

Is competition needed for ecological character displacement? Does displacement decrease competition?

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Interspecific competition for resources is generally considered to be the selective force driving ecological character displacement, and displacement is assumed to reduce competition. Skeptics of the prevalence of character displacement often cite lack of evidence of competition. The present article uses a simple model to examine whether competition is needed for character displacement and whether displacement reduces competition. It treats systems with competing resources, and considers cases when only one consumer evolves. It quantifies competition using several different measures. The analysis shows that selection for divergence of consumers occurs regardless of the level of between-resource competition or whether the indirect interaction between the consumers is competition (–,–), mutualism (+,+), or contramensalism (+,–). Also, divergent evolution always decreases the equilibrium population size of the evolving consumer. Whether divergence of one consumer reduces or increases the impact of a subsequent perturbation of the other consumer depends on the parameters and the method chosen for measuring competition. Divergence in mutualistic interactions may reduce beneficial effects of subsequent increases in the other consumer's population. The evolutionary response is driven by an increase in the relative abundance of the resource the consumer catches more rapidly. Such an increase can occur under several types of interaction.

KEY WORDS: Character displacement, competition, consumer–resource system, divergence, interspecific interaction.

Ecological character displacement has been defined as “the general process of phenotypic change induced or maintained by resource competition” (Schluter 2000a, p. 69). Most authors, including Schluter (2000a,b), restrict the definition to evolutionary change; thus it assumes the existence of genetic variation that will permit the evolutionary shift. The two questions given by the title may seem strange, given this definition and the history of the term “character displacement.” Ecological character displacement is usually understood to reduce the population dynamical effect of competition. Some authors have restricted character displacement to increased differences between traits in sympatry; that is, divergence. Schluter's relatively broad definition reflects the possibility that characters may converge in response to competition (Grant 1972) and there are several mechanisms that could in theory

produce convergence or parallel change (Abrams 1986, 1987a,b, 1990; Abrams and Matsuda 1994; Fox and Vasseur 2008). Nevertheless, divergence has far more empirical support (Schluter 2000a; Pfennig and Pfennig 2010, 2012), and some authors restrict the definition to divergence. This article primarily considers ecological scenarios under which divergence is expected; convergent displacement is mentioned briefly in the “Extensions and Modifications” section.

The assumed necessity of competition for character displacement is reflected in Schluter's (2000a,b) six requirements for documenting character displacement. One of these is to demonstrate that similar phenotypes actually do compete for resources. Schluter (2000a) noted that proof of competition was the evidence most frequently missing in purported cases of character



displacement. Several recent reviews have reemphasized the importance of competition for character displacement. Stuart and Losos (2013, p. 404) question the importance of character displacement because, “for most cases [published after the early 1980s] interspecific competition has not been documented and confounding mechanisms have not been ruled out.” They do not question the existence of character shifts, or overlapping use of resources, but argue that these cannot be validly claimed to represent character displacement without evidence of competition being present. In another prominent review, Losos and Ricklefs (2009, p. 832) claim that displacement is the result of “selection favoring adaptations that reduce competition between species, including morphological divergence and resource specialization.”

These claims raise three questions that surprisingly lack clear answers: (1) What is competition, and how can it be quantified?; (2) Is competition required for character displacement to be favored?; and (3) Does character displacement decrease competition? These questions are the focus of the remainder of this article.

What is Competition, and How Can it be Measured?

Competition in the ecological literature is always associated with mutually negative effects of two species on each other’s population size (Schoener 1982). It is also usually restricted to two mechanisms, exploitation and interference (Schoener 1983). Interference involves direct harm, whereas exploitation involves indirect effects via commonly used resources. Evolutionary biologists (Schluter 2000a; Pfennig and Pfennig 2012) have also restricted “competition” to mutually negative effects on population size. Character displacement has usually been restricted to situations involving exploitation. Mutually negative indirect effects via higher trophic levels (Holt’s 1977 apparent competition) do not represent competition by most definitions, although they have similar population-level effects (Chesson and Kuang 2008) and may produce similar evolutionary character shifts (Abrams 2000; Abrams and Chen 2002).

As documented by several reviews of experimental studies (Connell 1983; Schoener 1983; Denno et al. 1995), a single addition or removal of individuals of another species has been the most commonly used method to determine whether competition was present. The lack of mutually negative population effects implies an interaction other than competition. Paired positive effects (Levine 1976; Vandermeer 1980) are mutualism, whereas (+,–) effects on population size represent contramensalism (following Arthur and Mitchell 1989). Unlike competition, “mutualism” and “contramensalism” are not restricted to any particular mechanism. Inconsistencies between the treatment of mechanism and outcome in defining interactions were criticized in Abrams (1987c), but a generally agreed upon resolution of this problem has not emerged.

Both mutualism and contramensalism can arise from mutual resource exploitation when increased consumption of one of two competing resources reduces the competitive effect of that first resource on the second resource. This positive effect may be large enough to more than offset the first consumer’s increased consumption of the second resource. If the second resource is more important than the first resource in the diet of the second consumer species, the latter may benefit from higher numbers of the first consumer, which primarily uses resource 1. Early empirical examples of positive effects between consumers via their use of competing resources are provided by Davidson et al. (1984) and Dungan (1987).

In summary, both mutually negative (–,–) effects on population size and either shared resource exploitation or interference are required by the term “competition.” Character displacement is usually discussed in the context of exploitation competition (but see Abrams and Matsuda 1994). It has long been agreed that shared use of limiting resources that produces at least one positive effect does not constitute competition. (Theoretical treatments include Levine 1976; Vandermeer 1980, 2004; Abrams 1987c; Schoener 1993; Tsumura et al. 1993; Abrams and Nakajima 2007; and Abrams and Cortez 2015.) The evolutionary change in one consumer’s resource utilization traits in response to altered input, loss, or abundance of a second consumer has not been examined for noncompetitive interactions between consumers of shared resources. Even when the interaction is competitive, there has been little attention to how character displacement changes its strength. There appears to have been no attention to this question when the interaction via shared resource exploitation is something other than competition.

The above summary is incomplete because the nature and size of the perturbation used to determine the interspecific “effect” have not been specified. Such specification is required to determine the type of interaction and how its magnitude changes with character displacement. Schoener (1993, p. 366) stated that, “In the most precise existing theoretical formulation, an effect is defined as a change in equilibrium population size caused by a change in the input or abundance of another species.” However, subsequent work has shown that changed input or loss may have counterintuitive effects on abundance; that is, increased loss may increase abundance and increased input may decrease abundance. Abrams and Matsuda (2005) termed such counterintuitive outcomes “hydra effects.” One mechanism by which they may occur is a lowering of total resource productivity due to the change in the resource community caused by lower consumer mortality. It has also been shown that, for each type of perturbation to one consumer—abundance or input—the magnitude of the perturbation can alter the sign of its effect on the other consumer (Abrams et al. 1996; Abrams 1987c, 1998, 2001; Abrams and Nakajima 2007; Abrams and Cortez 2015). Even when there is no change

in sign, the magnitude of the perturbation to input or abundance will often change the population effect per unit of perturbation (Abrams et al. 1996; Abrams 1975, 2001). These possibilities are discussed in more detail below; see Abrams and Cortez (2015) for a recent analysis in the context of the consumer–resource system explored here.

Given these complications, both classifying an interaction and determining how it is changed by evolution require a measure of interaction strength. Our approach follows Abrams and Cortez (2015) in exploring the three most commonly used methods for measuring the effect of species *i* on species *j*. An effect on *j* may be measured by the change in the equilibrium (or long-term mean) population of species *j* produced by (1) a small change in the per capita mortality rate (or immigration rate) of consumer species *i*; (2) a small change in the population size of consumer species *i*; or (3) addition or removal of consumer species *i*. The first and second methods assume the initial state is a sympatric system, whereas the third may start with either allopatry or sympatry. These three methods are discussed in a more quantitative manner following presentation of the model, and are discussed in greater detail in Abrams and Cortez (2015). As noted above, the third method has been used in most empirical studies. However, method (1) is the standard theoretical method for measuring indirect effects in theoretical treatments of food webs (e.g., Novak et al. 2011).

