

Appendix from P. A. Abrams et al., “Competition-Similarity Relationships and the Nonlinearity of Competitive Effects in Consumer-Resource Systems” (Am. Nat., vol. 172, no. 4, p. 463)

Additional Competition-Similarity Relationships

This appendix presents competition-similarity relationships for five variants of the models presented in the main text. The first examines the impact of utilization curve shape. The second variant model looks at the impact of nonlinear density dependence in the growth of biotic resources. The third section deals with the combination of abiotic resources and asymmetric resource utilization curves. The last two sections discuss consumers that differ in the shapes of their utilization curves and unimodal rather than flat resource abundance distributions.

A Strongly Peaked Resource Utilization Curve: Biotic Resources

Here we assume that the utilization curve is characterized by a negative second derivative at all positions other than $x = y$. It is given by the following function (illustrated in Abrams et al. 2008):

$$C(x, y) = \begin{cases} 0 & \text{if } x < y \\ 12(x - y)^2 & \text{if } y < x < y + 1/2 \\ 12[1 - (x - y)]^2 & \text{if } y + 1/2 < x < y + 1 \\ 0 & \text{if } x > y + 1 \end{cases}$$

This has a positive second derivative with respect to x at all values where it is positive and a sharp peak at $y + 1/2$. The resulting competition-similarity relationships are shown in figure A1. The main qualitative difference between figure A1 and figure 2 is that α_{ij} is a unimodal function of mortality for low niche separations; this is reflected in the $d = 0.15$ curve lying above the corresponding curves for $d = 0.05$ or $d = 0.45$ at some positions on the niche axis. The shape of the utilization curve influences whether the increased resource exclusion caused by lowered mortality increases or decreases the effective resource overlap.

Biotic Resources with $\theta \neq 1$

Measurements of density dependence are usually characterized by an exponent, θ , that differs from 1 (Sibly et al. 2005). This results in nonlinear interactions at all consumer efficiencies. The steady state abundance of resource at position x is given by $[K(x)/r(x)][r(x) - C(x, y_i)N_i - C(x, y_j)N_j]^{(1/\theta)}$. Because competitive effects are based on the derivatives of these resource densities with respect to N , $\theta = 1$ represents a special case in which competitive effects are independent of consumer density, provided that the resource is present. All other values of θ imply that competitive effects change with N_i and hence depend on consumer mortality. As a result, all four measures of the competition coefficient differ from one another for all mortality rates across all separations. Larger mortality decreases N , which magnifies $\partial R/\partial N$ when $\theta > 1$. As a result, the effect of the resident on the invader is larger than the effect of the invader on the resident when mortality is high enough that all resources are present, as noted for the mortality rate $d = 0.45$ in figure A2A, which assumes $\theta = 3$. Exclusion of a significant number of resources reverses the magnitudes of these two effects. The corresponding case with $\theta = 1/3$ is shown in figure A2B.

The Combination of Abiotic Resources and Asymmetric Utilization Curves

The example presented here uses the same asymmetrical utilization curve as does figure 4 (exponents $e_1 = 3$ and $e_2 = 1$), but it assumes abiotic rather than logistic growth. Figure A3 shows the resulting competition-similarity relationships. The panels show the effect of species j (the species whose utilization curve is displaced to the right, to a higher position on the axis) on species i (the nondisplaced species). Because abiotic growth results in lesser weights (W in eq. [2b]) for more heavily used resources at all resource abundances, the first competition coefficient, α_{ij} , exceeds 1 for some displacements at all mortalities ($\alpha_{ij} > 1$ occurs only for low mortalities in figure 4). Asymmetry also magnifies the difference in competitive effects between resident and invader, compared with the corresponding system with bell-shaped utilization curves shown in figure 5.

