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Competition-Similarity Relationships and the Nonlinearity of Competitive Effects in Consumer-Resource Systems

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ABSTRACT: Much previous ecological and evolutionary theory about exploitative competition for a continuous spectrum of resources has used the Lotka-Volterra model with competition coefficients given by a Gaussian function of niche separation. Using explicit consumer-resource models, we show that the Lotka-Volterra model and the assumption of a Gaussian competition-similarity relationship both fail to reflect the impact of strong resource depletion, which typically reduces the influence of the most heavily used resources on the competitive interaction. Taking proper account of resource depletion reveals that strong exploitative competition between efficient consumers is usually a highly nonlinear interaction, implying that a single measure is no longer sufficient to characterize the process. The nonlinearity usually entails weak coupling of competing species when their abundances are high and equal. Rare invaders are likely to have effects on abundant residents much larger than those of the resident on the invader. Asymmetrical utilization curves often produce asymmetrical competition coefficients. Competition coefficients are typically non-Gaussian and are often nonmonotonic functions of niche separation. Utilization curve shape and resource growth functions can have major effects on competition-similarity relationships. A variety of previous theoretical findings need to be reassessed in light of these results.

Keywords: competition, competition coefficient, competitive asymmetry, consumer-resource interactions, resource overlap, resource utilization.

Competitive interactions determine both species diversity in natural communities and the morphological diversity of those species (Hutchinson 1959; MacArthur and Levins 1967; Schoener 1983; Ricklefs and Schluter 1993; Chesson 2000; Schluter 2000*a*, 2000*b*). The ability of a particular species to exist in a competitive community and the evolution of traits affecting its resource use are determined by how the population sizes of its competitors and interspecific differences in resource use affect the per capita growth rate of the focal species (MacArthur 1972; Abrams 1983; Schluter 2000*a*, 2000*b*). The consequences of exploitative competition are most often represented by a version of the Lotka-Volterra model in which competition coefficients are related to phenotypic similarity using a function proposed by MacArthur and Levins (1967). The Lotka-Volterra model implies that the per capita population growth rate of each species declines linearly with increases in its own density or those of its competitors. MacArthur and Levins's (1967) work established the convention that the competition coefficients between two competitors are Gaussian functions of the niche separation of the two species (e.g., Otto and Day 2007). This standard model is referred to as the LV-G model below.

Use of the LV-G model to describe exploitative competition should be based on either empirical evidence that it is an adequate approximation to natural competitive guilds or theoretical evidence that such a model is an adequate approximation to a wide variety of more detailed models describing the consumer-resource interactions explicitly. Empirical evidence provides, at best, mixed support for the LV-G model. Vandermeer (1969) was able to obtain reasonable fits to time series data on two competing protozoa using the Lotka-Volterra model, but a more detailed study of several systems of competing *Drosophila* (Ayala et al. 1973; Pomerantz et al. 1980) showed that per capita growth rates were highly nonlinear functions of population densities. Measurements of utilization curves have typically observed relationships that differ greatly from Gaussian (Wilson 1975; Grant 1986), and there appear to be no experiments examining how competition changes with niche separation, beyond a comparison of

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two pairs of species having different niche separation (Pacala and Roughgarden 1982).

On the theoretical side, MacArthur (1968, 1970, 1972) provided the only derivation of the LV-G model from a consumer-resource system. The latter system assumed Gaussian utilization curves, noninteracting nutritionally substitutable resources with logistic growth, and consumers with linear functional responses. Soon after MacArthur's studies appeared, other work showed that large deviations from the LV-G model could be obtained using models with different assumptions (Schoener 1974, 1976; Abrams 1975, 1977, 1980*a*, 1980*b*). Additional studies showed that MacArthur's derivation had made unwarranted assumptions about the lack of resource extinction (Hsu and Hubbell 1979; Abrams 1980*b*). Subsequent work has reemphasized these points by showing that the assumed lack of resource extinction could have a major effect on competition-similarity relationships (Abrams 1998, 2001; Abrams and Nakajima 2007).

The early critiques had little impact on subsequent competition theory, which has relied extensively on the LV-G model. The LV-G model is the basis of the vast majority of work on evolutionary responses to competition (e.g., Dieckmann and Doebeli 1999; Case and Taper 2000; Day 2000; Doebeli and Dieckmann 2000, 2003; Drossell and McKane 2000; Vincent and Brown 2005; Bolnick 2006; Scheffer and van Nes 2006; Konuma and Chiba 2007). It has also been assumed in the majority of work on the limiting similarity of competitors (e.g., May 1973, 1974; Scheffer and van Nes 2006; Szabó and Meszéna 2006). The Lotka-Volterra model (without the Gaussian competition-similarity relationship) has formed the basis of much work on the relationship between diversity and stability (Ives and Hughes 2002; Ives and Carpenter 2007). More generally, scalar measures of interaction strength, which are of little use if they change greatly with initial densities and perturbation sizes, continue to be widely used in studies of food webs (Berlow et al. 2004; Wootton and Emmerson 2005). This is a reflection of the predominance of the assumption of constant per capita effects, which is manifested in the linear decline in per capita growth rates with competitor densities in the Lotka-Volterra model. It is puzzling why early criticisms of this framework have been largely ignored. One possible reason is that most of the criticisms were derived from models having two discrete resources rather than the more popular conceptual model of a continuous spectrum of resources. Regardless of the reason for employing it, continued use of the LV-G model to draw biological conclusions about exploitative competition for a continuous spectrum of resources requires that we have a better understanding of the magnitude of deviations from that model, entailed by a more complete representation of the competitive process, and a better understanding of the ecological circumstances producing the largest deviations. Understanding the range of likely forms for the competition-similarity relationship is particularly important given recent results showing that even modest deviations from Gaussian functions can produce very different predictions in evolutionary models (Gyllenberg and Meszéna 2005; Doebeli et al. 2007; Pigolotti et al. 2007; Leimar et al. 2008). The impact of predation on the diversity of a prey community is one of a number of important ecological problems that are very sensitive to the linearity of competitive interactions and to the form of the competition-similarity relationship (Chase et al. 2002).

