

Opinion

Moving Character Displacement beyond Characters Using Contemporary Coexistence Theory

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Character displacement is one of the most studied phenomena in evolutionary biology, yet research has narrowly focused on demonstrating whether or not displacement has occurred. We propose a new experimental approach, adopted from the coexistence literature, that directly measures interspecific competition among sympatric and allopatric populations of species. Doing so allows increased ability to (i) test predictions of character displacement without biases inherent to character-centric tests, (ii) quantify its effect on the stability of coexistence, (iii) resolve the phenotypic pathways through which competitive divergence is achieved, and (iv) perform comparative tests. Our approach extends research to forms of character displacement not readily identified by past methods and will lead to a broader understanding of its consequences for community structure.

A Brief History of Character Displacement Research

High ecological similarity among species precludes stable coexistence [1], meaning that competing species will ultimately exclude one another unless differences that promote stabilization evolve [2]. The process by which **character** (see [Glossary](#)) shifts evolve in response to the presence of interspecific competition is known as **ecological character displacement** [3]; we refer to ecological character displacement as ‘character displacement’ for brevity henceforward, exclusive of reproductive character displacement [4]. Character displacement was classically considered a phenomenon that occurs primarily among closely related or incipient species [5], given their assumed ecological similarity, but has since been generalized to include distant relatives [6] and entire communities [7]. We do not wish to review the rich history of character displacement research, as this has been achieved elsewhere [8–10], but note that character displacement has been studied for about 50 years to understand its role in population divergence, speciation, diversification, and community structure [4].

Although character displacement remains central to understanding how genetic, phenotypic, and species diversity arise [4,8], most empirical tests do not go far beyond demonstrating its existence, often with unclear success. In 1992, Schluter and McPhail [11] outlined six criteria (see Box S1 in the Supplemental Information online) that must be met to rule out alternative explanations for patterns consistent with character displacement; >20 years and 144 case studies later, all six criteria were met in only 5% of studies [10]. Yet, theory continues to advance, providing predictions for when and how character displacement might play out [12–14], as well as its consequences for ecological communities [15]. For example, theory provides insight into how character displacement might manifest under different forms of competition (resource vs. apparent [16]) and in the presence of abiotic

Trends

Recent evaluations of tests of character displacement suggest major gaps in our understanding.

We advocate for adopting an experimental approach from the ecological literature to allow researchers to test long-standing theory about when, where, and how character displacement occurs.

The approach adopts an invasibility criterion, and in practice is assessed by measuring the population growth rate of a species when rare competing against a background of individuals of another species from either sympatric or allopatric populations.

We show how adopting this approach will provide unbiased demonstrations of whether character displacement is present, as well as reveal its evolutionary underpinnings and ecological consequences.

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gradients [14], as well as its consequences for resource use and the outcome of competition [17]. To keep pace, empiricists need methods that efficiently meet all six criteria while simultaneously being able to provide answers to classic and emerging questions beyond tests of whether character displacement does or does not exist.

We propose a new experimental framework, adopted from the contemporary coexistence literature in ecology, that can answer fundamental questions that underlie character displacement research as well as move the field forward in new directions. To achieve this, we first argue that traditional character-based approaches to character displacement introduce biases that underestimate its prevalence and provide a narrow perspective of the phenotypic pathways through which it is achieved. We then describe a specific type of competition experiment that allows tests of character displacement that are not contingent on understanding how character differences map onto competitive differences, and that meets Schluter and McPhail's [11] six criteria (Box S1). Finally, we detail how our method opens up new research avenues toward elucidating the evolutionary underpinnings and ecological consequences of character displacement. Overall, our goals are to bring to light rarely acknowledged limitations of existing character displacement research, to present a new method that overcomes those limitations identified by us and past research [10,11] using methods borrowed from community ecology, and to present testable predictions for how competitive differences between species might evolve in **sympatry**.

Sources of Bias in Traditional Character-Centric Tests of Character Displacement

We contend that character-centric tests of character displacement offer a biased perspective of its diversity and prevalence, and rely on assumptions about the relationships between characters, competition, and evolution that are often unsupported [18,19]. To demonstrate this argument, we break down a traditional case study of character displacement into three steps. Step 1: in the field, the researcher observes character differences among two species in sympatry that appear more exaggerated than in **allopatry**. Step 2: the researcher finds replicated sympatric and allopatric populations, and measures a suite of characters that might affect resource use and therefore mediate competition among species. Step 3: the researcher performs statistical tests to determine whether differences are significantly different in sympatry than in allopatry. The first step results in an accumulation of character displacement research on organisms in which there are initial observations that it might exist. Though this approach is not a problem for the inferences of individual studies, and is a feature of any study driven by natural history observations, it likely underestimates the phenomenon of character displacement as a whole and is biased toward its most conspicuous forms.

