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## EVOLUTION OF NICHE WIDTH AND ADAPTIVE DIVERSIFICATION

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**Abstract.**—Theoretical models suggest that resource competition can lead to the adaptive splitting of consumer populations into diverging lineages, that is, to adaptive diversification. In general, diversification is likely if consumers use only a narrow range of resources and thus have a small niche width. Here we use analytical and numerical methods to study the consequences for diversification if the niche width itself evolves. We found that the evolutionary outcome depends on the inherent costs or benefits of widening the niche. If widening the niche did not have costs in terms of overall resource uptake, then the consumer evolved a niche that was wide enough for disruptive selection on the niche position to vanish; adaptive diversification was no longer observed. However, if widening the niche was costly, then the niche widths remained relatively narrow, allowing for adaptive diversification in niche position. Adaptive diversification and speciation resulting from competition for a broadly distributed resource is thus likely if the niche width is fixed and relatively narrow or free to evolve but subject to costs. These results refine the conditions for adaptive diversification due to competition and formulate them in a way that might be more amenable for experimental investigations.

**Key words.**—Adaptive dynamics, competition, diversification, fitness minimum, frequency-dependent selection, niche width, sympatric speciation.

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Understanding the ecological mechanisms of diversification is a central problem in evolutionary ecology. Variability in the biotic environment is one possible cause of phenotypic diversification and subsequent speciation: variable environments can allow different specialized types to evolve and coexist. An important example of environmental variation is variation in the resources available for consumption. Indeed, selection acting on characters related to resource acquisition is thought to drive most cases of adaptive radiation (Schluter 2000).

A general theoretical framework for studying how resource variation can drive phenotypic diversification is to assume that individuals compete for a resource that varies continuously along a single axis and (in the absence of consumption) reaches highest densities for an intermediate value on this axis (Roughgarden 1976; Slatkin 1980; Case 1981; Doebeli 1996; Dieckmann and Doebeli 1999). This resource could, for example, consist of seeds that differ in size, with seeds of intermediate size being most common.

Importantly, these models assume that the resource is re-

plenishable. Its density or concentration can be depressed through consumption and in the absence of consumption increases up to a carrying capacity. It is further assumed that a phenotypic trait determines how well individual consumers acquire resource items of a certain type. In the case of seeds as the food items and birds as consumers, beak size could be the trait that determines the ability of individuals to consume seeds of a certain size. This implies that there is a trade-off between the consumption of different resource types. Phenotypes that use one type well are less efficient at using other types (e.g., because they have a beak that is suited for consuming small but not large seeds). Each individual can then be characterized by the type of resource it acquires most efficiently and by how fast acquisition efficiency drops for resources that differ from the optimal type. The first quantity can be interpreted as the niche position, the second as the niche width.

This ecological setting has been developed to study character displacement (e.g., Roughgarden 1976; Slatkin 1980; Case 1981). These studies address one aspect of phenotypic diversification: given a number of coexisting species, how does competition affect the spacing of the species on a continuous resource axis? More recently, this same ecological setting has been used to study sympatric speciation (Doebeli

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1996; Dieckmann and Doebeli 1999; Drossel and McKane 2000), which is another aspect of phenotypic diversification. Here, the question is the following: starting with one consumer species, can competition for a continuously distributed resource induce a splitting into several discrete phenotypic clusters, that is, daughter species? Results from these models, in which niche width was assumed to be fixed and non-evolving, can be interpreted as follows: if the variation in the resource is large compared to the niche width of the consumer, then splitting of the consumer into two or more phenotypic clusters is a typical outcome (Doebeli 1996; Dieckmann and Doebeli 1999). This demonstrates that this ecological situation can set the stage for adaptive speciation.

However, it is reasonable to assume that the niche width itself can readily respond to selection, a viewpoint that is supported by comparative (Funk and Bernays 2001; Nosil 2002) and experimental evidence (Bolnick 2001). The fact that the evolutionary outcome depends critically on the niche width of the consumer thus naturally raises the question of how evolution of the niche width affects diversification and speciation. Will resident consumers evolve wider niches, use the resources more completely, and thus prevent the evolutionary emergence of other phenotypes with different niche positions?

Here we model the evolution of niche width based on a general model by MacArthur (1972), which lies at the basis of most of the previous work on character displacement and adaptive diversification due to frequency-dependent competition. Even though MacArthur's original model describes the ecological dynamics of both consumer and resource, most of the derived models did not treat resource dynamics explicitly, but instead made the implicit assumption that similarity of resource use determines competitive effects, the usual assumption being that competition between two individuals decreases monotonically in a Gaussian fashion with increasing distance in the niche position (Roughgarden 1976; Slatkin 1980; Case 1981). It has been noted that this assumption is somewhat arbitrary and only derives from MacArthur's model under special circumstances (Taper and Case 1985; Abrams 1986).

In contrast, our models for the evolution of niche width are based on MacArthur's original model, extended to incorporate the dynamics of a continuous spectrum of resources (e.g., also envisaged by Case and Taper 1986). We model resource utilization, described by niche position and niche width, explicitly to determine the steady-state distribution that the resource will attain in the presence of a resident population with a given niche position and niche width. This, in turn, allows us to calculate the equilibrium density of the consumer, that is, its carrying capacity, as well as the competition coefficient between two different consumer types. This makes it possible to use invasion analysis and the analytical framework of adaptive dynamics (Dieckmann and Law 1996; Metz et al. 1996; Geritz et al. 1998) to study the evolutionary dynamics of niche position and niche width.

To obtain biologically meaningful results, one has to impose constraining relationships on resource utilization and thus on the form of the niche (otherwise all individuals would evolve maximal niche width). This is biologically realistic, because using diverse resource items (as opposed to consum-

ing just one type) likely reduces the efficiency or rate at which items of a given type can be consumed. We assume that uptake rates of different resource types (i.e., resource utilization) are described by a unimodal curve. The maximum of this curve is the niche depth, and the relationship between niche width and niche depth then determines whether widening the niche has inherent costs or benefits. If widening the niche is exactly compensated for by a reduction in niche depth, so that the total resource consumption is constant, there are no costs or benefits. Undercompensation leads to an increase in the total rate of resource uptake with widening of the niche, and thus corresponds to an inherent benefit of widening the niche. Overcompensation, on the other hand, corresponds to an inherent cost. We find that the costs or benefits of widening the niche are the principal determinant of the evolutionary outcome.

If widening the niche has benefits, then the resident evolves a niche width that shapes the resource distribution in such a way that selection on niche position is stabilizing. In contrast, if widening the niche width has a cost, a narrower niche will evolve that leaves substantial amounts of resources at the periphery of the resource distribution unconsumed. As a consequence, with a cost to widening the niche selection on niche position turns disruptive, a scenario that serves as a potential starting point for evolutionary diversification of the niche position. Such diversification was observed in corresponding individual-based simulations, which we used to confirm the predictions derived from the analytical theory.

Both the analytical and the individual-based models that we present are based on the assumption of asexual reproduction. In sexual populations, adaptive diversification is hindered by random mating. However, if the ecological conditions for adaptive diversification are satisfied, then assortative mating is favored by selection, and hence is often likely to evolve (Dieckmann and Doebeli 1999). Thus, understanding the ecological conditions that render the splitting of a lineage adaptive is an important ingredient for understanding adaptive, sympatric speciation. Our results suggest that adaptive speciation and the evolution of a wide niche are two alternative processes that can alleviate the effects of frequency-dependent competition for resources, and they specify the ecological conditions determining which of these two processes is more likely to occur.

## MODEL AND RESULTS

Our starting point is the consumer-resource system proposed by MacArthur (1972), which is, in one form or another, at the basis of most models of evolutionary divergence due to competition for resources. MacArthur envisaged a finite number of discrete resources, but it is straightforward to formulate the model for a continuous spectrum of resources, with different resource types characterized by a continuously varying quantity  $z$ . For example, if the resource is seeds of various sizes, then  $z$  could denote seed size, and  $F(z)$  would denote the density of seeds of size  $z$ . In the absence of the consumer, it is assumed that the resources  $F(z)$  grow logistically to carrying capacity  $S(z)$ :

$$\frac{dF(z)}{dt} = rF(z) \left[ 1 - \frac{F(z)}{S(z)} \right], \quad (1)$$

where, for simplicity, we have already assumed that the intrinsic growth rate of the resource is independent of  $z$ . For the most part, we assume in this paper that the carrying capacity  $S(z)$  is of Gaussian form,

$$S(z) = S_0 \exp\left(\frac{-z^2}{2\sigma_S^2}\right), \tag{2}$$

which makes it possible to derive analytical results. Equation (2) implies that the carrying capacity is highest at some intermediate value along the resource axis  $z$ , which we have arbitrarily set at  $z = 0$ , and declines with increasing distance from  $z = 0$  at a rate that is determined by  $\sigma_S$ . Importantly, the distribution of the resource is assumed to be spatially homogenous at all times, so that each consumer individual has always access to the whole range of resource types at densities corresponding to the momentary steady-state resource distribution.