Consumers That Differ in the Shapes of Their Utilization Curves

It is likely that any pair of competitors in nature will have some differences in the shapes of their utilization curves. The example shown in figure A4 consists of two asymmetric curves having the same basic form as in figure 4 of the main text, except that the two curves are skewed in different directions. Resource growth is logistic. The greatest overlap of the two utilization curves, as measured by equation (2a), occurs when the right-skewed curve (species j) is displaced approximately 0.4 units to the left of the left-skewed curve (species i). When mortality is high enough that all resources are present, this point of maximal overlap also results in maximal competition, measured as either α_{ij} or β_{ij} . For α_{ij} , the maximum strength of competition increases with decreasing mortality, and coefficients significantly >1 are possible. For β_{ij} , low mortality results in a strongly bimodal relationship between similarity and competition. With decreasing mortality, the strongest competition coefficient corresponds to ever-smaller displacements of the two utilization curves. The invasion competition coefficient, χ_{ij} , which is not shown here, also exhibits a complex, nonmonotonic response to resource separation.

Impact of a Nonuniform Resource-Abundance Spectrum

In this last scenario, we consider a nonuniform distribution of resource abundances. In this case, the weighting terms in equation (2b) differ because of differences in $K(x)$ and $R(x)$. Figure A5 assumes a Gaussian $K(x)$ having a standard deviation similar to that of the utilization curves; all other aspects of the model are identical to those in figure 2. The main effect of a unimodal resource distribution is that the strength of competition, when measured as α_{ij} , is a unimodal function of the niche separation, with values exceeding 1 for intermediate separations when the consumer mortality rate is sufficiently low. Another difference is that β_{ij} does not drop to 0 for intermediate separations at $d = 0.05$. However, 0 values for β_{ij} do occur for still lower mortalities. This case is complicated by the fact that greater separations change the abundance each competitor would attain in allopatry. The increase in α_{ij} with separation is in part a consequence of the decrease in allopatric population density when the consumer's utilization is not centered on the same position as the maximum of the K curve. A full consideration of all possible sets of nonuniform b , K , and r is beyond the scope of this appendix. However, simulations of a number of standard deviations of the Gaussian $K(x)$ and other unimodal curves, as well as calculations using a monotonically changing $b(x)$ or $r(x)$, suggest that these also result in nonlinear competition involving highly non-Gaussian relationships when consumers are efficient exploiters. Ackermann and Doebeli (2004) showed that non-Gaussian competition coefficients result from nonuniform carrying capacity curves, even when there is no resource exclusion in MacArthur's original system.

