Eco-evolutionary Feedback 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 trade-offs 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.

**Keywords:** competition, coevolution, eco-evolutionary dynamics, consumer-resource interactions, adaptation, community stability.

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**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, p. 55). A large body of theoretical (e.g., Lawlor and Smith 1976; Taper and Case 1985; Abrams 1986; Doebeli 1996; 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; Taper and Case 1985; Abrams 1986).

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; Basar et al. 2017; Germain et al. 2018; 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 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 the indirect effects of consumer-resource interactions, may yield new insight into 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 trade-offs 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 less resilience 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 \((C_{1,2})\) competing for two shared resources \((R_{1,2})\):

\[
\begin{align*}
\frac{dR_1}{dt} &= r_1 R_1 \left(1 - \frac{R_1}{K_1}\right) - F_{11}(R_1) C_1 - F_{12}(R_1) C_2, \\
\frac{dR_2}{dt} &= r_2 R_2 \left(1 - \frac{R_2}{K_2}\right) - F_{21}(R_2) C_1 - F_{22}(R_2) C_2, \\
\frac{dC_1}{dt} &= e_1 F_{11}(R_1) C_1 + e_1 F_{21}(R_2) C_1 - m_1 C_1, \\
\frac{dC_2}{dt} &= e_2 F_{12}(R_1) C_2 + e_2 F_{22}(R_2) C_2 - m_2 C_2,
\end{align*}
\]

(1)

where \(r_i\) represents the intrinsic growth rate of resource \(i\), \(K_i\) represents the carrying capacity of resource \(i\), \(e_j\) represents the conversion efficiency of resource \(i\) into consumer \(j\), and \(m_j\) represents the mortality rate of consumer \(j\). The term \(F_{ij}(R_i)\) 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; for an example, see Taper and Case 1985). Importantly, inferences about character displacement can be made only by comparing food webs with and without a competing consumer (Schluter and McPhail 1992). Therefore, I arbitrarily set \(C_j = 0\) 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 that their feeding rate increases linearly with resource abundance, such that

\[F_{ij}(R_i) = a_{ij} R_i,\]

(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

\[F_{ij}(R_i) = w_i a_{ij} R_i,\]

(3)

where \(w_i\) 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 \(w_i\) is a proportion, \(w_i + w_j = 1\). 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)

\[F_{ij}(R_i) = \frac{a_{ij} W_j R_i}{1 + a_{1j} h_{1j} W_1 R_1 + a_{2j} h_{2j} W_2 R_2},\]

(4)

where consumer \(j\)'s feeding rate on resource \(i\) is influenced by the abundance of each resource, the feeding rate saturates as resource abundances increase (due to handling time \(h_i\)), and consumer habitat preferences are modified by the relative abundance of resources, such that \(W_j = w_j R_j / (w_1 R_1 + w_2 R_2)\).

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 are given in supplement S1; supplements S1–S4 are available online). I say consumers have undergone divergent character displacement if their evolved attack rates are more specialized when evolving with versus without a competing consumer. Specialization of consumer \(j\) on resource \(i\) is measured as \(a_{ij} / (a_{ij} + a_{kj})\), where a value of 0.5 is a complete generalist \((a_{ij} = a_{kj})\) and a value of 1 is a complete specialist \((a_{ij} = 0)\). 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.

*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 eq. [1] are zero), and solving the system at this point gives equilibrium abundances for each resource ($R_i$) and each consumer ($C_j$). I also compared the local stability of these food webs using standard methods (Otto and Day 2007). This stability analysis derives the dominant eigenvalue, $\lambda_{\text{max}}$, of the matrix of partial derivatives of each species' population growth rate (given by eq. [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, $\lambda_{\text{max}}$, is the one closest to positive infinity and ultimately determines food-web stability. If $\lambda_{\text{max}} > 0$, then the food web is not locally stable. If $\lambda_{\text{max}} < 0$, 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 $-\lambda_{\text{max}}$ rather than $\lambda_{\text{max}}$ 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 ($r = r_i$ and $K = K_i$) as well as consumers ($e = e_i, h = h_i, m = m_j$) are equivalent, except that consumer attack rates and their habitat preferences (if present) are mirror images of each other ($a_{ij} = a_{21}, a_{12} = a_{21}, w_{ij} = w_{12}$). Note that I arbitrarily set $C_1$ as being preadapted to $R_1$ ($a_{11} > a_{21}$) while $C_2$ was a mirror image, being preadapted to $R_1$ ($a_{21} = a_{12}, a_{12} = a_{21}$). In each scenario, I assumed that consumer feeding rates increase linearly with resource abundance. I also relaxed this assumption and considered a more realistic functional response when resources occurred in different habitats ($b$).

