Predicting the effects of character displacement on food-web dynamics

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Model of resource competition

I analyzed a continuous-time model of two consumers (C_1, C_2) competing for two shared resources (R_1, R_2):

$$\frac{dR_1}{dt} = r_1 K_1 (1 - \frac{R_1}{K_1}) - F_{11}(R_1)C_1 - F_{21}(R_1)C_2$$

$$\frac{dR_2}{dt} = r_2 K_2 (1 - \frac{R_2}{K_2}) - F_{12}(R_2)C_1 - F_{22}(R_2)C_2$$

$$\frac{dC_1}{dt} = e_{11} F_{11}(R_1)C_1 + e_{12} F_{12}(R_2)C_1 - m_1 C_1$$

$$\frac{dC_2}{dt} = e_{21} F_{21}(R_1)C_2 + e_{22} F_{22}(R_2)C_2 - m_2 C_2$$

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]; Abrams [1986]). The general result of these analyses is that divergent character displacement in attack rates is an inevitable outcome of resource competition.

Here, I examine the effects of this inevitable divergence in attack rates on food-web dynamics. In particular, I examine how divergence in attack rates affect resource densities as well as the local stability of both resources and consumers. I do this by (i) deriving analytical expressions for the relationship between attack rates and food-web dynamics in different foraging scenarios and (ii) simulating the effects of competition on the eco-evolutionary dynamics of consumers and resources. For these simulations, I used an Adaptive Dynamics approach. At each evolutionary 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 with equal probability. The mutant's attack rate on the other resource was determined by the shape of the tradeoff (details below). Assuming this mutant consumer is 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 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 evolutionary limit (e.g. $\frac{a_{ii}}{a_{ii}+a_{ij}}$ is constrained to a maximum of 1 and minimum of 0). I show that the consequences of character displacement on food-web dynamics are not intuitive and depend critically on the foraging scenario and tradeoff in consumer attack rates.

Effect of character displacement on resource densities

I start by examing the effects of character displacement on the density of resources at equilibrium, which will also set the stage for a later analysis of food-web stability. In particular, I examine two different foraging scenarios: one where consumers forage for both resources simultaneously (e.g. MacArthur [1972]) and one where they cannot because resources occur in distinct habitats (e.g. Lawlor and Smith [1976]; McCann et al. [2005]). 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.

Consumers forage for both resources simultaneously

An inherent assumption in MacArthur's model of resource competition is that consumers can forage for both resources simultaneously. In essence, this implies that both resources occur within the same habitat. To gain analytical insight to this scenario, 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 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 isolates the effect of character displacement rather than any dependence on inherent differences in consumers or resources. I show that when both consumers and resources are present that the density of resources at equilibrium are equivalent ($R = R_1 = R_2$) and are determined by the following equation (*Mathematica* file with derivation available upon request):

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

Note that a key determinant of resource density is the consumer's total attack rate, $a_{ii} + a_{ij}$. Since the total attack rate is in the denominator, this implies that resource densities will decrease if evolution favors an increase in total attack rate. I assume that consumers are not

