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Issue: *The Year in Evolutionary Biology***Development and evolution of character displacement**

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Character displacement occurs when competition for either resources or successful reproduction imposes divergent selection on interacting species, causing divergence in traits associated with resource use or reproduction. Here, we describe how character displacement can be mediated either by genetically canalized changes (i.e., changes that reflect allelic or genotype frequency changes) or by phenotypic plasticity. We also discuss how these two mechanisms influence the tempo of character displacement. Specifically, we suggest that, under some conditions, character displacement mediated by phenotypic plasticity might occur more rapidly than that mediated by genetically canalized changes. Finally, we describe how these two mechanisms may act together and determine character displacement's mode, such that it proceeds through an initial phase in which trait divergence is environmentally induced to a later phase in which divergence becomes genetically canalized. This plasticity-first hypothesis predicts that character displacement should be generally mediated by ancestral plasticity and that it will arise similarly in multiple, independently evolving populations. We conclude by highlighting future directions for research that would test these predictions.

**Keywords:** adaptive divergence; competition; ecological developmental biology; genetic assimilation; genetics of adaptation; phenotypic plasticity

*Imagine a case in which two such species have been squeezed together in the same communities long enough for evolution to occur. When they first came into contact, they were elastic and could diverge in their habits enough to lessen competition. The differences were phenotypic, the result of environment and not genes. The compression occurred in traits that were relatively easy to change, most likely by a retreat from parts of the habitat and diet by one or both of the species. As the generations passed, genetic differences arose and hardened the distinction between the two species (Wilson, p. 174).<sup>1</sup>*

**Introduction**

Among evolutionary biology's most persistent challenges is to explain the origins of biodiversity. Darwin's<sup>2</sup> proposed solution to this problem was his "principle of divergence of character." According to this principle, all organisms face recurring competition for scarce resources, and this competition favors individuals that are least like their competitors

in resource use and associated traits. In other words, Darwin posited that competition is a primary agent of adaptive trait evolution. Moreover, Darwin argued that groups of organisms that compete should become increasingly dissimilar over time, possibly even transforming into separate species. Thus, selection deriving from competition, Darwin<sup>2</sup> held, is the primary engine of diversification.

Abundant evidence now indicates that such competition-induced selection can indeed promote adaptive—and divergent—trait evolution through an evolutionary process now known as *character displacement*.<sup>3–6</sup> Moreover, researchers have come to recognize that character displacement can be driven by not only resource competition (as Darwin proposed), but also by costly reproductive interactions, such as when different species hybridize or compete for reproductive trait space used in attracting mates.<sup>3,4,7</sup> Character displacement therefore assumes two forms: "ecological character displacement,"<sup>8,9</sup> which stems from resource competition, and "reproductive character displacement,"<sup>10</sup>

which stems from deleterious reproductive interactions. Both ecological and reproductive character displacement derive from selection stemming from any direct or indirect interactions between organisms that reduce each individual's access to either resources or successful reproductive opportunities and is therefore deleterious (on average) to all parties.<sup>11,12</sup> Because our arguments throughout this paper apply equally to either process, we do not treat ecological and reproductive character displacement separately here. Moreover, for the purposes of this paper, "competition" refers to either costly reproductive interactions or competition for resources.<sup>13</sup>

Because of its diversifying nature, character displacement is thought to play a vital role in the origins, maintenance, abundance, and distribution of biodiversity.<sup>5,6,13,14</sup> Yet, previous research has focused primarily on when or whether character displacement occurs.<sup>5–7</sup> By contrast, relatively little work has explored the proximate mechanisms of character displacement,<sup>13,14</sup> although this is changing. With the advent of new technology and approaches, investigators have more opportunities than ever to identify the genetic and developmental basis of character displacement in a greater diversity of systems.

Our goal in this paper is to examine the proximate mechanisms that underpin character displacement; discuss how these mechanism influence character displacement's speed; and evaluate how these alternative mechanisms interact and affect the means by which character displacement transpires. We focus specifically on contrasting genetically canalized trait evolution versus the expression and evolution of plasticity in mediating character displacement.

Before proceeding, however, we must make an important point. In particular, character displacement, by its nature, is a form of adaptive evolution. The mechanisms that underpin character displacement therefore do not differ from other forms of adaptive trait evolution. We do not intend to suggest otherwise in this paper, and in that sense, character displacement is not "special." Much of what we outline below applies to any other form of adaptive evolution and could be similarly applied to other contexts. What then is the need for understanding the proximate bases of character displacement *per se*?

Our answer to this question is twofold. First, the study of character displacement provides an ideal

context in which to study both the nature of adaptive evolution and its role in diversification.<sup>5,13,14</sup> Indeed, insights gained from the study of character displacement can contribute to the understanding of adaptive evolution more broadly. Yet, other types of interactions (e.g., predation<sup>15</sup> or parasitism<sup>16</sup>) are similarly suited for studying adaptive trait evolution. Nevertheless, such interactions are not generally expected to drive diversification in the same way that character displacement does. Indeed, as Darwin<sup>2</sup> first held, competitively mediated selection acts as a "wedge" that should continually drive interacting species apart within their respective communities. Thus, although adaptive evolution can be studied in other contexts, the study of character displacement provides powerful opportunities for relating adaptive evolution to diversification.

Second, whether or not character displacement arises can dictate a population's persistence. Unlike other forms of trait evolution where populations may persist in suboptimal states, the absence of character displacement can actually result in the local extinction of one species by another, specifically, via competitive exclusion<sup>17,18</sup> or reproductive exclusion.<sup>19,20</sup> In this paper, we suggest that alternative proximate mechanisms may actually be more or less likely to promote character displacement. If different mechanisms can influence the nature of character displacement, as well as whether or not it even occurs in the first place,<sup>13,14</sup> identifying these proximate mechanisms becomes crucial for evaluating when and why character displacement occurs. Thus, in contrast with other forms of adaptive trait evolution, where proximate mechanisms can be treated as a "black box" (i.e., the particular form of mechanism generating a trait may be interesting in its own right, but does not necessarily affect whether or not adaptive evolution occurs), a full understanding of character displacement's role in evolutionary diversification may ultimately rest on identifying its underlying mechanisms.

### Proximate mechanisms of character displacement

Character displacement arises when species come to differ from one another in traits associated with resource use or reproduction.<sup>8,21–25</sup> At the mechanistic level, how does such divergence arise?