We have not taken a position on the best method of measuring an interaction. All three measures provide useful insight because interactions generally cannot be fully described by a single number (Abrams 2001). As a consequence, the classification of an interaction as (–, –) may depend on the method chosen, and the quantitative change produced by evolution will almost always depend on the method. To evaluate the claim that competition is required for character displacement, we simply show that character displacement may often be favored in spite of none of the methods indicating competition. Abrams and Cortez (2015) demonstrated that all three categories of the between-consumer interaction (competition, mutualism, contramensalism) are possible for each of the three methods for the system studied here. In addition, the parameter range producing each type of interaction depends on the method used. We present most of our analysis for methods (1) and (2) because they are most amenable to analysis and because larger magnitude perturbations can often be understood as a succession of small magnitude perturbations.

The Model and Analysis

A number of articles (e.g., Lawlor and Maynard Smith 1976; Abrams 1986, 2006, 2012; Rueffler et al. 2006, 2007) have used models with two consumers and two resources to explore character displacement in the simplest possible setting that includes resource dynamics. However, all of these models with resource

dynamics have assumed that the resources do not interact with each other. Some analysis of evolution in similar models with between-resource competition has been carried out in the particular context of specialist–generalist competition (Abrams 2007; van Velzen and Etienne 2013). These two studies show that between-resource competition can produce qualitatively different consumer evolutionary responses than do comparable models with noninteracting resources.

The Model

ECOLOGICAL DYNAMICS

The main analysis is based on the simple system analyzed by Abrams and Cortez (2015), which has the following form:

$$\frac{dR_1}{dt} = R_1 (r_1 - k_1 (R_1 + \alpha q R_2)) - c_{11} R_1 N_1 - c_{21} R_1 N_2 \quad (1a)$$

$$\frac{dR_2}{dt} = R_2 (r_2 - k_2 (R_2 + (\alpha/q) R_1)) - c_{12} R_2 N_1 - c_{22} R_2 N_2 \quad (1b)$$

$$\frac{dN_1}{dt} = N_1 (b_{11} c_{11} R_1 + b_{12} c_{12} R_2 - d_1) \quad (1)$$

$$\frac{dN_2}{dt} = N_2 (b_{21} c_{21} R_1 + b_{22} c_{22} R_2 - d_2). \quad (1d)$$

The above equations describe two resources (R_1, R_2) that experience Lotka–Volterra interspecific competition and are fed upon by two consumer species (N_1, N_2), each of which has linear functional and numerical responses to both resources. The maximum per capita growth rate of each resource is r_i and the reduction in per capita growth with density is k_i . The competition coefficients for resources are expressed as a product of the geometric mean of the two coefficients, α , and an asymmetry parameter; q for the effect on resource 1 and $1/q$ for the effect on resource 2. Larger values of q reflect a higher per capita effect of resource 2 on resource 1 and a lower effect of 1 on 2. When competition between the resources is exploitative, α reflects the overlap in use of lower level resources (e.g., nutrients or foods) by the resource species, and q reflects the ratio of the mean food/nutrient uptake rate of resource 2 to that of resource 1.

The phenomenological representation of competition in the resource equations is somewhat at odds with the representation of indirect effects between consumers. However, using the Lotka–Volterra model to represent competition between resources greatly simplifies the analysis, and a full three-trophic level model with consumption of lower level resources will be examined in subsequent work. If the between-resource interaction is interference, or if it is exploitative for abiotic (not self-reproducing) resources, then the noncompetitive consumer interactions explored by Abrams and Cortez (2015) cannot occur. The Lotka–Volterra representation is a reasonable approximation in these cases.

The consumer equations (1c, 1d) assume a per capita capture (consumption) rate of resource j by consumer i given by c_{ij} and a corresponding resource conversion efficiency of b_{ij} . The parameter d_i is a constant, density independent per capita death rate (or metabolic loss rate) for consumer species i . In most of this analysis, we follow Abrams and Cortez (2015) in assuming all of the conversion efficiencies are equal, which allows them to be removed by scaling the R_i . The resulting equilibrium densities for equations (1) were derived in Abrams and Cortez (2015), and are given in the Appendix of the current article. Several modifications of this system have been considered in studies of ecological interactions between consumers, including the presence of direct density dependence in the mortality rates (Abrams 1986, 1987b), and type-II functional responses in the consumers (Abrams 1980; Vandermeer 2004). Some of these are treated briefly in the “Extensions and Modifications” section.

INTERACTION MEASURES

The three methods of measuring the interaction introduced in the “What is Competition?” section may be expressed in terms of equilibrium densities and their derivatives with respect to consumer per capita mortality rates. The measures of the effect of species i on species j that we used here are: method (1), $\partial N_j / \partial d_i$; method (2), $(\partial N_j / \partial d_i) / (\partial N_i / \partial d_i)$; method (3), $(N_{j, \text{symp}} - N_{j, \text{allo}}) / N_{i, \text{symp}}$, where “allo” and “symp” denote allopatric (alone) and sympatric (together). Methods (1) and (2) assume each N is the equilibrium sympatric density, whereas method (3) may start with either sympatry or allpatry. Expressions for the derivatives of densities with respect to mortality are given in the Appendix. For method (3), the expressions for sympatric populations are given by equations (A1, A2) and the more complicated allopatric population formulas are given in Appendix A of Abrams and Cortez (2015).

Method (2) is equivalent to $\partial N_j / \partial N_i$, evaluated at the equilibrium sympatric densities, but it may also be regarded as method (1) normalized by the effect of increased mortality of the perturbed consumer has on its own density. Methods (1) and (2) only differ in sign when species i has a hydra effect. Methods (1) and (3) can differ in sign when the allopatric equilibrium for species j involves exclusion of one of the resources. For the special case of Lotka–Volterra models (e.g., eqs. 1), methods (2) and (3) are equivalent, provided that both resources are present in allopatry. See Abrams and Cortez (2015) for more details.

EVOLUTIONARY DYNAMICS

The evolutionary component of the model describes how the capture rates c_{ij} change over time. The standard assumption in previous two-resource models of character displacement is that a trade-off relationship exists between the two capture rate constants for one (Abrams 2012) or both consumer species (Lawlor

and Maynard Smith 1976; Abrams 1986). Here we assume that a trade-off between the two capture rates, c_{11} and c_{12} , exists, and can be described by expressing c_{12} as a decreasing function of c_{11} . Other potential trade-offs are mentioned in the “Extensions and Modifications” section. In the context of a two-resource model, the resource use of a species is defined by its ratio of capture rates c_{i1}/c_{i2} . We can assume without loss of generality that in the initial state of the system, $c_{11} > c_{12}$. Divergence of consumer species 1 occurs if, following one of the positive perturbations to consumer species 2 discussed above, natural selection favors an increase in the ratio c_{11}/c_{12} when initially $c_{11}/c_{12} > c_{21}/c_{22}$, or a decrease in c_{11}/c_{12} when initially $c_{11}/c_{12} < c_{21}/c_{22}$. Equality of the two ratios ($c_{11}/c_{12} = c_{21}/c_{22}$) makes coexistence extremely unlikely, because it requires equal equilibrium resource densities in both allopatric systems. If such coexistence with neutral stability occurred in this system, equilibrium resource densities would be identical in sympatry and allopatry, and no evolutionary response would be produced.

In the main analysis we assume that each species is inherently better at capturing a different resource (“traditional” resource partitioning), so $c_{11} > c_{12}$ and $c_{21} < c_{22}$, implying $c_{11}c_{22} > c_{12}c_{21}$. Coexistence is possible, but under a narrower range of parameter values, when both species have higher capture rates of the same resource. This “defense-based” partitioning (Abrams and Cortez 2015) is considered in “Extensions and Modifications” section. Although we mainly consider cases in which all of the b_{ij} are equal, it should be noted that coexistence requires $b_{11}b_{22}c_{11}c_{22} > b_{12}b_{21}c_{12}c_{21}$ given that $c_{11}c_{22} > c_{12}c_{21}$.

