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# Coexistence and limiting similarity of consumer species competing for a linear array of resources

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**Abstract.** Consumer–resource systems with linear arrays of substitutable resources form the conceptual basis of much of present-day competition theory. However, most analyses of the limiting similarity of competitors have only employed consumer–resource models as a justification for using the Lotka–Volterra competition equations to represent the interaction. Unfortunately, Lotka–Volterra models cannot reflect resource exclusion via apparent competition and are poor approximations of systems with nonlogistic resource growth. We use consumer–resource models to examine the impact of exclusion of biotic resources or depletion of abiotic resources on the ability of three consumer species to coexist along a one-dimensional resource axis. For a wide range of consumer–resource models, coexistence conditions can become more restrictive with increasing niche separation of the two outer species. This occurs when the outer species are highly efficient; in this case they cause extinction or severe depletion of intermediate resources when their own niches have an intermediate level of separation. In many cases coexistence of an intermediate consumer species is prohibited when niche separation of the two outer species is moderately large, but not when it is small. Coexistence may be most likely when the intermediate species is closer to one of the two outer species, contrary to previous theory. These results suggest that competition may lead to uneven spacing of utilization curves. The implications and range of applicability of the models are discussed.

**Key words:** coexistence; competition coefficient; consumer–resource system; interspecific competition; limiting similarity; Lotka–Volterra model; nonlinearity.

## INTRODUCTION

The concept of limiting similarity, as introduced by MacArthur and Levins (1967), states that two competitors have to be separated by some minimum distance in a one-dimensional niche space for coexistence with a third, intermediate competitor to be possible. However, subsequent work (May 1974, Roughgarden 1974) on similar Lotka–Volterra models showed that this conclusion depended on the assumption that the intermediate species had the same carrying capacity as the two outer species. Permitting a greater carrying capacity of the intermediate species allowed coexistence for any degree of separation of the outer species, but the range of relative carrying capacities permitting coexistence was very narrow when the niche separation of the outer species was relatively small. (Niche separation is measured as the distance on the resource axis between the means of the two utilization curves.) This result suggested that the limiting similarity of MacArthur and Levins was not an absolute prohibition on coexistence of sufficiently similar species. The idea of an absolute limit

(where coexistence was impossible for small enough niche separations) was given another justification by May and MacArthur (1972). They added stochasticity to the same Lotka–Volterra system (see also May 1973, 1974), and suggested that environmental variability made indefinite coexistence impossible for sufficiently small niche separations of three or more species arranged along a one-dimensional niche axis. However, subsequent work again showed that none of these models had rigorously demonstrated the existence of a firm limit beyond which coexistence was impossible, or even highly unlikely (Abrams 1975, 1976, 1977, 1980*b*, 1983, Turelli 1978, 1981). In particular, the analysis of stochastic models of May and MacArthur had made unwarranted assumptions about the applicability of linear approximations that led directly to the conclusion of an absolute limit to similarity. While these reanalyses of the May–MacArthur models have gone unchallenged in the literature, they have been ignored by some recent authors who have discussed limiting similarity (e.g., Scheffer and van Nes 2006, May et al. 2007). Thus, the current state of the theory of coexistence of three competitors along a one-dimensional niche axis may be summarized as follows: Coexistence of all three is possible for any separation of the outer species in the array, but coexistence occurs over a narrower range of consumer carrying capacities (i.e., efficiencies) as the niche separation of the outer species become smaller.

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Because there did not appear to be any absolute limit to similarity for competitors that were linearly arrayed in niche space, Abrams (1983) proposed that the term “limiting similarity” should instead be used to describe the system-specific relationships between similarity and the range of conditions (parameter values) allowing coexistence. This conception of limiting similarity will be described here as a similarity–coexistence relationship. Regardless of how the term “limiting similarity” is defined, there seems to be nearly universal agreement that the range of conditions (i.e., the extent of parameter space) allowing coexistence decreases monotonically with decreasing niche separation of adjacent consumer species (e.g., May 1974, Abrams 1983). A recent analysis of many-species coexistence concluded that, while an absolute limit did not exist, “... the idea of shrinking the possibility of coexistence with increasing similarity is general” (Mészéna et al. 2006:79).

MacArthur realized that it was necessary to determine whether this model was consistent with more mechanistic models of resource consumption. Shortly after his seminal work with Levins, he derived a Lotka–Volterra model as an approximation to an explicit consumer–resource model (MacArthur 1968, 1970, 1972). This allowed him to relate the competition coefficients of the Lotka–Volterra model to the degree of overlap in the spectrum of utilized resources. The importance of a consumer–resource approach was reemphasized by several early studies showing that different consumer–resource models could lead to different conclusions regarding coexistence and similarity–competition relationships than did the MacArthur models (Abrams 1975, 1977, Schoener 1976). In his derivation, MacArthur made the tacit assumption that consumers were not efficient enough to cause extinction of any resources. It was pointed out by Hsu and Hubbell (1979) and Abrams (1980b) that such extinctions could occur. Subsequent work showed that, when resources do become extinct, many predictions of the Lotka–Volterra model are changed (Abrams 1998, 2001, Abrams and Nakajima 2007, Abrams et al. 2008a, b). However, the impact of such exclusion on the question of limiting similarity in a continuous linear niche space has not been examined. In this article we will use consumer–resource models similar to those introduced by MacArthur (1968, 1970, 1972) to determine: (1) whether an absolute limit to similarity exists; and (2) whether the range of consumer parameters allowing coexistence always declines as consumer species become more similar in their resource use. We pay particular attention to scenarios with high consumer efficiencies. Following MacArthur and Levins (1967), we examine cases with two or three competing consumer species.

