

Predicting the effects of character displacement on food-web dynamics

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Abstract

Introduction

3 Ecological character displacement is thought to be a key evolutionary process generating biodiversity (Dolph Schluter 2000; D. W. Pfennig and Pfennig 2010; but see Stuart and Losos 2013). Ecological character displacement describes the “process of phenotypic evolution in a species
6 generated or maintained by [exploitative] resource competition with one or more coexisting species” (Dolph Schluter 2000). Over the past 40 years, a large body of theoretical (e.g. Lawlor and Smith 1976; P A Abrams 1986; Doebeli 1996; Taper and Chase 1985) and empirical (reviewed in: Dolph
9 Schluter 2000; Dayan and Simberloff 2005; Stuart and Losos 2013) work has been generated to understand the scenarios under which exploitative competition for resources leads to the divergence of consumer foraging traits. The general result emerging from these studies is that, if resources are
12 nutritionally substitutable (Peter A Abrams 1987; Fox and Vasseur 2008) and there is no other strong source of density dependence acting on consumers (P A Abrams 1986), then resource competition drives the divergence of consumer foraging traits [Lawlor and Smith (1976); Taper and Chase
15 (1985)]. This process is not simply driven by ecological differences, but creates an eco-evolutionary feedback that drives further differentiation. This key insight was made by theoretical models that explicitly included resource dynamics as a mediator of competition in driving evolutionary change
18 (Lawlor and Smith 1976; P A Abrams 1986; Taper and Chase 1985).

Although explicit models of resources gave key insights to the evolution of character displacement, the ecological feedback onto consumer-resource dynamics have received surprisingly little attention. This is likely because character displacement has been primarily studied through the lens of
21 competition and coexistence theory [Lawlor1976; Germain2018]. For example, early theoretical work by Lawlor and Smith (1976) showed that ecological character displacement promotes coexistence by favoring specialized consumers that experience reduced interspecific competition. On
24 the other hand, specialization often increases a consumer’s ability to capture a specific resource. A well known consequence of increased foraging efficiency is resource suppression, which if
27 sufficient enough, can generate oscillations, and hence less stable, consumer-resource dynamics

[Rosenzweig 1971; Murdoch et al. 2003; McCann 2011]. NEED A LAST SENTENCE TO WRAP IT UP, HIGHLIGHTING HOW A FOOD-WEB PERSPECTIVE MAY YIELD NEW ECOLOGICAL INSIGHTS AND GIVE A CONTRASTING PERSPECTIVE TO COEXISTENCE THEORY. PERHAPS A I NEED TO INCLUDE A SENTENCE MID-WAY THROUGH SUGGESTING THAT A FOOD-WEB PERSPECTIVE MAY GIVE QUALITATIVELY DIFFERENT INSIGHTS. IT MAY BE NICE TO BRING IN THE SPATIAL COUPLING WORK OF MCCANN SUGGESTING THAT SPECIALIZATION CAN COUPLE FOOD-WEBS, BUT THIS WAS ONLY WITH ONE TOP PREDATOR (I.E. NO CONSUMERS... LOOK AT OLD TEXT FOR WORDING SUGGESTIONS.)

Here, I address this knowledge gap by building a mathematical model to examine 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 does character displacement affect food-web stability? To test the generality of these ecological effects, I examined three different foraging scenarios: (i) resources occur in the same habitat and consumers exhibit a linear functional response (e.g. MacArthur (1972); Lawlor and Smith (1976)); (ii) resources occur in different habitats and consumers exhibit a linear functional response (e.g. Lawlor and Smith (1976)); (iii) resources occur in distinct habitats and consumers exhibit a more realistic functional response (K S McCann, Rasmussen, and Umbanhowar 2005). I also explore the contingency of these effects to different assumptions about evolutionary trade-offs in consumer foraging traits. I focus on the ecological side of these dynamics because the evolutionary aspects have been well characterized (Lawlor and Smith 1976; Taper and Chase 1985; P A Abrams 1986). I show that the consequences of character displacement on food-web dynamics are not always intuitive and depend on the foraging scenario and tradeoff in consumer traits.

Methods and Results

Underlying Food-web Dynamics

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

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

where r_i represents the intrinsic growth rate of resource i , K_i represents the carrying capacity of resource i , e_{ji} represents the conversion efficiency of resource i into consumer j , and m_j represents the mortality rate of consumer j . $F_{ji}(R_i)$ represents consumer j 's feeding rate (i.e. functional response) on resource i . This model is a useful characterization of a scenario where consumers compete for two distinct resources (e.g. zooplankton and benthic invertebrates) rather than if resources are better characterized by a continuous trait distribution (e.g. seed size, see Taper and Chase (1985) for an example). In the scenario where consumer feeding rates increase linearly with resource density, such that $F_{ji}(R_i) = a_{ji}R_i$ where a_{ji} is the attack rate of consumer j on resource i , then this model becomes MacArthur's model of resource competition (MacArthur (1972)). The evolution of consumer attack rates in this model (and several extensions) have been analyzed in detail (Lawlor and Smith (1976); P A Abrams (1986)), with the general result being divergent character displacement. I say consumers have undergone divergent character displacement if there evolved attack rates are more specialized, defined as $|\frac{a_{ii}}{a_{ii}+a_{ij}} - 0.5|$, when evolving with a competing consumer. I focus here on the ecological consequences of this adaptive divergence.

72 To investigate the ecological consequences, I studied the effect of adaptive divergence in consumers
on resource densities and the stability of the entire food web at equilibrium. An equilibrium
is reached when the four rates of change in the above equations are 0, and solving the system
75 at this point gives equilibrium densities for each resource (\hat{R}_1, \hat{R}_2) and consumer (\hat{C}_1, \hat{C}_2). At
the coexistence equilibrium (i.e., where $\hat{R}_1, \hat{R}_2, \hat{C}_1, \hat{C}_2 > 0$), I calculated resource densities and
performed a linear stability analysis (Otto and Day 2007). This stability analysis derives the
78 dominant (largest in absolute value) eigenvalue, λ , which determines whether (and how readily) the
food web, when perturbed a small amount, will return to equilibrium (see supplementary material
for derivation). Together, these two measures indicate how ecological character displacement
81 affects resource densities and food-web stability.

