

Ecological character displacement destabilizes food webs

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Abstract

Ecological character displacement is an adaptive process that generally increases phenotypic
3 diversity. Despite the fact that this diversification is due to an eco-evolutionary feedback between
consumers competing for shared resources, its consequences for food-web dynamics have not
been examined. Here, I study a model of two consumers competing for two shared resources to
6 examine how character displacement in consumer attack rates affects resource abundances and the
resilience of food webs to perturbations. I found that character displacement always strengthened
consumer-resource interactions whenever consumers competed for resources that occurred in
9 different habitats. This increase in interaction strength resulted in lower resource abundances and
less resilient food webs. This occurred under different evolutionary tradeoffs and in both simple
and more realistic foraging scenarios. Taken together, my results show that the adaptive process of
12 character displacement 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 & 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 & Smith, 1976; Abrams, 1986; Doebeli, 1996;
18 Taper & Chase, 1985; McPeck, 2019) and empirical (reviewed in: Schluter, 2000; Dayan & Simberloff,
2005; Stuart & 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
21 nutritionally substitutable (Abrams, 1987; Fox & 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 & Smith, 1976; Taper & Chase, 1985). This adaptive
24 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
27 driving evolutionary change (Lawlor & Smith, 1976; Abrams, 1986; Taper & Chase, 1985).

Although models that included resources led to insights to the evolution of character displacement,
the ecological feedback onto consumer-resource dynamics has received surprisingly little attention.
30 This is likely because the ecological feedback has been primarily studied through the lens of
coexistence theory (Lawlor & Smith, 1976; Germain *et al.*, 2018; Bassar *et al.*, 2017; McPeck, 2019).
For example, early theoretical work showed that ecological character displacement promotes
33 coexistence by favoring specialized consumers that experience reduced interspecific competition
(Lawlor & Smith, 1976). Yet, this reduction in interspecific competition may, at the same time,
increase interspecific interactions between specialized consumers and their resources. Both food-
36 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;
39 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.

42 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
questions: (1) How does ecological character displacement affect resource abundances? (2) How
45 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.
I found that the adaptive process of character displacement often comes with an ecological cost;
48 resulting in food webs with lower resource availability and that are less resilient to perturbations.

Material and methods

Underlying Consumer-Resource Dynamics

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

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

54 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
the mortality rate of consumer j . $F_{ij}(R_i)$ represents consumer j 's feeding rate on resource i (i.e. func-
57 tional 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
& Chase (1985) for an example). Importantly, inferences about ecological character displacement
60 can only be made by comparing food webs with and without a competing consumer (Schluter

& McPhail, 1992). Therefore, I arbitrarily set $C_2 = 0$ to create a food-web without a competing
 63 consumer for these comparisons.

Foraging Scenarios

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

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

where a_{ij} is the attack rate of consumer j on resource i . This first scenario is the starting point
 69 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 (McCann *et al.*, 2005). The second scenario accounts for this spatial context (fig. 1
 72 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
 resource i is found (i.e. habitat preference). Note that since w_{ij} is a proportion that $w_{1,j} = 1 - w_{2,j}$.
 75 Finally, it is well known that consumer feeding rates often saturate at high resource abundances
 (Holling, 1959; Rosenzweig & 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.*,
 78 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 & 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 & Day, 2007). This stability analysis derives the dominant eigenvalue, λ_{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 ($a_{11} > a_{21}$; $w_{11} > 0.5$),