#### THE MODEL

Most of our analysis treats a consumer–resource model nearly identical in form to the one considered by MacArthur (1970, 1972); the model has a linear array of

three consumer species where the two outer species are equivalent except for the position of their utilization curves. A continuous linear array of logistically growing resources is used by the consumer species, each of which has independent linear functional responses to the resources it consumes. The utilization curve plots the relative value of the slope of a given consumer’s functional response to each resource against the resource parameter that determines that slope (e.g., size of a food item); here the utilization function is denoted by  $C$ , and resource position by  $x$ . Utilization curves having several different shapes are explored. We extend previous work by considering some systems in which resource growth is not logistic. For all models, the dynamics of consumers and resources at position  $x$  are described by

$$\frac{dR(x)}{dt} = f_x[R(x)] - \sum_{i=1}^3 C_i(x, y_i) N_i R(x) \quad (1a)$$

$$\frac{dN_i}{dt} = N_i [b_i \int C_i(x, y_i) R(x) dx - d_i]. \quad (1b)$$

Here  $R(x)$  is the density of resources at position  $x$  on the resource axis, and  $N_i$  is the density of consumer species  $i$ .

The resource use phenotype of consumer  $i$  is  $y_i$ , which denotes the position of its utilization curve on the resource axis. The resource utilization curve for consumer species  $i$  is  $C_i(x, y_i)$ , its resource conversion efficiency is  $b_i$  (assumed identical for all resources), and its per capita death rate is  $d_i$ . The integral in Eq. 1b is taken over the range of resource used by consumer species  $i$ , and it represents the total resource intake rate. The resource at position  $x$  has an instantaneous population growth rate in the absence of consumption that is described by  $f_x$ . In MacArthur’s model (1970), and in the initial analysis here,  $f_x$  is assumed to be a logistic function with parameters that are independent of  $x$  (i.e.,  $f_x = rR(x)[1 - R(x)/K]$ ). The identical growth functions allow both  $K$  and  $r$  to be scaled to one by measuring resource density in units of  $K$  and time in units of  $1/r$ . Throughout this article,  $y_i$  gives the smallest resource (the minimum  $x$ ) that is utilized by consumer  $i$ , and the utilization curve is only positive for  $x$  between  $y_i$  and  $y_i + 1$ . In this analysis, the consumer species are assumed to have identical shapes for their utilization curve, so we drop the subscript  $i$  on  $C$ . In most of the analysis, the utilization curve is given by the bell-shaped function,  $C(x, y_i) = 30(x - y_i)^2(1 - (x - y_i))^2$  for values of  $x$  between  $y_i$  and  $y_i + 1$ ;  $C = 0$  elsewhere. The curve is scaled (here by a factor of 30) so the total area under the curve is one; this makes the standard deviation  $\sim 0.189$ . An alternative utilization curve with a parabolic shape is also studied; this is given by  $C(x, y_i) = 6(x - y_i)(1 - (x - y_i))$  for values of  $x$  between  $y_i$  and  $y_i + 1$ , and  $C = 0$  elsewhere (the standard deviation is  $\sim 0.224$ ). We avoid the more commonly used Gaussian curves because of the biological implausibility of the long tails of this function (Wilson 1975), although we have repeated all of the

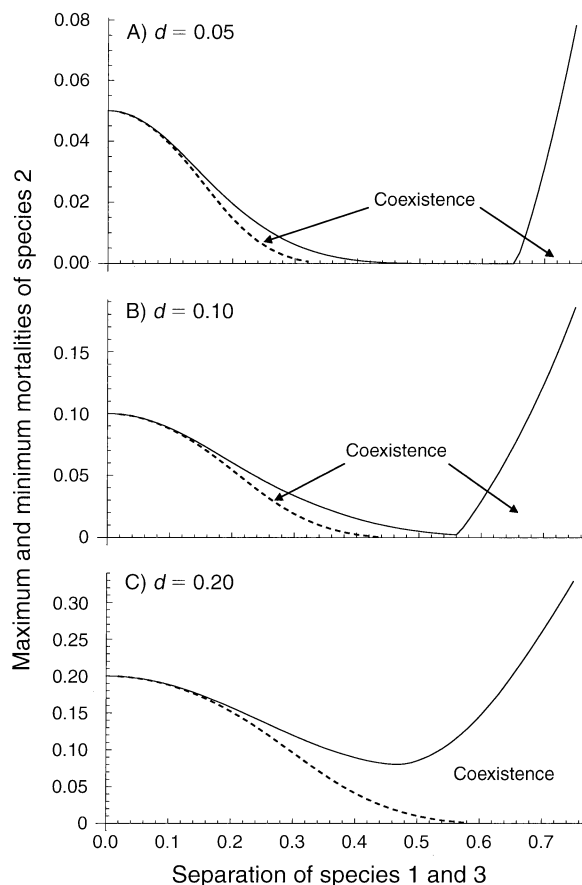


FIG. 1. The maximum (solid lines) and minimum (dashed lines) mortality rates of an exactly intermediate species (species 2), which allow it to coexist with two otherwise equivalent species (species 1 and 3) having the resource utilization curve separation given by the  $x$ -axis. The calculations assume logistic resource growth, and all consumer species have a bell-shaped utilization curve with a range of one unit on the resource axis [ $C(x, y_i) = 30(x - y_i)^2(1 - (x - y_i))^2$  for values of  $x$  between  $y_i$  and  $y_i + 1$ ;  $C = 0$  elsewhere]. Each panel of the figure illustrates a different mortality rate for the outer two species. The coexistence ranges for mortalities higher than 0.20 are similar in shape to those shown in panel C. Per capita mortality,  $d$ , is measured as a fraction of the maximum mortality allowing existence in the absence of competition. Niche separation is measured relative to the width (range) of the utilization curve for a given species.

work using a truncated Gaussian curve with a standard deviation of 0.189. The assumptions that  $C$  is independent of  $i$  and that the nonzero range of  $C$  is finite allow the niche “separation” between species  $i$  and  $j$  to be measured by  $|y_i - y_j|$ . The above assumptions about  $K$ ,  $b$ , and  $C$  imply that  $d < 1$  is required for a consumer to exist, since  $b$  (here set equal to one) multiplied by the maximum intake rate (the integral of  $CK$ , which is one) must be greater than the per capita mortality rate. These assumptions also imply that  $d$  is equal to the ratio of the per capita resource intake rate when the consumer population is at equilibrium and the intake rate when

the consumer population density is close to zero. Therefore,  $d$  measures the minimum resource intake required for population growth, and a low  $d$  implies a high efficiency of resource use.

