

Ecological character displacement and the study of adaptation

Jonathan B. Losos*

Department of Biology, Campus Box 1137, Washington University, St. Louis, MO 63130

The study of adaptation—a central issue in biology since before the time of Darwin—is currently enjoying a renaissance. Ridiculed two decades ago as following a panglossian paradigm (1) that promulgated “just so stories” rather than testing hypotheses, evolutionary biology has become a vibrant field in which a wide variety of methods—ranging from molecular developmental biology to manipulative field experiments—are used to rigorously test adaptive hypotheses (2). Nowhere is this more evident than in the study of ecological character displacement; a paper by Adams and Rohlf (3) in a recent issue of PNAS is one of a growing number of studies that have used integrative, multidisciplinary approaches and have demonstrated that ecological character displacement appears to be an important ecological and evolutionary phenomenon.

The theory of ecological character displacement was first explicitly developed by W. L. Brown and E. O. Wilson in 1956 (4). The idea underlying this theory is quite simple: Suppose that two very similar species come into contact. If resources are limiting, the species are likely to compete strongly. One possible outcome is competitive exclusion: the superior competitor will triumph and the inferior one will become extinct. But an alternative possibility is that natural selection will favor, in each population, those individuals whose phenotype allows them to use resources not used by members of the other species (Fig. 1). The result may be that the populations diverge in phenotype and resource use (hence the term displacement), thus reducing resource competition and permitting coexistence (Fig. 1).

Soon after the theory was promulgated, ecologists and evolutionary biologists were seeing evidence for character displacement everywhere. Because the theory of limiting similarity indicated that species that were too morphologically similar could not coexist (5), seemingly any difference between two sympatric species was interpreted as the evolutionary outcome of selection favoring divergence between sympatric species—character displacement was seen as a powerful and pervasive force structuring ecological communities. These interpretations corresponded nicely with the prevailing adaptationist thinking of the time that viewed almost all interspecific differences as the result of adaptation to different regimes of natural selection.

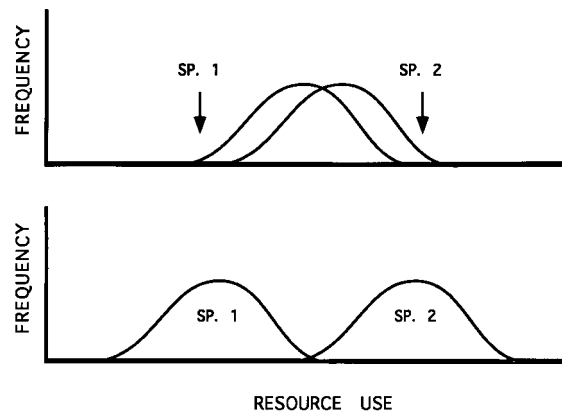


Fig. 1. (Upper) Two sympatric species with broadly overlapping distributions of resource use. If resources are limiting, then natural selection may favor individuals in each species with traits that allow each of them to use that portion of the resource spectrum not used by the other species, as indicated by the arrows. (Lower) The result may be that the species diverge in trait value and resource use, thus minimizing competition for resources.

placement was seen as a powerful and pervasive force structuring ecological communities. These interpretations corresponded nicely with the prevailing adaptationist thinking of the time that viewed almost all interspecific differences as the result of adaptation to different regimes of natural selection.

The decade from the mid-1970s to the mid-1980s were tumultuous times in both evolutionary biology and ecology. Even as the primacy of natural selection as the engine of evolutionary change was under attack (1, 6), parallel arguments were being leveled against character displacement. Statistical analyses showed that, in many cases, differences between sympatric species were no greater than would be expected by chance (7, 8). Moreover, even when sympatric species were significantly different in morphology, ecological character displacement was but one of many possible explanations. Some of these alternatives still relied on interspecific competition as the underlying cause (e.g., ref. 9), but others did not. Further, theoretical treatments suggested that the conditions under which ecological character displacement might occur were much more restrictive than previously appreciated (10–13). The net result was that character displacement’s importance as a force structuring communities was severely downgraded; many considered it to be a rare phenomenon for which few convincing examples could be found (e.g., refs. 14–16).

