

Ecological Character Displacement in Adaptive Radiation

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ABSTRACT: I give an overview of the observational and experimental evidence for ecological character displacement in adaptive radiation. Sixty-one published cases of character displacement involving closely related species (congeners) make up the observational data set. All cases involve divergence, even though parallel and convergent displacement are theoretically possible. Character ratios in sympatry were greatest when displacement was symmetric (mean 1.54) and least when asymmetric (mean 1.29), perhaps because the most symmetric resource distributions are also the broadest. Carnivores are vastly overrepresented in the data compared with other trophic groups, with herbivores the next most common category. I consider five hypotheses to explain this pattern, including the possibility that the likelihood of divergence via competition depends on position in food webs. Overall, the quality and completeness of observational data has improved in recent years, as judged by the extent to which individual cases satisfy six standard criteria. All but one of the criteria are met in over half the cases. Most often lacking is independent evidence that the species involved compete for resources. For this reason, we cannot be sure that divergence in sympatry is usually the result of resource competition rather than some other interaction. Field experiments on character displacement, which explore how interaction strength changes per unit change in phenotypic traits, are only just beginning. I summarize research on threespine sticklebacks that used experiments in ponds to test three predictions: that present-day differences between sympatric species are a “ghost” of competition past; that adding a competitor alters natural selection pressures on a species already present, favoring divergence; and that divergent natural selection stemming from resource competition is frequency dependent. In total, the evidence suggests that character displacement occurs frequently in nature, and it probably plays an important role in the evolution of diversity in many adaptive radiations.

Keywords: adaptive radiation, character displacement, coevolution of competitors, divergence, interspecific competition.

Interspecific resource competition has long been regarded as a major cause of phenotypic differentiation in adaptive

radiation. The idea is simple: depletion of shared resources by closely related, morphologically similar species would favor phenotypes exploiting new resources as yet untapped, leading to divergence. Darwin (1859) referred to the process many times, but Lack's (1947) study of the Galápagos finches really solidified the view. Lack presented several examples in which beak differences between species were greater where they occurred together (sympatry) than where they occurred separately (allopatry). His most memorable case was of the two ground finches *Geospiza fuliginosa* and *Geospiza fortis*. Both have similar beak sizes on islands where each occurs alone, but *G. fuliginosa* has a smaller beak and *G. fortis* a larger beak on islands where the two coexist. Brown and Wilson (1956) later compiled a list of similar examples from other birds and dubbed the phenomenon “character displacement.” These studies had a profound influence on evolutionary theory, and the idea that competition greatly influenced the evolution of diversity soon gained widespread acceptance.

Later views of competition's role in divergence were more skeptical. Doubts about its importance spread following a series of critiques that questioned the quality and completeness of the evidence and the conclusions that could be drawn from it. For example, Grant (1975) pointed out that two species with partly overlapping geographic ranges might exhibit greater differentiation in sympatry than allopatry if each was responding independently to the same environmental gradient. Arthur (1982) observed that, in most of the putative cases of character displacement available at the time, evidence was lacking that differences between sympatric and allopatric character states had a genetic basis. The patterns might instead have been the outcome of phenotypic plasticity, which, however interesting, is not character displacement. Developing statistical approaches suggested that morphological differences between species in sympatry were often not greater than would be expected purely by chance (Strong et al. 1979; Simberloff and Boecklen 1981). Randomly generated “null” assemblages of species often exhibited patterns similar to those seen in real communities. In other words, alleged instances of character displacement usually also had simple alternative explanations, and at that time, few data sets were complete enough to rule them out.

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The appeal of character displacement remained high, nevertheless, despite uncertainty over its importance. While the debates bred skepticism, they also spurred interest in locating fresh examples and in applying rigorous tests to cases both new and old. The outcome is that >70 cases of ecological character displacement have now been described. Tests against alternative hypotheses have increased dramatically, and experimental study of the process has begun at last. Recent overviews of selected subsets of cases (Taper and Case 1992; Robinson and Wilson 1994) are much more optimistic about its role in evolution.

Here, I summarize most of the available evidence for character displacement and its implications. This summary is based on a literature compilation whose details are given elsewhere (Schluter 2000). I evaluate the completeness of the observational evidence and examine it for patterns that might give clues to the circumstances that favor character displacement, noting especially its relationship to trophic level of putative competitors and the magnitude and symmetry of displacement. I also describe research on threespine sticklebacks in my own laboratory that has attempted to test experimentally predictions of the character displacement hypothesis. I conclude with a perspective of the importance of character displacement in adaptive radiation.

Definition

I define “ecological character displacement” as the process of phenotypic evolution in a species generated or maintained by resource competition with one or more coexisting species. By “resource competition,” I mean the negative impact of one phenotype on another arising from depletion of shared resources. Perhaps this definition is too narrow, as similar character shifts may result from apparent competition (“competition for enemy-free space”), a mutually detrimental interaction between prey species sharing a predator (Holt 1977; Abrams 2000, in this issue). One can go further and apply the term to shifts caused by other mutually antagonistic interactions as well, such as intraguild predation, interspecific killing, and behavioral interference. Here, I use the term in the more restricted, traditional sense. Nevertheless, an interesting question is whether resource competition, rather than one of these other interactions, is responsible for a given pattern suggesting character displacement. The distinction between competition and other interactions is blurred if interspecific killing or behavioral interference are adaptations to minimize interspecific resource competition. I focus on divergent character displacement because this is the most relevant to adaptive radiation. Convergent and parallel character displacement are theoretically possible (Abrams 1986, 1996), but there are no examples. I limit attention to studies of closely related spe-

cies (i.e., congeners) because these point to the role of competition at a relatively early stage of diversification.