We will quantify the ability of a species to coexist with others by the range of mortality rates that allows mutual invasion of the intermediate and outer species; this range will be referred to as the “coexistence bandwidth” (following Armstrong 1976; see also Abrams and Holt 2002). Mortality divided by conversion efficiency gives the resource intake rate producing zero population growth, so either parameter would yield the same measure of coexistence bandwidth. Here we only provide results using the mortality rate. In most of the analysis, we assume the two outer consumer species have an identical death rate,  $d_1$ , and the middle species has a death rate  $d_2$ . The coexistence bandwidth is then the range of values of  $d_2$  that allow coexistence of all three consumers. Values of  $d_2$  that lie above this range result in exclusion of the middle species, while  $d_2$  below this range produces exclusion of both outer species. An absolute limit to similarity occurs if the coexistence bandwidth is zero for a range of niche separations of the outer species.

MacArthur and Levins (1967) examined coexistence with an intermediate species whose utilization curve was equidistant from each of the two resident species. They assumed this was the point at which coexistence was most likely to occur. Here we explore this scenario, but also explore the full range of niche positions for the intermediate species. We calculated the equilibrium resource and consumer densities numerically using Mathematica 6.0.0 (Wolfram 2007). Results by Chesson (1990) and Haygood (2002) show that these equilibria will always be globally stable. These findings also justify the mutual invasion approach we use to determine coexistence.

## RESULTS

Our results show how the coexistence bandwidth is affected by the mortality rate of the outer consumers and by the functional forms of both the utilization curves and resource growth. For logistic resource growth, we are particularly interested in determining the impact of death rates that are low enough to produce resource exclusion. Fig. 1 shows the coexistence bandwidth for logistic resources that have identical growth parameters, and for consumers that have the bell-shaped utilization curve described in the paragraph following Eq. 1. The  $x$ -axis of the figure gives the niche separation of the two outer species. The middle species is assumed to be exactly intermediate between the outer species. The three panels are based on different mortality rates ( $d = 0.05, 0.10$ , and  $0.20$ ) for the outer species. In Fig. 1A the coexistence bandwidth is zero when the two outer species have resource separations between  $\sim 0.57$  and  $0.65$ ; for this range of separations it is impossible for the exactly intermediate species to exist regardless of its

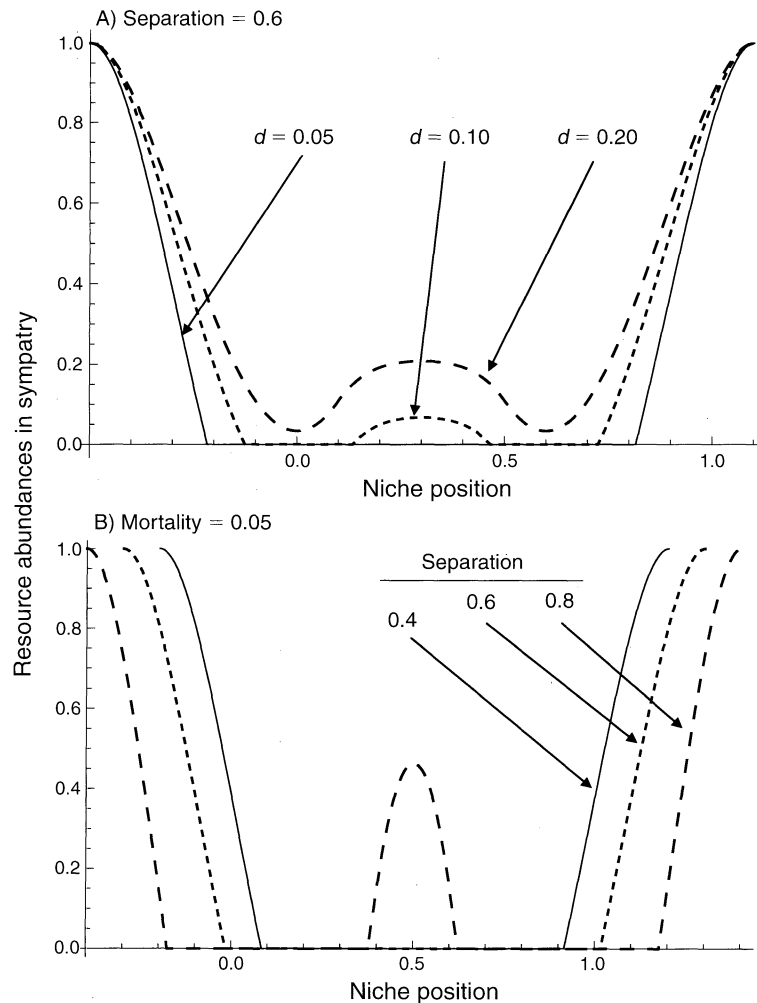


FIG. 2. The equilibrium resource abundances when the two outer consumers are at equilibrium in sympatry for the system described in Fig. 1. The outer consumers are located symmetrically on either side of the niche position at the middle of the  $x$ -axis (0.3 in Panel A and 0.5 in Panel B). Panel A assumes a niche separation of 0.6 and illustrates resource densities for three different mortality rates. Panel B assumes a mortality of  $d = 0.05$  and presents resource densities for three different separations. In Panel A, only the mortality of 0.05 produces a range of extinct resources with a span  $> 1$  on the resource axis. In Panel B, only a separation of 0.6 produces this result. Resource abundance is measured relative to a maximum abundance of 1. See Fig. 1 for an explanation of niche separation and mortality.