These debates—unpleasant as they sometimes were—served a good purpose: the study of evolutionary phenomena was recognized as an historical science—investigating what happened in the past thus requires an historical context (17–20). Moreover, investigating whether a trait arose as an adaptation requires examination of the hypothesis that natural selection led to the evolution of a trait in response to a particular selective situation. A wide variety of approaches—combining functional, experimental, and genetic methods—have been proposed as means to test this hypothesis (21, 22). One conclusion stands out from these methods: we cannot go back in time and expressly determine why a trait evolved. The best we can do is enumerate tests suggested by a particular adaptive hypothesis: the more such tests a hypothesis survives, the stronger may be our confidence in it.

Recent approaches to the study of character displacement exemplify this approach. Schluter and McPhail (23) outlined six tests of a hypothesis of ecological character displacement, which were further elaborated by Taper and Case (24):

(i) Differences between sympatric taxa are greater than expected by chance—i.e.,

See companion article on page 4106 in issue 8 of volume 97.

*E-mail: losos@biology.wustl.edu.



Fig. 2. *P. cinereus* and *P. hoffmani*. Photos are courtesy of R. W. Van Devender.

there is a deterministic phenomenon to explain.

(ii) Differences in character states are related to differences in resource use—if not, then the character divergence must have some other cause than the amelioration of competition for resources.

(iii) Resources are limiting, and interspecific competition for these resources is a function of character similarity.

(iv) Resource distributions are the same in sympatry and allopatry such that differences in character states do not simply reflect differences in resource availability—e.g., if some localities had an abundance of large and small insects, but few intermediate sized ones, one might expect two species to be able to coexist, one adapted to catching each size class of insects, whereas another locality with only intermediate sized insects might only be able to support one species. These differences might not be the result of character displacement, but of ecological tracking of resource availability.

(v) Differences must have evolved *in situ*—i.e., coexistence did not result from taxa evolving differences in allopatry that subsequently permitted range expansion and sympatry. Moreover, differences in sympatry must not result because character variation in both species is clinal and the geographic ranges of the species happen to overlap at the point where their morphological differences are greatest (25).

(vi) Differences must be genetically based—Phenotypic differences between sympatric and allopatric populations could result from a variety of nongenetic causes, including adaptive phenotypic plasticity and differences in survival and growth rates. Coexistence mediated by any of these nongenetic causes would certainly be interesting but would not qualify as character displacement.

Addressing all six of these tests in a single study is a challenging task, as it requires integrating a variety of different methods spanning the fields of ecology, genetics, and evolutionary biology. Nonetheless, an increasing number of studies are testing many of these hypotheses, as the paper by Adams and Rohlf illustrates (3).

Adams and Rohlf studied variation in body size and skull shape among populations of two small and closely related salamanders. *Plethodon cinereus* is widespread throughout the eastern United States whereas *Plethodon hoffmani* has a limited distribution “centered” in south-central Pennsylvania (Fig. 2). The species are for the most part allopatric; the range of *P. hoffmani* is surrounded on all sides by that of *P. cinereus*. This distribution, and the great similarity between the two species, suggests the possibility that lack of widespread sympatry is the result of competitive exclusion: the species are too similar ecologically to coexist. If this is the case, one might wonder what happens when populations of the two species come together at their range boundaries.

To find out, Adams and Rohlf sampled populations of both species in allopatry and in sympatry. They discovered that, in allopatry, the size of the two species was very similar. In sympatry, however, populations of *P. cinereus* were smaller, and populations of *P. hoffmani* were larger (Fig. 3). This is the hallmark of character displacement, but how well does this example hold up to the six tests outlined above?

(i) Is the pattern nonrandom? To test this hypothesis, Adams and Rohlf measured specimens from many allopatric populations of both species. They then computed the probability of finding differences as great as those actually observed if one randomly sampled one allopatric population from each species. The result: sympatric populations of the two species are more divergent than any possible pair of allopatric populations. The pattern is thus not a result of random sampling of existing morphological variation in the two species.

