

Predicting the effects of character displacement on food-web dynamics

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Manuscript elements: Figure 1, figure 2, figure 3, figure 4. All figures should be printed in color.

Keywords: competition; eco-evolutionary dynamics; ecological speciation; three-spine stickleback; zooplankton

Manuscript type: Note.

Prepared using an *Am. Nat.* inspired L^AT_EX template for Rmarkdown.

Abstract

Ecological character displacement is a key driver of diversification and adaptive radiation; however,
3 there has been little work examining the consequences of character displacement on the dynamics
of ecological communities. Given the growing recognition for the role of evolution in structuring
ecological communities, understanding how major evolutionary processes impact ecological dy-
6 namics is increasingly important. Here, we build a mathematical model to predict how exploitative
competition between two consumers for two resources affects the evolution of consumer attack
rates, and, in turn, consumer-resource population dynamics. Our model suggested that increasing
9 ecological character displacement decreases the equilibrium density of resources, and with suffi-
cient divergence, results in more oscillatory (destabilizing) consumer-resource dynamics. These
results suggest that ecological character displacement can eventually have a negative feedback on
12 food-web persistence in the absence of other processes.

Introduction

Ecological character displacement is thought to be a key evolutionary process generating biodiversity (Dolph Schluter 2000; D. W. Pfennig and Pfennig 2010; but see Stuart and Losos 2013). Ecological character displacement describes the “process of phenotypic evolution in a species generated or maintained by [exploitative] resource competition with one or more coexisting species” (Dolph Schluter 2000). Over the past 40 years, a large body of theoretical (e.g. Lawlor and Smith 1976; P A Abrams 1986; Doebeli 1996; Taper and Chase 1985) and empirical (reviewed in: Dolph Schluter 2000; Dayan and Simberloff 2005; Stuart and Losos 2013) work has been generated to understand the scenarios under which exploitative competition for resources leads to the divergence of consumer foraging traits. The general result emerging from these studies is that, if resources are nutritionally substitutable (Peter A Abrams 1987; Fox and Vasseur 2008) and there is no other strong source of density dependence acting on consumers (P A Abrams 1986), then resource competition drives the divergence of consumer foraging traits [Lawlor and Smith (1976); Taper and Chase (1985)]. This process is not simply driven by ecological differences, but creates an eco-evolutionary feedback that drives further differentiation. This insight was clearly by theoretical models that highlighted the importance of explicitly including resource dynamics as a mediator of competition in driving evolutionary change (Lawlor and Smith 1976; P A Abrams 1986; Taper and Chase 1985). Although character displacement is the result of an eco-evolutionary feedback, the ecological consequences of this process have received surprisingly little attention (Germain et al. 2018). Perhaps this is because early theoretical work suggested that character displacement was a potent stabilizing force in ecological communities (Lawlor and Smith 1976). This ecological outcome is also an intuitive one —character divergence reduces interspecific competition between consumers, promoting coexistence. However, inferences about the effect of character displacement, like the process itself, can only be made when comparing communities in the presence and absence of competition (criteria #3 for character displacement, D Schluter and McPhail 1992; Dolph Schluter 2000). Current inferences about the stabilizing effects of consumer divergence are only comparisons

about communities where there are two consumers, and even though, the focus is only on the stable coexistence of consumer species.

The consequence of this eco-evolutionary feedback for consumer coexistence has been well characterized (Lawlor and Smith 1976; Germain's work). Ecological character displacement has typically been considered to be a stabilizing factor in communities (Lawlor and Smith 1976). This is because divergence in foraging traits is thought to reduce the strength of interspecific competition between consumers. Reducing the strength of interspecific competition relative to intraspecific competition is a stabilizing force in consumer-resource systems. Consumer specialization on distinct resources suggests that there are niche differences between consumers. Mathematically, this is also often assumed to be the case, because using techniques such as evolutionary invasion analysis describe the ability for a consumer with a mutant allele to increase in abundance when rare, a demographic signature of niche differentiation. Therefore, if both consumers are able to invade when rare, then this suggests that they can coexist.

Character displacement involves evolutionary shifts in character states in response to competition (D Schluter and McPhail 1992; Dolph Schluter 2000). Theoretically, this is determined by comparing character changes in the presence and absence of a competitor. Empirically, this is determined by meeting several criteria that rule out other possible explanations (D Schluter and McPhail 1992; Dolph Schluter 2000). Importantly, current inferences about the effect of character displacement on community stability do not meet this criteria. For example, the inference that character displacement enhances species coexistence is only made in a scenario where consumers are competing. This type of stability is important, but it does not enable us to examine the effect of character displacement on community stability. As a consequence, I argue that the effect of character displacement on community stability remains an open question.

Indeed, ecological character displacement often results in the evolution of characters that enhance a consumer's ability to capture resources, which tends to destabilize consumer-resource interactions (Murdoch et al. 2003; McCann 2011). This occurs because increases in a consumer's attack rate

results in the resource being suppressed well below its carrying capacity, which if sufficient enough,
66 can generate oscillations, and hence less stable, consumer-resource dynamics (Rosenzweig 1971;
Murdoch et al. 2003). Experimental decreases in interaction strength between consumers and
resources has been shown to promote coexistence between consumers and resources (Luckinbill
69 1973). Moreover, there is broad support that specialized consumers, since they are tightly coupled
to their resources, tend to exhibit consumer-resource cycles, whereas this is not the case for
generalists (Murdoch et al. 2002). Therefore, although evolutionary responses to exploitative
72 competition may reduce the strength of interactions between consumers, they ultimately increase
the strength of interactions with their resources which can destabilize the direct consumer-resource
interaction (rather than the indirect consumer-consumer interaction). While prior models of
75 character displacement have included more realistic functional responses and spatial relationships
between consumers and resources, they have focused more on whether these factors alter patterns
of character displacement rather than the effects of character displacement on the stability of the
78 ecological community. As a consequence, it is currently unclear whether ecological character
displacement has a net stabilizing or destabilizing effect on ecological communities.