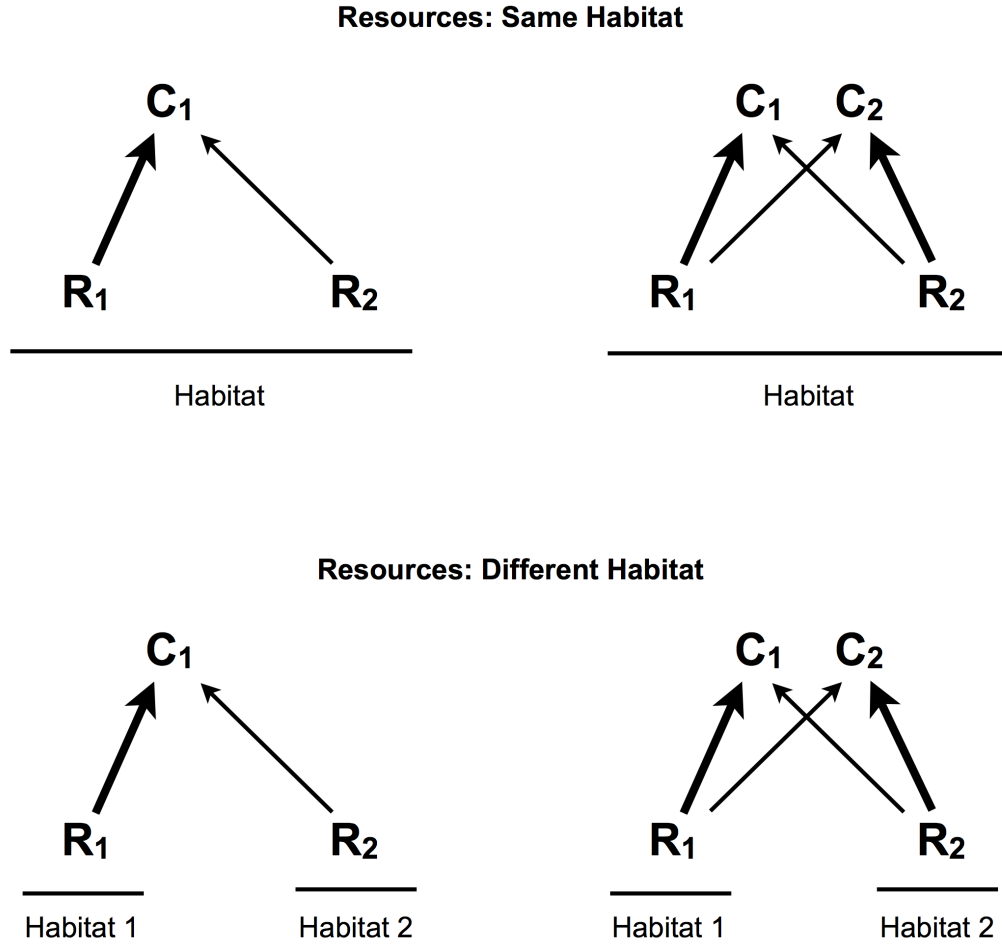


Figure 1: **Ecological foraging scenarios.** I examined whether the effect of ecological character displacement on food-web dynamics depended on whether consumers competed for resources that occurred in the same vs. different habitats. The width of each arrow corresponds to initial attack rates (a_{ij}) 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 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).

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 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 & 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 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 & 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 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 (https://github.com/mabarbour/ECD_model) and have been archived with Zenodo (INSERT DOI).