We assume that there is genetic variation for the relative values of the two-resource consumption rates of consumer 1, and that the additive genetic variance is small enough that the simplifying assumptions of an adaptive dynamics approach (Geritz et al. 1998) are valid. Under this approach, the rate of change of the trait (c_{11}) is proportional to the derivative of individual fitness with respect to the individual’s trait value. Evolutionary equilibrium occurs when this derivative is zero:

$$b_{11} \hat{R}_1 + b_{12} \frac{\partial c_{12}}{\partial c_{11}} \hat{R}_2 = 0, \tag{2}$$

where the carats denote the equilibrium values. If the trait c_{11} is under stabilizing selection, it follows that, at the equilibrium,

$$\frac{\partial^2 c_{12}}{\partial c_{11}^2} < 0 \tag{3}$$

Equations (2) and (3) imply that the equilibrium character value and the direction of change in that value produced by a perturbation to the competitor’s dynamics are both determined by the ratio of the two-resource densities. In system (1), the equilibrium resource densities in the four-species system are determined solely by the parameters that affect consumer dynamics; they are

not influenced by parameters that only affect resource dynamics (α, q, r_i, k_i). However, the resource population growth parameters are key determinants of the equilibrium consumer densities, and the indirect ecological interaction between them (see the Appendix). The presence of additional resources and/or direct density dependence of consumer growth would make equilibrium resource densities dependent on their growth parameters (see the “Extensions and Modifications” section).

Our analysis examines whether competition, as defined by any one or all of the commonly used measures, is needed for character displacement. We also examine how the evolutionary response of an adaptively evolving consumer affects the magnitudes of the interaction given by the three interaction measures.

Results

DOES CONSUMER SPECIES 1 DIVERGE IN RESPONSE TO A POSITIVE PERTURBATION OF SPECIES 2? YES

For our purposes, a “positive perturbation” is a parameter change that increases species 2’s per capita growth rate without altering its resource uptake rate constants, c_{ij} . (We exclude effects on uptake rates because they directly alter the interaction.) For methods (1) and (2), we assume that the positive perturbation to consumer 2 is a small decrease in its mortality. A small increase in immigration would have the same qualitative effects if it were present (Yodzis 1988, 1989). Method (3) assumes the initial state is consumer 1 alone and at equilibrium; the positive perturbation to species 2 is introducing it and allowing it to reach equilibrium (or its dynamic attractor). Importantly, these measures frequently differ in sign and magnitude from each other, and their signs and magnitudes are both affected by the two parameters describing resource competition.

Divergence occurs when the evolutionary equilibrium c_{11} increases following a positive perturbation to consumer 2. Under small mortality perturbations (methods 1 and 2), the change in the evolutionary equilibrium of c_{11} is obtained by implicit differentiation of equation (2), and is given by

$$-\frac{\partial \bar{c}_{11}}{\partial d_2} = \frac{b_{11} \frac{\partial \hat{R}_1}{\partial d_2} + b_{12} \frac{\partial c_{12}}{\partial c_{11}} \frac{\partial \hat{R}_2}{\partial d_2}}{b_{12} \hat{R}_2 \frac{\partial^2 c_{12}}{\partial c_{11}^2}} = \frac{-b_{11} d_1 [b_{11} b_{22} c_{11} c_{22} - b_{12} b_{21} c_{12} c_{21}]}{b_{12} (b_{11} c_{11} d_2 - b_{21} c_{21} d_1)^2 \frac{\partial^2 c_{12}}{\partial c_{11}^2}}, \quad (4)$$

where \bar{c}_{11} denotes the evolutionary equilibrium of c_{11} defined by equation (2). The second equality above involves substituting for the equilibrium resource densities (see the Appendix) and using equation (2) to substitute for the evolutionary equilibrium value of $\partial c_{12} / \partial c_{11}$. The fact that selection is stabilizing guarantees that the far right quantity must be positive. Thus, given the assumption that $c_{11} c_{22} > c_{12} c_{21}$, a small reduction of the death rate of

consumer 2 increases the evolutionary equilibrium of c_{11} . In other words, consumer 1 diverges; the ratio of utilization rates for consumer 1 (c_{11}/c_{12}) becomes larger, making it more different from the corresponding ratio (c_{21}/c_{22}) for species 2. A key property of equation (4) is that it does not depend on any of the parameters of the resource dynamics; in particular, it is independent of competition between the resources, even though the nature of resource competition is an important determinant of the indirect ecological interaction between consumer species, as reviewed above.

Adopting method (2) to measure the interaction does not alter the divergence implied by lower death rates in the other species. However, a small decrease in the mortality of consumer species 2 may decrease its population size (the hydra effect), which raises the issue of whether decreased mortality in this case should be considered a positive perturbation to consumer 2. If the population decrease were considered to be a negative perturbation to species 2, then the same perturbation (decreased d_2) would be negative in the context of method (1) and positive in the context of method (2). This contradiction seems undesirable. Even when it decreases the equilibrium population size, lower mortality increases a consumer’s maximum per capita growth rate and increases the amount of additional mortality needed to cause extinction. Both of these effects represent positive demographic perturbations. Thus we also consider decreased mortality to be a positive perturbation in the context of method (2); under this interpretation, divergence of consumer 1 is still the evolutionary response to a positive perturbation to consumer 2. Nevertheless, it is important to be aware that, when there is a hydra effect in consumer 2, a higher population size of that species will sometimes be associated with character convergence of consumer 1, rather than divergence.

Under method (3), the initial state is the allopatric system, here assumed to have only consumer 1. The positive perturbation to consumer 2 consists of introducing it, or reducing its mortality rate from an initial level that ensures its exclusion. Divergence occurs if the resulting evolutionary change in species 1 increases c_{11} . When both resources are present in the allopatric system, the results for method (1) must apply, so divergence must occur. However, divergence also occurs when consumer 1 in allopatry causes exclusion of the resource it catches at a higher rate, that is, resource 1, implying a minimum value for c_{11} in allopatry.

IS THE DIRECTION OF EVOLUTIONARY CHANGE RELATED TO THE SIGN OF THE INDIRECT ECOLOGICAL INTERACTION BETWEEN CONSUMER SPECIES UNDER EQUATIONS (1A–1D)? NO

For all three measures of indirect consumer interactions, mutualism and contramensalism between consumers are common when competition between resources is strong (α close to 1) or asymmetric ($q \gg 1$ or $\ll 1$); see Abrams and Cortez (2015). However,

the prediction of divergence in the previous section is independent of the signs of the indirect effects between the consumers. Thus, regardless of which method is used to quantify effects, and regardless of the signs of the indirect effects via resource use, character divergence always occurs.

The universality of divergence, embodied in equation (4), is not a consequence of small differences in the magnitude of the ecological interaction when comparing different measures of consumer competition or different degrees of resource competition. Figure 1 plots the three measures of consumer competition as a function of the resource competition coefficient for a system with symmetrical capture rates of the two consumers and asymmetrical resource competition. Most of the interaction coefficients change significantly as between-resource competition, α , changes from 0 to 1. In most of the cases shown, the coefficients change sign over this range. Nevertheless, there is selection for sympatric divergence in all cases, and the strength of selection is independent of resource competition for the two methods based on small perturbations.

The above “universal divergence” result would also not be very significant if there were only very narrow ranges of parameters that produced noncompetitive outcomes. Figure 2 shows that that is also not the case. Significant ranges of parameter space produce noncompetitive interactions by one or more measures of interaction strength. High levels of between-resource competition and highly asymmetric competition are both associated with noncompetitive interactions. Figure 2B also shows that the hydra effect, which causes sign differences between measures 1 and 2, is also associated with moderate to high between-resource competition and at least some asymmetry in that competition. More examples are analyzed in Abrams and Cortez (2015). One simple case when all three of the measures predict mutualism occurs in the system explored by Abrams and Nakajima (2007). Here the two consumers have symmetric resource use ($c_{11} = c_{22}$; $c_{12} = c_{21}$), and the resources have symmetric Lotka–Volterra competition (with competition coefficient $\alpha > 2c_{11}c_{12}/(c_{11}^2 + c_{12}^2)$). All three methods classify the interaction as mutualism when the consumers have relatively high death rates, but method (3) predicts competition when the consumers initially have sufficiently low death rates. Regardless of the initial death rate, there is selection for divergence in all of these cases.

