

The Effect of Competition Among Resources on  
Phenotypic Evolution of Consumers

by

Seiji Kumagai

Department of Biology  
Duke University

Date: \_\_\_\_\_

Approved:

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William G. Wilson, Supervisor

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Kathleen Donohue

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William F Morris

Thesis submitted in partial fulfillment of the requirements for the degree of  
Master of Science in the Department of Biology  
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ABSTRACT  
(Ecology)

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# Abstract

The pattern of competition among consumers is one of the important factors that determine if consumer traits diverge or remain monomorphic under natural selection. Despite its importance, a detailed understanding of the factors that can affect the pattern remains unclear. This problem is especially acute with regards to how resource dynamics affects consumer trait evolution. One aspect of resource biology known to affect the evolution is the shape of resource distribution. Here I investigate the effect of interacting resources on the trait evolution of consumers in an extension of previous models. I focus on competitive interactions among resources, and because resource competition alters the resource distribution, the evolutionary dynamics of consumers is also affected. What I find is that resource competition does not change a condition determining when the consumer traits to diverge, but change the pattern of divergence when the traits diverge.

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# 1

## Introduction

Interactions of organisms with their environments are important aspects of natural selection. Organisms face the direct interactions as well as the indirect feedback from the changed environment. Understanding mechanisms and consequences of such interactions has been a core question in biology. Recently the ability of organisms to induce environmental changes is increasingly emphasized in ecology (Jones et al., 1994, 1997; Wright and Jones, 2006). The changes in turn force the organisms to survive under a novel environmental condition. Furthermore, in a system where organisms and environmental factors affect dynamics of each other, the knowledge of such interactions may further the understanding of organismal evolution (Odling-Smee et al., 1996; Laland et al., 1999).

Among many types of ecological interactions, consumer-resource interactions have proven to be a useful framework to explore various aspects of evolutionary changes. Models based either explicitly or implicitly on consumer-resource dynamics have provided insight into character displacement, limiting similarity, and disruptive selection (MacArthur and Levins, 1967; Roughgarden, 1976; Slatkin, 1980; Case, 1981; Case and Taper, 1986; Doebeli, 1996; Abrams et al., 2008a,b; Abrams and Rueffler,

2009). Diversification of an originally monomorphic consumer population, often considered a prerequisite for speciation, may also be driven by competition for shared resources (Dieckmann and Doebeli, 1999; Drossel and McKane, 2000; Schluter, 2001; Ackermann and Doebeli, 2004).

Although these studies provide a wealth of insight, they commonly make simple assumptions pertaining to non-focal populations. For example, if a focal population is a consumer species, then resources are depicted as a collection of noncompeting groups. Therefore, the population density of one resource is not affected by direct interactions with the other resource. However, competition, along with predation, is one of the most important mechanisms of population regulation (Schoener, 1983; Sih et al., 1985; Chase et al., 2002). Although the relative importance of these two factors is debated (Sih et al., 1985; Gurevitch et al., 2000), competition among resources may substantially alter the resource distribution, and because resource distribution is important for defining the pattern of competition among consumers, competition among resources can change how consumers interact. This in turn may change the course of phenotypic evolution, especially divergence, in consumers (Ackermann and Doebeli, 2004; Baptistini et al., 2009; Pigolotti et al., 2010).

In order to address how competition among resources systematically affects the evolutionary outcome of competing consumers, we analyze an extension of a consumer-resource interaction model introduced by Ackermann and Doebeli (2004).



# 2

## Model and Results

To investigate the effect of competition among resources on the phenotypic evolution of consumers, I first construct an ecological model based on Ackermann and Doebeli (2004). I then construct an evolutionary model based on the ecological model.

### 2.1 Resource Dynamics

Resources are characterized by a single continuous trait whose phenotype is described by  $z$  such as body size. This trait governs three important aspects of resource biology. The first aspect affected by  $z$  is carrying capacity. Here I assume that the population density of the resources  $F(z)$  increases logistically in the absence of consumers. If the resource population is monomorphic,  $F(z)$  reaches the carrying capacity  $K(z)$ , which is modeled by a Gaussian function

$$K(z) = K_0 \exp\left[-\frac{z^2}{2\sigma_K^2}\right], \quad (2.1)$$

with spread  $\sigma_K$  and a constant  $K_0$  scaling the total population density.