Generally, the focus in character displacement has been on genetic differentiation between interacting

species and, within each such species, between populations in sympatry and allopatry with the other species.<sup>13</sup> Specifically, most research presumes that divergence is mediated exclusively by genetically canalized changes (i.e., divergence that reflects allelic or genotype frequency changes). This focus on genetic differentiation has seemingly arisen, in part, for two reasons. First, models of character displacement generally assume specific genetic architectures (e.g., single locus vs. multilocus)<sup>8,21</sup> and genetic processes (e.g., mutation, gene flow).<sup>24,26</sup> Empirical tests of the predictions of such alternative genetic models necessarily require investigations of the genetic basis of character displacement (see below for more detail). Second, a focus on genetic differentiation has also emerged because, among the widely accepted criteria used to define character displacement, is the requirement that putative cases of character displacement should reflect genetic differentiation of populations and species.<sup>4,23,27–30</sup>

Although genetically canalized traits have largely been the focus of proximate studies of character displacement, Wilson's<sup>1</sup> quote at the beginning of this paper highlights an alternative mechanism that can underpin displacement: namely, phenotypic plasticity. In the context of character displacement, plasticity is manifest as competitively mediated trait expression (i.e., trait expression that varies depending on the presence of competition). Although not generally considered in the theory of character displacement (except in models involving learning and cultural transmission<sup>31</sup>), plasticity can effectively generate trait divergence between species and thereby serve as an additional axis of variation on which selection can act to promote the evolution of traits that minimize competitive interactions between species. Indeed, because many populations exhibit heritable variation in whether and how individuals respond through environmentally induced change,<sup>32,33</sup> plasticity can itself evolve,<sup>34–36</sup> and plastic traits can therefore satisfy the criteria for demonstrating character displacement.<sup>37,38</sup> Thus, as we describe in greater detail later, evolved environmentally induced niche shifts can constitute character displacement.

Note, however, that genetic canalization and plasticity are not mutually exclusive mechanisms of trait production. Instead, these two proximate mechanisms are best thought of as occupying different positions along a continuum of environmental in-

fluences on trait production,<sup>39</sup> with strict genetic control of trait variation at one end of the continuum and with pure environmental induction of trait variation at the opposite end. In reality, most traits have both genetic and environmental components.<sup>40</sup> Moreover, plasticity in one or more traits is often required to hold another trait constant in the face of changing environmental conditions (thereby maintaining homeostasis),<sup>41</sup> further demonstrating the interdependence of these two influences on development.

Perhaps more importantly, these two proximate mechanisms are often evolutionarily interchangeable,<sup>42</sup> meaning that selection can slide trait regulation anywhere along this continuum.<sup>39,41,42</sup> Specifically, when genetic variation for the degree of environmental influence is present, then selection can act on this variation to promote the evolution of either increased or decreased environmental sensitivity.<sup>42</sup> If selection eliminates all environmental influences (i.e., if “genetic assimilation”<sup>43,44</sup> occurs), the end result is a genetically canalized trait (note that selection can also promote “epigenetic assimilation,” wherein trait expression becomes less sensitive to environmental influences due to inherited environmental effects,<sup>45</sup> such as a maternal effect,<sup>46</sup> cultural transmission,<sup>47</sup> or parasite transmission<sup>48</sup>).

With genetic assimilation, the evolution of a new trait does not require the emergence of new genes or new gene complexes; instead, selection acts on existing genetic architecture and epigenetic interaction.<sup>32,49,50</sup> In other words, a plastic trait can be converted into a canalized trait (or, alternatively, it can be converted into a trait that shows enhanced plasticity) through evolutionary adjustments in the regulation of trait expression. Experiments have demonstrated such evolutionary shifts in the degree to which populations are sensitive to environmental influences,<sup>34</sup> including the complete loss of plasticity,<sup>44</sup> and numerous examples of evolution by natural selection might be explained by genetic assimilation.<sup>42,51–53</sup>

Genetic assimilation might be a more common mechanism of character displacement than has been heretofore appreciated.<sup>39</sup> We will focus on the potential role of genetic assimilation in character displacement later in this paper. Before we do so, however, we briefly review separately the evidence for genetically canalized traits in character displacement and plasticity, respectively.

### Genetic mechanisms of divergence

Competitively mediated selection is expected to target genes that influence the expression of phenotypes involved in resource use or reproduction. Although relatively few studies have thus far identified these selective targets, the studies that have been conducted to date suggest that a diversity of genetic mechanisms can mediate character displacement. Four such mechanisms are briefly reviewed below.

First, character displacement might arise via a “single-allele mechanism.”<sup>54–56</sup> With such a mechanism, divergence arises between interacting species because the same allele in both species enhances existing differences between them. An allele that enhances sensory sensitivity to male sexual signals, for example, might render females better at identifying conspecific males and thereby promote reproductive character displacement. For instance, in fruit flies, *Drosophila pseudoobscura* and *D. persimilis*, a single allele potentially mediates species recognition.<sup>57</sup> Females of both species from sympatric populations exhibit greater discrimination against heterospecifics compared to females from allopatric populations.<sup>58</sup> This discrimination ability in both species appears to be at least partly mediated by a single allele at the *Coy-2* chromosomal region that enhances discrimination against heterospecifics (likely by influencing a female’s ability to detect species-specific olfactory cues).<sup>57,59</sup> Although additional mechanisms might also be involved in mate discrimination in these flies,<sup>59,60</sup> this system illustrates how costly reproductive interactions between species can be reduced by a single allele shared by both species.

Single-allele mechanisms may mediate ecological character displacement as well. Enhanced sensory sensitivity might also refine preexisting food preferences within different species and thereby reduce overlap between them in resource use. Moreover, a single allele might reduce dispersal tendencies, which could exaggerate differences between species in habitat use and thereby preclude interactions between them. Such possibilities will remain speculative, however, until more is known regarding the proximate mechanisms underlying traits that are involved in minimizing resource competition between species.

A second, slightly more complex mechanism—but one still involving a single locus—entails alternative alleles at a locus between the interacting

species that specifies divergent resource-use or reproductive traits. Such allelic differentiation at a single locus might suffice to reduce competitive or reproductive interactions between species. For example, passion-vine butterflies (genus *Heliconius*) show great diversity in wing color patterns. This genus has undergone rapid speciation,<sup>61</sup> but many of its constituent species have also converged in wing color pattern owing to Müllerian mimicry.<sup>62,63</sup> However, for species that use wing coloration in mate choice (such as *H. cydno* and *H. pachinus*, where males use wing color to discriminate conspecific from heterospecific mates<sup>64</sup>), such convergence in wing color pattern increases the risk of hybridization.<sup>65</sup> Thus, interacting species are expected to undergo reproductive character displacement as a means of reducing such costly interactions. Recent research suggests that a single locus might encode both mate preference and wing coloration.<sup>64</sup> Because pigments involved in wing coloration also occur in the eye (and affect perception of wing coloration),<sup>64</sup> a single gene affects both coloration and perception of—and preference for—that coloration.<sup>66</sup> Therefore, species that possess alternative alleles at a single locus can diverge in traits such as sexual signaling and mate choice that mediate character displacement. If that locus has pleiotropic effects, as in *Heliconius* butterflies, then divergence in multiple traits can arise simultaneously.

