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Principle of Divergence

David W. Pfennig
Department of Biology, University of North Carolina, Chapel Hill, NC, USA

Synonyms

Divergence of character; Character displacement

Definition

The "principle of divergence," first proposed by Darwin in *The Origin of Species,* is the hypothesis that divergent natural selection causes competitors to evolve to become more dissimilar from each other in resource use and associated traits.

Introduction

In *The Origin of Species,* Darwin (1859/2009) proposed his "principle of divergence of character" (a process now termed "character displacement"; Schluter 2000) to explain the origin and diversity of species. Darwin held that competition is a key driver of divergent selection: when organisms compete for scarce resources, natural selection favors those individuals that are least like their competitors. This divergent selection thereby causes competing groups of organisms (i.e., populations and species) to evolve to become more dissimilar from each other in resource use and associated traits. Darwin's ideas were groundbreaking, for none of his predecessors had viewed interactions between organisms as being important in evolution (Ridley 2005). Indeed, Darwin himself attached great importance to this idea. He wrote to his friend Joseph Hooker (8 June 1858, a year before the publication of *The Origin of Species*), "the 'Principle of Divergence,' … along with 'Natural Selection,' is the keystone of my book." At the same time, this principle remains relatively misunderstood. However, increasing evidence suggests that divergence of character (character displacement) might be central to the origins of diversity (Pfennig and Pfennig 2012).

Darwin's Principle of Divergence

> Divergence of character . . . is of high importance on my theory, and explains, as I believe, several important facts. (Darwin 1859/2009, p. 111)

> . . . it is the most closely-allied forms, – varieties of the same species, and species of the same genus or related genera, – which, from having nearly the same structure, constitution and habits, generally come into the severest competition with each other. Consequently, each new variety or species, during the progress of its formation, will generally press hardest on its nearest kindred, and tend to exterminate them. (Darwin 1859/2009, p. 110)

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> Natural selection, also, leads to divergence of character; for more living beings can be supported on the same area the more they diverge in structure, habits, and constitution, of which we see proof by looking at the inhabitants of any small spot or at naturalised productions. Therefore during the modification of the descendants of any one species, and during the incessant struggle of all species to increase in numbers, the more diversified these descendants become, the better will be their chance of succeeding in the battle of life. Thus the small differences distinguishing varieties of the same species, will steadily tend to increase till they come to equal the greater differences between species of the same genus, or even of distinct genera. (Darwin 1859/2009, pp. 127–128)