We begin by reviewing MacArthur's (1970) analysis of a particular consumer-resource model and then extend his general framework by properly accounting for the impact of resource depletion. We then present a range of numerical results for both logistic and nonlogistic resource growth to show how resource depletion changes the linearity of competitive effects and the relationship between similarity and competition.

Models

MacArthur's Model

A generalized version of MacArthur's (1972) two-consumer/multiple-resource system is as follows:

$$\frac{dR(x)}{dt} = R(x)f(R(x)) - \sum_{i=1}^{2} C_i(x)N_iR(x), \tag{1a}$$

$$\frac{dN_i}{dt} = N_i\left(b_i\int_{x\min}^{x\max} C_i(x)R(x)dx - d_i\right), \tag{1b}$$

where $R(x)$ is the population density of resource at position x on a one-dimensional resource axis and N_i is the abundance of consumer i. Resources at different positions are assumed to be nutritionally substitutable. The utilization function of consumer i is given by $C_i(x)$; this is the slope of the consumer's linear functional response to the resource at position x. The integral in equation (1b) is over the range of resources used by consumer i. The consumers have linear numerical responses with a conversion efficiency of resources into consumers, given by b_i, and a density-independent per capita death rate, d_i. (The parameter d_i may also be interpreted as the energy intake required for zero population growth.) We simplify the model by assuming that b_i is independent of resource position and is identical for both consumer species. This allows us to scale b to unity. Resource growth in MacArthur's analysis is logistic, so the per capita growth rate $f(R(x)) =$

$r(x)[1 - (R(x)/K(x))]$. MacArthur's (1970, 1972) analysis sets $dR(x)/dt = 0$ and solves for the resulting steady state values of $R(x)$, denoted $R^*(x)$. This yields $R^*(x) = [K(x)/r(x)][r(x) - C_1(X)N_1 - C_2(x)N_2]$. Substituting this formula into equation (1b) results in a model in which consumer densities are the only dynamic variables and the per capita growth rate of each consumer decreases linearly with its density and that of the other consumer (i.e., Lotka-Volterra competition). This linearity implies that the competition coefficient is independent of consumer population sizes. However, the resulting simplification is valid only when the resources have positive densities, a fact that is true only for sufficiently low consumer efficiency (high enough mortality, d). Given low efficiency and the additional simplifying assumption of a flat resource spectrum (i.e., equal b, r, and K for all resources), MacArthur's competition coefficient of species j on species i is

$$\alpha_{ij} = \frac{\int C_i(x)[\partial R^*(x)/\partial N_j]dx}{\int C_i(x)[\partial R^*(x)/\partial N_i]dx} = \frac{\int C_i(x)C_j(x)dx}{\int C_i(x)^2dx}, \tag{2a}$$

where both integrals extend over the range of resources used by species i and $R^*(x)$ denotes the steady state resource density at x. The right-hand expression arises because $\partial R^*/\partial N_k = -(K/r)C_k$ (for $k = i$ or j) when resources are logistic and at positive density, so the $-(K/r)$ factors cancel out of the numerator and denominator.

More generally, if all resources share a common per capita growth rate, $f(R(x))$, the steady state resource density is defined by $f(R^*(x)) - C_i(x)N_i - C_j(x)N_j = 0$. The effect of each N on $R^*(x)$ is determined by implicit differentiation of this equation when the steady state resource density is positive. This yields $\partial R^*/\partial N_k = C_k/[df/dR(x)]|_{R=R^*}$, assuming $R^* > 0$. If $R^* = 0$, $\partial R^*/\partial N_k = 0$. This generalization of equation (2a) can be expressed as follows:

$$\alpha_{ij} = \frac{\int C_i(x)C_j(x)W(x)dx}{\int C_i(x)^2W(x)dx}, \tag{2b}$$

where $W(x) = 1/[df/dR(x)]|_{R=R^*}$ if $R^*(x) > 0$ and $W(x) = 0$ if $R^*(x) = 0$.

If the utilization curves C_1 and C_2 have the same shape (but a different position), the competition coefficient formula is symmetrical under equation (2a); $\alpha_{ij} = \alpha_{ji}$. Assuming that Gaussian utilization curves have equal standard deviations, σ, expression (2a) simplifies to

$$\alpha_{ij} = \exp\frac{-(y_i - y_j)^2}{2\sigma^2}, \tag{3}$$

where y_i denotes the position of the utilization curve of species i on the resource axis. This derivation is the basis of the traditional assumption of a Gaussian competition function. Roughgarden (1974) showed that the Gaussian form of the competition coefficient could be changed somewhat by non-Gaussian resource utilization curves, but the impacts on the relationship between α_{ij} and niche separation demonstrated were relatively small for most curves having the same variance. Formulas (2a), (2b), and (3) are changed if resources at different positions on the axis differ in population growth parameters; in this case, each of the two integrands of equation (2a) is weighted by K/r (Ackermann and Doebeli 2004), where K is generally assumed to be a function of x.

The cancellation of the weighting terms in equation (2a) means that the effect of one more consumer on the per capita growth rates does not depend on population size, which leads to the linear relationship between consumer densities and per capita growth rate that defines the Lotka-Volterra model. However, because, in general, $W(x)$ depends on R^*, which in turn depends on the consumer densities, formula (2b) is a function of those consumer densities. The weighting terms change most dramatically with a change in consumer abundance if the resource at position x becomes extinct. If consumers have large enough densities and the resources are self-reproducing (biotic), then, at equilibrium, the most heavily exploited resources will be driven extinct via apparent competition (Holt 1977). Those resources will therefore have $W(x) = 0$; that is, they will not contribute to competition. If both consumers have high and similar population densities and relatively little niche separation, $W(x)$ is most likely to be 0 for resources that are taken up at a high rate by both consumers. This means that the weighting terms will generally reduce the numerator of expression (2b) more than the denominator because the $C_i(x)C_j(x)$ factors in the numerator in this case are more closely correlated with a zero resource density than are the $C_i(x)^2$ terms in the denominator. On the other hand, if consumer i is abundant and consumer j is rare, $W(x) = 0$ is more likely to characterize the largest values of $C_i(x)^2$ than the largest values of $C_i(x)C_j(x)$. This increases expression (2b) because it differentially decreases the denominator. When both consumer densities are high but niche separation is also high, the $W(x)$ terms reduce the denominator more than the numerator, again increasing the competition coefficient relative to what is predicted by equation (2a). In all cases, it is clear that the value of the competition coefficient is changed by the densities of the consumers because these determine the resource densities on which the $W(x)$ depend. In other words, the Lotka-Volterra model's key assumption of constant per capita competitive effects is no longer satisfied.

