

# Ecological character displacement destabilizes food webs

Matthew A. Barbour<sup>1,2,\*</sup>

1. University of Zurich, Department of Evolutionary Biology and Environmental Studies, 8057 Zurich, Switzerland;

2. University of British Columbia, Department of Zoology, Vancouver, BC V6T 1Z4, Canada;

\* Corresponding author; e-mail: matthew.barbour@ieu.uzh.ch

*Running title:* Character divergence destabilizes food webs

*Keywords:* competition; eco-evolutionary dynamics; consumer-resource interactions; adaptation; community stability

## 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 may come 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). A large body of theoretical (e.g. Lawlor and Smith, 1976; Abrams, 1986;  
18 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 conclusion has  
21 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, 1976; Taper  
24 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 led to 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 showed that ecological character displacement promotes  
coexistence by favoring specialized consumers that experience reduced interspecific competition  
(Lawlor and Smith, 1976). Yet, this reduction in interspecific competition may, at the same time,  
36 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 generate  
39 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 and evolutionary tradeoffs in consumer attack rates.  
48 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.

## Material and methods

### 51 Underlying Consumer-Resource Dynamics

To examine how ecological character displacement affects resource abundances and food-web stability, I analyzed a continuous-time model of two consumers ( $C_{j=1,2}$ ) competing for two shared  
54 resources ( $R_{i=1,2}$ ):

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

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

can only be made by comparing food webs with and without a competing consumer (Schluter  
 63 and McPhail, 1992). Therefore, I arbitrarily set  $C_2 = 0$  to create a food-web without a competing  
 consumer for these comparisons.

## Foraging Scenarios

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

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

69 where  $a_{ij}$  is the attack rate of consumer  $j$  on resource  $i$ . This first scenario is the starting point  
 for many models of resource competition (MacArthur, 1972); however, it does not reflect many  
 food webs where consumers are mobile and their foraging behavior links resources that occur in  
 72 different habitats (McCann et al., 2005). The second scenario accounts for this spatial context (fig. 1  
 bottom) and takes the form:

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

where  $w_{ij}$  represents the proportion of time consumer  $j$  spends foraging in a habitat where only  
 75 resource  $i$  is found (i.e. habitat preference). Note that since  $w_{ij}$  is a proportion that  $w_{1,j} = 1 - w_{2,j}$ .  
 Finally, it is well known that consumer feeding rates often saturate at high resource abundances  
 (Holling, 1959; Rosenzweig and MacArthur, 1963; Murdoch et al., 2003; McCann, 2011) and that  
 78 consumers do not usually spend a fixed proportion of time in a particular habitat (McCann et al.,  
 2005). The third scenario accounts for these biological realities and takes the form (derived by  
 McCann et al., 2005):

$$F_{ij}(R_i) = \frac{a_{ij}W_{ij}R_i}{1 + a_{1,j}h_{1,j}W_{1,j}R_1 + a_{2,j}h_{2,j}W_{2,j}R_2} \quad (4)$$

where consumer  $j$ 's feeding rate on resource  $i$  is influenced by the abundance of each resource; saturates as resource abundances increase (due to handling times  $h_{ij}$ ); and consumer habitat preferences are modified by the relative abundance of resources, such that:  $W_{ij} = \frac{w_{ij}R_i}{w_{1,j}R_1 + w_{2,j}R_2}$ .

Previous studies have analyzed the evolution of consumer attack rates in the first two foraging scenarios using an Adaptive Dynamics approach, with the general result being character divergence (Lawlor and Smith, 1976; Abrams, 1986). 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). I say consumers have undergone character divergence if their evolved attack rates are more specialized when evolving with vs. without a competing consumer. Specialization of consumer  $j$  on resource 1 is measured as  $\frac{a_{1,j}}{a_{1,j} + a_{2,j}}$ , where a value of 0.5 is a complete generalist ( $a_{1,j} = a_{2,j}$ ), and a value of 1 is a complete specialist ( $a_{2,j} = 0$ ). Values less than 0.5 indicate specialization on the other resource.

## 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 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 ( $\hat{R}_i$ ) and each consumer ( $\hat{C}_j$ ). I also compared the local stability of these food webs using standard methods (Otto and Day, 2007). This stability analysis derives the dominant eigenvalue,  $\lambda_{max}$ , of the matrix of partial derivatives of all differential equations with respect to all variables evaluated at equilibrium. If  $-\lambda_{max} > 0$ , then the food web will return to equilibrium after a small perturbation (i.e. locally stable), with more positive values indicating a faster return time. If  $-\lambda_{max} < 0$ , then the food web is not locally stable.

