

# Ecological character displacement destabilizes food webs

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## Abstract

Ecological character displacement is an adaptive process that generally increases phenotypic  
3 diversity. Despite the fact that this diversification is due to an eco-evolutionary feedback between  
consumers competing for shared resources, its consequences for food-web dynamics have not  
been examined. Here, I study a model of two consumers competing for two shared resources to  
6 examine how character displacement in consumer attack rates affects resource abundances and the  
resilience of food webs to perturbations. I found that character displacement always strengthened  
consumer-resource interactions whenever consumers competed for resources that occurred in  
9 different habitats. This increase in interaction strength resulted in lower resource abundances and  
less resilient food webs. This occurred under different evolutionary tradeoffs and in both simple  
and more realistic foraging scenarios. Taken together, my results show that the adaptive process of  
12 character displacement often comes with the ecological cost of decreasing food-web resilience.

## Introduction

Ecological character displacement is an important adaptive process in generating biodiversity  
15 (Schluter, 2000; Pfennig and Pfennig, 2010). This process is due to “phenotypic evolution in a  
species generated or maintained by [exploitative] resource competition with one or more coexisting  
species” (Schluter, 2000). Over the past 40 years, a large body of theoretical (e.g. Lawlor and Smith,  
18 1976; Abrams, 1986; Doebeli, 1996; Taper and Chase, 1985; McPeck, 2019) and empirical (reviewed  
in: Schluter, 2000; Dayan and Simberloff, 2005; Stuart and Losos, 2013) work has examined which  
scenarios lead to phenotypic divergence or convergence of competing consumers. The general  
21 result has been that, if resources are nutritionally substitutable (Abrams, 1987; Fox and Vasseur,  
2008) and there is no other strong source of density dependence acting on consumers (Abrams,  
1986), then resource competition drives the adaptive divergence of competitors (Lawlor and Smith,  
24 1976; Taper and Chase, 1985). This adaptive process is not simply a response to static differences in  
resource distributions, but creates an eco-evolutionary feedback that drives further differentiation.  
This crucial insight was made by theoretical models that explicitly included resource dynamics as a  
27 mediator of competition in driving evolutionary change (Lawlor and Smith, 1976; Abrams, 1986;  
Taper and Chase, 1985).

Although models that included resources gave insights to the evolution of character displacement,  
30 the ecological feedback onto consumer-resource dynamics has received surprisingly little attention.  
This is likely because the ecological feedback has been primarily studied through the lens of  
coexistence theory (Lawlor and Smith, 1976; Germain et al., 2018; Bassar et al., 2017; McPeck,  
33 2019). For example, early theoretical work by Lawlor and Smith (1976) showed that ecological  
character displacement promotes coexistence by favoring specialized consumers that experience  
reduced interspecific competition. Yet, this reduction in interspecific competition may, at the same  
36 time, increase interspecific interactions between specialized consumers and their resources. Both  
food-web theory and empirical studies have shown that increasing the strength of consumer-  
resource interactions often suppresses the abundance of resources, which if sufficient enough, can

39 generate oscillations and less stable consumer-resource dynamics (Rosenzweig, 1971; Luckinbill,  
1973; Murdoch et al., 2002, 2003; McCann, 2011). Thus, a food-web perspective, which accounts for  
both the direct and indirect effects of consumer-resource interactions, may yield new insight to the  
42 ecological consequences of character displacement.

Here, I address this knowledge gap by studying a mathematical model that examines how ecological  
character displacement affects consumer-resource dynamics in a food-web context. I address two  
45 questions: (1) How does ecological character displacement affect resource abundances? (2) How  
does character displacement affect food-web stability? To test the generality of these effects, I  
explored different ecological foraging scenarios (fig. 1) and evolutionary tradeoffs in consumer  
48 attack rates (fig. 2). I found that the adaptive process of character displacement often comes with  
an ecological cost; resulting in food webs with lower resource availability and that are less resilient  
to perturbations.

## 51 **Material and methods**

### **Underlying Consumer-Resource Dynamics**

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

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

where  $r_i$  represents the intrinsic growth rate of resource  $i$ ,  $K_i$  represents the carrying capacity of  
 57 resource  $i$ ,  $e_{ij}$  represents the conversion efficiency of resource  $j$  into consumer  $i$ , and  $m_i$  represents  
 the mortality rate of consumer  $i$ .  $F_{ij}(R_j)$  represents consumer  $i$ 's feeding rate on resource  $j$  (i.e. func-  
 tional response). This model is a useful characterization of a scenario where consumers compete for  
 60 two distinct resources (e.g. zooplankton and benthic invertebrates in lakes) rather than if resources  
 are better characterized by a continuous trait distribution (e.g. seed size, see Taper and Chase (1985)  
 for an example).