We now envisage a consumer that is characterized by how it uses the resources  $F(z)$  along the  $z$ -axis, that is by its utilization function. This function describes the relative effort a consumer invests in harvesting resources of type  $z$ . If all resource types would be equally common (i.e., if the resource distribution was flat), then the utilization curve would describe the distribution of resources consumed by an individual. If, as in our model, the resource distribution is not flat, then the distribution of resources actually consumed by an individual depends both on the effort spent on the different resource types (given by the utilization curve) and the momentary density of the different types.

Again for purposes of analytical tractability, we assume that the utilization curve is of Gaussian form and is determined by two phenotypic properties of the consumer: the position of the maximum,  $x$ , and the standard deviation,  $y$ . The consumer  $(x,y)$  uses resources at position  $z = x$  most intensively, and the intensity of utilization declines with increasing distance from  $z = x$  at a rate that is determined by  $y$ . Thus, whereas  $x$  determines the preferred position along the resource axis,  $y$  determines the degree of specialization, with small  $y$  corresponding to specialists and large  $y$  corresponding to generalists.  $x$  thus denotes the niche position, while  $y$  is a measure for the niche width. Given the phenotype  $(x,y)$  of the consumer, utilization  $a_{x,y}(z)$  of resources of type  $z$  is described by the function

$$a_{x,y}(z) = \frac{\exp(-c \cdot y)}{\sqrt{2\pi}y} \exp\left[\frac{-(z-x)^2}{2y^2}\right]. \tag{3}$$

In this expression,  $c$  is a measure of the costs or benefits of larger niche widths  $y$ . This can be seen by considering the integral,  $\int_z a_{x,y}(z) dz$ , which is a measure of the total effort devoted to resource consumption of all types  $z$ . If  $c = 0$ , then  $\int_z a_{x,y}(z) dz = 1$  for all phenotypes  $(x,y)$ . If  $c > 0$ , then  $\int_z a_{x,y}(z) dz$  decreases as  $y$  increases, indicating a cost of becoming more generalist in resource utilization. In contrast, if  $c < 0$ , then  $\int_z a_{x,y}(z) dz$  increases as  $y$  increases, indicating an inherent benefit for generalists, and thus a cost of specialization. Both scenarios are biologically plausible. Note that even without costs to generalists (i.e.,  $c = 0$ ), widening the utilization curve nevertheless leads to a decrease in niche depth, that is, in the maximum of the function  $a_{x,y}(z)$ . How-

ever, this decrease occurs at a rate that is exactly compensated for by the widening of the curve so that the total effort  $\int_z a_{x,y}(z) dz$  is independent of the phenotype  $(x, y)$ . The terms ‘‘cost’’ and ‘‘benefit’’ thus refer to changes in total effort, given by the integral of the utilization curve.

The presence of consumer  $(x, y)$  changes the dynamics of the resources to

$$\frac{dF(z)}{dt} = rF(z) \left[1 - \frac{F(z)}{S(z)}\right] - F(z)a_{x,y}(z)N_{x,y}. \tag{4}$$

Here  $N_{x,y}$  is the density of consumers with phenotype  $(x, y)$ , so that  $a_{x,y}(z)N_{x,y}$  is the rate at which resources of type  $z$  are consumed. Figure 1 illustrates the basic ecological setup of the interaction between resource and consumer. Of course, the consumer density  $N_{x,y}$  itself changes over time due to resource consumption, and according to MacArthur’s (1972) model the population dynamics of  $N_{x,y}$  are given by

$$\frac{dN_{x,y}}{dt} = RN_{x,y} \left[ b \int_z a_{x,y}(z)F(z) - m \right]. \tag{5}$$

In this equation  $b$  represents the net energy gained per food item acquired, so that the total energy acquired per individual is  $b$  times the total amount of resources acquired,  $\int_z a_{x,y}(z)F(z)$ . For simplicity we assume that all resource types contribute equally to energy gain, so that  $b(z) = b$  is a constant. The total amount of energy available for reproduction is the total gain minus  $m$ , the per individual costs for maintenance. Finally,  $R$  is the number of individuals that are produced per unit of energy available for reproduction. Note that the quantities  $R$ ,  $m$ , and  $b$  could, in principle, all depend on the phenotype  $(x,y)$ , but we assume here that this is not the case.

### Consumer Carrying Capacity

To derive the evolutionary dynamics, the consumer equation first has to be brought into logistic form, which is done using equations (4) and (5). The arguments are the same as those used in Schoener (1974) and consist of a time scale separation between the dynamics of the resources and that of the consumer, so that the resource can always be assumed to be in its equilibrium state. This essentially corresponds to assuming that the consumer birth rate  $R$  is much smaller than the intrinsic growth rate  $r$  of the resource. Consequently, one first finds, for a given consumer density  $N_{x,y}$ , the nonzero solution  $\hat{F}(z)$  of the resource equation (4) (this solution is illustrated in Fig. 1C). One then substitutes this solution into equation (5), which yields a logistic equation for  $N_{x,y}$  of the form (see Appendix 1 for details)

$$\frac{dN_{x,y}}{dt} = R_{x,y}N_{x,y} \left(1 - \frac{N_{x,y}}{K_{x,y}}\right). \tag{6}$$

This logistic equation of population growth allows one to interpret  $R_{x,y}$  as the intrinsic growth rate and  $K_{x,y}$  as the carrying capacity of a consumer population that is monomorphic for phenotype  $(x, y)$ .

General analytical expressions for  $R_{x,y}$  and  $K_{x,y}$  are given in Appendix 1. For all the analyses presented in this paper, the numerical value of the parameters  $r$  and  $b$  in equations (4) and (5) is irrelevant, so that, without loss of generality, we can set these parameters equal to unity. In this case, using

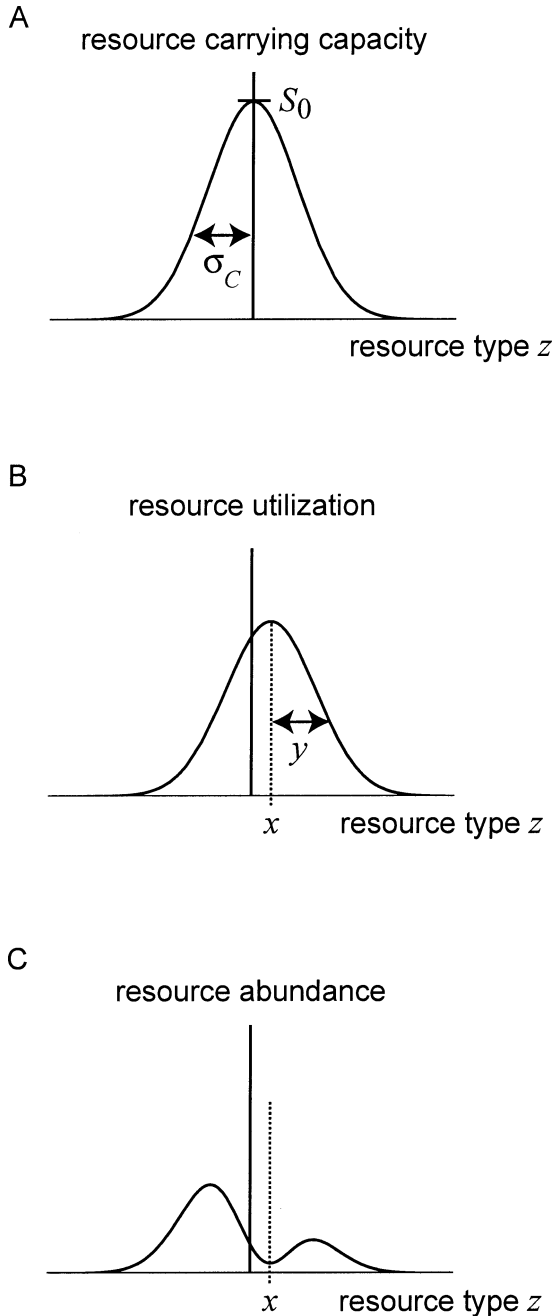


FIG. 1. The ecological setup for resource utilization. (A) Distribution of the resource in the absence of a consumer. The resource is distributed along a continuous  $z$ -axis. As there is no consumer, all resource types are at their carrying capacity, a Gaussian curve with standard deviation  $\sigma_S$  and maximum  $S_0$  at  $z = 0$ . (The position of the maximum at  $z = 0$  is indicated by the vertical line in all three panels.) (B) Utilization curve of a consumer with phenotype  $(x, y)$ . The utilization curve describes the effort spend in harvesting resources of type  $z$ . The consumer  $(x, y)$  spends most of its effort on resources of type  $z = x$ . For resources differing from  $x$ , its effort declines in a Gaussian fashion at a rate determined by  $y$ . (C) Steady-state distribution of the resource from (A) in the presence of the consumer with phenotype  $(x, y)$  whose utilization curve is shown in (B). The consumer depresses the resource below its carrying capacity. The strongest depression occurs at  $z = x$ , the position where the consumer spends most of its harvesting effort.

equations (2) and (3) for the functions  $S(z)$  and  $a_{x,y}(z)$  in the expression for  $K_{x,y}$  (eq. A3), one gets

$$K_{x,y} = 2y\sqrt{2\pi}\sqrt{2\sigma_S^2 + y^2}\exp\left(\frac{x^2 + 4c\sigma_S^2y + 2cy^3}{2\sigma_S^2 + y^2}\right) \times \left[ \frac{-m}{\sigma_S S_0} + \frac{\exp\left(-\sigma_S y - \frac{x^2}{2\sigma_S^2 + 2y^2}\right)}{2\sqrt{\sigma_S^2 + y^2}} \right]. \quad (7)$$

This expression calculates the carrying capacity, that is, the equilibrium density, of a consumer with phenotype  $(x, y)$ , given the resource parameters  $\sigma_S$  and  $S_0$ , the consumer parameter  $m$ , and the cost parameter  $c$ . It is important to note that, as a function of the niche position  $x$ , the consumer carrying capacity  $K_{x,y}$  does not necessarily have a maximum at  $x = 0$  corresponding to the maximum of the carrying capacity of the resource. In other words, a consumer phenotype that most prefers the resource with the highest carrying capacity does not necessarily attain the highest equilibrium density.