I examine the effects of this inevitable divergence in attack rates on food-web dynamics by (i)
deriving analytical expressions for the relationship between attack rates and food-web dynamics
84 and (ii) simulating the effects of competition on the eco-evolutionary dynamics of consumers
and resources. To gain analytical insight, I assume that resources are equivalent ($r = r_1 = r_2$ and
 $K = K_1 = K_2$) as well as consumers ($e = e_{11} = e_{12} = e_{21} = e_{22}$; $m = m_1 = m_2$), except that consumer
87 attack rates are mirror images of each other ($a_{ii} = a_{11} = a_{22}$; $a_{ij} = a_{12} = a_{21}$). While this scenario is
arguably simplistic, it allows me to isolate the effects of ecological character displacement.

To simulate eco-evolutionary dynamics, I used an Adaptive Dynamics approach. At each evolution-
90 ary time step, I created a mutant consumer by randomly choosing a consumer and modifying its
attack rate on one resource by either subtracting or adding a small constant (0.001 in the following
simulations) with equal probability. The mutant's attack rate on the other resource was determined
93 by a tradeoff, such that $(a_{ii}/A)^n + (a_{ij}/A)^n = 1$, where A is the total investment in attack rates
and n describes the shape of the tradeoff (Sargent and Otto 2006). This function has the useful
property that it differentiates between cases where intermediate combinations of a_{ii} and a_{ij} are
96 higher, on average, than the extremes (when $n > 1$, green line in Fig. 1) or, conversely, where the
two extremes are higher, on average, than intermediate investments (when $n < 1$, orange line Fig.

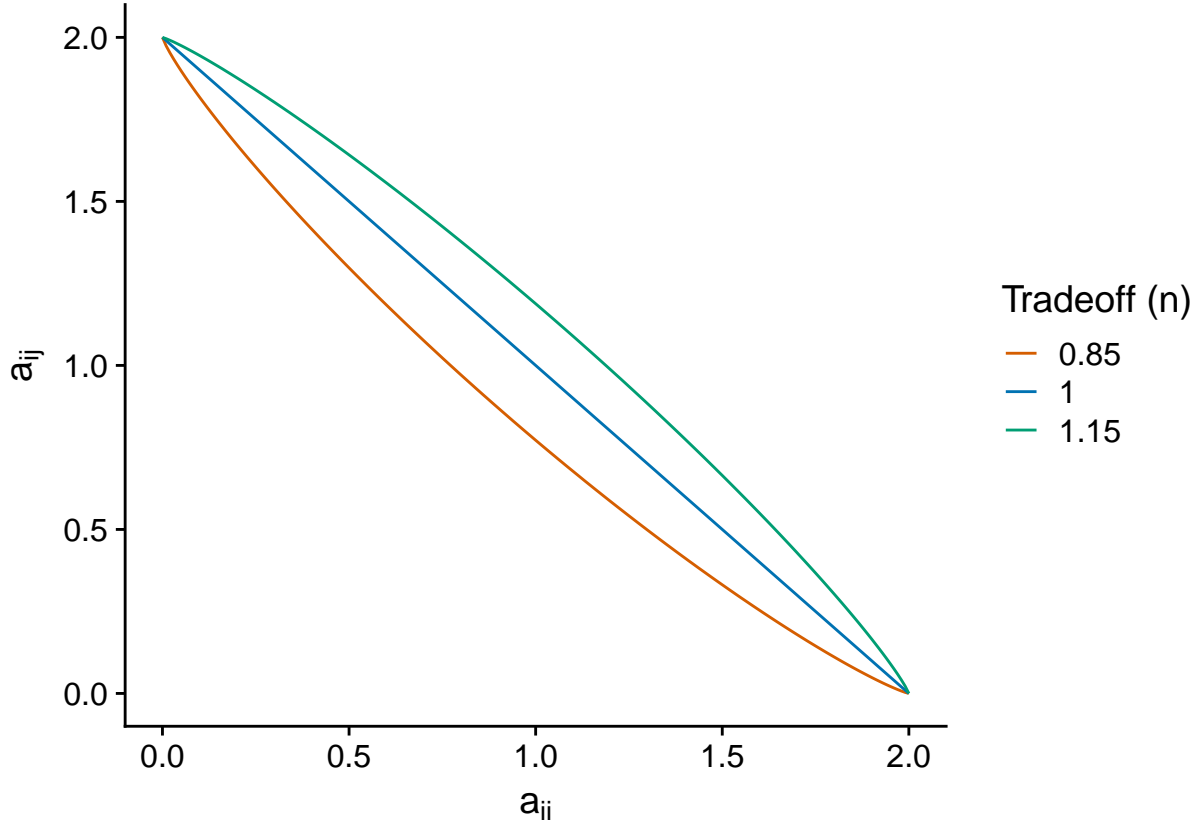


Figure 1: Tradeoff forms for consumer attack rates.

1). When $n = 1$, the tradeoff function is linear, and all combinations of a_{ii} and a_{ij} have the same
 99 total attack rate (blue line in Fig. 1). 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
 102 the resident consumer to the mutant attack rate and allowed consumer and resource dynamics
 to reach a steady state. I then repeated the simulation up to 10,000 times, which was sufficient
 for consumers to either reach an evolutionary stable strategy (ESS, Smith and Price 1973) or an
 105 evolutionary limit (e.g. $\frac{a_{ij}}{a_{ii}+a_{ij}}$ is constrained to a maximum of 1 and minimum of 0).

Consumers Forage For Both Resources Simultaneously

When both consumers and resources are present, the density of resources at equilibrium are equivalent ($\hat{R} = \hat{R}_1 = \hat{R}_2$) and are determined by the following equation (derivation in supplementary material):

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

A key determinant of resource density in this model is the consumer's total attack rate, $a_{ii} + a_{ij}$.