Here, I address this knowledge gap by building a mathematical model to examine how ecological
81 character displacement affects consumer-resource dynamics in a food web context. I address two
question: (1) How does ecological character displacement affect resource abundances? (2) How
does character displacement affect food-web stability? I show that the consequences of character
84 displacement on food-web dynamics are not intuitive and depend critically on the foraging scenario
and tradeoff in consumer attack rates.

Methods and Results

87 Model of resource competition

To examine how ecological character displacement affects consumer-resource interactions and food-web dynamics, I analyzed a continuous-time model of two consumers (C_1, C_2) competing for
90 two shared resources (R_1, R_2):

$$\begin{aligned}\frac{dR_1}{dt} &= r_1 K_1 \left(1 - \frac{R_1}{K_1}\right) - F_{11}(R_1)C_1 - F_{21}(R_1)C_2 \\ \frac{dR_2}{dt} &= r_2 K_2 \left(1 - \frac{R_2}{K_2}\right) - F_{12}(R_2)C_1 - F_{22}(R_2)C_2 \\ \frac{dC_1}{dt} &= e_{11}F_{11}(R_1)C_1 + e_{12}F_{12}(R_2)C_1 - m_1 C_1 \\ \frac{dC_2}{dt} &= e_{21}F_{21}(R_1)C_2 + e_{22}F_{22}(R_2)C_2 - m_2 C_2\end{aligned}$$

where r_i represents the intrinsic growth rate of resource i , K_i represents the carrying capacity of resource i , e_{ji} represents the conversion efficiency of resource i into consumer j , and m_j represents
96 the mortality rate of consumer j . $F_{ji}(R_i)$ represents consumer j 's feeding rate (i.e. functional response) on resource i . This model is a useful characterization of a scenario where consumers compete for two distinct resources (e.g. zooplankton and benthic invertebrates) rather than if
99 resources are better characterized by a continuous trait distribution (e.g. seed size, see Taper and Chase (1985) for an example). In the scenario where consumer feeding rates increase linearly with resource density, such that $F_{ji}(R_i) = a_{ji}R_i$ where a_{ji} is the attack rate of consumer j on resource i ,
102 then this model becomes MacArthur's model of resource competition (MacArthur (1972)). The evolution of consumer attack rates in this model (and several extensions) have been analyzed in detail (Lawlor and Smith (1976); P A Abrams (1986)). The general result of these analyses is that
105 divergent character displacement in attack rates is an inevitable outcome of resource competition.

Here, I examine the effects of this inevitable divergence in attack rates on food-web dynamics. In particular, I examine how divergence in attack rates affect resource densities as well as the local

108 stability of both resources and consumers. I do this by (i) deriving analytical expressions for the
relationship between attack rates and food-web dynamics in different foraging scenarios and (ii)
simulating the effects of competition on the eco-evolutionary dynamics of consumers and resources.
111 For these simulations, I used an Adaptive Dynamics approach. At each evolutionary time step, I
created a mutant consumer by randomly choosing a consumer and modifying its attack rate on
one resource by either subtracting or adding a small constant with equal probability. The mutant's
114 attack rate on the other resource was determined by the shape of the tradeoff (details below).
Assuming this mutant consumer is rare, I then determined whether the mutant had higher relative
fitness than the resident consumer, and thus could invade and replace the resident consumer. If the
117 mutant was able to invade, I updated the attack rate of the resident consumer to the mutant attack
rate and allowed consumer and resource dynamics to reach a steady state. I then repeated the
simulation up to 10,000 times, which was sufficient for consumers to either reach an evolutionary
120 stable strategy (ESS, Smith and Price (1973)) or an evolutionary limit (e.g. $\frac{a_{ij}}{a_{ii}+a_{ij}}$ is constrained to a
maximum of 1 and minimum of 0).

Resource densities

123 I start by examining the effects of character displacement on the density of resources at equilibrium,
which will set the stage for a later analysis of food-web stability. In particular, I examine two
different foraging scenarios: one where consumers forage for both resources simultaneously (e.g.
126 MacArthur (1972)) and one where they cannot because resources occur in distinct habitats (e.g.
Lawlor and Smith (1976); K S McCann, Rasmussen, and Umbanhowar (2005)). I say consumers
have undergone divergent character displacement if there evolved attack rates are more specialized,
129 defined as $|\frac{a_{ij}}{a_{ii}+a_{ij}} - 0.5|$, when evolving with a competing consumer.

