Ecological character displacement destabilizes food webs

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Abstract

Ecological character displacement is an adaptive process that generally increases phenotypic 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 received little attention. Here, I study a model of two consumers competing for two shared resources to 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 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 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 (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; Doebeli, 1996; Taper and Case, 1985; McPeek, 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 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 and Case, 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 mediator of competition in driving evolutionary change (Lawlor and Smith, 1976; Abrams, 1986; Taper and Case, 1985).

Although models that included resources led to insights about the evolution of character displacement, 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; McPeek, 2019). For example, early theoretical work showed that 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, 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 oscillations

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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 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. Specifically, I sought to answer the question: how does character displacement in consumer attack rates affect resource abundances and food-web stability? To test the generality of these effects, I explored different ecological foraging scenarios and evolutionary tradeoffs in consumer attack rates. 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

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 resources ($R_{i=1,2}$):

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

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

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the mortality rate of consumer j. $F_{ij}(R_i)$ represents consumer j's feeding rate on resource i (i.e.,

its 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 where resources are better characterized by a continuous trait distribution (e.g., seed size; see Taper and Case (1985) for an example). Importantly, inferences about character displacement can only be made by comparing food webs with and without a competing consumer (Schluter and McPhail, 1992). Therefore, I arbitrarily set $C_2 = 0$ to create a food-web without a competing consumer for these comparisons.

Foraging scenarios

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

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

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 different habitats (Holt, 1984). The second scenario accounts for this spatial context (Fig. 1b) and takes the form:

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

where w_{ij} represents the proportion of time consumer j spends foraging in a habitat where only resource i is found (i.e., its 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 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):

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

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 time h_{ij}); and consumer habitat preferences are modified by the relative abundance of resources, such that: $W_{ij} = w_{ij}R_i/(w_{1,j}R_1 + w_{2,j}R_2)$.

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 divergent character displacement (Lawlor and Smith, 1976; Abrams, 1986). I also used an Adaptive Dynamics approach to analyze the evolution of consumer attack rates in the third foraging scenario, and I too observed divergent character displacement (detailed analysis given in Appendix S1). I say consumers have undergone divergent character displacement 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 $a_{1,j}/(a_{1,j} + a_{2,j})$, 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. Since I did not observe convergent character displacement in any of the foraging scenarios I analyzed, I refer to divergent character displacement as simply (ecological) character displacement throughout the rest of the text.
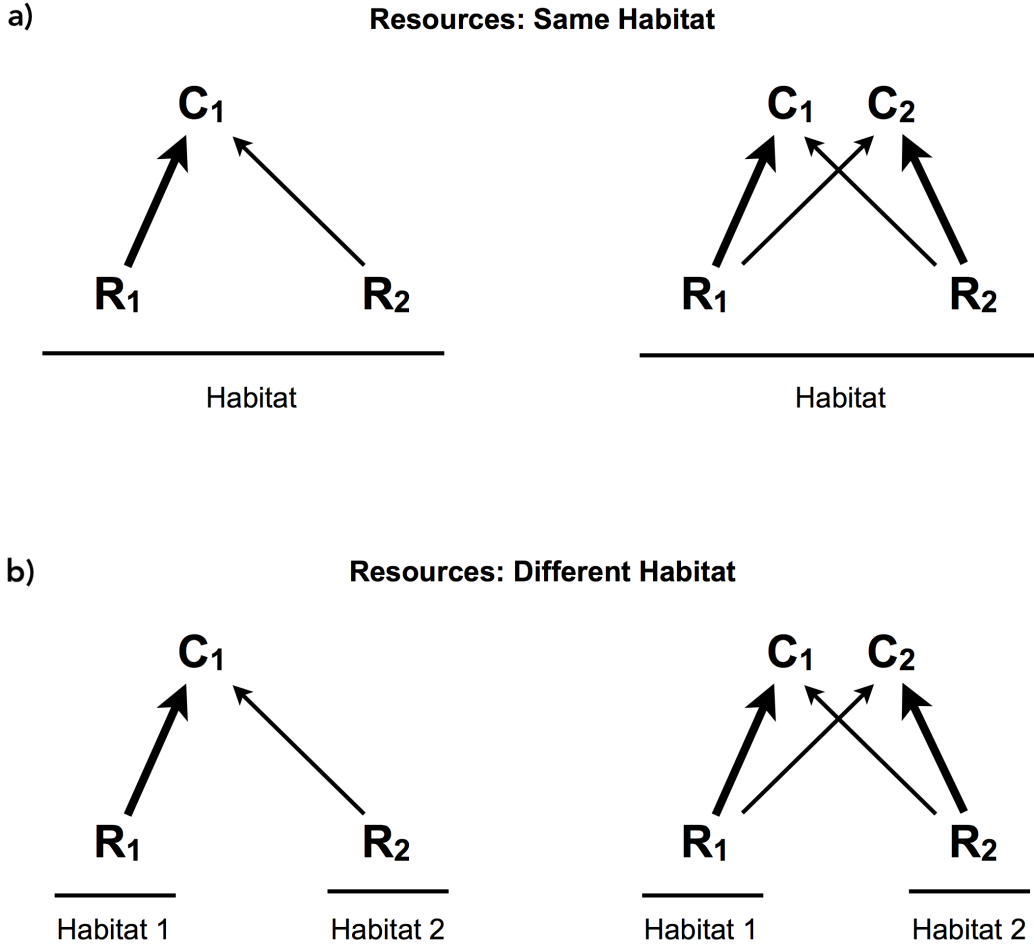
a)
Resources: Same Habitat

