is disruptive selection, which arises when extreme phenotypes have a fitness advantage over more intermediate phenotypes (Mather 1953). By favoring extreme phenotypes, disruptive selection

maintains, and may even increase, variation in natural populations (Rueffler et al. 2006). Indeed, such selection could ultimately result in the evolution of resource or mating polymorphism—alternative phenotypes within the same population that differ in resource use or in mate acquisition tactics (Andersson 1994; Smith and Skúkason 1996).

Although numerous agents can generate disruptive selection, intraspecific competition for resources or mates has long been viewed as a leading cause (Rosenzweig 1978; Wilson and Turelli 1986; Day and Young 2004; Rueffler et al. 2006). Such disruptive selection on traits associated with resource use or reproduction thereby favors divergence in these characters within populations (Smith 1993; Medel et al. 2003; Bolnick 2004; Pfennig et al. 2007; Bolnick and Lau 2008; Calsbeek and Smith 2008; Hendry et al. 2009; Martin and Pfennig 2009). The resulting trait evolution, arising from interactions *within* species, is analogous to that stemming from interactions *between* species (Dayan and Simberloff 2005) and can be considered “intraspecific character displacement” (*sensu* West-Eberhard 2003).

Once a population has undergone *intraspecific* character displacement, it may, in turn, be more prone to undergo *interspecific* character displacement, for at least two reasons. First, intraspecific character displacement may favor the evolution of alternative resource-use or mate-acquisition phenotypes (Martin and Pfennig 2009). The evolution of such alternative phenotypes, prior to interactions between species, may fuel rapid character displacement via differential success of the alternative phenotypic variants (Figure 3) (Rice and Pfennig 2007; Barrett and Schluter 2008). Second, even when disruptive selection does not favor distinct morphs, it does tend to maintain, and even increase, both phenotypic and genetic variation in natural populations (Mather 1953; Rueffler et al. 2006). As noted in the previous section, such abundant standing variation increases the chances that interspecific character displacement will occur (Rice and Pfennig 2007).

PHENOTYPIC PLASTICITY

In the previous section, we focused on a selective agent—intraspecific competition—that favors variation within populations. Such variation might predispose populations to subsequently undergo interspecific character displacement. However, it is also important to consider the proximate mechanisms that generate such variation. Elucidating these proximate mechanisms is vital, because different proximate mechanisms can influence the speed at which new phenotypic variants arise. Therefore, different proximate mechanisms may ultimately influence the speed of character displacement, and thereby determine whether character displacement even occurs in the first place. In particular, any proximate mechanism that facilitates divergence in resource-use or reproductive phenotypes may render character displacement more likely to transpire, as opposed to competitive or reproductive exclusion.

An important proximate mechanism for rapidly generating new phenotypic variants is phenotypic plasticity. Phenotypic plasticity is the ability of an individual organism to react to an environmental stimulus with a change in phenotype (reviewed in West-Eberhard 2003). Phenotypic plasticity enables organisms to respond rapidly to the presence of heterospecifics by altering their phenotype adaptively (Robinson and Wilson 1994; Agrawal 2001; Pfennig and Murphy 2002; Fordyce 2006; Pfennig et al. 2006). For example, when faced with resource competition or reproductive interactions from a heterospecific, individuals of many species facultatively express alternative resource-acquisition or reproductive phenotypes that lessen competition or reproductive interactions (Werner and Hall 1976; Pfennig and Murphy 2002; Pfennig 2007). Such rapid shifts in resource-acquisition or reproductive traits have not traditionally been considered character displacement, because phenotypic plasticity is often regarded as a nongenetic response that is incapable of mediating adaptive evolution (Grant 1972; Arthur 1982; Schluter 2000). However, the magnitude

and direction of a plastic response is often genetically variable and, consequently, subject to natural selection and evolutionary change (Schlichting and Pigliucci 1998; West-Eberhard 2003; DeWitt and Scheiner 2004).

Moreover, intergenerational plasticity—specifically, maternal effects—might actually promote a form of “canalization,” in which trait differences between species and populations persist, even when individuals are reared under common conditions (Pfennig and Martin 2009). Maternal effects occur when the phenotype of a female influences the phenotype of her offspring, independent of the direct effects of her genes on her offspring’s phenotype (Mousseau and Fox 1998). Because these effects can be acted upon by selection (McAdam and Boutin 2004) and can, in turn, cause information to be conveyed reliably between generations (Rossiter 1996; Agrawal et al. 1999; Plaistow et al. 2006; Allen et al. 2008), they may play an important role in mediating adaptive evolution (Jablonka and Lamb 1995; Maynard Smith 1998).

Maternal effects can facilitate either form of character displacement, but they may be especially important in mediating ecological character displacement. Ecological character displacement causes interacting species to utilize different resources (Schluter 2000; Day and Young 2004). When resource quality is asymmetric, one species will gain the more profitable resource, whereas the other will be forced to utilize a less profitable resource (e.g., Pfennig and Pfennig 2005; Grant and Grant 2006). Consequently, females of the latter species may mature at a smaller body size or in poorer condition (Gorbushin 1996; Pfennig and Pfennig 2005; Grant and Grant 2006), and, as a result, they may produce offspring that are also smaller and in poorer condition, purely because of a maternal effect (e.g., Pfennig and Martin 2009). Because of this maternal effect, the offspring may ultimately express a resource-use phenotype dissimilar to that expressed by the other species, as resource use is often correlated with body size.