The second aspect affected by  $z$  is the extent of competition between members of different phenotypes. When the population is polymorphic, individuals of different

phenotypes may compete (inter-phenotypic competition) in addition to the competition between individuals of the identical phenotypes (intra-phenotypic competition). I am interested in evolutionary outcomes of inter-phenotypic competition in resources on consumers, which is hereafter referred as “competition among resources” or “resource competition.” These two terms are used interchangeably.

The strength of inter-phenotypic competition between two phenotypes  $z_1$  and  $z_2$ ,  $\alpha(z_1, z_2)$ , depends on phenotypic similarity, with  $\alpha$  decreasing from  $d = |z_1 - z_2| = 0$  as  $d$  increases. This situation may arise if, for example, the resources are a group of insects, and the corresponding trait is body size. If body size and dietary preference are correlated, organisms with similar body size forage on similar food items. In this case a single trait may reasonably capture both the carrying capacity and mode of competition among resources. In order to keep my model simple, I use the competition function of MacArthur and Levins (1967)

$$\alpha(z_1, z_2) = \alpha(d) = \exp \left[ -\frac{d^2}{2\sigma_\alpha^2} \right], \quad (2.2)$$

where  $\sigma_\alpha$  describes the extent of competition. As  $d$  decreases,  $\alpha(z_1, z_2)$  approaches unity from below. Competition is intra-phenotypic at  $z_1 = z_2$ , and  $\alpha$  is exactly unity. Therefore, it is possible to interpret  $\alpha$  as the relative strength of population regulation of inter-phenotypic competition to intra-phenotypic competition.

Finally, population dynamics of the resources in the absence of consumers is expressed as:

$$\frac{dF(z)}{dt} = rF(z) \left( 1 - \frac{F(z) + \int_Z \alpha(z, \zeta) F(\zeta) d\zeta}{K(z)} \right), \quad (2.3)$$

where  $r$  is resource intrinsic rate of growth. The domain of possible phenotypes is defined as  $Z = (-\infty, +\infty)$  to keep analysis simple. The integration is taken over the entire domain of resource phenotypes.

The last aspect of biology affected by  $z$  is the functional response of consumers. However, full description of consumption requires several aspects of consumer biology, and this is discussed next.

## 2.2 Consumer-Resource Interactions and Consumer Dynamics

Consumers are characterized by two traits: niche position and niche width. The niche position  $x$ , which has an identical domain with  $z$ , governs the optimal resource phenotypes. Consumers use resources most efficiently if  $z = x$ . The niche width  $y$  governs the degree of specialization. A small  $y$  indicates a high degree of specialization; consumers with a small  $y$  are highly efficient in capturing resources of phenotype  $z$  when  $|z - x|$  is small, dropping rapidly as  $|z - x|$  increases. On the other hand, a large value of  $y$  denotes a generalist; consumers with a large  $y$  are not as effective as those with a small  $y$  when  $|z - x|$  is small, however, their efficiency remains relatively higher when  $|z - x|$  increases.

Again, in order to keep my model simple, a Gaussian function is used to describe the consumer's resource utilization function:

$$a_{x,y}(z) = \frac{\exp[-cy]}{\sqrt{2\pi y}} \exp\left[-\frac{(x-z)^2}{2y^2}\right], \quad (2.4)$$

where the parameter  $c$  is a measure of whether specialists are better foragers ( $c > 0$ ) or not ( $c < 0$ ) and  $y$  has a domain  $Y = (0, +\infty)$ . Thus,  $c$  controls a specialist-generalist trade-off. I assume that  $c$  depends on a fixed consumer trait and that the trait is non-evolvable. Then, the integral of  $a_{x,y}(z)$  over  $z$  provides the total capture rate. If  $c = 0$ , the integral is unity for all consumer phenotypes. If  $c < 0$ , the integral is larger for large  $y$  than small  $y$ . This condition is a bias toward generalists. If  $c > 0$ , the integral is smaller for large  $y$  than small  $y$ ; This is a bias against generalists.