'Darwinian demons' (Law [1979]) and thus the evolution of their attack rates are subject to certain constraints. I modelled these constraints such that $\left(a_{ii}/A\right)^n + \left(a_{ij}/A\right)^n = 1$, 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 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. 1). When $n = 1$, the tradeoff function is linear, and all combinations of a_{ii} and a_{ij} have the same total attack rate (blue line in Fig. 1).
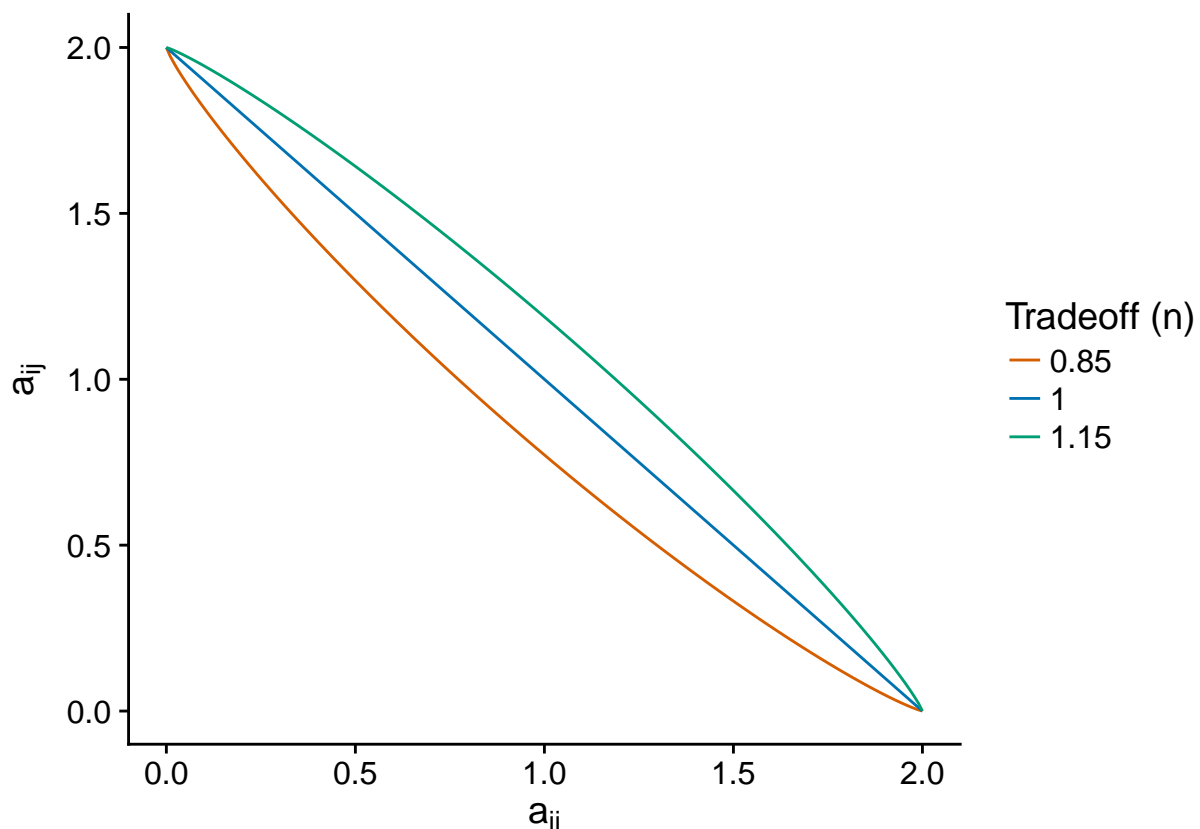

