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Quick guide

Character displacement

David W. Pfennig* and Karin S. Pfennig

What is character displacement? Character displacement is trait evolution that arises as a result of natural selection acting to lessen competition between species.

How does it come about? When species occur in the same location, they often compete, for instance by vying for limited resources such as food or mates. As competition is costly, natural selection favours individuals with traits (morphological or behavioral) that enable them to minimize competition with other species, for instance by accessing resources that are not used by other species. Over generations, such selection can cause competing species to diverge (Figure 1A,B). Moreover, as a fundamental precept of ecology is that species cannot share the same niche and stably coexist, these niche shifts also increase the likelihood of species coexistence.

Who came up with this idea? Like much in evolutionary biology, the idea traces to Darwin, who in his *On the Origin of Species* noted that "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..." Darwin's 'divergence of character' is now referred to as 'character displacement,' a term coined by William Brown and E.O. Wilson in 1956.

How do you study character displacement? Character displacement is often inferred rather than actually observed, most commonly when species are more dissimilar in traits involved in resource acquisition or reproduction where they occur together (sympatry) than where each occurs alone (allopatry; Figure 1C). For example, in a classic study, David Lack observed that different species of finches on the Galápagos Islands differ in the size and shape of their beaks (they use their beaks to obtain food, but beak shape can also affect their song, which they use to attract mates). Notably, species differ more when sympatric than when allopatric. Peter and Rosemary Grant documented this process actually evolving. On one of the Galápagos Islands, the medium ground finch lived alone until the large ground finch invaded and began to outcompete them for their preferred food (large seeds). This selection favoured medium ground finches with smaller beaks because they could harvest smaller seeds that were less in demand. The Grants documented an evolutionary shift toward smaller beak size in medium ground finches, demonstrating that character displacement had occurred. Character displacement has now been documented in many plants and animals.

Are there different forms of character displacement? There are two main forms. The most familiar (envisioned by Darwin) is 'ecological character displacement', which is trait evolution arising from resource competition. However, selection can also act to lessen costly reproductive interactions between species, such as when one species interferes with another species' ability to obtain high-quality mates, or when separate species interbreed and produce low-fitness hybrids. This can lead to 'reproductive character displacement' – which minimizes deleterious *reproductive* interactions between species. For example, in spadefoot toads (Figure 1D), female *Spea multiplicata* prefer mates with faster calls because they sire high-quality offspring. However, these calls happen to resemble those of another species, *Spea bombifrons*. Thus, in sympatry, where there is risk of hybridization, *S. multiplicata* have evolved a preference for slower calls to minimize mating with the wrong species.

How does character displacement evolve? Generally, it is assumed to arise through changes in allele frequencies at genes underlying the divergent traits. Essentially, selection favours individuals that are most dissimilar from their competitors, and thus alleles that encode