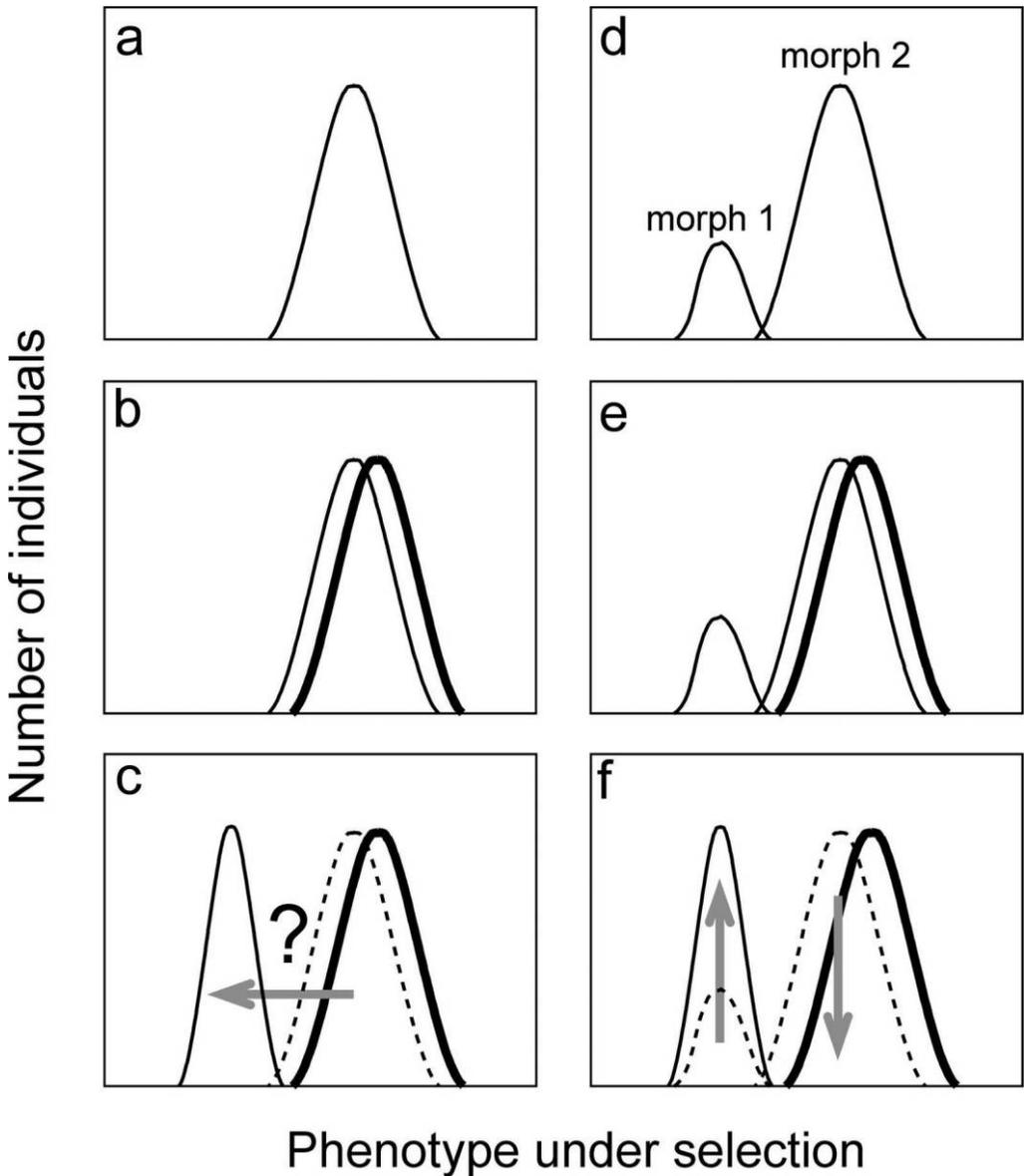


FIGURE 3. ABUNDANT STANDING VARIATION PROMOTES CHARACTER DISPLACEMENT

(a) and (d) represent a focal species—species 1, whose trait distribution is indicated by the bell-shaped curve(s). Initially, species 1 occurs alone in allopatry, either as a monomorphic species (a) or as a polymorphic species (d) consisting of alternative resource-use or reproductive morphs (morphs 1, 2), one of which is, at first, rarer than the other. Later (b, e), a superior competitor, species 2, whose trait distribution is indicated by the heavy bell-shaped curve, becomes sympatric with species 1 as a result of one species invading the other's habitat. 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 reproductive traits (reproductive character displacement). In both cases, the trait distributions of species 1 before selection are shown by the dashed bell-shaped curves. When there is little standing variation prior to encountering the heterospecific (c), character displacement unfolds only if novel phenotypes that are more dissimilar to the competitor arise and spread in sympatry following the invasion of species 2. Because such novel phenotypes, if they do not already exist in the population, can only be generated through mutation, recombination, or introgression—all

Moreover, because maternal effects can be transmitted reliably between generations (as aforementioned), these differences in trait expression between populations in sympatry with a heterospecific competitor and those in allopatry may persist even when individuals are experimentally reared under common conditions. Such a pattern would give the misleading appearance that genetic differences underlie these trait differences. Thus, trait differences between populations undergoing character displacement may be underlain entirely by a maternal effect (for a possible example, see Pfennig and Martin 2009).