### 63 Foraging Scenarios

I studied three different foraging scenarios (fig. 1). In the first, I assume that consumers can forage  
 for both resources simultaneously and their feeding rates increase linearly with resource abundance,  
 66 such that:

$$F_{ii}(R_i) = a_{ii}R_i \quad (2)$$

where  $a_{ii}$  is the attack rate of consumer  $i$  on resource  $i$ . This first scenario is the starting point  
 for many models of resource competition (MacArthur, 1972); however, it does not reflect many  
 69 food webs where consumers are mobile and their foraging behavior links resources that occur in  
 different habitats (McCann et al., 2005). A simple extension that accounts for this spatial context  
 takes the form:

$$F_{ii}(R_i) = w_{ii}a_{ii}R_i \quad (3)$$

72 where  $w_{ii}$  represents the proportion of time consumer  $i$  spends foraging in a habitat where only  
 resource  $i$  is found (i.e. habitat preference). Note that since  $w_{ii}$  is a proportion that  $w_{ij} = 1 - w_{ii}$ .  
 Finally, it is well known that consumer feeding rates often saturate at high resource abundances  
 75 (Holling, 1959; Rosenzweig and MacArthur, 1963; Murdoch et al., 2003; McCann, 2011) and that

consumers do not usually spend a fixed proportion of time in a particular habitat (McCann et al., 2005). To account for these biological realities, I consider a more realistic functional response  
 78 (derived by McCann et al., 2005):

$$F_{ii}(R_i, R_j) = \frac{a_{ii}W_{ii}R_i}{1 + a_{ii}h_{ii}W_{ii}R_i + a_{ij}h_{ij}W_{ij}R_j} \quad (4)$$

where consumer  $i$ 's feeding rate on resource  $i$  is influenced by the abundance of each resource;  
 81 saturates as resource abundances increase (due to handling times  $h_{ii}$ ,  $h_{ij}$ ); and consumer habitat preferences are modified by the relative abundance of resources, such that:  $W_{ii} = \frac{w_{ii}R_i}{w_{ii}R_i + (1-w_{ij})R_j}$ .

Previous studies have analyzed the evolution of consumer attack rates in the first two foraging  
 84 scenarios using an Adaptive Dynamics approach, with the general result being character divergence (Lawlor and Smith, 1976; Abrams, 1986). I say consumers have undergone character divergence if there evolved attack rates are more specialized, measured as  $|\frac{a_{ii}}{a_{ii}+a_{ij}} - 0.5|$ , when evolving  
 87 with a competing consumer. I also used an Adaptive Dynamics approach to analyze character displacement in the third foraging scenario, and I too observed character divergence (detailed analysis in Appendix S1 of Supplementary Information).

## 90 Food-web Dynamics

Given that character divergence occurred across these foraging scenarios, I focus here on its consequences for food-web dynamics. To do this, I analyzed differences in resource abundances  
 93 and food-web stability at equilibrium. An equilibrium is reached when the rates of change in equation 1 are 0, and solving the system at this point gives equilibrium abundances for each resource ( $\hat{R}_1, \hat{R}_2$ ) and each consumer ( $\hat{C}_1, \hat{C}_2$ ). Importantly, inferences about ecological character  
 96 displacement can only be made by comparing food webs with and without a competing consumer (Schluter and McPhail, 1992). Therefore, I compared resource abundances between food webs with