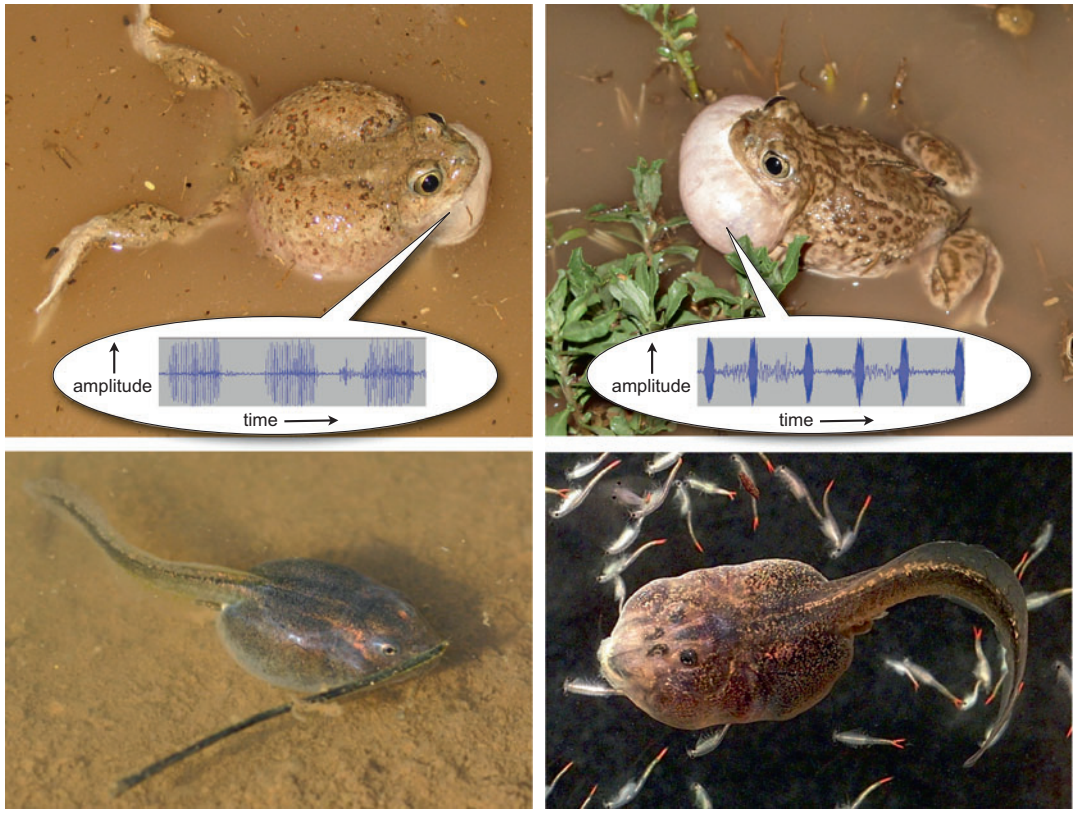
Why do even closely related species typically differ in ecologically relevant traits (Fig. 1)? Darwin first suggested that such differences reflected the action of a ubiquitous agent of selection: competition ("competition" is used here to refer to any direct or indirect interaction between groups of organisms that reduces access to vital resources and that is therefore deleterious – on average – to all parties.) According to Darwin, 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. Consequently, groups of organisms that compete should evolve to become more dissimilar. Darwin dubbed this idea "divergence of character" or the "principle of divergence."

Darwin considered divergence of character to be "of high importance" (first quote above) for three reasons. First, it explained why even closely related species tend to differ from each other. Because "the most closely-allied forms . . . come into the severest competition with each other" (second quote above), competitively mediated divergent natural selection acts strongest between individuals that are the most similar – ecologically, phenotypically, and phylogenetically. Second, it explained the origin of species. According to Darwin, selection that minimizes competition between "varieties" could drive divergence between them until they became separate species (third quote above). Finally, it explained why evolution has generated a "tree-like" typology (Ridley 2005). By continually disfavoring individuals that are phenotypically intermediate between two competing species, competitively mediated selection causes species to diverge from each other and the history of life to resemble a tree, with numerous, diverging branches.

In the 150 years since the publication of *The Origin of Species*, Darwin's claims have been largely substantiated. In particular, researchers have gathered evidence (described below) suggesting that selection acting to lessen competitive interactions can lead to divergent trait evolution – a process now known as "character displacement" (sensu Brown and Wilson 1956; Grant 1972; Schluter 2000). [As an aside, there is disagreement in the literature as to whether or not "divergence of character" and "character displacement" describe the same process; for a discussion of this controversy, and a review of the evidence suggesting that these two terms are synonymous, see Pfennig and Pfennig 2010.]

A widely used approach for demonstrating character displacement (i.e., divergence of character) is to compare populations of the same species that co-occur with another species (i.e., "sympatry") versus those that occur in the other species' absence (i.e., "allopatry"). Because selection to lessen competition between any two species will only act in sympatry, character displacement should produce a distinctive pattern in which species pairs are more dissimilar in sympatry than in allopatry. The classic example comes from seed-eating finches from the Galápagos islands, where several species have been found to differ more in beak morphology (the primary resource-acquisition trait) where they are sympatric with each other than where they are allopatric (Grant 1972). Numerous other such cases – in taxa as diverse as insects and mammals – have now been documented (Schluter 2000).

However, species can differ for evolutionary reasons other than selection, and for selective reasons other than to avoid competition. Thus, a major challenge is to rule out other causes that could produce the same patterns as character displacement. One approach for doing so is to establish rigorous criteria, which, when met, make a compelling case for character displacement.