Consumers forage for both resources simultaneously: An inherent assumption in MacArthur's
model of resource competition is that consumers can forage for both resources simultaneously. In
132 essence, this implies that both resources occur within the same habitat. To gain analytical insight

to this scenario, I assume that resources are equivalent ($r = r_1 = r_2$ and $K = K_1 = K_2$) as well as consumers ($e = e_{11} = e_{12} = e_{21} = e_{22}$; $m = m_1 = m_2$), except that consumer attack rates are mirror images of each other ($a_{ii} = a_{11} = a_{22}$; $a_{ij} = a_{12} = a_{21}$). While this scenario is arguably simplistic, it isolates the effect of character displacement rather than any dependence on inherent differences in consumers or resources. I show that when both consumers and resources are present that the density of resources at equilibrium are equivalent ($R = R_1 = R_2$) and are determined by the following equation (*Mathematica* file with derivation available upon request):

$$\hat{R} = \frac{1}{a_{ii} + a_{ij}} \cdot \frac{m}{e}$$

Note that a key determinant of resource density is the consumer's total attack rate, $a_{ii} + a_{ij}$. Since the total attack rate is in the denominator, this implies that resource densities will decrease if evolution favors an increase in total attack rate. I assume that consumers are not 'Darwinian demons' (Law (1979)) and thus the evolution of their attack rates are subject to certain constraints. I modelled these constraints such that $(a_{ii}/A)^n + (a_{ij}/A)^n = 1$, where A is the total investment in attack rates and n describes the shape of the tradeoff (Sargent and Otto (2006)). This function has the useful property that it differentiates between cases where intermediate combinations of a_{ii} and a_{ij} are higher, on average, than the extremes (when $n > 1$, green line in Fig. 1) or, conversely, where the two extremes are higher, on average, than intermediate investments (when $n < 1$, orange line Fig. 1). When $n = 1$, the tradeoff function is linear, and all combinations of a_{ii} and a_{ij} have the same total attack rate (blue line in Fig. 1).

Previous work has shown that consumers undergo divergent character displacement regardless of the shape of the tradeoff (Lawlor and Smith (1976); P A Abrams (1986)). Interestingly, I find that the shape of the tradeoff qualitatively affects the relationship between character displacement and resource density (Fig. 2). For example, if consumer's are constrained by a linear tradeoff (blue lines), then there is no net change in total attack rate (Fig. 2A) and character displacement has no effect on resource densities (Fig. 2B). If the tradeoff is concave down (green lines), then

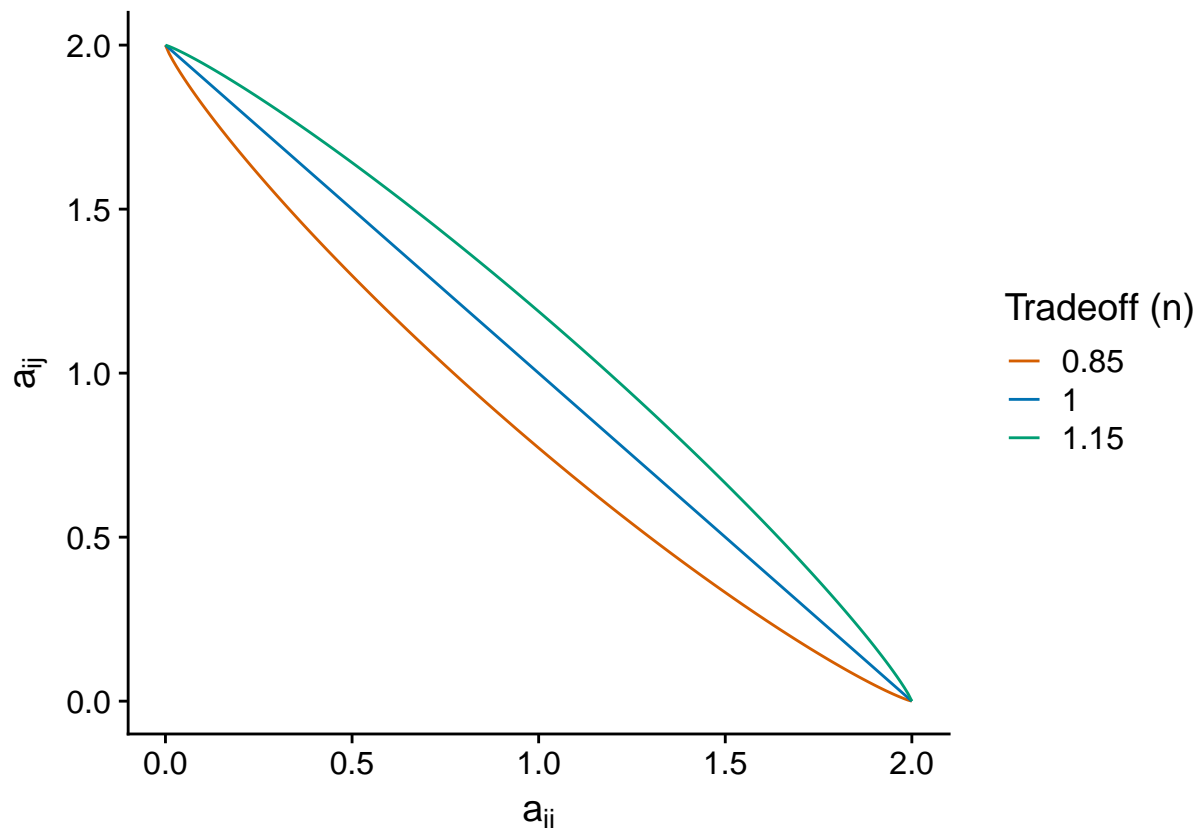


Figure 1: Tradeoff forms for consumer attack rates.

resource abundances can actually increase under character displacement (Fig. 2B). This is because the total attack rate of consumers is maximized at intermediate values ($a_{ii} = a_{ij}$) and decreases as consumers diverge (Fig. 2A). Note that detecting this effect in nature would likely be difficult, since a concave-down tradeoff results in relatively small displacement relative to other tradeoff shapes (Lawlor and Smith (1976); green points in Fig. 2A,B). When the tradeoff is concave up (orange lines), character displacement suppresses resource densities due to the increase in total attack rates (Fig. 2A,B). Although the equation I derived for resource density was for the scenario where both consumers and both resources are present, it predicts well the density of resources when a single consumer reaches its ESS (triangles on respective colored lines in Fig. 2B). This is because a single consumer evolves to be a generalist that has equal attack rates on each resource (triangles at 0.5 along x-axis in Fig. 2A), resulting in equivalent resource densities.