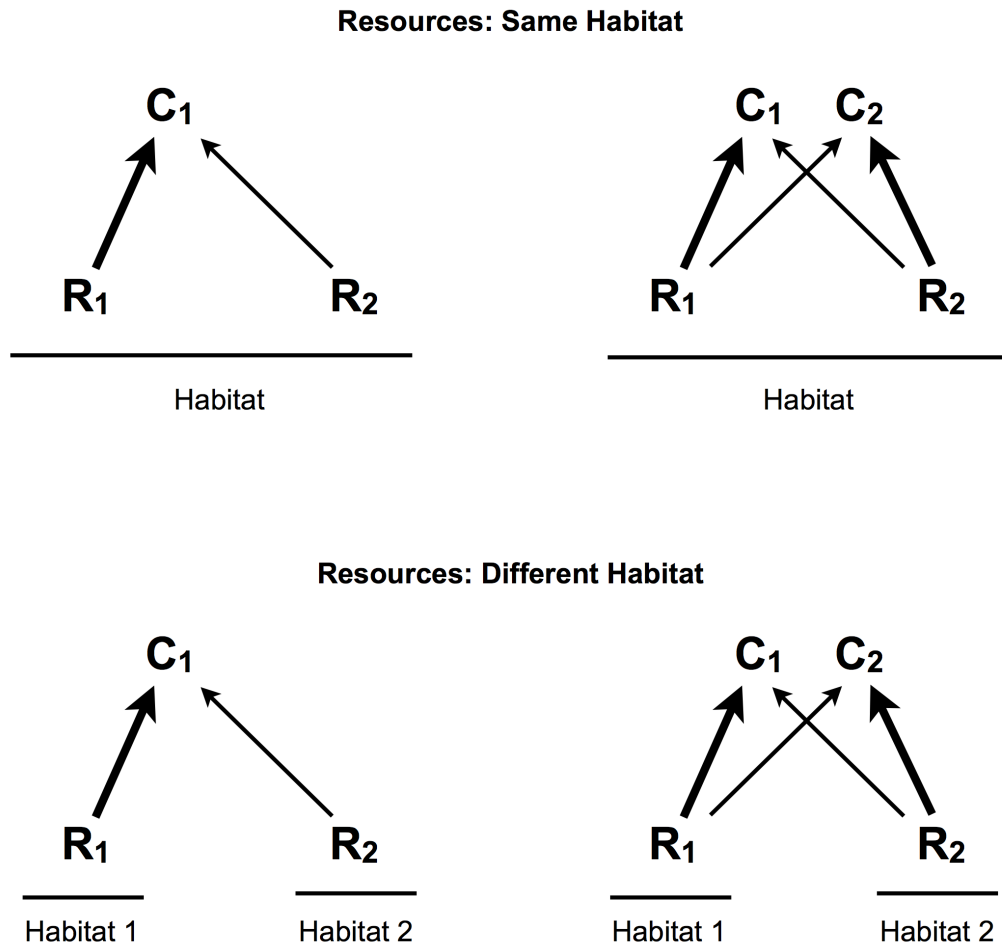


Figure 1: **Ecological foraging scenarios.** I examined whether the effect of ecological character displacement on food-web dynamics depended on whether consumers competed for resources that occurred in the same vs. different habitats. The width of each arrow corresponds to initial attack rates ( $a_{ij}$ ,  $a_{ji}$ ) of consumers. Note that  $C_i$  was always pre-adapted to  $R_i$  ( $a_{ii} > a_{ij}$ ). In each scenario, I assumed consumer feeding rate increased linearly with resource abundance. I also relax this assumption and consider a more realistic functional response when resources occurred in different habitats.

( $\hat{R}_1, \hat{R}_2, \hat{C}_1, \hat{C}_2 > 0$ ) and without ( $\hat{R}_1, \hat{R}_2, \hat{C}_1 > 0$ ) a competing consumer. I also compared the local  
 99 stability of these food webs using standard methods (Otto and Day, 2007). This stability analysis  
 derives the dominant eigenvalue,  $\lambda$ , which determines whether (and how readily) the food web  
 will return to equilibrium after a small perturbation.

102 When possible, I derived analytical expressions for the relationship between consumer attack  
 rates and food-web dynamics. To do this, I simplified the model by assuming that resources are  
 equivalent ( $r = r_1 = r_2$  and  $K = K_1 = K_2$ ) as well as consumers ( $e = e_{11} = e_{12} = e_{21} = e_{22}$ ;  
 105  $h = h_{11} = h_{12} = h_{21} = h_{22}$ ;  $m = m_1 = m_2$ ), except that consumer attack rates and their habitat  
 preferences (if present) are mirror images of each other ( $a_{ii} = a_{11} = a_{22}$ ;  $a_{ij} = a_{12} = a_{21}$ ;  $w_{ii} =$   
 $w_{11} = w_{22}$ ). Controlling for other sources of variability allowed me to isolate the general effects  
 108 of character divergence. All mathematical derivations were conducted in Mathematica (Wolfram  
 Research Inc., 2018) and are provided in the Supplementary Information (Appendix S1-3).

To gain insight to the eco-evolutionary feedback generated by character displacement, I conducted  
 111 simulations using an Adaptive Dynamics approach. Specifically, at each evolutionary time step, I  
 created a mutant consumer by randomly choosing one and modifying its attack rate on one resource  
 by either subtracting or adding a small constant (0.01 in the following simulations) with equal  
 114 probability. The mutant's attack rate on the other resource was determined by a tradeoff, 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  
 117 between cases where intermediate combinations of  $a_{ii}$  and  $a_{ij}$  are higher than the extremes (when  
 $n > 1$ , green line in fig. 2) or, conversely, where the two extremes are higher than intermediate  
 investments (when  $n < 1$ , orange line fig. 2). When  $n = 1$ , the tradeoff function is linear, and all  
 120 combinations of  $a_{ii}$  and  $a_{ij}$  have the same total attack rate (blue line in fig. 2). Assuming the mutant  
 consumer was 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 mutant was  
 123 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 stable strategy (ESS, Smith and Price, 1973) or an evolutionary limit (e.g.  $\frac{a_{ii}}{a_{ii}+a_{ij}}$  is constrained to a maximum of 1 and minimum of 0). Unless otherwise noted, I conducted simulations with the following parameter values:  $r = 1$ ;  $K = 4$ ;  $e = 0.8$ ;  $m = 1$ ;  $A = 2$ ;  $h = 0.4$ ; and  $w_{ii} = 0.6$ . I set an initial value of  $a_{ii} = 1.2$  and  $a_{ij}$  depended on the value of  $n$ . I set initial consumer and resource abundances to:  $R_1 = R_2 = 2$ ;  $C_1 = C_2 = 1$ . All simulations were conducted in R (R Core Team, 2018) and the code to reproduce these simulations is publically available on GitHub ([https://github.com/mabarbour/ECD\\_model](https://github.com/mabarbour/ECD_model)).