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 ( $r = r_i$  and  $K = K_i$ ) as well as consumers ( $e = e_{ij}$ ;  $h = h_{ij}$ ;  $m = m_j$ ), except that consumer attack rates and their habitat preferences (if present) are mirror images of each other ( $a_{11} = a_{22}$ ;  $a_{12} = a_{21}$ ;  $w_{11} = w_{22}$ ). Note that I arbitrarily set  $C_1$  as being pre-adapted to  $R_1$  ( $a_{11} > a_{21}$ ;  $w_{11} > 0.5$ ),

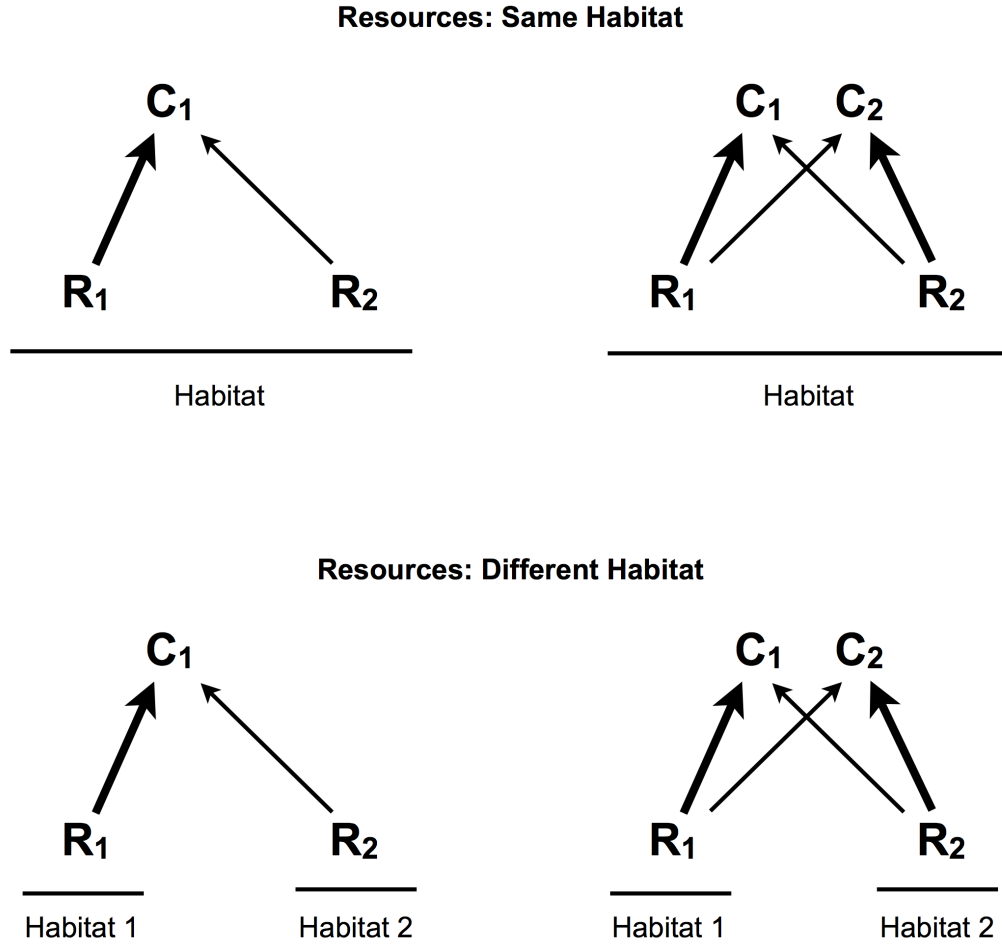


Figure 1: **Ecological foraging scenarios.** I examined whether the effect of ecological character displacement on food-web dynamics depended on whether consumers competed for resources that occurred in the same vs. different habitats. The width of each arrow corresponds to initial attack rates ( $a_{ij}$ ) of consumer  $j$  on resource  $i$ . Note that  $C_1$  was pre-adapted to  $R_1$  ( $a_{11} > a_{21}$ ), while  $C_2$  was a mirror image, being pre-adapted to  $R_2$  ( $a_{22} > a_{12}$ ). In each scenario, I assumed consumer feeding rates increased linearly with resource abundance. I also relax this assumption and consider a more realistic functional response when resources occurred in different habitats.

and therefore  $C_2$  was pre-adapted to  $R_2$ . Controlling for other sources of variability allowed me to  
111 isolate the general effects of character divergence. All mathematical derivations were conducted in  
Mathematica (Wolfram Research Inc., 2018) and are provided in the Supplementary Information  
(Appendix S1-3).