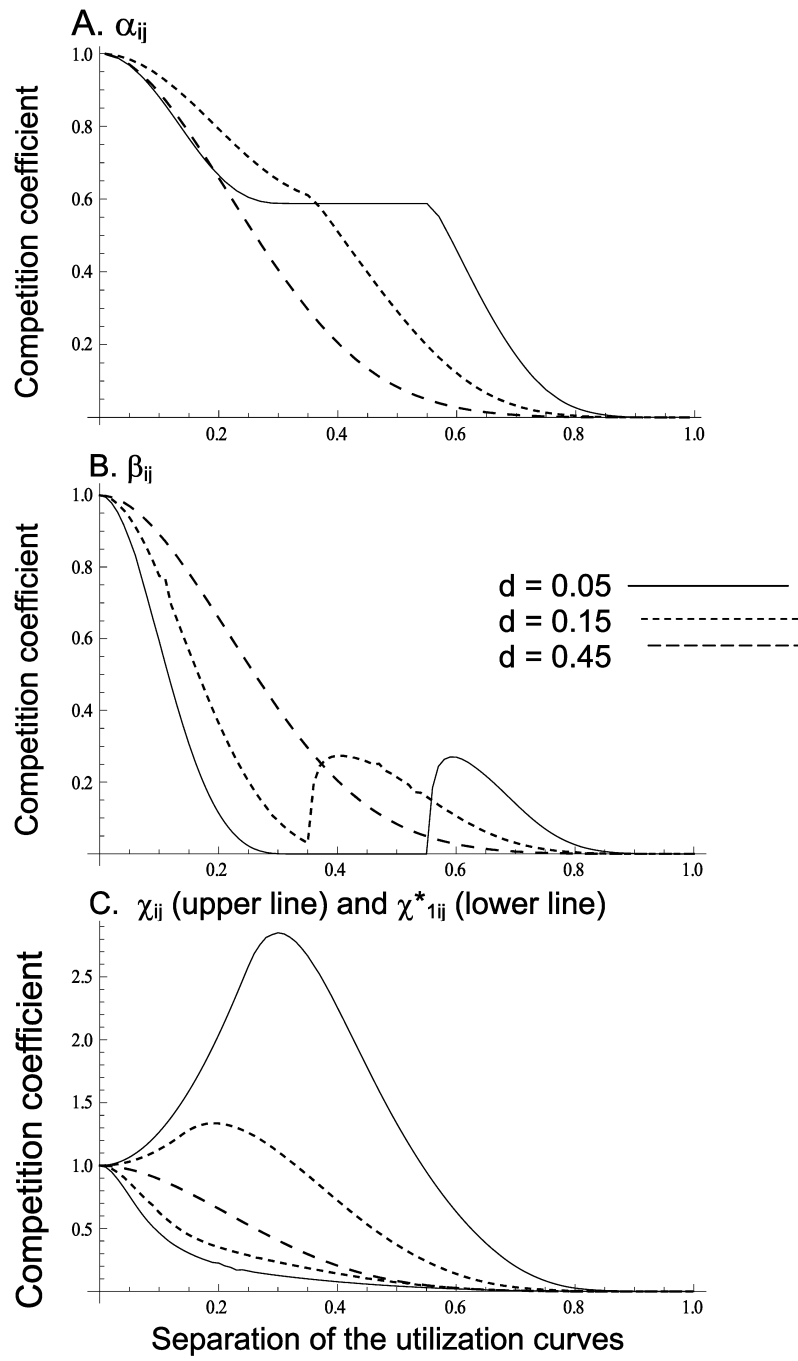


Figure A1: Competition-similarity relationships produced by the tent-shaped utilization curve described in “A Strongly Peaked Resource Utilization Curve: Biotic Resources.” The format matches that of figure 2.

