# Introduction to the Symposium: Species Interactions and Adaptive Radiation

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The purpose of this supplement is to explore the effects of interactions between species on the evolution of diversity, with an emphasis on lineages undergoing adaptive radiation. By "adaptive radiation," I mean the relatively rapid proliferation of new species from a single ancestor accompanied by expansion to new resources and environments and by divergence in phenotypic traits used to exploit those environments. The process may have many causes, but here we focus on the role of interactions between members of the diversifying lineage. Adaptive radiation is a good place to center an inquiry into the evolutionary consequences of species interactions because so much of ecological diversity, perhaps even most of it, has arisen by adaptive radiation. Species interactions, especially competition, have also been regarded as important causes of phenotypic differentiation in adaptive radiation. Finally, interactions play an important role in several ecological theories of speciation, especially sympatric speciation.

Here, I give a brief background on current ideas about species interactions and divergence, which provide the twin motivations for this issue. The history begins with Darwin (1859, p. 105), who sensed that interspecific competition for resources was one of the fundamental processes of phenotypic differentiation: "Natural selection … leads to divergence of character, for more living beings can be supported on the same area the more they diverge in structure, habitats, and constitution." Lack's (1947) study of the Galápagos finches solidified this view and helped make it the consensus among most naturalists by around the middle of the twentieth century. Lack regarded divergence between competitors as the last stage of each evolutionary cycle that produced two coexisting species from a single ancestor. As evidence, he presented several examples in which beak differences between closely related species were greater where the species occurred together (sympatry) than where they occurred separately (allopatry; a phenomenon later named "character displacement"; Brown and Wilson 1956): "The meeting of two forms in the same region to form new species must … result in subdivision of the food or habitat, and so to increased specialization. The repetition of this process has produced the adaptive radiation of Darwin's finches" (Lack 1947, p. 83). One finds little discussion of the role of other interactions, such as predation, in his writings nor in those of Mayr (1942, 1963), Simpson (1944, 1953), and the other naturalists of the modern synthesis. The emphasis was clearly on resource competition.

A consensus on competition's role in divergence held for another 20 yr or so but then began to unravel and was eventually replaced by an enduring skepticism in the minds of many biologists over the importance of competition and the frequency of character displacement in nature. Various factors produced the decline, but two main causes set the stage. The first was a growing realization that the empirical evidence for character displacement was surprisingly weak. Cases involving enhanced levels of phenotypic differentiation between two species in sympatry compared to two species in allopatry may be explained by processes other than character displacement. For example, Grant (1975) showed that two species with partly overlapping geographic ranges might exhibit greater divergence in sympatry than allopatry even if each was responding independently to a spatial gradient in some feature of environment. Most putative cases of character displacement were found to be too incomplete to rule out such alternative hypotheses. Later, doubts were raised over whether differences in sympatry were exaggerated at all. New analyses suggested that morphological differences between sympatric species were not usually greater than those seen in randomly generated "null" communities of species (Strong et al. 1979; Simberloff and Boecklen 1981). The validity of these analyses was hotly debated (see Gotelli and Graves 1996 for a

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Am. Nat. 2000. Vol. 156, pp. S1–S3. 
0003-0147/2000/15604S-0001$03.00. 

review of technical issues and contrasting perspectives), but whatever its limitations, the approach exposed serious deficiencies in the argument for character displacement. These controversies did not center on adaptive radiation specifically, but the majority of examples involved ecologically differentiated, closely related species (congeners).

Gathering doubts over the supremacy of interspecific competition in natural communities was a second factor underlying the demise of the earlier consensus on character displacement. Some researchers regarded competition as too weak and intermittent to be a significant force in divergence (Wiens 1977). Others felt that, while competition probably occurred, it was frequently overpowered by other interactions such as predation (Connell 1980). Experiments and observational studies settled the question somewhat by showing that interspecific competition is indeed common (Connell 1983; Schoener 1983; Gurevitch et al. 1992), making the idea of character displacement more plausible. However, the growing database of experimental studies also revealed that competition was but one of many direct and indirect species interactions occurring in nature, all of which too may have significant impacts on divergence. Two-species models of competition gave way to representations of nature in which "webs" of species interacted both directly (e.g., as predator and prey) and indirectly via resources (competition), shared predators (e.g., "apparent competition"), and indirect mutualists.

These lines of thought have left us with two questions that need to be addressed. First, how important is competition in evolutionary divergence? Is character displacement a common event in adaptive radiation, or has its importance been overblown? Is it a general and common phenomenon, responsible for divergence in many systems, or is it a peculiar feature of a few radiations? Second, which other interactions also favor divergence? Should researchers of adaptive radiation follow the ecologists' lead and give up on simple two-species models of competition-induced divergence, in favor of an expanded study of interaction webs and their evolutionary consequences?

This supplement addresses these issues with a combination of theoretical and empirical studies. The first three articles approach the question of the prevalence of character displacement and the methods we should use to elucidate it. The first (Schluter 2000, in this issue) summarizes the comparative and experimental evidence for character displacement and its implications. There are now over 70 described cases in the literature: what do these tell us about the importance of competition in divergence? Hansen et al. (2000, in this issue) advance the empirical study of character displacement with a novel statistical method that overcomes a serious deficiency afflicting almost all published tests: separate populations are not statistically independent when they are connected by gene flow or shared history. Pollination traits in flowers of the tropical vines *Dalechampia* serve as their test case. Travisano and Rainey (2000, in this issue) use a model experimental system to explore the environmental conditions that favor ecological and morphological diversification and elucidate the kinds of interactions responsible for the spread and persistence of different bacterial morphs. The next two articles address the role of interactions other than competition in divergence. Abrams (2000, in this issue) presents a theoretical study of evolutionary responses to shared predation, including the possibility of character divergence driven by "apparent competition" (Holt 1977). Pellmyr and Leebens-Mack (2000, in this issue) analyze how the evolved mutualism between yuccas and yucca moths facilitated the rise of new yucca moth species that exploit the association. The final article by Doebeli and Dieckman (2000, in this issue) picks up a third line of inquiry related to the first two: how strong ecological interactions may cause not only phenotypic divergence but the origin of new species even in the absence of geographic barriers to gene flow. They present a mathematical framework that can be applied to many types of interactions. Their ideas are directly applicable to adaptive radiations known or suspected to have taken place largely in sympatry but also to those in which the speciation process was begun in allopatry and completed in sympatry.

The overarching goal of this collection of works is to make progress toward fulfilling the two objectives, in the hopes that this brings us closer to a fuller understanding of species interactions and their evolutionary consequences.

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