(ii) Are morphological differences related to differences in resource use? Adams and Rohlf found that, in sympatry,

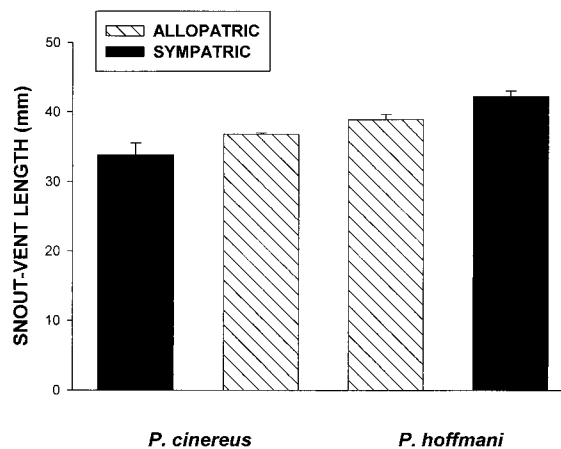


Fig. 3. Body size (as represented by snout-vent length) in allopatric and sympatric populations of the two species. In allopatry, populations are similar in size, but in sympatry, *P. hoffmani* is larger and *P. cinereus* is smaller (data courtesy of D. C. Adams).

P. cinereus eats smaller prey and *P. hoffmani* larger prey than each eats in allopatry. Why might this be? The authors note that the morphological feature that differed most between sympatric populations is the relative size of two bones in the head, the squamosal and dentary (which did not differ in allopatric populations of the two species). Adams and Rohlf suggest that this variation may have important functional consequences: salamanders with short squamosals relative to their dentaries (as is the case with sympatric *P. hoffmani*) should be able to snap their jaws shut quickly, but with little force, whereas long-squamosaled salamanders (sympatric *P. cinereus*) should be slow, but powerful. Plethodontid salamanders initially capture their prey by contact with their tongue. However, prey are then manipulated in different ways depending on their size: large prey are detained by rapid closure of the jaw, whereas small prey are moved to the back of the mouth and immobilized by pressure between the tongue and the teeth on the roof of the mouth. Hence, the differences in skull morphology and prey use of sympatric salamanders may be related to differences in bone dimensions. This is particularly clear for *P. hoffmani*, which eats large prey and should be able to close its jaws rapidly. Whether the force *P. cinereus* generates in jaw closure is related to the pressure generated at the back of mouth is less clear—direct biomechanical investigation is an obvious next step.

(iii) Interspecific competition is implicated by the observation that both species consumed fewer prey in sympatry than they did in allopatry. Whether character divergence has lessened these competitive effects, however, remains to be established.

(iv) Insect sampling indicated that, at least at a very crude level, no obvious differences in resource availability exist between sympatric and allopatric localities.

(v) Did the differences actually evolve in sympatry, or did they evolve before the attainment of sympatry and allow subsequent invasion and coexistence? One approach to addressing this question is to use phylogenetic analysis to reconstruct the historical timing of morphological evolution (26–30). In this case, however, such analyses are unnecessary: because no allopatric populations exist in which *P. cinereus* is as small as it is in sympatry and only one allopatric population exists that is slightly larger than the smallest sympatric population of *P. hoffmani* (based on a personal communication provided by D. C. Adams), the only reasonable conclusion is that these differences evolved in sympatry. Also, size distributions do not change in an obviously clinal fashion in either species, thus discounting this alternative possibility.

(vi) Are the differences genetically based? No data are available to address this question.

Like any good study of adaptation in a hypothetico-deductive framework, these results do not prove the case for character displacement; rather, they just indicate that the hypothesis thus far cannot be rejected. And, like any good study, this work suggests further hypotheses to be tested. Three obvious tests come to mind. First, if interspecific competition is truly the force that has driven this divergence, then if one placed allopatric populations of the two species together, they should compete more strongly than do the sympatric species, which are divergent in morphology (along these lines, the evidence on interspecific competition presented in this study is suggestive, but manipulative experiments would more clearly demonstrate competitive effects of one species on the other). Moreover, if one had enough patience, such manipulations could actually be used to measure selection and microevolutionary change. Over the course of several generations, one would expect to see selection favoring

differences among the species; even small-scale morphological responses might be detectable. Such manipulative approaches have long been a staple of community ecology, but only recently have been added to the arsenal of evolutionary ecologists (e.g., refs. 31 and 32).

Second, this work predicts specifically that each sympatric species will be more efficient at capturing prey of a particular type. Although biomechanical theory suggests that this may be the case, there is no substitute for direct evaluation of such a prediction. Finally, investigation of the genetic basis of differences between sympatric populations are needed to evaluate other, nongenetic, explanations.

In summary, the data support the hypothesis of character displacement, but more predictions remain to be investigated. Adams and Rohlf are appropriately conservative in concluding that “these data provide strong evidence that character displacement may be proposed as a causal mechanism to explain current morphological differences between sympatric populations of these species.”