Figure 1: Tradeoff forms for consumer attack rates.

Previous work has shown that consumers undergo divergent character displacement regardless of the shape of the tradeoff (Lawlor and Smith [1976]; Abrams [1986]). Interestingly, I

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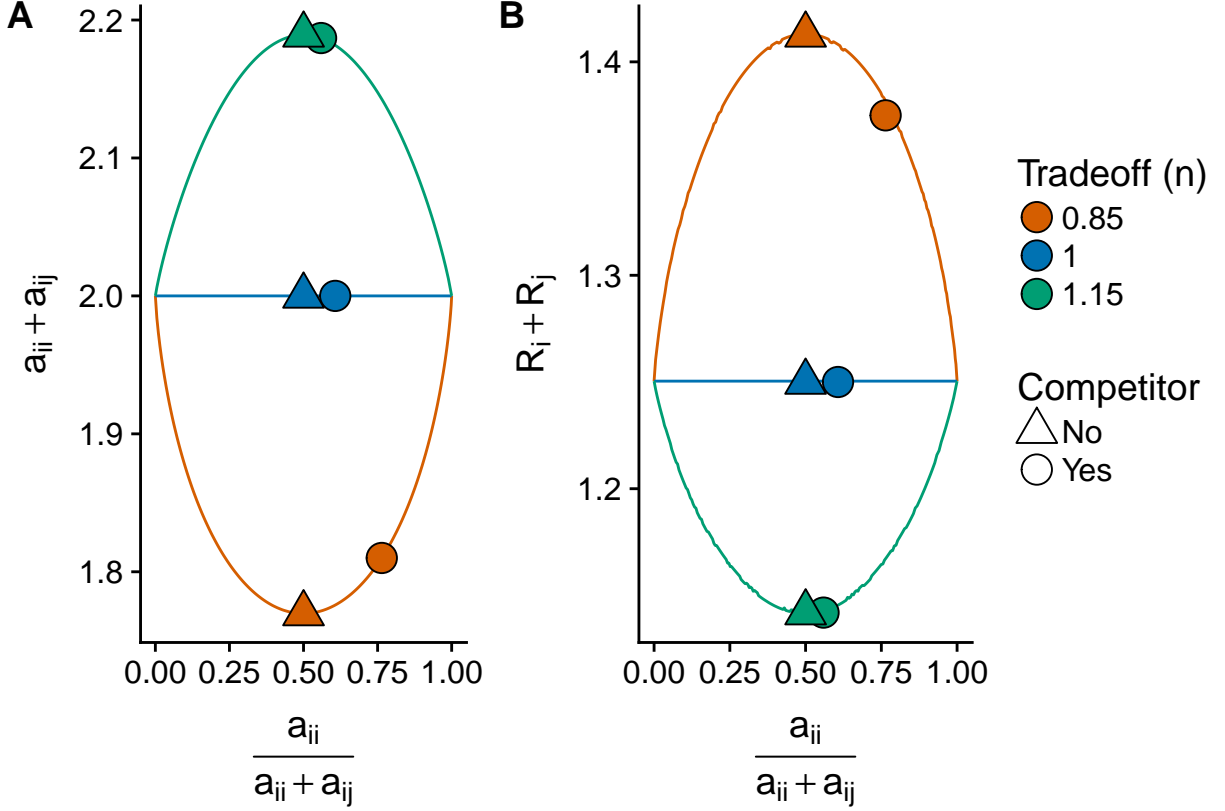
Figure 2: Effect of character displacement on total attack rates (A) and resource densities (B) when consumers can forage for both resources simultaneously.