114 To gain insight to the eco-evolutionary feedback generated by character displacement, I conducted  
simulations using an Adaptive Dynamics approach. Specifically, after letting consumer and  
resource abundances reach a steady state, I created a mutant consumer by randomly choosing one  
117 and modifying its attack rate on one resource by either subtracting or adding a small constant (0.01  
in the following simulations) with equal probability. The mutant's attack rate on the other resource  
was determined by a tradeoff, such that  $(a_{1,j}/A)^n + (a_{2,j}/A)^n = 1$ , where  $A$  is the total investment  
120 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  $a_{1,j}$   
and  $a_{2,j}$  are higher than the extremes (when  $n > 1$ , green line in fig. 2) or, conversely, where the  
123 two extremes are higher than intermediate investments (when  $n < 1$ , orange line fig. 2). When  
 $n = 1$ , the tradeoff function is linear, and all combinations of  $a_{1,j}$  and  $a_{2,j}$  have the same total attack  
rate (blue line in fig. 2). Assuming the mutant consumer was rare, I then determined whether the  
126 mutant had higher relative fitness than the resident consumer, and thus could invade and replace  
the resident consumer. If the mutant was able to invade, I updated the attack rate of the resident  
consumer to the mutant attack rate and allowed consumer and resource abundances to reach a  
129 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.  $\frac{a_{ij}}{a_{1,j}+a_{2,j}}$  is constrained to a maximum of 1 and minimum of 0). Unless otherwise noted, I  
132 conducted simulations with the following parameter values:  $r = 1$ ;  $K = 4$ ;  $e = 0.8$ ;  $m = 1$ ;  $A = 2$ ;  $h =$   
 $0.4$ ; and  $w_{11} = w_{22} = 0.6$ . I set an initial value of  $a_{11} = a_{22} = 1.2$ , while  $a_{12}$  and  $a_{21}$  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  
135 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)).