efficiency. If we assume a truncated Gaussian curve with the same standard deviation, this range is reduced to 0.58–0.63. Fig. 1B, C show that the pattern in Fig. 1A is dependent on low mortalities (high efficiencies). Panels B and C indicate that coexistence of the intermediate species is possible for some range of mortalities of the middle species, although that range may be quite narrow for some separations of the outer species (e.g., separation close to 0.55 in Fig. 1B, which assumes  $d = 0.1$ ).

Fig. 2 shows the distributions of resource abundances produced by the two outer species; these distributions reveal how the coexistence bandwidths in Fig. 1 arise. Fig. 2A, which assumes a niche separation of 0.6, shows the resource abundance distribution for three mortality rates. When  $d = 0.05$  resources are extinct over an interval of length 1.08 centered on the midpoint between

the two outer consumers. Extinction is due to the high combined consumption of these resources by the two outer consumer species. An exactly intermediate consumer would therefore not have any resources available within its range; this condition is obviously sufficient to prevent invasion of the middle species. The other two consumer mortality rates illustrated in Fig. 2A allow positive densities for a range of intermediate resources, which permits invasion by an intermediate consumer that has a low enough mortality rate. For a low mortality of the outer consumers (e.g.,  $d = 0.05$ ), their niche separation determines which resources are extinct at equilibrium. If the utilization curves of the outer species are separated by  $< 0.57$  units, then the interval of extinct resources is  $< 1$  in width. In this case a central species can invade and survive on the resources available

TABLE 1. Mortalities and niche separations producing an absolute limit to similarity for two different utilization curves  $C(x, y)$ .

Mortality rate	Separations producing ranges of extinct resources >1 unit in width	Maximum width of range of extinct resources
Model 1; bell-shaped; $C(x, y) = 30(x - y)^2[1 - (x - y)]^2$		
0.06	0.63	1.0
0.05	0.57–0.65	1.08
0.025	0.43–0.73	1.30
0.0125	0.33–0.79	1.46
Model 2; parabolic; $C(x, y) = 6(x - y)[1 - (x - y)]$		
0.07	0.67–0.68	1.01
0.05	0.53–0.74	1.21
0.025	0.35–0.82	1.47
0.0125	0.24–0.88	1.64

Note: Niche separation is measured as the distance on the resource axis between the means of the two utilization curves. See *The model* and the *Results* sections for further explanation.

in the tails of its utilization curve. If the two outer species are separated by an interval longer than 0.65, an isolated range of extant resources exists around the midpoint between the ranges of the two outer species. This central set of resources allows invasion of a sufficiently efficient middle species. Thus, 0.57–0.65 is the range of outer-curve separations for which there is an “absolute” limit to similarity for an exactly intermediate species when  $d=0.05$ . Fig. 2B examines the impact of consumer niche separation on the resource abundance distribution, given  $d=0.05$ . Too small a separation (0.4) only produces a relatively short interval of the resource axis where resources are extinct, while too large a separation (0.8) allows the existence of resources that are close to midway between the maxima of the two utilization curves.

Coexistence becomes more difficult with increasing niche separation when the upper boundary of the coexistence region decreases more rapidly than the lower boundary. In Fig. 1 this occurs for separations large enough that the lower boundary is close to zero (i.e., when the outer species are relatively immune to exclusion by the intermediate one). The upper boundary decreases because, as the separation of the outer species expands, the increase in total population size of the two outer species exceeds the decrease in the sum of their utilization constants,  $C$ . This phenomenon is reversed at high separations, when the population sizes of the outer species approach their carrying capacities. The lower boundary of the coexistence region hits zero (and therefore cannot decrease further) when each outer species is able to exist on the resources that it uses exclusively, and therefore cannot be excluded by the intermediate species, regardless of its efficiency. Under previous analyses of the Lotka-Volterra model (e.g., May 1973, 1974), the lower boundary of the coexistence region always decreased more rapidly than the upper boundary at low niche separations. In addition, neither boundary reached zero. These features are consequences of the inability of the Lotka-Volterra model to reflect

resource exclusion and the absence of exclusive resources when the utilization curves have infinite tails.

The qualitative features of Fig. 1 do not depend sensitively on utilization curve shape. Similar results for truncated Gaussian curves were mentioned in the first paragraph of the *Results* section. Table 1 presents some results comparing the utilization curves used in Figs. 1 and 2 with results for the parabolic utilization curve given previously. For both utilization curves, the consumer mortality must be lower than some threshold value for the interval of extinct resources to be wider than the range of the utilization curve for the intermediate species; the length of the interval increases with decreasing mortality. Similarly, for both utilization curves, the range of niche separations for the outer species resulting in extinct resource over a sufficient interval increases as the mortality rate of the outer species decreases. The figures presented in Table 1 show that the parabolic utilization curve produces an absolute limit to similarity over a wider range of mortality rates and, for a given mortality rate, produces limits over a wider range of consumer niche separations. The curvature of the utilization function determines how far apart the two outer curves must be before the resources halfway between the maxima of the two curves have positive densities. Curves characterized by negative second derivatives, like the parabola, increase the range of niche separations where the resources are extinct (Table 1; Abrams et al. 2008a). Conversely, if the utilization curves have positive second derivatives at all positions on the resources axis, as in the Laplace distribution (Roughgarden 1974) and similar distributions in Abrams et al. (2008b), then much lower mortalities are required to produce an absolute limit.