Kinds of Data

The evidence for character displacement in nature is observational, experimental, and predictive. By “observational,” I mean studies of pattern in existing species assemblages. By “experimental,” I mean experimental tests of predictions of character displacement, not experiments testing resource competition per se. Experiments on character displacement include measurement of change in natural selection and phenotypic evolution with change in the density of competing species or change in the strength of competition as the phenotype of competitors is varied. This approach has been little attempted but is, in my view, the most important future direction of research. The “predictive” approach uses optimality or evolutionary models to generate quantitative expectations of mean phenotypes under character displacement and compares them with expectations from other models that do not include competition. The approach has been used only twice, in *Cnemidophorus* lizards (Case 1979) and Galápagos ground finches (Schluter and Grant 1984; Schluter et al. 1985), and in both cases, the results conformed to predictions of character displacement. Here, I focus on the observational evidence and recent experimental results.

Observational Data

The most common pattern detected is exaggerated divergence in sympatry, whereby phenotypic differences between two or more species are greater where the species coexist (sympatry) than where they occur separately (allopatry). Examples include beak sizes of the two Galápagos ground finches mentioned earlier, body sizes of solitary and paired *Anolis* lizards on small islands of the Lesser Antilles (Schoener 1970; Losos 1990), and growth performance of sympatric and allopatric stork's bill *Erodium* (Martin and Harding 1981).

The next most common pattern is overdispersion of trait means (or constant size ratios), whereby the mean phenotypes of ecologically similar species tend to be evenly spaced along a size or other phenotypic trait axis. Examples include canine diameters in the wild *Felis* cats of Israel (Dayan et al. 1990), mandible lengths of *Odontochila* and *Therates* tiger beetles (Pearson 1980), and flowering times of *Acacia* trees (Stone et al. 1996). No realistic theory of character displacement would predict size ratios that are truly constant (Abrams 1990), but competition is regarded as a likely explanation when species trait means tend to be overdispersed, provided that ancillary information such as resource use points the same way.

The third and rarest pattern is “species-for-species matching,” defined as unusually similar guild structures or phenotype distributions between sets of species that have evolved independently. Matching is not the same as convergence, which only requires that extant communities be more similar today than was the case between their ancestors. Matching does not imply that species phenotypes are overdispersed within any community (nevertheless, overdispersion may lead to matching). Rather, it implies that trait means are assigned to species in communities in a consistent way, implying in turn that the members of each community interact, perhaps as resource competitors (Schluter 1990). Examples include the independent evolution of similar sets of ecomorphs in *Anolis* of large islands in the Greater Antilles (Williams 1972; Losos et al. 1998), the repetitive origin of benthic-limnetic species pairs in fishes of northern lakes (Schluter and McPhail 1993; Robinson and Wilson 1994; Schluter 1996b), and the matched distributions of body sizes in finchlike birds of Mediterranean habitats (Schluter 1990).

Criteria for Observational Evidence

Six standard criteria listed below have come to be recognized as important for demonstrating character displacement with observational data. These criteria are from a compilation by Schluter and McPhail (1992) of the most significant criteria raised by earlier researchers (e.g., Grant 1972, 1975; Strong et al. 1979; Arthur 1982; see also Taper and Case 1992). I scored studies in the literature according to which of these criteria have been met: First, phenotypic differences between populations and species should be wholly or partly genetic. Second, chance should be ruled out as an explanation of the pattern. Third, population and species differences should represent evolutionary shifts, not just species sorting. Fourth, shifts in resource use should match changes in morphology or other phenotypic traits. Fifth, environmental differences between sites of sympatry and allopatry should be controlled. Sixth, independent evidence should be gained that similar phenotypes compete for resources.

A demonstration of heritable phenotypic variation within a population is not sufficient to satisfy the first criterion, which is about between-population differences. This first criterion is an issue mainly in cases of exaggerated divergence in sympatry. I assume the criterion is satisfied in all cases of trait overdispersion and species-for-species matching because these patterns are based on mean phenotype distributions of species living in the same environment. Even if phenotypic plasticity adjusts species means in response to niche use and competition, a genetic component is necessary to maintain differences between means of different species.

Ruling out chance (second criterion) requires rejection of a statistical null hypothesis, and this in turn requires some form of replication. Testing exaggerated divergence in sympatry requires comparison of means over multiple independent sympatric and allopatric populations. Trait overdispersion is tested by comparing the size spacing of species in a community with that in a “null” distribution of phenotypes generated by random sampling from a formal probability distribution (e.g., uniform or lognormal) or from an empirical distribution obtained by randomizing observed trait values. Gotelli and Graves (1996) review the alternative approaches that have been used and their underlying assumptions. Species-for-species matching is tested by asking whether differences between the phenotype distributions of two or more communities are significantly smaller than expected in random or randomized assemblages. Replication in the latter two kinds of tests is provided by the multiple species making up each community. I ignored the problem that statistical tests of character displacement are uncorrected for the nonindependence of replicate populations or species arising from phylogeny or gene flow. The method of Hansen et al. (2000, in this issue) provides a solution to this problem for statistical tests of exaggerated divergence in sympatry.