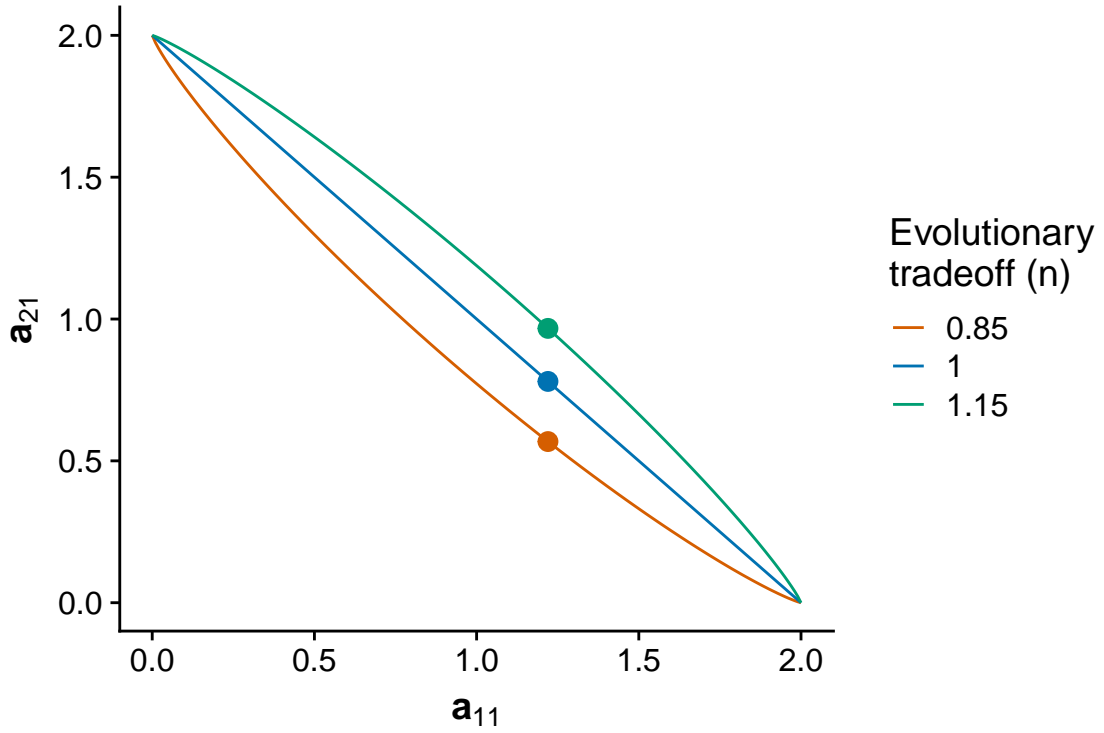


Figure 2: **Evolutionary tradeoffs in consumer attack rates.** In each foraging scenario, I explored the effects of three different tradeoffs: intermediate combinations of attack rates ($a_{1,j}, a_{2,j}$) are higher than the extremes (green line, $n > 1$); extreme combinations of attack rates are higher 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