The limit to similarity at low mortality rates reflected in Fig. 1A and Table 1 differs significantly from the absolute limit predicted by much of the previous literature. In the present case, coexistence of two competitively similar but displaced “outer” consumer species with an exactly intermediate consumer is possible when the two outer species have utilization curves that

are either very close to each other, or highly displaced, but not for intermediate separations. In other words, there is both a limiting similarity and a limiting dissimilarity of the outer species where coexistence with an exactly intermediate third species becomes possible. The coexistence bandwidth at low to moderate separations is rather narrow in all panels of Fig. 1, but it is difficult to translate this into a probability of coexistence of three species. The range of mortalities allowing coexistence at some moderately small separations represents a significant fraction of mortality rate for the outer species, suggesting that coexistence is not difficult. However, the upper limit of that range is generally much lower than mortality of the outer species (e.g., for a niche separation of 0.25 in Fig. 1A). This suggests that an intermediate species that is able to coexist is not likely to be closely related to the outer species.

So far we have only considered coexistence when the intermediate species is exactly midway between the outer species. We now examine situations when the intermediate species has a utilization curve closer to that of one of the two outer species. Numerical results show that coexistence is always possible for some range of niche positions of the intermediate species. Fig. 3A is based on the same system as Fig. 1A ( $d = 0.05$ ) for a separation of 0.6 between the two outer species. However, Fig. 3A shows that three-species coexistence is possible when the utilization curve of the intermediate species is located asymmetrically with respect to the outer species. This figure is representative of all the examples we have examined in which an equidistant intermediate species is always excluded. In all of these cases, coexistence is possible for a range of niche separations close to either resident, and impossible for a range of separations close to the midway point between the two outer species. An asymmetrical location close to one outer species allows the intermediate consumer access to some nonextinct resources. Because it has fewer resources available, the intermediate species must be more efficient than the outer species ( $d_2 < d_1$ ). However, the maximum bandwidth within the zone of coexistence is characterized by  $d_2$  much lower than  $d_1$ , again suggesting that a coexisting intermediate species would usually not be closely related to the outer ones. Fig. 3B presents the range of mortalities allowing coexistence calculated assuming that no resources go extinct. Here the bandwidth is always nonzero and is maximized at the midway point (0.30). Because the consumer carrying capacities are given by  $1 - d$  in this example, the distance between the two lines in Fig. 3B also describes the width of the range of carrying capacities allowing coexistence in the Lotka-Volterra model of MacArthur and Levins (1967) when the outer species have a carrying capacity of 0.95.

In most previous work on limiting similarity, similarity has been measured using " $d/w$ ," the ratio of the separation of utilization curves to their standard

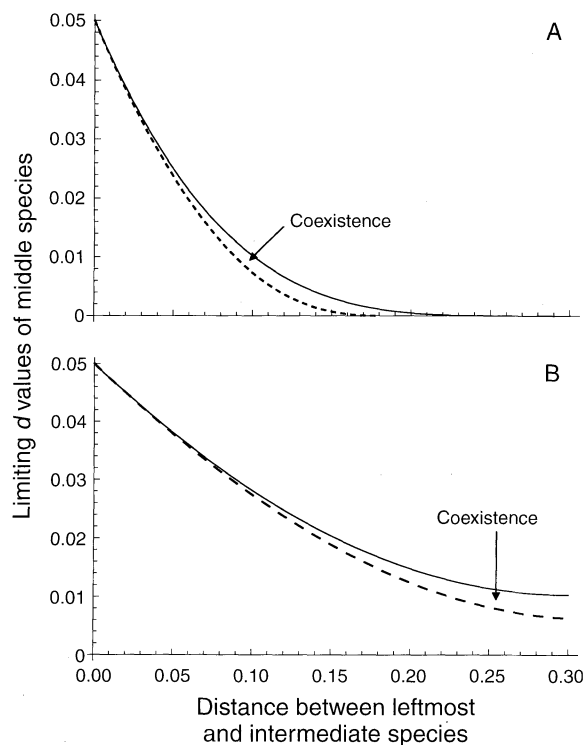


FIG. 3. (A) The limiting mortalities of an intermediate species that allow coexistence of three species, plotted as a function of the separation of the leftmost species and the intermediate species. The two outer species have resource utilization curves separated by a distance of 0.6 on the resource axis and have per capita mortality rates of 0.05. All three species have the same bell-shaped utilization curve assumed in Figs. 1 and 2. Coexistence is possible for per capita mortality rates of the intermediate species that lie between the solid and dashed curves. An identical figure describes coexistence boundaries when the intermediate species is closer to the rightmost resident species. Coexistence is impossible for any separation between  $\sim 0.25$  and  $0.3$ , although the persistence boundaries are so narrow for separations between  $0.2$  and  $0.25$  that coexistence is biologically unrealistic for such cases. (B) The corresponding limits on  $d$  if calculation were based on the MacArthur and Levins (1967) Lotka-Volterra model, for which  $K = 1 - d$ . This implicitly assumes that the resources all have positive densities, which is not the case for  $d = 0.05$ . Because  $K = 1 - d$ , the width of the interval of mortalities allowing coexistence is exactly equal to the width of the interval of carrying capacities. Panel B implies that, when mortality is high enough that all resources persist, the coexistence bandwidth is greatest when the middle species is equidistant from the two outer species. Distance is niche separation, measured relative to the width of a single utilization curve. Per capita mortality,  $d$ , is measured relative to the maximum mortality that allows existence of a single consumer species.