The second step relies on our ability to understand the characters that mediate competitive interactions, and can underestimate instances of character displacement in three scenarios. First, one might measure characters that are unimportant to differences in resource use among competing species (Figure 1A), missing those few characters that have responded to character displacement. Although a partial solution is to measure many characters, doing so inflates the risk of committing type I errors and might still miss important characters that are less obvious or difficult to measure. In a recent test of character displacement in plants, two of 11 characters showed greater character divergence in sympatry than in allopatry [20]. If those two characters had been overlooked, then character divergence in sympatry would have been missed, which highlights the potential for character choices to influence discovery rates. Second, univariate character differences among species can map poorly onto resource-use differences if resource partitioning is achieved via character combinations (Figure 1B) [21]. In annual plants, for example, the characters that underlie resource partitioning are multidimensional [22],

Glossary

Allopatry: regions in landscapes in which two species do not co-occur.

Character: an observable feature or phenotypic trait of an organism; could be morphological, physiological, behavioral, or phenological.

Ecological character

displacement: the process by which interspecific competition drives evolutionary change, giving rise to character shifts among populations of a given species in regions where its distribution overlaps with one or more competitors relative to regions of allopatry.

Evolutionary rescue: evolution allows the recovery of a population that had been declining to extinction.

Fitness difference: differences in the competitive abilities and intrinsic population growth rates among two competing species, which reduce the possibility of stable coexistence.

Note that ecological 'fitness differences' are not the same as individual fitness in an evolutionary context.

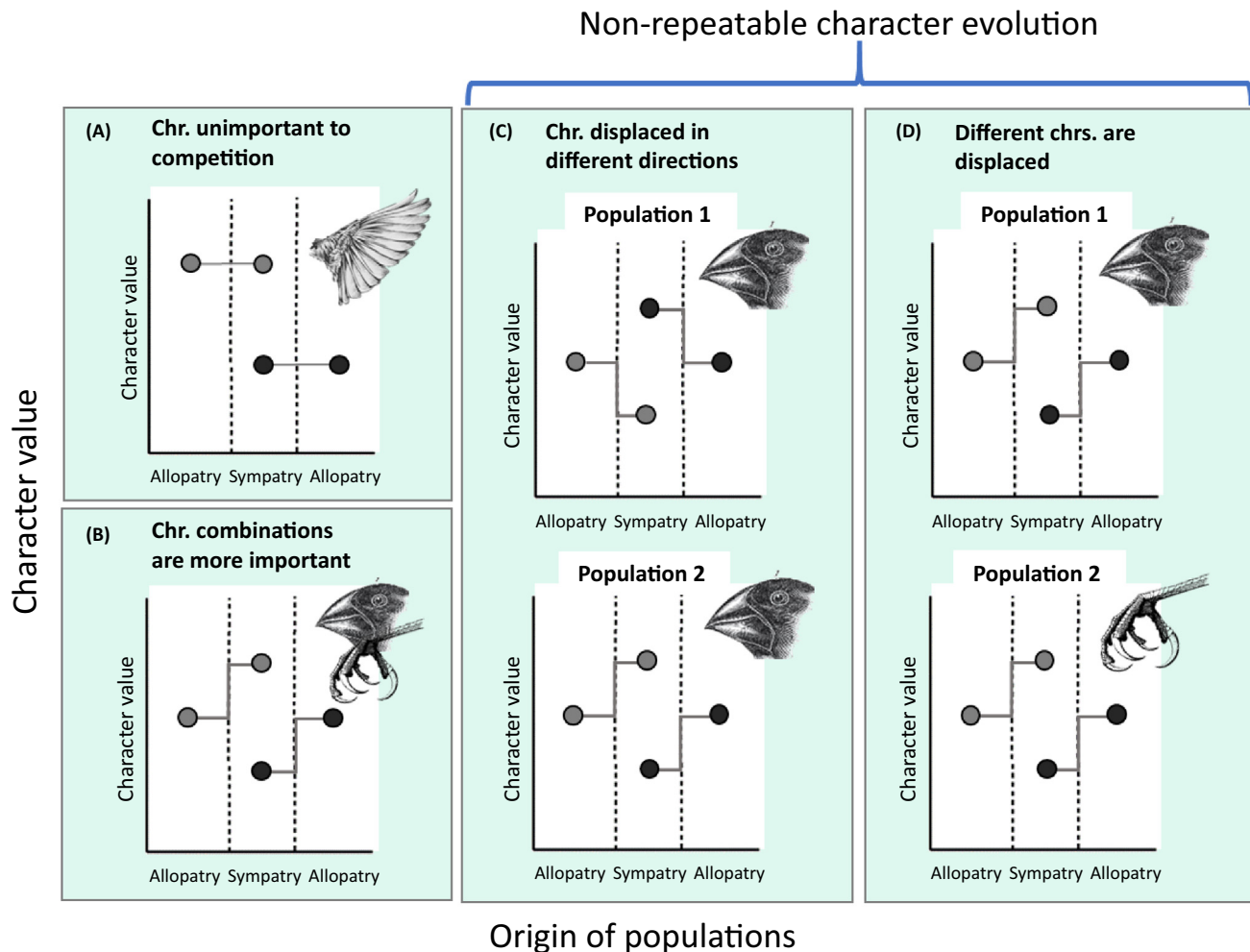
Intrinsic population growth rate: the growth rate of a population when at low abundance and not experiencing competition.