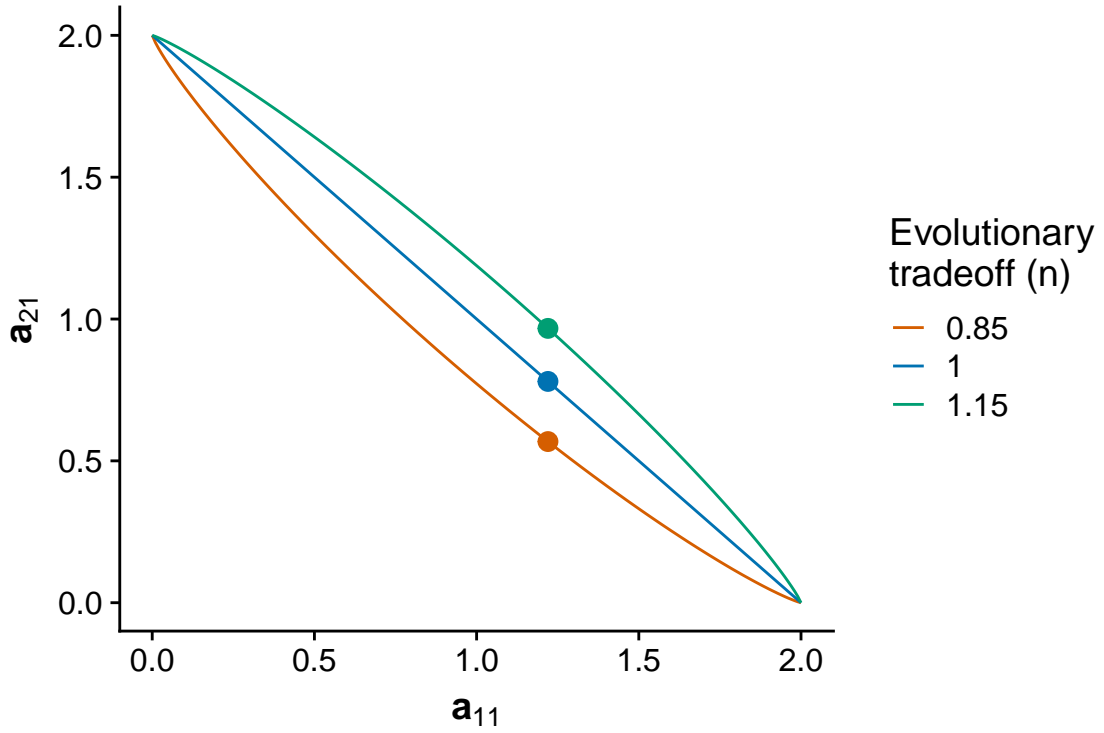


Figure 2: **Evolutionary tradeoffs in consumer attack rates.** In each foraging scenario, I explored the effects of three different tradeoffs: intermediate combinations of attack rates ( $a_{1,j}, a_{2,j}$ ) are higher than the extremes (green line,  $n > 1$ ); extreme combinations of attack rates are 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 for  $C_1$ , which was pre-adapted to  $R_1$  ( $a_{11} > a_{12}$ ).

## 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):

$$\hat{R} = \frac{1}{a_{1,j} + a_{2,j}} \cdot \frac{m}{e} \quad (5)$$

A key determinant of resource abundance in this scenario is the consumer's total attack rate,  $a_{1,j} + a_{2,j}$ . Therefore, the effect of character displacement on food-web dynamics depends on how the shape of the tradeoff function influences the evolution of consumer attack rates.

I found that the shape of the tradeoff function qualitatively affects the relationship between character displacement and resource abundances in this scenario (fig. 3 middle left). 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 top left) and character displacement has no effect on resource abundances (fig. 3 middle left). If the tradeoff is concave down (green lines), then resource abundances can actually increase under character displacement (fig. 3 middle left). This is because the total attack rate of consumers is maximized at intermediate values ( $a_{1,j} = a_{2,j}$ ) and decreases as consumers diverge (fig. 3 top left). When the tradeoff is concave up (orange lines), character displacement suppresses resource abundances due to the increase in total attack rates (fig. 3 top left). 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 evolutionary stable strategy (ESS; triangles on respective colored lines in fig. 3 middle left). 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 left panels), 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 middle left), there is a decrease in food-web stability (fig. 3 bottom left). Character divergence may

not affect or even increase food-web stability (blue and green lines in fig. 3 bottom left); however, evolution does not favor strong divergence in these scenarios (blue and green points in fig. 3), which dampens these contingent effects. Note that the dip in stability occurs when both consumers evolve to be generalists, a situation that is not favored in any of the foraging scenarios we examined (fig. 3 bottom).

### 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):

$$\hat{R} = \frac{1}{w_{1,j}a_{1,j} + w_{2,j}a_{2,j}} \cdot \frac{m}{e} \quad (6)$$

This equation implies that if consumers evolve to become specialists on resources that occur in their preferred habitat (e.g.  $w_{1,j} > 0.5$  and  $a_{1,j} > a_{2,j}$ ), then the effective attack rate of consumers ( $w_{1,j}a_{1,j} + w_{2,j}a_{2,j}$ ) will always increase, regardless of the tradeoff (fig. 3 top right). Thus, character divergence always results in resource suppression (fig. 3 middle right). 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 ESS (triangles in fig. 3 middle right). In contrast, resource abundances reach a similar value when consumers evolve in the presence of a competitor (circles in fig. 3 middle right), 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 middle right). 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 right panels).

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):

$$\hat{R} = \frac{1}{w_{1,j}a_{1,j} + w_{2,j}a_{2,j}} \cdot \frac{m}{e - hm} \quad (7)$$

And since evolution favors consumer divergence onto their preferred resources (see Appendix S1), the effective attack rate of consumers ( $w_{1,j}a_{1,j} + w_{2,j}a_{2,j}$ ) will always increase, resulting in lower resource abundances and decreased food-web stability (Appendix S4).