Finally, I assume a I Holling's type I functional response, for which resource acquisition is linearly dependent on both resource and consumer densities. Combining the

above assumptions with the resource population dynamics (Eqn. (2.3)), consumer-resource population dynamics is described by a system of integro-differential equations

$$\frac{dF(z)}{dt} = rF(z) \left( 1 - \frac{F(z) + \int_Z \alpha(z, \zeta) F(\zeta) d\zeta}{K(z)} \right) - a_{x,y}(z) F(z) N_{x,y}, \quad (2.5)$$

$$\frac{dN_{x,y}}{dt} = RN_{x,y} \left( b \int_Z a_{x,y}(z) F(z) dz - m \right), \quad (2.6)$$

where  $N_{x,y}$  is the population density of consumers, whose niche position and width are  $x$  and  $y$ , respectively. Here,  $b$  is the amount of energy extracted from a single item of the resources assumed independent of resource trait  $z$ , and a product of  $b$  and the number of resource units consumed gives the total energy intake. Similarly,  $m$  represents maintenance, or the subsistence level of resource acquisition, and the difference between intake and expenditure gives the amount of energy diverted toward reproduction. Finally,  $R$  identical offspring are reproduced given a unit amount of energy available for reproduction.

### 2.3 Equilibrium Distribution of Resources

To reduce the complexity of the system and to facilitate its analysis, I assume that the resource dynamics occur at a much faster rate than that of the consumers, meaning that any change in resource density occurs instantaneously relative to the timescale of the consumer dynamics. Under this quasiequilibrium assumption, the resource density immediately reaches its equilibrium level after any change in the consumer density. Obtaining the equilibrium resource distribution is trivial when  $\sigma_\alpha = 0$  as the model collapses to a standard logistic equation. It can also be easily shown that there is only one non-trivial distribution when  $\sigma_\alpha > 0$ . Thus, this assumption allows substitution of the equilibrium resource distribution for the actual resource distribution in Eqn. (2.6).

To find the equilibrium resource distribution, I set the left hand side of Eqn. (2.5) equal to zero simultaneously for all  $z$ . Then, rearranging the equation leads to the following Fredholm integral equation of the second kind:

$$\hat{F}(z) + \int_Z \alpha(z, \zeta) \hat{F}(\zeta) d\zeta = \frac{K(z)}{r} (r - a_{x,y}(z) N_{x,y}), \quad (2.7)$$

where  $\hat{F}(z)$  is the equilibrium resource density of phenotype  $z$ . A solution for this integral equation can be expressed in terms of a Neumann series given by:

$$\hat{F}(z) = \sum_{i=0}^{\infty} (-1)^i A^i K(z) - N_{x,y} \sum_{i=0}^{\infty} (-1)^i A^i K(z) a_{x,y}(z), \quad (2.8)$$

where  $A^0 f = f$ ,  $A^1 f = \int_Z \alpha(z, \zeta) f(\zeta) d\zeta$ , and  $A^i f = A(A^{i-1} f)$  for a function  $f(z)$ . Higher terms with  $i > 0$  vanish at the limit of no competition, and my model coincides with Ackermann and Doebeli (2004) for  $\sigma_\alpha = 0$ . The infinite series converges if  $A^1 < 1$ , so it is valid for  $\sigma_\alpha < 1/\sqrt{2\pi} \approx 0.4$  in my model. Fig. 2.1 illustrates how resource competition reduces the equilibrium resource density for all  $z$ . In addition, because competition is density-dependent, resource density is depressed more severely around  $z = 0$ , where the density is high. In contrast, where  $|z|$  is large, resource density is low (Fig. 2.1a) and is less affected. As a result, the equilibrium resource distribution becomes flatter than the original carrying capacity. Moreover, strong competition decreases the total population density by about a half, and the rate of decline becomes slightly less toward higher  $\sigma_\alpha$  (Fig. 2.1b).