C_1

R_1 R_2

_____
              Habitat

C_1 C_2

R_1 R_2

_____
              Habitat

b)
Resources: Different Habitat

C_1

R_1 R_2

_____   _____
  Habitat 1   Habitat 2

C_1 C_2

R_1 R_2

_____   _____
  Habitat 1   Habitat 2

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 (a) vs. different habitats (b). Note that inferences about character displacement can only be made by comparing food webs with (right) and without (left) a competing consumer, so I arbitrarily set $C_2 = 0$ for these comparisons. The width of each arrow corresponds to the initial attack rate (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 ($a_{22} = a_{11}$; $a_{12} = a_{21}$). 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 (b).

Food-web dynamics

Given that character displacement 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 there is no change in the population growth rates of consumers and resources (i.e., 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 each species' population growth rate (given by equation 1) with respect to each species' abundance evaluated at equilibrium. All eigenvalues must be negative for the food web to be locally stable; however, the dominant eigenvalue, $\lambda_{\max}$, is the one closest to positive infinity and ultimately determines food-web stability. If $\lambda_{\max} > 0$, then the food web is not locally stable. If $\lambda_{\max} < 0$, then the food web will return to equilibrium after a small perturbation (i.e., it is locally stable), with more negative values indicating a faster return time (i.e., greater stability). I chose to plot $-\lambda_{\max}$ rather than $\lambda_{\max}$, so that increasing values would indicate greater stability, which I felt was a more intuitive way to present the results.

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 ($a_{11} > a_{21}$; $w_{11} > 0.5$), and therefore C_2 was pre-adapted to R_2. Controlling for other sources of variability allowed me to isolate the general effects of character displacement. All mathematical derivations were conducted in Mathematica (Wolfram Research Inc., 2018) and are provided in Appendices S1-3.

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

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resource abundances reach a steady state, 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 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 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 two extremes are higher than intermediate investments (when $n < 1$, orange line in 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 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 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., $a_{ij}/(a_{1,j} + a_{2,j})$ is constrained to a maximum of 1 and minimum of 0).