## Results

### Resources occur in same habitat

In this first scenario (equation 2), the abundance of resources at equilibrium are equivalent when both consumers and resources are present ( $\hat{R} = \hat{R}_1 = \hat{R}_2$ ), and are determined by the following equation (derived in Appendix S2):

$$\hat{R} = \frac{1}{a_{ii} + a_{ij}} \cdot \frac{m}{e} \quad (5)$$

A key determinant of resource abundance in this model is the consumer's total attack rate,  $a_{ii} + a_{ij}$ . Therefore, the effect of character displacement on food-web dynamics depends on how the tradeoff influences the evolution of consumer attack rates.

My simulations show that the shape of the tradeoff qualitatively affects the relationship between character displacement and resource abundances (fig. 3). For example, if consumer's are constrained by a linear tradeoff (blue lines), then there is no net change in total attack rate (fig. 3) and character displacement has no effect on resource abundances (fig. 3). If the tradeoff is concave down (green lines), then resource abundances can actually increase under character displacement

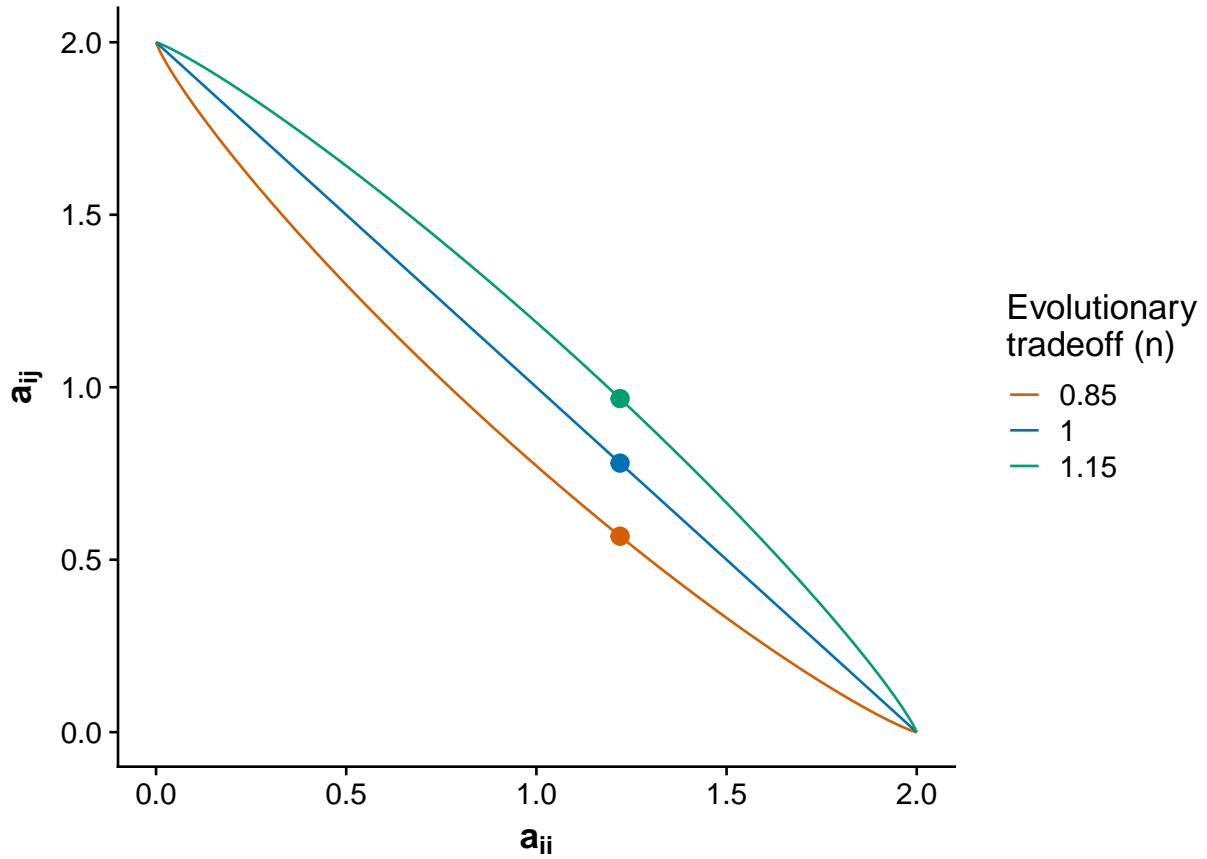


Figure 2: **Evolutionary tradeoffs in consumer attack rates.** In each foraging scenario, I explored the effects of three different tradeoffs: intermediate combinations of attack rates ( $a_{ii}$ ,  $a_{ij}$ ) are higher than the extremes (green line,  $n > 1$ ); extreme combinations of attack rates are higher than intermediate investments (orange line,  $n < 1$ ); and all combinations of attack rates have the same total attack rate (blue line,  $n = 1$ ). Points corresponding to attack rates at the beginning of the simulation. Note that  $C_i$  was always pre-adapted to  $R_i$  ( $a_{ii} > a_{ij}$ ).

(fig. 3). This is because the total attack rate of consumers is maximized at intermediate values ( $a_{ii} = a_{ij}$ ) and decreases as consumers diverge (fig. 3). When the tradeoff is concave up (orange lines), character displacement suppresses resource abundances due to the increase in total attack rates (fig. 3). Although the equation I derived for resource abundances was for the scenario where both consumers and both resources were present, it accurately predicts the abundance of resources when a single consumer reaches its ESS (triangles on respective colored lines in fig. 3). 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. 3), resulting in equivalent resource abundances.