Character displacement involves evolutionary shifts in character states in response to competition (third criterion), but biased extinction of phenotypically similar species may yield a similar pattern. For example, if a series of species pairs is assembled on islands of an archipelago, and if one of the two species goes extinct on those islands where the colonists are overly similar, then a pattern is created in which sympatric species are more different from each other than are allopatric species. I ruled out biased extinction if, for example, trait differences in sympatry exceeded the span among allopatric populations or if mean phenotypes of member species varied over several communities exhibiting trait overdispersion.

Character displacement arises from depletion of shared resources (competition), and hence, a connection to resource use must be shown (fourth criterion). Tests of exaggerated divergence in sympatry require a demonstration of a shift in resource use between sympatry and allopatry. Tests of species overdispersion and matching require evidence that spacing of resource utilization correlates with the distribution of mean phenotypes.

Controlling for differences between environment (fifth criterion) ensures that a pattern suggesting character displacement is not merely the outcome of species evolving independently to environmental changes (e.g., Grant 1975). It is impossible to rule out all conceivable environmental agents, but attempts should be made to test effects of the most obvious factors such as resource dis-

tribution. For example, the evidence for character displacement in Galápagos ground finches is not diminished when differences between islands in seeds, the finches' main resource, are controlled (Schluter and Grant 1984; Schluter et al. 1985). I scored cases of character displacement according to whether or not at least one likely influential environmental factor was controlled. Clearly, this is not the same as ruling out all environmental differences, but it is a start.

Finally, a case for character displacement is greatly advanced if the interaction proposed to drive it, resource competition, is demonstrated (sixth criterion). Such a demonstration would not rule out the possibility that other interactions are also present and influencing divergence, but it would nevertheless satisfy an important precondition for character displacement. I allowed both experimental and observational evidence for competition. Tests of this criterion represent one area in which experiments have contributed to the study of otherwise purely observational data. However, such evidence is available in only a handful of cases (see "Criteria Met").

These criteria provide a yardstick against which the completeness of observational evidence for character displacement may be evaluated. Their value lies in the recognition that character displacement is not the only explanation for exaggerated divergence in sympatry, trait overdispersion, and species-for-species matching. Fulfilling a criterion just means that the corresponding alternative hypothesis has been tested and rejected at least once. Meeting five of the six criteria is no guarantee that the sixth too will be upheld. Moreover, satisfying all six criteria does not prove character displacement—we are dealing with observational evidence here. Nevertheless, a case is increasingly compelling as, one by one, the most likely alternative hypotheses fail upon testing.

Patterns in Observational Data

Seventy-two cases of character displacement that fulfill at least one of the six above criteria were found in the literature. They are listed in full in Schluter (2000). Sixty-one of these cases included congeneric species. The latter set provides the database for the summaries below. The remaining 11 cases include no congeneric species, and they are not considered further here. A "case" refers to a unique pair of species in tests of exaggerated divergence in sympatry, a unique assemblage of species in tests of trait overdispersion, or a unique set of assemblages in tests of species-for-species matching. The data set does not include any case that failed one or more tests of the criteria. For example, body sizes of dytiscid beetles show a significant pattern of trait overdispersion, but experimental study suggested that food limitation was absent at natural beetle

densities (Juliano and Lawton 1990a, 1990b). If so, then resource competition cannot be the mechanism behind trait overdispersion, and the case was excluded from my survey (it would nevertheless be interesting to know what interaction lay behind this pattern, as it may be more widespread). Thirty-three of the 61 studies included in the survey were of exaggerated divergence in sympatry, 25 were of trait overdispersion, and three were of species-for-species matching (Schluter 2000).

Criteria Met

Fulfilling only one of the criteria is not a major feat, but fortunately such studies are in the minority. Most satisfy at least three, and 22 (36%) fulfill four or more. A few cases meet all six criteria. They include threespine sticklebacks (*Gasterosteus*; Schluter and McPhail 1992; Pritchard 1998), Galápagos ground finches (*Geospiza*; Schluter and Grant 1984; Schluter et al. 1985), heteromyid rodents from deserts of the southwestern United States (*Dipodomys*, *Perognathus*, and *Chaetodipus*; Brown and Munger 1985; Dayan and Simberloff 1994; Heske et al. 1994), fish species pairs in postglacial lakes (Schluter and McPhail 1993; Robinson and Wilson 1994), and *Anolis* lizards of the Greater and Lesser Antilles (Schoener 1970; Williams 1972; Pacala and Roughgarden 1985; Losos et al. 1998).

Which criteria are most often fulfilled and which are most often lacking? Chance has been ruled out as an explanation of the pattern in >80% of the cases (51 of 61 cases; fig. 1). At the other extreme, independent evidence that species compete has been gained in only 14 of 61 cases (23%; fig. 1). This evidence is experimental in 10 cases, but even in these, it is not always clear that the

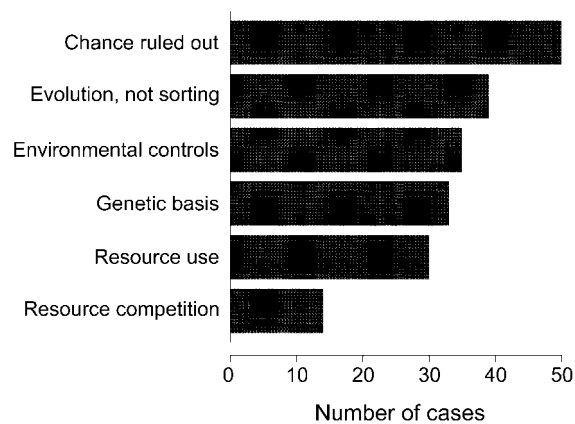


Figure 1: Number of observational studies satisfying each of the six criteria for observational evidence. Data are from Schluter (2000) and include 61 studies that include closely related species (congeners).

mutually antagonistic interaction responsible for the experimental effect is indeed resource competition, not some other interaction. For example, behavioral interference may be an important proximate factor in competition experiments (e.g., *Gerbillus*). Remaining criteria, including the criterion that the displacement should have a genetic basis, are fulfilled in roughly half the cases. This represents a vast improvement since Arthur's (1982) review.