In contrast to mechanisms (such as those above) that depend either on a single allele or on alternative alleles at a single locus (with or without pleiotropy), a third mechanism arises when character displacement is under the control of multiple, divergent loci. A possible example comes from pied flycatchers (*Ficedula hypoleuca*) and collared flycatchers (*F. albicollis*), which have undergone reinforcement of female preferences and male coloration.<sup>67</sup> Such divergence appears to be mediated by multiple, divergent loci.<sup>68</sup> Similarly, character displacement between benthic and limnetic species of stickleback fish (*Gasterosteus aculeatus* complex<sup>27</sup>) involves multiple traits that appear to be encoded by numerous loci: F<sub>1</sub> hybrids are intermediate in morphology between the two parent species, and these differences persist over multiple generations in a common laboratory environment.<sup>69–72</sup>

At present, it is unclear how commonly character displacement arises through the different

mechanisms above. Theoretical models suggest that character displacement (reproductive character displacement or reinforcement, in particular) will be more likely to arise under a one-allele mechanism than a two-allele mechanism.<sup>55</sup> However, other models suggest that character displacement can also arise when mediated by multiple loci.<sup>21,22</sup>

Given that character displacement typically entails complex suites of traits,<sup>73,74</sup> one might expect that competitively mediated selection would target multiple loci. Nevertheless, a key (theoretical and empirical) challenge has been to explain how such a mechanism would persist in the face of recombination, which would tend to break up coadapted gene complexes that encode species differences.<sup>75,76</sup> This is particularly problematic in species that exchange genes (as has been documented in species that have undergone character displacement, including sticklebacks,<sup>77</sup> spadefoot toads,<sup>78</sup> Darwin's finches,<sup>79</sup> and nightingales<sup>80</sup>), because hybridization tends to "scramble" allelic combinations at loci that isolate species. One possibility is that the loci encoding species differences might reside in areas that are protected from recombination,<sup>75,76,81,82</sup> such as inside chromosomal inversions,<sup>81</sup> near the chromosome's centromere,<sup>82</sup> or on sex chromosomes.<sup>67</sup>

In the three previous mechanisms (i.e., single-allele, multiple alleles at a single-locus, and multiple-loci mechanisms), the genes involved in mediating character displacement encode for proteins that produce the trait(s) that undergo divergence (e.g., cuticular hydrocarbons used in mate recognition in fruit flies; color pigments in butterflies). In other words, character displacement involves changes in the protein-encoding regions of the genome. Yet, differences in protein-coding sequences are not the only means by which species could become differentiated.<sup>83–88</sup> Instead, species might diverge in cis-regulatory (noncoding) regions that are involved in resource use or reproduction. Thus, a fourth mechanism involves divergence in regions of the genome that regulate the expression of the genes that encode for displaced traits between species.

A putative example comes from Darwin's finches, which have undergone both ecological and reproductive character displacement in the size and shape of their beaks<sup>89,90</sup> (the size and shape of an individ-

ual's beak determines not only which resources it can use,<sup>89</sup> it can also affect the production of male song, which is used in territorial defense and mate attraction).<sup>91</sup>

Recent studies of how bird beaks form developmentally point to the possible genetic targets of divergent selection in this system. Beak development is influenced by several genes that encode a series of signaling molecules, including fibroblast growth factor 8 (*Fgf8*) and sonic hedgehog (*Shh*). These two gene products influence the expression of a third signaling molecule, bone morphogenetic protein 4 (*Bmp4*), which governs differences between species in beak depth.<sup>92,93</sup> These two gene products also affect the expression of the gene calmodulin (*CaM*), which encodes for a calcium-binding protein involved in apoptosis that influences beak length.<sup>93</sup>

Although any one of these four genes could conceivably serve as a target of selection during character displacement, these genes are also involved in several crucial metabolic processes (e.g., *CaM* is involved in numerous, vital cellular processes). Thus, any changes in these genes would likely have deleterious consequences. Consequently, it is unlikely that selection would favor alternative alleles at these genes in different species and populations. Instead, character displacement has likely occurred when selection brought about changes in the regulation of these genes.<sup>89</sup>

Regulatory mutations are similarly thought to be involved in competitively induced divergence in pheromones (specifically, cuticular hydrocarbons) that are used in mate choice in the *Drosophila serrata* complex.<sup>94</sup> Such regulatory mutations have also been implicated in mediating reproductive character displacement (specifically, floral-color divergence) in the Texas wildflower, *Phlox drummondii*.<sup>95</sup> Although the role of regulatory mutations during adaptation remains controversial,<sup>96,97</sup> such mutations are increasingly viewed as being important during adaptive population divergence.<sup>88,98</sup>

In sum, studies of the genetic targets of competitively mediated selection have revealed a diversity of genetic mechanisms, which appear to differ in the degree to which they facilitate character displacement. However, we still do not know whether one mechanism is more prevalent than the others in mediating character displacement. Although putative examples exist for each mechanism, additional

work across a diversity of systems is critically needed to determine whether some genetic mechanisms are more likely to underpin character displacement than others as predicted by theory.<sup>55</sup> In the next section, we consider an alternative mechanism that might be effective at mediating character displacement: phenotypic plasticity.

### *Mechanisms of environmentally induced divergence*

In contrast to reflecting genetically canalized differences, divergent traits might alternatively arise through phenotypic plasticity. Specifically, rather than being produced constitutively (as with the genetic mechanisms described earlier), divergent traits might be expressed facultatively, such that they are produced in an individual only when it experiences competition from a heterospecific (e.g., see Fig. 1). Although relatively few studies have explicitly considered plasticity's role in character displacement (notwithstanding Wilson's<sup>1</sup> quote at the outset of this paper), such environmentally contingent niche shifts may play an underappreciated role in mediating character displacement.<sup>13,14,99</sup> Here we discuss two different mechanisms by which plasticity may promote character displacement. Before we do so, we begin with a caveat.