The effect of character displacement on resources corresponds to its impact on food-web stability. For example, when character displacement decreases resource abundances (orange points in fig. 3), there is a decrease in food-web stability (fig. 3). Character divergence may not affect or even increase food-web stability (blue and green lines in fig. 3); however, evolution does not favor strong divergence in these scenarios (blue and green points in fig. 3), which dampens these contingent effects.

## Resources occur in different habitats

In the second foraging scenario (equation 3), I again see that resource abundances are equivalent when both consumers and resources are present ( $\hat{R} = \hat{R}_1 = \hat{R}_2$ ), but are now determined by the following equation (derived in Appendix S3):

$$\hat{R} = \frac{1}{w_{ii}a_{ii} + (1 - w_{ii})a_{ij}} \cdot \frac{m}{e} \quad (6)$$

This equation implies that if consumers evolve to become specialists on resources that occur in their preferred habitat (e.g.  $w_{ii} > 0.5$  and  $a_{ii} > a_{ij}$ ), then the effective attack rate of consumers ( $wa_{ii} + (1 - w_{ii})a_{ij}$ ) will always increase, regardless of the tradeoff (fig. 3). Thus, character divergence always results in resource suppression (fig. 3). 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 an evolutionary stable strategy (ESS,  
triangles in fig. 3). In contrast, resource abundances reach a similar value when consumers evolve  
in the presence of a competitor (circles in fig. 3), because character displacement tends to reach a  
constraint of complete specialization. It is worth noting that resource abundances 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. 3). This is because consumers  
actually evolve to be slightly specialized on the resources that occur in their non-preferred habitat  
(deviation of triangles from 0.5 along x-axis in fig. 3).

As seen previously, the effect of character displacement on resource abundances qualitatively  
corresponds to its effect on food-web stability (fig. 3). Specifically, character divergence decreases  
food-web stability, regardless of the tradeoff in attack rates. 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 (fig. 3). For example, when the tradeoff  
is concave up (orange), the initial two-consumer food web (small circle) is more stable than when  
there is only one consumer (small triangle); however, this pattern switches by the end of the  
eco-evolutionary simulation (large points).

### **Adding a more realistic functional response**

In the third foraging scenario (equation 4), I observed the same general effect of character divergence  
as the previous scenario (resources in different habitats, but linear functional response). This  
is because resource abundances at equilibrium are governed by a similar dynamic (derived in  
Appendix S1):