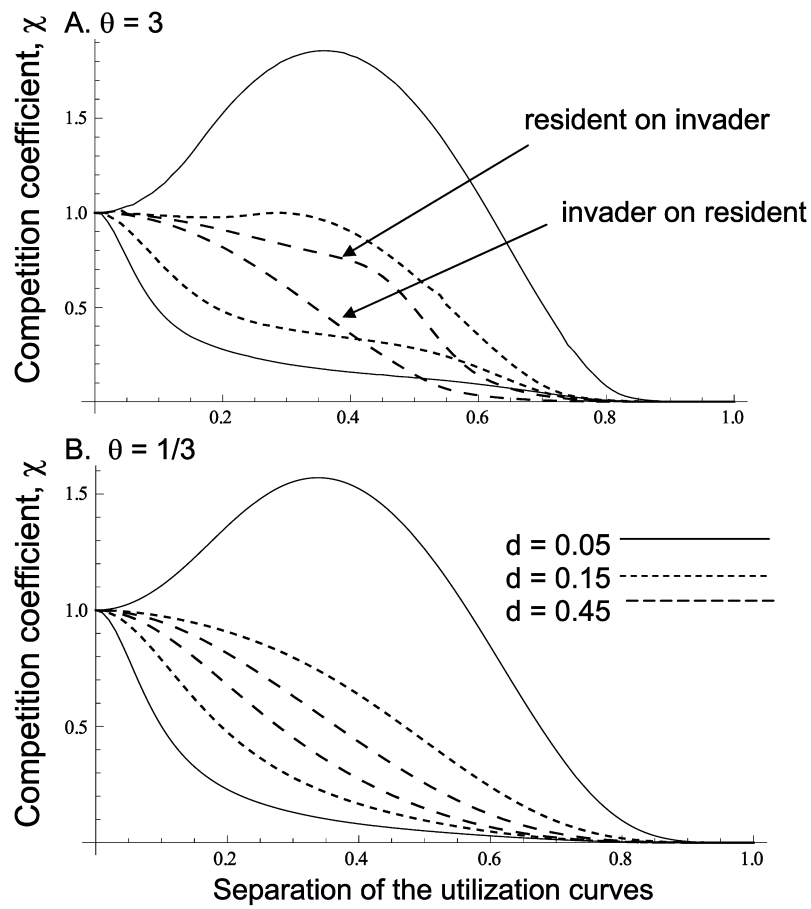


Figure A2: Competition-similarity relationships for the θ -logistic model using the invasion competition coefficients (χ_{ij} and χ_{ij}^*) for three different consumer mortalities. The system is identical to that illustrated in figure 2C, except that $\theta = 3$ in A and $\theta = 1/3$ in B. In all cases but one, the upper line of a given style gives the effect of the invader on the resident, while the lower line gives the effect of the resident on the invader. However, for $d = 0.45$ (long-dashed line) in A, the magnitudes of the two effects are reversed.