The reason for this somewhat counterintuitive fact is that having highest utilization rate of the resource with the highest carrying capacity can lead to overexploitation, and thus to a disproportionately high consumer pressure on other resources, resulting in an overall reduction of the consumer carrying capacity (e.g., Slobodkin 1968; Rosenzweig 1973; Abrams 1983; Matessi and Gatto 1984; Holt 1985). A typical example of the consumer carrying capacity  $K_{x,y}$  is shown in Figure 2 for a case with  $c = 0$  (no costs for widening the niche). If the carrying capacity is viewed as a function of the niche position  $x$ , then  $K_{x,y}$  has a minimum at  $x = 0$  and two symmetric maxima on either side of this minimum for intermediate values of the niche width  $y$ , whereas  $K_{x,y}$  is unimodal with a maximum at niche position  $x = 0$  for small as well for large  $y$ . As a function of  $y$ ,  $K_{x,y}$  always has a maximum at some intermediate  $y$ -value: extreme specialization implies utilization of too few resource types, whereas extreme generalists use too many unproductive resource types. (The dot in the figure indicates the position of the evolutionary equilibrium for the given parameters; see section *Convergence stability* below.)

#### Competition Coefficients

To study the evolution of the traits  $x$  and  $y$ , we need to be able to compare resident and mutant phenotypes that differ in these traits. This implies that we need to determine the competition coefficients of two competing consumer types. The method of calculating competition coefficients from MacArthur's (1972) model is straightforward and again follows the exposition in Schoener (1974).

The dynamics of consumer type  $(x, y)$  in the presence of a competitor  $(u, v)$  are given by

$$\frac{dN_{x,y}}{dt} = R_{x,y}N_{x,y} \left[ 1 - \frac{N_{x,y} + \beta(x, y, u, v) \cdot N_{u,v}}{K_{x,y}} \right], \quad (8)$$

where  $\beta(x, y, u, v)$  is the relative competitive impact of a consumer individual of type  $(u, v)$  on consumers of type  $(x, y)$  (see Appendix 1).

Using equations (2) and (3) for the functions  $S(z)$ ,  $a_{x,y}(z)$ ,

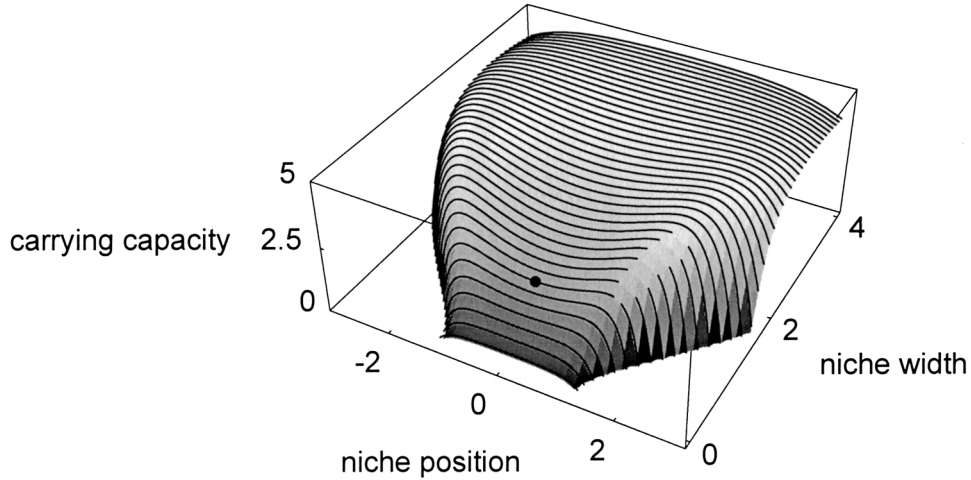


FIG. 2. Carrying capacity  $K_{x,y}$  given by equation (7), as a function of the niche position ( $x$ -axis) and the niche width ( $y$ -axis). The dot indicates the position of the evolutionary equilibrium (eq. 14). Note that at this equilibrium, the carrying capacity has a local minimum as a function of the niche position. Parameter values:  $m = 0.05$ ,  $\sigma_S = 0.5$ ,  $S_0 = 1.5$ .

and  $a_{u,v}(z)$ , we can evaluate equation (A7) for  $\beta(x, y, u, v)$  to obtain

$$\begin{aligned} \beta(x, y, u, v) &= \exp\left[ c \cdot (y - v) \right. \\ &\quad + \left. \left( \{-2\sigma_S^4(u - x)^2 + v^2x^2y^2 \right. \right. \\ &\quad \quad \left. \left. + \sigma_S^2y^2(-3u^2 + 2ux + x^2) - u^2y^4\right) \right. \\ &\quad \left. \div \{2(2\sigma_S^2 + y^2)[v^2y^2 + \sigma_S^2(v^2 + y^2)]\} \right] \\ &\quad \times \frac{y\sqrt{2\sigma_S^2 + y^2}}{\sqrt{v^2y^2 + \sigma_S^2(v^2 + y^2)}}. \end{aligned} \tag{9}$$

This is a rather complicated expression, but an important insight can be gained straightaway: the competition coefficient is not symmetric in the two types ( $x,y$ ) and ( $u, v$ ). In other words, in general  $\beta(x, y, u, v) \neq \beta(u, v, x, y)$ . In particular, this means that the competitive effect that one consumer ex-

erts on another depends not only on the distance between the consumer's niches, but also on the niche positions of the two competitors relative to the resource.

To illustrate the competitive effect of a given type ( $x,y$ ) on varying phenotypes ( $u,v$ )—a perspective that will be used in the next section for assessing the competitive effect of a resident ( $x,y$ ) on mutants ( $u,v$ )—Figure 3 shows the competition coefficient  $\beta(u,v,x,y)$  as a function of  $u$  and  $v$  for a fixed competitor ( $x,y$ ). In this figure we assumed  $c = 0$  (no costs for widening the niche), and the focal phenotype ( $x,y$ ) whose effect on other phenotypes is shown has its niche position at the maximum of the resource distribution, that is,  $x = 0$  (the focal phenotype is indicated by the dot and again corresponds to the evolutionary equilibrium; see section *Convergence stability* below). The figure shows that for large enough values of the niche width  $v$ , the competitive effect of the focal type ( $x,y$ ) on ( $u,v$ ) has a minimum at  $u = x$  and increases with increasing distance  $|u - x|$ . That competitive

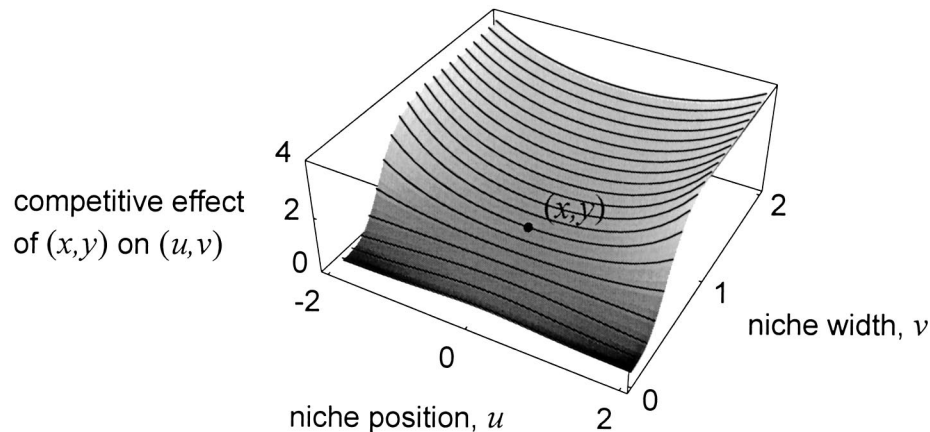


FIG. 3. Competition coefficient  $\beta(u,v,x,y)$ , given by equation (9), as a function of the niche position ( $u$ -axis) and the niche width ( $v$ -axis). The function measures the competitive impact of a fixed focal phenotype ( $x,y$ ) on varying phenotypes ( $u,v$ ). The focal phenotype is indicated by the dot and corresponds to the position of the evolutionary equilibrium (eq. 14). Note that the competitive impact of this focal type on other types typically increases with increasing distance in niche position  $|u - x|$ . Parameter values are the same as in Figure 2.

effects increase with increasing phenotypic distance is counterintuitive at first, but is due to the competitive asymmetry mentioned above, which implies that individuals with a niche position at the resource maximum tend to have relatively more exploitative impact on other individuals the farther the niche positions of these individuals are from the resource maximum. In contrast, for small values of the niche width  $v$ , competitive effects decrease with increasing distance  $|u - x|$ . As a function of the niche width  $v$ , competitive effects increase monotonically, which makes sense because increasing  $v$  implies in any case a larger niche overlap with the focal phenotype  $(x,y)$ .