The Adaptive Dynamics approach I use here is one of several possible approaches for studying the eco-evolutionary dynamics of interacting species. A strength of this approach is that it enables me to gain analytical insight to the effects of character displacement in more realistic foraging scenarios. This is much less tractable in quantitative genetic (Taper and Case, 1985; McPeek, 2017) or explicit genetic (Doebeli, 1996) models of character displacement, which is why the foraging scenarios previously examined have been limited (but see McPeek, 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). In addition, I assume that there is no intraspecific variation within interacting species, despite the fact that intraspecific variation is a common feature of natural populations and often has important ecological consequences (Bolnick et al., 2011; Des Roches et al., 2018). Still, models that explicitly include resource dynamics

inevitably show that resource competition results in character displacement, regardless of whether
a quantitative genetic or Adaptive Dynamics approach is used (Lawlor and Smith, 1976; Taper
and Case, 1985). Therefore, it should still serve as a good starting point for studying the ecological
consequences of character displacement (but see **Caveats** section in the discussion).

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 $w_{11} = w_{22} = 0.6$. 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 simulations were conducted in R (R Core Team, 2018) and the
code to reproduce these simulations is publically available on GitHub and has been archived with
Zenodo (please contact journal office for links).

Results

Resources occur in the 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):

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

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. 3a,b). For example, if
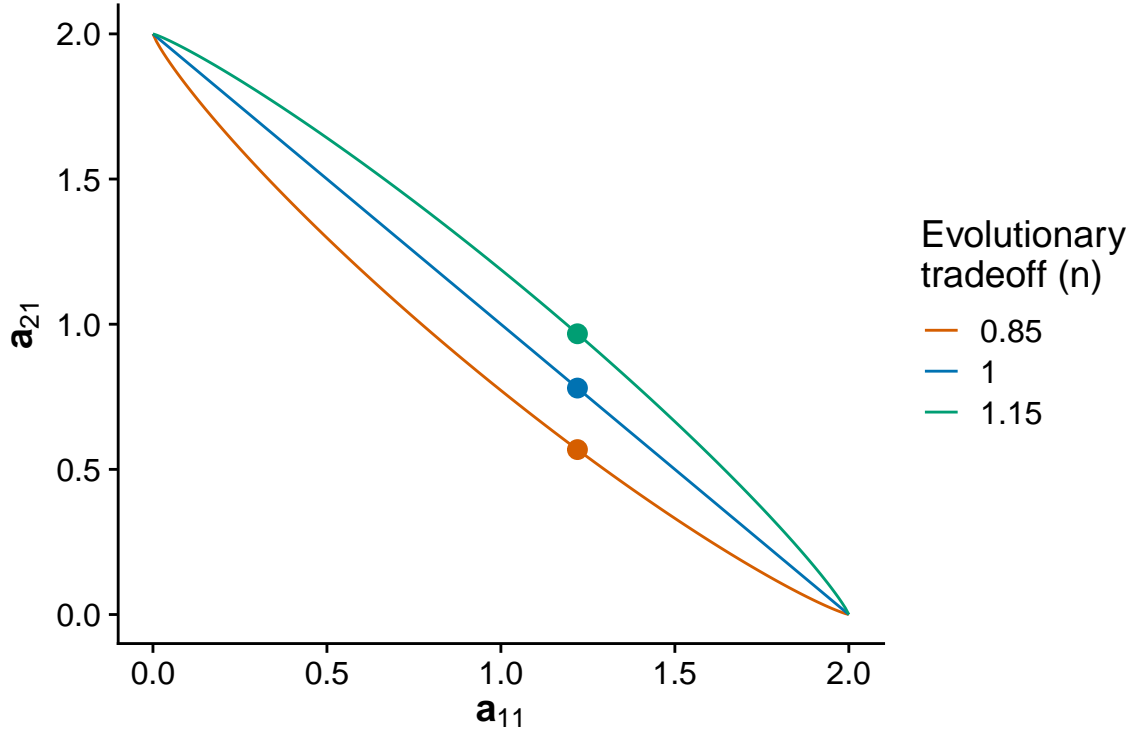consumer's are constrained by a linear tradeoff (blue lines), then there is no net change in total

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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 ($a_{11} > a_{12}$). Note that C_2 was a mirror image of C_1, being pre-adapted to R_2 ($a_{22} = a_{11}$; $a_{12} = a_{21}$).