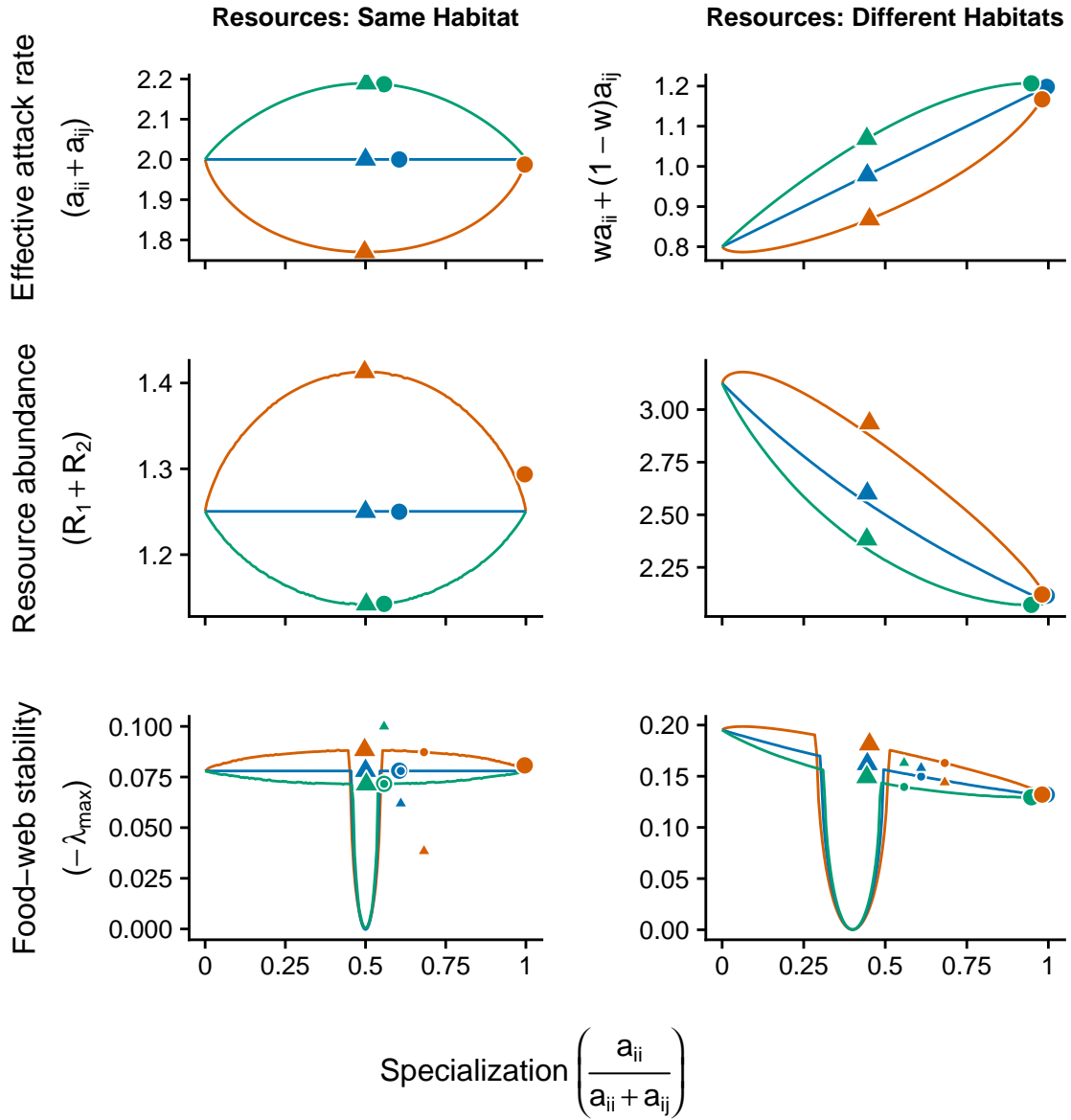


Figure 3: **Effect of character displacement on food-web dynamics under different evolutionary tradeoffs and foraging scenarios.** Different line colors correspond to different tradeoffs in attack rates (green,  $n = 1.15$ ; blue,  $n = 1$ ; orange,  $n = 0.85$ ). Large circles (two consumers) and triangles (one consumer) correspond to the end points of the eco-evolutionary simulation, whereas as small shapes correspond to the starting points (only in stability panels). In both foraging scenarios, feeding rates increase linearly with resource abundance, but the equation for effective attack rate is different.

$$\hat{R} = \frac{1}{wa_{ii} + (1 - w)a_{ij}} \cdot \frac{m}{e - hm} \quad (7)$$

And since evolution favors consumer divergence onto their preferred resources (see Appendix S1), the effective attack rate of consumers ( $wa_{ii} + (1 - w)a_{ij}$ ) will always increase, resulting in lower resource abundances and decreased food-web stability (Appendix S4).

In first two foraging scenarios, character displacement influences food-web stability, but all of the food webs ultimately return to a stable equilibrium (because  $\lambda_{max} < 0$ , see Appendix S2-3). In this more realistic model, however, whether the food web is locally stable depends on consumer and resource parameters. Specifically, I found that the two-consumer food web will transition from having a locally stable equilibrium to a limit cycle under the following conditions (derived using Routh-Hurwitz criteria in Appendix S1):

$$w_{ii}a_{ii} + (1 - w_{ii})a_{ij} > \frac{e + hm}{hK(e - hm)} \quad (8)$$

Thus, character displacement always pushes the food web toward an unstable structure in this more realistic foraging scenario (fig. 4). Note that I stopped the simulation in the four-species food web once it became locally unstable. I do not simulate beyond this point as this would require making assumptions about the dynamics of mutant consumers in variable environments, which is beyond the scope of this work.

## **Robustness to consumer asymmetry**

The previous analytical results and simulations make a strong assumption that competing consumers start off as perfect mirror images of each other (i.e. symmetry). Yet, theory indicates a predictable asymmetry between initial consumer attack rates. This predictable asymmetry emerges from a process of community assembly where a single consumer invades a system, reaches an ESS as a generalist, followed by the invasion of a second, more specialized, consumer. This theoretical