DOES DIVERGENCE IN ONE CONSUMER ALWAYS DIMINISH THE COMPETITIVE (OR OTHER) EFFECT OF THE SECOND CONSUMER? NO

We begin by defining the meaning of the question in the above heading. The two alternative interpretations are: (1) Does the evolutionary change in one consumer cause its population to change in a direction that counteracts or enhances its original (ecological) response to the perturbation of the other consumer?; and (2)

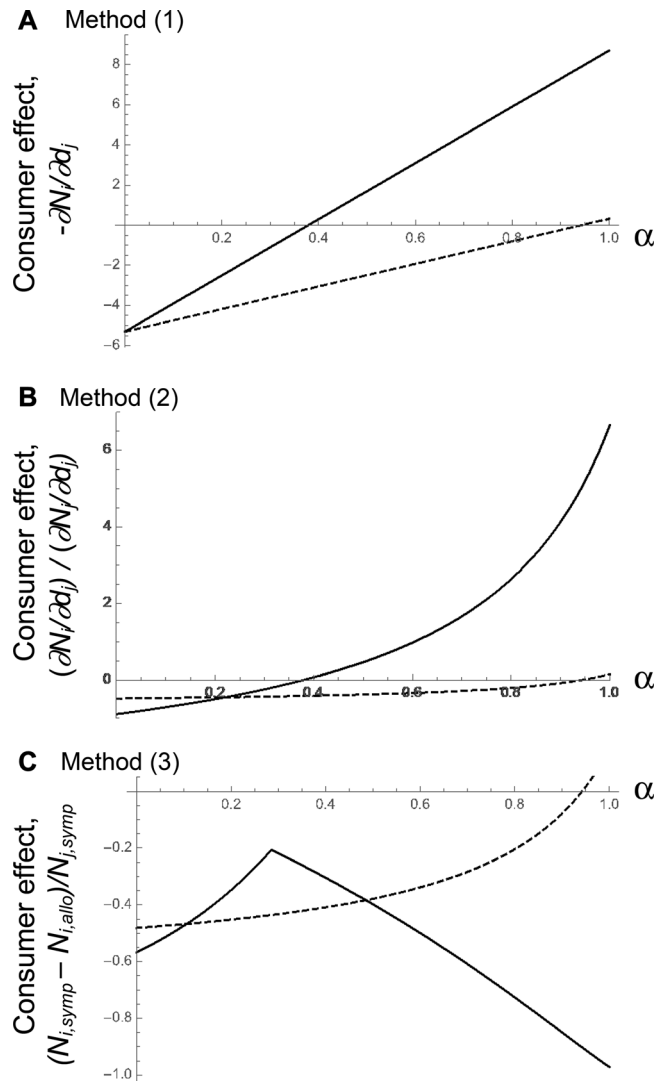


Figure 1. Three measures of the effect of each consumer species on the other as a function of α , the geometric mean of the competition coefficients between the two resources. In all panels, the solid line is the effect of consumer 2 on consumer 1, whereas the dashed line is the effect of 1 on 2. Panel A gives the effects based on the mortality of the other species (method (1)). Panel B gives the same quantity scaled by the intraspecific effect of mortality (method (2)). Finally, panel C gives the effect of addition of the other species, scaled by the equilibrium population of the added species (method (3)). Formulas for these measures are given in the figure. In all cases the parameters are: $r_1 = k_1 = 3.5$; $r_2 = k_2 = 3.9$; $c_{11} = 0.7$; $c_{12} = 0.27$; $c_{21} = 0.36$; $c_{22} = 1$; $d_1 = 0.22$; $d_2 = 0.31$; $q = 2$. All N 's denote equilibrium population size.

Does the evolutionary change reduce the population-level effect of a subsequent additional perturbation to the other consumer? For both questions, it is of interest to compare cases initially characterized by positive or negative effects of a positive perturbation to the other (nonevolving) consumer.

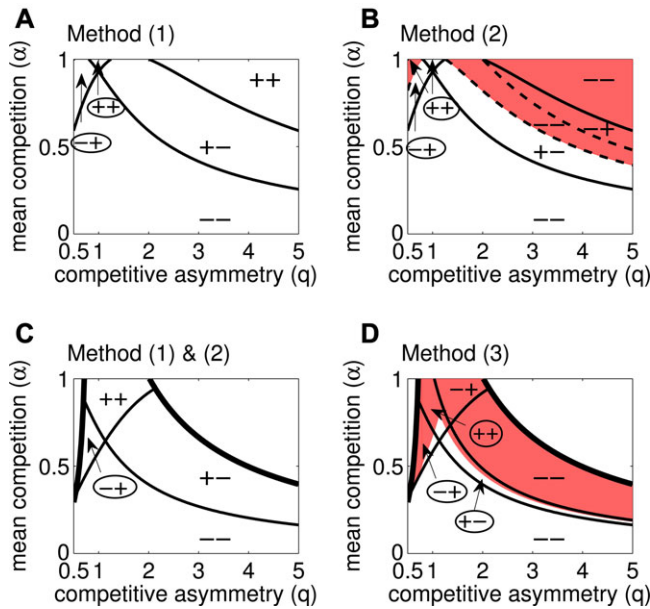


Figure 2. Examples of the dependence of interaction classification on resource competition parameters for the three interaction quantification methods. In all panels, black solid and dashed lines denote parameter values where one of the interactions switches signs. Dashed lines correspond to parameter values above which one or both consumers exhibit a hydra effect. For each region, the first symbol denotes the effect of consumer 2 on 1 and the second denotes the effect of consumer 1 on 2. Panels A and B compare methods (1) and (2). In panel B, methods (1) and (2) differ in the red region, where one or both consumers exhibit a hydra effect. Panels C and D compare all three methods for a different set of parameters. In panel C, methods (1) and (2) predict the same interaction signs for all parameters shown. In panel D, red regions denote where both prey cannot coexist with one of the predators in allopatry; method (3) can produce signs that differ from methods (1) and (2) in those regions. The parameter values for panels (A, B) are: $r_1 = r_2 = k_1 = k_2 = 1$, $c_{11} = 1.25$, $c_{12} = 1$, $c_{21} = 1$, $c_{22} = 2$, $d_1 = d_2 = 0.2$. For panels (C, D) they are: $r_1 = 3.5$, $r_2 = 3.5$, $k_1 = 3.5$, $k_2 = 4.5$, $c_{11} = 1$, $c_{12} = 0.5$, $c_{21} = 0.3$, $c_{22} = 1.2$, $d_1 = 0.3$, $d_2 = 0.5$.

The first question is concerned with how divergence affects the population size of the evolving species (consumer 1); that is, how evolution modifies the ecological effect of the original perturbation. Equation (A5) in the Appendix shows that the evolutionarily favored change in capture rates produces a decrease in the equilibrium population size of the evolving consumer (here species 1) in response to a lower death rate of consumer 2. This decrease is the result of greater specialization due to divergence, which reduces the resource base for the evolving species. The population decrease means that evolution of species 1 increases the competitive effect of species 2 in those cases where the original effect on consumer 1 is negative. Abrams (2012) presents a special case of this result. If the original effect of the perturbation

is positive, the evolutionary decrease in population size will reduce that positive effect. As above, we consider a decrease in death rate to be a positive perturbation to consumer 2, even when there is a hydra effect that decreases its population size as a result. However, it should be noted that a hydra effect means that a higher population size of consumer 2 will be associated with convergence and that convergence will increase the population size of consumer 1. Note also that, if both consumer species can evolve, and they both diverge, the negative effect on N_1 due to species 1's evolution may be reversed by the positive effect due to consumer 2's divergence (examples in Abrams 1986).