Consumers cannot forage for both resources simultaneously: Most models of character displacement have assumed a scenario where consumers can forage for both resources simultaneously (e.g. Taper and Chase (1985); P A Abrams (1986)). This assumption may be valid for some foraging scenarios (e.g. Darwin's finches foraging for seeds); however, in many situations consumers forage for resources that occur in different habitats, and thus cannot forage for both simultaneously. The only character displacement model that I am aware of that modeled resources in different habitats was one examined by Lawlor and Smith (1976). This model takes the same form as the previous model, except now the consumer's feeding rate takes the form:

$$F_{ji}(R_i) = w_{ji}a_{ji}R_i$$

where w_{ji} represents the proportion of time consumer j spends foraging in a habitat where only resource j is found (i.e. habitat preference). Note that since w_{ji} is a proportion that $w_{jj} = 1 - w_{ji}$. As with attack rates, I assume that consumer habitat preferences are mirror images of each other ($w = w_{11} = w_{22}$).

Lawlor and Smith (1976) found that consumers still underwent divergent character displacement

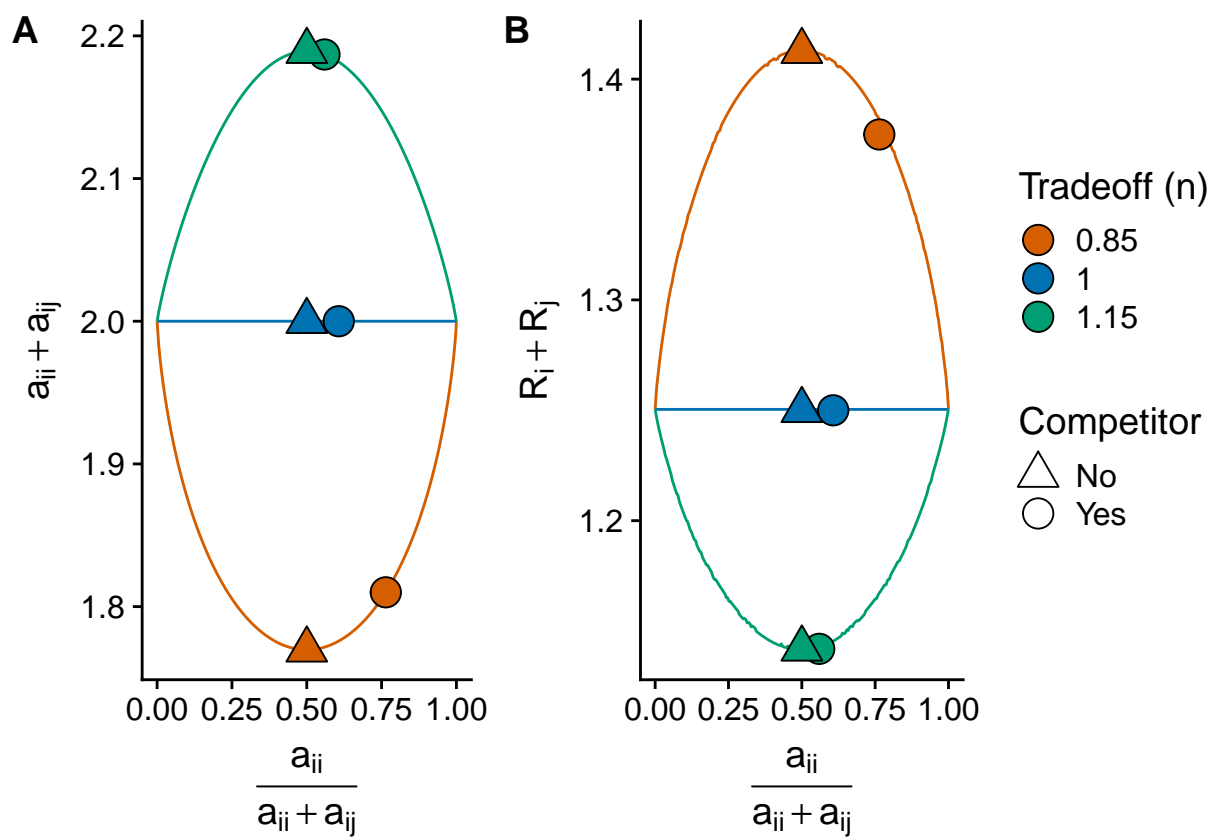


Figure 2: Effect of character displacement on total attack rates (A) and resource densities (B) when consumers can forage for both resources simultaneously.

regardless of whether consumers could or could not forage for resources simultaneously. I find that the foraging scenario qualitatively affects the relationship between character displacement and resource densities. To demonstrate this, note that again resource densities are equivalent at equilibrium ($R = R_1 = R_2$ when both consumers and resources present), but are now determined by the following equation (*Mathematica* file with derivation available upon request):

$$\hat{R} = \frac{1}{wa_{ii} + (1 - w)a_{ij}} \cdot \frac{m}{e}$$

This equation implies that if consumers evolve to become specialists on resources that occur in their preferred habitat (e.g. $w > 0.5$ and $a_{ii} > a_{ij}$), then character displacement will always increase the effective attack rate of consumers ($wa_{ii} + (1 - w)a_{ij}$), regardless of the tradeoff (Fig. 3A). Thus, character displacement always results in resource suppression if consumers are competing for resources that occur in different habitats (Fig. 3B). Note that the shape of the tradeoff can modify the effect of character displacement. This is not so much due to the tradeoff affecting the magnitude of displacement (it does, but the effect is minor), but because the form of the tradeoff affects resource abundances when a single consumer has reached its ESS (triangles in Fig. 3B). In contrast, resource densities reach a similar value when consumers evolve in the presence of a competitor (circles in Fig. 3B), because character displacement tends to reach a constraint of complete specialization.