Consumers *cannot* forage for resources simultaneously

Most models of character displacement have assumed a scenario where consumers can forage for both resources simultaneously (e.g. Taper and Chase [1985]; 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 forage for both simultaneosly. The only character displacement model that I am aware of that modeled resources in different 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 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 ($w = w_{11} = w_{22}$).

Lawlor and Smith [1976] found that consumers still underwent divergent character displacement regardless of whether consumers could or could not forage for resources simultaneously. I find that the foraging scenario qualitatively affects the relationship between character displacement and resource densities. To demonstrate this, note that again resource densities are equivalent at equilibrium ($R = R_1 = R_2$ when both consumers and resources present), but are now determined by the following equation (*Mathematica* file with derivation available upon request):

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

This equation implies that if consumers evolve to become specialists on resources that occur in their preferred habitat (e.g. $w > 0.5$ and $a_{ii} > a_{ij}$), then character displacement will always increase the effective attack rate of consumers ($wa_{ii} + (1-w)a_{ij}$), regardless of the tradeoff (Fig. 3A). Thus, character displacement always results in resource suppression if consumers are competing for resources that occur in 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 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.

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.

It is worth noting 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 slightly specialized on the resources that occur in their non-preferred habitat (deviation of triangles from 0.5 along x-axis in Fig. 3B).
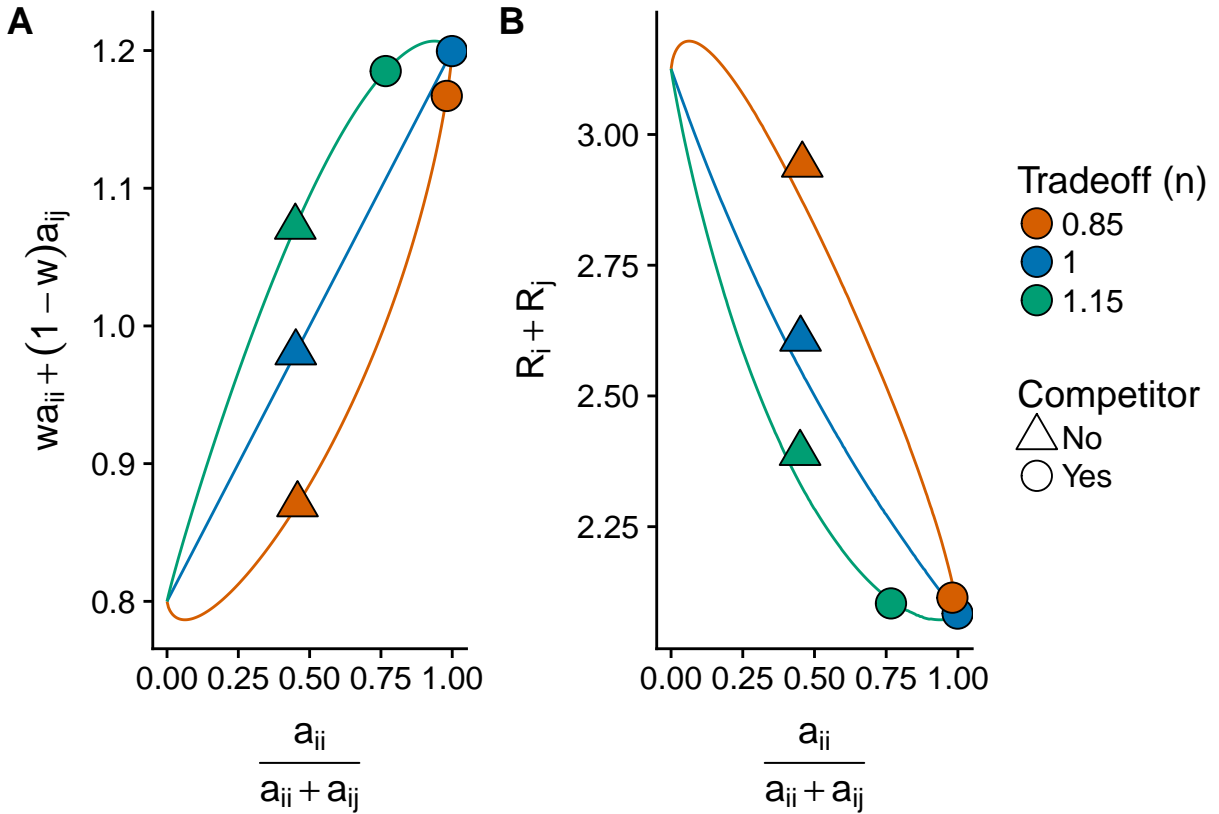

Figure 3: Effect of character displacement on effective attack rates (A) and resource densities (B) when consumers cannot forage for resources simultaneously.

The effect of the foraging scenario on the relationship between character displacement and resource densities appears to be quite general. For example, even if I consider a more realistic consumer functional response (derived by McCann et al. [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 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. 5 in Appendix). This is because resource competition always leads to character divergence and equilibrium resource densities are governed by similar dynamics (*Mathematica* file with derivations available upon request):

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

Effect of character displacement on food-web stability

Of the prior models of character displacement, only Lawlor and Smith [1976] examine the effect of character displacement on the ecological stability of the system. They conducted a detailed theoretical analysis of three different metrics of stability: (i) stable coexistence of consumers, defined as the mutual invasibility of each consumer; (ii) global stability of consumers, defined as the continued coexistence of both consumers when resource dynamics are perturbed; and (iii) local stability, defined as the rate at which the four-species food web

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returned to equilibrium after a small perturbation to species abundances. Note that the first two metrics correspond to the stable coexistence of consumers, while the third metric measures the stability of the entire food web. Lawlor and Smith [1976] found that character displacement enhanced the stable coexistence of consumers, yet had a small negative effect on the local stability of the food web.

Lawlor and Smith [1976]'s work gave fundamental insight to the effect of character displacement on ecological stability; however, none of their stability analyses compared food webs with and without a competing consumer. Such comparisons are necessary for inferring the effects of ecological character displacement, a point that has been made clear in the criteria to demonstrate character displacement (Schluter [2000]; Schluter and McPhail [1992]). In fact, the first two metrics of stability can only be assessed when both consumers are present because it examines the effect of divergence on coexistence, which requires both consumers to be present. In contrast, local stability can be compared in food webs with and without a competing consumer, and thus provides a useful benchmark for examining the effects of character displacement on food-web stability.

