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COMMENT

Character displacement is a pattern: so, what causes it?

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Character displacement was originally defined simply as a pattern – divergence between two species in sympatry but not allopatry – and it was recognized that multiple processes might generate this pattern. However, over time, character displacement has come to be nearly synonymous with the process of adaptive divergence between species caused by selection stemming from resource-competitive interactions (and if not, then from reproductive interactions). This tight link between character displacement and resource competition has generated, and continues to generate, imprecision and confusion in the literature. Here, to address this problem, we suggest unlinking character displacement – the pattern – from any specific process (e.g. natural selection arising from species interactions). That is, character displacement should be documented as a pattern, agnostically with respect to process. Purposeful, direct investigation of what process generated character displacement then naturally follows. This has the benefit of acknowledging that there can be many different avenues to divergence in sympatry.

ADDITIONAL KEYWORDS: character displacement – competition – ecological character displacement – reproductive character displacement – species interactions.

INTRODUCTION

The ecology and evolution literature is replete with hundreds of cases where two species – usually closely related, ecologically similar species – show divergence from one another when they co-occur in sympatry but are indistinguishable where they exist separately in allopatry. In 1956, Brown and Wilson coined a name for this pattern – character displacement [unless noted otherwise, the use of character displacement in this manuscript refers to the pattern of divergence in sympatry relative to allopatry] – and proposed two processes by which selection for such divergence could arise, reinforcement and resource competition (Brown & Wilson, 1956). In the six decades since, resource competition has become tightly linked with the term 'character displacement' such that character displacement and resource competition-driven divergence are nearly synonymous (P.R. Grant, personal communication; Stuart & Losos, 2013).

Problematically, the interchangeability between character displacement (that is, the pattern) and resource competition has meant that resource competition is commonly inferred when only divergence in sympatry has been shown (Connell, 1980; Simberloff & Boecklen, 1981; Stuart & Losos, 2013). Such straightforward inference has inhibited the investigation of the causes of character displacement patterns, thereby slowing progress toward understanding the many ways in which divergence evolves. Indeed, Brown and Wilson (Brown & Wilson, 1956) and many others (e.g. (Simberloff & Boeklen, 1981); reviewed in (Grant, 1972) (Schluter, 2000), (Pfennig & Pfennig 2012)) have pointed out that numerous other ecological and evolutionary processes besides resource competition can result in character displacement [Table 1; reviewed in (Schluter, 2000)]. So, while documenting the pattern is often straightforward,

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Table 1. Processes that could generate a pattern of character displacement, and how the processes differ in their target of selection (if selection is involved) and outcomes, all under the pattern-based definition of character displacement we advocate here

Process qualifier	Source and outcome of selection
Ecological (resource-competitive*) (Brown & Wilson, 1956)	Selection favours divergence in resource-related traits to reduce interspecific competition for limited resources
Reinforcement** (Brown & Wilson, 1956)	Selection favours divergence in sexual traits to reduce unprofitable interspecific matings
Agonistic (Grether *et al.*, 2009)	Selection favours divergence in resource or sexual traits to reduce deleterious aggressive interactions
Intraguild predation (IGP)*** (Polis, Myers, & Holt, 1989)	Selection favours divergence in resource use traits to reduce predation among competitors
Apparent competition (Holt, 1977)	Selection favours divergence in resource use traits to avoid shared predators (i.e. competition for enemy-free space)
Ecological sorting (Case, 1979)	Coexistence following secondary contact is facilitated by prior divergence in allopatry
Phenotypic plasticity (Pfennig & Martin, 2009)	Divergence is not constitutive but stems from selection for an alternative phenotype in sympatry****
Gradient adaptation (Grant, 1972; Meiri, Simberloff, & Dayan, 2011)	Divergence in sympatry stems from differential adaptation by each species along an environmental gradient
Chance (Simberloff & Boecklen, 1981)	Divergence arises from random sampling of populations, not selection

*We propose this as a more descriptive name for ecological character displacement, given the ambiguity of the "ecological" qualifier. **That is "reproductive". ***For an intriguing wrinkle on intraguild predation, see interspecific killing (Hoogland & Brown, 2016). ****Of course, divergence in the expression of plasticity can be genetically based and evolve.

discerning the processes causing character displacement is more difficult (Stuart & Losos, 2013).

Here, we trace a brief history of character displacement to understand how it changed meanings to refer to the process of divergence due to natural selection from species interactions. We then emphasize a pattern-based definition in line with the original definition that unlinks character displacement from a specific selective force. Our focus on pattern is in contrast to arguments to define character displacement as a process (Grant, 1972) (Pfennig & Pfennig, 2009, 2012), but, as explained below, we believe that disentangling the pattern from the process results in a simpler nomenclature, and more importantly, actually promotes a more thorough investigation of the ecological and evolutionary forces that cause divergence. Our goal is to encourage researchers to recognize that documenting the pattern of character displacement (across a landscape or through time) is just the first step in a broader task of distinguishing between a variety of processes that might generate such patterns.