These results do lead to an interesting prediction that could be tested either experimentally or with field data. If consumers are competing for resources that occur in different habitats, then greater character displacement corresponds to a greater decrease in resource densities (line trajectories in Fig. 3B). This prediction likely only applies to comparisons within species where there is likely little difference in the shape of the tradeoff among populations.

It is worth noting that in this foraging scenario, resource densities are consistently higher at the single consumer ESS compared to the predictions I derived for when both consumers are present (deviation of triangles from respective colored lines in Fig. 3B). This is likely because consumers actually evolve to be slightly specialized on the resources that occur in their non-preferred habitat

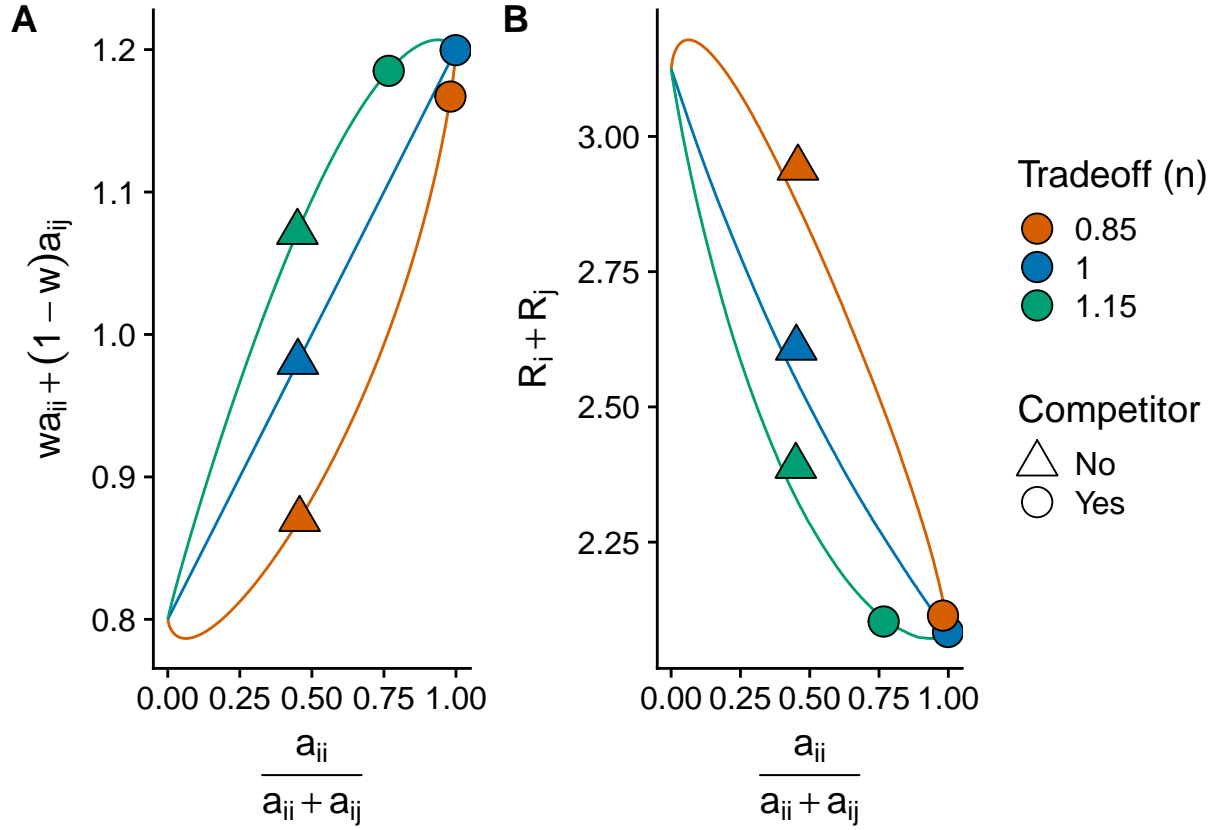


Figure 3: Effect of character displacement on effective attack rates (A) and resource densities (B) when consumers cannot forage for resources simultaneously.

(deviation of triangles from 0.5 along x-axis in Fig. 3B).