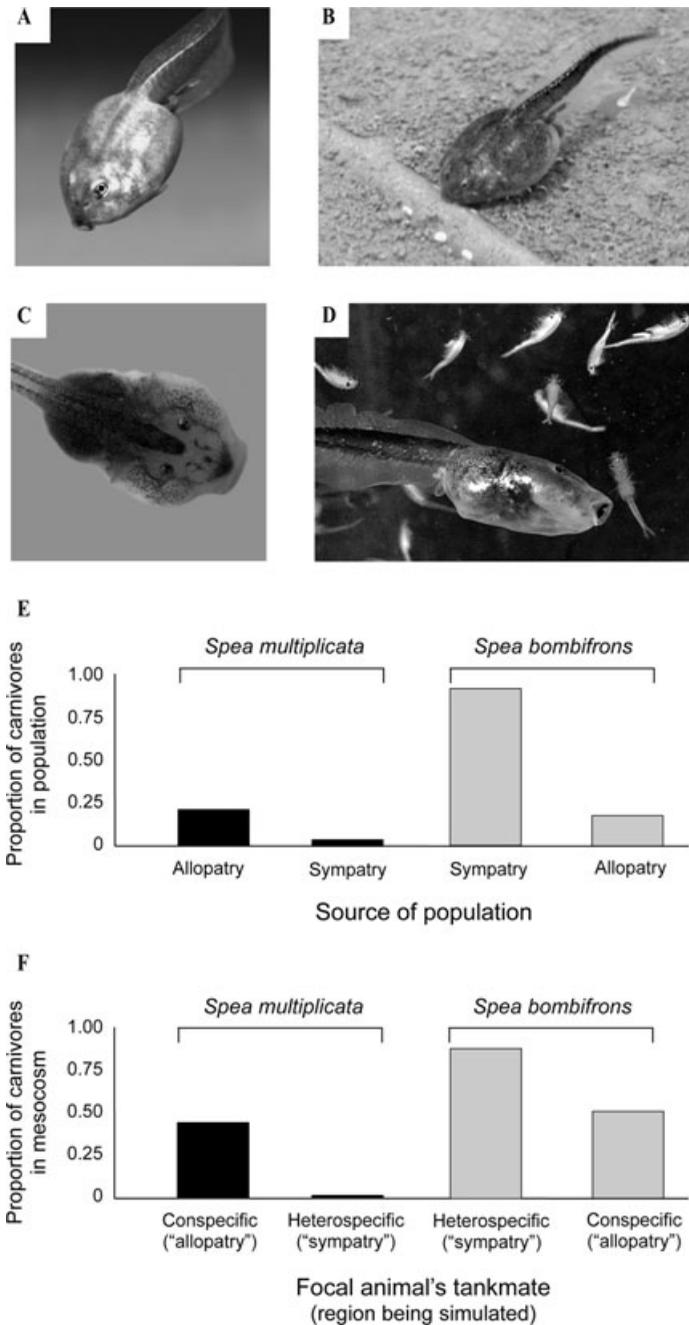
In particular, competitively mediated plasticity may or may not constitute character displacement.<sup>37,38</sup> Character displacement is defined as trait evolution that arises as an adaptive response to resource competition or deleterious reproductive interactions between species.<sup>4,5,9,13,14,100</sup> Competitively mediated plasticity therefore constitutes character displacement only when it has actually evolved in direct response to competitively mediated selection and when it lessens competitive interactions between heterospecifics.

Even when environmentally induced traits have not themselves undergone character displacement, they can still be critical to the process. Specifically, lineages that respond to heterospecific competitors through facultative adjustments in their phenotype may be less likely to go extinct via competitive or reproductive exclusion. Indeed, plasticity is increasingly viewed playing a critical role in shielding populations from extinction when confronted with changing environments.<sup>39,101,102</sup> In the context of competitive interactions, plasticity might enable individuals to produce resource-use or reproduc-

tive phenotypes that are less like the phenotypes expressed by their competitors. In this way, competitively mediated plasticity might provide a mechanism for reducing the frequency and intensity of competitive interactions. Thus, even in the absence of character displacement, plasticity may promote species coexistence through resource partitioning<sup>103</sup> or reproductive partitioning. Such a process could serve to promote developmentally mediated species sorting, in which species express different phenotypes at contact, but not owing to preexisting canalized differences.<sup>104,105</sup>

Many organisms appear to possess the ability to respond to heterospecifics through facultative adjustments of their phenotype.<sup>42,103,106–109</sup> For example, when confronted with a heterospecific competitor, the individual members of many species of plants facultatively express traits that reduce interspecific competition, such as altering the spatial positioning of their roots,<sup>110–113</sup> modifying the width of their leaves,<sup>114</sup> or adjusting their physiology.<sup>115</sup> Similarly, when faced with a heterospecific competitor, many species of fish<sup>109</sup> and amphibians<sup>37,38</sup> facultatively express resource-use morphologies that differ from those expressed by the heterospecific. Some species can even facultatively adjust their mate preferences in the presence of heterospecifics, thereby reducing costly reproductive interactions between species.<sup>116</sup> Of such cases, several systems have illustrated that plasticity does mediate character displacement,<sup>37,38,99,109,117,118</sup> via two different mechanisms.

First, plasticity may underlie character displacement when competitively mediated selection leads to the evolution of a reaction norm that minimizes competitive interactions. Under this mechanism, selection acts on underlying heritable variation in either the tendency to respond to competitors in the first place or the manner in which individuals express these responses (or both) in propelling competitively mediated trait evolution (i.e., character displacement). Such evolved shifts in environmentally induced resource-use or reproductive traits can satisfy the widely accepted criteria for demonstrating character displacement.<sup>37</sup> In particular, experiments have demonstrated that these induced shifts are indeed caused by the presence of a heterospecific competitor *per se* (Fig. 1) and that they lessen costly interactions with the heterospecific that induces them.<sup>37,116</sup> Furthermore,



**Figure 1.** An experimental demonstration of how phenotypic plasticity might mediate ecological character displacement. Spadefoot toad tadpoles (*Spea multiplicata* and *S. bombifrons*) typically occur as (A) an omnivore morph, (B) which specializes on plant material and detritus, and (C) a morphologically distinctive carnivore morph, (D) which specializes on, and is induced by, anostracan fairy shrimp. (E) In allopatric populations, each species produces similar, intermediate frequencies of both morphs. However, in sympatry, *S. multiplicata* shift to producing mostly omnivores, whereas *S. bombifrons* shift to producing mostly carnivores; that is, these two species have undergone character displacement in morph production. (F) Similar niche shifts can be experimentally recreated in the lab. When allopatric individuals are reared with a single conspecific and fed limited amounts of both shrimp and detritus, they produced similar proportions of both morphs (as in natural allopatric populations; see panel E). By contrast, when the two species are experimentally combined, *S. multiplicata* shift to producing mostly omnivores, whereas *S. bombifrons* shift to producing mostly carnivores (as in natural sympatric populations). These facultative niche shifts appear to reflect differences between species in ability to capture and consume shrimp, an environmental cue that induces carnivores.

experimentally induced shifts often mirror, in magnitude and direction, the fixed phenotypic differences between naturally occurring sympatric and allopatric populations (e.g., see Fig. 1). Finally, facultative shifts have been shown to evolve in sympatry versus allopatry.<sup>38,116</sup>