Low weighting of heavily exploited resources is not confined to situations in which resources actually become extinct. This can be seen by considering a case with chemostat dynamics of the resources: $dR/dt = I - ER - C_iN_iR - C_jN_jR$. Here, the per capita growth rate, f, that determines the weighting factors in equation (2b) is $(I/R) - E$. Thus, $1/f' = -R^2/I$. As a result, more heavily exploited resources (low R^*) have smaller-magnitude weighting factors in expression (2b). Because many resource populations are class structured or spatially structured, with only some subset being vulnerable to a consumer, the dynamics of the susceptible groups can often be intermediate between logistic and chemostat growth (Abrams and Walters 1996; Turchin and Hanski 2001). Such cases also have lower-magnitude weighting factors for heavily exploited resources in equation (2b). It is easy to verify, for example, that adding a small immigration rate for all resources in the logistic-resource model, although it prevents extinction, still results in very low $W(x)$ for those resources that would have become extinct in the absence of immigration.

It is possible for the weighting factors in equation (2b) to increase as resource densities decline. This occurs under the θ-logistic model (Ayala et al. 1973), $dR/dt = rR[1 - (R/K)^\theta]$, when $\theta > 1$. Here $f' = -\theta rR^{\theta-1}/K^\theta$, so $1/f'$ becomes larger as R^* declines. Even in these cases (which Sibly et al.'s [2005] review suggests are only one-third as common as $\theta < 1$), the weighting factor in equation (2b) is 0 when a resource is excluded. The reduced density dependence reflected by large θ also increases the fraction of resources excluded, all else being equal (Holt 1977). Class structure or immigration may also result in lower-magnitude weightings of heavily exploited resources in spite of $\theta > 1$. Values of $\theta < 1$ always result in lower weighting of more heavily exploited resources. Thus, although it is not universal, a lesser contribution of heavily exploited resources to competition is expected to be much more common than either no weighting or heavier weighting. Any type of differential weighting makes competitive relationships nonlinear because the absolute and relative exploitation rates of different resources change with the changes in the abundances of either consumer species. In addition, the relationship between niche separation and competition will be changed because increasing separation implies changes in the set of resources that is most heavily exploited. Finally, differential weighting of resources implies that the shape of the utilization curves, which has a major effect on which resources are most heavily exploited, will also have a significant effect on competitive interactions. All of these consequences are illustrated below.

Numerical Exploration of the Impacts of Resource Depletion on Competition

The results in this section illustrate the implications of resource depletion for three issues: the nonlinearity of competitive interactions, the impact of consumer mortality (or, more generally, efficiency) on the strength of competition, and the relationship between the niche separation of two consumer species and the amount of competition between them.

Competition Coefficients

The dependence of competitive effects on the population sizes of the two competing species implies that multiple measures of competition are needed to describe the interaction. We deal with this problem by calculating the competitive effect using three different combinations of initial population sizes and population perturbations: first, the impact of introducing or removing one competitor on the equilibrium density of the other when the second is initially at its single-species (allopatric) equilibrium; second, the impact of a small perturbation in the population density of one consumer (competitor) species on the equilibrium population density of the other when both competitors are at their sympatric equilibrium; and, finally, the pair of impacts due to a small change in density when one species is at its allopatric equilibrium and the other is a rare invader. The second and third quantities represent "local" measures of competition based on small changes in density, while the first is a "global" measure based on the impact of addition or removal. The first measure (here denoted α_{ij}) is the most common way of quantifying competition in empirical studies. It is calculated as $\alpha_{ij} = (N_{i\mathrm{A}} - N_{i\mathrm{S}})/N_{j\mathrm{S}}$, where A denotes allopatry, S denotes sympatry, and all densities are measured at equilibrium. The second measure (denoted β_{ij}) is the usual definition of competition coefficients for nonlinear models, and it determines the extent to which the dynamics of the species are coupled near equilibrium: $\beta_{ij} = (\partial g_i/\partial N_j)/(\partial g_i/\partial N_i)|_{N_i=N_{i\mathrm{S}};N_j=N_{j\mathrm{S}}}$, where g_i is the per capita growth rate of consumer species i. When formula (2b) is evaluated at the sympatric equilibrium, it yields β_{ij}. The third pair of measures represents the effect sizes of an invading species on a resident (χ_{ij}) and the resident on the invader (χ^*_{ij}) during the early stages of invasion; these are among the most important effects in an applied context. These measures are given by $\chi_{ij} = (\partial g_i/\partial N_j)/(\partial g_i/\partial N_i)|_{N_j=0;\,N_i=N_{i\mathrm{A}}}$ and $\chi^*_{ij} = (\partial g_i/\partial N_j)/(\partial g_i/\partial N_i)|_{N_i=0;N_j=N_{j\mathrm{A}}}$.

All of these competition coefficients are unity when species 1 and 2 have identical resource utilization curves, and all are 0 when the utilization curves of the two species do not overlap. The three formulas are identical to each other for all overlaps when the two species obey Lotka-Volterra equations; this is a consequence of the linear effect of density on per capita growth rate. A large difference between any pair of the measures (including that between χ_{ij} and χ^*_{ij}) implies significant nonlinearity in competitive effects.