Character Ratios

Character ratios in sympatry are variable and not always large (range 1.03–1.98), with a mean ratio of 1.36 (median 1.30). This range is similar to that seen in random assemblages (Eadie et al. 1987). Therefore, the magnitude of character ratios provides little information about whether size differences in sympatry show a pattern consistent with character displacement. Size ratios of adjacent species in cases of trait overdispersion are smaller on average (1.27) than in cases of exaggerated divergence in sympatry (1.41). However, cases of trait overdispersion also represent larger assemblages than those involving exaggerated divergence in sympatry (up to 13 species instead of just two), and this alone is expected to yield smaller ratios, all else being equal.

Symmetry of Displacement

The symmetry of displacement is quantifiable when measurements from sympatry and allopatry are available for both members of a pair of species showing exaggerated divergence in sympatry. According to some theories, asymmetry should be associated with greater divergence and symmetry with less divergence, all else being equal. This expectation arises from quantitative genetic theories of character displacement that found that skew in resource abundance distributions (i.e., those that peak toward one extreme endpoint of the resource gradient) tends to facilitate character displacement whereas symmetric resource distributions tend to hinder it (Slatkin 1980; Milligan 1985). Skewed resource distributions also lead to a co-evolutionary equilibrium in which one species exploits the most frequent resources in both sympatry and allopatry whereas the other species (the rarer) exploits the peak resources in allopatry but shifts markedly away from the peak in sympatry. This theoretical prediction is not necessarily robust because only a few scenarios leading to asymmetric character displacement have been modeled and because other parameters besides resource skew may also influence the magnitude of displacement (e.g., width of the resource distribution).

Symmetry was computed as the ratio of the displacements for each species, the smaller divided by the larger.

The displacement for each species was calculated as the natural log of the ratio of its trait mean in sympatry and its mean in allopatry, the larger divided by the smaller. Symmetry ranged from 0 (only one of two species shifted from allopatry to sympatry) to 1 (both species shifted equal amounts). Data were sufficient to allow calculation of symmetry in only 15 cases. Nevertheless, a pattern emerged that was opposite in direction to that initially expected (fig. 2). Character ratios in sympatry were greatest when displacement was symmetric (mean 1.54) and least for the asymmetric displacements (mean 1.29; Mann-Whitney $U = 51$, $P = .006$).

A possible explanation for this finding is that resource breadth, not resource symmetry, is the main determinant of the magnitude of displacement. Wide resource distributions favor large displacements (Slatkin 1980; Doebeli 1996). To account for the results, the widest resource distributions in nature must then also be more symmetric than narrower resource distributions. Too little information is available on resources to permit a test of this hypothesis. However, it is telling that several of the largest and most symmetric displacements are from depauperate environments: *Gasterosteus* sticklebacks in northern lakes, *Anolis* lizards on islands of the Lesser Antilles, *Cnemidophorus* lizards on islands in the Sea of Cortez, and *Geospiza* finches from the Galápagos Islands. The resource gradient may be effectively widest in these circumstances because few other taxa vie for it.

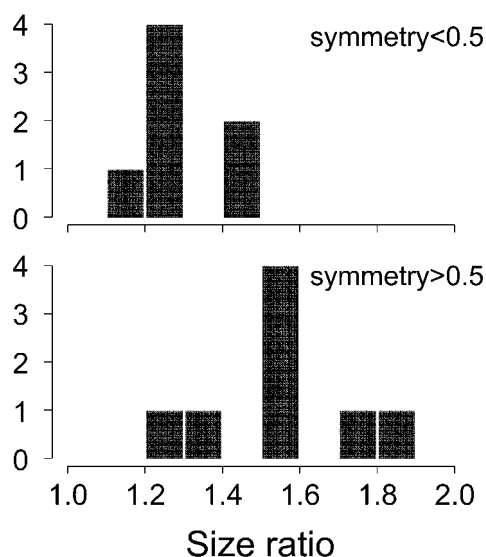


Figure 2: Character ratios in sympatry in the least symmetric displacements (< 0.5) compared with those in the most symmetric displacements (> 0.5). See text for details on the calculation of symmetry. Data are from Schluter (2000) and are based on 15 studies that include closely related species (congeners).

Trophic-Level Effects

The most striking pattern is the vast overrepresentation of carnivores compared with other trophic groups (fig. 3). Herbivores (mainly granivores) are the next most frequent trophic category followed by primary producers (plants). Cases of character displacement in microbivores and detritivores are scarce. The reasons for an association with trophic level are unknown. At least five hypotheses come to mind.

Hypothesis 1. Character displacement is most frequent at those trophic levels experiencing the strongest and most frequent interspecific competition. Carnivores experience stronger competition than other trophic levels because theirs is the only level limited mainly by resources.

Hypothesis 2. Foods consumed by carnivores are nutritionally substitutable whereas those at lower trophic levels are not. When resources differ in essential nutrients, as might be true for herbivores and plants, character displacement is more complex and may include convergence (Abrams 1987, 1996).