The above discussion suggests that phenotypic plasticity can mediate rapid phenotypic divergence between species. Phenotypic plasticity might also promote the evolution of genetic differences that stabilize such phenotypic differences (West-Eberhard 2003). If individuals in a population begin to facultatively express a novel phenotype that lessens costly interactions with a heterospecific, and if there is underlying genetic variation in the degree to which individuals respond to heterospecifics, then selection should favor those alleles or gene combinations that best stabilize, refine, and extend the new trait's expression (a process known as "genetic accommodation") (West-Eberhard 2003). Thus, under persistent selection to minimize competition or reproductive interactions with heterospecifics, divergent traits that are initially plastic may eventually become genetically canalized (i.e., "fixed") in the population (Pfennig and Murphy 2000, 2002). Furthermore, phenotypic shifts mediated by phenotypic plasticity may shield populations from extinction via competitive or reproductive exclusion as genetic evolution proceeds.

In summary, phenotypic plasticity plays a potentially important role in facilitating character displacement (Wilson 1992; Pfennig and Murphy 2002), and plastic traits themselves may be the targets of selection that initially diverge rapidly between species (i.e., they may undergo character displacement) (Pfennig and Murphy 2000, 2002). Additionally, plasticity can promote canalized character displacement (*sensu* Pfennig and Murphy 2002) or buffer populations from extinction while the evolution of such canalization proceeds (*sensu* West-Eberhard 2003).

In the above section, we have just explored the causes of character displacement by highlighting some diverse factors that might give rise to it. By fostering character displacement, as opposed to extinction through competitive or reproductive exclusion, these factors could ultimately explain why some communities or taxonomic groups are more diverse than others. Therefore, any factors that contribute to character displacement may have far-reaching implications beyond simply mediating trait divergence between species. Below, we explore such evolutionary and ecological implications in more detail.

CONSEQUENCES OF CHARACTER DISPLACEMENT

As described above, character displacement results in divergent traits between interacting species, as well as divergent traits within each species between allopatric and sympatric populations (Figure 2b). This hallmark pattern is not the only significant outcome of character displacement, however. Indeed, character displacement may contribute to broader patterns of diversity. For example, as our

of which are relatively slow processes—competitive or reproductive exclusion are more likely to occur than character displacement. By contrast, when there is abundant standing variation (f), character displacement unfolds when the phenotypic variant that is more dissimilar to the competitor (morph 1) is selectively favored and thereby increases in frequency at the expense of the alternative morph. Because such a process can unfold rapidly (e.g., potentially within a single generation), character displacement, as opposed to exclusion, is more likely to transpire. Although we have illustrated this process as involving discrete morphs, which may have arisen through intraspecific character displacement, it could also occur in populations expressing a wide range of continuously distributed phenotypes. Modified from Rice and Pfennig (2007).

earlier discussion indicated, whether or not character displacement occurs depends on a number of evolutionary and proximate factors. Consequently, some groups may be more likely to undergo character displacement—and therefore may be more diverse—than others. Yet, character displacement's role in generating such macroevolutionary patterns of differential taxonomic diversity is largely unknown (but see Schluter 2000). Similarly, the ecological and evolutionary implications that stem from character displacement remain relatively unexplored.

Here, we discuss how character displacement can influence four key evolutionary processes: correlated evolution, sexual selection, speciation, and extinction. By influencing how these processes unfold, character displacement has potentially far-reaching impacts beyond mere trait divergence between species.

CORRELATED EVOLUTION

During character displacement, sympatric and allopatric populations diverge in traits involved in resource use or reproduction (Figure 2b). However, populations may also diverge in traits that are not directly involved in resource acquisition or reproduction, owing to correlated evolution with those traits that are actually targeted by selection (*sensu* Conner and Hartl 2004). Such divergence in correlated traits can accentuate differences between interacting species and, within each species, between populations in sympatry and allopatry. As we describe below, these differences could, in turn, enhance reproductive isolation among these groups.

When correlated evolution in response to heterospecifics arises from pleiotropy, fitness trade-offs can arise between the benefits of avoiding deleterious interactions with heterospecifics and the costs accrued in other fitness components (Pfennig and Pfennig 2005). For example, both reproductive and ecological character displacement have caused spadefoot toads to evolve smaller body size in the presence of a heterospecific competitor (Pfennig and Pfennig 2005). This shift in size appears to

have arisen as a by-product, rather than as a direct target, of character displacement (Pfennig and Pfennig 2005). Yet, the shift to reduced body size in sympatry is associated with reduced offspring survival, female fecundity, and sexual selection on males (Pfennig and Pfennig 2005). Thus, character displacement may sometimes represent the “best of a bad situation” in that it lessens competition but at a cost: individuals in sympatry with the displaced phenotype may have higher fitness than those without the displaced trait because they experience reduced competition, but they may have reduced fitness relative to individuals in allopatry (Pfennig and Pfennig 2005).