In the 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):

$$w_{1,j}a_{1,j} + w_{2,j}a_{2,j} > \frac{e + hm}{hK(e - hm)} \quad (8)$$

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

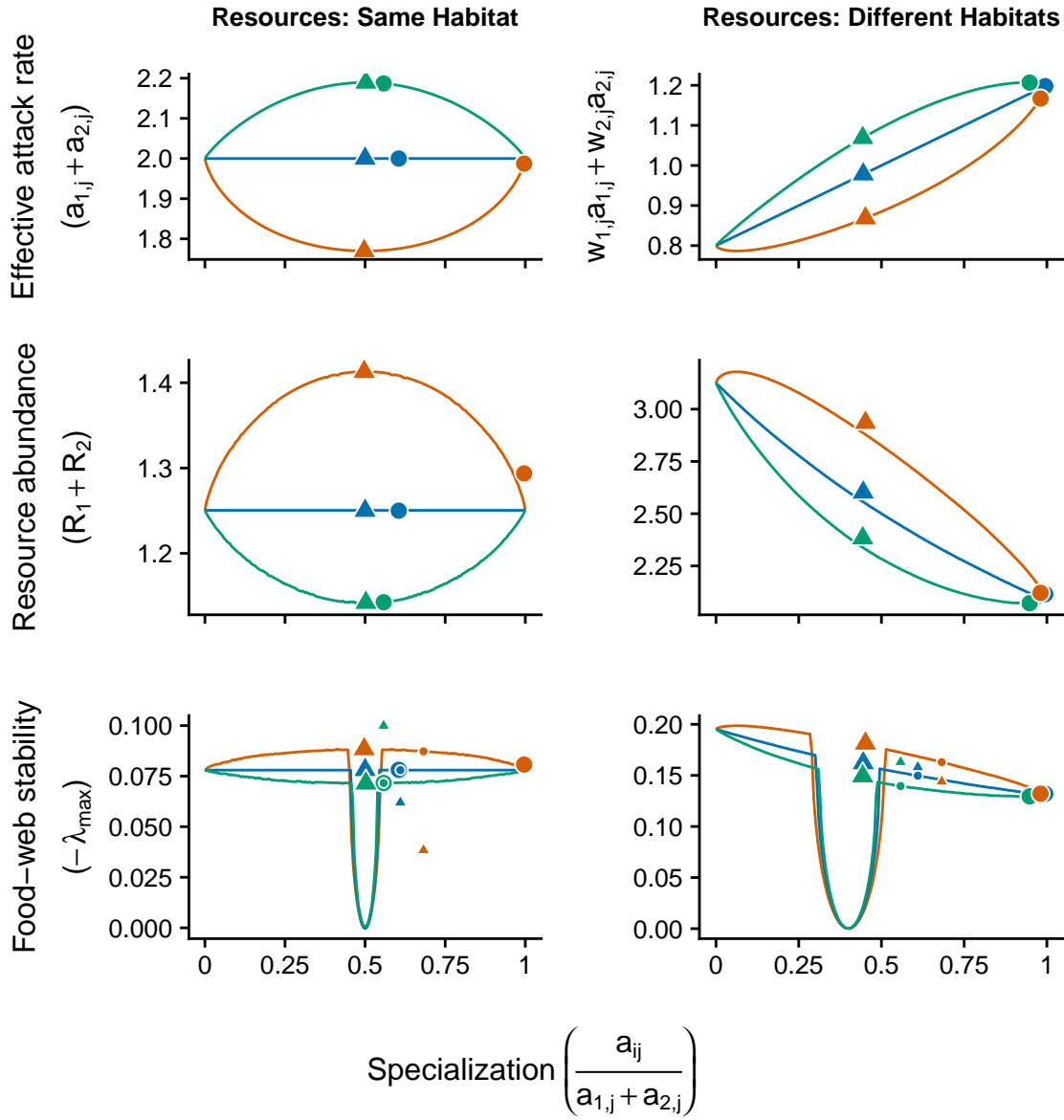


Figure 3: **Effect of character displacement on food-web dynamics under different evolutionary tradeoffs and foraging scenarios.** Lines show predicted values when both consumers and resources are present. Different line colors correspond to different tradeoffs in attack rates (green,  $n = 1.15$ ; blue,  $n = 1$ ; orange,  $n = 0.85$ ). Large circles (two consumers) and triangles (one consumer) correspond to the end points of the eco-evolutionary simulation for  $C_1$ , 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.