Hypothesis 3. Greater species richness at lower trophic levels dilutes the outcome of competition between pairs of species, rendering displacements smaller and less detectable.

Hypothesis 4. Character shifts in sympatry are not mainly the result of resource competition at all, but rather are evolutionary responses to intraguild predation, interspecific killing, and other direct antagonisms. Such behaviors are perhaps most prevalent among carnivores.

Hypothesis 5. Variation between trophic levels in the frequency of cases may result from simple detection bias. Character displacement is most easily detected when species differ in easily measured morphological traits that map linearly onto resource utilization. Perhaps this is more often true of carnivores than other trophic levels.

Detection bias is probably part of the story. Simple relationships between morphology and resource use in carnivores seem to be overrepresented in the literature compared with species at other trophic levels. Simple linear relationships are also commonly described in granivores, which make up the majority of the herbivore cases. Straightforward relationships between phenotype and resource use are far less frequently described for folivores, plants, and detritivores. Little evidence is available to test the other hypotheses. Note, however, that many of the carnivores in the data are not top predators but are intermediate-level predators that are themselves preyed upon (by diseases but also by other carnivores), detracting from the first explanation.

Experimental Tests

The above sections reveal that observational evidence for character displacement is burgeoning and that the mag-

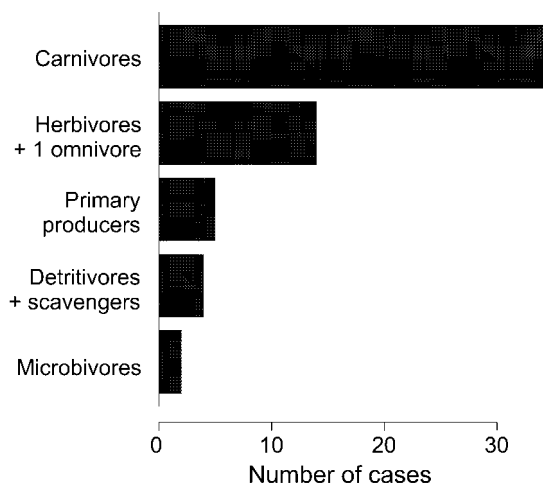


Figure 3: Frequency of cases of character displacement in species at different trophic levels in community food webs. “Carnivores” refers to animals that eat other animals, whether vertebrate or invertebrate. “Herbivores” includes consumers of any plant parts such as seeds, leaves, or fruits. Data are from Schluter (2000) and are only from studies including closely related species (congeners).

nitude and frequency of displacement varies greatly with trophic level and other circumstances. However, the causes of these patterns are uncertain. In particular, we require more direct evidence that resource competition is the main cause of exaggerated divergence in sympatry, trait overdispersion, and species-for-species matching. Information on mechanism remains the category of evidence in shortest supply (fig. 1). Experiments have confirmed the existence of a competitive interaction between species in 10 of 61 cases of character displacement. Yet, field experiments on competition are not rare (Connell 1983; Schoener 1983; Gurevitch et al. 1992), a fact that should inspire efforts to assess resource competition’s role in other putative cases of character displacement.

There is a further reason to conduct experiments that goes beyond the desire just to fulfill one more criterion for character displacement. Experiments allow us to test stronger predictions of the hypothesis than simply that species compete. Most important, they allow us to explore how interaction strength has changed during the putative character displacement sequence and to investigate how natural selection pressures on a species are altered when a second, closely related species is present in the environment.

Here I summarize experiments on threespine sticklebacks (*Gasterosteus aculeatus* species complex) designed to test three related predictions of the character displacement hypothesis. Where relevant, I point to comparable results from other systems. I limit attention to experiments that

address observed cases of character displacement in nature. A different class of experiments uses model laboratory systems to understand how interaction leads to character divergence and polymorphism (Helling et al. 1987; Taper and Case 1992; Rainey and Travisano 1998; Travisano and Rainey 2000, in this issue).

Sympatric Threespine Sticklebacks

Several experiments were carried out to test the hypothesis that character displacement promoted morphological and ecological divergence of sympatric sticklebacks inhabiting small post-Pleistocene lakes of coastal British Columbia, Canada. The system has been described in detail in Schluter and McPhail (1992), McPhail (1994), and Schluter (1996a). Briefly, pairs of species are found in several lakes. In each case one of the species is limnetic, foraging primarily on zooplankton in the water column, and the other is benthic, foraging on invertebrates in the sediments or clinging to vegetation. Each limnetic species is small and slender and has many long gill rakers and a narrow gape. Each benthic species is larger and more robust and has fewer, shorter gill rakers and a wider gape. Solitary stickleback species occurring in nearby lakes similar in size to those containing pairs are intermediate in morphology (but closer on average to the benthic than to the limnetic) and consume both zooplankton and benthic invertebrates. Morphological differences between populations and species persist in the laboratory, and at least some of these appear to have a polygenic basis (Hatfield 1997).