Fitness trade-offs associated with the benefits of avoiding deleterious interactions with heterospecifics, on the one hand, and the costs accrued in other fitness components, on the other hand, may have at least three important consequences. First, depending on the nature of the trade-off and the strength of selection to avoid heterospecific interactions, trade-offs may constrain the evolution of adaptive traits that reduce heterospecific interactions (*sensu* Conner and Hartl 2004). That is, pleiotropic interactions may limit evolutionary divergence in response to heterospecifics. Variation within and between species in fitness trade-offs may explain why character displacement varies among populations or why it is sometimes expressed asymmetrically between the interacting species (Schluter 2000; Cooley 2007). Second, such fitness trade-offs may explain why traits that evolve in sympatry often do not spread back into allopatry, even in the face of high gene flow (Servedio and Noor 2003; Higgie and Blows 2007). Finally, because fitness trade-offs may cause individuals in sympatry to have reduced fitness relative to those in allopatry (as in the spadefoot toad example), sympatric populations may be at a higher risk for extinction relative to allopatric populations (Pfennig and Pfennig 2005; see also Webb 2003; Gröning and Hochkirch 2008). We will return to this point below.

SEXUAL SELECTION

Sexual selection explains much of the diversity in sexual signals and mating behaviors in sexually reproducing organisms (Andersson 1994), and character displacement can have a profound influence on sexual selection. When character displacement alters the expression of mate choice or traits used in sexual signaling or male competition, it necessarily impacts the expression of sexual selection among populations that differ in their interactions with heterospecifics (Boughman 2001, 2007; Pfennig and Ryan 2007). Indeed, character displacement may impact sexual selection in at least two ways. First, character displacement can preclude mate choice for male traits that are indicative of mate quality and thereby alter the underlying fitness consequences of mate choice and sexual signaling (Higgie and Blows 2008; Pfennig 1998, 2000). Second, character displacement can alter the targets of sexual selection in populations that differ in their interactions with heterospecifics, without necessarily affecting the fitness accrued through mating decisions or mate attraction. We discuss each of these impacts separately below.

First, character displacement potentially alters sexual selection by precluding the expression of mate choice for fitness-enhancing conspecific mates (Pfennig 1998, 2000; Higgie and Blows 2008). Generally, females should choose mates that provide them with fitness benefits, such as increased numbers of offspring or higher-quality offspring (Andersson 1994). If reproductive character displacement favors the evolution of preferences that ensure mating with the correct species, the resulting preferences that evolve via character displacement may not be those that also enable females to select high-quality conspecific mates (Pfennig 1998, 2000; Higgie and Blows 2007, 2008). For example, sexual selection theory generally predicts that females prefer males with more elaborate or costly signals that are indicative of a male's ability to confer benefits to a female (Andersson 1994; Bradbury and

Vehrencamp 1998). If, however, heterospecifics possess elaborate traits, character displacement may promote the evolution of preferences for less exaggerated signals (Ryan and Rand 1993; Pfennig 1998; e.g., Pfennig 2000; Rosenthal et al. 2002; Higgie and Blows 2008). By adopting such preferences, females may avoid costly heterospecific interactions, but they may concomitantly forego information about a prospective conspecific mate's ability to convey additional fitness benefits (for examples, see Pfennig 2000, 2008; Higgie and Blows 2007, 2008).

Such trade-offs will not always arise via character displacement (Pfennig 1998). For example, if males with the most elaborate characters are also the most dissimilar from heterospecifics, sexual selection and character displacement reinforce each other (Pfennig 2000). However, when trade-offs do arise, their effects may be far-reaching. As with the pleiotropic effects described above, trade-offs in mate choice can explain why divergent mating traits that evolve in sympatry do not spread back into allopatry via gene flow (Pfennig and Pfennig 2005; Higgie and Blows 2007). Indeed, when trade-offs in mate choice arise, sympatric and allopatric populations can experience nearly opposing patterns of mate choice-mediated sexual selection. Consequently, not only will mate preferences diverge between sympatry and allopatry, but sexual signals—and any correlated traits—will also diverge (Howard 1993; Hoskin et al. 2005; Pfennig and Pfennig 2005; Pfennig and Ryan 2006; Higgie and Blows 2007, 2008; Lemmon 2009). As we will discuss, such divergence in mating behavior can lead to reproductive isolation and, ultimately, speciation of allopatric and sympatric populations (Howard 1993; Hoskin et al. 2005; Pfennig and Ryan 2006; Lemmon 2009). Furthermore, over time, selection may favor the resolution of trade-offs by promoting the evolution of preferences for multiple traits that enable females to avoid heterospecific interactions while simultaneously assessing conspecific quality (Pfennig 1998). Thus, character displacement can contribute not only to

divergence in a given aspect of a signal, but it can also indirectly promote the evolution of multiple or complex signals for discriminating mates (Pfennig 1998; Gerhardt and Huber 2002; Hebets and Papaj 2005).

A second major way that character displacement may impact sexual selection is by altering the targets of sexual selection in sympatry versus in allopatry (e.g., Gerhardt 1994; Pfennig 2000; Higgie and Blows 2007). As we describe below, character displacement can lead to morphological changes in resource-use traits that concomitantly alter the production of sexual signals (e.g., Podos 2001; Huber and Podos 2006). These novel sexual signals might, in turn, become targets for further elaboration by direct sexual selection because of their attractiveness to the opposite sex, for instance, or their effectiveness in competition among conspecifics for mates (Andersson 1994). Moreover, because ecological and reproductive character displacement often promote habitat shifts, occupancy of these novel habitats will tend to promote new patterns of sexual selection (*sensu* Endler and Basolo 1998; Boughman 2002). The nature of mate preferences and sexually selected traits often covary with habitat, as the transmission and the perception of sexual signals are typically habitat-dependent (Wiley 1994; Bradbury and Vehrencamp 1998; Endler and Basolo 1998; Boughman 2002). Thus, any shifts in habitat use that are mediated by character displacement will likely be accompanied by shifts in patterns of sexual selection (Boughman 2007).