*Adaptive Dynamics*

Based on the ecological components developed in the previous sections, we now construct a model for the evolutionary dynamics of the phenotypes  $x$  and  $y$  using the theory of adaptive dynamics (Dieckmann and Law 1996; Metz et al. 1996; Geritz et al. 1998). The basic quantity needed to derive the adaptive dynamics is the invasion fitness, a function that describes the growth rate of a rare mutant phenotype  $(u,v)$  that appears in a resident population that is monomorphic for a resident phenotype  $(x,y)$ . To determine the invasion fitness function, it is assumed that the monomorphic resident is at ecological equilibrium, and hence its density is equal to its carrying capacity  $K_{x,y}$ . Moreover, the mutant is assumed to be so rare that its own density is unimportant for its dynamics during the invasion attempt. Consequently, the dynamics of the mutant density  $N_{u,v}$  is described by equation (8) adopted for the mutant type  $(u,v)$ :

$$\frac{dN_{u,v}}{dt} = R_{u,v}N_{u,v} \left[ 1 - \frac{\beta(u, v, x, y)K_{x,y}}{K_{u,v}} \right]. \tag{10}$$

Thus, the per capita growth rate of the mutant, that is, the invasion fitness  $f(x,y,u,v)$  of the mutant  $(u,v)$  in the resident  $(x,y)$ , is given by

$$f(x, y, u, v) = R_{u,v} \left[ 1 - \frac{\beta(u, v, x, y)K_{x,y}}{K_{u,v}} \right]. \tag{11}$$

The invasion fitness is then used to calculate the selection gradients for the two evolving traits. Both selections gradients are functions of the resident trait values  $(x,y)$ . We denote the gradient for trait  $x$  by  $s_1(x,y)$ , and the gradient for trait  $y$  by  $s_2(x,y)$ . These gradients are determined as

$$s_1(x, y) = \left. \frac{\partial f}{\partial u} \right|_{u=x, v=y} \quad \text{and} \tag{12a}$$

$$s_2(x, y) = \left. \frac{\partial f}{\partial v} \right|_{u=x, v=y}. \tag{12b}$$

Under certain simplifying assumptions, the selection gradients can be used to derive a deterministic model for the evolutionary dynamics of the two traits  $x$  and  $y$ . These assumptions are spelled out in detail in Dieckmann and Law (1996) and in Metz et al. (1996). Crucial among these assumptions are that mutations are small and occur sufficiently rarely so that residents can always be assumed to be monomorphic and in their ecological equilibrium state. It is also assumed that successful invasion of a mutant leads to re-

placement of the current resident by the mutant. These assumptions may seem restrictive, but numerical simulations of underlying stochastic, individual-based models indicate that the deterministic adaptive dynamics derived from these assumptions typically yield very accurate descriptions of the evolutionary dynamics (Dieckmann and Law 1996; see below).

In addition to the selection gradients, the evolutionary dynamics of the two traits  $x$  and  $y$  is also affected by the constraints imposed by the covariance matrix  $\mathbf{G}$ . This matrix describes the variance and covariance structure of the mutations that arise in a given resident. Here, we assume that the number and effect of mutations is independent of the resident and that there is no mutational covariation between niche position and niche width. Relaxing these assumptions does not alter our main conclusions (Appendix 2).

Under these assumptions, the adaptive dynamics of the two traits is simply given by

$$\frac{dx}{dt} = s_1(x, y) \quad \text{and} \tag{13a}$$

$$\frac{dy}{dt} = s_2(x, y). \tag{13b}$$

We have emphasized throughout that evolutionary change in our models is driven by frequency-dependent selection. Frequency dependence manifests itself in equations (13a,b) for the adaptive dynamics through the fact that the direction of evolutionary change depends on the current resident population. The course of evolution is thus determined by the frequency distribution of individuals with different phenotypes. In our models, this distribution is constrained to be zero for all phenotypes other than the resident phenotypes.

*Convergence Stability*

To find the equilibrium points of the evolutionary dynamics in the two-dimensional trait space  $(x,y)$  given by equations (13a,b), we have to find solutions  $x^*$  and  $y^*$  of the equations and  $s_1(x^*,y^*) = 0$  and  $s_2(x^*,y^*) = 0$ . It is possible to prove the following facts analytically. The adaptive dynamics have a unique equilibrium point  $(x^*,y^*)$  with  $x^* = 0$  independent of the value of the cost parameter  $c$ . For  $c = 0$  we have

$$y^* = y_{crit} = \sqrt{\left( \frac{\sigma_S^5 \cdot S_0}{2m} \right)^{2/5} - \sigma_S^2}. \tag{14}$$

This value is denoted by  $y_{crit}$  for reasons that will become clear later. For now it suffices to say that if there are costs to generalists, that is, if  $c > 0$ , then  $y^* < y_{crit}$ , that is, the niche width evolves to lower values. The opposite is true if there are costs to specialists ( $c < 0$ ), in which case  $y^* > y_{crit}$ . The selection gradient  $s_1$  on niche position satisfies  $s_1(x,y) > 0$  for  $x < x^*$ , and  $s_1(x,y) < 0$  for  $x > x^*$ , independent of the niche width  $y$ . Therefore, in the two-dimensional phenotype space  $(x,y)$  the adaptive dynamics will always converge onto the line given by  $x = x^* = 0$ . On this line the adaptive dynamics is given by the one-dimensional system  $dy/dt = s_2(0, y)$ . Furthermore, it is always true that  $(\partial s_2 / \partial y)|_{x=x^*, y=y^*} < 0$ , which means that along the line  $x = 0$ , the singular point  $y^*$  is locally stable for this one-dimensional

system. Finally, since the singular point  $(x^*, y^*)$  is unique, so that there are no other equilibria on the line  $x = x^* = 0$ , it follows that this point is also globally stable.

Thus, the evolutionary dynamics always converges to a point in trait space at which the niche position  $x^*$  matches the resource with the highest carrying capacity. It is important to note that this also happens when the carrying capacity of the consumer,  $K_{x,y}$ , does not have a maximum at  $x = 0$ , so that the consumer does not necessarily maximize its carrying capacity during the evolutionary process. The significance of the value  $y^*$  to which the width of the utilization curve evolves will become clear in the next section.

### Evolutionary Stability

It is an elementary fact in adaptive dynamics theory that convergence stability does not imply evolutionary stability and vice versa (see Metz et al. 1996; Geritz et al. 1998). In particular, convergent stable singular points can be evolutionarily unstable. Such a singular point is called an ‘‘evolutionary branching point,’’ at which invasion of nearby mutants gives rise to evolutionary diversification into diverging lineages (e.g., Dieckmann and Doebeli 1999). Investigating the evolutionary stability of convergent stable singular points therefore addresses our primary question of when our ecological setup can give rise to adaptive diversification.

We therefore want to test for evolutionary stability of the attractor  $(x^*, y^*)$ , that is, we must address the question of whether nearby mutant trait values can invade. This is done by considering second derivatives of the invasion fitness function  $f(x, y, u, v)$  given by equation (11) with respect to the mutant trait values and evaluated at the singular point  $(x^*, y^*)$ . More precisely, evolutionary stability is determined by the Hessian matrix  $\mathbf{H}^*$  of second derivatives of  $f$  at the singular point  $(x^*, y^*)$ :

$$\mathbf{H}^* = \begin{pmatrix} \left. \frac{\partial^2 f}{\partial u^2} \right|_{u=x^*, v=y^*} & \left. \frac{\partial^2 f}{\partial u \partial v} \right|_{u=x^*, v=y^*} \\ \left. \frac{\partial^2 f}{\partial v \partial u} \right|_{u=x^*, v=y^*} & \left. \frac{\partial^2 f}{\partial v^2} \right|_{u=x^*, v=y^*} \end{pmatrix}. \quad (15)$$

The equilibrium  $(x^*, y^*)$  is evolutionarily stable if  $\mathbf{H}^*$  is negative definite, that is, if both eigenvalues of this symmetric, real-valued matrix are negative (Leimar 2001). In the present case, one can show that

$$\mathbf{H}^* = \begin{pmatrix} h_1 & 0 \\ 0 & h_2 \end{pmatrix}, \quad (16)$$

with  $h_1 = \partial^2 f / \partial u^2|_{u=x^*, v=y^*}$  and  $h_2 = \partial^2 f / \partial v^2|_{u=x^*, v=y^*}$ .