attack rate (Fig. 3a) and character displacement has no effect on resource abundances (Fig. 3b). If the tradeoff is concave down (green lines), then resource abundances can actually increase under character displacement (Fig. 3b). 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. 3a). When the tradeoff is concave up (orange lines), character displacement suppresses resource abundances due to the increase in total attack rates (Fig. 3a,b). 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. 3b). 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. 3a), 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. 3b), there is also a decrease in food-web stability (Fig. 3c). Character displacement may not affect or even increase food-web stability (blue and green lines in Fig. 3c); however, evolution does not favor strong divergence in these scenarios (blue and green points in Fig. 3a), which dampens these contingent effects. Note that the dip in stability toward a dominant eigenvalue of zero is an artifact of the two consumers becoming ecologically identical ($a_{11} = a_{21} = a_{12} = a_{22}$) on identical resources, and effectively become neutral species (McPeek and Siepielski, 2019). Although neutrality is an ecological possibility, it is never favored by evolution in these models since character displacement occurred across all the foraging scenarios I examined.

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):

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

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. 3d). Thus, character displacement always results in resource suppression (Fig. 3e). 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. 3e). In contrast, resource abundances reach a similar value when consumers evolve in the presence of a competitor (circles in Fig. 3e), 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. 3e). This is because consumers actually evolve slightly specialized attack rates on the resources that occur in their non-preferred habitat (deviation of triangles from 0.5 along x-axis in Fig. 3d).

As seen previously, the effect of character displacement on resource abundances qualitatively corresponds to its effect on food-web stability (Fig. 3f). Specifically, character displacement 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. 3c). 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). As with the previous model, the dip in stability corresponds to the situation where consumers are effectively identical ($w_{11}a_{11} = w_{21}a_{21} = w_{12}a_{12} = w_{22}a_{22}$) and become neutral species, which is never favored in these models.

It is worth noting that the scales are different between the left and right columns of Figure 3. When resources occur in different habitats (relative to the same habitat), the consumer's effective attack rate is lower because it is multiplied by the proportion w_{ij}. This results in relatively higher resource abundances and more stable food webs compared to when resources occur in the same habitat, and corresponds to the inherent stabilizing role of spatial heterogeneity in food webs (Holt, 1984; McCann et al., 2005).

Adding a more realistic functional response

In the third foraging scenario (equation 4), I observed the same general effect of character displacement 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):

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

And since evolution favors character displacement toward 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, Fig. S1).

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 become unstable under the following conditions (derived using Routh-Hurwitz criteria in Appendix S1):