Therefore, the ecological consequences of character displacement depend on how the tradeoff influences the evolution of consumer attack rates.

My simulations show that the shape of the attack-rate tradeoff qualitatively affects the relationship between character displacement and resource density (Fig. 2). For example, if consumer's are constrained by a linear tradeoff (blue lines), then there is no net change in total attack rate (Fig. 2A) and character displacement has no effect on resource densities (Fig. 2B). If the tradeoff is concave down (green lines), then resource abundances can actually increase under character displacement (Fig. 2B). This is because the total attack rate of consumers is maximized at intermediate values ($a_{ii} = a_{ij}$) and decreases as consumers diverge (Fig. 2A). When the tradeoff is concave up (orange lines), character displacement suppresses resource densities due to the increase in total attack rates (Fig. 2A,B). Although the equation I derived for resource density was for the scenario where both consumers and both resources are present, it accurately predicts the density of resources when a single consumer reaches its ESS (triangles on respective colored lines in Fig. 2B). 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. 2A), resulting in equivalent resource densities.

The effect of character displacement on resource density closely matches its impact on food-web stability (Fig. ??). For example, when character displacement results in resource suppression (orange), there is a corresponding decrease in stability. Similarly, if character displacement does not influence resource densities (blue), then there is no corresponding effect on stability. Curiously,

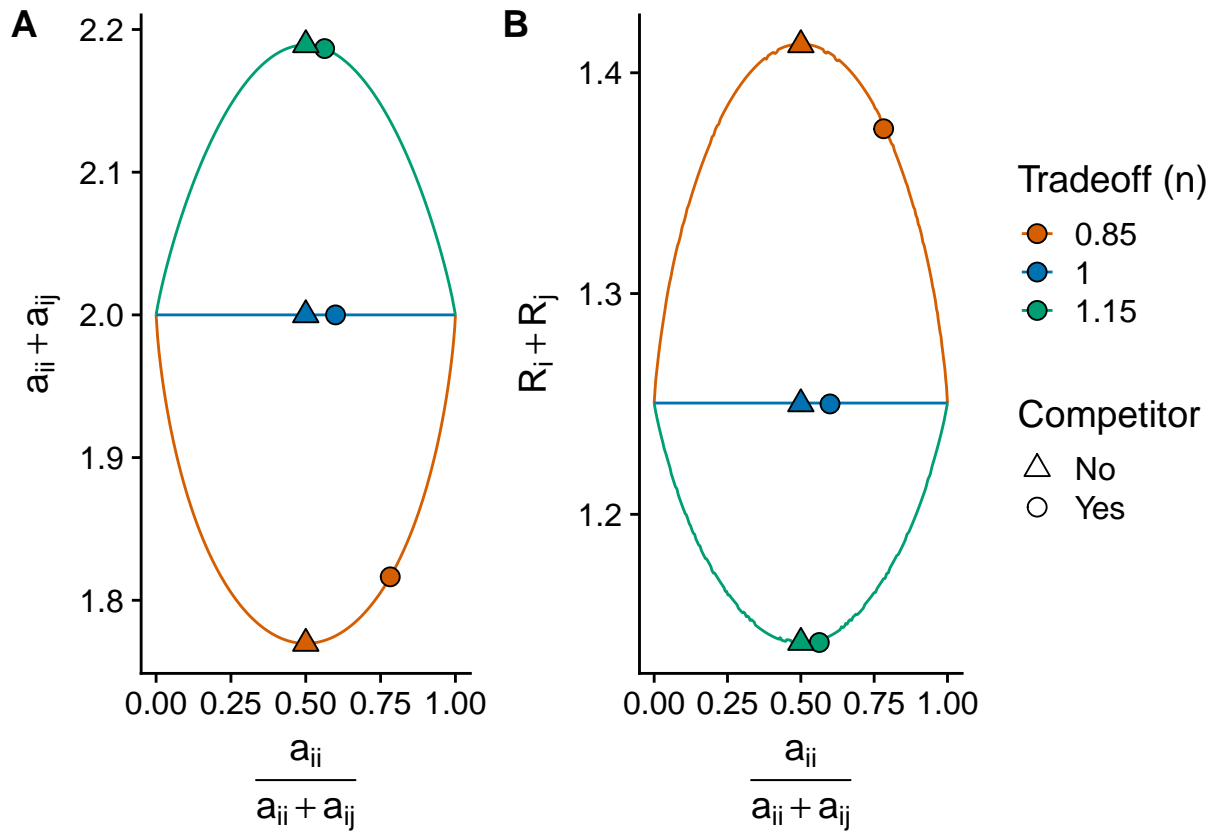
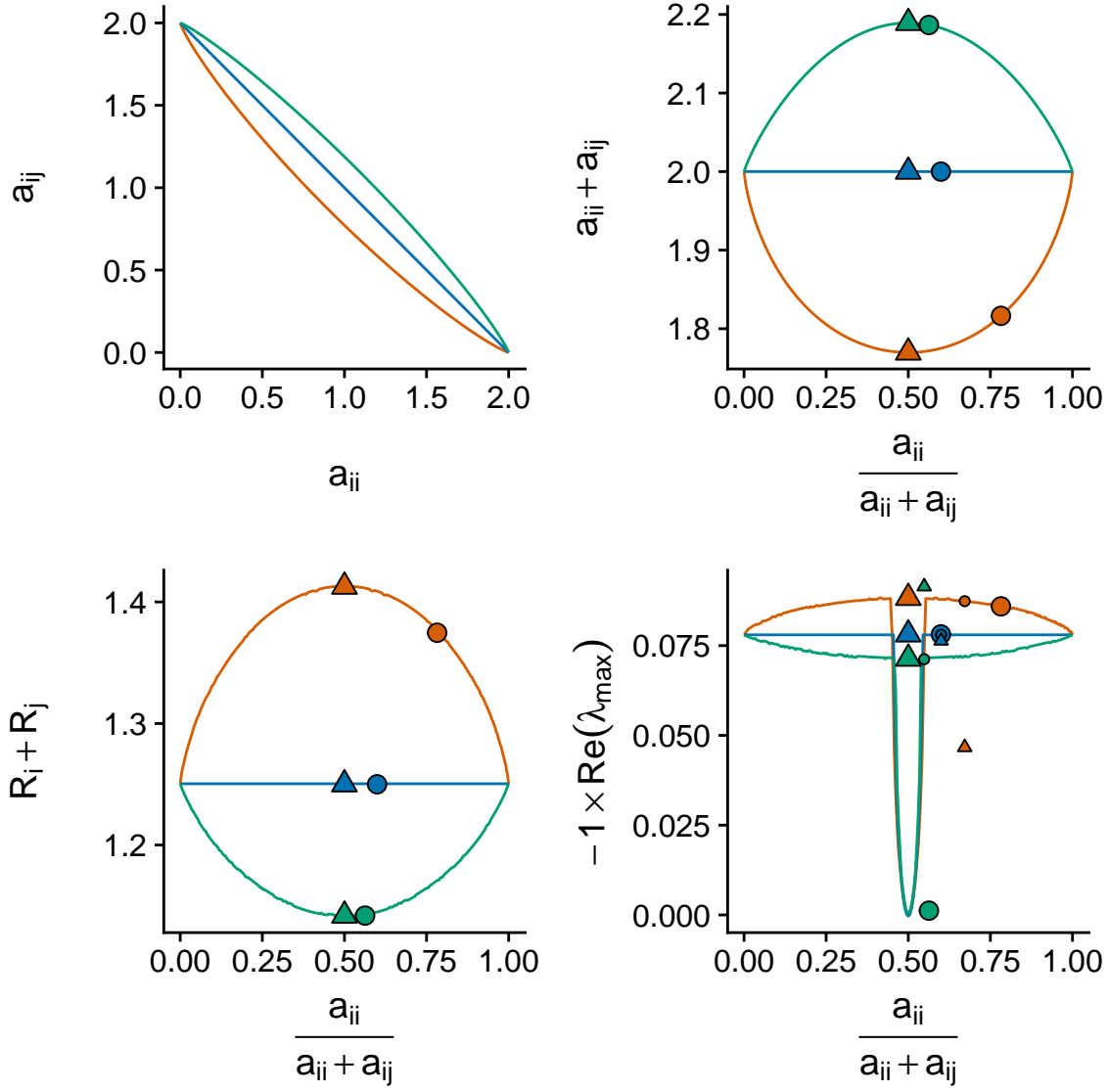