One can also show that, independent of the value of the cost parameter  $c$ , it is always true that  $h_2 < 0$ . Thus, the singular point always represent a fitness maximum with respect to variation in the  $y$ -direction. The central result of this paper is that the propensity for disruptive selection on niche position, and thus for an adaptive split into two diverging lineages, is determined by the costs or benefits for widening the niche. Without costs or benefits (i.e., if  $c = 0$ ), the resident population evolves a niche width  $y^* = y_{crit}$  that is precisely wide enough to annihilate any disruptive selection on the

niche position. In other words, one can show that for  $c = 0$ ,  $h_1 = 0$  in the Hessian  $\mathbf{H}^*$ . Further analysis of higher order derivatives, as well as the results of the individual-based model (see below), indicate that in the absence of costs or benefits for generalists, the attractor  $(x^*, y^*)$  is indeed evolutionarily stable and thus represents the final outcome of the evolutionary process.

Assuming no costs or benefits for generalists represents a structural instability, in that it implies that the niche width is exactly neutral with respect to the total rate of resource uptake. Considering cases with  $c \neq 0$  reveals that the case without costs represents a dividing line between two different evolutionary regimes. More precisely, if  $c > 0$ , so that there are costs for specialization, the singular niche width  $y^*$  is larger than  $y_{crit}$ , which implies  $h_1 < 0$  in the Hessian  $\mathbf{H}^*$ . This means that the singular point  $(x^*, y^*)$  is evolutionarily stable. Thus, a benefit to generalization lets the niche width evolve to a value that is large enough to overcompensate the disruptiveness on the trait  $x$  that is due to frequency-dependent competition. As a consequence, the trait  $x$  experiences stabilizing selection at the equilibrium of the adaptive dynamics, and this equilibrium represents the endpoint of the evolutionary process.

In contrast, if  $c < 0$ , so that there is a cost to widening the niche, the singular niche width  $y^*$  is smaller than  $y_{crit}$ , and one can show that this implies that  $h_1 > 0$  in the Hessian  $\mathbf{H}^*$ . In other words, with a cost to generalism a population at the singular point  $(x^*, y^*)$  experiences disruptive selection on the niche position. Thus, a cost to generalism prevents the niche width from evolving to a value that is large enough to neutralize the disruptiveness on the trait  $x$  that arises due to frequency-dependent competition. As a consequence, the trait  $x$  will undergo evolutionary branching.

Overall, we can see that the cost or benefits for generalists determine the evolutionary outcome. The neutral case without costs or benefits delimits the conceptual border for evolutionary branching: the model exhibits disruptive selection on the niche position with costs to generalists but stabilizing selection when there are benefits for generalists.

### Individual-Based Models

We tested the analytical predictions derived in the previous sections using an individual-based model based on the logistic dynamics of the consumer given by equation (6). For simplicity, the individual-based model is set in discrete time, so that all individuals can be updated synchronously. To approximate the assumption of infinitely small mutations made for the analytical model, we chose the mutations in the individual-based model to be of small effect. The individual-based model is described in Appendix 3.

Figure 4 illustrates four typical evolutionary scenarios resulting from this individual-based model. In the first scenario, we assumed a fixed niche width for all individuals at some value  $y_{fixed}$ . In Figure 4A,  $y_{fixed} > y^*$ , where  $y^*$  is the evolutionary equilibrium in the case where there are no costs or benefits for increasing  $y$  ( $c = 0$ ). In this case, the fixed niche width is too large, that is, frequency dependence is too weak, for competition to induce disruptive selection on the niche position, hence the equilibrium  $x^* = 0$  is evolutionarily sta-

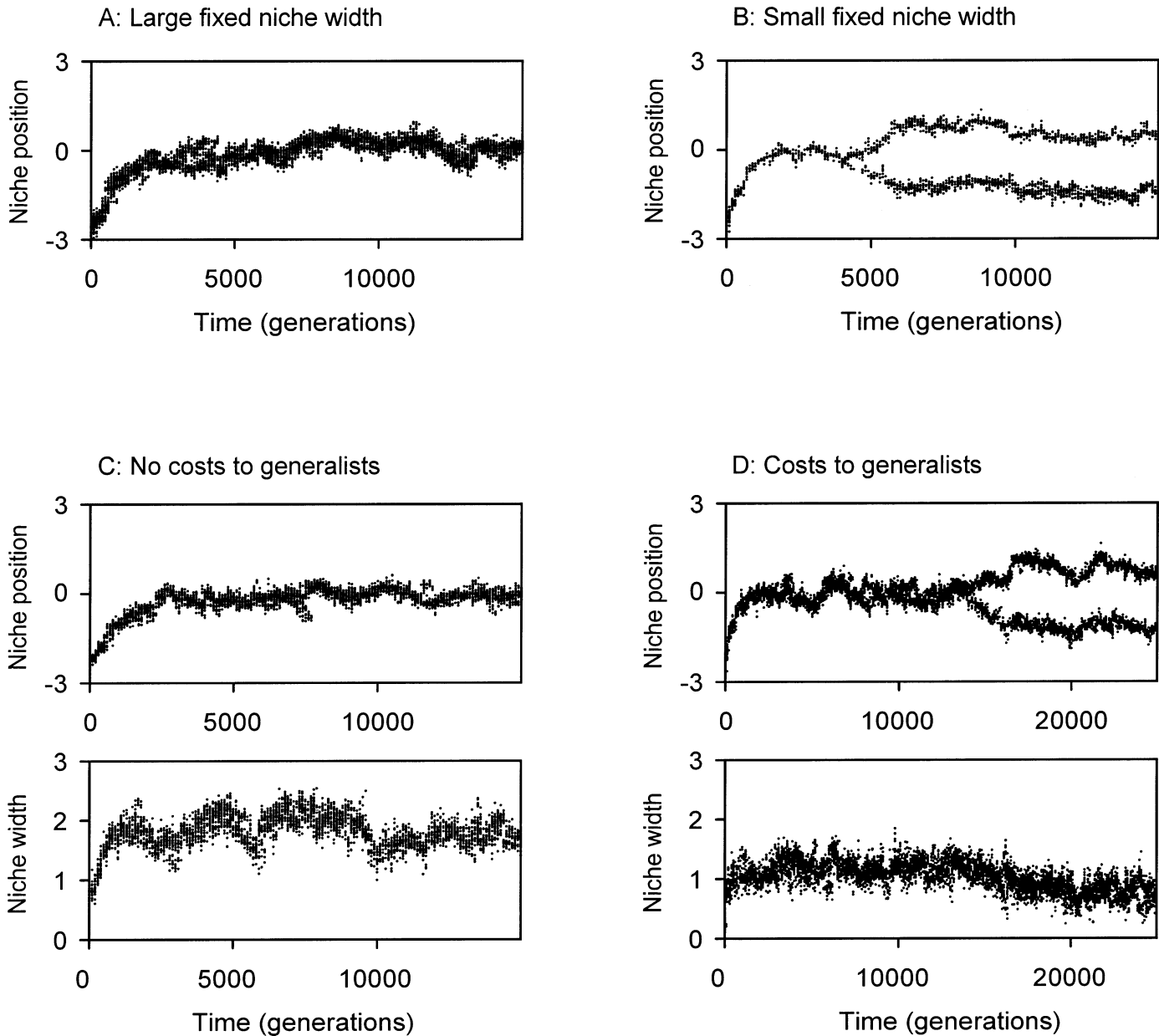


FIG. 4. Examples of evolutionary trajectories generated by the individual-based model. (A) No diversification in niche position if the niche width is fixed at a value  $y_{fixed} > y_{crit}$ , where  $y_{crit}$ , given by equation (14), is the evolutionary equilibrium in the case where there are no costs or benefits for increasing  $y$  ( $c = 0$ ). (B) Evolutionary branching in niche position if the niche width is fixed at a value  $y_{fixed} < y_{crit}$ . (C) No diversification in either trait, niche position or niche width, if the niche width is free to evolve, and if there are no costs to generalists ( $c = 0$ ). (D) Evolutionary branching in niche position if the niche width is free to evolve but there is a cost to generalists ( $c = 0.6$ ). Note that diversification occurs in the form of distinct phenotypic clusters, rather than in the form of a single cluster that is continuously polymorphic. Also note that diversification in niche position is accompanied by a general decrease in the niche width. For all figures, the runs were started with a population of 200 individuals whose phenotypes were drawn from a Gaussian distribution with variance 0.1 and with mean equal to  $-2.5$  for the niche position and  $0.5$  for the niche width. In every generation, offspring experienced mutations with probability 0.01 independently in each evolving trait; if a mutation occurred, the mutant phenotype was drawn from a Gaussian distribution with the parental phenotype as mean and with variance 0.1. Every 100th generation, the different phenotypes present in the population are displayed. Parameter values:  $\lambda = 1.5$ ,  $m = 0.2$ ,  $\sigma_S = 1$ ,  $S_0 = 12$ , which implies that  $y^* \approx 1.702$ . In (A)  $y_{fixed} = 2.5$ , while in (B)  $y_{fixed} = 0.7$ .