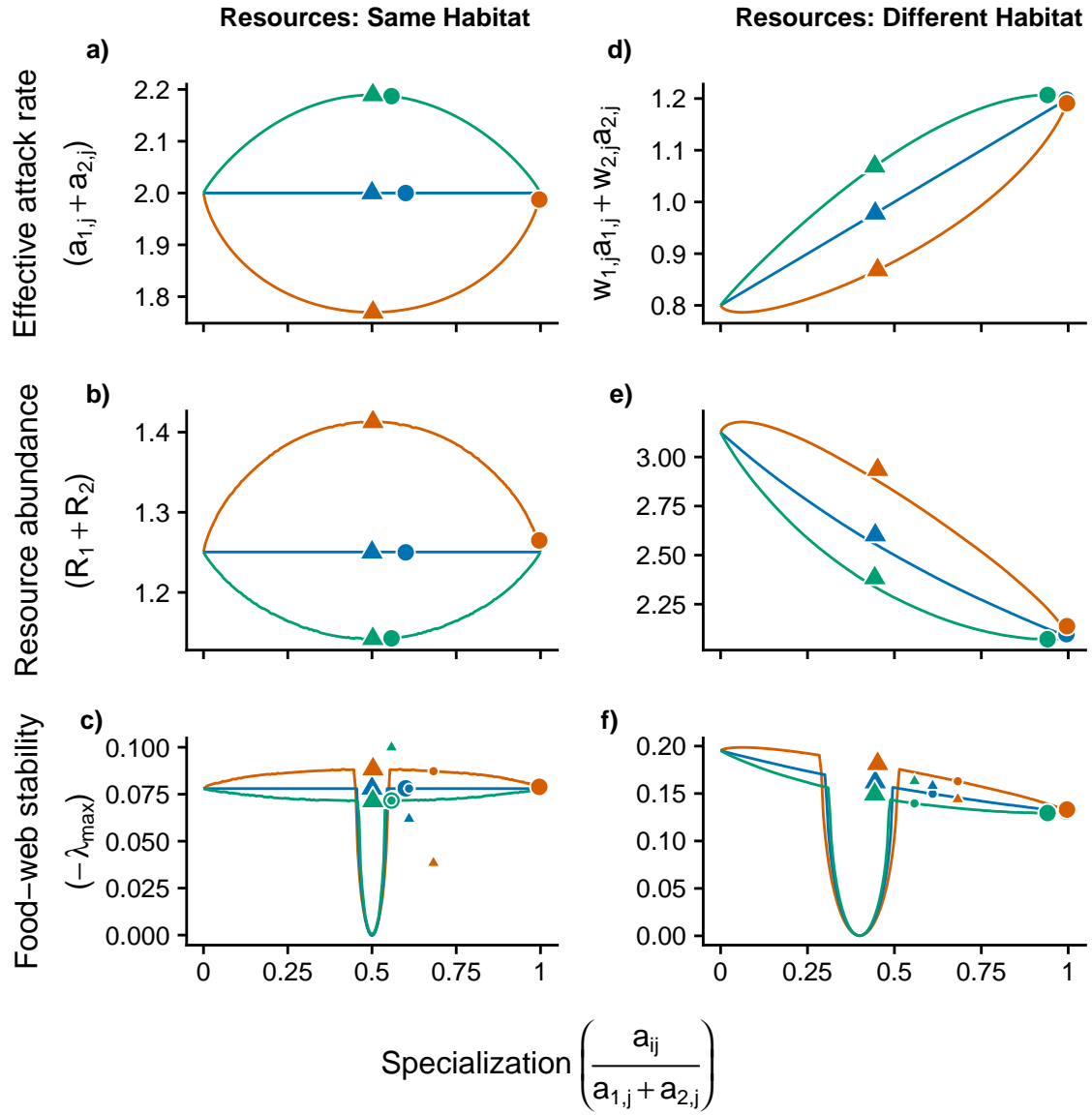$$w_{1,j}a_{1,j} + w_{2,j}a_{2,j} > \frac{e + hm}{hK(e - hm)} \tag{8}$$

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 (the choice to display C_1 was arbitrary), whereas 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 the effective attack rate is different.