Below, I plot the results from the same simulations I did previously except now local stability ($-1 \times \text{Re}(\lambda_{max})$) is on the y-axis (Fig. 4). In general, I find that resource supression goes hand-in-hand with local stability, a tendency that has been noted by others (Murdoch et al. [2003]; McCann [2011]). Whenever character displacement results in resource suppression, I observe a decrease in local stability (Fig. 4). 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. 4). Note that I reach the same fundamental conclusions when I incorporated a more realistic functional response for the consumers (Fig. 6 in Appendix).
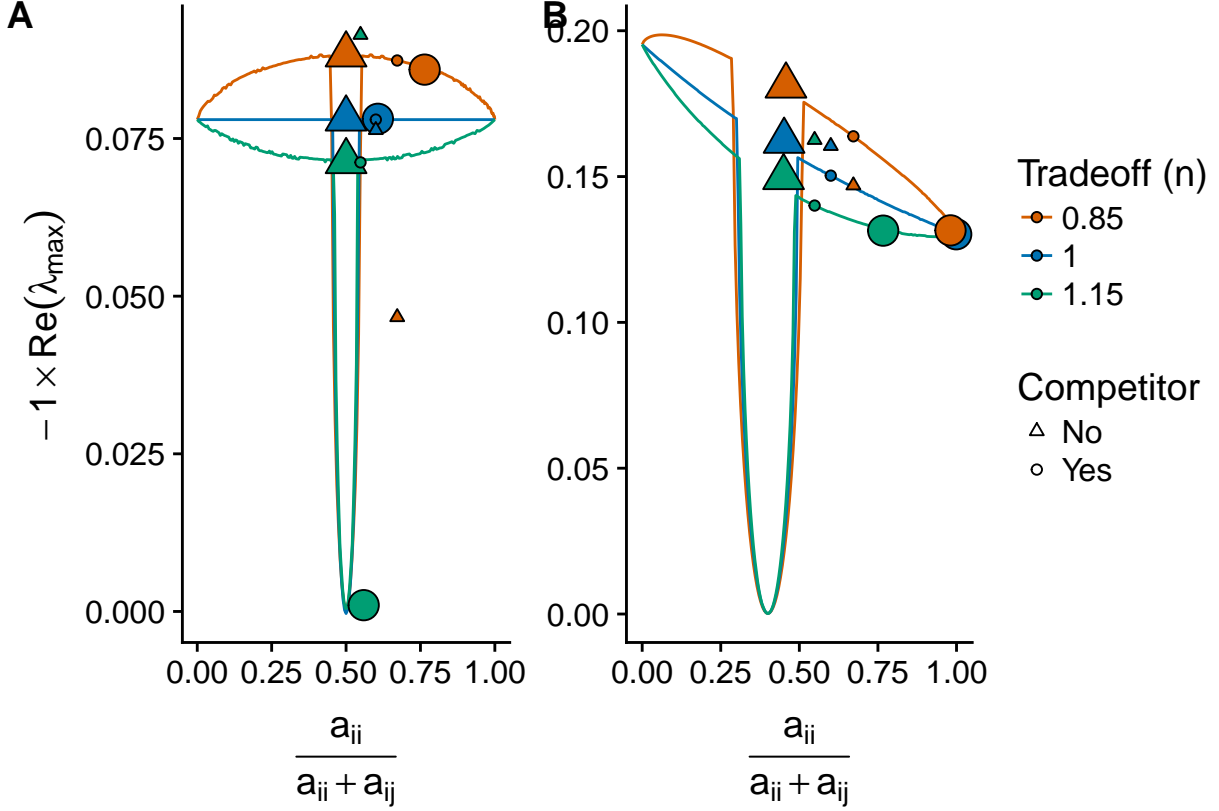
Figure 4: Effect of character displacement on local stability when consumers can (A) and cannot (B) forage for both resources simultaneously. Small and large points correspond to initial and evolved strategies, respectively.

I conducted the previous simulations on a scenario where the food web remains locally stable $(\mathrm{Re}(\lambda_{max}) < 0)$. 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 (McCann et al. [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):

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

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.

Predictions for threespine stickleback

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. 5B). Prior work in threespine stickleback suggests that the evolution of stickleback attack rates are constrained by a concave-up tradeoff (Schluter [1993]; Arnegard et al. [2014]) and that stickleback ecotypes are competing for resources that occur in different habitats (benthic vs. limnetic, 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 et al. [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 et al. [2003]; 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.