Utilization Curves

In most of the analysis, we assume that different consumer species have curves, C, with identical shapes but (usually) different positions on the resource axis. We measure the position of the utilization curve of species i by y_i, which gives the minimum resource position x that is used by the consumer. Thus, we can represent $C_i(x)$ by $C(x, y_i)$. The range of positive values of C is assumed to be 1 unit on the resource axis, from y_i to $y_i + 1$, and the area under the curve is assumed to equal 1. This rescaling has no impact on the results obtained. We have examined models with a variety of different utilization curves, but only two will be illustrated in the text (for other cases, see the appendix in the online edition of the *American Naturalist*). Both curves are instances of the general formula,

$$C(x,y) = \begin{cases} 0 & \text{if } x < y \\ \dfrac{(x-y)^{e_1}[1-(x-y)]^{e_2}}{\beta(e_1+1, e_2+1)} & \text{if } y < x < y+1\,, \\ 0 & \text{if } x > y+1 \end{cases} \quad (4)$$

where the exponents, e_i, are positive and β is Euler's β function. (This β, which lacks subscripts, is unrelated to the measure of competition, β_{ij}.) These assumptions mean that C has the form of a β probability density function. If $e_1 = e_2 = 0$, equation (4) specifies a uniform distribution. If $0 < e_1$ and $e_2 \leq 1$, C has a negative second derivative with respect to x for all x. When $e_1 = e_2 > 1$, C describes a bell-shaped curve where the inflection point (transition from positive to negative second derivative) is closer to the maximum of the curve for larger values of e. Unequal values of the exponents result in asymmetric curves that are skewed to the right or left, depending on the relative values of the two exponents. We concentrate on two cases: $e_1 = e_2 = 2$ and $e_1 = 3$, $e_2 = 1$. Figure 1 displays these two curves when $y = -0.5$.

Resource Growth Functions

Our main distinction here is between resources that can be excluded and those that cannot; these will be represented by the logistic and chemostat models, respectively. The θ logistic with $\theta \neq 1$ is considered in the appendix. To simplify calculations, we assume $r = K = 1$ for all resources when growth is logistic and $I = E = 1$ for all resources under chemostat growth. In the logistic model with a uniform resource spectrum, $r = 1$ can be achieved by scaling time, and $K = 1$ can be achieved by scaling resource density. This scaling affects d, which becomes inversely proportional to K (see, e.g., Abrams and Holt 2002).

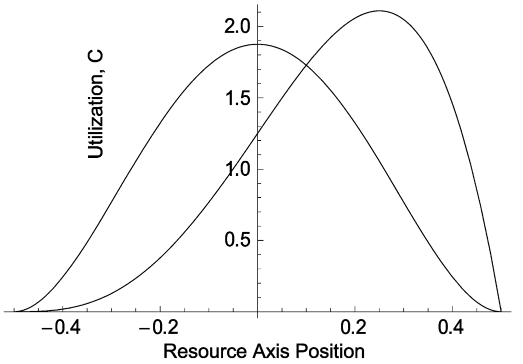

Figure 1: The two resource utilization curves based on equation (4) employed in most examples: the bell-shaped function with exponents $e_1 = e_2 = 2$ and the asymmetrical, right-skewed function C_1 with exponents $e_1 = 3$ and $e_2 = 1$. The range of resource use in each case is from −0.5 to +0.5 on the resource axis.

General Methods of Analysis

We examine how the level of resource depletion affects the outcome of competition between consumer species. The level of resource depletion is determined by consumer efficiency. Here, we use "efficiency" to mean the average proportion by which consumers reduce resource populations below their carrying capacity. In a system with one consumer and one logistic resource, this proportion is $d/(bCK)$. Because we have scaled b and K and have assumed that the integral of C is 1, efficiency can be varied only by changing d, with lower d implying higher efficiency. Given the values assumed for the other parameters, $d < 1$ is required for the consumer to exist. The lowest value of d we examine is $d = 0.05$; this is low enough to produce extinction of a wide range of heavily used resources in models with biotic resource dynamics (fig. 3). Varying efficiency via changes in b, C, or K has qualitatively similar effects.

All of the analysis presented here is based on numerical determination of equilibria of equations (1), carried out using Mathematica, version 6.0 (Wolfram 2007). In a few of the cases considered, analytical solutions were possible, and these confirmed the numerical results. The analysis assumes that the systems have globally stable equilibria, which has been shown for these sorts of consumer-resource models by Chesson (1990) and Haygood (2002).

Results

We examine the impact of different consumer efficiencies (d_i) on the linearity of competitive interactions and on the relationship between niche separation and competition. We can show both of these effects in a single figure by plotting each of the measures of competition (α_{ij}, β_{ij}, χ_{ij}, and χ^*_{ij}) as a function of niche separation for three different consumer mortality rates. This yields 12 competition-similarity relationships. Comparison of any single measure at the three mortality rates reveals the impact of mortality (or, equivalently, the degree of resource depletion) on that competition coefficient. Differences between the competition-similarity relationships at a particular mortality reveal the nonlinearity of the interaction at that mortality.

Competition in Models with Logistic Growth

We begin by examining the bell-shaped curve given by equation (4) with exponents $e_1 = e_2 = 2$. Figure 2 shows the three competition coefficients as a function of the separation between the two resource utilization curves (from 0 to 1) for three different mortality rates. The highest mortality shown ($d = 0.45$) is representative of cases with all resources present (true for $d > 0.2$). In this case, formula (2a) gives the competition coefficient, which is identical for all three measures shown. For the two lower mortalities ($d = 0.05$ and $d = 0.15$), some resources are extinct at both single- and two-consumer equilibria. Resource extinctions have two effects. First, the competition coefficient as a function of niche separation differs significantly from the nearly Gaussian relationship produced at high death rates (fig. 2, *long-dashed lines*). Second, the three measures of competition differ from one another, implying nonlinear competitive effects. Some of the competition-similarity relationships at the lowest mortality are not even monotonically decreasing with increased separation of the resource utilization curves; there is a perfectly flat nonzero segment in figure 2*A*, a flat zero segment in figure 2*B*, and increasing segments in figure 2*B* and 2*C*.