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This inequality indicates that 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 two-consumer 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.
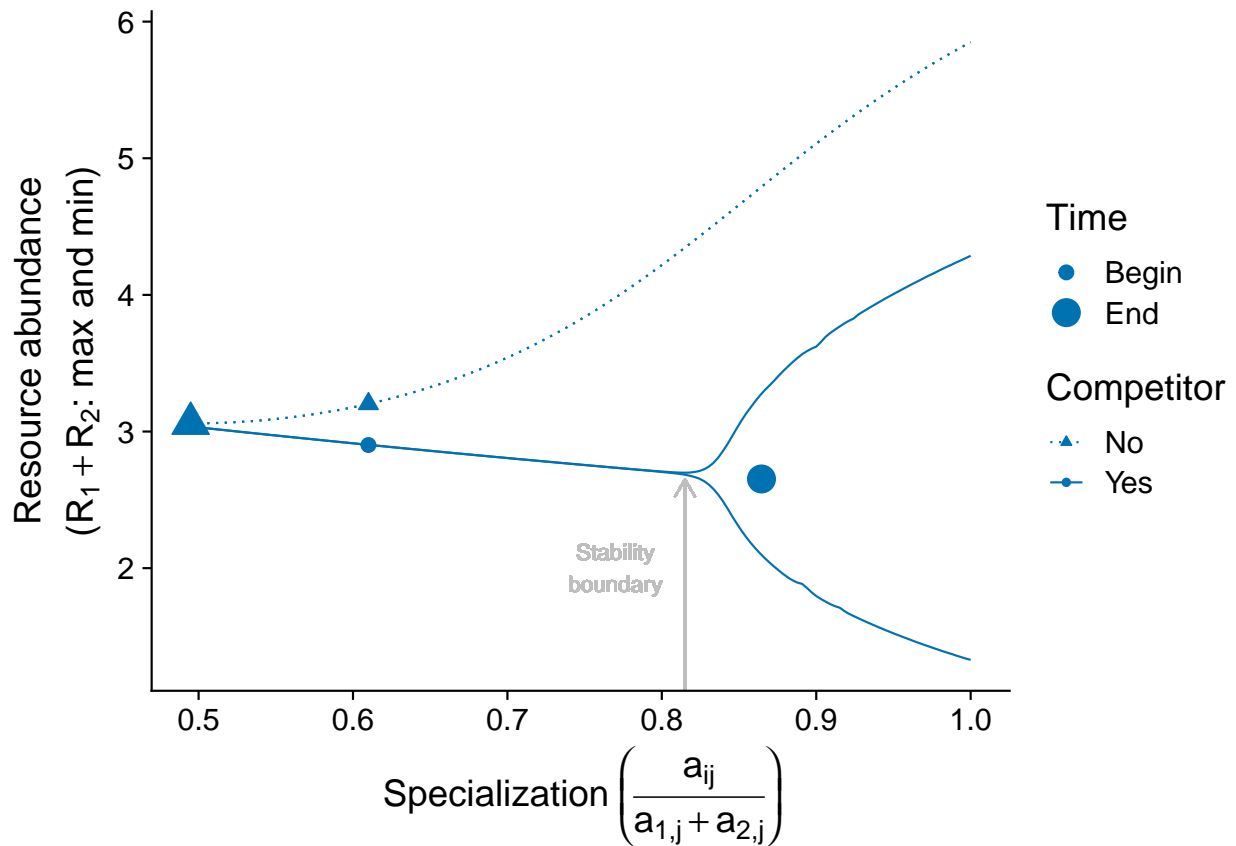

Figure 4: **Character displacement creates an unstable food web**. Lines illustrate the effect of character displacement across the range of specialization for C_1 (the choice to display C_1 was arbitrary), while the points are the results of an eco-evolutionary simulation. Note that I increased the total investment in attack rates ($A = 3.3$) to create a scenario that could result in an unstable food web. Although I specified a linear tradeoff in attack rates for this simulation, different tradeoff shapes do not qualitatively alter these results (see Appendix S4, Fig. S1).

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., there is 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, evolves to be a generalist that can equally attack both resources, 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, Fig. S2-3).

Discussion

Resource abundances

One of the criteria used to demonstrate ecological character displacement is that "sites of sympatry [two consumers] and allopatry [one consumer] should not differ greatly in food [resource abundances], climate, or other environmental features affecting the phenotype" (Schluter and McPhail, 1992). In contrast, my results indicate that character displacement causes predictable differences in resource abundances. In fact, the ecological and evolutionary scenarios that favored the largest character displacement always decreased the relative abundance of resources. For example, if mobile consumers compete for resources that occur in different habitats, then character

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displacement always resulted in lower resource abundances. Threespine stickleback, one of the classic examples of character displacement, exemplify this foraging scenario (Schluter and McPhail, 1992; Schluter, 2000). Stickleback must move between the pelagic and littoral zones of a lake when foraging for zooplankton and benthic invertebrates, respectively. The theory developed here predicts that resource abundances will be lower in lakes where competing stickleback have undergone character displacement compared to lakes with only a single species of stickleback. 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 that many cases of ecological character displacement may result in lower resource availability.

Similarly, the evolutionary tradeoff that favored character displacement decreased resource availability 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 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 large displacements, and is thus less likely to detect in nature.