As a result of the above effects of character displacement on sexual selection, sympatric and allopatric populations will potentially diverge in mating behaviors that were not necessarily the direct targets of selection to reduce heterospecific interactions. Because mate choice plays a critical role in reproductive isolation (Coyne and Orr 2004), divergent patterns of sexual selection in sympatry versus allopatry could ultimately contribute to speciation (Howard 1993; Hoskin et al. 2005; Pfennig and Ryan 2006; Lemmon 2009). Thus, character displacement may initiate speciation

between populations that differ in their interactions with heterospecifics (Howard 1993; Hoskin et al. 2005; Pfennig and Ryan 2006; Lemmon 2009), and this is the topic that we turn to next.

SPECIATION

Character displacement potentially plays a critical role in speciation in two ways. First, character displacement can finalize speciation between already divergent groups (Servedio and Noor 2003; Coyne and Orr 2004; Grant and Grant 2008). Second, character displacement can initiate divergence and reproductive isolation between populations that differ in their interactions with heterospecifics (Howard 1993; Hoskin et al. 2005; Pfennig and Ryan 2006; Pfennig and Rice 2007; Lemmon 2009). We discuss each of these avenues to speciation in turn.

Character displacement has long been regarded as important in completing the process of speciation (Coyne and Orr 2004; Grant and Grant 2008). Ecological character displacement, for example, should cause differentiated but potentially interbreeding populations (i.e., incipient species) to diverge in resource acquisition traits (Grant and Grant 2008). Specialization on alternate resources may reduce contact between the two incipient species, thus allowing for the accumulation of genetic differences between them that, in turn, contributes to enhanced isolation (Coyne and Orr 2004; Grant and Grant 2008; Price 2008). Moreover, if the two species interbreed and produce hybrids of low fitness, reproductive character displacement will cause divergence in reproductive traits, thereby precluding hybridization (Dobzhansky 1940; Howard 1993; Servedio and Noor 2003; Coyne and Orr 2004). This process of reinforcement will therefore finalize speciation by promoting the evolution of complete reproductive isolation (Dobzhansky 1940; Howard 1993; Servedio and Noor 2003; Coyne and Orr 2004).

Character displacement can also *initiate* speciation, but this route has received relatively little attention from researchers

(but see Howard 1993; Hoskin et al. 2005; Pfennig and Ryan 2006; Pfennig and Rice 2007; Lemmon 2009). Character displacement may instigate speciation by driving the evolution of divergent traits between populations that differ in their interactions with heterospecifics (Howard 1993; Hoskin et al. 2005; Pfennig and Ryan 2006; Pfennig and Rice 2007; Lemmon 2009). Because individuals in sympatry will experience a different selective environment than conspecifics in allopatry, conspecific populations in these two types of environments are expected to diverge in resource-use or reproductive traits (Howard 1993; Hoskin et al. 2005; Pfennig and Ryan 2006; Pfennig and Rice 2007; Lemmon 2009), and such divergence may indirectly promote speciation via two non-mutually exclusive routes.

First, character displacement may promote the evolution of post-mating barriers to gene flow between sympatric and allopatric populations (Pfennig and Rice 2007). In particular, as an indirect consequence of character displacement between species, offspring produced by matings between conspecific individuals from *different* selective environments (i.e., sympatric male/female x allopatric male/female) may express an intermediate phenotype that is less well-adapted to either selective environment than that expressed by offspring produced by matings between individuals from the *same* selective environment (i.e., sympatric male/female x sympatric male/female or allopatric male/female x allopatric male/female) (sensu Rice 1987; Hatfield and Schluter 1999; Rundle 2002). For example, individuals produced by matings across sympatry and allopatry may express intermediate resource acquisition phenotypes that make them competitively inferior in either sympatry or allopatry (e.g., Pfennig and Rice 2007). Similarly, individuals produced from matings across sympatry and allopatry may engage in mating behaviors that are inappropriate for either selective environment (sensu Hatfield and Schluter 1996; Vamosi and Schluter 1999; Svedin et al. 2008; van der Sluijs et al. 2008). Such mal-

adaptation essentially serves as a post-mating barrier to gene flow between populations in different selective environments.

Second, character displacement may promote the evolution of pre-mating barriers between sympatric and allopatric populations. During reproductive character displacement, female preferences or male traits may become so divergent that females in sympatry fail to recognize allopatric males as acceptable mates (or vice versa). Consequently, populations in sympatry and allopatry will become reproductively isolated from each other (Howard 1993; Hoskin et al. 2005; Pfennig and Ryan 2006). Likewise, ecological character displacement can contribute to pre-mating barriers between conspecific populations in sympatry versus allopatry if shifts in habitat or resource use preclude mating between them (Rundle and Schluter 2004).