PATTERN

In 1953, Brown and Wilson published a paper about geographical variation and the subspecies concept (Wilson & Brown, 1953). This collaboration launched them into a number of "megathought discussions" (Brown, 1986), and they became particularly interested in one of Wilson's findings in his revision of the ant genus *Lasius*, namely that "certain pairs of species, distinct morphologically and ecologically where they occurred together … were in other regions replaced by populations that appeared to be intermediate to … the same two species" (Wilson, 1955; Brown, 1986). Brown and Wilson began collecting evidence for this pattern, which Brown had started calling "character displacement", leading to a 1955 paper in which the idea and phrase were first coined (Wilson & Brown, 1955). By 1956, the pair was ready to publish a general description of

> … a seldom-recognized and poorly known speciation phenomenon that we consider to be of potential major significance in animal systematics. This condition, which we have come to call 'character displacement,' may be roughly described as follows. Two closely related species have overlapping ranges. In the parts of the ranges where one species occurs alone, the populations of that species are similar to the other species and may even be very difficult to distinguish from it. In the area of overlap, where the two species occur together, the populations are more divergent and easily distinguished, i.e., they 'displace' one another in one or more characters. The characters involved can be morphological, ecological, behavioral, or physiological; they are assumed to be genetically based. (Brown & Wilson, 1956)

In this description, Brown and Wilson defined character displacement as a pattern: divergence in sympatry.

That is, for a phenotypic trait X in each of two species, in sympatry, they are divergent ($\left|\overline{X}_1 - \overline{X}_2\right| > 0$), while in allopatry they are not ($\left|\overline{X}_1 - \overline{X}_2\right| \cong 0$), where $\overline{X}_1$ and $\overline{X}_2$ are the population means for trait X for species 1 and 2, respectively. [One alternative mathematical formulation is $|\overline{X}_{1A} - \overline{X}_{2A}| < |\overline{X}_{1S} - \overline{X}_{2S}|$, where $_A$ and $_S$ represent allopatry and sympatry, respectively. This is slightly different from Brown and Wilson's verbal description of the pattern, allowing two species to be different from each other in allopatry and asking whether the two species are *even more* different in sympatry. This 'exaggerated divergence' formulation is both more general and biologically realistic.] To document this pattern, one need not presuppose that the trend is driven by any one process, for example natural selection, sexual selection, drift, ecological sorting, biased migration, and so on.

Several processes initially proposed

Brown and Wilson also considered process, describing a pair of "interaction[s] in the history of the [species] pair…", with character displacement arising "most often as a product of the genetic and ecological interaction of two (or more) newly evolved cognate species during their period of first contact" (Brown & Wilson, 1956). The first interaction they considered was "*reinforcement* of the reproductive barriers [italics by (Brown & Wilson, 1956)]. It may happen that the species continue to interbreed to some extent, and either the resulting inseminations are ineffectual, or the hybrids produced are inviable or sterile, resulting in what geneticists have termed 'gamete wastage.' Consequently, any further ethological or genetic divergence reducing this wastage will be strongly favored by selection." The second process Brown and Wilson considered was "*ecological character displacement* [italics by (Brown & Wilson, 1956)]. It seems clear from an *a priori* basis that any further ecological divergence lessening competition between the overlapping populations will be favored by natural selection if it has a genetic basis." Thus, character displacement was originally proposed as a pattern arising from two species-interaction driven processes: (1) natural selection to reduce unprofitable interspecific matings (reinforcement; we consider reinforcement and reproductive character displacement – RCD – to be the same process. Some authors consider reinforcement to be nested within a broader concept of RCD (Pfennig & Pfennig, 2009, 2012)), and (2) natural selection to reduce interspecific competition (ecological character displacement; as resource competition became the dominant paradigm in ecology through the 1960s-1980s (Schoener, 1982), the rather vague adjective, "ecological", became synonymous with resource competition in the character displacement literature).

One process gets defined

Grant formally linked the pattern of divergence in sympatry to divergent selection arising from species interactions by redefining character displacement as the "process by which a morphological character state of a species changes under natural selection arising from the presence, in the same environment, of one or more species similar to it ecologically and/or reproductively" (Grant, 1972). By defining character displacement thus, a pattern of divergence in sympatry can only be called character displacement (*sensu* Grant) if it stems from divergent natural selection imposed by an interacting species. That is, Grant argued that species interactions had to be involved (Grant, 1972). [Though carefully defined by Grant, such that divergent natural selection could come from any kind of species interaction, today, to many workers, one cannot call a pattern of divergence character displacement unless one has proved competition (or reinforcement), even if it is clear that some yet-to-be-determined species interaction is present.]

Was it necessary to restrict the source of divergence to only selection from species interactions? Brown and Wilson clearly were focusing on species interactions: character displacement "aris[es] most often as a product of the … interaction of … species…", with "two important ways in which the sympatric populations can interact…" (Brown & Wilson, 1956). However, "most often" and "ways in which" indicate that other events besides species interactions could also generate a pattern of divergence in sympatry that still constitutes character displacement (Brown, 1986).