The second question above asks whether divergence decreases the effect of future (positive) perturbations to consumer 2. Most previous work has assumed that divergence in species 1 will in fact reduce the effect of such perturbations on species 1's population size. This assumption is based on the idea that divergence decreases overlap in resource utilization, which is usually associated with lower competition. In models lacking competition between resources, divergence does in fact decrease competition as measured by method (2) (e.g., Lawlor and Maynard Smith 1976; Abrams 1986). The effect of evolutionary divergence when there is significant resource competition is more complicated. The simplest results can be obtained by using method (1). The Appendix (eq. A7) gives the expression for the effect of a small amount of divergence of consumer 1 on the method (1) measure of consumer 2's effect on consumer 1. This expression confirms that, for sufficiently low competition between resources, divergence of consumer species 1 reduces the impact of subsequent decreases in consumer 2's mortality; that is, it reduces consumer competition. However, greater competition between resources (when $q \geq 1$, given $c_{ii} > c_{ij}$) means the effect of consumer 2 on 1 is positive. When the effect is small and positive, divergence increases its magnitude, but divergence decreases the magnitude of positive effects at still higher levels of resource competition. Divergence of species 1 also affects the impact of a mortality change in species 2 on 2's own density, which is given by equation (A8a) in the Appendix. That equation shows that the intraspecific effect is reduced by divergence when competition between resources is low, but the reverse may happen under high between-resource competition. The first case increases the magnitude of the method (2) interspecific effect, whereas the second case decreases its magnitude. Divergence of consumer 1 may also increase or decrease its own intraspecific effects (eq. A8b).

The effects of divergence on the method (1) measure of interaction are illustrated in Figure 3, which is based on an example with moderate resource partitioning and asymmetric resource competition. The black lines give the predivergence method (1) effects of species 2 on 1 (solid) and 1 on 2 (dashed), both as a function of the strength of resource competition (α). The between-consumer interaction is competitive at low α ,

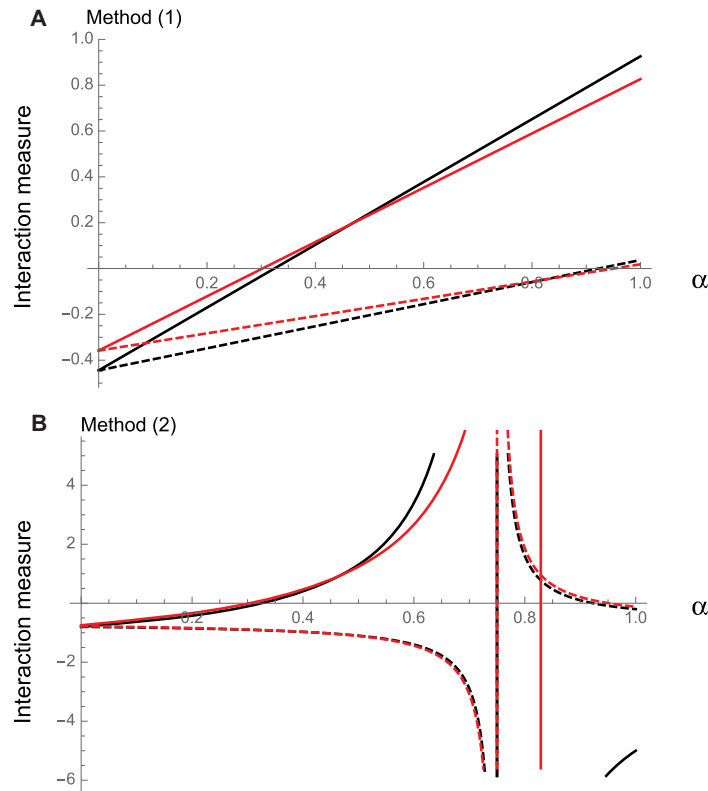


Figure 3. The impact of divergence of consumer species 1 on their interspecific interactions for a range of between-resource competitive interactions, given by the geometric mean resource competition coefficient, α . The interactions are measured using method (1) in panel A and method (2) in panel B. The solid line gives the effect of decreased d_2 on N_1 , whereas the dashed lines give the effect of decreased d_1 on N_2 . The parameters are: $r_1 = 3$; $k_1 = 1$; $r_2 = 2$; $k_2 = 1$; $c_{11} = 2$; $c_{12} = 1$; $c_{21} = 1$; $c_{22} = 2$; $d_1 = 0.5$; $d_2 = 0.5$; $q = 3$. The red lines show the interaction measures after species 1's resource use traits diverge so that $c_{11} = 2.1$ and $c_{21} = 0.9$. In panel B, the measures of effects on species 1 at high α are too large in negative magnitude to appear on the graph.

contramensalistic at intermediate α , and mutualistic at high α . The red lines give the corresponding effects following a small magnitude divergence of consumer 1 (where c_{11} is increased by 0.1 and c_{12} is decreased by the same amount because $\partial c_{12}/\partial c_{11} = -1$ at the evolutionary equilibrium given by eq. 2). The comparison of the differently colored lines implies that divergence decreases the magnitudes of both negative effects that occur when there is a competitive interaction due to low resource competition. Divergence can change the effect of reduced d_2 on species 1 from negative to positive for $0.302 < \alpha < 0.324$. Small positive effects (when $0.324 < \alpha < 0.464$) on consumer 1 are increased by divergence, whereas large positive effects (for $\alpha > 0.464$) are decreased. The nonevolving consumer 2 (dashed line in Fig. 2) experiences a smaller negative effect due to consumer 1's divergence for $\alpha < 0.822$; an increased magnitude negative effect for $0.822 < \alpha < 0.923$; a change to a small negative rather than a small positive effect for $0.923 < \alpha < 0.951$; and a decreased magnitude (and small) positive effect for $\alpha > 0.951$. Other effects of divergence on interaction strength and sign occur for other parameter values, but the decrease in the magnitude of competitive effects at low resource competition is general.

Figure 3B corresponds to Figure 3, but uses method (2) to measure interspecific effects. Recall that method (2) provides a measure of relative changes in density of the two consumers in response to decreased mortality of the second consumer. The qualitative responses to divergence are similar when between-resource competition is relatively low; for $\alpha < \sim 0.3$, both interspecific effects are negative and both have lower magnitudes following divergence. (These decreases are mostly on the order of 10–15%, but are difficult to see because of the large y-axis range required in this figure.) Method (2's) division of the interspecific by the intraspecific response changes the measures considerably at higher α values because the intraspecific effects in the denominator become very small. Each consumer experiences a hydra effect (decreased density in response to decreased mortality) when $\alpha > 0.75$ in the original system, and intraspecific effects of mortality are therefore very small in magnitude close to $\alpha = 0.75$. Moreover, the evolutionary divergence of consumer 1 has a significant effect on the threshold value of α , above which a hydra effect occurs in consumer 2. Figure 3B shows that a slight divergence of species 1 shifts the threshold α where the hydra effect in species 2 occurs from 0.75 to 0.828. Because of the small magnitude of

intraspecific consumer effects when α is close to 0.75, small absolute changes in parameters have a large impact on the ratio (measure 2). Thus, a small divergence has a large impact on the method (2) measure when resource competition is close to $\alpha = 0.75$.

A final question is whether a larger magnitude perturbation, such as addition or removal of a consumer species (method 3) results in qualitatively different effects of evolutionary responses on interaction strengths. This question is difficult to address because of the potential range of shapes of the evolutionary trade-off, and the possibility of exclusion of one resource when only one consumer is present. The first problem means that the full extent of evolutionary change after one species is added or removed cannot be determined without knowing the exact trade-off. The second problem means that the effect of evolution generally changes abruptly when the nature of the allopatric equilibrium changes due to resource exclusion. A full treatment would require a separate article. However, as an illustration of the range of potential effects, Figure 4 explores an example in which there is strong symmetric between-resource competition, and a symmetric pattern of resource utilization by the consumers ($c_{11} = c_{22}$ and $c_{12} = c_{21}$). The ecological interactions correspond to those treated in the ecological study by Abrams and Nakajima (2007). The example in the figure assumes $c_{11} + c_{12} = 4$. The interaction as measured by method (1) or (2) changes from competition to mutualism when the consumer's overlap in resource use becomes sufficiently low ($c_{11} > 2.4588$ in the figure). The two panels show the effect of a small evolutionary divergence (dashed line) on the method (3) measure of competition for cases with highly (Fig. 4A) or moderately (Fig. 4B) efficient consumers. In panel A, the interaction is competitive with a large effect size that increases in magnitude as resource partitioning becomes greater. This pattern is driven largely by the resource exclusion in allopatry, which leads to high consumer population sizes with highly unequal capture rates (Abrams 1998). In panel B, the interaction switches from competitive for high consumer overlap to mutualistic with lower overlap (larger c_{11}). Here, a small evolutionary divergence of species 1 increases the magnitude of the negative effect of species 2 at very high overlap in resource use ($2.1 < c_{11} < 2.18$). It decreases the magnitude of competition for a range of somewhat lower overlaps ($2.18 < c_{11} < 2.77$). For still lower overlaps divergence changes weak competition to weak mutualism ($2.77 < c_{11} < 2.82$); increases the magnitude of mutualism ($2.82 < c_{11} < 2.94$); and, for the lowest overlaps, decreases mutualism ($c_{11} > 2.94$).