Competition among resources also affects the pattern of consumption. Fig. 2.2 shows the distribution of resources eaten by a monomorphic consumer population, whose niche position is slightly off center ( $y = 0.5$ ). Similar to the equilibrium distribution of resources, competition flattens the distribution of captured resources. This flattening can be observed in the case of a narrow  $y$  (Fig. 2.2a) or a broad  $y$

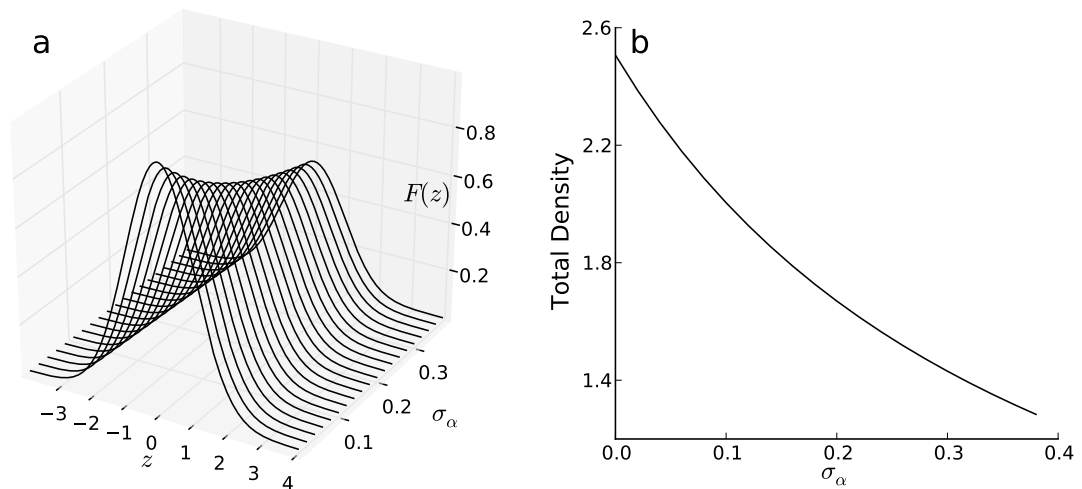


FIGURE 2.1: Equilibrium distributions of resources without consumers. Equilibrium resource densities are plotted as a function of resource phenotype  $z$  and the extent of competition among resources  $\sigma_\alpha$ . High  $\sigma_\alpha$  indicates widespread and intensive competition between resources (a) and its total population size (b). Parameters:  $x = 0.6$ ,  $r = 1$ ,  $K_F = 1$ ,  $\sigma_{K_F} = 1$ , and  $N_{x,y} = 1.1$ .

(Fig. 2.2b). The equilibrium resource distribution under the presence of monomorphic consumers is either unimodal, when  $y$  is small (Fig. 2.2c), or bimodal, when  $y$  is large (Fig. 2.2d). In both cases, consumers capture more resources near  $z = 0$  than near their niche position because the resource density is high enough to compensate for the lower capture rate. of

Fig. 2.2 also shows that inter-phenotypic competition in resources reduces the amount of resources eaten by consumers. This reduction again is most prominent where the predation is the most intense. Therefore, competition among resources affects both the resource distribution and the pattern of predation.

## 2.4 Simplified Consumer Dynamics

Substituting  $\hat{F}(z)$  obtained from Eqn. (2.8) into Eqn. (2.6) yields a simplified model for consumer dynamics. After some rearrangement, we obtain the logistic form of

consumer dynamics

$$\frac{dN_{x,y}}{dt} = r_{x,y}N_{x,y} \left( 1 - \frac{N_{x,y}}{K_{x,y}} \right). \quad (2.9)$$

General expressions for  $r_{x,y}$  and  $K_{x,y}$  are given by:

$$r_{x,y} = R(b \sum_{i=0}^{\infty} (-1)^i \langle a_{x,y}, A^i K \rangle - m), \quad (2.10)$$

$$K_{x,y} = \frac{r(b \sum_{i=0}^{\infty} (-1)^i \langle a_{x,y}, A^i K \rangle - m)}{b \sum_{i=0}^{\infty} (-1)^i \langle a_{x,y}, A^i K a_{x,y} \rangle}. \quad (2.11)$$

$\langle f, g \rangle = \int_Z f(z)g(z)dz$  is an inner product of two functions  $f(z)$  and  $g(z)$  over  $Z$ .