Figure 2: Effect of character displacement on total attack rates (A) and resource densities (B) when consumers can forage for both resources simultaneously.

this match between impact on resources and stability breakdowns with the concave down tradeoff (green).



132

Consumers *cannot* forage for both resources simultaneously

The only character displacement model that I am aware of that modeled resources in different
 135 habitats was one examined by Lawlor and Smith (1976). This model takes the same form as the
 previous model, except now the consumer's feeding rate takes the form:

$$F_{ji}(R_i) = w_{ji}a_{ji}R_i$$

where w_{ji} represents the proportion of time consumer j spends foraging in a habitat where only
 138 resource j is found (i.e. habitat preference). Note that since w_{ji} is a proportion that $w_{jj} = 1 - w_{ji}$.
 As with attack rates, I assume that consumer habitat preferences are mirror images of each other
 ($w = w_{11} = w_{22}$). In Lawlor and Smith (1976)'s detailed evolutionary analysis of this model, they
 141 again always observe divergent character displacement.

To examine the ecological consequences of this model, I again derive the equilibrium solution when
 both consumers and both resources are present. Again, resource densities are equivalent at this
 144 equilibrium ($\hat{R} = \hat{R}_1 = \hat{R}_2$ when both consumers and resources present), but are now determined
 by the following equation (derivation in supplementary material):

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

This equation implies that if consumers evolve to become specialists on resources that occur in their
 147 preferred habitat (e.g. $w > 0.5$ and $a_{ii} > a_{ij}$), then the effective attack rate of consumers ($wa_{ii} +$
 $(1 - w)a_{ij}$) will always increase, regardless of the tradeoff (Fig. 3A). Thus, character displacement
 always results in resource suppression if consumers are competing for resources that occur in
 150 different habitats (Fig. 3B). 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
 153 a single consumer has reached its ESS (triangles in Fig. 3B). In contrast, resource densities reach a
 similar value when consumers evolve in the presence of a competitor (circles in Fig. 3B), because
 character displacement tends to reach a constraint of complete specialization. It is worth noting
 156 that in this foraging scenario, resource densities 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. 3B). This is likely because consumers actually evolve to be
 159 slightly specialized on the resources that occur in their non-preferred habitat (deviation of triangles
 from 0.5 along x-axis in Fig. 3B).