Principle of Divergence, Fig. 1 Interacting species often differ in ecologically relevant traits, and these differences are often thought to reflect divergence of character (character displacement). For example, in areas where they co-occur, Mexican spadefoot toads (*Spea multiplicata*; *top left*) and Plains spadefoot toads (*S. bombifrons*; *top right*) diverge in both mating calls (*inset*: call spectrograms) and resource use, with *S. multiplicata* tadpoles developing into an omnivore morph that mainly eats plants (*bottom left*) and *S. bombifrons* tadpoles developing into a distinctive carnivore morph that specializes on animals (*bottom right*)

A number of studies have applied such criteria to make a strong case for character displacement (Schluter 2000). A second approach is to use experiments to confirm observations consistent with character displacement. Several such experimental studies have demonstrated that natural selection favors character displacement (reviewed in Schluter 2000; Pfennig and Pfennig 2012). Finally, the strongest support for character displacement is to actually observe its evolution in the wild following the invasion of one species into the habitat of another. Recent studies of Galápagos finches and *Anolis* lizards have provided such support (e.g., see Grant and Grant 2006; Stuart et al. 2014). In short, the available data suggest that resource competition can indeed promote divergent trait evolution, just as Darwin initially proposed in developing his principle of divergence. Additionally, ample empirical evidence (reviewed in Pfennig and Pfennig 2012) supports Darwin's claim that the intensity of divergent selection increases the more similar two species are to each other ecologically, phenotypically, and phylogenetically.

Darwin also maintained that competition promotes divergence within species. Here, too, his ideas have been validated. Indeed, selection acting to reduce such intraspecific competition can promote divergence within species through a process that is the intraspecific analog to interspecific character displacement (Pfennig and Pfennig 2012). In some cases, intraspecific character

displacement can lead to the evolution of discrete phenotypes within populations that differ in resource use. Numerous examples of such "resource polymorphism" have been documented (Pfennig and Pfennig 2012). For example, many species of fish have evolved alternative ecomorphs that specialize on benthic versus limnetic niches.

Character displacement might also promote speciation. One way it might do so is by *finalizing* speciation. Under the classical allopatric model of speciation (Coyne and Orr 2004), speciation begins when populations in allopatry start to diverge from one another. When such populations come into secondary contact, character displacement can finalize speciation by accentuating divergence between them. For possible examples, see Coyne and Orr (2004). Character displacement might also *initiate* speciation by promoting reproductive isolation between conspecific populations that occur in sympatry versus allopatry with another species (Pfennig and Pfennig 2012). Because individuals in sympatry will experience a different selective environment than conspecifics in allopatry, populations in these two types of environments should also diverge. Such divergence might indirectly promote speciation through the evolution of either post-mating or pre-mating barriers to gene flow between sympatric and allopatric populations. For possible examples, see Pfennig and Pfennig (2012). In sum, although speciation is difficult to observe directly, theoretical and empirical studies suggest that character displacement can indeed promote speciation (reviewed in Coyne and Orr 2004; Pfennig and Pfennig 2012; Schluter 2000).

Finally, in developing his principle of divergence, Darwin focused solely on *resource* competition. Yet, similar selective pressures can also act to lessen costly *reproductive* interactions between species, such as when one species interferes with another's ability to obtain high-quality mates or when separate species engage in costly mismatings with each other (i.e., hybridization). This selection operates on traits associated with reproduction, and it can lead to a form of trait evolution known as "reproductive character displacement" (in contrast to "ecological character displacement," which operates on traits associated with resource use). Indeed, as shown in Fig. 1, such selection can generate divergence rivaling that generated by resource competition. Reproductive character displacement might even serve as the critical link between divergence in resource use and the origin of species (Pfennig and Pfennig 2012).

Conclusion

In developing the principle of divergence, Darwin (1859/2009) maintained that the origin of species, and the evolution of trait differences between them, stem from divergent selection acting to minimize competitive interactions between initially similar individuals. Although Darwin failed to appreciate that similar selective pressures could also act to lessen reproductive interactions, his principle of divergence (i.e., character displacement) is well supported (Grant 1972; Pfennig and Pfennig 2012; Schluter 2000) and is thought to play a key role in generating biodiversity (Pfennig and Pfennig 2012).

Cross-References

- ▶ Charles Darwin
- ▶ Natural Selection
- ▶ Sexual Selection

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