deviation. May (1973, 1974) suggested the rough rule that  $d/w > 1$  was required for coexistence to be likely, and that rule is still widely quoted (e.g., Scheffer and van Nes 2006, May et al. 2007). Assume that coexistence of all three species considered here is defined as "likely" if the range of mortalities of the intermediate species that allows coexistence is at least 20% as large as mortality of the outer species. Given the standard deviation of 0.189

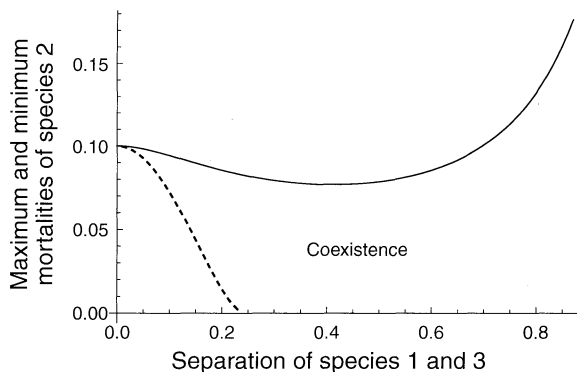


FIG. 4. The coexistence bandwidth under the same assumptions as in Fig. 1B but for a system with abiotic rather than logistic resource growth. The resource growth equation has parameters  $I = 1$  and  $E = 1$ , for input rate and exit rate. The outer consumer species both have a mortality  $d = 0.10$ . The coexistence bandwidth increases from a separation of zero to  $\sim 0.23$  units on the resource axis, at which point the lower boundary of  $d_2$  reaches zero. At this point, the bandwidth is 0.0832 units of mortality. At larger separations, the intermediate species cannot exclude the outer species regardless of its mortality. The bandwidth then decreases until the maximum  $d_2$  reaches its minimum value of 0.0769 at a separation of 0.41. The bandwidth increases for larger separations but does not exceed the value at a separation of 0.23 until separation reaches 0.58. See Fig. 1 legend for definitions of niche separation and mortality,  $d$ .

for the utilization curve used in Fig. 1, the minimum separation of the two outer species required for likely coexistence represent  $d/w$  measures of 3.55, 3.12, and 2.17 in Fig. 1A, B, C, respectively. Following invasion by the intermediate species, these correspond to interspecies  $d/w$  values of 1.78, 1.56, and 1.08. Only the spacing for Fig. 1C (where no resources went extinct) corresponds well to the traditional rule.

Before leaving the case of logistic resources, we discuss coexistence in a system having only two consumer species. In a two-species system with utilization curves having finite, nonidentical ranges, each species has some exclusively utilized resources. Persistence on this range of exclusively utilized resources is always possible once mortality is sufficiently low. Thus, for two species having very low mortality rates and a moderate separation of their utilization curves, exclusion of one species cannot be produced by lowering the death rate of the other. Furthermore, there is no absolute limit to similarity; there is always some range of mortality rates of one species allowing coexistence, given a fixed mortality of the other species. It is also true that the bandwidth increases with increasing niche separation in this case.

#### Model variations

Here we consider three variations of the framework introduced in the section titled *The model* to determine whether the results are robust to these changes in the form of the model.

*Nonuniform carrying capacity function.*—So far, we have assumed a uniform resource spectrum, but it is more common to assume that resource productivity is a unimodal function of position on the resource axis. Calculations were therefore made assuming a Gaussian distribution of resource carrying capacities having a maximum at position zero on the resource axis. To maintain a constant total productivity over the range of resources that could be used by two overlapping “outer” species, the maximum value of the  $K$  function was adjusted for different standard deviations so that the integral from  $-1$  to  $+1$  was constant. The outer consumers were assumed to be located symmetrically on opposite sides of the maximum of the resource distribution. This means that the equilibrium allopatric population densities of the consumers decrease as their niche separation increases, because the resource they capture at the highest rate has a smaller  $K$ . As a result, a lower mortality rate of the outer consumer species is required for intermediate resources to be driven extinct. This does not eliminate the phenomenon of an absolute limiting similarity, but it does mean that such a limit requires lower mortality rates. For example, if the standard deviation of the  $K$  distribution is 0.18 (close to the standard deviation of the bell-shaped utilization curve employed here), and the separation of utilization curves is 0.6, a mortality rate less than  $\sim 0.032$  is required for an absolute limit to similarity (compared to a mortality between 0.05 and 0.06 in the case of a flat resource distribution). The change in the coexistence bandwidth for increasing separation of the outer species is similar to that for the case of a flat resource distribution illustrated here.

*Abiotic resource growth.*—The abiotic resource growth model assumes that  $f_x$  in Eq. 1a is given by  $I(x) - ER$ , where  $I(x)$  and  $E$  are an input rate and an exit rate per unit resource density. In spite of its name, this model frequently applies to living organisms that can move in and out of vulnerable states (Abrams 1977, Abrams and Walters 1996). The fact that resources with a nonzero  $I$  cannot go extinct implies that an absolute limit to similarity cannot occur. The absolute limit shown previously requires that resources are completely absent from a large interval on the resource axis. Nevertheless, the two phenomena underlying the decline in coexistence bandwidth with increasing separation of the outer species shown for logistic resource growth still occur with abiotic growth. The upper boundary of the bandwidth decreases over a range of low to intermediate separations because the net exploitation of intermediate resources increases. The lower boundary decreases more rapidly than the upper boundary at low separations, but then reaches zero once separation is great enough that each of the outer species can exist on their exclusive resources alone. The result is that in many systems the coexistence bandwidth initially expands with greater niche separations, and then contracts, before expanding again at high separations. Under the logistic model of resource growth, this



phenomenon was only observed when resource exclusion occurred for some range of the resource axis.