Although the effects of evolutionary divergence on measure (3) in other systems will differ from those shown in Figure 4, it is clear that divergence can increase or decrease both competitive and mutualistic effects. One major difference between measure (3) and measures (1) and (2) is that divergence can increase subsequent consumer competition even when there is no competition between resources. This result is implicit in

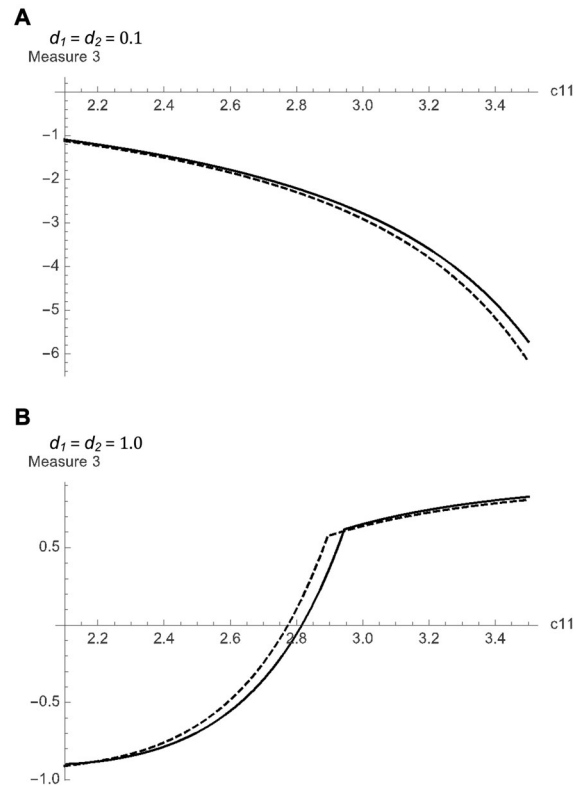


Figure 4. The effect of divergence on the method (3) measure of competition, which compares sympatric and allopatric populations. The solid line gives the predivergence measure for the effect of consumer 2 on 1, and the dashed line gives the measure following an increase of c_{11} by 0.05 over the original value given on the x-axis (with the same decrease in c_{12}). The predivergence system has symmetrical resource use by the two consumers with an initial state characterized by $c_{11} = c_{22}$, $c_{12} = 4 - c_{11}$, and $c_{21} = 4 - c_{22}$. Resource competition is high and symmetrical; $q = 1$ and $\alpha = 0.9$. The other parameters are $r_1 = r_2 = k_1 = k_2 = 1$, with consumer death rates given in the figure.

the analysis of Abrams (1998). That study showed that, for efficient consumers with symmetrical resource use patterns and no competition between resources, there are larger competitive effects between species with greater differences between their relative consumption rates. In this case divergence leads to a greater difference between sympatric and allopatric populations because the allopatric population becomes larger as the resource utilization becomes more asymmetrical. Figure 4 would be very similar if it had assumed no between-resource competition.

EXTENSIONS AND MODIFICATIONS OF THE BASIC MODEL (EQS. 1)

Equations (1) may be extended in several directions. The resource growth model need not be logistic, although biotic growth (self-reproduction) is required to have between-resource competition. Mutual use of noninteracting abiotic resources always produces

competitive interactions between consumers. We do not know exactly how nonlinearity in the per capita growth rates of biotic resources would affect the results. However, phenomena similar to those described under equations (1) occur with nonlinear density dependence in resource growth. One of the most important extensions of equations (1) is adding intraspecific density dependence in the mortality rates of the consumer species. Such density dependence allows the stable coexistence of two species having identical resource use traits. As shown by Abrams (1986, 1987b), the presence of intraspecific density dependence can alter the direction of evolutionary response in one consumer to a perturbation in the population growth rate or density of a second consumer in models lacking between-resource competition. For 2-consumer–2-resource systems intraspecific density dependent mortality makes parallel change more likely. Adding intraspecific density dependence to both consumers is also a rough representation of systems having an additional resource or resources that are caught by methods that are unaffected by the evolving trait.

Adding linear density dependence of consumer death rates into equations (1) still allows explicit solution of equilibrium densities, and it makes equilibrium densities of the two resources dependent on the resource growth parameters. Expressions for the derivatives of the equilibrium densities in response to mortality become more complicated. However, it is not difficult to show that noncompetitive ecological interactions between consumers still occur over a wide range of parameters when the resources compete. Divergence is still by far the most likely response in resource utilization for two consumers each of which has a higher capture rate for a different resource. It is common for divergence to reduce population size, although increases are also possible. If the example used in Figure 3 is changed so that each species has linearly density dependent mortality similar in magnitude to the density independent mortality in the original system, the signs of the interconsumer effects and their directions of change with greater resource competition are quite similar to those shown in Figure 3; Figure A1 in the Appendix presents results for this case.

Although the analysis here has concentrated on traditional resource partitioning, the two basic results for equations (1)—that divergence is favored and that it decreases the population density of the diverging species—also apply to “defense-based” partitioning, under which both species initially have their highest capture rate on the same resource. The direction of adaptive evolution specified by equation (4) changes sign at the same point that $c_{11}c_{22} - c_{12}c_{21}$ changes sign, implying that divergence also occurs under defense-based partitioning. The change in population size with mortality of the other species is given by expression (A5) in the Appendix; population size still decreases with divergence because the sign of this expression is not altered by a change in sign of $c_{11}c_{22} - c_{12}c_{21}$. However, if strong intraspecific density dependence exists, parallel character shifts in sympatry often oc-

cur when there is defense-based partitioning (Abrams 1986). It is not known how evolution changes interaction strengths in similar systems with convergent displacement due to nutritionally essential, rather than substitutable resources (Abrams 1987a; Fox and Vasseur 2008).

Under other modifications of equations (1), shared resource use can produce evolutionary change following sympatry, without changing the equilibrium consumer populations. It is possible that another type of resource limits consumer population size. For example, the two consumers could each be regulated by the availability of distinct types of nesting sites while sharing a common set of foods. This scenario may be modeled by a very nonlinear increase in consumer mortality (or decrease in natality) over a narrow range of population sizes close to a threshold value. A similar situation can come about when each consumer is limited by a different specialist predator. If one of the consumer populations experiences a change in its equilibrium density due to altered mortality of its specialist predator or altered abundance of nesting sites, changes in the relative abundances of the shared lower trophic level resources are expected, even though the other consumer will not change its equilibrium population density. In these cases, the expectation of divergence still applies for the nutritionally substitutable resources we have modeled here. These cases differ from those considered under the main scenario here in that evolutionary change in resource use of the nonperturbed species will not significantly alter its equilibrium population size.

The approach considered here differs from most previous analyses of character displacement in that it considers evolutionary change in only one of the consumer species. Doing so allows the selective forces and ecological responses to be analyzed in the simplest possible scenario. Understanding this scenario is necessary for assigning the cause of population changes when both consumers exhibit evolutionary shifts in resource use. The net result of evolution when both consumer species have similar magnitudes of evolutionary response to each other can be very different from the single-species evolution models. The earlier analysis of Abrams (Appendix 3, 1986) found that coevolutionary character displacement in the same ecological model (with no resource competition) often increased (but did not maximize) the population sizes of both consumers. The results here show that this increase should be attributed to the divergence of the other consumer species; the amount of the population increase in a particular consumer is actually diminished by its own evolutionary divergence.