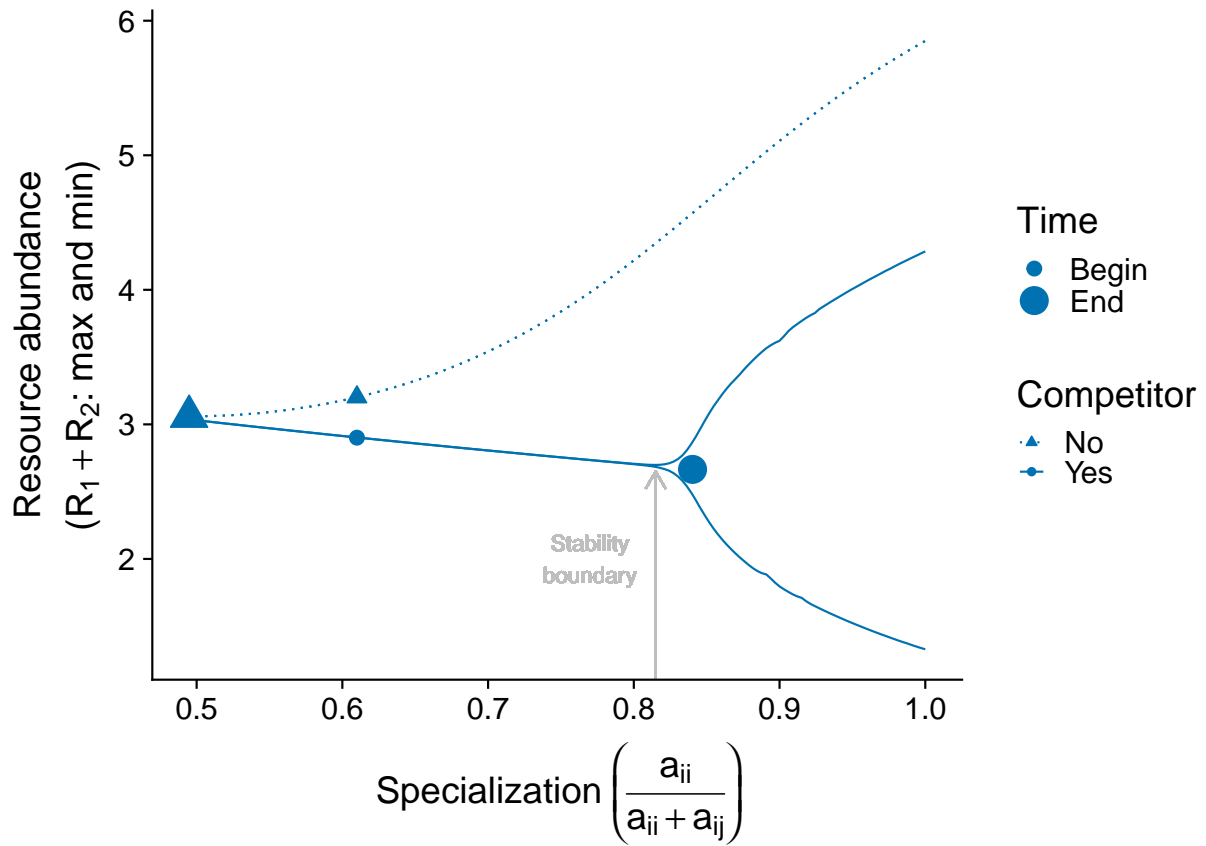


Figure 4: **Character divergence creates an unstable food web.** Lines illustrate the effects of character divergence across the range of specialization, while the points are the results of an eco-evolutionary simulation. Note that I increased the total investment in attack rates ( $A = 3.3$ ) to create a scenario that could result in an unstable food web.

scenario has been hypothesized as the sequence of events leading to character displacement in threespine stickleback in small coastal lakes of British Columbia (Schluter and McPhail, 1992; Schluter, 2000).

To test whether my results were robust to this asymmetry, I used the evolved attack rates at the end of the simulations with one consumer as the starting values for one of the two consumers. I did this for all foraging scenarios and tradeoffs previously examined. I found that my previous inferences are robust to including consumer asymmetry across different foraging scenarios and tradeoffs (Appendix S4).

## Discussion

### Resource abundances

One of the criteria used to demonstrate character displacement is that “sites of sympatry [two consumers] and allopatry [one consumer] should not differ greatly in food, ...” (Schluter and McPhail, 1992). In contrast, my results suggest that ecological character displacement causes predictable differences in resource abundances. In fact, the ecological and evolutionary scenarios that favored the greatest character divergence always decreased the abundance of resources. For example, the magnitude of character displacement was highest when mobile consumers competed for resources that occur in different habitats. An empirical example of this is threespine stickleback that have diverged into limnetic and benthic species with specialized traits to forage on zooplankton and benthic invertebrates, respectively (Schluter and McPhail, 1992; Schluter, 2000). These two resource types occur in distinct zones of the lake (pelagic and littoral), therefore stickleback must move between these zones when foraging for resources. Interestingly, a disproportionate number of the documented cases of character displacement involve carnivores (Schluter, 2000) that are larger, and likely more mobile, than their resources (McCann et al., 2005), suggesting many cases of ecological character displacement may result in lower resource availability.



234 Similarly, the evolutionary tradeoff that favored character divergence resulted in lower resources  
across all foraging scenarios. Although data on the shape of the tradeoff in consumer foraging  
traits is scarce, two classic examples of character displacement, Darwin's finches and threespine  
237 stickleback, both appear to exhibit a tradeoff where extreme trait values increase the net foraging  
rate of consumers (Schluter et al., 1985; Arnegard et al., 2014). While it is theoretically possible that  
character displacement does not alter (or even increase) resource abundances, this was limited to  
240 the simplest, and arguably least realistic, foraging scenario and under tradeoffs that did not favor  
large displacements, and thus less likely to detect in nature. Taken together, my results call for  
empirical work to test these clear theoretical predictions and suggest a revision is needed for one of  
243 the criteria used to demonstrate character displacement.

## Food-web Stability

My most striking result was that character divergence made food webs less resilient to perturbations.  
246 In fact, under the most realistic foraging scenario, character divergence can even result in an  
unstable food web. The mechanism underlying this destabilization is quite general. Character  
divergence generally increases the strength of consumer-resource interactions, but does not alter the  
249 strength of intraspecific interactions. This relative increase in interspecific interactions, combined  
with the natural oscillatory tendency of consumer-resource dynamics (Lotka, 1925; Volterra, 1926),  
creates a food-web structure that is less resilient to perturbations (Chesson and Kuang, 2008; Rip  
252 and McCann, 2011; McCann, 2011).