Fig. 4 is an example of this phenomenon for a model with abiotic resource growth having a uniform abundance distribution ( $I(x) = E = 1$ ), assuming the standard bell-shaped utilization curve used in Fig. 1. While the coexistence bandwidth is relatively wide for even moderate separations, it does contract by  $\sim 7.5\%$  as niche separation increases from  $\sim 0.23$  to  $0.41$ . The bandwidth does not exceed its value for a separation of  $0.23$  until separation exceeds  $\sim 0.58$ . The shape of these boundaries is relatively insensitive to the parameters of the model. Most biological resources are likely to have growth equations consisting of biotic and abiotic elements. Immigration of the resource from other habitats that lack consumers, or transitions of resource into a vulnerable size/age class represent “abiotic” elements in models of living resources. In such a case, the contraction of the coexistence bandwidth with increasing niche separation will be intermediate between the large values shown in Fig. 1 and the more modest values shown in Fig. 4.

*Unequal efficiencies of outer consumer species.*—There are many ways that systems with unequal efficiencies of the two outer species can differ from the one considered here. However, unequal mortality does not eliminate the phenomenon of an absolute limit to similarity. If either of the two outer species has a high enough mortality, there will be intermediate resources and the absolute limit will not exist. However, absolute limits do not require that the mortalities of the outer species be approximately equal. If, for example, the two outer species are separated by a distance of  $0.6$ , and the previous model is modified so that  $d_3$  (the mortality of species 3) differs from  $d_1$  (with  $d_1 = 0.05$ ), an intermediate zone of resource exclusion  $>1$  unit in width on the resource axis occurs for all values of  $d_3$  between just above zero to just below  $0.09$ . In this case, it is again possible for invasion and coexistence to occur if the intermediate species is closer to the higher mortality resident, and its own mortality falls within a narrow range of values.

## DISCUSSION

### *Can an absolute limit to similarity exist?*

The original analysis of limiting similarity by MacArthur and Levins (1967) proposed that invasion and coexistence of an intermediate species is impossible for some range of separations of two resident competitors. This conclusion rests on the assumption of equal consumer efficiencies, required for equal consumer carrying capacities (May 1974, Abrams 1975). This does not seem to be warranted. Without this assumption, there is no absolute limit to similarity in the Lotka-Volterra model used by MacArthur and Levins (1967), as shown by May (1974). May’s (1974) analysis of this deterministic model suggested that the coexistence bandwidth decreased with decreasing separation

of resource utilization curves, a conclusion supported by subsequent studies (e.g., Abrams 1975, 1983, Mesz  na et al. 2006). The reanalysis of MacArthur’s consumer–resource model (and variations thereof) presented here do not agree with previous results on either the absolute or relative conceptions of limiting similarity. In each case, the difference in results is a consequence of taking into account the impact of resource exclusion and/or depletion on the competition between consumer species.

Our results show that an absolute limiting similarity can exist in cases where consumers are efficient and have one-dimensional partitioning of biotic resources. However, this result must be qualified by noting that there is always a possibility for invasion and coexistence by intermediate species that fall within a restricted range of niche positions that are closer to one of the resident species and have efficiencies of resource utilization sufficiently higher than either resident (e.g., sufficiently lower mortalities). These separations allow the middle species access to some resources, and the lower mortality gives it the competitive advantage required to avoid exclusion by the closer of the two outer species. Low resource immigration rates prevent the “absolute” limit that can occur under the pure logistic model, but the mortalities of the intermediate species that are required for coexistence are so low, and the range of those mortalities is so narrow, that coexistence conditions are biologically implausible.

### *Coexistence bandwidth can decrease with increasing niche separation*

Our results also show that a broad range of models and parameters can result in the coexistence bandwidth decreasing with greater separation of the outer two species in a linear array of three species. This outcome is associated with high consumer efficiencies (e.g., low mortalities), and is observed for an intermediate range of separations of the outer two species. Over this range of niche separations, moving the utilization curves of two consumers further apart can result in a broader range of severely depleted or extinct resources. High consumer efficiency implies that the maximum mortality of the intermediate species allowing coexistence decreases rapidly with increasing niche separation. The minimum mortality decreases rapidly at low separations, but then decreases more slowly (or does not change) because this minimum approaches (or reaches) zero when the outer consumers have high enough efficiency and niche separation.

### *Higher order interactions*

The Lotka-Volterra model assumes that the competition coefficients between any pair of species are independent of the presence or absence of any other competitors. Consumer–resource models with small numbers of resources suggest that this is generally not the case (Abrams 1980a). The models analyzed here also

exhibit a strong dependence of the competition coefficients characterizing a pair-wise interaction on the presence or absence of additional competitors. Because competition coefficients are based on consumption of extant resources, these coefficients are bound to change with species addition or removal when the range of extinct resources changes. In the system considered here, depletion or extinction of intermediate resources by an intermediate consumer will reduce competition between the outer species.

#### *Relationship to other literature*

Two papers have results that superficially appear similar to those presented here, but are actually quite different. Roughgarden (1974) analyzed variants of the MacArthur and Levins (1967) Lotka-Volterra model, and showed that if the intermediate species had a carrying capacity somewhat greater than the residents, invasion by the intermediate species could be possible at both high and low, but not intermediate, separations of the outer species. This was termed a "similarity barrier," and it is reflected here in the fact that upper limit of  $d_2$  is minimized by intermediate separations in Figs. 1 and 4 in this paper. However, Roughgarden's "similarity barrier" did not measure the coexistence conditions for all three species; it measured only invasion of the middle species. While Roughgarden (1974) also suggested that three-species coexistence should be easier for both large and small separations of the outer species, this was not supported by quantitative analysis, and was not observed in our reanalysis of analogous consumer-resource models, even when resources did not go extinct. In the second related paper, Abrams (1998) analyzed competition using two-consumer-two-resource models in which extinction of resources was considered, and showed that the change in population density caused by the competing consumer was maximized at intermediate levels of similarity. However, that article did not treat the conditions required for coexistence.