The main features of the relationships in figure 2 for the lower two mortalities can be understood by considering the spectrum of resource densities produced when $d = 0.05$, which is representative of low consumer mortality rates. In allopatry, a single consumer drives the resources in the middle 58% of its utilization range extinct; these are the resources most heavily used. Resources are present for only approximately 0.21 units of the axis on each end of the range used. This is the same as the resource-abundance spectrum at the sympatric equilibrium when the two consumers have 0 separation. Figure 3 shows how the spectrum of resource densities at the sympatric equilibrium changes as the two utilization curves move apart (separations of 0.1, 0.5, and 0.7). At a separation of 0.1, the two consumers have overlap for extant resources in both tails of their utilization curves. At a separation of 0.5, the zone of overlap has no extant resources. When the separation is 0.7, some resources again exist in the zone of overlap of the utilization curves; here the combined utilization rate of the two consumers is not sufficient to cause extinction. This explains why β_{ij} drops to 0 in figure 2 for intermediate separations (where there are no extant resources in the zone of overlap) but then increases again at moderately large separations. Similarly, the fact that α_{ij} is constant over a range of intermediate niche separations results because, for this entire range of sepa-

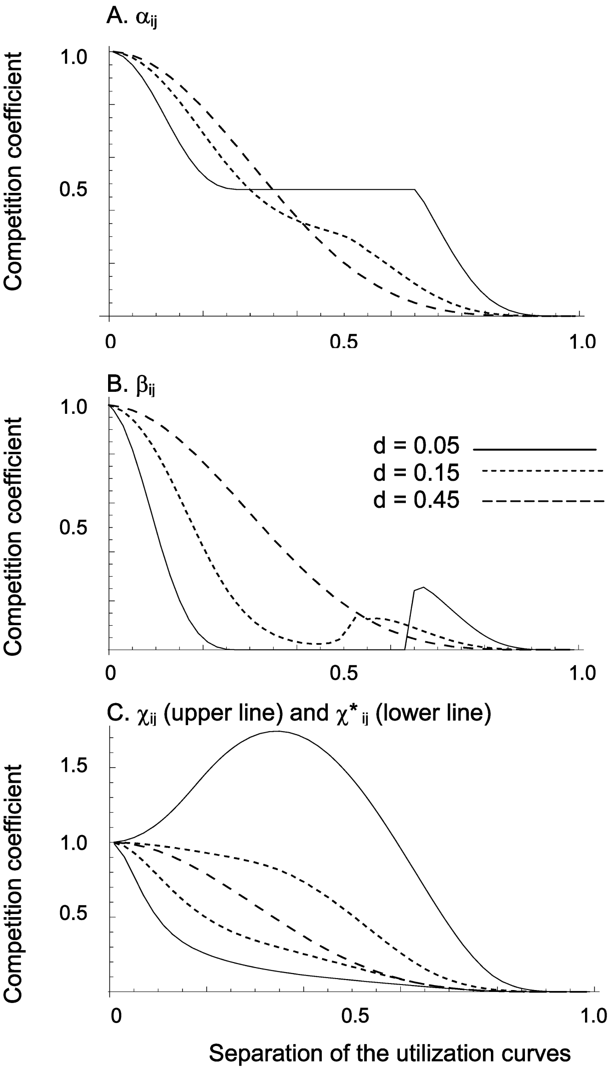

Figure 2: Competition-similarity relationships for three different measures of the competition coefficient. The system has logistic resources and bell-shaped utilization curves C_1 with $e_1 = e_2 = 2$. In each panel, the three lines designate different mortality rates. In *C*, there are two lines for each of the two lower mortalities; the upper line represents the effect of the invader on the resident relative to the resident on itself (χ_{ij}), while the lower line represents the effect of the resident on the invader relative to the invader on itself (χ^*_{ij}). The competition coefficients are independent of the direction of displacement of utilization curve 2 relative to curve 1.

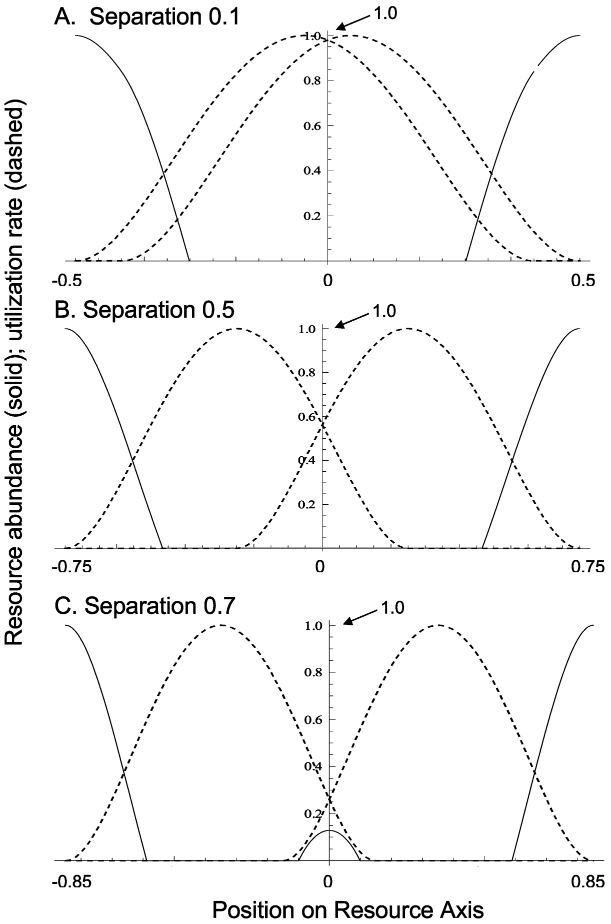

Figure 3: Resource distributions produced by three different utilization curve separations in the system from figure 2 with a mortality of $d = 0.05$. In all cases, the utilization curves have been placed so that 0 on the resource axis is exactly intermediate between the two curves. The utilization curves (*dashed lines*) have been rescaled so their maximum value is 1. *A–C* show increasing separations of the curves.

rations, sympatry completely eliminates one of the two "tails" of extant resources.

Another property of α_{ij} and β_{ij} in figure 2 is that competition increases with mortality at low separations and decreases with mortality at high separations. Both phenomena are explained by the increase in the range of extinct resources as mortality declines. At low niche separation and low mortality, overlapped resources are often weighted by 0 because they are the most heavily used. At high niche separation and low mortality, the extinct resources are in the nonoverlapped category (see fig. 3*C*), which reduces the denominator of equation (2b) without affecting the numerator, thus increasing β_{ij} relative to cases with higher mortality. The value of β_{ij} is always less than or equal to the value of α_{ij}. This is because α_{ij} is influenced by the larger competitive effects that apply when species densities are very unequal as well as the effects that apply close to the sympatric equilibrium.