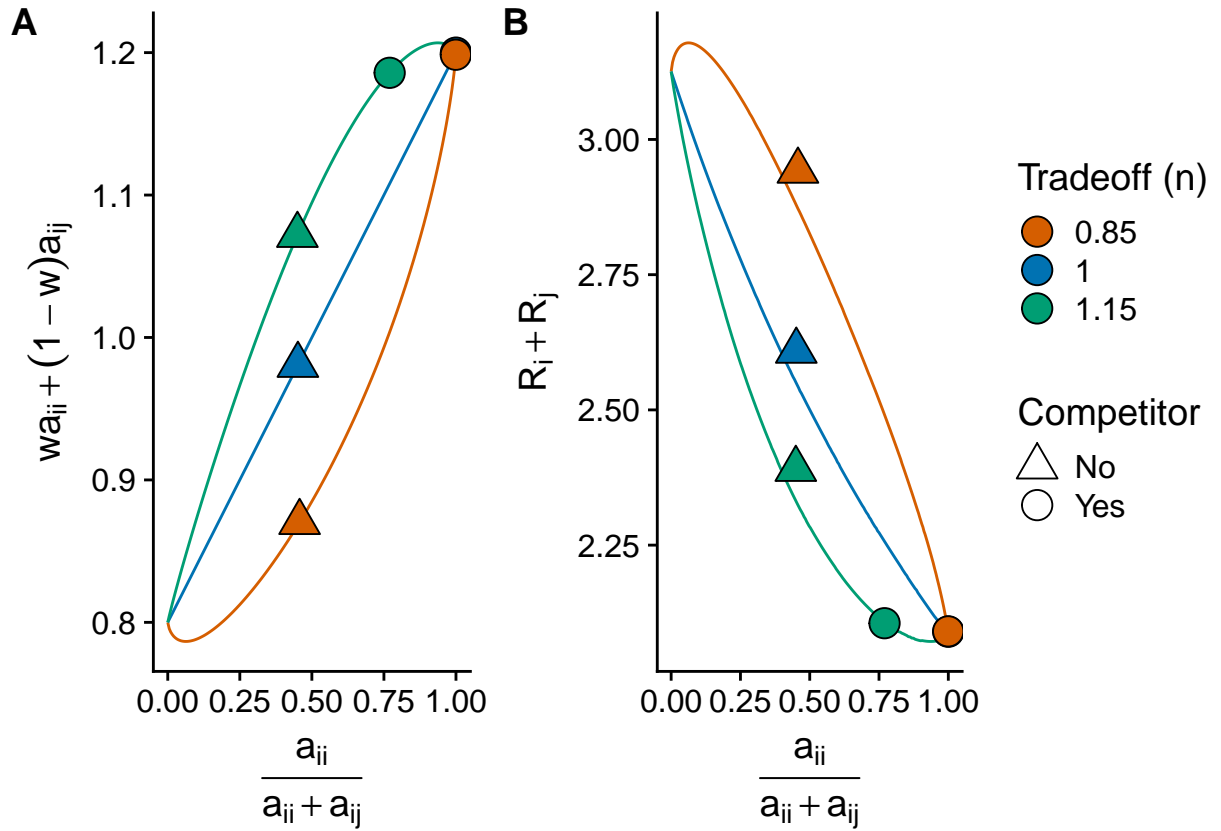
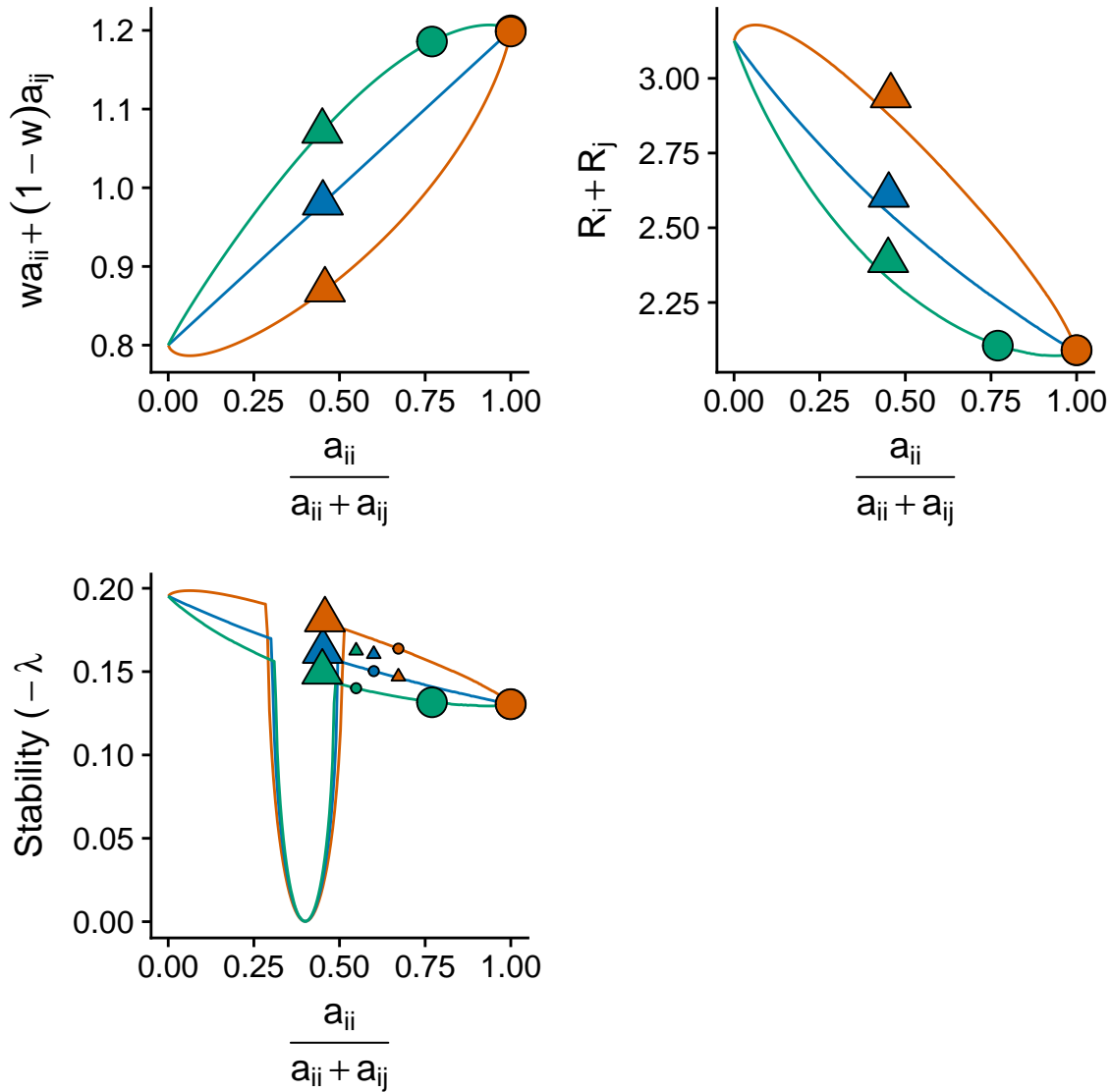


Figure 3: Effect of character displacement on effective attack rates (A) and resource densities (B) when consumers cannot forage for resources simultaneously.