Other relevant points

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 (Abrams [1987]; Fox and Vasseur [2008]).
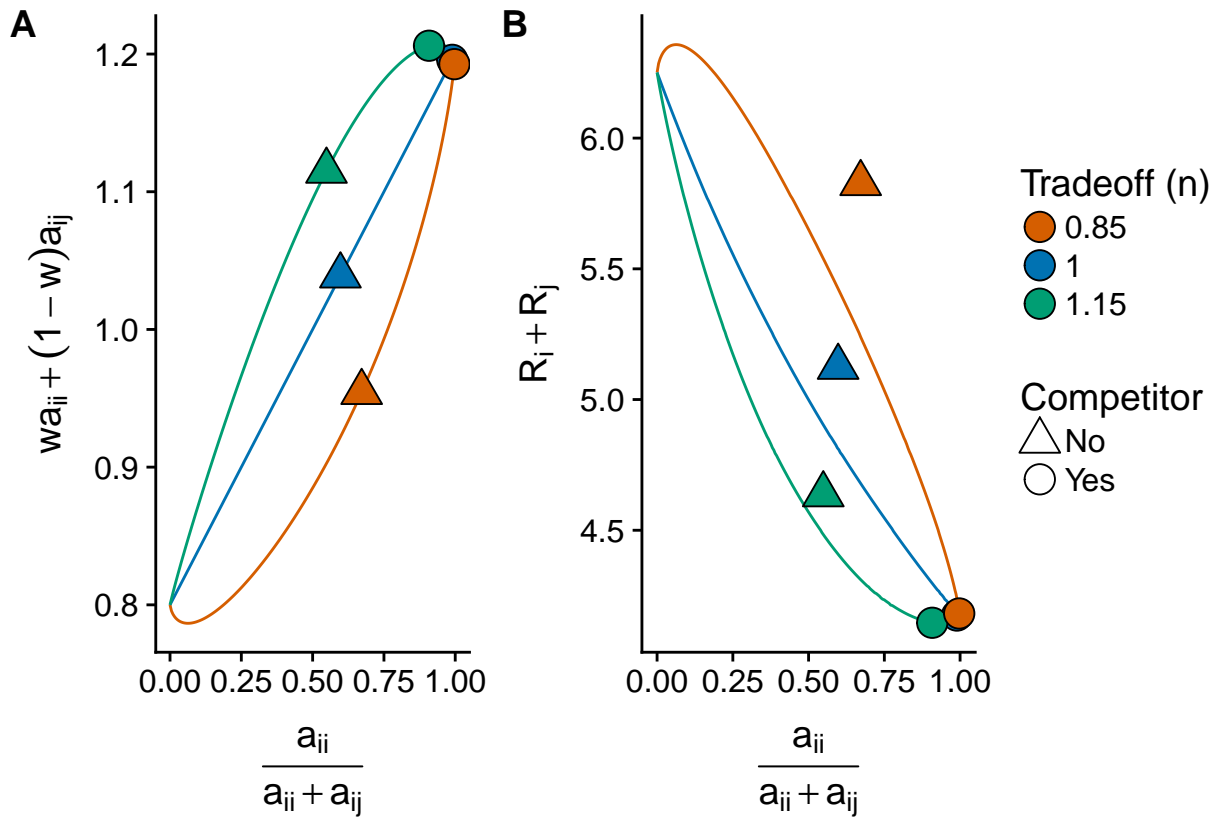
Appendix: More realistic functional response