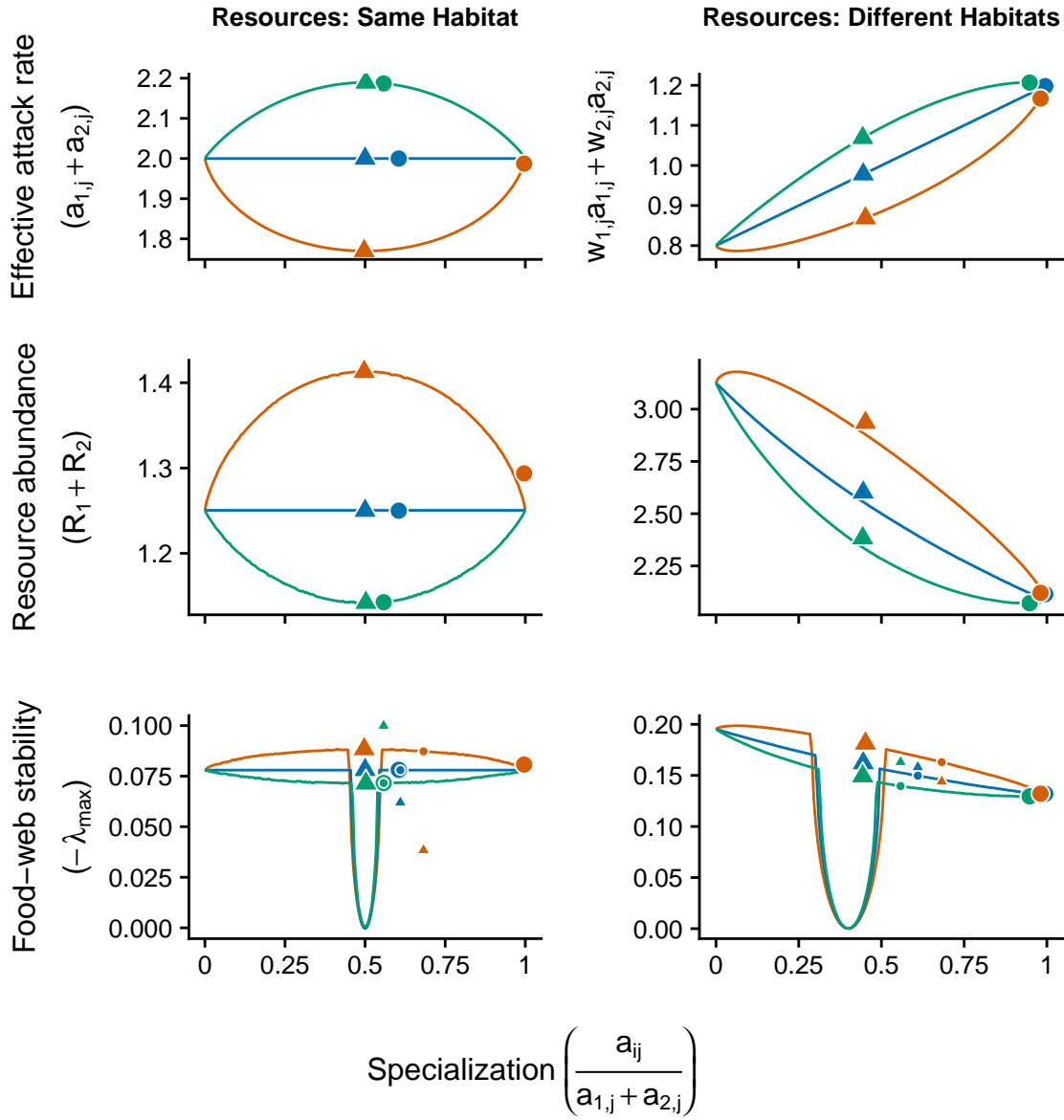


Figure 3: **Effect of character displacement on food-web dynamics under different evolutionary tradeoffs and foraging scenarios.** Lines show predicted values when both consumers and resources are present. Different line colors correspond to different tradeoffs in attack rates (green, $n = 1.15$; blue, $n = 1$; 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.