The experiments were designed around a historical scenario proposed by McPhail for the origin of species pairs (Schluter and McPhail 1992; McPhail 1993, 1994). He suggested that each pair formed by a process of double invasion and character displacement (fig. 4A). A key part of this scenario is that the intermediate form resulting after the first invasion by the marine ancestor was displaced toward a more benthic lifestyle when the marines invaded lakes a second time. The second invader did not evolve an intermediate phenotype like that attained the first time but instead retained a shape closer (although not identical) to that of the marine ancestor. The broad features of this historical sequence are supported by nuclear genes (allozymes and microsatellites; McPhail 1984, 1992; Taylor and McPhail 2000) and measurements of salinity tolerance (Kassen et al. 1995). An alternate scenario involving character displacement and sympatric speciation following a single colonization is supported by mtDNA results. However, we suspect these results are contaminated by mitochondrial gene flow between populations after the second invasion (Taylor et al. 1997; Taylor and McPhail 2000). Modifications of this double-invasion scenario that are also consistent with the molecular data are possible (Kas-

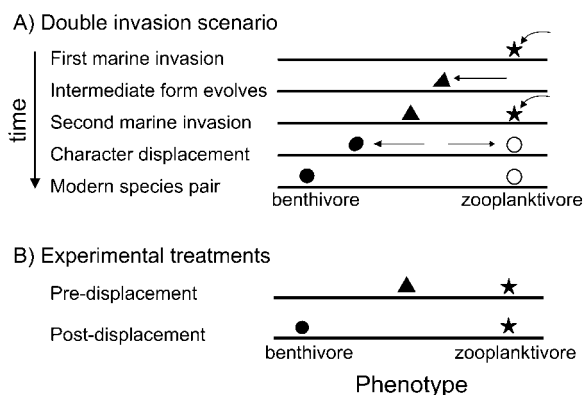


Figure 4: A, Hypothesized double invasion and character displacement sequence for the origin of stickleback species pairs. Curving arrows at the right indicate invasion events by the marine ancestor. Symbols indicate the mean position of a population along a resource-based morphological continuum: marine, *solid star*; intermediate, *solid triangle*; benthic, *solid circle*; and limnetic, *open circles*. B, Experimental treatments simulate stages in (A) before and after character displacement. Modified from Pritchard and Schluter (in press).

sen et al. 1995), but they do not critically affect the design of our experiments.

The experiments were carried out in a series of ponds on the campus of the University of British Columbia (Schluter 1994). Each pond is 23 m × 23 m, and its depth slopes gradually to 3 m in the center. The ponds were constructed in 1991 and seeded with plants and invertebrates from Paxton Lake on Texada Island, British Columbia (an 11-ha lake used as the source of experimental limnetic and benthic populations). Ponds are sand lined and edged with limestone extracted from surface mines near Paxton Lake. The ponds are not intended to be identical to wild lakes but only to mimic natural conditions well enough that they may serve as tools to study species interactions. All invertebrates found in the diets of experimental fish were characteristic of the species in the wild. Fish predators of sticklebacks are absent in the ponds, but insect predators are common. Predation by piscivorous birds (herons, kingfishers, and mergansers) is present but sporadic. Each pond can sustain thousands of sticklebacks over multiple generations, and life cycles in the ponds are similar to those in native lakes (D. Schluter, unpublished observations).

Experiment 1: The Ghost of Competition Past

This experiment tested the prediction that the intensity of competition experienced by species should decline as divergence proceeded, yielding descendants whose present-day interactions are a “ghost” of their former strength (see

Connell 1980). This expectation is a standard assumption of character displacement theory, but it has rarely been tested. Pritchard and Schluter (in press) tested the prediction by recreating historical and contemporary stages of the postulated character displacement sequence, taking advantage of the availability of the ancestral marine species in the ocean. The experiment ran in the summer of 1995 and lasted 7 wk. The marine species was the target. It was placed together with intermediate sticklebacks from Cranby Lake, Texada Island (pre-displacement treatment), or benthic sticklebacks from Paxton Lake (post-displacement treatment) in three divided ponds (fig. 4B). We used the intermediate form from Cranby Lake because the lake is similar to Paxton Lake in location, size, productivity, vegetation characteristics, and prey types available. The Cranby lake population has a low salinity tolerance, like the present-day benthics, suggesting that it formed around the time of the first invasion to lakes presently containing two species (Kassen et al. 1995). The experimental design held the phenotype of the zooplanktivore constant between treatments so that any treatment effects may be attributable to changes in the first invader, the form that departs most from the ancestral state (Schluter and McPhail 1992; Pritchard and Schluter, in press).

The “ghost” prediction was confirmed. Growth rate and degree of habitat specialization of the marine species was higher in the postdisplacement treatment than in the pre-displacement treatment, suggesting a decline in the strength of resource competition through time (fig. 5). An alternate interpretation is that benthics are indirect mutualists that somehow facilitate growth of marines in the postdisplacement treatment, perhaps by depleting the density of invertebrate predators and competitors of zooplankton, the main food of marine sticklebacks. Such indirect effects are rarely considered and may be influential in promoting divergence in many systems. However, this alternative does not accord well with other stickleback experiments in these ponds, which indicate that growth depression is the inevitable net result of adding sticklebacks to ponds regardless of phenotype. Our results, therefore, suggest that competition strength fell as divergence proceeded.