Figure 5: Effect of character displacement on total attack rates (A) and resource densities (B) when consumers exhibit a more realistic functional response.
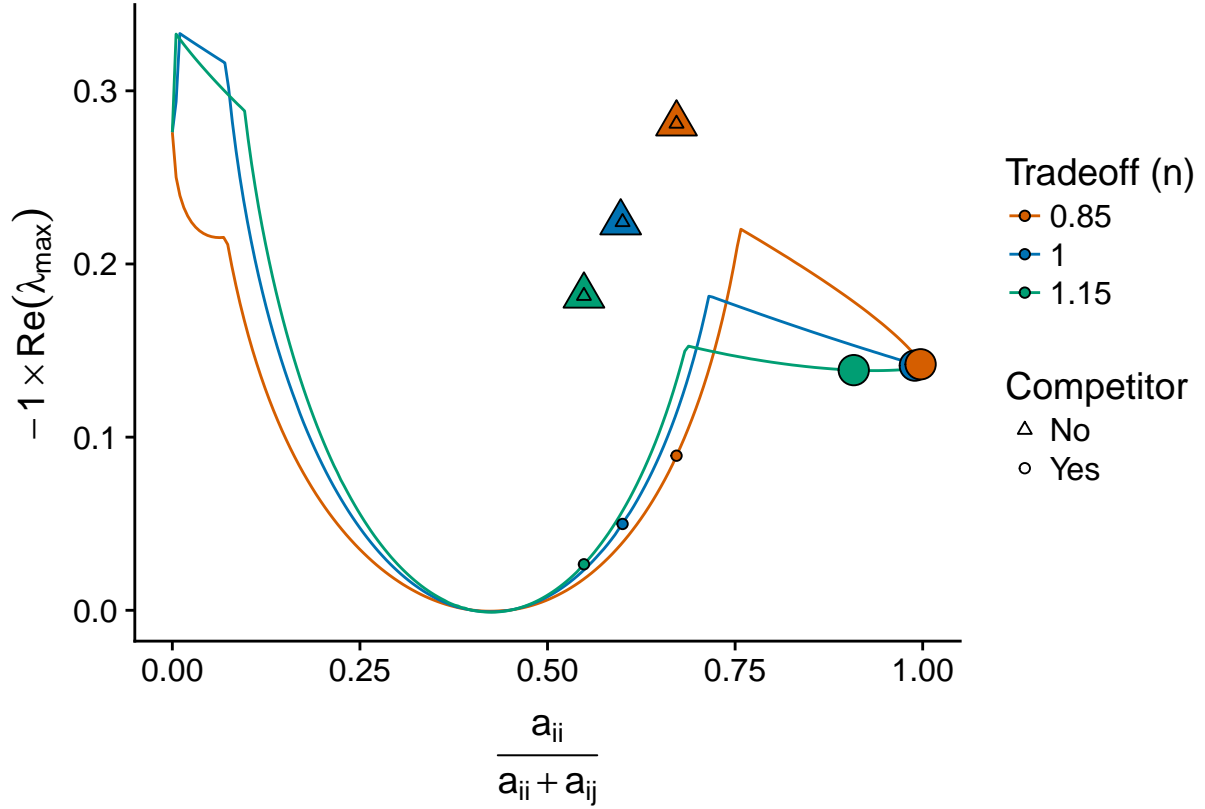
Figure 6: Effect of character displacement on local stability when consumers exhibit a more realistic functional response.

References

P A Abrams. Character displacement and niche shift analyzed using consumer-resource models of competition. *Theor. Popul. Biol.*, 29(1):107–160, February 1986.

Peter A Abrams. Alternative models of character displacement and niche shift. i. adaptive shifts in resource use when there is competition for nutritionally nonsubstitutable resources. *Evolution*, 41(3):651–661, 1987.

Matthew E Arnegard, Matthew D McGee, Blake Matthews, Kerry B Marchinko, Gina L Conte, Sahriar Kabir, Nicole Bedford, Sara Bergek, Yingguang Frank Chan, Felicity C

Jones, David M Kingsley, Catherine L Peichel, and Dolph Schluter. Genetics of ecological divergence during speciation. *Nature*, 511(7509):307–311, July 2014.

Jeremy W Fox and David A Vasseur. Character convergence under competition for nutritionally essential resources. *The American Naturalist*, 172(5):667–680, 2008.

Gabriel Gellner, Kevin S McCann, and Alan Hastings. The duality of stability: towards a stochastic theory of species interactions. *Theor. Ecol.*, 9(4):477–485, December 2016.

Richard Law. Optimal life histories under Age-Specific predation. *Am. Nat.*, 114(3):399–417, 1979.

Lawrence R Lawlor and J Maynard Smith. The coevolution and stability of competing species. *Am. Nat.*, 110(971):79–99, 1976.

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

K S McCann, J B Rasmussen, and J Umbanhowar. The dynamics of spatially coupled food webs. *Ecol. Lett.*, 8(5):513–523, May 2005.

Kevin S McCann. *Food webs (MPB-50)*. Princeton University Press, 2011.

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

Risa D Sargent and Sarah P Otto. The role of local species abundance in the evolution of pollinator attraction in flowering plants. *Am. Nat.*, 167(1):67–80, January 2006.

D Schluter and J D McPhail. Ecological character displacement and speciation in sticklebacks. *Am. Nat.*, 140(1):85–108, July 1992.

Dolph Schluter. Adaptive radiation in sticklebacks: Size, shape, and habitat use efficiency. *Ecology*, 74(3):699–709, April 1993.

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

J Maynard Smith and G R Price. The logic of animal conflict. *Nature*, 246:15, November 1973.

Mark L Taper and Ted J Chase. Quantitative genetic models for the coevolution of character displacement. *Ecology*, 66(2):355–371, April 1985.

P Yodzis and S Innes. Body size and Consumer-Resource dynamics. *Am. Nat.*, 139(6): 1151–1175, 1992.