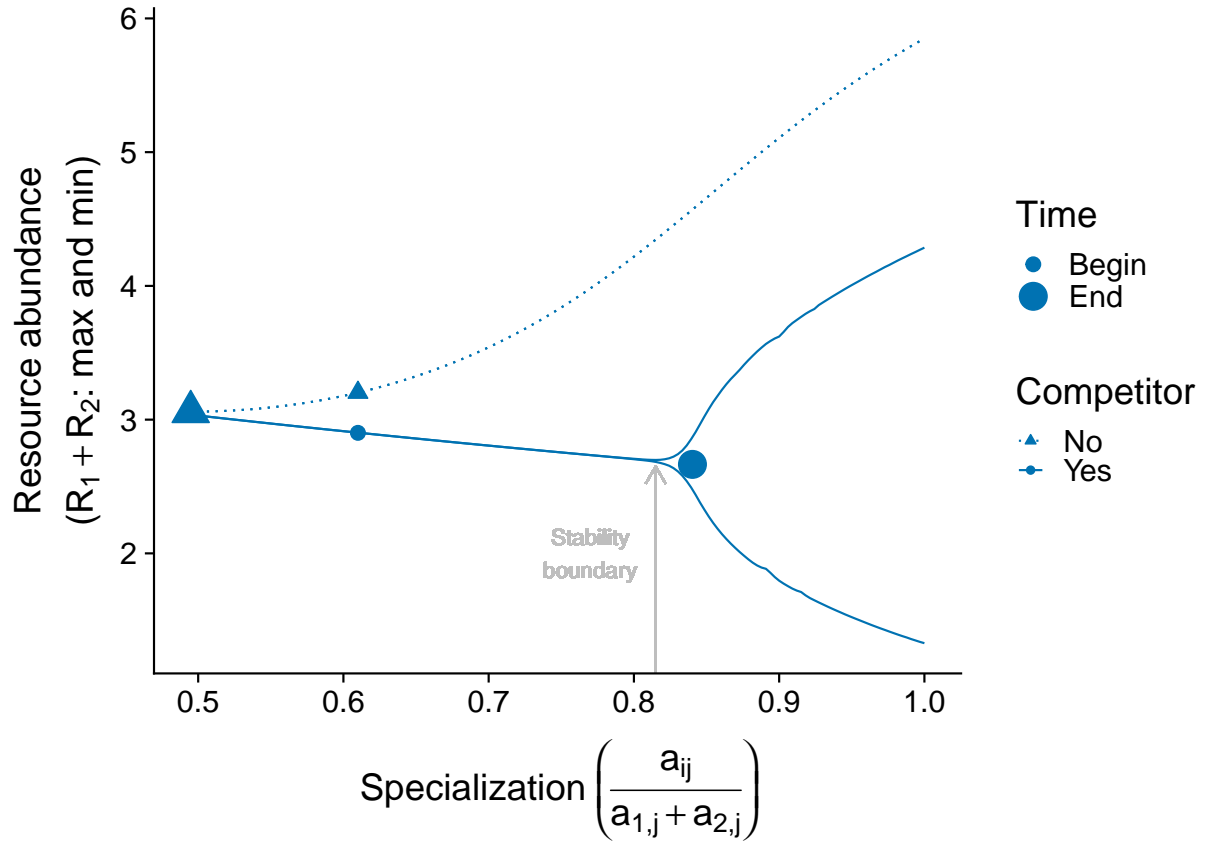


Figure 4: **Character divergence creates an unstable food web.** Lines illustrate the effects of character divergence across the range of specialization, while the points are the results of an eco-evolutionary simulation. Note that I increased the total investment in attack rates ($A = 3.3$) to create 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 & 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 & 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 & 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 & Kuang, 2008; Rip &
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 & 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 & 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 & 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 &
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 & 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 & 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 & 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 & 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 & Smith, 1976; Taper & 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 & 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.

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References

- Abrams, P.A. (1986). Character displacement and niche shift analyzed using consumer-resource
357 models of competition. *Theor. Popul. Biol.*, 29, 107–160.
- Abrams, P.A. (1987). Alternative models of character displacement and niche shift. i. adaptive shifts
in resource use when there is competition for nutritionally nonsubstitutable resources. *Evolution*,
360 41, 651–661.
- Arnegard, M.E., McGee, M.D., Matthews, B., Marchinko, K.B., Conte, G.L., Kabir, S. *et al.* (2014).
Genetics of ecological divergence during speciation. *Nature*, 511, 307–311.
- 363 Bassar, R.D., Simon, T., Roberts, W., Travis, J. & Reznick, D.N. (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
366 food webs. *Oikos*, 124, 1583–1588.
- Borrelli, J.J., Allesina, S., Amarasekare, P., Arditi, R., Chase, I., Damuth, J. *et al.* (2015). Selection on
stability across ecological scales. *TREE*, 30, 417–425.
- 369 Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31,
343–366.
- Chesson, P. & Kuang, J.J. (2008). The interaction between predation and competition. *Nature*, 456,
372 235–238.
- Connell, J.H. (1980). Diversity and the coevolution of competitors, or the ghost of competition past.
Oikos, 35, 131–138.
- 375 Dayan, T. & Simberloff, D. (2005). Ecological and community-wide character displacement: the
next generation. *Ecol. Lett.*, 8, 875–894.
- Doebeli, M. (1996). An explicit genetic model for ecological character displacement. *Ecology*, 77,
378 510–520.
- Feulner, P.G.D. & Seehausen, O. (2018). Genomic insights into the vulnerability of sympatric
whitefish species flocks. *Mol. Ecol.*