The effect of character displacement on resource densities qualitatively matches its negative effect of food-web stability (Fig. ??). 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 (compare initial (small points) with evolved strategies (large points), Fig. ??).

For example, when the tradeoff is concave up (orange), then the four-species (small circle) food web actually starts off as less stable than the three-species one (small triangle), but the eco-evolutionary dynamics cause a switch in the pattern once they reach their evolutionary stable strategies (large

points).



Adding A More Realistic Functional Response

171 Thus far I have consider a simple type I functional response of consumers foraging for resources in either the same or distinct habitats.

For example, even if I consider a more realistic consumer functional response (derived by K S

174 McCann, Rasmussen, and Umbanhowar (2005)):

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

where consumer feeding rates on resource i are influenced by both resource densities; saturate as resource densities increase (due to handling time h); and consumer habitat preferences are modified
 177 by relative resource densities, such that:

$$W_{ii} = \frac{wR_i}{wR_i + (1 - w)R_j}$$

I still observe the same qualitative relationship between character displacement and resource suppression (Fig. 4 in Appendix). This is because resource competition always leads to character
 180 divergence and equilibrium resource densities are governed by similar dynamics (*Mathematica* file with derivations available upon request):

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

I conducted the previous simulations on a scenario where the food web remains locally stable
 183 ($\text{Re}(\lambda_{\max}) < 0$). Is it possible that character displacement would ever result in a locally unstable food web? To gain analytical insight to this question, I examined the conditions governing the local stability of the four-species food web when consumers exhibit a more realistic functional response
 186 (K S McCann, Rasmussen, and Umbanhowar (2005)). I show that the four-species food web will transition from having a locally stable equilibrium to a limit cycle under the following conditions (*Mathematica* file with derivation available upon request):

$$wa_{ii} + (1 - w)a_{ij} > \frac{e + hm}{hK(e - hm)}$$

189 Previously, I showed that character displacement always increases the effective attack rate of consumers ($wa_{ii} + (1 - w)a_{ij}$), regardless of the the shape of the tradeoff (Fig. 3A). Thus, character

displacement is capable of pushing food webs to a point where they are locally unstable. (it simple
192 depends on the choice of parameter, I could put a situation where evolution pushes it toward local
instability, or even the hopf bifurcation.)

Discussion

195 I find that the foraging scenario qualitatively affects the relationship between character displace-
ment and resource densities.

Most models of character displacement have assumed a scenario where consumers can forage for
198 both resources simultaneously (e.g. Taper and Chase 1985; P A Abrams 1986). This assumption
may be valid for some foraging scenarios (e.g. Darwin's finches foraging for seeds); however, in
many situations consumers forage for resources that occur in different habitats, and thus cannot
201 forage for both simultaneously (K S McCann, Rasmussen, and Umbanhowar 2005).

The effect of the foraging scenario on the relationship between character displacement and resource
densities appears to be quite general.

204 Note that detecting this effect in nature would likely be difficult, since a concave-down tradeoff
results in relatively small displacement relative to other tradeoff shapes (Lawlor and Smith (1976);
green points in Fig. 2A,B).

207 Previous work has shown that consumers undergo divergent character displacement regardless of
the shape of the tradeoff (Lawlor and Smith (1976); P A Abrams (1986)).

Important point: Criteria 5 in D Schluter and McPhail (1992) does not make sense since character
210 displacement usually alters resource distributions. Think about this more.

Lawlor and Smith (1976) found that consumers still underwent divergent character displacement
regardless of whether consumers could or could not forage for resources simultaneously.

213 These results do lead to an interesting prediction that could be tested either experimentally or with

field data. If consumers are competing for resources that occur in different habitats, then greater character displacement corresponds to a greater decrease in resource densities (line trajectories in Fig. 3B). This prediction likely only applies to comparisons within species where there is likely little difference in the shape of the tradeoff among populations.

In general, I find that resource suppression goes hand-in-hand with local stability, a tendency that has been noted by others (Murdoch, Briggs, and Nisbet (2003); Kevin S McCann (2011)).

The scenario where the relationship between character displacement and resource suppression is the strongest is when the tradeoff in attack rates is concave-up and consumers are competing for resources that occur in different habitats (orange points in Fig. 3B and Fig. 4B). Prior work in threespine stickleback suggests that the evolution of stickleback attack rates are constrained by a concave-up tradeoff (Dolph Schluter (1993); Arnegard et al. (2014)) and that stickleback ecotypes are competing for resources that occur in different habitats (benthic vs. limnetic, D Schluter and McPhail (1992)). Thus, I predict that ecological character displacement in sticklebacks would suppress resource densities and decrease local stability.

While measuring resource densities is relatively straightforward, measuring stability is notoriously difficult. One of the more easy to acquire empirical metrics of stability is the coefficient of variation ($CV = \frac{\sigma}{\mu}$) as this only requires measurements of resource (or consumer) densities over time. Interestingly, there is a close correspondence between the coefficient of variation and the local stability of a food web (Gellner, McCann, and Hastings (2016)). Thus, I predict that character displacement in threespine stickleback will increase the CV of resource (or consumer) densities.

Consumer and resource densities in these dynamical models can be interpreted from either a population or biomass perspective (Yodzis and Innes (1992); Murdoch, Briggs, and Nisbet (2003); Kevin S McCann (2011)). For the stickleback system, you have data on seasonal dynamics of resources in terms of both abundances and biomass. Within a season, I do not expect stickleback abundances to be coupled to the abundances of zooplankton and benthic invertebrates, given that stickleback reproduce annually whereas zooplankton and benthic invertebrates can reproduce

many times within a season. Instead, I expect that stickleback biomass will be coupled to the biomass of zooplankton and benthic invertebrates within a season. This is because there will be lots of young stickleback at the beginning of the season, and they will eat a lot of resources and grow in size as the season progresses. If this is true, I also expect to see the largest negative effect of stickleback on resource densities late in the season.