ble. In contrast, consider  $y_{fixed} < y^*$  in Figure 4B: now the fixed niche width is not large enough to offset the disruptive selection generated by frequency-dependent competition, hence the system exhibits evolutionary branching into two distinct niche position clusters. Phenomenologically, this sce-

nario corresponds to cases in which frequency-dependent competition leads to evolutionary branching in the models of Dieckmann and Doebeli (1999). However, in contrast to those models, we have chosen an example where the consumer carrying capacity actually has a minimum for the niche

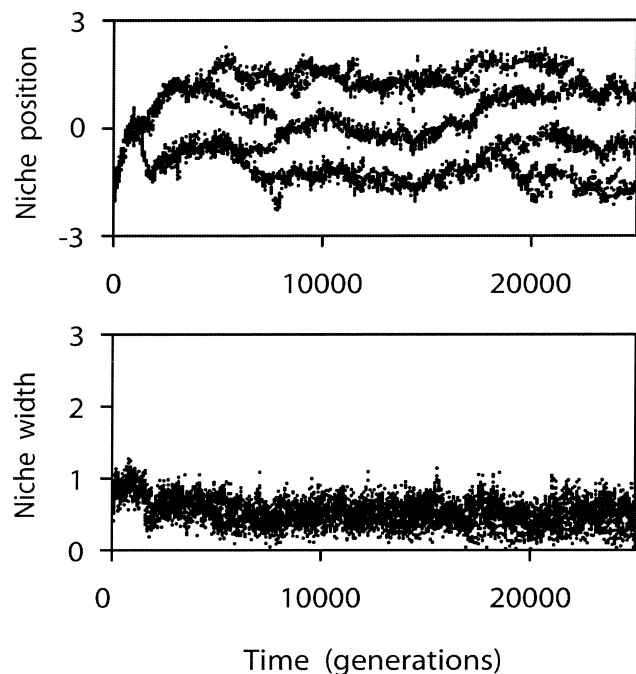


FIG. 5. Multiple branching if costs to generalists are high. Evolution of very narrow niches facilitates greater diversification in niche position. Note again that diversification occurs in the form of distinct phenotypic clusters, rather than in the form of a single cluster that is continuously polymorphic. Parameter values: same as in Figure 4D, except that  $c = 1.25$ .

position  $x^* = 0$  corresponding to the maximal resource carrying capacity (cf. Fig. 2). Despite that, the niche position first evolves to the equilibrium  $x^* = 0$  and subsequently undergoes diversification. It is also worth noting that branching occurs at  $x^* = 0$  despite the fact that nearby mutant experience higher competitive impacts from the resident at  $x^* = 0$  than resident individuals themselves (cf. Fig. 3).

Figure 4C shows the evolutionary dynamics of the individual-based model in the case in which both the niche position  $x$  and the niche width  $y$  are free to evolve and in which increasing  $y$  has no costs or benefits ( $c = 0$ ). As predicted by the analytical theory, the system converges to the evolutionary attractor  $(x^*, y^*)$  given by  $x^* = 0$  and  $y^* = y_{crit}$  (eq. 14), which represents the final evolutionary outcome. In particular, no branching occurs.

Finally, Figure 4D shows the evolutionary dynamics of  $x$  and  $y$  when there is a cost to having higher  $y$ , that is, to being a generalist ( $c > 0$ ). Again as predicted by the analytical theory, the niche position undergoes evolutionary branching, while the niche width does not. Instead, concomitant with the evolutionary diversification in niche position, the niche width becomes smaller in both emerging clusters. Figure 5 illustrates that with even higher costs, niches become so narrow as to allow for multiple evolutionary branching: because the niches are smaller, there is room for more phenotypic clusters with respect to niche position. The two clusters emerging from the primary branching event are again evolutionarily unstable and hence give rise to secondary branching. Due to the symmetry of the system, secondary branching should occur in both primary branches, but in the example

shown there is only room for one additional (intermediate) cluster. Stochastic effects therefore lead to occasional extinction or merging of intermediate clusters, so that diversification results in three branches for most of the time, with intermittent occurrences of a fourth phenotypic species. The fact that higher costs to generalists lead to more coexisting phenotypic species is reminiscent of classic results from the theory of limiting similarity, according to which smaller niche widths allow more species to coexist (May and MacArthur 1972).

## DISCUSSION

We were interested in the conditions under which competition for a continuously distributed resource can lead to processes of evolutionary diversification in which the splitting of a lineage is an adaptive response to frequency-dependent selection. In our models, competition is frequency-dependent because the strength of competition depends on the amount of niche overlap between different individuals. The amount of niche overlap, in turn, depends on the positions and the widths of the individuals' niches, and we developed models to study evolutionary changes in niche width and niche position.

In our models, individuals are characterized by their resource utilization curve, which determines the rates at which an individual is using different types of a continuously varying resource. The utilization curve is described by two quantities: its center (the niche position) and its width (the niche width). We assumed that these quantities are phenotypic traits and studied their evolution using the framework of adaptive dynamics (Metz et al. 1996; Geritz et al. 1998). This analytical approach was complemented with individual-based models.

We found that in an initial phase the niche position evolved to match the maximum of the resource curve, even if this niche position corresponds to a local minimum of the consumer carrying capacity. Subsequent evolution of the niche position depended on the costs or benefits for increases in niche width. If increasing the niche width has benefits, then one single resident population evolved that covered the resource distribution to an extent that did not allow the invasion of individuals with alternative niche positions. If, however, increasing the niche width had costs, the utilization curve of the resident population remained relatively narrow, leaving substantial amounts of resources on both sides of the maximum of the resource curve. The analytical model predicted that this would lead to disruptive selection on the niche position. The individual-based model corroborated this by showing that this situation indeed led to the invasion of individuals with niche positions to the left and right side of the resource curve (Fig. 4). As a consequence, two evolutionarily diverging clusters of individuals with different niche positions became established, corresponding to a process of adaptive diversification.

Our results indicate that adaptive speciation is indeed a probable outcome of competition for a continuously distributed resource, corroborating the results by Doebeli (1996), Dieckmann and Doebeli (1999), and Drossel and McKane (2000). The general agreement in the outcome between these

earlier models and ours is not trivial, because there are a number of important differences in the modeling approaches, as will be discussed below. In fact, we believe that the approach presented here is both mathematically more general and ecologically more realistic, because it explicitly includes the resource in the basic ecological dynamics that drives the evolutionary process.

#### *Generality of Our Model*

Due to the inclusion of resource dynamics and because it describes the evolutionary dynamics of a pair of traits rather than of a single trait, the adaptive dynamics model presented here is more complicated than earlier models for diversification due to frequency-dependent competition. Nevertheless, the predictions emerging from our models regarding the conditions for adaptive speciation are actually simpler than for example those obtained in Dieckmann and Doebeli (1999). In that model, which assumes unimodal consumer carrying capacities and symmetric competition, evolutionary branching occurs if the width of the carrying capacity curve is larger than the width of the competition function. Thus, conditions for evolutionary diversification are expressed in terms of two parameters that may be difficult to determine in real biological systems, because they involve measuring population properties and properties of groups of interacting individuals. In contrast, in our models the conditions for diversification are expressed in terms of single parameter measuring the relative costs of widening individual diet breadth.

To make our model of the evolution of niche widths and positions analytically tractable, we had to make a number of simplifying assumptions. In particular, we assumed that various parameters describing the ecological dynamics of the consumer and the resource are independent of consumer phenotype or resource type. We expect that our general results regarding the effect of evolutionary change in the niche width on the selection profile for niche position are robust with regard to assumptions about variation in these parameters. For the consumer, only the distribution of energy contained in resource items along the resource axis is relevant. As long as resource consumption can be molded by evolutionary change in the niche width as envisaged here, the results should not change qualitatively.

For the same reason, we expect that the results are independent of the exact form of the resource distribution and utilization curve. In our model, the resource curve in absence of the consumer has the same shape as the utilization curve. One might think that this fact is responsible for the annihilation of selection on niche position observed in the case of no costs for widening the niche. However, there are two lines of evidences suggesting that this is not the case. First, the evolutionary dynamics is driven by the actual distribution of the resource in the presence of the consumer rather than by the initial distribution without consumer. The resource distribution in presence of a consumer is not Gaussian, but typically bimodal (Fig. 1). Second, it is possible to analyze situations where the resource distribution and the utilization curve are not of the same form and to show that selection on niche position still vanishes. For example, if in the Gaussian expression for the resource carrying capacity, equation

(2), the term  $(z - z_0)^2$  (describing the decline of the resource carrying capacity with increasing distance from the maximum at  $z_0$ ) is replaced by terms  $(z - z_0)^4$  or  $(z - z_0)^8$ , the resulting adaptive dynamics model has exactly the same qualitative properties as with Gaussian resource carrying capacities. This indicates that the robust result is that as long as there is a shape parameter of the utilization curve influencing the niche width, then, in the absence of costs, this parameter will evolve so as to exactly compensate for disruptive selection on niche position.