The effect of the foraging scenario on the relationship between character displacement and resource densities appears to be quite general. For example, even if I consider a more realistic consumer functional response (derived by K S McCann, Rasmussen, and Umbanhowar (2005)):

$$F_{ii}(R_i, R_j) = \frac{a_{ii}W_{ii}R_i}{1 + a_{ii}hW_{ii}R_i + a_{ij}hW_{ij}R_j}$$

where consumer feeding rates on resource i are influenced by both resource densities; saturate as resource densities increase (due to handling time h); and consumer habitat preferences are modified by relative resource densities, such that:

$$W_{ii} = \frac{wR_i}{wR_i + (1-w)R_j}$$

I still observe the same qualitative relationship between character displacement and resource
 213 suppression (Fig. 5 in Appendix). This is because resource competition always leads to character
 divergence and equilibrium resource densities are governed by similar dynamics (*Mathematica* file
 with derivations available upon request):

$$\hat{R} = \frac{1}{wa_{ii} + (1-w)a_{ij}} \cdot \frac{m}{e - hm}$$

216 Food-web stability

Of the prior models of character displacement, only Lawlor and Smith (1976) examine the effect
 of character displacement on the ecological stability of the system. They conducted a detailed
 219 theoretical analysis of three different metrics of stability: (i) stable coexistence of consumers,
 defined as the mutual invasibility of each consumer; (ii) global stability of consumers, defined as
 the continued coexistence of both consumers when resource dynamics are perturbed; and (iii) local
 222 stability, defined as the rate at which the four-species food web returned to equilibrium after a
 small perturbation to species abundances. Note that the first two metrics correspond to the stable
 coexistence of consumers, while the third metric measures the stability of the entire food web.
 225 Lawlor and Smith (1976) found that character displacement enhanced the stable coexistence of
 consumers, yet had a small negative effect on the local stability of the food web.

Lawlor and Smith (1976)'s work gave fundamental insight to the effect of character displacement on
 228 ecological stability; however, none of their stability analyses compared food webs with and without
 a competing consumer. Such comparisons are necessary for inferring the effects of ecological
 character displacement, a point that has been made clear in the criteria to demonstrate character
 231 displacement (Dolph Schluter (2000); D Schluter and McPhail (1992)). In fact, the first two metrics

of stability can only be assessed when both consumers are present because it examines the effect of divergence on coexistence, which requires both consumers to be present. In contrast, local stability
 234 can be compared in food webs with and without a competing consumer, and thus provides a useful benchmark for examining the effects of character displacement on food-web stability.

Below, I plot the results from the same simulations I did previously except now local stability
 237 $(-1 \times \text{Re}(\lambda_{\max}))$ is on the y-axis (Fig. 4). In general, I find that resource suppression goes hand-in-hand with local stability, a tendency that has been noted by others (Murdoch, Briggs, and Nisbet (2003); Kevin S McCann (2011)). Whenever character displacement results in resource suppression,
 240 I observe a decrease in local stability (Fig. 4). This is not simply a consequence of having an additional consumer in the system, but emerges from the eco-evolutionary feedback between character displacement and resource suppression (compare initial (small points) with evolved
 243 strategies (large points), Fig. 4). Note that I reach the same fundamental conclusions when I incorporated a more realistic functional response for the consumers (Fig. 6 in Appendix).

I conducted the previous simulations on a scenario where the food web remains locally stable
 246 $(\text{Re}(\lambda_{\max}) < 0)$. Is it possible that character displacement would ever result in a locally unstable food web? To gain analytical insight to this question, I examined the conditions governing the local stability of the four-species food web when consumers exhibit a more realistic functional response
 249 (K S McCann, Rasmussen, and Umbanhowar (2005)). I show that the four-species food web will transition from having a locally stable equilibrium to a limit cycle under the following conditions (*Mathematica* file with derivation available upon request):

$$wa_{ii} + (1 - w)a_{ij} > \frac{e + hm}{hK(e - hm)}$$

252 Previously, I showed that character displacement always increases the effective attack rate of consumers $(wa_{ii} + (1 - w)a_{ij})$, regardless of the the shape of the tradeoff (Fig. 3A). Thus, character displacement is capable of pushing food webs to a point where they are locally unstable.