A second general mechanism by which plasticity may promote character displacement is when it is transmitted reliably across generations and thereby forms the basis of an alternative inheritance system on which adaptive evolution can unfold. There are two types of transgenerational plasticity that may be important in mediating character displacement. The first are maternal effects, which occur when a female's phenotype influences her offspring's phenotype, independent of the direct effects of her coding sequences on her offspring's phenotype.<sup>46,119–123</sup> Because they can be induced by interspecific competition,<sup>117,120</sup> mediate adaptive phenotypic change,<sup>46,121,122,124,125</sup> and be transmitted reliably across generations,<sup>126</sup> maternal effects might play an underappreciated role in promoting character displacement.<sup>117</sup> A second form of transgenerational plasticity is cultural inheritance, mediated by learning. In many animals, for example, preference for conspecific mates is learned.<sup>89,127,128</sup> Likewise, many animal species learn to use new food resources.<sup>129,130</sup> Once a population acquires such learned mate or food preferences, these preferences can be transmitted across generations and even reinforce differences between species, thereby mediating ecological or reproductive character displacement.<sup>127,130</sup> Such a situation is illustrated in Darwin's finches, where learning played a crucial role in mediating reproductive character displacement.<sup>127</sup>

In sum, plasticity may play a role in mediating character displacement. However, more empirical and theoretical work is needed to determine whether and how each of the above mechanisms contributes to character displacement. For the remainder of the paper, we consider some ways in which plasticity may play an important role in character displacement. In particular, we contrast plasticity and genetic canalization in terms of their effects on the rapidity with which character displacement can occur. Although the two mechanisms are by no means mutually exclusive, they differ in important ways that can ultimately affect when and how character displacement occurs.

## Tempo and mode of character displacement

As we highlighted in the Introduction, character displacement is a form of adaptive evolution, and the earlier mechanisms are therefore not unique to character displacement. Nevertheless, the mechanisms mediating character displacement may determine when and how it occurs. In this section, we focus on this issue.

We first consider each mechanism's impacts on the speed of character displacement. We do so, because character displacement is a time-limited process. Populations experiencing competition are often at risk of competitive or reproductive exclusion. Therefore, populations that do not respond sufficiently rapidly to the presence of competition risk extinction. Indeed, a meta-analysis by Schluter<sup>5</sup> indicated that some taxa are more likely to undergo character displacement than others. Although such variation may reflect researcher bias in terms of the systems chosen to study character displacement, such a pattern may also indicate that character displacement is more likely to occur in some conditions versus others. One such condition that may be important is the ease and rapidity with which character displacement takes place. Thus, consideration should be given to the differential rate by which genetically canalized versus plastic traits are likely to evolve, in addition to the other conditions that appear to facilitate character displacement (e.g., strong selection, certain genetic architectures, and initial trait differences).<sup>21,25,131,132</sup> Such differences in the speed of evolution for these different proximate mechanisms could therefore explain when character displacement is more—or less—likely to occur.

### *Why proximate mechanisms likely differ in speed of divergence*

A key factor that determines the speed of character displacement is the amount of standing variation in the trait(s) under divergent selection.<sup>21,131,132</sup> When abundant standing variation is present in a population that encounters a heterospecific competitor, competitively mediated selection could act on this variation, filtering out those variants that are the most similar to the heterospecific competitor and preserving those that are most dissimilar. This process fuels character displacement,<sup>13,132</sup> and, if standing variation is abundant and selection is

strong, then the rate of such an evolutionary response could be rapid in that it could transpire in a handful of generations (Darwin's finches provide a possible example of such rapid evolution<sup>133</sup>).

When standing variation is depleted (or is initially absent), however, character displacement, like any other form of adaptive evolution, may be precluded.<sup>5,132,134</sup> In particular, for character displacement to proceed, new variants must be introduced into the population. If divergence depends entirely on genetically canalized differences, new variants must be introduced into the population via mutation, recombination, or gene flow from another conspecific population or another species (through hybridization).

All three of the above means of acquiring new variants are likely to either transpire relatively slowly or, ironically, simultaneously counteract character displacement even as they provide the raw material necessary for character displacement to proceed. For example, the waiting time for favorable, new mutations to arise and spread in a population can take many generations.<sup>135</sup> Indeed, many genetic models of character displacement predict that the pace of evolution will be slow, especially during the early phase of divergence.<sup>21,22</sup> Yet, if character displacement transpires slowly, the risk of competitive or reproductive exclusion increases.<sup>13</sup> Moreover, although recombination and gene flow can potentially introduce favorable, new genetic variants into a population more quickly than does mutation, these processes will typically affect only a few individuals in any given generation. Perhaps more critically, theory has shown that high rates of gene flow and recombination actually reduce a population's ability to respond to competitors, because maladaptive gene combinations over time swamp adaptive combinations.<sup>26</sup> Thus, even though variants might be introduced that are favored by competitively mediated selection, the population may continue to receive an influx of gene combinations that ultimately prevent local adaptive to competition.

By contrast, divergence driven by phenotypic plasticity might promote a rapid adaptive response to competitors, for at least three reasons. First, an important consequence of environmentally induced phenotypes is that their expression can reveal cryptic genetic variation—genetic variation that is normally not visible as phenotypic variation.<sup>136</sup> Indeed, hidden reaction norms (variation that is pheno-

typically expressed only after an organism experiences changes in environmental conditions) may store an evolutionarily significant pool of cryptic genetic variation upon which selection may act.<sup>33</sup> Therefore, with plasticity, abundant standing variation (which could fuel divergent trait evolution) can be released and exposed to selection as soon as a population experiences competition.<sup>33,137</sup> Essentially, the waiting time between when a population begins to experience competitively mediated selection and when it begins to express variation on which selection can act to produce an adaptive response to competitors is negligible—the process by which new variants are produced occurs over developmental time or over the course of an individual's lifetime (as with learning) rather than over generations.

Second, environmentally induced changes typically occur in numerous individuals simultaneously<sup>42</sup> (especially when a population experiences exploitative competition). This situation contrasts markedly with a mechanism in which the production of new divergent traits requires the introduction of new genetic variants, which typically arise in just a few, or even just one, individual (see above). Moreover, because individuals often differ in whether and how they respond to an environmental cue (such as the presence of a heterospecific competitor), this variation increases the likelihood and speed of an evolutionary response. Although this line of argument has been developed most prominently by West-Eberhard<sup>42,108,138,139</sup> to explain rapid adaptive evolution generally, the application of these ideas to the realm of character displacement could be fruitful, because it potentially broadens the conditions under which character displacement is predicted to occur.