#### *Variation between Individuals and Sexual Reproduction*

Adaptive lineage splitting and the evolution of a wide utilization curve can be seen as two alternative processes, and the costs associated with widening the utilization curve determine which of the two processes is more likely to occur. These two processes interact antagonistically. If a wide utilization curve is either assumed or can evolve without costs then adaptive diversification is not observed. However, if the conditions for speciation are fulfilled, then the speciation event tends to lead to a decrease in the width of the utilization curve (Fig. 4D).

In fact, there is a third process that could lead to a match between the total utilization of the consumer community and the resource curve, which can be illustrated by considering a situation with a wide resource distribution. Without costs for widening the niche, all individuals will evolve wide and congruent niches. The populationwide utilization curve (the sum over the individual utilization curves) is Gaussian with a large variance. What happens now if costs for large niche widths keep the individual utilization curves narrow? If within- and between-individual variation were replaceable, one would assume that between-individual variation would simply compensate for the constrained within-individual variation (Taper and Case 1985). In this case, one would expect a population to evolve in which all individuals have narrow utilization curves, but in which the positions of the maxima of the utilization curves, that is, the niche positions, would vary in such a way that the population would have the same populationwide utilization curve as before.

However, this is not what happens in our individual-based models, which show that when the adaptive dynamics model predicts evolutionary branching, the populations diversify into distinct clusters with respect to niche position, rather than into a highly polymorphic population with continuously varying niche positions that cover a whole range of resources (Figs. 4D,E). This is the fundamental and somewhat surprising result of studies on adaptive diversification by means of evolutionary branching (Metz et al. 1996; Geritz et al. 1998). Discrete clusters evolve because of the disruptiveness that emerges in a population at the branching point. Disruptiveness in turn results when the resident population at the maximum of the resource carrying capacity depresses resources to such an extent that mutant consumers can invade whose niche positions allow them to take advantage of the more abundant resources to either side of resident niche. Our results thus illustrate the limitations of a populationwide perspective, which would not capture essential features of the evolutionary invasion process studied here. This leads to the

insight that within- and between-individual variation in resource use are not replaceable in evolutionary terms.

In our models, the emergence of discrete clusters is facilitated by the fact that, throughout our analysis, we have assumed a consumer that reproduces asexually. Asexual reproduction facilitates diversification as compared to sexual reproduction, as the latter leads to continuous production of intermediate types, preventing the formation of discrete phenotypic classes. Given this, will sexual populations thus evolve continuously varying niche positions that match the niche distribution? The answer depends on the balance between different biological properties of the evolving population. One reaction to disruptive selection might be a diversification of the niche position through an increase in the genetic variation. Widening the variation in niche position between individuals decreases disruptive selection on this trait and might thus bring further diversifying evolution to a halt.

Alternatively, there are biological processes that promote the emergence of discrete diverging clusters rather than a wide unimodal niche distribution within the population. One important process is the evolution of assortative mating. Previous models (Doebeli 1996; Dieckmann and Doebeli 1999; Kondrashov and Kondrashov 1999; Drossel and McKane 2000) have shown that disruptive selection on the characteristics of resource consumption leads selection for assortative mating with respect to these traits. As a consequence of assortative mating, there is little or no gene flow between groups, so that the formation of these groups corresponds to adaptive speciation. Thus, despite being asexual, our models are also relevant for understanding adaptive speciation in sexual populations, because they inform us about the conditions that make lineage splitting an adaptive response to ecological interactions, and hence about the conditions that potentially favor the evolution of reproductive isolation through assortative mating.

#### *Costs of Being a Generalist*

Our analysis shows that competition for resources with a broad distribution is likely to lead to adaptive diversification if consuming a wide range of resources is either costly or prevented by constraints. Under what circumstances do we expect substantial costs for niche generalism to arise? This question traces back to the question of why having a wide utilization curve should have costs in terms of the niche depth in the first place. These costs are a manifestation of general trade-offs in the ability to deal with different types of resources, trade-offs that are central to every discussion of resource generalism versus specialism. They are often postulated, but typically difficult to demonstrate (Futuyma and Moreno 1988).

Several processes could cause such trade-offs. It is possible that the efficient handling of a resource requires morphological (Smith 1987; Schluter 1995; Schondube and del Rio 2003; Svanback and Eklov 2003) or physiological (Schoonhoven and Meerman 1978) adaptations that impair the handling of other, different resources. Alternatively, perception and information processing might become inefficient if the range or resources targeted is large (Courtney 1983; Bernays

2001). Finally, if resources are spatially distributed and similar resources clustered, then consuming a wide range of resources results in increased expenditures in terms of time and energy for traveling.

It is difficult to make general predictions about when such costs outweigh the benefits of a widened diet. It is therefore difficult to predict under what circumstances and how often competition for resources can set the stage for adaptive speciation in natural situations. Even if costs to generalists can be measured unequivocally in a given context, these costs might themselves change in the course of evolution in a way that alters the outcome. Nevertheless, it seems possible to find out whether special ecological situations are likely to lead to costs to generalists, so that one could then test whether these situations are frequently associated with speciation events. Such information could for example be obtained from evolution experiments with microorganisms such as *Escherichia coli*. Indeed, in a recent review Kassen (2002) argued that such experiments have yielded evidence for both costs to generalists and costs to specialists. It seems feasible that the same experimental systems could also be used to test whether adaptive diversification is indeed observed under suitable circumstances.

#### *Comparison to Previous Models of Diversification Due to Resource Competition*

In contrast to many previous models that used a continuously distributed resource to study evolution of consumer populations, we treated the resource dynamics explicitly. This has a number of important and perhaps nonintuitive consequences that are absent in the earlier models. One consequence of this approach is that the carrying capacity of the consumer is not necessarily maximized if the center of the utilization curve, that is, the niche position, is at the maximum of the resource distribution. Most previous models assumed that a Gaussian resource distribution would lead to a carrying capacity curve that is also Gaussian (Roughgarden 1976; Slatkin 1980; Case 1981; Doebeli 1996; Dieckmann and Doebeli 1999). Here we found that, for a part of the parameter space, the consumer carrying capacity is in fact bimodal, with a local minimum at the position where the resource distribution has a maximum. Intuitively, this scenario is similar to one in which overharvesting leads to a reduction in yield.

Because initially the niche position always evolves to the maximum of the resource curve, this means that evolution does not necessarily maximize consumer carrying capacity, as has been noted before in different contexts (e.g., Slobodkin 1968; Rosenzweig 1973; Abrams 1983; Matessi and Gatto 1984; Holt 1985). A similar effect arises with respect to the niche width. As can be seen in Figure 2, the niche width at the evolutionary equilibrium is much smaller than the niche width that would maximize the consumer carrying capacity. These two effects can be seen as manifestation of the ‘‘tragedy of the commons,’’ where individual interests lead to a situation where a shared resource is inefficiently used (Hardin 1968).

A second consequence of modeling resource dynamics and resource utilization explicitly is that competition coefficients

are generally not symmetric, and hence do not only depend on the distance between niche positions of competing individuals. Traditionally, it has been assumed that competition is maximal for coinciding niche positions and decreases in a Gaussian fashion with increasing distance between the niche positions (Slatkin 1980; Doebeli 1996; Dieckmann and Doebeli 1999; Drossel and McKane 2000). However, basing competition on the dynamics of the shared resource reveals that the niche position of an individual relative to the resource distribution matters for the individual's competitive effect on others. The closer an individual's niche position to the maximum of the resource carrying capacity, the stronger is the individual's competitive impact on coexisting individuals. This effect can be so strong that it overcomes the reduction in competition resulting from increasing distance between the niches of two individuals. In this case, an individual that resides at the maximum of the resource carrying capacity exerts a weaker competitive effect on individuals with similar niche position than on individuals with distant niche position. Abrams (1998) reported a similar effect for a situation where individuals compete for three discrete resources.

It is worth noting that in our models, one obtains the symmetric competition coefficients of earlier models by making the assumption that the resource distribution is flat, so that all resource types are equally abundant, and that all individuals have the same, fixed niche width. A flat resource distribution implies that the consumer carrying capacity is flat, that is, independent of the niche position. Assuming both symmetric competition and unimodal consumer carrying capacities, as has been done in most existing models for character displacement and adaptive speciation, is therefore not consistent with the version of MacArthur's (1972) model studied here. Overall, our results put in perspective some widespread ideas about the consequences of competition for a shared, continuously distributed resource, supporting the notion of Chesson (1990) and Abrams (1998) that much can still be learned from MacArthur's consumer-resource model in its original form.