Discussion

Brown and Wilson (1956) coined the term “character displacement,” but identified it based on the pattern of increased character differences in sympatry, without specifying a mechanism. Most subsequent works (Grant 1972; Taper and Case 1985, 1992;

Abrams 1986; Schluter 2000a; Pfennig and Pfennig 2010, Stuart and Losos 2013) have restricted the ecological variety of displacement to evolutionary responses to exploitative competition for resources. Much of this literature fails to consider the fact that shared use of limiting resources can produce mutualism or contramensalism when the resources themselves compete (Vandermeer 1980; Davidson et al. 1984; Schoener 1993). The results presented here suggest that all types of interactions based on common use of shared substitutable resources are expected to produce divergent character displacement, even when they do not qualify as competition. Recent work (Abrams and Cortez 2015) suggests that noncompetitive interactions via shared use of limiting resources occur for a wide range of parameters in simple models. Thus it may be common for interactions other than competition to produce character displacement. The selective pressure for divergence comes from changes in the relative abundances of the two resources, and it is not necessary that the indirect interaction be competition for such changes to occur. Although this result is shown in the context of a very simple model, it does not depend critically on the assumptions of that model. Nevertheless, there are many cases that require additional investigation, including structured populations, nonsubstitutable resources, and various nonlinear functional and numerical responses.

Any interaction that changes the relative abundances of different resource types should produce shifts in characters that have genetic variability in their relative intake rates of those resources. In the model considered here, the sign of a change in the mortality rate of a second consumer is a better predictor of divergence in a focal consumer than is the sign of its change in population density. Mortality is more predictive because the resource abundances at equilibrium change in a determinate direction with the death rate of the other consumer, but not with its density. A change in the density of the other consumer can often be associated with either a decrease or an increase in the ratio of resource abundances, depending on whether the perturbed species is characterized by a hydra effect (increased population size with increased mortality). The nature of the between-resource competition is one of the main factors determining whether a hydra effect occurs (Abrams and Cortez 2015).

The second question in the title of this article is also answered in the negative. At least in the context of small reductions in the mortality of the perturbed consumer species, the other consumer species' adaptive evolutionary response diminishes its own density. If the ecological effect of the perturbed consumer on the other consumer is negative, then this evolutionary shift increases the competitive effect of the perturbed species on the other. Thus, under the normal definition of competition (mutually negative effects on population size), character displacement in the model considered here enhances rather than diminishes competition experienced by the evolving species. In the current model, the effect

of one consumer on the other may be positive, and the favored evolutionary response then often reduces the positive effects of the other consumer on the evolving species.

Another interpretation of "evolution reducing competition" is that divergence reduces the negative impact of subsequent positive perturbations to other consumer. This interpretation is valid for the model considered here provided there is little or no between-resource competition. However, the situation again becomes more complicated when between-resource competition is moderate or high. In these cases, the favored evolutionary divergence may increase or decrease subsequent ecological effects, whether they are negative or positive. If competition is measured as the ratio of inter- to intraspecific effects of a small perturbation (method (2)), then even a small amount of divergence can produce large increases in the negative impacts of subsequent mortality perturbations to the other consumer, as shown in Figure 3.

In summary, we argue that character displacement should be thought of as an evolutionary response to the shift in the relative abundances of different resources caused by another consumer's utilization of those resources. Cases of divergent character shifts in sympatry should not be dismissed as being independent of another consumer species just because of lack of evidence of competition between the species. The negative answers to both questions in the title argue that character displacement should not be thought of as an adaptive response to reduce competition. Divergence may increase competitive effects and may also reduce the positive effects of another consumer on the evolving species.

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Appendix

The conversion efficiencies b_{ij} are assumed equal here, and are removed by scaling resource densities. The resulting equilibrium consumer densities are then:

$$\hat{N}_1 = \frac{\left[\alpha (k_2 c_{21} (c_{22} d_1 - c_{12} d_2) + k_1 q^2 c_{22} (c_{21} d_1 - c_{11} d_2)) + q ((c_{11} c_{22} - c_{12} c_{21})(r_1 c_{22} - r_2 c_{21}) + c_{12} c_{22} d_2 k_1 + c_{11} c_{21} d_2 k_2 - c_{21}^2 d_1 k_2 - c_{22}^2 d_1 k_1) \right]}{q(c_{11} c_{22} - c_{12} c_{21})^2} \quad (A1)$$

$$\hat{N}_2 = \frac{\left[\alpha (k_1 c_{12} q^2 (c_{11} d_2 - c_{21} d_1) + k_2 c_{11} (c_{12} d_2 - c_{22} d_1)) + q ((c_{11} c_{22} - c_{12} c_{21})(r_2 c_{11} - r_1 c_{12}) + c_{21} c_{11} d_1 k_2 + c_{22} c_{12} d_1 k_1 - c_{12}^2 d_2 k_1 - c_{11}^2 d_2 k_2) \right]}{q(c_{11} c_{22} - c_{12} c_{21})^2} \quad (A2)$$

The corresponding equilibrium densities of the resources are:

$$\hat{R}_1 = \frac{c_{22} d_1 - c_{12} d_2}{c_{11} c_{22} - c_{12} c_{21}} \quad (A3a)$$

$$\hat{R}_2 = \frac{c_{11} d_2 - c_{21} d_1}{c_{11} c_{22} - c_{12} c_{21}} \quad (A3b)$$

In all of the above expressions we assume $c_{11} c_{22} > c_{12} c_{21}$.

When evolving traits in consumer species 1 link its two capture rates, and the system is at an ecological and evolutionary

equilibrium with an intermediate value of c_{11} , the derivative of c_{12} with respect to c_{11} satisfies:

$$\frac{\partial c_{12}}{\partial c_{11}} = -\frac{\hat{R}_1}{\hat{R}_2} = \frac{c_{22} d_1 - c_{12} d_2}{c_{21} d_1 - c_{11} d_2} \quad (A4)$$

If one takes the derivative of the equilibrium population of consumer 1, equation (A1), with respect to c_{11} and substitutes the evolutionary equilibrium value of $\partial c_{12} / \partial c_{11}$ provided by equation (A4), one obtains the following, which gives the effect of divergence of species 1 on its population size:

$$\frac{\partial \hat{N}_1}{\partial c_{11}} \Big|_{c_{11}=\hat{c}_{11}} = \frac{d_2 \left[\alpha (k_2 c_{21} (c_{22} d_1 - c_{12} d_2) + k_1 q^2 c_{22} (c_{21} d_1 - c_{11} d_2)) + q ((c_{11} c_{22} - c_{12} c_{21})(r_1 c_{22} - r_2 c_{21}) + c_{12} c_{22} d_2 k_1 + c_{11} c_{21} d_2 k_2 - c_{21}^2 d_1 k_2 - c_{22}^2 d_1 k_1) \right]}{q(c_{21} d_1 - c_{11} d_2)(c_{11} c_{22} - c_{21} c_{12})^2} \quad (A5)$$

A comparison with expression (A1) shows that the sign of (A5) is identical to that of equation (A1), that is, \hat{N}_1 , which must be positive. The latter factor must be negative due to the requirement that the equilibrium R_2 must be positive. Thus, parameters that allow the two consumers to coexist also guarantee that divergence (which is always favored) reduces the equilibrium population size of the diverging consumer.