A third reason why plasticity might mediate rapid character displacement is that the ability to respond to competition through plasticity may already exist in a given population, having evolved as an adaptive response to intraspecific competition. For example, forms of plasticity present within species that may mediate character displacement between species include phytochrome-mediated shade-avoidance responses in plants,<sup>114</sup> resource polymorphism in many species of fish and amphibians,<sup>140</sup> and mating polymorphism in many invertebrate and vertebrate species.<sup>141,142</sup> Note that, in some populations, intraspecific competition may also

favor genetically canalized variation, such as a genetic polymorphism,<sup>143,144</sup> on which competitively mediated selection can act. However, unless this constitutively expressed variation is maintained in a population by selection, it is at risk of being lost over time. By contrast, with environmental induction, unexpressed (cryptic) genetic variation can be “protected” from selection or chance loss until it is released by a change in the environment.<sup>33</sup>

The presence of preexisting plasticity (and underlying cryptic genetic variation) is important, because as noted in the Introduction, the evolution of a new divergent trait (such as an alternative morphology or behavior that reduces competitive interactions with a heterospecific) need not require new genes or new gene complexes. Instead, selection can repurpose existing genetic pathways and developmental mechanisms and thereby drive rapid, divergent trait evolution. In the context of character displacement, if a population has already evolved the ability to respond to intraspecific competition via environmentally induced changes, the same mechanisms involved in such a response might be co-opted to mediate adaptive divergence between heterospecific competitors (i.e., character displacement). Indeed, empirical data exist (described later) to suggest that intraspecific variation generated by plasticity might form the basis for interspecific variation during character displacement. Essentially, preexisting plasticity (and the underlying developmental mechanisms) might enable character displacement to evolve rapidly along lines of least resistance.<sup>145</sup>

Above, we contrasted the speed with which character displacement arises via genetic canalization versus competitively mediated plasticity. However, as noted earlier, these alternative proximate mechanisms of character displacement are not mutually exclusive and will potentially evolve in concert. Yet, because of the difference in speed with which they can occur, plasticity may initially underpin competitively mediated divergence, with genetic canalization evolving subsequently.<sup>1,118</sup> We describe how this sequence of events might unfold in the next section.

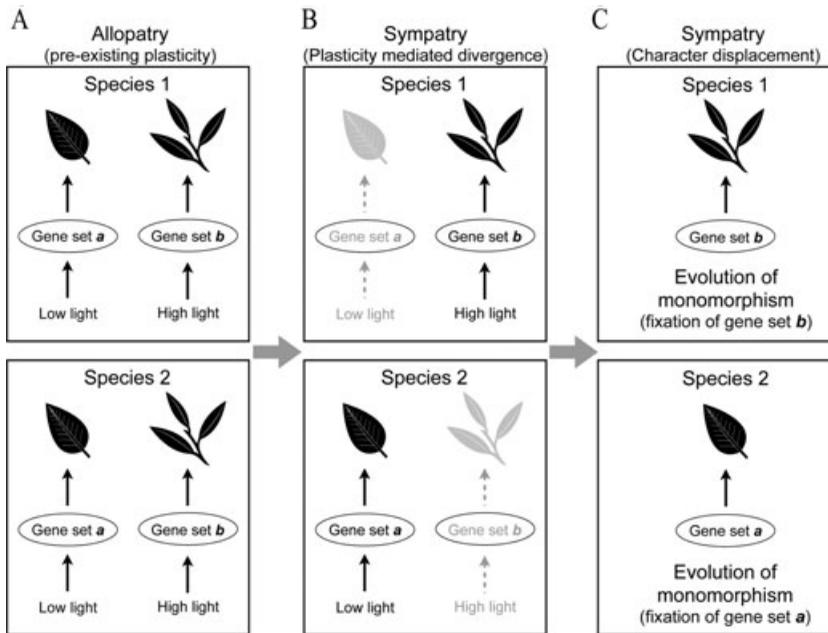
### *Evolution of character displacement: plasticity first?*

Evolutionary biologists have long hypothesized that phenotypic plasticity might precede, and even promote, the genetically canalized traits that arise dur-

ing adaptive evolution.<sup>32,39,42,44,53,138,146–152</sup> This “plasticity-first” hypothesis rests on the argument that, if selection acts on quantitative genetic variation regulating the expression of initially environmentally dependent traits, it can lead to the evolution of either enhanced plasticity or, alternatively, even the loss of plasticity, that is, genetic assimilation.<sup>44</sup> Such loss might result as an incidental by-product of selection favoring a single phenotypic trait (or an extreme phenotype in a continuum) to the exclusion of all other phenotypes.<sup>43,44,153</sup> Alternatively, plasticity might be lost when the alleles that underlie it are lost through stochastic processes. In particular, when an environmental change results in one trait rarely being produced in a population (such as when, in the presence of a competitor, an individual fails to produce a resource-use or reproductive trait expressed in the competitor’s absence; Fig. 1), then alleles that regulate expression of this “hidden” phenotype would not be exposed to selection and would therefore be at greater risk of chance loss.<sup>154,155</sup>

That such genetic assimilation could serve as a mechanism of character displacement has not been heretofore generally appreciated,<sup>13,14</sup> despite Wilson’s<sup>1</sup> suggestion, quoted at the outset of the paper. Yet, consider two species that possess preexisting plasticity in resource-use or reproductive phenotypes. Once in sympatry, each species might facultatively express a different subset of the initial phenotypes (Fig. 2). Over time, each species might lose plasticity and become fixed (either through selection or chance) for a different alternative phenotype.<sup>152</sup> Character displacement might begin with an initial phase in which each species evolves the expression of competitively induced plastic phenotypes and then subsequently transition to genetically canalized traits that minimize competitive interactions with the alternate species (Fig. 2).

This plasticity-first hypothesis, of course, is not the only way in which character displacement might evolve—plasticity might not play any role in some species or populations, whereas in other species, plasticity might play a solitary role by mitigating against selection for any further genetically canalized divergence.<sup>156</sup> However, character displacement might be first mediated by plasticity for two reasons. First, those populations that initially express plasticity might be more likely buffered from extinction while genetically canalized



**Figure 2.** How character displacement might evolve from an initial phase in which trait divergence is environmentally induced to one in which divergence is based on genetically canalized differences and thereby becomes expressed constitutively. (A) Initially, two interacting species may express plasticity in resource-use or reproductive phenotypes. In this case, two species of plants facultatively produce different-sized leaves as an adaptive response to different light levels. (B) When they come into sympatry and compete (e.g., for photons), each species may begin to facultatively express a different subset of the initial phenotypes. Here, Species 1 overtops Species 2, thereby gaining increased access to photons, which triggers the facultative production in Species 1 of small leaves only. By contrast, because it is shaded by Species 1, Species 2 facultatively produces larger leaves only (in each case, the expressed phenotype—and underlying genes—are shown in black, whereas the unexpressed one is shown in gray). If individuals within the same population harbor genetic variation in the degree to which they respond to environmental cues, and if these reaction norms evolve in response to competitively mediated selection and thereby minimize competition between species, then such evolved environmentally induced shifts would constitute character displacement. (C) Over time, both species may lose this preexisting plasticity and become fixed for a different alternative phenotype, possibly because of the loss (through selection or chance) of alleles or gene combinations underlying the nonexpressed phenotype. Thus, character displacement might proceed through an initial phase in which trait divergence is environmentally induced to a later phase in which divergence becomes genetically canalized. Essentially, during character displacement, each species may evolve from expressing a wide range of phenotypes to becoming genetically canalized for a narrower range of phenotypes (in this case, as each species evolves from being polymorphic for leaf shape to being monomorphic).