Although I used an Adaptive Dynamics approach here, I expect that these theoretical predictions would apply to models that assumed a different genetic architecture of attack rates (e.g. quantitative genetics). I expect this because, time and time again, models that explicitly include resource dynamics inevitably show that resource competition results in divergent character displacement, regardless of the genetic architecture of traits (see synthesis by Taper and Chase (1985)). Finally, my conclusions only apply to biological resources that are nutritionally substitutable. It would be interesting to extend these current analyses to non-substitutable resources where convergent character displacement is expected (Peter A Abrams (1987); Fox and Vasseur (2008)).

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References

- 261 Abrams, P A. 1986. "Character Displacement and Niche Shift Analyzed Using Consumer-Resource
Models of Competition." *Theor. Popul. Biol.* 29 (1): 107–60.
- Abrams, Peter A. 1987. "Alternative Models of Character Displacement and Niche Shift. I. Adaptive
264 Shifts in Resource Use When There Is Competition for Nutritionally Nonsubstitutable Resources." *Evolution* 41 (3). Wiley Online Library: 651–61.
- Arnegard, Matthew E, Matthew D McGee, Blake Matthews, Kerry B Marchinko, Gina L Conte,
267 Sahriar Kabir, Nicole Bedford, et al. 2014. "Genetics of Ecological Divergence During Speciation." *Nature* 511 (7509): 307–11.
- Dayan, Tamar, and Daniel Simberloff. 2005. "Ecological and Community-Wide Character Displace-
270 ment: The Next Generation." *Ecol. Lett.* 8 (8). Blackwell Science Ltd: 875–94.
- Doebeli, Michael. 1996. "An Explicit Genetic Model for Ecological Character Displacement." *Ecology* 77 (2). Ecological Society of America: 510–20.
- 273 Fox, Jeremy W, and David A Vasseur. 2008. "Character Convergence Under Competition for
Nutritionally Essential Resources." *The American Naturalist* 172 (5). The University of Chicago
Press: 667–80.
- 276 Gellner, Gabriel, Kevin S McCann, and Alan Hastings. 2016. "The Duality of Stability: Towards a
Stochastic Theory of Species Interactions." *Theor. Ecol.* 9 (4): 477–85.
- Lawlor, Lawrence R, and J Maynard Smith. 1976. "The Coevolution and Stability of Competing
279 Species." *Am. Nat.* 110 (971). [University of Chicago Press, American Society of Naturalists]: 79–99.
- MacArthur, R H. 1972. *Geographical Ecology: Patterns in the Distribution of Species*. Biology /
[Princeton University Press]. Princeton University Press.
- 282 McCann, K S, J B Rasmussen, and J Umbanhowar. 2005. "The Dynamics of Spatially Coupled Food

Webs." *Ecol. Lett.* 8 (5). Blackwell Science Ltd: 513–23.

McCann, Kevin S. 2011. *Food Webs (Mpb-50)*. Princeton University Press.

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

Otto, Sarah P, and Troy Day. 2007. *A Biologist's Guide to Mathematical Modeling in Ecology and*
288 *Evolution*. Princeton University Press.

Pfennig, David W, and Karin S Pfennig. 2010. "Character Displacement and the Origins of Diversity." *Am. Nat.* 176 Suppl 1 (December): S26–44.

291 Sargent, Risa D, and Sarah P Otto. 2006. "The Role of Local Species Abundance in the Evolution of Pollinator Attraction in Flowering Plants." *Am. Nat.* 167 (1): 67–80.

Schluter, D, and J D McPhail. 1992. "Ecological Character Displacement and Speciation in Stickle-
294 backs." *Am. Nat.* 140 (1): 85–108.

Schluter, Dolph. 1993. "Adaptive Radiation in Sticklebacks: Size, Shape, and Habitat Use Efficiency." *Ecology* 74 (3): 699–709.

297 ———. 2000. "Ecological Character Displacement in Adaptive Radiation." *Am. Nat.* 156 (S4): S4–S16.

Smith, J Maynard, and G R Price. 1973. "The Logic of Animal Conflict." *Nature* 246 (November).
300 Nature Publishing Group: 15.

Stuart, Yoel E, and Jonathan B Losos. 2013. "Ecological Character Displacement: Glass Half Full or Half Empty?" *Trends Ecol. Evol.* 28 (7): 402–8.

303 Taper, Mark L, and Ted J Chase. 1985. "Quantitative Genetic Models for the Coevolution of Character Displacement." *Ecology* 66 (2). Ecological Society of America: 355–71.

Yodzis, P, and S Innes. 1992. "Body Size and Consumer-Resource Dynamics." *Am. Nat.* 139 (6).
306 [University of Chicago Press, American Society of Naturalists]: 1151–75.