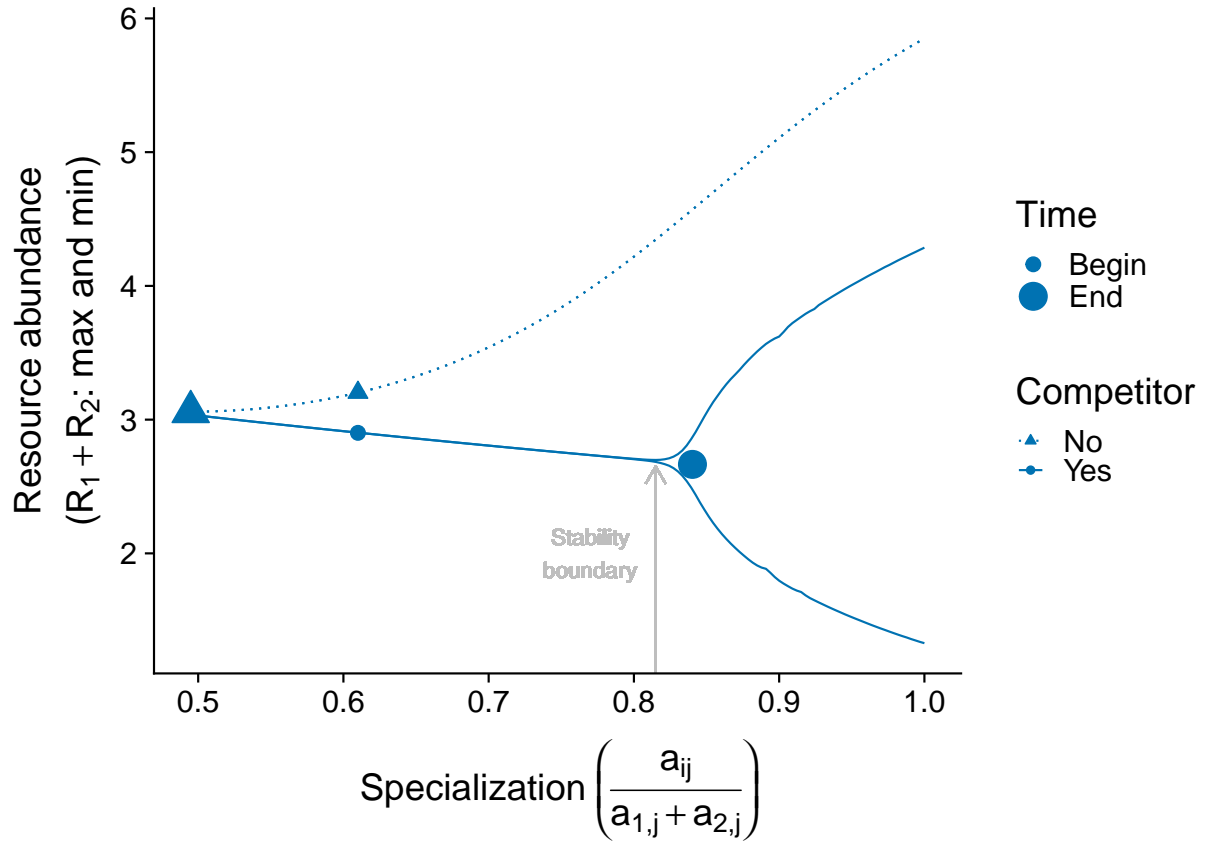


Figure 4: **Character divergence creates an unstable food web.** Lines illustrate the effects of character divergence across the range of specialization, while the points are the results of an eco-evolutionary simulation. Note that I increased the total investment in attack rates ( $A = 3.3$ ) to create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

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 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.

Similarly, the evolutionary tradeoff that favored character divergence resulted in lower resources

243 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  
246 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  
the simplest, and arguably least realistic, foraging scenario and under tradeoffs that did not favor  
249 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  
the criteria used to demonstrate character displacement.

## 252 **Food-web Stability**

My most striking result was that character divergence made food webs less resilient to perturbations.  
In fact, under the most realistic foraging scenario, character divergence can even result in an  
255 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  
strength of intraspecific interactions. This relative increase in interspecific interactions, combined  
258 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  
and McCann, 2011; McCann, 2011).

261 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  
is favored in food webs that are either highly productive, easy to find and capture resources, or  
264 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  
food-web resilience, as they increase the strength of consumer-resource interactions relative to  
267 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  
270 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.

273 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  
276 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  
279 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  
282 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  
285 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  
288 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  
291 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  
294 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).  
297 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

Although I model the indirect effects of coevolution between consumers, I do not account for potential coevolution between consumers and resources. In the context of my model, I would expect prey to evolve traits that reduce consumer attack rates. Thus, prey evolution would act to counter the effects of character displacement on resource abundance and food-web stability. Note that this does not negate my general conclusion that ecological character displacement decreases resource abundances and stability; however, this process may itself create another eco-evolutionary feedback between consumers and resources. This may actually help maintain dramatic examples of character divergence and prevent them from destabilizing systems, because it allows consumer traits to become decoupled from their attack rate. Examining this decoupling would be ideal in a quantitative genetic model that can explicitly track trait dynamics, but it would not fundamentally change the conclusions presented here.