traits evolve that harden the distinction between species.<sup>13,14</sup> When faced with a new, superior competitor, populations lacking the ability to respond through plasticity might simply undergo reproductive or competitive exclusion before canalized differences evolve.<sup>157</sup> Second, even in populations where plasticity successfully minimizes competitive interactions with heterospecifics, genetic canalization of such traits might be favored if plasticity has costs.<sup>158,159</sup>

This plasticity-first hypothesis has two key implications for the way in which character displacement occurs. First, character displacement may not always proceed slowly. As noted previously, although most

models of character displacement predict that divergence will occur slowly, observations of natural populations have revealed that character displacement can proceed rapidly (i.e., within a few generations).<sup>78,133,160–164</sup> This discrepancy between the models and the data may arise, because most models assume that divergence is based on genetically canalized differences, which (as noted earlier) can evolve slowly. If, instead, divergence is mediated by plasticity, then character displacement might generally proceed rapidly. Although such rapid divergence can also be explained in terms of abundant standing genetic variation (see above), the incorporation of plasticity into models of character displacement

could increase the parameter space over which character displacement can occur.

Second, character displacement that is mediated by plasticity and followed by genetic assimilation should generate repeated evolution of the same ecotype (specifically, one that minimizes interspecific competition) in multiple, independently evolving sympatric populations. Such parallel evolution of reproductive or ecological traits among independently evolving sympatric populations that are experiencing similar selective pressures from competition (“parallel character displacement”) has indeed been documented in a number of systems.<sup>165–170</sup> Although the plasticity-first hypothesis does not uniquely predict parallel character displacement (standing variation in genetically canalized traits could respond similarly to the same selective pressures across different populations),<sup>166</sup> if stochastic processes (mutation, recombination) serve as the basis of variation in genetically canalized traits that mediate character displacement, then such parallel evolution becomes less likely: populations will be more likely to evolve different routes in response to competitors. By contrast, with preexisting plasticity, the same sets of phenotypes are repeatedly revealed when individuals in different, independent populations experience similar selective pressures from competition. Thus, the environment might play a critical role in not only exerting parallel selection pressures in different populations, but also in generating parallel distributions of traits on which selection acts.<sup>14,39</sup>

### *Empirical support for the plasticity-first hypothesis*

Several systems in which character displacement has been documented appear to conform to the plasticity-first scenario. Specifically, we highlight research on three systems, in which competitively induced plasticity appears to have preceded the evolution of canalized genetic differences.

The first case comes from stickleback fish (*G. aculeatus* complex). Two species occur together in certain small coastal lakes in southwestern Canada: one expresses a “benthic” phenotype, whereas the other expresses a “limnetic” phenotype.<sup>171</sup> These two species are thought to have arisen following the invasion from the ocean of an ancestral limnetic ecotype into lakes that already contained an

intermediate ecotype. Following this invasion, both ecological and reproductive character displacement resulted in the parallel evolution of a new benthic ecotype within each such lake, which replaced the ancestral, intermediate ecotype.<sup>171</sup>

Recall from above that the phenotypic differences between these benthic and limnetic ecotypes appear to reflect genetically canalized differences. Recent experiments have revealed, however, that diet-induced plasticity is present in marine sticklebacks,<sup>172</sup> which are thought to represent the ancestral colonists.<sup>171</sup> More importantly, this diet-induced plasticity generates phenotypes that resemble the benthic and limnetic ecotypes found in modern-day (derived) freshwater populations.<sup>172</sup> This recent work indicates that trait divergence between ecotypes was initially environmentally induced, but ultimately may have become genetically canalized. Such plasticity in resource-use traits has been similarly detected in dozens of species of freshwater fish,<sup>109,173–175</sup> including in many that have undergone character displacement,<sup>109</sup> indicating that this route to character displacement is likely not unique to sticklebacks.

A second such example comes from two species of North American spadefoot toads (*Spea multiplicata*, *S. bombifrons*), which have undergone ecological character displacement in tadpole trophic morphology.<sup>37,38,99,163,169,176</sup> Where they co-occur, almost all individuals of one species (*S. multiplicata*) develop into an omnivore morph, which feeds mostly on detritus, whereas almost all individuals of the other species (*S. bombifrons*) develop into a distinctive carnivore morph, which specializes on eating anostracan shrimp and other tadpoles (Fig. 1).

The proximate mechanism of character displacement appears to differ for these two species. In *S. multiplicata*, the phenotypic differences between sympatric and nearby allopatric populations appear to reflect a condition-dependent maternal effect.<sup>117</sup> By contrast, in *S. bombifrons*, the phenotypic differences between sympatric and allopatric populations appear to reflect genetically canalized differences.<sup>118</sup>

In allopatric populations (i.e., ancestral, pre-displacement populations), however, both species have the capacity to respond adaptively to the presence of the other species through phenotypic plasticity. Yet, despite the fact that individuals from allopatric populations of both species have the capacity

to produce both carnivores and omnivores,<sup>99,163</sup> when allopatric *S. multiplicata* are experimentally exposed to *S. bombifrons*, they facultatively produce mostly omnivores (Fig. 1F), which is similar to the pattern of morph expression found among *S. multiplicata* in naturally occurring, populations in sympatry (Fig. 1E). Conversely, when allopatric *S. bombifrons* are experimentally exposed to *S. multiplicata*, they facultatively produce mostly carnivores (Fig. 1F), which is similar to the pattern of morph expression found among *S. bombifrons* in naturally occurring, populations in sympatry (Fig. 1E). Finally, phylogenetic analyses have found that sympatry is the derived condition in this system.<sup>169</sup> Thus, experimentally initiated niche shifts in ancestral (allopatric) populations mirror in direction and magnitude the canalized shifts observed in derived (sympatric) populations.

Because plasticity in allopatry is ancestral, these data suggest that character displacement in spadefoots might have evolved from an initial phase in which trait divergence was environmentally induced (as observed in modern-day allopatric populations) to one in which divergence became either developmentally canalized (as in modern-day sympatric populations of *S. multiplicata*, where character displacement is mediated by a maternal effect<sup>117</sup>) or genetically canalized (as in modern-day sympatric populations of *S. bombifrons*, where character displacement appears to be mediated by genetic shifts<sup>118</sup>). Presumably, sympatric populations of these two species differ in the mechanism of character displacement because they differ in the length of time that each has been in sympatry,<sup>118</sup> with sympatric populations of *S. bombifrons* having been in sympatry longer than sympatric populations of *S. multiplicata* (due to a range expansion by *S. bombifrons* into the region where character displacement occurs).<sup>177</sup>

Spadefoots therefore highlight two points: (1) they are consistent with the plasticity-first hypothesis for character displacement; and (2) they show that canalized differences need not be strictly genetic. Regarding the second point, a maternal effect in *S. multiplicata* (a form of transgenerational plasticity<sup>178</sup>) has led to canalized differences between the species in morph production in sympatry. Thus, rather than being genetically canalized, the phe-

notypic differences in *S. multiplicata* appear to be epigenetically canalized. As noted earlier, epigenetic assimilation (such as that mediated by a maternal effect) may be an evolutionary precursor to genetic assimilation (recall from above that sympatric populations of *S. multiplicata* have only recently experienced competitively mediated selection imposed by *S. bombifrons*).