A problem with a process-based definition restricted to species interactions is how to discuss patterns of divergence in sympatry that do not arise from species interactions. One could come up with new terms for each such pattern-process, but that risks obscuring the clear relationships among the processes – that is, they are all trying to explain divergence in sympatry. Brown and Wilson's pattern-based approach, in contrast, allows any process that generates divergence in sympatry to be considered and compared and synthesized under a single umbrella: (the pattern of) character displacement.

"Qualified" character displacement denotes process

Thus, in our opinion, we should return to the original pattern-based definition of character displacement,

unlinking it from the processes that generate it. Agnostic to process, one should first test whether $|X_1 - X_2| > 0$ is true in sympatry but not in allopatry. Then, process should be investigated to determine what kind of character displacement has occurred (Table 1). [Grant argued that linking pattern to process was advantageous, in part, because different patterns of divergence could be considered representative of the same selective process. Yet, by reporting mechanism through a qualifier as described below, our approach also works for the other named patterns of character displacement, like trait over-dispersion and species-for-species matching (Schluter, 2000) (Grant, 1972), or cases where divergence increases through time in areas of newly established sympatry. (Grant, 1972).]

How does one denote the various processes driving character displacement if the pattern has been discovered? The nomenclature under our approach is straightforward. Indeed, researchers have already begun to solve this question by putting qualifying adjectives in front of the term "character displacement". For example, divergence resulting from selection to reduce resource competition has been called "ecological" character displacement (Schluter, 2000); to reduce unprofitable matings (i.e. reinforcement) has been called "reproductive" character displacement (Pfennig & Pfennig, 2009) and to reduce aggressive encounters has been called "agonistic" character displacement (Grether *et al.*, 2009). In each of these cases, the qualifier denotes the type of process underlying divergence in sympatry. Thus, under a return to Brown and Wilson's original pattern-based definition, all we must do is adapt the "qualifier" approach by extending the list of qualifiers to describe new processes (Table 1).

How are we to determine the source of divergence itself? Schluter and McPhail codified a set of criteria for testing whether character displacement results from resource competition, and is therefore "ecological" character displacement [Appendix 1; (Schluter & McPhail, 1992)]. Similar criteria have been put forth for reinforcement (Waage, 1979; Hopkins, 2013) and "agonistic" character displacement (Grether *et al.*, 2009). This criterion approach can be modified for all the processes in Table 1 (see Table A1), thereby providing a rigorous way to discern among potential processes. We note here that these criteria do not explicitly require measurement of divergent selection to confirm process (for those processes that depend on selection). However, in concert with criteria 6 (what is the source of selection) and 4 (how traits are related to selection) (Appendix Table A1), testing whether there is a cost of coexisting in sympatry and whether trait divergence lessens that cost would bolster a hypothesized selective process. In other words, is mean fitness for at least one of the species positively related to trait divergence: $\frac{d\bar{w}}{d(|\bar{X}_1 - \bar{X}_2|)} > 0$, where the numerator represents the change in average fitness. [See Slatkin (1980) for detailed theoretical treatment of ecological character displacement. Reviewed in Schluter (2000).] Of course, character displacement may be a result of selection in the distant past. If the populations have diverged sufficiently, ongoing selection for displacement might not be measurable, except by experimental tests artificially generating less-displaced populations or natural experiments that do the same (Hopkins, 2013; Stuart & Losos, 2013).

CONCLUSION

We know that our inclusive, pattern-based definition runs against common usage (Grant, 1972); nevertheless, we feel that the benefit of describing character displacement as a pattern, and then pursuing process, outweighs any drawbacks that come from changing common usage (Grant, 1972; Pfennig & Pfennig, 2012). First, character displacement can be documented and named clearly without requiring process, so as to make findings relevant (and searchable) for syntheses and meta-analyses and to spur future research. Second, there are testable criteria to distinguish among processes once the pattern is documented (Tables 1 and A1), and the kind of process can be easily noted with a qualifier. But, third, if not all the criteria are met, character displacement is not void as it would be under the existing process-based definition where selection must be shown. Rather the pattern can still be published with careful discussion of those processes that are consistent with any criteria the researchers have tested in their study. Fourth, this framework requires trait divergence, rather than just trait evolution, so other phenomena like character convergence (Grant, 1972) and red-queen escalation are excluded and can be examined separately.

Ecologists and evolutionary biologists are motivated to (1) describe the natural world to find patterns that govern biological diversity and (2) understand the proximate and ultimate processes that generate these patterns. By unlinking character displacement from resource competition, and species interactions generally, we hope to facilitate both these goals.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Appendix 1. Criteria for 'ecological' character displacement, modified from (Schluter & McPhail, 1992).
Table A1. Criteria applied to all processes.