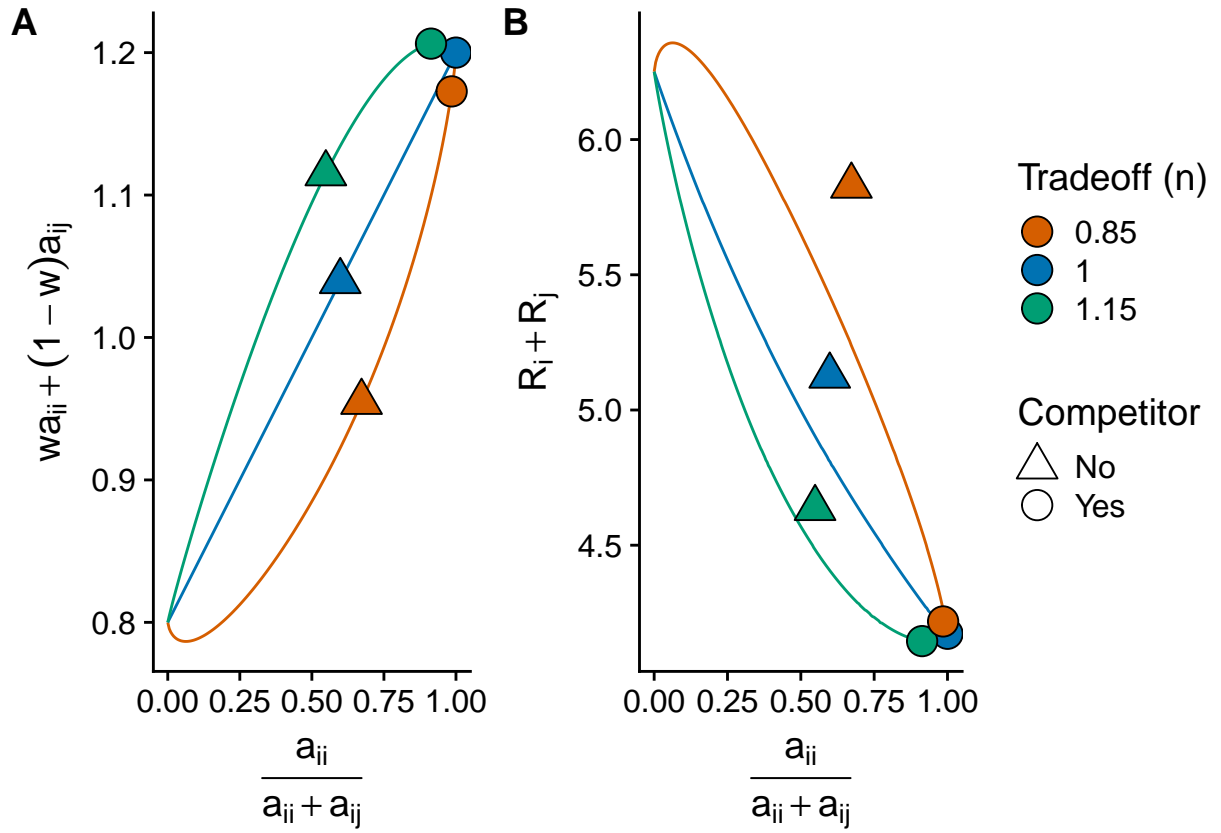


Figure 4: Effect of character displacement on total attack rates (A) and resource densities (B) when consumers exhibit a more realistic functional response.

Appendix: More realistic functional response

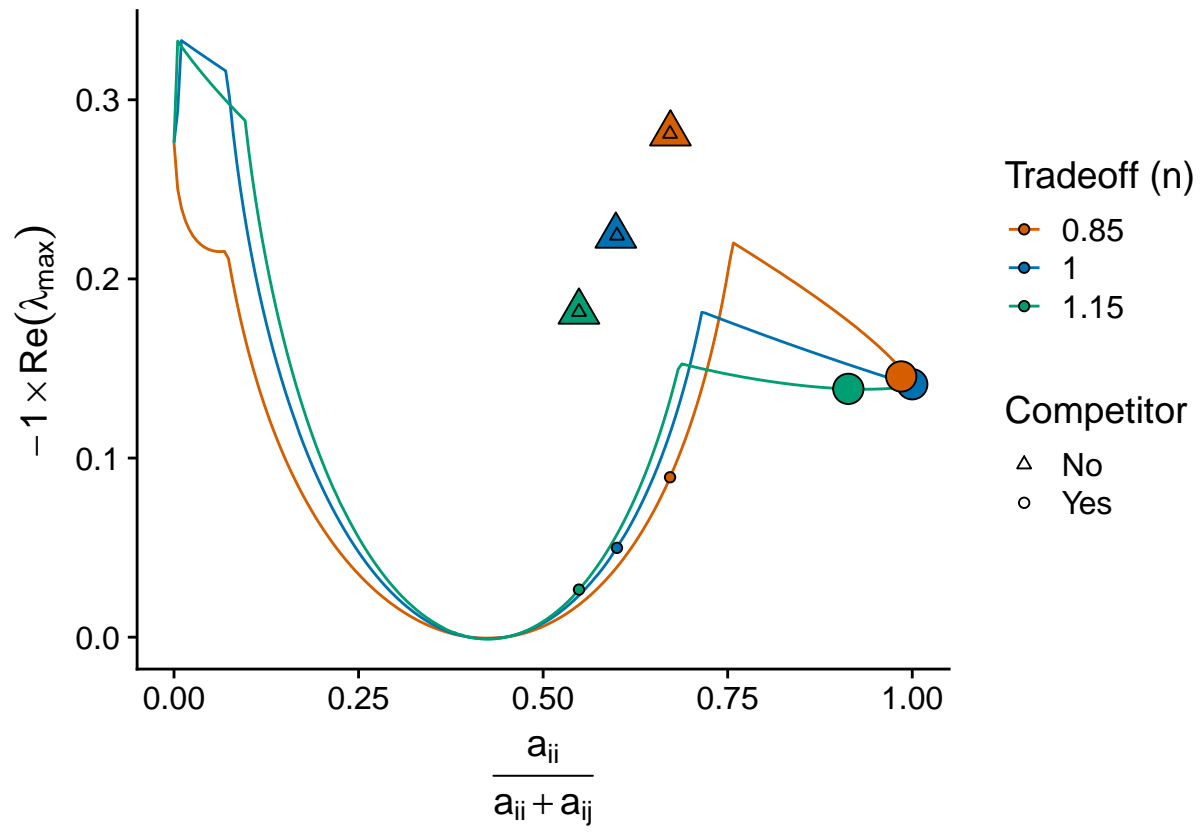


Figure 5: Effect of character displacement on local stability when consumers exhibit a more realistic functional response.