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 ($a$) or different ($b$) habitats. Note that inferences about character displacement can be made only 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 preadapted to $R_1$ ($a_{11} > a_{21}$) while $C_2$ was a mirror image, being preadapted to $R_1$ ($a_{21} = a_{12}, a_{12} = a_{21}$). In each scenario, I assumed that consumer feeding rates increase linearly with resource abundance. I also relaxed this assumption and considered a more realistic functional response when resources occurred in different habitats ($b$).
in Mathematica (Wolfram Research 2018) and are provided in supplements S1–S3.¹

To gain insight into 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 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 trade-off, such that \((a_{1j}/A)^n + (a_{2j}/A)^n = 1\), where \(A\) is the total investment in attack rates and \(n\) describes the shape of the trade-off (Sargent and Otto 2006). This function has the useful property that it differentiates between cases where intermediate combinations of \(a_{1j}\) and \(a_{2j}\) 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 trade-off function is linear, and all combinations of \(a_{1j}\) and \(a_{2j}\) have the same total attack rate (blue line in fig. 2). Assuming that 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., \(a_{ij} = (a_{1i} > a_{2j})\) 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 into 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 timescales 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

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¹ Code that appears in The American Naturalist is provided as a convenience to readers. It has not necessarily been tested as part of peer review.
as a good starting point for studying the ecological consequences of character displacement (but see “Caveats” in the discussion section).

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 \( R_i = R_j = 2 \) and \( C_i = C_j = 1 \). All simulations were conducted in R (R Core Team 2018), and the code to reproduce these simulations is publicly available on GitHub (https://github.com/mabarbour/ECD_model) and has been archived on Zenodo (https://doi.org/10.5281/zenodo.3928098).

Results

Resources Occur in the Same Habitat

In the first scenario (eq. [2]), the abundance of resources at equilibrium are equivalent when both consumers and resources are present \( (R = R_i = R_j) \) and are determined by the following equation (derived in supplement S2):

\[
\dot{R} = \frac{1}{a_{11} + a_{22}} \cdot \frac{m}{e}.
\]

A key determinant of resource abundance in this scenario is the consumer’s total attack rate, \( a_{11} + a_{22} \). Therefore, the effect of character displacement on food-web dynamics depends on how the shape of the trade-off function influences the evolution of consumer attack rates.

I found that the shape of the trade-off function qualitatively affects the relationship between character displacement and resource abundances in this scenario (fig. 3a, 3b). For example, if consumers are constrained by a linear trade-off (blue lines), then there is no net change in total attack rate (fig. 3a) and character displacement has no effect on resource abundances (fig. 3b). If the trade-off 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 (when \( a_{11} = a_{22} \)) and decreases as consumers diverge (fig. 3a). When the trade-off is concave up (orange lines), character displacement suppresses resource abundances as a result of the increase in total attack rates (fig. 3a, 3b). 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. 3b). This is because a single consumer evolves to be a specialist that has equal attack rates on each resource (triangles at 0.5 along the 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 \( (a_{11} = a_{22} = a_{12} = a_{21}) \) on identical resources, and they 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 of the foraging scenarios I examined.

Resources Occur in Different Habitats

In the second foraging scenario (eq. [3]), I again see that resource abundances are equivalent when both consumers and resources are present \( (R = R_i = R_j) \) but are now determined by the following equation (derived in supplement S3):

\[
\dot{R} = \frac{1}{w_{1j}a_{1j} + w_{2j}a_{2j}} \cdot \frac{m}{e}.
\]

This equation implies that if consumers evolve to become specialists on resources that occur in their preferred habitat (e.g., \( w_{1j} > 0.5 \) and \( a_{1j} > a_{2j} \)), then the effective attack rate of consumers \( (w_{1j}a_{1j} + w_{2j}a_{2j}) \) will always increase, regardless of the trade-off (fig. 3d). Thus, character displacement always results in resource suppression (fig. 3e). Note that the shape of the trade-off can modify the effect of character displacement. This is not so much due to the trade-off affecting the magnitude of displacement (it does, but the effect is minor) but because the form of the trade-off 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 with 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 nonpreferred habitat (deviation of triangles from 0.5 along the 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 trade-off 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. 3f). For example, when the trade-off 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). In both foraging scenarios, feeding rates increase linearly with resource abundance, but the equation for the effective attack rate is different.