Invasibility framework: population growth rates of a focal population or species when grown at low relative frequencies in competition with another population or species.

Non-repeatable character evolution: the idiosyncratic evolution of different character states in independent populations in response to similar ecological pressures.

Stabilizing difference: the magnitude to which intraspecific competition is greater than interspecific competition, which increases negative frequency dependence and thus increases the stability of coexistence.

Sympatry: regions in landscapes in which two species co-occur.



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Figure 1. Four Scenarios in Which Focusing on Specific Characters Would Miss Instances of Character Displacement. Focal characters are depicted in the corner of each panel. The characters that are measured might be (A) unimportant to competitive interactions, or (B) important only as part of multivariate character combinations. Non-repeatable character displacement would be missed by traditional tests if (C) single characters are displaced in different directions in different sympatric populations (e.g., beak size decreases in population 1 of species A but increases in population 2), or if (D) different characters are displaced in different sympatric populations (e.g., beak size diverges among species in population 1 but limb size diverges in population 2). Light gray points = populations of species A, dark gray points = populations of species B, Chr. = character.

suggesting that evolution of differences that partition resources might also be multidimensional. Third, theory predicts that character divergence is only one outcome of the process of character displacement; character convergence and parallel shifts are also possible [3,13,17], but empirical examples are rare [20,23]. The compounding problem of missing important characters and important combinations of characters means that less conspicuous or less intuitive but important forms of character displacement are underestimated.

The third step assumes that character divergence via character displacement proceeds repeatedly in the same direction and involves the same characters – that species A always increases, while species B always decreases in character *x* in response to competition. However, what matters to competitive interactions is not the direction of character evolution,

or even the evolution of differences in single characters, but rather how resource-use differences evolve among species, which could be achieved via multiple phenotypic solutions [24]. We argue that character displacement encompasses (i) the evolution of similar absolute differences in character x among species A and B in sympatry, but in variable directions (Figure 1C), as well as (ii) the evolution of different characters in different populations (Figure 1D). Although our argument is consistent with existing definitions of character displacement, instances of **non-repeatable character evolution** have not been considered in theoretical or empirical treatments of character displacement, and cannot be detected by the statistical averaging of characters among replicated sympatric populations. Disentangling repeatable versus non-repeatable phenotypic evolution is key to providing a full picture of how selection has led to phenotypic divergence in competitive environments [25].

For the reasons detailed above, we argue that the existing literature underestimates the prevalence of character displacement and offers a biased perspective of the phenotypic pathways through which it is achieved. We do not suggest that evolution of specific characters is unimportant to understanding the phenomenon of character displacement; the fact that many forms of character evolution are possible in response to competition suggests a rich opportunity to study the relative importance of alternative phenotypic pathways to character displacement. Later, we discuss how characters could be invoked secondarily to a new experimental approach to understand the individual and combined effects of specific characters.

A New Approach to Testing Predictions of Character Displacement

Experimental tests of interspecific competition are needed to move character displacement research forward without the biases inherent to character-centric tests. Such experiments would allow tests of a fundamental prediction of character displacement [26]: that interspecific competition is weaker among competitors that evolved in sympatry than those that evolved in allopatry. Testing that character displacement shapes competitive interactions remains the least frequently met of Schluter and McPhail's [11] six criteria [10] despite it being the key criterion that links pattern to process [27]. Although weakened interactions in sympatry are the expectation if character displacement results in resource divergence [5], convergence in resource use (increased overlap of resource use in sympatry compared with allopatry [3]) might prevail in some circumstances, even in the presence of some divergence [13,17]. In the main text, we restrict our discussion to character displacement that results in divergence of resource use, but provide an in-depth comparison of character divergence versus convergence during the evolution of competitive interactions in Box S2 and Box 1 (viewed from the perspective of contemporary coexistence theory).