Differentiation between conspecific populations in sympatry versus allopatry is especially likely to occur if character displacement generates the kinds of fitness trade-offs described above. By precluding the spread of traits from sympatry into allopatry, such trade-offs essentially generate a selective barrier between sympatry and allopatry that fosters local adaptation (Pfennig and Pfennig 2005). Moreover, because of reduced gene flow between sympatry and allopatry, populations in these divergent selective environments may accumulate further differences that exaggerate both pre- and post-mating isolation between them. Thus, speciation between sympatric and allopatric populations may arise as an indirect consequence of selection for divergence between species during interspecific character displacement (Howard 1993; Hoskin et al. 2005; Pfennig and Ryan 2006; Pfennig and Rice 2007; Lemmon 2009).

Although we have focused above on interactions between pairs of species, character displacement may also drive numerous, rapid speciation events. If, for example, a given species interacts with different heterospecifics across different populations, local evolution of mating behaviors in response to these interactions may isolate

these conspecific populations and generate speciation among them (i.e., creating “speciation cascades”) (Pfennig and Ryan 2006). Thus, multiple speciation events—and possibly even adaptive radiations (Schluter 2000)—may arise as a by-product of interactions between species.

COEXISTENCE VERSUS EXTINCTION

Generally, character displacement is expected to promote species coexistence by reducing interactions that would be detrimental to overall fitness and that would otherwise lead to competitive or reproductive exclusion (Losos 2000). Yet, even when character displacement promotes coexistence, reduced survival and reproductive rates in populations in sympatry may occur as a result of character displacement (Pfennig and Pfennig 2005). Consequently, sympatric populations may experience a higher extinction risk than conspecific populations in allopatry (for review and discussion of how adaptive evolution can lead to extinction risk, see Kokko and Brooks 2003; Webb 2003). Character displacement can contribute to enhanced extinction risk when it involves trade-offs between the benefits of avoiding heterospecific interactions and the costs of expressing the displaced phenotype (Pfennig and Pfennig 2005). The costs that accrue to individuals in sympatry may reduce population fitness and thereby render sympatric populations more likely to go extinct (Pfennig and Pfennig 2005). For example, as we discussed earlier, ecological character displacement may result in one species being displaced onto a novel resource that is of inferior quality or that is more ephemeral than the pre-displacement resource. Lower-quality resources may support smaller populations that are more susceptible to stochastic extinction events, thus rendering sympatric populations at higher extinction risk relative to allopatric populations. Likewise, displacement onto a more ephemeral resource may make sympatric populations more susceptible to stochastic extinction events than allopatric populations.

Reproductive character displacement also could engender costs if the displaced phenotypes, such as male signals or female preferences, are more costly to express (for discussion of mate choice for costly signals, see Andersson 1994). More costly signals could reduce reproductive rates and limit population size (Kokko and Brooks 2003). Additionally, extinction risk may depend on how males trade-off sexual and viability selection (Kokko and Brooks 2003). Novel sexual signaling in sympatry may be more susceptible to trade-offs that enhance the risk of extinction relative to populations in allopatry. Moreover, as described above (see SEXUAL SELECTION), avoidance of heterospecifics may preclude females from selecting high-quality mates and may reduce sympatric female fitness relative to allopatric female fitness (Pfennig 2000; Higgie and Blows 2008; Pfennig 2008). Such trade-offs can reduce female fecundity, rates of reproduction, and even offspring growth or survival (Pfennig 2000, 2008). Indeed, if character displacement suppresses condition-dependent sexual selection in sympatry, sympatric populations may be less able to adapt to changing environments (*sensu* Lorch et al. 2003). Relative to conspecifics in allopatry, those in sympatry may be smaller, slower growing, and less able to respond to changes in the environment (Pfennig and Pfennig 2005). As a result, populations that have undergone character displacement may be more likely to experience extinction.

In summary, character displacement generally promotes species coexistence (Losos 2000). Depending on the way that character displacement unfolds, however, it may also counterintuitively enhance the risk of extinction in populations that are sympatric with heterospecifics relative to those that are not (Pfennig and Pfennig 2005; see also Kokko and Brooks 2003; Webb 2003). Thus, the distributions of many species may be patchier in areas where they are sympatric with a heterospecific than in areas where they are allopatric, and this patchy distribution may be associated with stochastic factors, rather than with the deterministic processes of

competitive or reproductive exclusion. Moreover, persistence of sympatric populations may be more variable in both space and time. Indeed, coexistence between species may be more dynamic than originally thought, with sympatric populations experiencing chance extinction, followed by recolonization and coexistence. That is, the outcome of heterospecific interactions may not be merely one or the other of two alternatives: coexistence or exclusion. Instead, character displacement may promote coexistence while increasing the likelihood of chance extinction.

RELATIONSHIP BETWEEN ECOLOGICAL AND REPRODUCTIVE CHARACTER DISPLACEMENT

Throughout this article, we have referred to character displacement—rather than to, specifically, ecological or reproductive character displacement—when the concepts being discussed apply to either process. Although the two processes are similar in many ways, relatively few studies have examined how they interact (for notable exceptions, see research on stickleback fish [reviewed in Rundle and Schluter 2004] and Darwin's finches [reviewed in Grant and Grant 2008]). However, because species that compete for resources likely interact during mating (Schluter 2000; Rundle and Schluter 2004; Grant and Grant 2008; Price 2008), reproductive and ecological character displacement may often become intertwined. Below, we discuss how these two types of character displacement may affect one another.