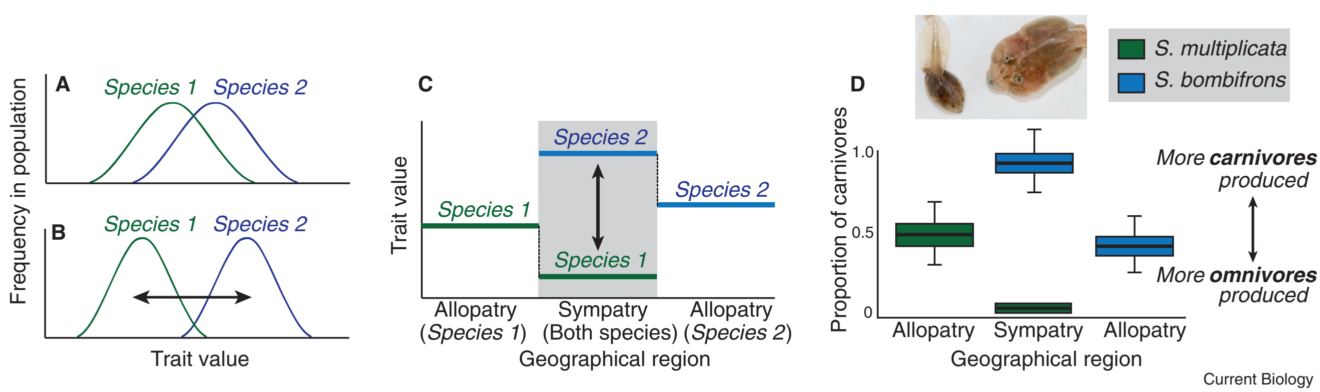

Figure 1. How character displacement evolves and is detected.
(A) When co-occurring species overlap in traits associated with resource use or reproduction (indicated here by overlapping bell-shaped curves), natural selection favours individuals most dissimilar from the other species, potentially causing (B) species to diverge. (C) This process can produce a pattern in which species are more dissimilar in sympatry (shaded region), where there is selection for divergence, than in allopatry, where there is no such selection. (D) For example, two species of spadefoot toads, *Spea multiplicata* and *S. bombifrons*, each produce two different types of tadpoles: a small-headed omnivore morph (the tadpole on the left), which feeds mostly on plants and detritus, and a large-headed carnivore morph (the tadpole on the right), which feeds mostly on large animal prey. Where each species occurs in allopatry, they produce similar, intermediate frequencies of omnivores and carnivores. However, where they occur in sympatry, *S. multiplicata* shifts to producing mostly omnivores, whereas *S. bombifrons* shifts to producing mostly carnivores. In so doing, these two species reduce competition for food and are thereby able to coexist.

these divergent traits. As the frequency of dissimilar individuals increases, so does the frequency of these alleles. Support for this model comes from several systems, including the Galápagos finches. Yet, an adaptive response to competition need not arise solely through genetic changes — such a response might instead reflect environmentally induced phenotypic change, 'phenotypic plasticity.' Many species can facultatively alter their resource use or reproductive traits to lessen competition with other species. Character displacement might thus evolve from an initial phase of environmentally induced differences until divergent traits become genetically fixed. Support for this model comes from sticklebacks, spadefoot toads and anole lizards.

Is character displacement controversial? Most researchers accept the basic idea, but controversy has arisen over how common character displacement actually is. Central to this debate is the realization that numerous selective and non-selective factors can cause species to exhibit exaggerated divergence in sympatry (Figure 1C). Most researchers therefore now rely on additional evidence to make a compelling case for character displacement.

Why is character displacement important? As character displacement increases the chances of species coexistence, it can play a key role in structuring ecological communities. It has also been implicated in the formation of new species and in large-scale evolutionary phenomena, such as adaptive radiation. Thus, character displacement may be central in the origin, maintenance and distribution of biodiversity.

Where can I find out more?

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Department of Biology, University of North Carolina, Chapel Hill, NC 27599, USA.
*E-mail: dpfennig@unc.edu

Q & A

John Peever

John Peever is a Professor in the Department of Cell and Systems Biology at the University of Toronto. He completed his PhD in neurobiology in the Department of Physiology at the University of Toronto in 2001 and a postdoctoral fellowship in the Department of Psychiatry and Biobehavioral Sciences at UCLA in 2004. His research examines how and why we sleep, with a particular focus on identifying the brain mechanisms that control rapid eye movement (REM) sleep and how their dysfunction underlies narcolepsy and REM sleep behavior disorder. Peever is also an advocate for promoting the awareness of sleep in health and disease through his roles as Vice President of the Canadian Sleep Society and Chair of the National Training Program in Sleep Medicine and Biology. Outside of science, he is a husband to David LeRoy, dog dad, hobby farmer, beekeeper, horseman, and antique admirer.

What turned you on to biology in the first place? My interest in brain biology started when I was six. I have an incredibly vivid memory of my first visit to the school library and picking up a book entitled *The Brain*. I took it home and read it cover to cover. I recall saying to my parents — although they don't recall this — that I wanted to be a brain surgeon. Initially, I thought that I'd be a neurologist. So, I decided to go to university and streamed into pre-medical school courses. But as time moved on, I realized that I was petrified of hospitals. So, I abandoned my initial dream of being a neurologist. But I wondered: how could I study the brain but not be a medical doctor? Then I started taking basic biology and neuroscience courses and was slowly introduced to basic research. Eventually, I realized that I could study the brain at a research level. The rest is history.

And what drew you to your specific field of research? I'm not sure, but I've always been fascinated by sleep. My earliest memory about sleep is from when I was 10. I recall lying in bed thinking "where do I go when I sleep?", "why do I wake up in the morning?", and "why do I dream about flying so much?" I didn't think much about sleep again until I was an undergraduate student, when I started experiencing sleep paralysis. I'd wake up after a bad dream but be unable to move or speak even though I wanted to. These terrifying experiences sparked my interest in sleep biology. I started reading about sleep and more specifically REM sleep because sleep paralysis arises from dreaming sleep. Given that there was no internet at this point, I had to skulk the library stacks for information. I quickly came across the seminal work of Allan Hobson, William Dement, and Michel Jouvet, who were studying REM sleep. Their work was fascinating, but what really got me hooked was how little we know about how and why we experience REM sleep.

If you had to choose a different field of biology, what would it be? That's a tough question to answer because so many things fascinate me. But if I could do a '180', I'd probably study the biology of aging. I find it fascinating how obsessed we are with age and aging. We devote — sadly — so much of our waking lives to worrying about it. Just look at how many books and movies are devoted to the subject. I lived in Los Angeles during the rise of plastic surgery and was fascinated to see how people would literally carve up their faces just to look a few years