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APPENDIX 1

*Deriving the Consumer Carrying Capacity and the Competition Coefficients*

To derive a logistic equation for the consumer dynamics, one finds, for a given consumer density  $N_{x,y}$ , the nonzero solution  $\hat{F}(z)$  of the resource equation (4) (this solution is illustrated in Fig. 1C). One then substitutes this solution into equation (5), which yields:

$$\begin{aligned} \frac{dN_{x,y}}{dt} &= RN_{x,y} \left[ b \int_{-\infty}^{\infty} a_{x,y} \hat{F}(z) dz - m \right] \\ &= RN_{x,y} \left\{ b \int_{-\infty}^{\infty} a_{x,y}(z) [r - a_{x,y}(z) N_{x,y}] \frac{S(z)}{r} dz - m \right\}. \end{aligned} \quad (A1)$$

If we set

$$R_{x,y} = R \left[ b \int_{-\infty}^{\infty} a_{x,y}(z) S(z) dz - m \right] \quad \text{and} \quad (A2)$$

$$K_{x,y} = \frac{r \left[ b \int_{-\infty}^{\infty} a_{x,y}(z) S(z) dz - m \right]}{b \int_{-\infty}^{\infty} [a_{x,y}(z)]^2 S(z) dz}, \quad (A3)$$

the population dynamic equation for the consumer becomes

$$\frac{dN_{x,y}}{dt} = R_{x,y} \cdot N_{x,y} \cdot \left( 1 - \frac{N_{x,y}}{K_{x,y}} \right). \quad (A4)$$

Thus, the consumer (x,y) grows logistically to carrying capacity  $K_{x,y}$ , and its intrinsic growth rate is  $R_{x,y}$ . Note that for a given resource distribution  $S(z)$  and a given utilization type  $a_{x,y}(z)$ , both  $R_{x,y}$  and  $K_{x,y}$  become negative for large  $m$ , which means that the consumer would not be able to grow. We also note that the expression for  $K_{x,y}$  is equivalent to equation (9) in Schoener (1974).

For the resource distributions  $S(z)$  and the utilization curves  $a_{x,y}(z)$  given by equations (2) and (3), an expression for  $K_{x,y}$  is given in the main text, and  $R_{x,y}$  can be calculated as

$$R_{x,y} = R \left[ \frac{b\sigma_S S_0 \exp\left(-\sigma_S y - \frac{x^2}{2\sigma_S^2 + 2y^2}\right)}{2\sqrt{\sigma_S^2 + y^2}} - m \right]. \quad (A5)$$

This implies that as a function of the niche position, the intrinsic growth rate has a maximum at  $x = 0$ , corresponding to the maximum of the resource carrying capacity. This is intuitively clear, as the intrinsic growth rate can be viewed as describing exponential growth in the absence of competitors. In contrast, the carrying capacity  $K_{x,y}$  need not have an maximum at  $x = 0$  (see main text).

If two consumer types (x,y) and (u,v) are present, then the dynamics of the resource is, in analogy to equation (4), described by

$$\begin{aligned} \frac{dF(z)}{dt} &= rF(z) \left[ 1 - \frac{F(z)}{S(z)} \right] \\ &\quad - F(z) [a_{x,y}(z) N_{x,y} + a_{u,v}(z) N_{u,v}], \end{aligned} \quad (A6)$$

where  $N_{x,y}$  and  $N_{u,v}$  are the densities of the two consumers, and  $a_{x,y}$  and  $a_{u,v}$  are their respective utilization functions. Solving this equation for given  $N_{x,y}$  and  $N_{u,v}$  yields equilibrium resource densities  $\hat{F}(z)$  that can be substituted into the population dynamic equation (5) for consumer (x,y). After some algebraic manipulation, this yields the expression

$$\frac{dN_{x,y}}{dt} = R_{x,y} N_{x,y} \left[ 1 - \frac{N_{x,y} + \beta(x, y, u, v) N_{u,v}}{K_{x,y}} \right], \quad (A7)$$

where

$$\beta(x, y, u, v) = \frac{\int_{-\infty}^{\infty} a_{x,y}(z) a_{u,v}(z) S(z) dz}{\int_{-\infty}^{\infty} [a_{x,y}(z)]^2 S(z) dz} \quad (A8)$$

is the relative competitive impact of a consumer individual of type (u,v) on consumers of type (x,y). Note that this equation implies  $\beta(x, y, x, y) = 1$ , as it should be.

We note that we can recover the symmetric competition coefficients so pervasively used in competition models by assuming that  $c = 0$  (no costs for widening the niche), that all competitors have a fixed width  $y_0$  of the utilization function, and by considering the limit when  $\sigma_S \rightarrow \infty$ , that is, when the carrying capacity of the resource is independent of  $z$ . In this case it is easy to see from equation (9) that

$$\beta(x, y_0, u, y_0) = \exp\left[\frac{-(u-x)^2}{4y_0^2}\right]. \quad (A9)$$

This is the symmetric competition coefficient derived by Roughgarden (1979). It is important to note that such symmetry of competitive impacts between interacting types only occurs under the assumption of constant resource carrying capacities, which in turn imply constant consumer carrying capacities as a function of the position of the preferred resources  $x$ . Thus, while models that contain both the symmetric competition coefficients (A9) and a nonconstant consumer carrying capacity (as a function of  $x$ ) may be biologically plausible, such models cannot be derived from the basic MacArthur (1972) model used here.

APPENDIX 2

*The Covariance Matrix G*

The covariance matrix  $\mathbf{G}$  describes the variance and covariance structure of the mutations. Together with the selection gradients  $s_1(x, y)$  and  $s_2(x, y)$ , it determines the evolutionary rate of change in  $x$  and  $y$  as follows:

$$\begin{pmatrix} \frac{dx}{dt} \\ \frac{dy}{dt} \end{pmatrix} = \mathbf{G} \begin{bmatrix} s_1(x, y) \\ s_2(x, y) \end{bmatrix}. \quad (A10)$$

In general, the matrix  $\mathbf{G}$  has entries that may depend on the current resident trait values (x,y), for example, because the number of new mutations occurring in a particular resident may depend on the population size. Here we will assume that the matrix  $\mathbf{G}$  is the identity matrix,

$$\mathbf{G} = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}. \quad (A11)$$

The results about the existence and local stability of the singular point  $(x^*, y^*)$  remain valid for nontrivial covariance matrices  $\mathbf{G}$ , that is, for the more general adaptive dynamics given by equation (A10).

This is true because, on the one hand,  $(x^*, y^*)$  is of course still an equilibrium of this dynamics and, on the other hand, the Jacobian matrix at this equilibrium is  $\mathbf{J}' = \mathbf{G} \cdot \mathbf{J}^*$ , where  $\mathbf{J}^*$  is the Jacobian matrix of the dynamical system (13) at the equilibrium  $(x^*, y^*)$ . One can show that  $\mathbf{J}^*$  is of the form

$$\mathbf{J}^* = \begin{pmatrix} j_1 & 0 \\ 0 & j_2 \end{pmatrix}, \quad \text{with}$$

$$j_1 = \left. \frac{\partial s_1}{\partial x} \right|_{x=x^*, y=y^*} < 0 \quad \text{and}$$

$$j_2 = \left. \frac{\partial s_2}{\partial y} \right|_{x=x^*, y=y^*} < 0.$$

Since  $\mathbf{G}$  must be symmetric and must have positive entries in the diagonal, it is easy to see from this that both eigenvalues of the Jacobian  $\mathbf{J}'$  must have negative real parts, and hence that  $(x^*, y^*)$  is always locally stable for the system (A10).

APPENDIX 3

*Individual-Based Model*

To make the transition from the continuous-time logistic equation (6) to a discrete time model, we took advantage of the fact that the logistic equation  $dN/dt = rN [1 - (N/K)]$  is dynamically equivalent to the discrete-time Beverton-Holt dynamics given by

$$N' = \frac{\lambda N}{1 + \frac{\lambda - 1}{K} N}, \tag{A12}$$

where  $N$  and  $N'$  are population densities in successive generations, and  $\lambda = \exp(r)$  (see Yodzis 1989; dynamic equivalence implies that the population time series generated by the discrete model is obtained through sampling of the trajectory of the continuous model at unit time intervals). Accordingly, in the individual-based model the survival probability of an individual with phenotype  $(x, y)$  from one generation to the next is given by

$$\frac{1}{1 + \frac{\exp(R_{x,y}) - 1}{K_{x,y}} N_{eff}}. \tag{A13}$$

Here  $R_{x,y}$  and  $K_{x,y}$  are given by equations (A5) and (7), respectively, and the effective density  $N_{eff}$  that the individual experiences due to competition from other individuals is

$$N_{eff} = \sum_{(u,v)} \beta(x, y, u, v), \tag{A14}$$

where the sum runs over all individuals  $(u, v)$  in the population. After survival of all individuals is determined probabilistically according to equation (A13), the surviving individuals each give birth to a Poisson distributed number of offspring with mean  $\lambda = \exp(R_{x,y})$  and then die. With probability  $\mu$  an offspring's  $x$  trait is different from the parent's trait, in which case the offspring trait is chosen from a normal distribution with mean the parent trait and variance  $\sigma_\mu$ , and similarly for the  $y$  trait.