ECOLOGICAL CHARACTER DISPLACEMENT IN PHENOTYPIC TRAITS AS A PROMOTER OF REPRODUCTIVE CHARACTER DISPLACEMENT

Ecological character displacement can promote reproductive character displacement when shifts in resource-use traits also alter the production of signals used for reproduction (Huber and Podos 2006; Grant and Grant 2008). If these shifts in signal production reduce deleterious reproductive interactions between species, then ecological selection essentially jump-

starts reproductive character displacement. For example, shifts in resource use that lead to changes in bird beak and larynx morphology can cause concomitant shifts in a sexual signal (i.e., bird song) that is directly involved in species recognition (Podos and Nowicki 2004; Grant and Grant 2008; Price 2008). Indeed, in the medium ground finch *Geospiza fortis*, populations that consist of a large-beaked morph and a small-beaked morph—which feed on large and small seeds, respectively—produce distinct song types (Huber and Podos 2006). Females apparently use these different song types during mate choice and mate assortatively with males of their own beak type (Huber et al. 2007). Thus, ecological selection can also alter sexual signals in a way that affects mate choice, and potentially, reproductive isolation (Podos 2001; Podos and Nowicki 2004; Podos et al. 2004; Huber et al. 2007; Grant and Grant 2008).

Although the above example focuses on acoustic signals, shifts in resource use could foster similar changes in other sensory modalities used in sexual signaling. In particular, shifts in resource use could affect visual or olfactory sexual signals depending on how dietary components (e.g., carotenoids) are incorporated into sexual displays. In many fish species, for instance, male coloration is diet-dependent (see discussion and references in Andersson 1994; Olson and Owens 1998), and coloration can also play an important role in species recognition (e.g., Seehausen and van Alphen 1998; Boughman 2001). If ecological character displacement causes divergence in resource use, male signaling can be affected if the dietary components used to generate a given signal are no longer available or are too costly to acquire based upon the new diet (Boughman 2007). Consequently, resource shifts may be accompanied by shifts in sexual signals, which can then be maintained and further elaborated via reproductive character displacement if they serve to minimize deleterious reproductive interactions between species.

Although recent work has focused on

how resource shifts can alter male signals, morphological and physiological changes that accompany ecological character displacement can also directly affect female perception and, therefore, female mate choice (sensu Endler and Basolo 1998; Ryan 1998; Boughman 2002). Changes in jaw morphology to capture prey, divergence in olfactory or visual sensitivity to localize prey, and even shifts in overall body size for specializing on different resources that result from ecological character displacement could all simultaneously alter female perception and discrimination of male signals (Endler and Basolo 1998; Ryan 1998; Boughman 2002). For example, changes in ear morphology caused by changes in jaw structure or body size could affect female perception of and preferences for male calls (Ryan 1990, 1998; Boughman 2002). Thus, ecological character displacement could directly alter female mate preferences and thereby initiate or perpetuate reproductive character displacement, if such preferences also minimize reproductive interactions.

ECOLOGICAL CHARACTER DISPLACEMENT IN HABITAT USE AS A PROMOTER OF REPRODUCTIVE CHARACTER DISPLACEMENT

The above discussion illustrates how resource shifts can directly alter male sexual signals or female mate preferences, thus promoting reproductive character displacement. However, ecological character displacement may also mediate indirect divergence in reproductive characters. In particular, because habitat critically affects the attenuation and perception of signals (Wiley 1994; Bradbury and Vehrencamp 1998; Boughman 2002; Gerhardt and Huber 2002), shifts in habitat use associated with ecological character displacement may promote selection for the evolution of novel sexual signals that are more suited to the new foraging habitat. The sympatric anoles *Anolis cooki* and *A. cristatellus*, for example, display divergent UV light sensitivity that appears to enable them to co-occur in a partitioned light microhabitat (Leal and Fleishman 2002), and such divergent microhabitat use may facilitate co-

occurrence by enabling them to partition resources (Leal and Fleishman 2002). UV reflectance of male dewlaps has also diverged so that these dewlaps contrast most against the light microhabitat in which each species resides, thereby facilitating species recognition (Leal and Fleishman 2002). Presumably, divergent habitat use simultaneously selects for signals that optimize communication in the novel habitat while also minimizing reproductive interactions between species (Leal and Fleishman 2002). In this way, ecological character displacement may indirectly foster the evolution of divergent reproductive characters that minimize reproductive interactions.

Changes in habitat or resource use via ecological character displacement may also generate changes in female mate preferences that promote reproductive character displacement. Such changes could occur in two ways. First, novel habitats may exert direct selection on females to evolve preferences for male traits that are most efficiently detected in those new habitats (Endler and Basolo 1998; Boughman 2002). Second, novel habitats or resources may exert natural selection on female sensory systems to better identify prey (Ryan 1998; Boughman 2002). These shifts in sensory sensitivity could indirectly alter patterns of female mate choice (Ryan 1990, 1998; Endler and Basolo 1998; Boughman 2002, 2007). If such preferences reduce sexual interactions between species, they may be further enhanced by reproductive character displacement.