There is a persistent idea (Dayan and Simberloff 2005) that competition should result in even spacing of utilization curves (i.e., niche positions). This is supported by the MacArthur and Levins (1967) parameterization of the Lotka-Volterra model, in that the maximum range of parameters allowing coexistence occurs at a niche position midway between that of the two outer species. However, this is not predicted by consumer-resource models of highly efficient consumers. As shown in Fig. 3A, intermediate niche positions that are significantly closer to one of the outer species are most favorable to coexistence when consumers are efficient and niche separation is moderate. The implication is that conditions that are symmetric around a particular position on the resource axis can result in an asymmetric distribution of consumer species in the absence of any constraints on the characteristics of those consumers. This may be related to observed uneven size distributions (Holling 1992). It differs from

the phenomenon of long transient coexistence of clumps of consumers in the Lotka-Volterra model of Scheffer and van Nes (2006).

#### *Possible extensions*

Multidimensional resource partitioning requires further analysis. However, at least for small numbers of species, low mortalities enhance coexistence when each consumer species has some exclusively used resources (Schoener 1976, Abrams 1977), as is true in the case of two consumers in the current model. Exclusive resources result from utilization functions that are finite in extent and do not overlap completely. In this case, a sufficiently low mortality would allow the consumers to persist on the exclusive resources alone, and thus prevent any absolute limit to similarity. Higher mortalities mean that some of the shared resources must also be obtained for a positive equilibrium consumer density. Unfortunately, the topic of resource partitioning has not been a popular topic of empirical research in recent years (Schoener [1974] provides an early review), so the nature of multidimensional partitioning is still poorly quantified. The impacts of resource depletion and exclusion also need to be reconsidered in models that have a continuous resource spectrum for situations in which coexistence is influenced by environmental variability (Abrams and Holt 2002), and for cases where the resources compete with each other (Abrams and Nakajima 2007).

Several recent models have analyzed coexistence within large linear arrays of competitors (e.g., Gyllenberg and Meszéna 2005, Scheffer and van Nes 2006, Szabó and Meszéna 2006), and the present analysis could be extended to include more consumer species. However, resource partitioning along a single axis seldom characterizes more than a small number of competing species (Schoener 1974, Abrams 1983). Careful studies of small groups (<10 species) of competitors have revealed multidimensional partitioning (Abrams et al. 1986, Abrams 1987). Diamond's (1975) description of eight competing fruit pigeons seems to be the largest group of species for which linear partitioning has even been proposed, and resource partitioning in that system is poorly understood. Thus, the issue of coexistence in very large linear arrays of species is of questionable biological relevance, and was not treated here.

#### *Relationship to real competitive communities*

In the context of the simple models considered here, the absolute limit to similarity and declining coexistence bandwidth with increasing similarity are both most likely when the scaled mortality rate,  $d$ , is low. It is therefore important to discuss whether the low values of  $d$  assumed in many of the calculations here are biologically realistic. This can be judged by comparing these values to the ratio of resource densities with and without consumers in empirical studies. Because of the scaling of parameters ( $b = 1$ ;  $K = 1$ ; sum or integral of  $C$

$= 1$ ),  $d$  is equal to this ratio in a system with a single resource species. In a system with many resources having equal equilibrium densities in the absence of consumption,  $d$  gives a weighted average of equilibrium resource densities in the presence of the consumer, where the weights are  $C(x)$ . Because  $C(x)$  has a negative covariance with  $R(x)$  at equilibrium with the consumer (and the integral of  $C(x)$  is unity), the mean resource density,  $R(x)$  must be larger than  $d$ . As a result, the ratio of mean total resource density in the presence of a consumer species to mean resource density in the absence of consumers is greater than or equal to  $d$ . To judge whether a  $d$  value on the order of 0.1 is biologically reasonable, we can look at the average reduction in resource (prey) densities produced by their consumers (predators) in empirical studies. Measurements of resource reductions in laboratory microcosms are frequently several orders of magnitude lower than equilibrium abundances in the absence of consumers (Holyoak and Lawler 1996), suggesting that values of  $d$  close to 0.001 are not unrealistically low, at least for some systems. In fact, Shurin et al. (2002) documented an average reduction of resources to  $\sim 6\%$  of their pre-consumer levels in field studies of predator density manipulations for benthic assemblages in lentic ecosystems. Because the consumer abundance is measured in units of  $K$ , increasing the resource carrying capacity sufficiently will result in a very low value of the scaled mortality parameter  $d$ . This implies that fertilizing resources should have effects similar to reducing death rates. Bimodal or multimodal size-abundance distributions similar to those shown in Fig. 2 have been observed (Holling 1992, Havlicek and Carpenter 2001), but the mechanism producing them is not known. Complete absence of certain sizes classes over a wide range of sizes does not appear to have been observed. However, this is not surprising, as resources of a given size are likely to include many that are well-defended or otherwise unusable.

The theory of limiting similarity is difficult to test because key parameters cannot be manipulated in an experimental setting. Observed patterns of niche separation are generally influenced by the limited variation in resource use traits of potential community members, as well as their evolution in sympatry. Both of these processes are likely to lead to a level of similarity in resource use that is less than maximal, and both are likely to vary significantly based on many factors other than those we have considered. However, there are potentially testable predictions from the theory developed here. For example, our results suggest that high resource use efficiency is likely to reduce the ability of consumer species at intermediate niche positions to invade communities. In addition, evolutionary divergence in the resource use of two resident species may reduce the possibility of invasion at intermediate positions. Our results also suggest that increased mortality of all consumers is most likely to lead to the

exclusion of intermediate consumer species in a linear array. These ideas could potentially be tested using microcosms. Finally, the theory developed here should aid in understanding the basis of observed multimodal size distributions within a trophic level.

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