Only two other studies have compared competition intensity between species in different phenotype combinations (not necessarily representing extremes of a character displacement sequence). Competition was stronger between the two sympatric species of *Anolis* lizard on the Caribbean island of St. Maarten, where morphological and ecological separation is small, than between two species on St. Eustatius, where differences in body size and perch use are greater (Pacala and Roughgarden 1985). Competition between the two salamander species *Plethodon jordani* and *Plethodon glutinosus* was greater in the Great

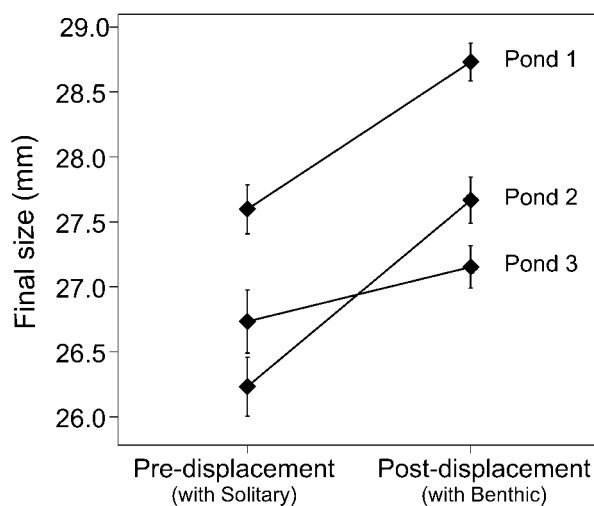


Figure 5: Mean growth of marine sticklebacks in two pond treatments representing early and late stages of a hypothesized character displacement sequence (fig. 4B). Modified from Pritchard and Schluter (in press).

Smoky Mountains, where altitudinal ranges of the two species abut without overlapping, than in the Balsam Mountains, where altitudinal ranges overlap extensively (Hairston 1980).

Experiment 2: Natural Selection Promotes Divergence

The goal of the second experiment was to test whether natural selection favored divergence between sympatric stickleback species (Schluter 1994). This experiment has been reviewed before (Schluter 1996a) and will not be elaborated here. I give a brief overview of crucial elements because the next experiment tests a related expectation and builds upon the same design.

The experiment tested another prediction stemming from the double invasion scenario (fig. 4A): that addition of a zooplanktivore (second invader) should alter natural selection pressures in a solitary population having an intermediate phenotype, favoring the more benthic phenotypes within it. The target of the experiment was the intermediate stickleback from Cranby Lake, Texada Island. This population was hybridized to limnetics and benthics before introduction to increase its levels of phenotypic variation and thereby to achieve a more sensitive measurement of changing natural selection pressures. Hybridization further enabled us to mark different trophic phenotypes within the target form using traits (armor and gill raker number) not susceptible to developmental plasticity that might otherwise have arisen from shifts in habitat use and diet. The intermediate population was placed either

alone (preinvasion treatment) or with the limnetic species from Paxton Lake (postinvasion treatment) in two divided ponds. The density of the target was held constant between treatments to ensure that any changes in selection detected may be attributed solely to the addition of the zooplanktivore. As a consequence, the total density of fish was higher in the preinvasion treatment. The hypothesis of character displacement makes the prediction that phenotypes in the intermediate population that are most similar to the limnetic species in morphology and habitat use should be most affected by the addition. The goal of the experiment was to test this prediction (Schluter 1994). The experiment was carried out over 3 mo in the summer of 1993.

As predicted by character displacement, addition of the zooplanktivore differentially depressed the growth rate of those individuals within the target population that were closest to the added competitor in morphology and diet (Schluter 1994). The effect of the addition on target phenotypes diminished gradually with increasing morphological distance away from the limnetic, with no growth depression in the most benthic phenotypes within the target population. The growth differential was steepest in the pond where density of the competitor was highest by the end of the experiment.

Experiment 3: Frequency-Dependent Natural Selection

The last experiment tested a third prediction of the character displacement hypothesis: that natural selection generated by interspecific competition should be frequency dependent (D. Schluter, unpublished data). I tested the prediction by determining whether the phenotype of the added competitor influenced the direction of selection within the intermediate species. The target of the experiment was again the stickleback from Cranby Lake, manipulated as before by hybridization to increase phenotypic variation. This species was placed on both sides of three divided ponds. Limnetics from Paxton Lake were added to one side of each pond, and benthics from the same lake were added to the other. The density of the target was again held constant to ensure that differences in selection detected between treatments may be attributed to the identity of the added competitor. Because competitors were added to both sides, total fish densities were now also equal at the start of the experiment.

Unlike the previous experiment, the treatments of the current design do not replicate stages in the putative history of stickleback species pairs (cf. fig. 4A). There was no attempt to make this experiment "historically correct" as in the case of the previous two experiments. Instead, my goal was to assess whether the identity of the second invader made a difference, that is, whether competition

for zooplankton was a key component of the events that transpired after the proposed double invasion or whether instead any added competitor would have produced the same effect. The experiment was carried out over 3 mo in the summer of 1996.

The relationship between growth rate and phenotype differed between treatments, confirming the expectation that the impact of species addition on the target was frequency dependent (fig. 6). Adding limnetics instead of benthics to a pond side reduced the growth rate of the most limnetic-like phenotypes within the intermediate population and elevated the growth rate of the most benthic-like phenotypes. Conversely, adding benthics instead of limnetics depressed growth of the most benthic-like phenotypes and raised the growth rate of the most limnetic-like phenotypes. Figure 6 shows the relationship when data from the three ponds are combined, but the result was the same within each replicate (D. Schluter, unpublished data). It is not possible to determine which competitor species, limnetic or benthic, exerted stronger selection because the experiment included no replicates in which the intermediate species alone was present. Nor can we assume that the observed relationship between growth rate and phenotype in the intermediate-only treatment in 1993 (0 slope; Schluter 1994) would also have occurred in 1996. Nevertheless, there is an indi-