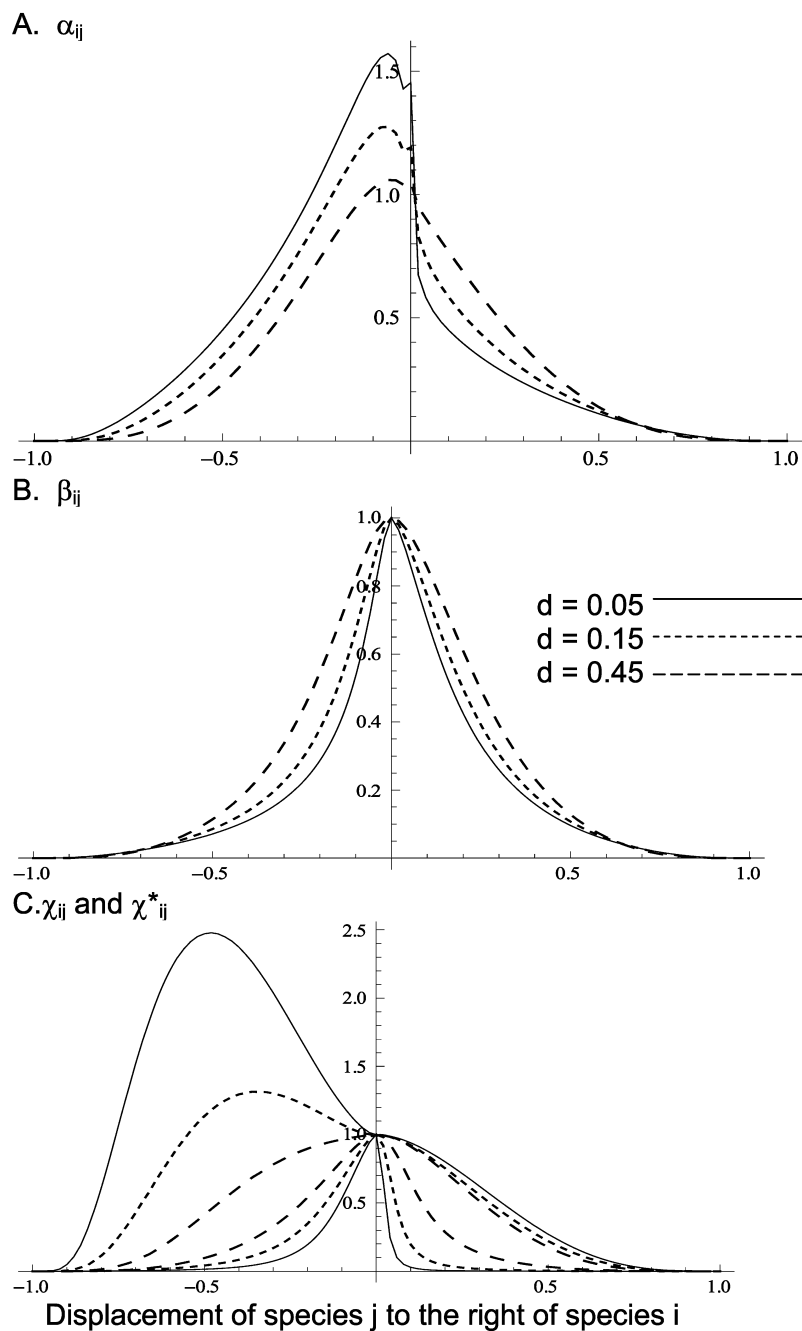


Figure A3: Competition-similarity relationships in a model with abiotic resources and asymmetrical utilization curves. The effect of the invader on the resident (χ_{ij}) is the upper curve of a given line style in C; the resident's effect on the invader (χ_{ij}^*) is the lower curve.

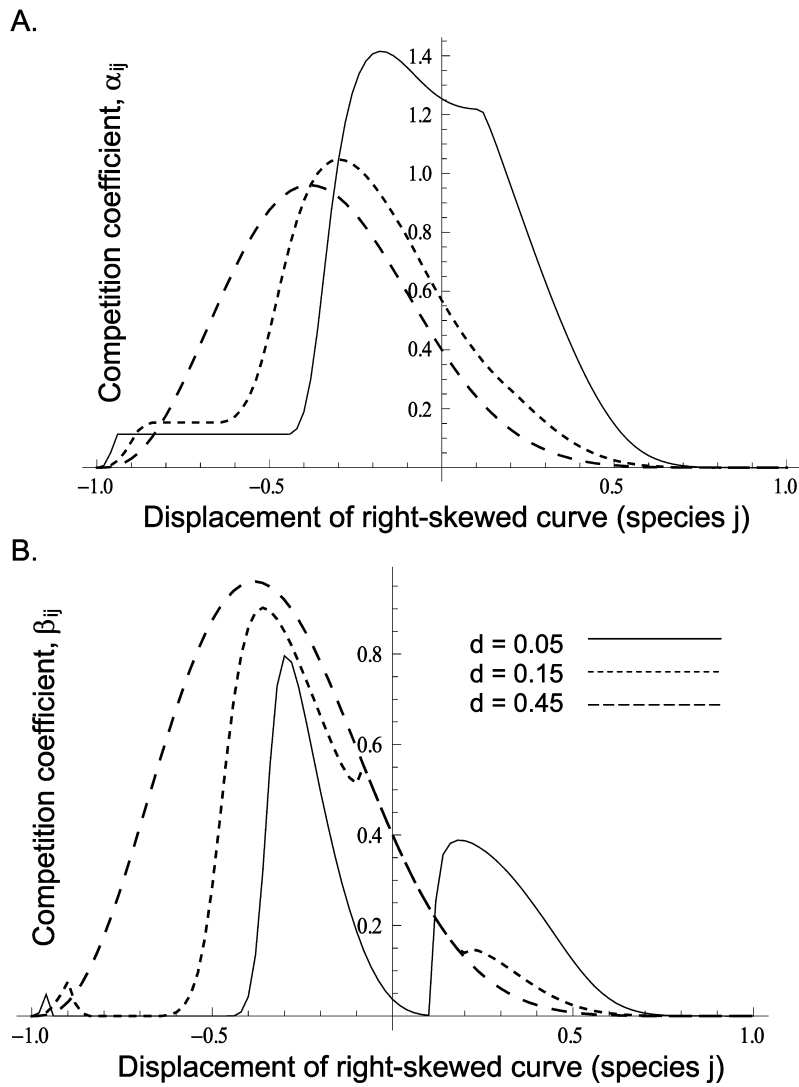


Figure A4: The coefficients α_{ij} and β_{ij} for logistically growing resources, a uniform carrying capacity, and competitors with oppositely skewed resource utilization curves. These are the right-skewed curve shown in figure 1, $C_j(x, y_j) = 20(x - y_j)^3[1 - (x - y_j)]$, and the similar left-skewed function, $C_i(x, y_i) = 20(x - y_i)[1 - (x - y_i)]^3$. The figure gives the impact of the right-skewed species (species j) on the left-skewed species (species i) relative to the left-skewed species on itself as a function of the displacement of species j relative to species i ($y_i = 0$; the X-axis corresponds to y_j).