Although many experimental designs exist to test competitive interactions among species, a way forward in character displacement research is to use tests of the **invasibility criterion**, which offer high inferential power [28,29]. To assess the invasibility criterion, population growth rates are measured when each species is rare and their competitors are at their single-species equilibrium population sizes (or are abundant if equilibrium population sizes are difficult to know *a priori*; see Supplemental Information), such that competition is mostly interspecific for the rare species. The more intensely a species experiences interspecific competition, the lower its population growth rate will be when rare while growing with a competitor (λ_{rare} ; Figure 2A). This method can be applied to test the consequences of coevolutionary history on interspecific competition by assessing the invasibility criterion among populations that either co-occur in sympatry (reciprocally for populations of species A and B that overlap geographically; orange region of Figure 2B) or are allopatric and have no history of interaction (reciprocally for

populations of species *A* and *B* that do not overlap geographically; red and yellow regions of Figure 2B). Though this approach is not appropriate for all study organisms, the goal of employing it is not to be able to test character displacement on all organisms or even on the same organisms as past studies. Rather, the goal is to be able to test character displacement across taxa even if the characters being displaced are not obvious or measurable. Figure S1 provides a decision tree to aid researchers in determining whether a given system is appropriate for invasibility experiments.

Statistically, a model to test character displacement could use λ_{rare} as the response variable, and population origin (sympatry or allopatry), species, and their interaction as predictor variables. A main effect of population origin without an interaction would be evidence that the process of character displacement has shaped the strength of interspecific competition, whereas an interaction would indicate that character displacement is present but asymmetrical between species. Note that our definition of character displacement is most aligned with that of Grant [3], which is based on differences among populations within species based on history of sympatry or allopatry with a competitor, rather than Brown and Wilson's [5] definition of differences among species in sympatry versus allopatry. Although we contend that any direction of change could be interpreted as evidence of character displacement, resource-use divergence in sympatry predicts that species evolve higher λ_{rare} in sympatry than λ_{rare}

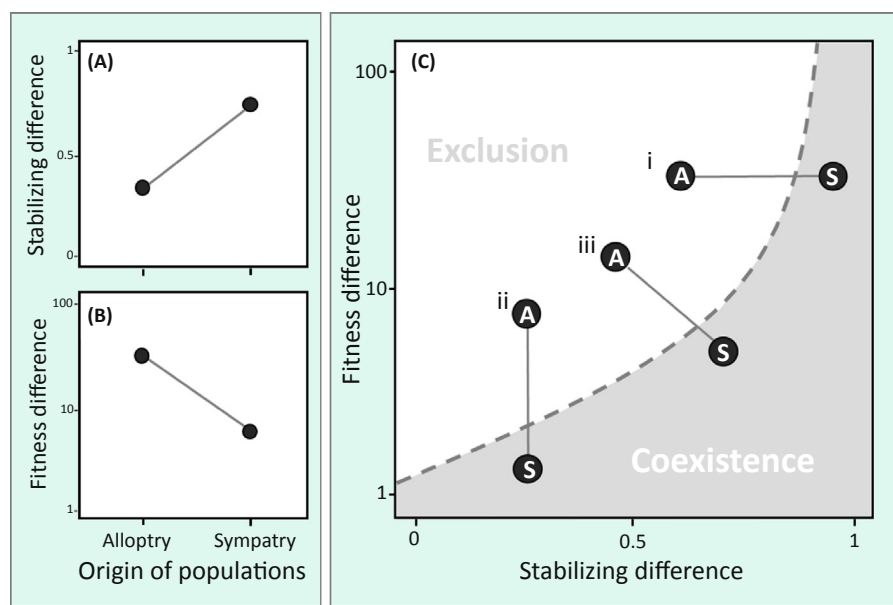
Box 1. Disentangling Divergent versus Convergent Character Displacement

Abrams [13] theoretically demonstrated that character divergence among species in response to competition is only one form of character displacement, and, perhaps counterintuitively, that competition can also drive convergence in characters [17]. For example, co-occurring weasels (*Mustela* spp.) converge in dentition in sympatry, a character associated with dietary niches [23]. The basic premise is that, to coexist in sympatry, species must be different enough to partition resources, but not so different that they compete poorly under the specific conditions and resources available at a given locality [17,46]. Individuals of an inferior competitor that use resources more similarly to superior competitors will have higher fitness [46], causing species to converge in resource use and the mediating characters. Although character convergence in response to interspecific competition is often dismissed as a special case, character displacement has been understudied in organisms in which it is most likely to emerge, such as those for which resources are not substitutable (e.g., plants) [17].