- 381 Fox, J.W. & Vasseur, D.A. (2008). Character convergence under competition for nutritionally
essential resources. *Am. Nat.*, 172, 667–680.
- 384 Germain, R.M., Williams, J.L., Schluter, D. & Angert, A.L. (2018). Moving character displacement
beyond characters using contemporary coexistence theory. *TREE*, 33, 74–84.
- 387 Hairston Jr, N.G., Ellner, S.P., Geber, M.A., Yoshida, T. & Fox, J.A. (2005). Rapid evolution and
the convergence of ecological and evolutionary time: Rapid evolution and the convergence of
ecological and evolutionary time. *Ecol. Lett.*, 8, 1114–1127.
- Hatfield, T. (2001). Status of the stickleback species pair, *gasterosteus* spp., in hadley lake, lasqueti
island, british columbia. *Can. Field Nat.*, 115, 579–583.
- 390 Hendry, A.P. (2016). *Eco-evolutionary Dynamics*. Princeton University Press.
- Holling, C.S. (1959). Some characteristics of simple types of predation and parasitism. *Can. Entomol.*,
91, 385–398.
- 393 Lawlor, L.R. & Smith, J.M. (1976). The coevolution and stability of competing species. *Am. Nat.*,
110, 79–99.
- Lotka, A.J. (1925). *Elements of Physical Biology*. Williams & Wilkins Company.
- 396 Luckinbill, L.S. (1973). Coexistence in laboratory populations of *paramecium aurelia* and its
predator *didinium nasutum*. *Ecology*, 54, 1320–1327.
- 399 MacArthur, R.H. (1972). *Geographical Ecology: Patterns in the Distribution of Species*. Biology /
[Princeton University Press]. Princeton University Press.
- May, R.M. (1973). *Stability and complexity in model ecosystems*. vol. 6 of *Monographs in Population
Biology*. Princeton University Press.
- 402 McCann, K.S. (2011). *Food Webs*. vol. 50 of *Monographs in Population Biology*. Princeton University
Press.
- 405 McCann, K.S., Rasmussen, J.B. & Umbanhowar, J. (2005). The dynamics of spatially coupled food
webs. *Ecol. Lett.*, 8, 513–523.

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

408 McPeck, M.A. (2019). Limiting similarity? the ecological dynamics of natural selection among resources and consumers caused by both apparent and resource competition. *Am. Nat.*, pp. E000–E000.

411 Murdoch, W.W., Briggs, C.J. & Nisbet, R.M. (2003). *Consumer-resource Dynamics*. Monographs in Population Biology. Princeton University Press.

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

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

417 Pfennig, D.W. & Pfennig, K.S. (2010). Character displacement and the origins of diversity. *Am. Nat.*, 176, S26–44.

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

Rip, J.M.K. & McCann, K.S. (2011). Cross-ecosystem differences in stability and the principle of energy flux. *Ecol. Lett.*, 14, 733–740.

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

426 Rosenzweig, M.L. & MacArthur, R.H. (1963). Graphical representation and stability conditions of Predator-Prey interactions. *Am. Nat.*, 97, 209–223.

Rudman, S.M. & Schluter, D. (2016). Ecological impacts of reverse speciation in threespine stickleback. *Curr. Biol.*, 26, 490–495.

429 Sargent, R.D. & Otto, S.P. (2006). The role of local species abundance in the evolution of pollinator attraction in flowering plants. *Am. Nat.*, 167, 67–80.

Schluter, D. (2000). Ecological character displacement in adaptive radiation. *Am. Nat.*, 156, S4–S16.

- 432 Schluter, D. & McPhail, J.D. (1992). Ecological character displacement and speciation in sticklebacks.
Am. Nat., 140, 85–108.
- Schluter, D., Price, T.D. & Grant, P.R. (1985). Ecological character displacement in darwin's finches.
435 *Science*, 227, 1056–1059.
- Smith, J.M. & Price, G.R. (1973). The logic of animal conflict. *Nature*, 246, 15.
- Stuart, Y.E. & Losos, J.B. (2013). Ecological character displacement: glass half full or half empty?
438 *TREE*, 28, 402–408.
- Taper, M.L. & Chase, T.J. (1985). Quantitative genetic models for the coevolution of character displacement. *Ecology*, 66, 355–371.
- 441 Taylor, E.B., Boughman, J.W., Groenenboom, M., Sniatynski, M., Schluter, D. & Gow, J.L. (2006).
Speciation in reverse: morphological and genetic evidence of the collapse of a three-spined
stickleback (*Gasterosteus aculeatus*) species pair. *Mol. Ecol.*, 15, 343–355.
- 444 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.