Finally, a third example consistent with the plasticity-first hypothesis for character displacement comes from *Anolis* lizards from the Greater Antilles. When different species occur together, they differ in microhabitat use.<sup>179,180</sup> Specifically, on islands where they are sympatric, different species of *Anolis* occur as different ecomorphs, which partition their habitat in different ways, residing (for example) in tree crowns (crown-giant ecomorph), on trunk/crowns (trunk-crown ecomorph), on the trunk/ground (trunk-ground ecomorph), and on twigs (twig ecomorph).<sup>179,180</sup> Different ecomorphs tend to differ in body size and limb length, and manipulative experiments have revealed that at least two species possess the ability to facultatively change limb length in response to different-diameter perches.<sup>181</sup>

Although species differences in limb length might have evolved (at least partly) through a process of species sorting<sup>105</sup> (in which species differences might have arisen through the differential invasion into a habitat of species that happen to differ, or through the differential extinction of species that happen to be too similar to coexist), some differences also have potentially evolved through character displacement,<sup>105,182</sup> and this process might have begun with environmentally induced niche shifts.<sup>181</sup> This system therefore serves as one in which the plasticity-first hypothesis could be tested more extensively.

In sum, several case studies provide evidence that is consistent with the plasticity-first hypothesis for character displacement. Nevertheless, much more work is needed to assess how general this mechanism is for explaining character displacement. As we discuss in more detail later, additional theoretical and empirical work is needed to fully consider plasticity's role in character displacement, and to determine if competitively mediated plasticity ultimately leads to the sort of genetically canalized traits

described in the section earlier on genetic mechanisms of divergence.

### Conclusions and future directions

Despite character displacement's importance in helping to explain how new species arise, diversify, and coexist,<sup>5,6,13,14</sup> relatively little is known of the proximate mechanisms that mediate character displacement. Indeed, from a proximate perspective, the focus in studies of character displacement has been on understanding how—and what kinds of—genetically canalized differences evolve between populations and species.<sup>5</sup> Yet, increasing evidence suggests that character displacement can alternatively arise through competitively induced phenotypic plasticity.<sup>13,14</sup> It is important to recognize that plasticity can mediate character displacement, because, in some populations and species, plasticity might represent the sole means by which adaptive, divergent traits arise. Perhaps more importantly, from an evolutionary perspective, character displacement might often unfold rapidly as it transitions from an initial phase in which species differences arises through phenotypic plasticity to one in which such divergence is underlain by genetically canalized differences.<sup>118</sup>

With recent theoretical and technical advances, now is a propitious time to both identify the mechanisms of character displacement and critically evaluate how different mechanisms interact during character displacement. Indeed, a number of key questions regarding the proximate basis of character displacement remain unanswered. Here, we highlight five specific questions that promise to provide fruitful avenues for future research.

First, what are the proximate mechanisms of character displacement in diverse taxa? At present, much of what we know comes from studies of relatively few organisms. Additional research on a greater variety of taxa is needed to clarify whether the mechanisms that have already been identified are present in diverse taxa, or whether these mechanisms are unique to the few taxa that have been studied thus far. Generally, there is insufficient data upon which to conclude whether some mechanisms are more prevalent than others.

Second, do different proximate mechanisms generate differences in the ease with which (and, hence, the likelihood that) character displacement occurs? In contrast to genetically canalized differences, shifts

underlain by phenotypic plasticity might generally occur more rapidly and affect many more individuals simultaneously.<sup>42</sup> Consequently, because competitively mediated plasticity buffers populations from extinction via competitive or reproductive exclusion,<sup>157</sup> it might increase the likelihood that character displacement will transpire to completion.<sup>13</sup> Additional theoretical and empirical approaches are required to evaluate these predictions. For example, experimental or comparative studies could be used to determine whether, when confronted with a novel competitor, populations (or species) consisting of more plastic genotypes undergo character displacement more rapidly (and more readily) than those consisting of less plastic genotypes. Indeed, this question would be ideally suited for experimental evolution studies with rapidly evolving organisms, such as microbes.<sup>183,184</sup>

Third, does phenotypic plasticity sometimes impede character displacement? Evolutionary biologists have long argued that phenotypic plasticity can dampen selection for diversification, for two reasons.<sup>156</sup> First, plasticity allows a single genotype to produce multiple phenotypes in response to different environmental (and hence, selective) regimes, and thus genetic alternatives are not required for attaining alternative fitness optima, such as those associated with populations in sympatry with a competitor versus those in allopatry. Second, different genotypes can produce the same phenotype via plastic responses, thereby hiding genetic differences between them from selection. Future theoretical and empirical research should seek to evaluate whether there are conditions under which competitively induced plasticity impedes, rather than facilitates, character displacement. In other words, an organism might be so plastic in its responses to competitors that no further evolution transpires. In such a case, plasticity may be more likely to mediate species sorting rather than character displacement.

Fourth, can competitively induced phenotypes lose their environmental sensitivity over evolutionary time and thereby undergo genetic assimilation? Experimental studies with rapidly evolving organisms might also prove informative for addressing this question.<sup>34</sup> Moreover, additional work comparing ancestral populations with derived populations that have undergone character displacement would be valuable in addressing this question.

Finally, does character displacement proceed initially by the evolution of plastic traits and subsequently transition to a phase in which genetically canalized traits evolve and mediate competitive interactions between species? If so, systems in which contact is recent should be more likely to display character displacement in plastic traits, whereas in systems where contact is older, trait differences should be mediated by genetically canalized differences. Addressing this issue is contingent, in part, on answering the fourth question above. Nevertheless, future research should aim to identify additional systems in which to evaluate the plasticity-first hypothesis for the evolution of character displacement. Only by doing so it will be possible to ultimately determine the conditions under which this route occurs and how common it is.

In addressing the above questions, equal emphasis should be placed on doing so in the contexts of both ecological character displacement and reproductive character displacement. Whether the relative importance of alternative mechanisms, and the nature of their interaction, is the same for these two forms of character displacement is itself an open question.

Additional research into the proximate bases of character displacement promises to have far-reaching ramifications. Indeed, because character displacement is central in the origins, abundance, and distribution of biodiversity,<sup>5,6,13,14</sup> understanding its causes can help illuminate some of the most fundamental issues in evolutionary biology and ecology, including how new species arise, how they diversify, and how they coexist.

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## Conflicts of interest

The authors declare no conflicts of interest.

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