Although invasibility is the net effect of divergence or convergence in resource use (Box S2), it cannot disentangle their relative magnitudes. However, with a few additional experimental treatments, invasibility experiments can be extended to quantify the magnitudes of two types of competitive differences that are likely to diverge and converge as a consequence of character displacement. Specifically, the strength of interspecific competition estimated via invasibility experiments can be viewed as the net outcome of competitive differences that stabilize coexistence and those that destabilize it, termed '**stabilizing differences**' and '**fitness differences**', respectively [31,47]. Stabilizing differences are the phenomenological outcome of resource partitioning between two species on population dynamics [31], and are calculated from the relative intensities of interspecific compared with intraspecific competition. Coexistence is increasingly stabilized as their ratio approaches 0, by introducing negative frequency dependence that buffers populations from exclusion when rare. By contrast, fitness differences arise from competitive asymmetries between two species in a given resource environment [31], and are estimated by the products of **intrinsic population growth rate** and competitive response ratios [37].

The net outcome of competition – coexistence or the eventual competitive dominance of one species over the other – is determined by the relative magnitudes of stabilizing differences that act to promote coexistence and fitness differences that act to preclude it. When fitness differences increase through increased differences in competitive ability or intrinsic population growth rates between two species, stable coexistence is only possible if those increases are balanced by existing stabilizing differences or the evolution of increased stabilizing differences. Though we will not detail the specific methods of how stabilizing and fitness differences are calculated, they generally include three components: (i) quantifying population growth rates when each species is rare (competing mainly with heterospecifics) and abundant (competing mainly with conspecifics), (ii) rearing each species at low densities in the absence of competitors, and (iii) fitting competition models to those data to parameterize the competition coefficients and intrinsic population growth rates. More specific methodological details can be found in published examples that use annual plants [37], perennial plants [48], plankton [49], and mollusks [50].

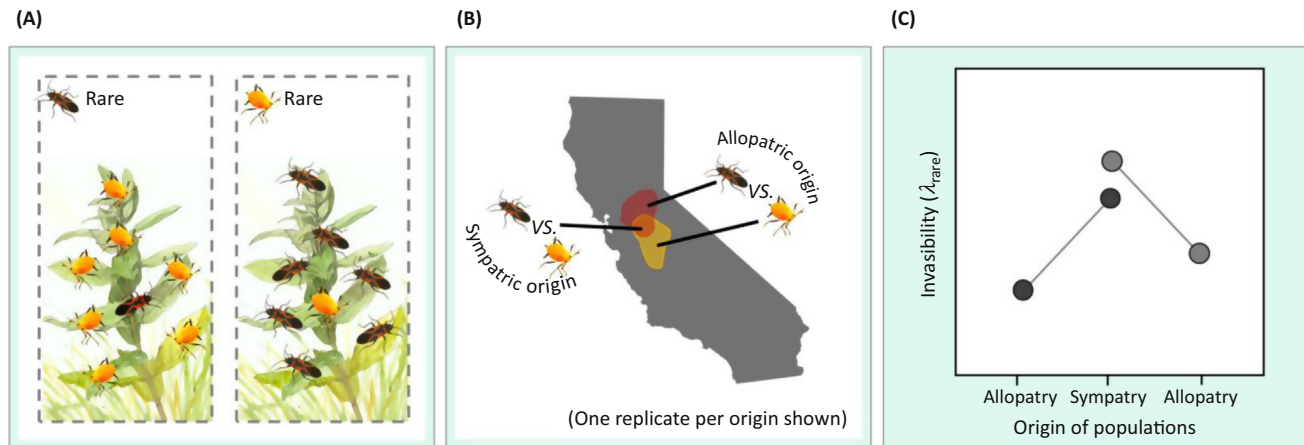
Though the microevolution of stabilizing differences and fitness differences has not been explored beyond verbal models [15], we predict that these quantities diverge and converge as a consequence of character displacement, respectively. Because stabilizing differences arise via resource partitioning, and character divergence via character displacement is thought to confer divergence in resource use, then stabilizing differences should evolve to be higher among population pairs that originate from sympatry than those that originate from allopatry (Figure 1A). Fitness differences, by contrast, are promoted by competitive asymmetries that arise because species differ in how effectively they acquire resources that are most limiting to population growth. Because character convergence is thought to minimize such competitive asymmetries, fitness differences should be lower among population pairs that originate from sympatry than those that originate from allopatry (Figure 1B). Note that character displacement could result only in resource-use divergence [only stabilizing differences evolve; Figure 1C (i)], only in resource-use convergence [only fitness differences evolve; Figure 1C (ii)], or some combination [both types of differences evolve; Figure 1C (iii)], and in all cases, coexistence is increasingly stabilized. A scenario in which only one type of difference is under selection in sympatry [Figure 1C (i) and (ii)] is most likely if fitness differences are small enough or stabilizing differences are large enough in allopatry, respectively, prior to coevolution. Empirical research is needed to test these predictions.