In sticklebacks, for example, a benthic ecomorph forages and mates in the littoral zone where red coloration is more difficult to detect. A limnetic ecomorph, by contrast, occurs in open water where red coloration is more discernable (Boughman 2001). Benthic females are less sensitive to variation in red than are limnetic females, and, unlike limnetic females, benthic females do not tend to prefer redder males (Boughman 2001, 2007; Boughman 2002). Male red coloration, in turn, is "tuned" to female perception of red color—males are redder in populations where females are

actually sensitive to, and thus prefer, redder males (Boughman 2001, 2007). Perhaps more critically, the extent to which a given limnetic/benthic species pair is reproductively isolated is negatively correlated with female red sensitivity and preference in a given population (Boughman 2001). Thus, shifts in mate preference tied to different habitats dictate the degree to which reproductive divergence occurs (Boughman 2001). Generally, shifts in resource or habitat use via ecological character displacement may play a critical role in initiating and promoting reproductive character displacement by fostering changes in mate preferences and sexual signals that minimize reproductive interactions between species.

REPRODUCTIVE CHARACTER DISPLACEMENT AS A PROMOTER OF ECOLOGICAL CHARACTER DISPLACEMENT

Although most empirical work has focused on how shifts in resource or habitat use may dictate shifts in reproductive characters (e.g., Boughman 2001; Podos 2001; Huber and Podos 2006; Boughman 2007), the reverse scenario could unfold. The evolution of reproductive characters stemming from selection to minimize reproductive interference could also cause divergence in traits associated with resource acquisition (Konuma and Chiba 2007). If, for example, species segregate in space or time to avoid reproductive interactions, they may be concomitantly exposed to novel, underutilized resources, thereby possibly leading to a shift in traits associated with resource use.

Moreover, mate preferences to avoid interactions with heterospecifics may promote the evolution of traits involved in the production of those signals (e.g., body size, beak morphology), which could, in turn, cause a shift in resource use and associated traits (Konuma and Chiba 2007). In the anole example above, for instance, the evolutionary chain of events is unclear. Although habitat partitioning in different light environments may have fostered the evolution of sexual signals that resulted in reproductive trait divergence, the converse

also could have occurred. That is, reproductive interactions may have generated divergence in perception and signaling that, in turn, fostered habitat and resource partitioning (Leal and Fleishman 2002).

TEASING APART REPRODUCTIVE AND ECOLOGICAL CHARACTER DISPLACEMENT: CAVEATS

As we have discussed, reproductive and ecological character displacement can promote each other. However, correlated evolution in either sexual signals or resource acquisition traits in response to direct selection on the alternative type of trait does not constitute character displacement (Coyne and Orr 2004). For example, the correlated evolution of sexual signals in response to selection to minimize resource competition would not represent reproductive character displacement, *per se*; divergence in reproductive traits would only constitute reproductive character displacement if these traits also become the targets of selection to minimize reproductive interactions. Caution must therefore be exercised when studying character displacement in systems that display divergence in both reproductive and resource-use traits (Rundle and Schluter 1998; Coyne and Orr 2004).

Nevertheless, two species that are similar enough to compete for resources will also likely utilize similar habitat for mate acquisition (Schluter 2000; Rundle and Schluter 2004; Grant and Grant 2008; Price 2008). Thus, initial changes to resource-use traits or sexual signals brought about by one form of character displacement will also fuel the alternate form of character displacement, if these differences are subsequently maintained or enhanced by selection to minimize interspecific interactions. As ecological and reproductive character displacement become intertwined, the degree to which one leads to the other may become obscured (Schluter 2000). Studies specifically aimed at delineating the relative contribution of each process are needed in order to determine if both types of character displacement are occurring in

a given system (e.g., Rundle and Schluter 1998).

Finally, although we have focused on how reproductive and ecological character displacement might reinforce each other, each process can potentially preclude the other from occurring. The inhibition of one process by the other may be especially likely when either process generates habitat partitioning, either spatially or temporally. When habitat partitioning arises via one process, selection to minimize interactions via the alternate process is effectively shut down. Essentially, the operation of one process negates the selective pressure for the other process to occur.

CONCLUSIONS

The consensus that has emerged from previous work is that character displacement is taxonomically widespread and that it can act to lessen both competitive and reproductive interactions between species (Howard 1993; Schluter 2000; Servedio and Noor 2003; Coyne and Orr 2004; Dayan and Simberloff 2005; Gröning and Hochkirch 2008). Having established that character displacement occurs, researchers can now move on to sorting out which factors facilitate it. Because character displacement can drive speciation and adaptive radiations (Schluter 2000; Grant and Grant 2008), understanding which species are especially prone to undergoing character displacement may help explain why some taxonomic groups are more diverse than others. Understanding when charac-

ter displacement proceeds—and when it does not—may therefore reveal how microevolutionary processes generate macroevolutionary patterns of diversity.

Similarly, by understanding how and when character displacement is likely to occur, we may gain insights into patterns of species coexistence, community diversity, and potentially large-scale patterns of species distribution. Character displacement necessarily mediates species coexistence (Losos 2000), and it has the further potential to alter population dynamics, extinction risk, and, concomitantly, species ranges (Brown 1995; Thompson 2005; Gröning and Hochkirch 2008). Studying character displacement can, therefore, potentially reveal how the fitness consequences of interactions between species ultimately translate into macroecological patterns of species richness, distributions, and diversity. Thus, the process of character displacement, by which individuals optimize fitness in response to heterospecifics, provides a unifying framework for understanding the origins, abundance, and distribution of biodiversity.

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