Another potential caveat is that I explored my model in a setting that makes many assumptions about resource and consumer symmetry (but see consumer asymmetry section). Prior work has shown that allowing for resource asymmetry, for example, may decrease the magnitude of character displacement (Abrams, 1986). This is because this asymmetry creates an asymmetry in resource abundances, which dampens the effects of character divergence. Again though, this may dampen the effects of divergence, but should not change the qualitative relationship we observed of ecological character displacement decreasing resource abundances and food-web stability.

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  
330 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 pace of character divergence, but this should not qualitatively change its effect  
333 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;  
336 Fox and Vasseur, 2008).

## Conclusions

Here, I show that an adaptive process that generates phenotypic diversity generally makes that  
339 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  
342 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  
345 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.

## Acknowledgements

348 This work was inspired by discussions with Seth Rudman, Dolph Schluter, Ben Gilbert, and Kevin  
McCann. Sally Otto provided much help in early analyses of the mathematical model. I would  
not have been able to take the theory as far as I did without her guidance and encouragement. For  
351 funding support, I thank the University of British Columbia (Four-Year Fellowship to M.A. Barbour),  
NSERC (Discovery grant to Greg Crutsinger), and the Swiss National Science Foundation (grant  
31003A\_160671 to Jordi Bascompte).

## References

Abrams, P. A. 1986. Character displacement and niche shift analyzed using consumer-resource models of competition. *Theoretical Population Biology* 29:107–160.

———. 1987. Alternative models of character displacement and niche shift. i. adaptive shifts in resource use when there is competition for nutritionally nonsubstitutable resources. *Evolution* 41:651–661.

Arnegard, M. E., M. D. McGee, B. Matthews, K. B. Marchinko, G. L. Conte, S. Kabir, N. Bedford, S. Bergek, Y. F. Chan, F. C. Jones, D. M. Kingsley, C. L. Peichel, and D. Schluter. 2014. Genetics of ecological divergence during speciation. *Nature* 511:307–311.

Bassar, R. D., T. Simon, W. Roberts, J. Travis, and D. N. Reznick. 2017. The evolution of coexistence: Reciprocal adaptation promotes the assembly of a simple community. *Evolution* 71:373–385.

Borrelli, J. J. 2015. Selection against instability: stable subgraphs are most frequent in empirical food webs. *Oikos* 124:1583–1588.

Borrelli, J. J., S. Allesina, P. Amarasekare, R. Arditi, I. Chase, J. Damuth, R. D. Holt, D. O. Logofet, M. Novak, R. P. Rohr, A. G. Rossberg, M. Spencer, J. K. Tran, and L. R. Ginzburg. 2015. Selection on stability across ecological scales. *Trends in Ecology and Evolution* 30:417–425.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31:343–366.

Chesson, P., and J. J. Kuang. 2008. The interaction between predation and competition. *Nature* 456:235–238.

Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:131–138.

Dayan, T., and D. Simberloff. 2005. Ecological and community-wide character displacement: the next generation. *Ecology Letters* 8:875–894.

Doebeli, M. 1996. An explicit genetic model for ecological character displacement. *Ecology* 77:510–520.

Feulner, P. G. D., and O. Seehausen. 2018. Genomic insights into the vulnerability of sympatric  
381 whitefish species flocks. *Molecular Ecology* .

Fox, J. W., and D. A. Vasseur. 2008. Character convergence under competition for nutritionally  
essential resources. *The American Naturalist* 172:667–680.

384 Germain, R. M., J. L. Williams, D. Schluter, and A. L. Angert. 2018. Moving character displacement  
beyond characters using contemporary coexistence theory. *Trends in Ecology and Evolution*  
33:74–84.

387 Hairston, N. G., Jr, S. P. Ellner, M. A. Geber, T. Yoshida, and J. A. Fox. 2005. Rapid evolution and  
the convergence of ecological and evolutionary time: Rapid evolution and the convergence of  
ecological and evolutionary time. *Ecology Letters* 8:1114–1127.

390 Hatfield, T. 2001. Status of the stickleback species pair, *gasterosteus* spp., in hadley lake, lasqueti  
island, british columbia. *Canadian Field-Naturalist* 115:579–583.