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Figure 1. Predicted Consequences of Character Displacement for Coexistence Mechanisms. (A) Stabilizing differences arising from resource partitioning among species are predicted to increase as a consequence of character displacement (i.e., divergence in resource use [15,46]) – stabilizing differences are bounded by 0 and 1, with 1 meaning that population dynamics of both competitors are strongly negative frequency dependent and stable coexistence is likely. (B) Fitness differences arising from competitive asymmetries among species are predicted to decrease as a consequence of character displacement [i.e., convergence in resource use [15,46]) – fitness differences are bound between 1 (competitive symmetry) and infinity (competitive asymmetry). (C) Coexistence outcomes (defined by mutual invasibility; coexistence = shaded region, competitive exclusion = unshaded region) depend on the relative strengths of stabilizing differences and fitness differences. Character displacement is predicted to move sympatric population pairs ('S') further into the shaded region compared with allopatric population pairs ('A'), either through (i) increased stabilizing differences, (ii) decreased fitness differences, or (iii) both.

between allopatric populations in response to competition ($\lambda_{\text{rare[sympatric]}} > \lambda_{\text{rare[allopatric]}}$; Figure 2C). However, it is possible that emerging empirical evidence will highlight a mismatch between theory and data; a recent study found no difference in invasibility among sympatric and allopatric populations of experimentally evolved seed beetles despite evolution in resource use [30]. Whether this outcome is general and also emerges in retrospective tests of character displacement in the field are not known.



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Figure 2. Demonstrating Character Displacement Using Invasibility Experiments. (A) To test invasibility, population growth rates are estimated while each species is rare and its competitor is at carrying capacity (or ‘abundant’ if carrying capacities are not known, see Supplemental Information). (B) To test character displacement using the invasibility framework, the competitive trials shown in panel A must be performed in four treatments: 1. Species $A_{rare[sympatric]}$ versus Species $B_{abundant[sympatric]}$; 2. $B_{rare[sympatric]}$ versus $A_{abundant[sympatric]}$; 3. $A_{rare[allopatric]}$ versus $B_{abundant[allopatric]}$; and 4. $B_{rare[allopatric]}$ versus $A_{abundant[allopatric]}$. Replication can be achieved by sampling additional populations in each colored region to compete multiple unique pairs of sympatric and allopatric populations (one replicate per origin shown). (C) Character displacement that results in resource-use divergence is present when a species’ ability to increase its population when rare (λ_{rare}) is greater when sympatric population pairs compete compared with allopatric ones (aka treatments 1 vs. 3 and 2 vs. 4); see Box S2 for predictions consistent with character displacement via convergence in resource use. Light gray points = populations of species A, dark gray points = populations of species B.

The invasibility framework overcomes many shortcomings of prior approaches (Box S1) and has six additional advantages to assessing character displacement and tests of competition more generally. First, differences among populations of species are inferred via population growth responses, which can be viewed as the phenomenological outcome of all characters that underlie those differences [31]. As a result, the invasion framework is not contingent on an *a priori* understanding of the ecological importance of specific characters, and competitive differences consistent with character displacement can emerge even if character displacement is multidimensional or non-repeatable. Second, by examining the population growth rates of species when rare and primarily interacting with heterospecific individuals, invasibility experiments isolate the effect of interspecific competition while holding total density constant [32].

Third, as we discuss below, the invasibility criterion allows a clear assessment of the role of character displacement for the stability of coexistence. That character displacement stabilizes coexistence among species that would otherwise exclude one another (given enough time and without dispersal) is often assumed but rarely tested. Fourth, the method itself is straightforward to perform, analyze, and interpret relative to other competition designs [32]. It is particularly useful for species with slow population dynamics or long generation times, for which the multigenerational experiments needed to explore population dynamics and reach equilibrium population sizes are not feasible. Thus, the experimental design we have proposed serves as a base model for how invasibility experiments can be used to test predictions of character displacement, and can be modified to test a diversity of questions (see Outstanding Questions). Fifth, invasibility outcomes can be extended to test the evolutionary consequences of other interactions affecting coexistence, such as apparent competition via predators, parasites, or mutualists (e.g., [33]). Finally, evaluating character displacement via population growth rates, a currency common to a diversity of taxa, would facilitate comparative explorations of factors that influence its strength.

A key consideration in experimental tests of competitive differences is the small spatial and temporal scales of inference, which are limited to the resource environment in which competition is measured. In community ecology, this limitation is viewed as a current challenge to understanding the mechanisms that maintain diversity at local and regional scales, and across temporally fluctuating environments [34]. In the context of character displacement, however, inferences made at the local scale have clear utility given that character displacement by definition manifests in sympatry, and sympatry by definition is the scale at which species interact. Although differentiation can occur in sympatry via partitioning of microhabitats, a phenomenon sometimes referred to as ‘microallopatry’ [35], invasibility experiments can accommodate this form of differentiation either by using mesocosms that incorporate microhabitat heterogeneity (e.g., fish reared in ponds with benthic and limnetic zones [26] or seasonal variation in growing conditions [36]) or by replicating the experiment across relevant microhabitats that vary through space (e.g., plants competing in deep and shallow soils [20]) or time (e.g., simulating interannual rainfall [37]).