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 with when resources occur in the same habitat, and it 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 (eq. [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
supplement S1):

$\frac{1}{w_{1,i}a_{1,i} + w_{2,i}a_{2,i}} \cdot \frac{m}{e - hm}$.

(7)

And since evolution favors character displacement toward
their preferred resources (see supplement S1), the effective
attack rate of consumers $(w_{1,i}a_{1,i} + w_{2,i}a_{2,i})$ will always in-
crease, resulting in lower resource abundances and de-
creased food-web stability (fig. S1; figs. S1–S3 are available
online).

In the first two foraging scenarios, character displace-
ment influences food-web stability, but all of the food
webs ultimately return to a stable equilibrium (because
$-\lambda_{\text{max}} > 0$; see supplements S2, S3). In this more realistic
model, however, whether the food web is locally stable
depends on consumer and resource parameters. Specifi-
cally, I found that the two-consumer food web will be-
come unstable under the following conditions (derived
using Routh-Hurwitz criteria in supplement S1):

$w_{1,i}a_{1,i} + w_{2,i}a_{2,i} > \frac{e + hm}{hK(e - hm)}$.

(8)

This inequality indicates that character displacement al-
ways 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 environ-
ments, which is beyond the scope of this work.

Robustness to Consumer Symmetry

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 symme-
try). 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 and evolves to be a gen-
eralist that can equally attack both resources, which is fol-
lowed by the invasion of a second, more specialized con-
sumer. This theoretical scenario has been hypothesized
as the sequence of events leading to character displace-
ment 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 asymme-
try, I used the evolved attack rates at the end of the sim-
ulations with one consumer as the starting values for one
of the two consumers. I did this for all foraging scenarios
and trade-offs previously examined. I found that my pre-
vious inferences are robust to including consumer asym-
metry across different foraging scenarios and trade-offs
(figs. S2, S3).

![Figure 4: Character displacement creates an unstable food web. Lines illustrate the effect of character displacement across the range of specialization for $C_i$ (the choice to display $C_i$ 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 trade-off in attack rates for this simulation, different trade-off shapes do not qualitatively alter these results (see fig. S1).](image-url)
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, p. 86). 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 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 with 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 trade-off that favored character displacement decreased resource availability across all foraging scenarios. Although data on the shape of the trade-off in consumer foraging traits are scarce, two classic examples of character displacement, Darwin’s finches and threespine stickleback, both appear to exhibit a trade-off 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 the least realistic, foraging scenario and occurred under trade-offs that did not favor large displacements, and it is thus less likely to be detected 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 it 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 that abundances will be more variable (see "Food-Web Stability"). 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 eq. [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 trade-off in consumer attack rates will determine the impact of character displacement (see fig. 3a–3c).

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 fig. 1 of Schluter 2000). 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 is 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 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; McCann 2011; Rip and 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 either are highly productive, are easy to find and capture resources, or are under weak abiotic stress. This corresponds to higher values of $K$ (productivity) or $A$ (investment in attack rates) or to 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 and lower consumer mortality both increase the relative strength of consumer-resource interactions, which predictably destabilizes food webs (McCann 2011; Rip and 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 with 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 invisibility; Chesson 2000). In the context of character displacement, a shortcoming of this mutual invisibility 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.

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 of variation (CV) in abundance, corresponds to changes in the dominant eigenvalue of consumer-resource interactions (Gellner et al. 2016). The CV is an indicator of temporal variability and requires data on the mean ($\mu$) and standard deviation ($\sigma$) of population abundance over time ($CV = \sigma/\mu$). I predict that character displacement would increase the CV (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 to time series of consumer and resource abundances in order to directly estimate the dominant eigenvalue of the food web (see eq. [22] in Ives et al. 2003).

**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 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 quantitative genetic model that explicitly tracks 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 "Robustness to Consumer Asymmetry"). Prior work has shown that allowing for resource asymmetry, for example, may decrease the magnitude of character 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 apply only to food webs with biotic resources that are nutritionally substitutable. It would be interesting to extend these current analyses to nonsubstitutable 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 into the patterns of biodiversity we see in nature.

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Statement of Authorship

M.A.B. conceived the study, derived analytical solutions, performed simulations, and wrote the article.

Data and Code Availability

No new data were used. All code used to produce this article and simulations within are publicly available on GitHub (https://github.com/mabarbour/ECD_model) and has been archived on Zenodo (https://doi.org/10.5281/zenodo.3928098).

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Female threespine sticklebacks from Paxton Lake. Top, a benthic female; bottom, a limnetic female. Photo credit: Diana J. Rennison.