Hendry, A. P. 2016. *Eco-evolutionary Dynamics*. Princeton University Press.

393 Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. *The Canadian*  
*Entomologist* 91:385–398.

Lawlor, L. R., and J. M. Smith. 1976. The coevolution and stability of competing species. *The*  
396 *American Naturalist* 110:79–99.

Lotka, A. J. 1925. *Elements of Physical Biology*. Williams & Wilkins Company.

Luckinbill, L. S. 1973. Coexistence in laboratory populations of *paramecium aurelia* and its predator  
399 *didinium nasutum*. *Ecology* 54:1320–1327.

MacArthur, R. H. 1972. *Geographical Ecology: Patterns in the Distribution of Species*. *Biology /*  
[Princeton University Press]. Princeton University Press.

402 May, R. M. 1973. Stability and complexity in model ecosystems, vol. 6 of *Monographs in Population*  
*Biology*. Princeton University Press.

McCann, K. S. 2011. *Food Webs*, vol. 50 of *Monographs in Population Biology*. Princeton University  
405 Press.

McCann, K. S., J. B. Rasmussen, and J. Umbanhowar. 2005. The dynamics of spatially coupled food webs. *Ecology Letters* 8:513–523.

408 McPeck, M. A. 2017. *Evolutionary Community Ecology*. Monographs in Population Biology. Princeton University Press.

———. 2019. Limiting similarity? the ecological dynamics of natural selection among resources  
411 and consumers caused by both apparent and resource competition. *The American Naturalist*  
pages E000–E000.

Murdoch, W. W., C. J. Briggs, and R. M. Nisbet. 2003. *Consumer-resource Dynamics*. Monographs  
414 in Population Biology. Princeton University Press.

Murdoch, W. W., B. E. Kendall, R. M. Nisbet, C. J. Briggs, E. McCauley, and R. Bolser. 2002. Single-species models for many-species food webs. *Nature* 417:541–543.

417 Otto, S. P., and T. Day. 2007. *A Biologist's Guide to Mathematical Modeling in Ecology and Evolution*. Princeton University Press.

Pfennig, D. W., and K. S. Pfennig. 2010. Character displacement and the origins of diversity. *The*  
420 *American Naturalist* 176:S26–44.

R Core Team. 2018. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

423 Rip, J. M. K., and K. S. McCann. 2011. Cross-ecosystem differences in stability and the principle of energy flux. *Ecology Letters* 14:733–740.

Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in  
426 ecological time. *Science* 171:385–387.

Rosenzweig, M. L., and R. H. MacArthur. 1963. Graphical representation and stability conditions of Predator-Prey interactions. *The American Naturalist* 97:209–223.

429 Rudman, S. M., and D. Schluter. 2016. Ecological impacts of reverse speciation in threespine stickleback. *Current Biology* 26:490–495.

- 432 Sargent, R. D., and S. P. Otto. 2006. The role of local species abundance in the evolution of pollinator attraction in flowering plants. *The American Naturalist* 167:67–80.
- Schluter, D. 2000. Ecological character displacement in adaptive radiation. *The American Naturalist* 156:S4–S16.
- 435 Schluter, D., and J. D. McPhail. 1992. Ecological character displacement and speciation in sticklebacks. *The American Naturalist* 140:85–108.
- Schluter, D., T. D. Price, and P. R. Grant. 1985. Ecological character displacement in darwin's finches. 438 *Science* 227:1056–1059.
- Smith, J. M., and G. R. Price. 1973. The logic of animal conflict. *Nature* 246:15.
- Stuart, Y. E., and J. B. Losos. 2013. Ecological character displacement: glass half full or half empty? 441 *Trends in Ecology and Evolution* 28:402–408.
- Taper, M. L., and T. J. Chase. 1985. Quantitative genetic models for the coevolution of character displacement. *Ecology* 66:355–371.
- 444 Taylor, E. B., J. W. Boughman, M. Groenenboom, M. Sniatynski, D. Schluter, and J. L. Gow. 2006. Speciation in reverse: morphological and genetic evidence of the collapse of a three-spined stickleback (*gasterosteus aculeatus*) species pair. *Molecular Ecology* 15:343–355.
- 447 Volterra, V. 1926. Fluctuations in the abundance of a species considered mathematically. *Nature* 118:558.
- Wolfram Research Inc. 2018. *Mathematica*, Version 11.0. Champaign, IL.