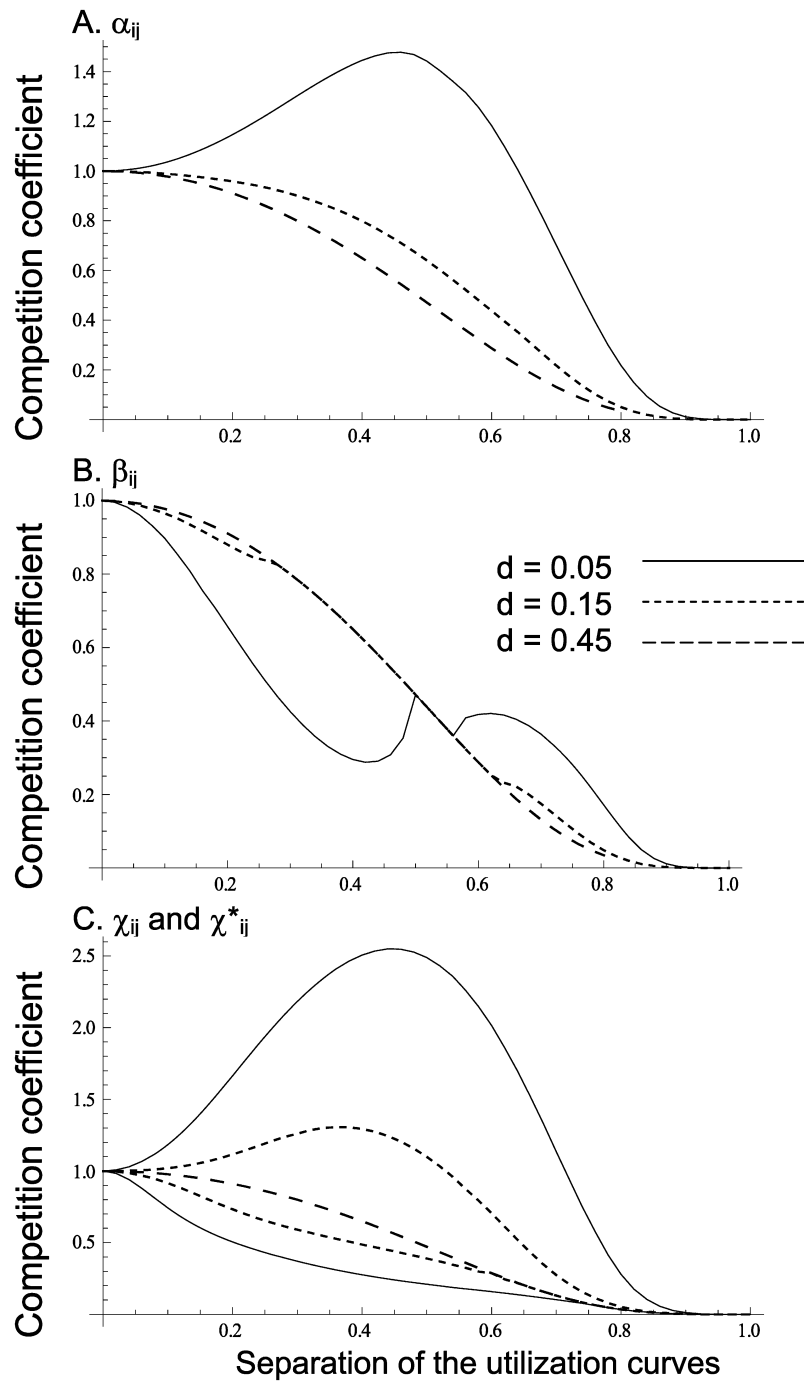


Figure A5: Competition-similarity relationships for a unimodal resource carrying capacity curve. Utilization curves are as in figure 2. The carrying capacity at position x is a Gaussian function of x with 0.15 SD and a maximum (at $x = 0$) of 2.6619. The species are assumed to be located symmetrically with respect to the peak of the K curve.