More generally, this study is one of a burgeoning literature testing the hypothesis of character displacement in many different contexts. Naysayers may argue that few of these studies are able to convincingly examine all six criteria, but such work is difficult, as it involves so many disparate fields. Nonetheless, the evidence continues to accumulate (e.g., refs. 33 and 34), and as long as each case is treated as a hypothesis, with further studies required to address unanswered questions, then continuing work in this area should clarify the evolutionary and ecological importance of character displacement.

I gratefully acknowledge T. Schoener and D. Wake for insightful comments, R. W. Van Devender for photographs, D. C. Adams for information, and the National Science Foundation for support.

- Gould, S. J. & Lewontin, R. (1979) *Proc. R. Soc. London Ser. B* **205**, 581–598.
- Rose, M. R. & Lauder, G. V. (1996) *Adaptation* (Academic, San Diego).
- Adams, D. C. & Rohlf, F. J. (2000) *Proc. Natl. Acad. Sci. USA* **97**, 4106–4111.
- Brown, W. L., Jr. & Wilson, E. O. (1956) *Syst. Zool.* **5**, 49–64.
- MacArthur, R. H. & Levins, R. (1967) *Am. Nat.* **101**, 377–385.
- Gould, S. J. (1982) *Science* **216**, 380–387.
- Simberloff, D. S. & Boecklen, W. (1981) *Evolution (Lawrence, Kans.)* **35**, 1206–1228.
- Boecklen, W. & NeSmith, C. (1985) *Evolution (Lawrence, Kans.)* **39**, 695–698.
- Case, T. J. & Sidell, R. (1983) *Evolution (Lawrence, Kans.)* **37**, 832–849.
- Roughgarden, J. (1979) *Theory of Population Genetics and Evolutionary Ecology: An Introduction* (MacMillan, New York).
- Slatkin, M. W. (1980) *Ecology* **61**, 163–177.
- Abrams, P. A. (1986) *Theor. Pop. Biol.* **29**, 107–160.
- Abrams, P. A. (1987) *Am. Nat.* **130**, 271–282.
- Simberloff, D. (1983) in *Coevolution*, eds. Futuyma, D. J. & Slatkin, M. (Sinauer, Sunderland, MA), pp. 404–430.
- Walter, G. H., Hulley, P. E. & Craig, A. J. F. K. (1994) *Oikos* **43**, 246–248.
- Arthur, W. (1987) *The Niche in Competition and Evolution* (Wiley, New York).
- Lauder, G. V. (1981) *Paleobiology* **7**, 430–442.
- Felsenstein, J. (1985) *Am. Nat.* **125**, 1–15.
- Baum, D. A. & Larson, A. (1991) *Syst. Zool.* **40**, 1–18.
- Larson, A. & Losos, J. B. (1996) in *Adaptation*, eds. Rose, M. R. & Lauder, G. V. (Academic, Chicago), pp. 186–219.
- Arnold, S. J. (1983) *Amer. Zool.* **23**, 347–361.
- Greene, H. W. (1986) *Fieldiana Zool. New Ser.* **31**, 1–12.
- Schluter, D. & McPhail, J. D. (1992) *Am. Nat.* **140**, 85–102.
- Taper, M. L. & Case, T. J. (1992) *Oxford Surv. Evol. Biol.* **8**, 3–109.
- Grant, P. R. (1972) *Biol. J. Linn. Soc.* **4**, 39–68.
- Losos, J. B. (1990) *Evolution (Lawrence, Kans.)* **44**, 558–569.
- Richman, A. D. & Price, T. (1992) *Nature (London)* **355**, 817–821.
- Radtkey, R. R. (1969) *Evolution (Lawrence, Kans.)* **50**, 604–623.
- Butler, M. & Losos, J. B. (1997) *Evolution (Lawrence, Kans.)* **51**, 1623–1635.
- Giannasi, N., Thorpe, R. S. & Malhotra, A. (2000) *Mol. Ecol.* **9**, 193–202.
- Schluter, D. (1994) *Science* **266**, 798–801.
- Reznick, D. N., Shaw, F. H., Rodd, F. H. & Shaw, R. G. (1997) *Science* **275**, 1934–1937.
- Dayan, T. & Simberloff, D. (1994) *Ecology* **75**, 1063–1073.
- Robinson, B. W. & Wilson, D. S. (1994) *Am. Nat.* **144**, 596–627.