The competition coefficients at invasion, χ_{ij} and χ^*_{ij}, are also sensitive to consumer mortality, as shown in figure 2*C*. At a mortality >0.2, the strength of competition is independent of which species is the invader and which the resident ($\chi_{ij} = \chi^*_{ij}$) because all resources are present at positive densities. This equality is broken when the consumer mortality rate is low enough that some resources become extinct ($d = 0.15$ and $d = 0.05$ in fig. 2*C*). For these low mortalities, the effect of the invader on the resident relative to the resident's impact on itself (fig. 2*C*, *upper line*) can increase and reach levels much greater than 1 with increasing separation of utilization curves. The zone of overlap of the two utilization curves includes equal ranges where the resident has a higher C than the invader and vice versa. However, many or all of the resources within that zone that are consumed at a greater rate by the (abundant) resident are extinct. Thus, for most of the extant overlapped resources, the invader has a consumption rate much larger than that of the resident. This leads to a large effect of the invader on the resident. Conversely, the effect of the resident on the invader is very small in these cases; the resident has lower consumption rates of the resources that are shared and available.

The patterns shown in figure 2 are robust to many potential changes in the model. Preventing resource extinction by adding a small rate of external immigration for all resources has little effect on any of the curves in figure 2, provided that the immigration rate is much less than the maximum per capita growth rate of the resource ($rK/4$). It is the fact that the extinct resources are not contributing to competition that drives the effects shown in figure 2, and this relative lack of impact on competition still applies when a low rate of immigration maintains these resources at low densities. Changing the shape of the utilization curve can alter some of the details of how α_{ij} and β_{ij} change with mortality (as shown in the appendix), but most phenomena shown in figure 2 appear to be robust for all symmetrical, unimodal utilization curves we have explored. Changing the assumption that conversion efficiency is identical for all resources also changes the shapes of competition-similarity relationships but does not make competition coefficients any less dependent of the level of resource depletion (P. A. Abrams, unpublished data).

Competitive interactions produced by asymmetrical resource utilization curves are predicted to be symmetrical under MacArthur's (1970, 1972) analysis. However, that is not the case for his (and our) model when resources become extinct. Figure 4 shows the same analysis as in figure 2 but uses the asymmetrical utilization function shown in figure 1. Figure 4 illustrates two significant dif-

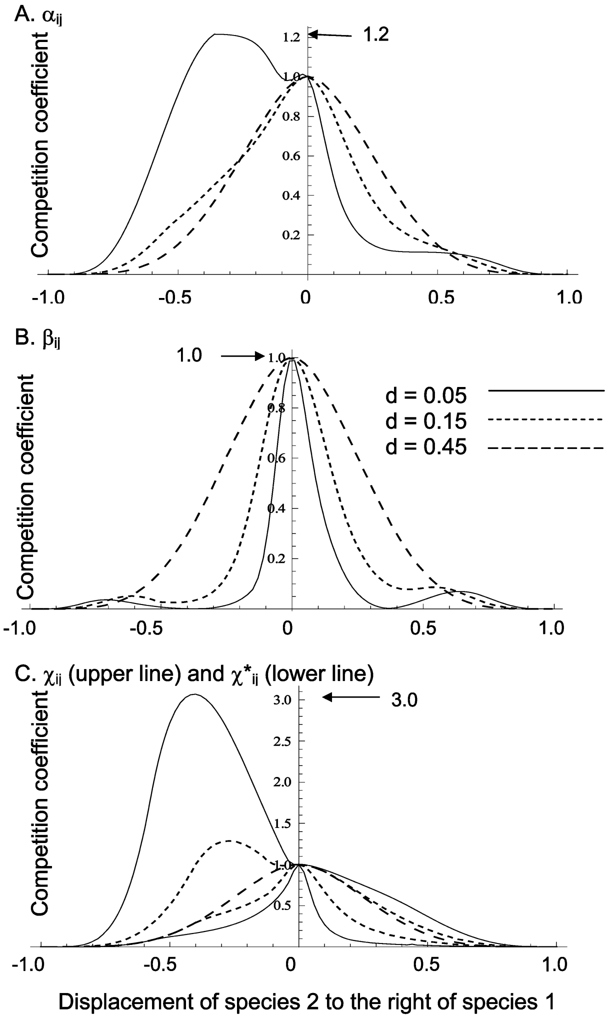

Figure 4: The three competition-similarity relationships assuming logistic growth and the asymmetrical utilization curve from figure 1 (exponents $e_1 = 3$ and $e_2 = 1$). Mortality rates and line styles are the same as in figure 2. Because the direction of displacement matters, the *X*-axis has positive and negative values, with positive values reflecting displacement of species 2 to the right of species 1 and negative values reflecting displacement of species 2 to the left of species 1. In *C*, the upper of the two lines with a given style shows the impact of the invader on the resident (χ_{ij}), and the lower line shows the impact of the resident on the invader (χ^*_{ij}).

ferences compared with the results for symmetrical utilization given by figure 2. First, when mortality is low enough that resources are excluded, the competitive effects are asymmetrical. Thus, the competitive effect of species *j* on species *i* must be illustrated for displacements of species *j* both to the left and to the right of species *i* along the resource axis. (This means that for a given pair of species, the two competition coefficients are located equal distances on either side of the origin.) A second difference between figures 2 and 4 is that in figure 4, α_{ij} does not always have a maximum at zero separation. The impact of the species located lower on the resource axis on the higher species can increase with increasing separation and can greatly exceed 1 at intermediate separations. The density of the competitor having a higher niche position is typically greatly decreased in sympatry because the highest consumption rates of the lower species coincide with the resource that contributes most to the population growth (i.e., the nonextinct resources) of the higher species. As in figure 2*C*, the coefficients χ_{ij} and χ^*_{ij} diverge when mortality is low, with the invader having a larger effect on the resident than vice versa. This is again because when the resident species *i* is abundant and the invader is rare, the largest values of $C_i(x)^2$ in the denominator of equation (2b) are associated with $W(x) = 0$ because these resources are extinct. The asymmetrical utilization curve makes χ_{ij} and χ^*_{ij} asymmetrical with respect to the direction of displacement. Low consumer mortalities and displacements of species 2 in the direction opposite the direction of utilization curve skew can produce very large effects of invader on resident. These effects can increase with increasing niche separation. For $d = 0.05$, the competition coefficient of an invader with a negative displacement of approximately -0.45 can be more than three times larger than the competition coefficient between identical species.