The effect of the divergence on interspecific effects measured by method (1) is examined in this paragraph. For the case with equal conversion efficiencies, Abrams and Cortez (2015) show that the effect of a small decrease in d_2 on the equilibrium density of consumer 1 is:

$$-\frac{\partial \hat{N}_1}{\partial d_2} = -\frac{q(c_{12}c_{22}k_1 + c_{21}c_{11}k_2) - \alpha(c_{12}c_{21}k_2 + c_{11}c_{22}k_1q^2)}{q(c_{11}c_{22} - c_{12}c_{21})^2}, \tag{A6a}$$

and the corresponding effect of that mortality on the density of consumer 2 is:

$$-\frac{\partial \hat{N}_2}{\partial d_2} = \frac{q(c_{21}^2k_1 + c_{11}^2k_2) - \alpha c_{12}c_{11}(k_2 + k_1q^2)}{q(c_{11}c_{22} - c_{12}c_{21})^2}. \tag{A6b}$$

Similarly, the effects of reduced mortality of consumer 1 are:

$$-\frac{\partial \hat{N}_1}{\partial d_1} = \frac{q(c_{21}^2k_2 + c_{22}^2k_1) - \alpha c_{22}c_{21}(k_2 + k_1q^2)}{q(c_{11}c_{22} - c_{12}c_{21})^2} \tag{A6c}$$

$$-\frac{\partial \hat{N}_2}{\partial d_1} = -\frac{q(c_{12}c_{22}k_1 + c_{21}c_{11}k_2) - \alpha(c_{11}c_{22}k_2 + c_{12}c_{21}k_1q^2)}{q(c_{11}c_{22} - c_{12}c_{21})^2}. \tag{A6d}$$

These four derivatives allow measurement of the interspecific interaction by methods (1) and (2). Here we examine the effect of divergence on the method (1) measure of the effect of consumer 2 on consumer 1. The effect of a slight divergence at the evolutionary equilibrium can be described by modifying (A6a) by an increase in c_{11} by δ and a decrease in c_{12} by $\delta(R_1/R_2)$, where the resources are at their equilibrium densities. If we denote the perturbed equilibrium density of consumer 1 with these changes in c_{1i} by \hat{N}_1^* , the effect of an increase in δ evaluated at $\delta = 0$ is:

$$\frac{\partial}{\partial \delta} \left(-\frac{\partial \hat{N}_1^*}{\partial d_2} \right) = \frac{\left[-q(c_{22}^2d_1k_1 + c_{12}c_{22}d_2k_1 + c_{21}^2d_1k_2 + c_{21}c_{11}d_2k_2) + \alpha(c_{12}c_{21}d_2k_2 + c_{21}c_{22}d_1k_2 + q^2k_1(c_{11}c_{22}d_2 + c_{21}c_{22}d_1)) \right]}{q(c_{11}c_{22} - c_{12}c_{21})^2(c_{21}d_1 - c_{11}d_2)}. \tag{A7}$$

The above expression must be positive when resource-level competition is absent ($\alpha = 0$). In other words, divergence increases (makes smaller in magnitude) the negative effect of species 2 on species 1. Note that equation (A7) is equivalent to $\partial/\partial c_{11}(\partial \hat{N}_1/\partial d_2)|_{c_{11}}$, given that c_{12} is expressed as a function of c_{11} . If the numerator of (A7) becomes positive for $\alpha < 1$, (A7) itself is negative, and divergence decreases the effect of species 2 on 1 for high α . Expressions (A6a) and (A7) simplify when the only asymmetry in the system is the asymmetry in resource competition ($q > \text{or} < 1$). In this case, the two consumers have symmetrical c_{ij} values, and the equilibrium densities of the two resources are equal. The effect of consumer 2 on 1 changes from negative to positive when $2c_{ii}c_{ij}q = \alpha(q^2c_{ii}^2 + c_{ij}^2)$. The effect of divergence on the interaction effect (A7) changes from positive to negative when $q(c_{ij} + c_{ii})^2 = \alpha(c_{ij}^2 + c_{ij}c_{ii} + q^2(c_{ii}^2 + c_{ij}c_{ii}))$. Figure 3 provides an example showing such a case, where $q = 3$, $c_{ii} = 2$, and $c_{ij} = 1$. The critical α where the interspecific impact (A6a) changes from negative to positive is $12/37$; divergence decreases the interspecific effect for $\alpha < 27/57$, whereas it increases the effect for larger α . This means that the magnitude of consumer competition is reduced by divergence when there is low resource competition, and the magnitude of consumer mutualism is also reduced at high resource competition.

One can also quantify the effect of a small amount of divergence by species 1 on the intraspecific effect of mortality on one or both consumers, given by equations (A6b, A6c). The resulting formulas for the effect of species 1's divergence on both species' intraspecific effects are:

$$\frac{\partial}{\partial \delta} \left(-\frac{\partial \hat{N}_2^*}{\partial d_2} \right) = \frac{d_1 [2q(c_{12}c_{22}k_1 + c_{21}c_{11}k_2) - \alpha(c_{12}c_{21} + c_{11}c_{22})(k_2 + k_1q^2)]}{q(c_{11}c_{22} - c_{12}c_{21})^2(c_{21}d_1 - c_{11}d_2)} \tag{A8a}$$

$$\frac{\partial}{\partial \delta} \left(-\frac{\partial \hat{N}_1^*}{\partial d_1} \right) = \frac{2d_2 [q(c_{22}^2k_1 + c_{21}^2k_2) - \alpha c_{21}c_{22}(k_2 + k_1q^2)]}{q(c_{11}c_{22} - c_{12}c_{21})^2(c_{21}d_1 - c_{11}d_2)}. \tag{A8b}$$

Expression (A8a) implies that the effect of divergence by species 1 on the measure (1) intraspecific effect of (the nonevolving) consumer 2 is to decrease that intraspecific effect when α is small (and the effect, eq. (A6b), is positive), and increase it when α (and q) are sufficiently large that the effect (A6b) is negative (i.e., divergence diminishes the hydra effect). Expression (A8b)

is the effect of species 1's divergence on its own (measure (1)) intraspecific effect. Although the exact switchover points differ from those for consumer species 2, divergence decreases the

positive effect of reduced consumer mortality that occurs with low between-resource competition, and decreases the negative effect of lower mortality at high resource competition.

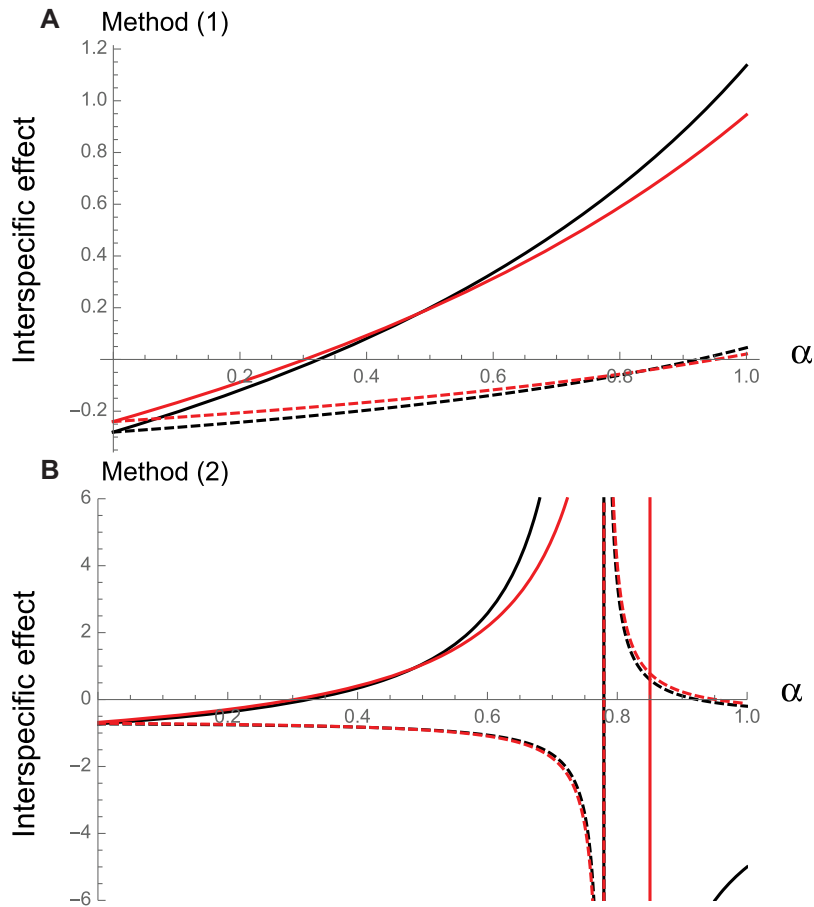


Figure A1. The interspecific interaction measures showing effects of a small decrease in d_2 on consumer species 1 (solid) and species 2 (dashed). Black lines are the predivergence measures and red lines are the same measures following a small magnitude divergence in species 1. Parameters are as in Figure 3B in the text, with the addition of intraspecific density-dependent mortality of $-0.5N_i$ for each consumer.