An Agenda for Future Character Displacement Research

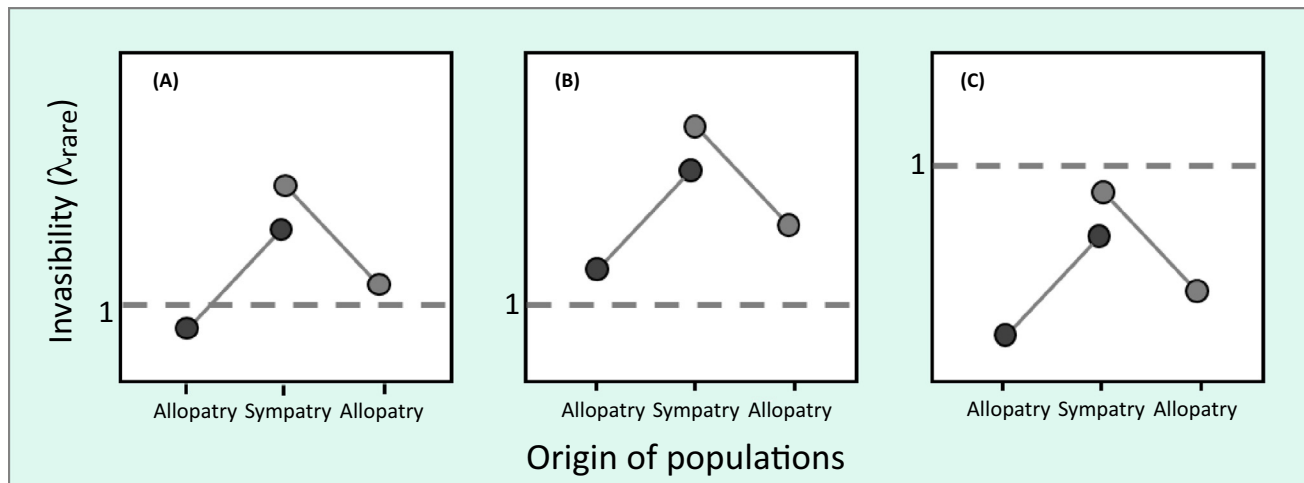
We have argued that the outcome of invasibility experiments can reveal the net effect of character displacement on the intensity of interspecific competition, even in cases in which the specific underlying characters are not readily identifiable and when character displacement results in both divergence and convergence in resource use [3] (Box S2). Such experiments would bridge a critical gap between theory and empirical research. In the following sections, we detail two additional research avenues at the intersection of ecology and evolution that can be explored using the invasibility framework.

Is Character Displacement an Evolutionary Pathway to Species Coexistence?

A major unanswered question is the degree to which character displacement facilitates species coexistence. To aid our discussion, it is critical to first note that ‘coexistence’ does not simply include all species found to co-occur in a specific area, but rather, only those species whose populations are buffered from extinction at low abundance. Many species might be found together that have no intrinsic mechanism that stabilizes coexistence, such as species whose populations are maintained via dispersal from elsewhere [38] or those in which exclusion is inevitable but takes time to play out [39]; Siepielski and McPeck [29] refer to these species as ‘co-occurring’ but not ‘coexisting’. In other words, we consider the effect of character displacement on the mechanisms that stabilize coexistence among competing species, rather than on their probability of co-occurring by any mechanism.

We have thus far discussed the invasibility framework only in terms of its ability to quantify the intensity of interspecific competition, but its greatest utility is its application to predicting the stability of coexistence [29]. The invasibility test simulates population dynamics when species are driven to low abundance or disperse to new sites, and are thus rare relative to their competitors. To relate the invasibility criterion to coexistence, one must examine where λ_{rare} falls relative to a persistence threshold ($\lambda = 1$, dashed lines in Figure 3); above this threshold, populations should increase and below it they should decline to extinction. Coexistence is predicted when both species can increase in population size when rare (both $\lambda > 1$), whereas coexistence is absent if one or both species decrease in population size when rare ($\lambda < 1$).