There are many ways of elaborating and extending the model of biotic resources considered here. The appendix considers θ-logistic resource growth with $\theta \neq 1$ (fig. A2 in the appendix), asymmetrical utilization curves that differ in their direction of their skew (fig. A4 in the appendix), and a Gaussian rather than a flat *K* function (fig. A5 in the appendix). Although all of these can produce some features that differ from the results in figures 2 and 4, they support the general conclusion that high levels of resource exploitation produce nonlinear interactions, highly non-Gaussian competition functions, and asymmetrical competition when utilization curves are asymmetric.

Abiotic Resources

In this section, we investigate the effect of abiotic (chemostat) resource dynamics on competition. Figure 5 shows the dependence of the three competition coefficients on utilization curve separation for abiotic resources assuming the same utilization function as in figure 2. The coefficients α_{ij} and β_{ij} (fig. 5*A*, 5*B*) differ from a Gaussian function less than when resource growth is logistic. More specifically, there is no longer any range of niche overlaps where these coefficients stay constant or increase with decreasing niche overlap. This is because abiotic resources cannot be driven extinct, so the weighting factors $W(x)$ typically have a smaller range of magnitudes. As with logistic growth,

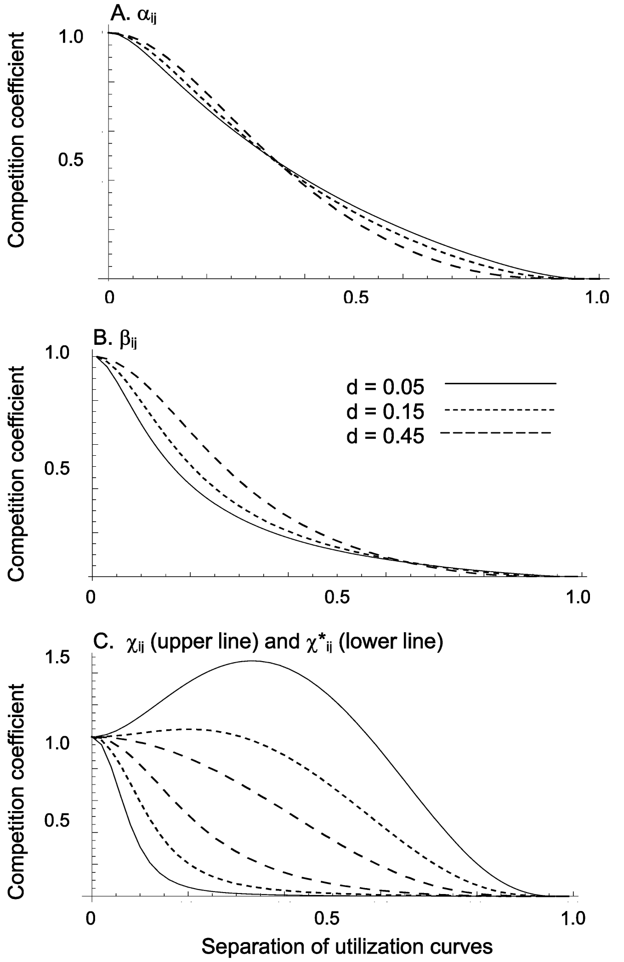

Figure 5: Competition-similarity relationships for three measures of competition in a system with abiotic rather than logistic resource growth; otherwise, the assumptions are identical to those in figure 2.

increasing mortality reduces competition coefficients when resource utilization curves are only slightly shifted but increases competition when there is greater niche separation. Another feature shared with the logistic resource model is that at low mortalities, the local formula for the competition coefficient β_{ij} declines much more rapidly with increasing separation than does the corresponding global formula for α_{ij}. The competition-similarity relationships measured at invasion, χ_{ij} and χ^*_{ij} (fig. 5*C*), have many of the features shown for the logistic model in figure 2*C*. In both figures, the weighting factors increase the competition coefficient of the invader on the resident and decrease that of the resident on the invader. However, in the abiotic resource model, χ_{ij} and χ^*_{ij} differ from each other even at high mortality rates (shown for $d = 0.45$). This is because for abiotic resources, unlike logistic resources, the impact of a particular resource on the competition coefficient is a continuously decreasing function of the level of depletion. Asymmetry in the resource utilization function has most of the same features in this case as in the corresponding results for logistic resources, shown in figure 4; the corresponding figure for abiotic resources is shown in the appendix (fig. A3).

Discussion

MacArthur's (1968, 1970, 1972) analysis of consumer species competing for an array of logistically growing, nutritionally substitutable resources seemed to provide a justification for using Lotka-Volterra equations to describe exploitative competition. His derivation also suggested that the competition coefficient in the Lotka-Volterra model could be calculated from resource utilization curves using equation (2a) (this article), which often leads to an approximately Gaussian relationship between the separation of utilization curves and the competition coefficient. MacArthur's results became the ecological foundation of most work on evolutionary responses to competition, beginning with that by Roughgarden (1976) and Slatkin (1980), and continuing to the present day (Otto and Day 2007). Lotka-Volterra models also underlie a good deal of theory on the relationship between diversity and stability (Ives and Carpenter 2007).