My predictions could be tested with an experiment that puts consumers that have and have not undergone character displacement in a common resource setting and comparing their effect on resource abundances. One experiment with threespine stickleback has actually done this, although they focused more on the community composition of zooplankton and benthic invertebrates as well as ecosystem properties (Harmon et al., 2009). Their reported data on average resource abundances support my prediction that character displacement in stickleback would decrease total resource abundances (compare totals for "BL" vs. "G" in Table 1 of Harmon et al., 2009). For future tests, I want to emphasize that it is important to measure resource abundances over time, as I also predict

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that abundances will be more variable (see **Food-web stability** section). I specifically predict that character displacement would decrease time-averaged resource abundances. An even more explicit test would be to apply a first-order multivariate autoregressive model to obtain equilibrium estimates of resource abundances (see equation 15 in Ives et al., 2003). An advantage of using this type of statistical model is that one can also estimate the effective attack rate of consumers, which I predict to be increased by character displacement in most foraging scenarios. In designing an experiment to test this theory, it is important to keep in mind the amount of available space for consumers. For example, a mesocosm experiment may effectively constrain resources to be in the same habitat for the consumer, in which case I predict that the shape of the tradeoff in consumer attack rates will determine the impact of character displacement (see Fig. 3a-c).

Although a well-designed experiment would be an ideal test, the same methods described above could be applied to observational data from the field. In fact, field data may already be available that could be used to test the effects of character displacement (Schluter, 2000). For example, the criterion that my theory questions is the third most frequently assessed of the six criteria (see "Environmental controls" in Figure 1 of Schluter, 2000). The data from studies that measured resources could be used to test my prediction that character displacement decreases resource abundances. Although my theory calls into question part of this criterion, I agree with its intention, which was to ensure that character displacement was not due to species evolving independently to different environments (Schluter and McPhail, 1992).

Food-web stability

My most striking result was that ecological character displacement made food webs less resilient to perturbations. In fact, under the most realistic foraging scenario, character displacement can even result in an unstable food web. The mechanism underlying this destabilization is quite general. Character displacement generally increases the strength of consumer-resource interactions, but does not alter the strength of intraspecific interactions. This relative increase in interspecific

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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 and McCann, 2011; McCann, 2011).

Interestingly, the ecological conditions that favor character displacement are those that are already the least resilient to perturbations. For example, McPeek (2019) showed that character displacement 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 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 displacement will not only occur in, but also cause, the least stable food-web structures.

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 (i.e., 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.

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344 Testing the effect of character displacement on food-web stability will be inherently more difficult than for resource abundances. Fortunately, a common empirical metric of stability, the coefficient

346 of variation in abundance (CV), corresponds to changes in the dominant eigenvalue of consumer-resource interactions (Gellner et al., 2016). The coefficient of variation is an indicator of temporal

348 variability and requires data on the mean (μ) and standard deviation (σ) of population abundance over time (CV $= \sigma/\mu$). I predict that character displacement would increase the coefficient of

350 variation (across most foraging scenarios) in each consumer and resource population. As with resource abundances, a more explicit test would be to apply multivariate autoregressive models

352 to time series of consumer and resource abundances in order to directly estimate the dominant eigenvalue of the food web (see equation 22 in Ives et al., 2003).

354 **Caveats**

Although I model the indirect effects of coevolution between consumers, I do not account for

356 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

358 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

360 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

362 character displacement 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

364 quantitative genetic model that explicitly tracks trait dynamics, but it would not fundamentally change the conclusions presented here.

366 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

368 shown that allowing for resource asymmetry, for example, may decrease the magnitude of character

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displacement (Abrams, 1986). While this may dampen the amount of divergence, it should not qualitatively change the relationship I observed.

One assumption that warrants further consideration is that I do not allow for intraspecific variation. Models of character displacement that allow trait variation to evolve actually predict that consumers will exhibit more trait variation in the absence of a competitor (Taper and Case, 1985). On the one hand, increased trait variation would impose a greater fitness load for the single consumer, which would weaken its top-down effect on resources (Schreiber et al., 2011). This would act to magnify my predicted effects of character displacement on resource abundances and food-web stability. On the other hand, if the increased trait variance has a large heritable component, then rapid evolution may generate oscillatory or chaotic dynamics in the single consumer food web (Schreiber et al., 2011), which could negate my predicted effects of character displacement on food-web stability. Finally, 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 convergent character displacement 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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