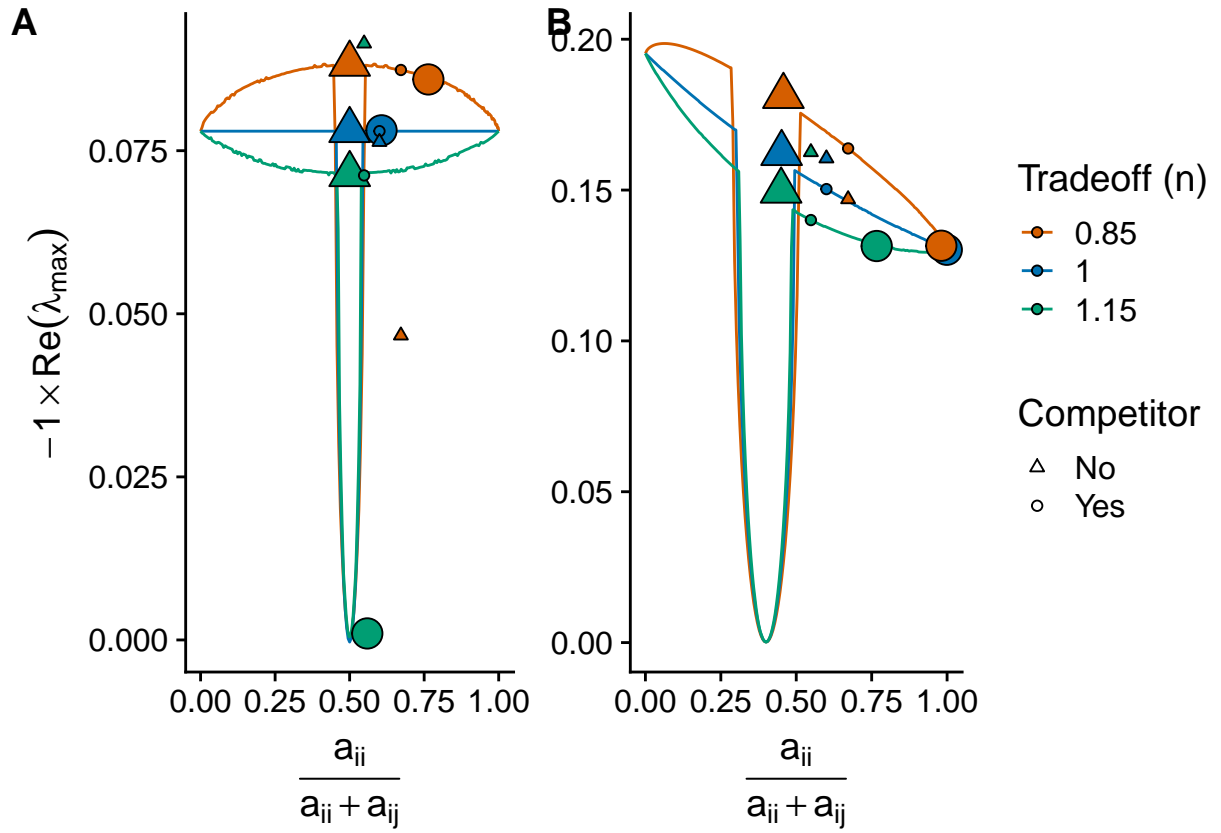


Figure 4: Effect of character displacement on local stability when consumers can (A) and cannot (B) forage for both resources simultaneously. Small and large points correspond to initial and evolved strategies, respectively.

Discussion

Important point: Criteria 5 in D Schluter and McPhail (1992) does not make sense since character displacement usually alters resource distributions. Think about this more.

Predictions for threespine stickleback

The scenario where the relationship between character displacement and resource suppression is the strongest is when the tradeoff in attack rates is concave-up and consumers are competing for resources that occur in different habitats (orange points in Fig. 3B and Fig. 5B). Prior work in threespine stickleback suggests that the evolution of stickleback attack rates are constrained by a concave-up tradeoff (Dolph Schluter (1993); Arnegard et al. (2014)) and that stickleback ecotypes are competing for resources that occur in different habitats (benthic vs. limnetic, D Schluter and McPhail (1992)). Thus, I predict that ecological character displacement in sticklebacks would suppress resource densities and decrease local stability.

While measuring resource densities is relatively straightforward, measuring stability is notoriously difficult. One of the more easy to acquire empirical metrics of stability is the coefficient of variation ($CV = \frac{\sigma}{\mu}$) as this only requires measurements of resource (or consumer) densities over time. Interestingly, there is a close correspondence between the coefficient of variation and the local stability of a food web (Gellner, McCann, and Hastings (2016)). Thus, I predict that character displacement in threespine stickleback will increase the CV of resource (or consumer) densities.

Consumer and resource densities in these dynamical models can be interpreted from either a population or biomass perspective (Yodzis and Innes (1992); Murdoch, Briggs, and Nisbet (2003); Kevin S McCann (2011)). For the stickleback system, you have data on seasonal dynamics of resources in terms of both abundances and biomass. Within a season, I do not expect stickleback abundances to be coupled to the abundances of zooplankton and benthic invertebrates, given that stickleback reproduce annually whereas zooplankton and benthic invertebrates can reproduce

many times within a season. Instead, I expect that stickleback biomass will be coupled to the biomass of zooplankton and benthic invertebrates within a season. This is because there will be lots of young stickleback at the beginning of the season, and they will eat a lot of resources and grow in size as the season progresses. If this is true, I also expect to see the largest negative effect of stickleback on resource densities late in the season.

Other relevant points

Although I used an Adaptive Dynamics approach here, I expect that these theoretical predictions would apply to models that assumed a different genetic architecture of attack rates (e.g. quantitative genetics). I expect this because, time and time again, models that explicitly include resource dynamics inevitably show that resource competition results in divergent character displacement, regardless of the genetic architecture of traits (see synthesis by Taper and Chase (1985)). Finally, my conclusions only apply to biological resources that are nutritionally substitutable. It would be interesting to extend these current analyses to non-substitutable resources where convergent character displacement is expected (Peter A Abrams (1987); Fox and Vasseur (2008)).

Acknowledgement

The content of this paper was greatly enhanced by numerous conversations with Seth Rudman. Sally Otto provided much help in early analyses of the mathematical model and I would not have been able to take the theory as far as I did without her guidance and her pushing me.