In this article we have analyzed a family of explicit consumer-resource models very similar to those used by MacArthur (1970). However, in contrast to MacArthur, we allowed for consumer efficiencies that led to the extinction of the most heavily used part of the resource spectrum, and we investigated nonlogistic resource growth. Our results show that each of these simple and reasonable deviations from MacArthur's original assumptions destroys the linearity of competitive effects (competition coefficients independent of density) that characterizes the Lotka-Volterra model. The resulting effects of initial densities and size of the density perturbation on the calculated magnitude of the competition coefficients are far from trivial when consumer efficiency is high. Simply changing the initial densities of the two species can often change at least one of the two competition coefficients manyfold and can change the coefficients by an absolute amount much greater than 1. Because the competition coefficient gives the response of the population size of one species divided by the perturbation in the population of the competing species that caused that response, this result implies that accurate predictions of population responses at one set of densities generally cannot be made on the basis of effects measured at other densities. The same biological features that lead to nonlinearity also lead to competition-similarity relationships that are characterized by competition increasing as niche separation increases. When consumer efficiency is high, competition-similarity relationships can be multimodal and usually cannot be adequately approximated by a Gaussian function. Here, we have modeled high efficiency by low mortality, but high resource carrying capacities, high mean consumption rates, or high conversion efficiencies have equivalent effects (results for a two-resource system in Abrams 1998, 2001).

Several generalizations apply to the type of nonlinearities that occur in consumer-resource models such as those considered here. The comparison of α_{ij} and β_{ij} shows that a small change in the density of one species at an equilibrium with similar abundances of both species usually produces a much smaller change in the population of the second species than does a larger change in abundance. Studies involving species removal may therefore overestimate competitive effects near a sympatric equilibrium, while studies examining systems near equilibrium are likely to underestimate the consequences of removal. Similarly, extrapolation of an observed large per capita impact of a rare introduced competitor on a resident is likely to overestimate its ultimate effect on the resident. Our analysis also predicts that greater consumer efficiency, which can arise because of low mortality, increases the nonlinearity of competitive effects and usually increases their asymmetry if utilization curves are asymmetric. Lower mortality can either increase or decrease the competition coefficient, contrary to the common assumption that competition is generally increased by low consumer mortality (e.g., Gallet et al. 2007). "A Strongly Peaked Resource Utilization Curve: Biotic Resources" in the appendix shows that unimodal responses of the competition coefficient to mortality are also possible.

The conclusion that heavily exploited resources should be weighted lightly in calculating competition coefficients applies to all cases of pure biotic (self-reproducing) resources because they are subject to extinction at high exploitation rates. Exploitation of resources in models with abiotic growth or biotic growth with $\theta < 1$ reduces their contribution to competition, regardless of the level of exploitation. This is also true of most models where growth is a combination of biotic and abiotic functions (e.g., Turchin and Hanski 2001).

The high consumer efficiencies that produce the largest nonlinearities in our models do not appear to be rare. For example, protist-bacteria predator-prey systems in the laboratory typically have equilibrium prey densities three orders of magnitude below prey carrying capacity (Holyoak and Lawler 1996), and Shurin et al. (2002) found an average 17-fold reduction in herbivore abundance following predator introduction in field studies of trophic cascades in lentic communities. The limited number of empirical measurements of competitive effects using different pairs of consumer densities suggests that nonlinear relationships are common. Relatively few experiments have measured competition at multiple densities, but those that have been carried out have usually shown that competitive effects are highly nonlinear (Ayala et al. 1973; Pomerantz et al. 1980). These, and the fact that nonlinearity has been produced by all of the consumer-resource models analyzed here (and earlier ones; Schoener 1974, 1976; Abrams 1975, 1977, 1980*a*, 1980*b*, 1998, 2001), make a strong case for expecting nonlinearity. While nonlinearity per se is hardly surprising, the magnitudes and specific nature of the nonlinearity shown here do not seem to have been appreciated.

In most competition theory, asymmetry in competition coefficients is assumed to be due to one species having a higher mean consumption rate than a second species (e.g., Slatkin 1980; Taper and Case 1992). The results here suggest that asymmetry in competition coefficients can also arise because of unequal abundances (e.g., an invader and a resident). Asymmetry also characterizes all measures of competition (even those involving equal consumer densities) when the utilization curves are asymmetrical and consumer efficiency is high. This may contribute to the high frequency of asymmetric interactions observed in nature (Schoener 1983).

Nonlinearities and their dependence on mortality (efficiency) have important implications for understanding competitive communities. There have already been several demonstrations that non-Gaussian competition functions significantly change coexistence conditions in multispecies systems and also change the evolutionary responses of resource-related characters of competitors (Ackermann and Doebeli 2004; Gyllenberg and Meszéna 2005; Meszéna et al. 2006; Szabó and Meszéna 2006; Doebeli et al. 2007; Pigolotti et al. 2007; Leimar et al. 2008). To our knowledge, published theory that examines non-Gaussian functions still assumes that competition decreases with increasing niche separation. Our results suggest that decreasing relationships are not universal; the implications of nonmonotonic relationships for multispecies coexistence are unknown. Theory on indirect effects in multispecies competition has generally been based on the Lotka-Volterra model (Lawlor 1979) and is likely to be misleading for competition in consumer-resource systems. The asymmetry of invader and resident effects is expected to affect theory on how competition influences range limits (Case and Taper 2000).

Elsewhere we show that the nonlinearities demonstrated here usually produce unimodal relationships between the level of consumer mortality and the strength of disruptive selection generated by intraspecific competition (Abrams et al. 2008). MacArthur's analysis instead predicts flat or monotonically decreasing relationships (Ackermann and Doebeli 2004). The limiting similarity of competitors

(MacArthur and Levins 1967; Abrams 1983) is also strongly affected by phenomena explored here (Abrams and Rueffler 2008). Finally, the lower competition that accompanies high similarity and high efficiency in our models suggests that investigations of the relationship between species diversity and stability based on the Lotka Volterra model (e.g., Ives and Hughes 2002: Loreau et al. 2003; Ives and Carpenter 2007) may have overestimated the instability of many-species communities.

We are not advocating that the Lotka-Volterra model be abandoned completely. MacArthur's assumptions are likely to be approximately satisfied in some systems, and the Lotka-Volterra model is clearly the simplest method for incorporating competition into a multispecies model when the exact nature of that competition plays a small role in the analysis (see, e.g., Abrams and Nakajima 2007). However, results that can be produced by consumer-resource models only under very special circumstances should not form the basis of general theory on exploitative competition. In closing, it should be added that resource depletion is not the only factor producing nonlinear exploitative competition. Other sources of nonlinearity include nonlinear consumer functional responses (Abrams 1980*b*) and adaptive choice of resources (Rosenzweig 1981, 1991; Abrams 1987).

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