Interestingly, the ecological conditions that favor character divergence are those that are already  
the least resilient to perturbations. For example, McPeck (2019) showed that character divergence  
255 is favored in food webs that are either highly productive, easy to find and capture resources, or  
under weak abiotic stress. This corresponds to higher values of  $K$  (productivity) or  $A$  (investment  
in attack rates), or lower values of  $m$  (abiotic stress). Each of these corresponding changes decrease  
258 food-web resilience, as they increase the strength of consumer-resource interactions relative to

intraspecific interactions. For example, increasing productivity reduces intraspecific competition in resource populations while increasing the flux of energy to consumers, resulting in the paradox of enrichment (Rosenzweig, 1971). Similarly, higher feeding rates or lower consumer mortality both increase the relative strength of consumer-resource interactions, which predictably destabilizes food webs (Rip and McCann, 2011; McCann, 2011). This suggests that the most dramatic examples of character divergence will not only occur in, but also cause, the least stable food-web structures.

A handful of empirical patterns support the hypothesis that character divergence decreases food-web resilience. For example, a single species of threespine stickleback lives in hundreds of small coastal lakes of British Columbia, but the species pair, where character divergence has resulted in specialized limnetic and benthic species, are only known from six lakes in four independent watersheds (Schluter and McPhail, 1992; Schluter, 2000). Perhaps many lakes had a species pair in the past, but have lost a species due to a less resilient food-web structure (Borrelli, 2015; Borrelli et al., 2015). The species pair are known to be vulnerable to perturbations, as they have gone extinct in two of the six lakes after the introduction of nonnative species (Hatfield, 2001; Taylor et al., 2006; Rudman and Schluter, 2016). The vulnerability of the stickleback system also corresponds with the fact that aquatic food webs have several properties that make them less resilient to perturbations, such as higher productivity and more efficient energy transfer to consumers (Rip and McCann, 2011). Detecting the ghost of competition past (Connell, 1980) may be quite difficult, but it could be possible with recent advances in genomics. For example, Feulner and Seehausen (2018) detected genomic signatures of hybridization in sympatric whitefish species following periods of eutrophication. Perhaps solitary stickleback in some lakes retain genomic signatures of having been a habitat specialist in the past.

My results contrast, but do not necessarily contradict, the notion from coexistence theory that character displacement contributes to species coexistence (Lawlor and Smith, 1976). Rather than studying resilience, coexistence theory usually studies the mutual ability of consumers with different phenotypes to invade when rare (mutual invasibility, Chesson, 2000). In the context of

character displacement, a shortcoming of this mutual invasibility measure is that it does not allow a comparison between food webs with and without a competing consumer. Such comparisons are necessary for inferring the effects of character displacement, a point that has been made clear in the criteria to demonstrate character displacement (Schluter and McPhail, 1992; Schluter, 2000). Although the addition of a consumer to a food web can decrease its resilience in the absence of evolution (May, 1973), my results are primarily driven by an eco-evolutionary feedback between consumer evolution and resource abundances.

## Caveats

I studied this eco-evolutionary feedback between consumers and resources using an Adaptive Dynamics approach. A strength of this approach is that it enabled me to gain analytical insight to the effects of character divergence in a more realistic foraging scenario. This is much less tractable in quantitative genetic (Taper and Chase, 1985; McPeck, 2017) or explicit genetic (Doebeli, 1996) models of character displacement, which is why the foraging scenarios previously examined have been limited (but see McPeck, 2017). A weakness, however, is that I assume a separation of time scales between ecological and evolutionary dynamics, an assumption that is becoming less tenable (Hairston et al., 2005; Hendry, 2016). I also do not explicitly model an underlying phenotypic trait for consumer attack rates nor do I allow for intraspecific variation. That being said, my theoretical predictions are likely robust to these assumptions. This is because models that explicitly include resource dynamics inevitably show that resource competition results in character divergence, regardless of whether a quantitative genetic or Adaptive Dynamics approach is used (Lawlor and Smith, 1976; Taper and Chase, 1985). A quantitative genetic model may certainly show differences in the magnitude of character divergence, but this should not qualitatively change its effect on food-web dynamics. It is important to note that my conclusions only apply to food webs with biotic resources that are nutritionally substitutable. It would be interesting to extend these current analyses to non-substitutable resources where character convergence is expected (Abrams, 1987; Fox

and Vasseur, 2008).

## Conclusions

Here, I show that an adaptive process that generates phenotypic diversity generally makes that diversity more susceptible to future extinctions. This destabilizing effect emerges from an eco-evolutionary feedback involving direct and indirect interactions between species in a food-web context. This result contrasts with the current notion that patterns of phenotypic diversity are solely the result of evolutionary constraints imposed by mutation, natural selection, gene flow, and genetic drift. In particular, my result supports the recent suggestion that food-web stability can impose an ecological constraint on phenotypic diversity that is agnostic to these evolutionary processes (Borrelli et al., 2015). I expect that identifying when and where this ecological constraint arises will yield novel insight to the patterns of biodiversity we see in nature.

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