Although some authors predict that character displacement necessarily leads to coexistence among species that would otherwise exclude each other [40,41], empirical evidence testing this prediction is lacking. If this prediction is true, then character displacement might provide **evolutionary rescue** to populations [34,35], facilitating coexistence among species that



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Figure 3. Relating Evidence of Character Displacement via Invasibility Experiments to Coexistence Outcomes. Character displacement that results in divergent resource use is present when a species' ability to increase its population when rare (λ_{rare}) is greater among sympatric population pairs than allopatric ones; stable coexistence is predicted when both species maintain population growth rates above 1 (dashed line) when rare. Here we illustrate three outcomes: (A) character displacement in sympatry increases the likelihood of coexistence among species that would otherwise exclude each other, (B) character displacement has no effect on coexistence outcomes but increases the stability of coexistence, meaning that sympatric population pairs should reach larger, more even abundances than allopatric ones, and (C) neither sympatric nor allopatric population pairs coexist stably; co-occurrence in sympatry is either transient or maintained via dispersal. Light gray points = populations of species A, dark gray points = populations of species B.

would not otherwise coexist [42], such as when species are competitively asymmetric prior to evolution in sympatry (i.e., $\lambda_{rare[sympatric]} > 1 > \lambda_{rare[allopatric]}$; Figure 3A). However, two other outcomes are possible. First, both sympatric and allopatric population pairs might coexist if species are preadapted in allopatry to coexist upon contact, with character displacement increasing the stability of coexistence (i.e., $\lambda_{rare[sympatric]} > \lambda_{rare[allopatric]} > 1$; Figure 3B). By increased stability, we mean a strengthening of negative frequency-dependent population growth rates, or λ_{rare} of both species that increasingly exceed 1. Second, stable coexistence might not be possible for either sympatric or allopatric population pairs, even if character displacement has brought λ_{rare} closer to 1 (i.e., $1 > \lambda_{rare[sympatric]} > \lambda_{rare[allopatric]}$; Figure 3C). In this case, a state of 'sympatry' reflects co-occurrence but not coexistence, and might be transient in the absence of further character displacement. In other words, assessments using λ_{rare} simultaneously allow inferences about whether competitive interactions have evolved in response to coevolutionary history (i.e., $\lambda_{rare[sympatric]} \neq \lambda_{rare[allopatric]}$), and if so, the consequences of this evolution for coexistence outcomes (i.e., where λ_{rare} fall relative to 1). As discussed earlier, all three outcomes are consistent with character displacement theory under resource-use divergence (i.e., that interspecific competition should be weaker among sympatric population pairs compared with allopatric ones [15]), yet not all outcomes lead to stable coexistence.

How Do Specific Characters Contribute to Competitive Divergence?

Rather than abandoning traditional explorations of character evolution in response to competition, we suggest that characters be measured as a complement to the invasibility framework to identify the phenotypic pathways through which character displacement is achieved, and the contributions of individual characters to total competitive divergence. Specifically, when competitive divergence is estimated via invasibility experiments on replicated sympatric and allopatric population pairs, one could simultaneously measure characters that would be measured in a traditional study of character displacement. The analyses might take the form

of multiple regression, where for example, effect sizes of how λ_{rare} responds to a history of sympatry or allopatry are regressed against effect sizes of how specific characters also respond to a history of sympatry or allopatry. Doing so would identify what fraction of total competitive divergence is attributable to specific characters, as well as how much variance in competitive divergence remains unexplained, potentially due to missing important characters or character combinations (Figure 1). Partitioning the relative contributions of specific characters would reveal whether character displacement is achieved via large effects of few characters or small effects of many characters, conceptually analogous to questions about whether adaptation is achieved via few genes of large effect or many mutations of small effect [43]. We note that the ‘phenomenon first’ workflow proposed here (first test emergent effects on competitive divergence and then identify causal characters) is analogous to the approach taken by the related study of reproductive isolation, where degree of isolation is first quantified and its underlying ecological and genetic drivers are then partitioned [44]. Note that although these types of analyses can only be performed in systems with highly replicated sympatric versus allopatric pairs due to the statistical power needed to perform multiple regression, doing so would provide invaluable answers to questions that have not been asked because methods that explicitly link character differences to resource-use differences had not been clear.

Concluding Remarks

We have suggested a new empirical approach to better test predictions of character displacement while allowing new insight into its mechanistic underpinnings and its ecological consequences. The approach will allow character displacement to be examined with greater inferential power in a diverse subset of organisms that are amenable to experimental tests. This includes some classic model organisms of past character displacement research (e.g., *Anolis* lizards [45]), as well as organisms that have been underrepresented thus far (e.g., plants and insects). Theoretical treatment of character displacement continues to advance in new directions – the challenge now falls on empiricists to test classic and emerging theory, for which the invasibility framework offers a way forward.

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Supplemental Information

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Outstanding Questions

How prevalent is character displacement across species, and does it depend on species' life histories, landscape characteristics, or taxonomy?

How often does character displacement provide evolutionary rescue for species that could not otherwise stably coexist?

How strongly do specific characters explain differences in the strength of interspecific competition among population pairs that are sympatric versus those that are allopatric?

How does character displacement interact with local adaptation to abiotic conditions?

How does character displacement play out in diverse communities with many species? How might invasibility experiments be applied to identify community-wide character displacement?

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