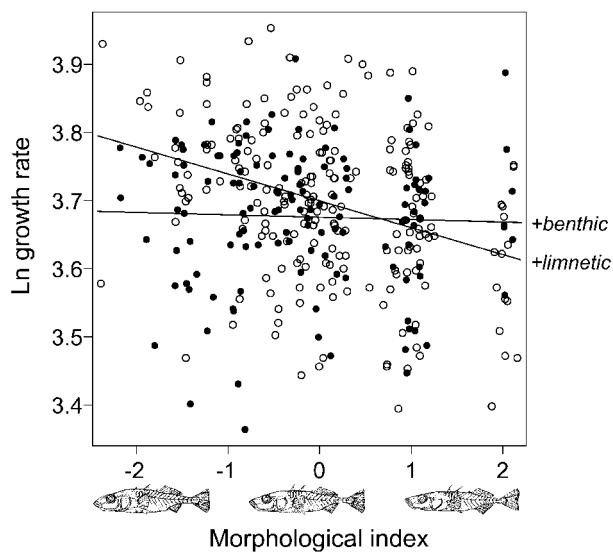


Figure 6: Growth rate (mm/90 d) of different phenotypes of the intermediate species in the presence of the benthic species (*solid circle*) and the limnetic species (*open circle*). The X-axis is a composite index representing trophic variation along the limnetic-benthic axis, with more benthic-like individuals on the left and the more limnetic-like individuals on the right. This graph combines data from three ponds, all of which showed the same pattern. From D. Schluter, unpublished data.

cation that the target species experienced competition, and possibly therefore selection, in both treatments of the current design. Regression lines of growth against phenotype for the two treatments crossed near the middle of the range of phenotypes present (fig. 6), with mean growth rate of the target equal in both treatments. This contrasts with the previous experiment in which the control and treatment regression lines crossed at the left end of the phenotype distribution, at the most benthic-like phenotypes. Therefore, the benthic treatment of the current experiment did not duplicate the control treatment of the previous experiment, suggesting that the benthic species as well as the limnetic species impacted the target but in opposite ways.

Discussion

The observational evidence for character displacement was extracted from a published body of literature that presents mainly the positive cases but few of the negative ones. Furthermore, I have not included negative cases in my survey, and I have not kept a running tally of examples that once looked promising but then later failed one or more tests of the criteria (e.g., the *Sitta* nuthatches; Grant 1975). Published negative cases are few, but this low count probably does not adequately represent the frequency of adaptive radiations in nature in which resource competition played little or no role in divergence. For this reason, I am unable to estimate the proportion of divergence events in nature in which significant character displacement occurred. Nevertheless, the positive cases summarized here are sufficiently numerous to indicate that character displacement is not a rare or peculiar phenomenon in nature. Very likely it is common, and it probably plays an important part in the evolution of diversity in many adaptive radiations. A view still encountered in the ecological literature, that little or no evidence exists for character displacement, is unsustainable.

The study of character displacement nevertheless has a long way to go. Key evidence is still lacking in most of the cases that have been described, particularly about mechanisms. In all but a few cases, tests are lacking of whether species indeed interact as resource competitors. Establishing the mechanism of interaction is especially crucial now that it is clear other interactions such as “apparent competition” arising from shared predation (a.k.a. “competition for enemy free space”; Holt and Lawton 1994) may also lead to character displacement (Brown and Vincent 1992; Abrams 2000, in this issue; Doebeli and Dieckmann 2000, in this issue). The contribution of shared predation and other interactions to divergent selection in adaptive radiation is completely unstudied experimentally, yet well worth investigating.

Additionally, the literature on which my survey is based provides little information, observational or experimental, of the circumstances that promote character displacement and those that hinder it. Variation between different trophic levels in the number of cases is the most striking indication of context-dependent character displacement and hints that position in food webs may be an important determinant. Before we can be sure of this, however, the influence of simple detection bias must be ruled out. A discovered link between symmetry and magnitude of displacement also indicates external influences on character displacement that have yet to be clearly identified. As well, character displacement theory predicts parallel shifts and even convergence under more complex scenarios of competition between species (Abrams 1986, 1996), but there are no examples.

Finally, we still know far too little about the dynamics of competition and selection. This is partly because we continue to rely too heavily on observational studies of pattern for our information. The sticklebacks reveal the feasibility of experimental studies, and I am optimistic that considerable progress in the future will come from manipulations of species composition and measurements of resulting changes in selection pressures and the direction of evolution. Experiments promise stronger tests of character displacement not just because they implement controls and replication but also because they allow tests of novel predictions that cannot be tested in any other way. Assessing how interaction strength changes at different putative stages of divergence is crucial to understanding its causes. Experiments also provide measurements of the basic processes involved in character displacement, including natural selection itself.

This study has focused on the role of competition between close relatives in differentiation. The other side of competition between relatives is “ecological opportunity,” an abundance of niches in a region little populated by competing taxa. Simpson (1953) and other naturalists of his day viewed ecological opportunity as the major regulator of the rate and extent of adaptive radiation. For diversification to occur, it was felt that the adaptive landscape of similar niches “must be occupied by organisms for some reason competitively inferior to the entering group or it must be empty” (Simpson 1953, p. 207). Most of the conclusions drawn from studies of character displacement between close relatives also apply to tests of the role of competing taxa in divergence and adaptive radiation. The quality of evidence for character displacement between species in different genera, families, or higher taxa is similar to that between more closely related species but examples are fewer. Evidence that resource competition is indeed the mechanism promoting divergence between distantly related species is usually absent. The evidence link-

ing phenotypic differentiation with ecological opportunity is almost entirely qualitative, perhaps because ecological opportunity is difficult to detect a priori and because detailed measurements have not been made. This is particularly true of examples from contemporary taxa. These patterns are summarized in greater detail elsewhere (Schluter 2000).

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