Appendix: More realistic functional response

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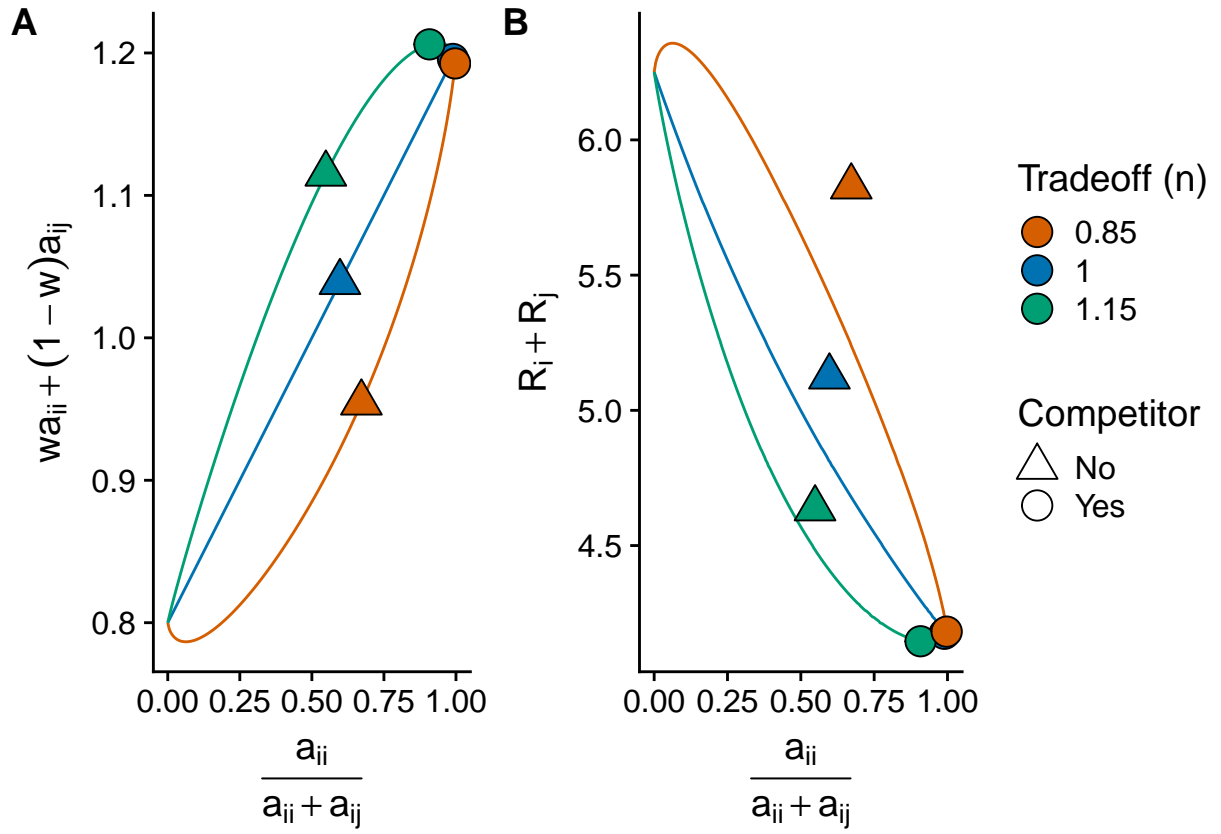


Figure 5: Effect of character displacement on total attack rates (A) and resource densities (B) when consumers exhibit a more realistic functional response.

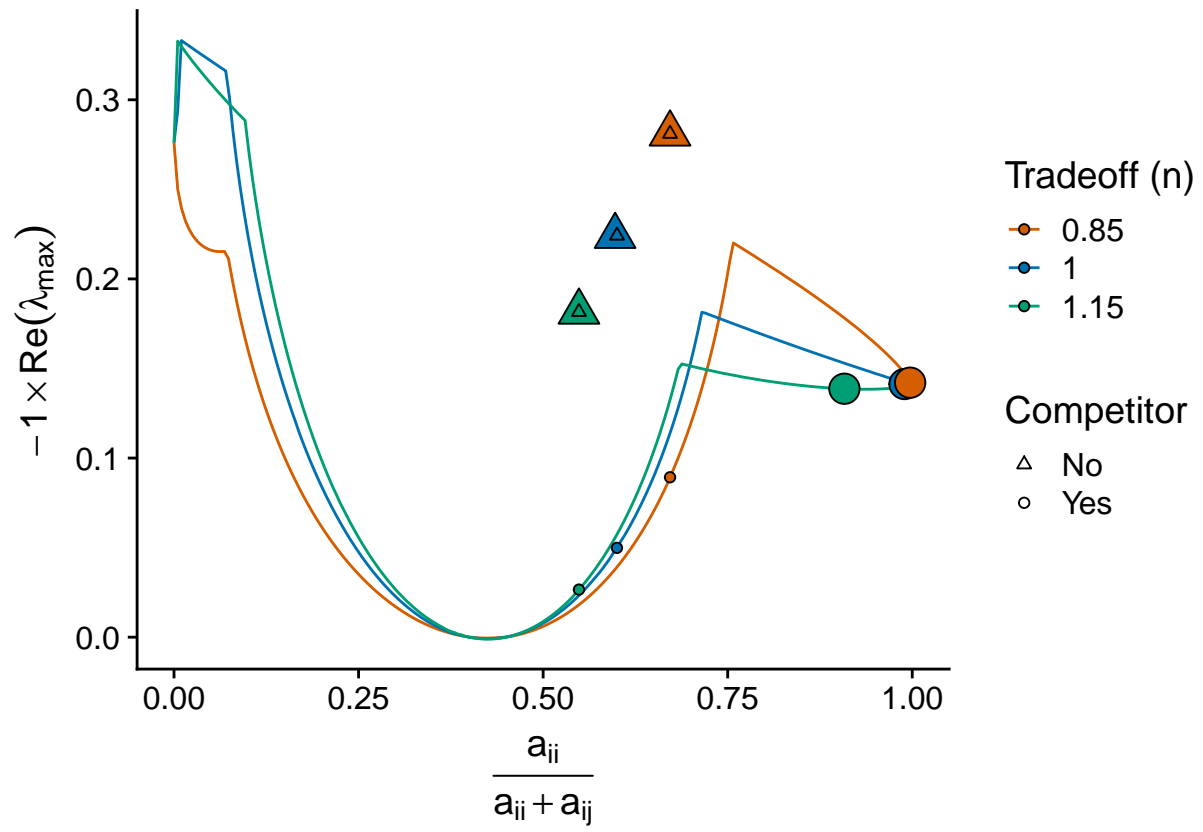


Figure 6: Effect of character displacement on local stability when consumers exhibit a more realistic functional response.

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