When a mutation occurs upon reproduction of consumers, the consumer population consists of two phenotypes, the original phenotype and a mutant phenotype. The mutant consumers, defined by phenotype  $(u, v)$ , compete with the resident consumers  $(x, y)$ . The competitive effect of the consumers  $(u, v)$  on  $(x, y)$  is denoted by  $\beta(x, y, u, v)$ ,

$$\beta(x, y, u, v) = \frac{\sum_{i=0}^{\infty} (-1)^i \langle a_{x,y}, A^i K a_{u,v} \rangle}{\sum_{i=0}^{\infty} (-1)^i \langle a_{x,y}, A^i K a_{x,y} \rangle}. \quad (2.12)$$

Derivations of  $r_{x,y}$ ,  $K_{x,y}$ , and  $\beta(x, y, u, v)$  are a straightforward extension of Ackermann and Doebeli (2004), and the dynamics of consumers for the focal phenotype  $(x, y)$  becomes:

$$\frac{dN_{x,y}}{dt} = r_{x,y}N_{x,y} \left( 1 - \frac{N_{x,y} + \beta(x, y, u, v)N_{u,v}}{K_{x,y}} \right). \quad (2.13)$$

## 2.5 Evolution of Consumer Phenotype

The next step is to describe evolutionary dynamics of the niche position and width of consumers using the theory of adaptive dynamics (Dieckmann and Law, 1996; Metz et al., 1996; Geritz et al., 1998). This theory utilizes an invasion fitness function which describes the fitness of rare mutants  $(u, v)$  in a population that consists of

resident phenotypes  $(x, y)$ . When the fitness is positive, the frequency of the mutants increases in the population, and when negative, the mutants perish. Under some simplifying assumptions the theory postulates that evolutionary trajectories can be traced by following the fitness gradient. Several important assumptions are involved. First, mutation occurs at very low rate. Before the next mutation appears in a population, the first mutation is either lost or fixed. Thus, just before the arrival of a new mutation, a population is at equilibrium. Second, and perhaps more importantly, a mutant phenotype differs from that of a wild-type parent only by a small amount. Third, a successful invasion is equated with fixation of the mutation in the population, completely replacing the resident phenotype.

The invasion fitness is obtained by assuming that the magnitude of population regulation exerted by rare mutants is negligible and that the resident phenotypes are at equilibrium. These assumptions lead to the following frequency-dependent invasion fitness

$$f(x, y, u, v) = r_{u,v} \left( 1 - \frac{\beta(u, v, x, y)K_{x,y}}{K_{u,v}} \right). \quad (2.14)$$

Now, assuming that the rates of phenotypic evolution are equivalent to the gradients of the invasive fitness function, a set of ordinary differential equations

$$\frac{dx}{dt} = \left. \frac{\partial f}{\partial u} \right|_{u=x, v=y}, \quad (2.15)$$

$$\frac{dy}{dt} = \left. \frac{\partial f}{\partial v} \right|_{u=x, v=y}, \quad (2.16)$$

for the niche position and width respectively, describes the time evolution of consumer's phenotypic evolution.

At an evolutionary equilibrium, Eqns. (2.15) and (2.16) simultaneously vanish. The point is known as a convergent stable strategy if the population initially evolves toward the point. The niche position always evolves toward  $\hat{x} = 0$ , where the hat



indicates a convergent stable strategy. This point corresponds to the highest density of resources at  $z = 0$ . On the other hand, we have to numerically find  $\hat{y}$ . Fig. 2.3a shows that the convergent niche width becomes narrower as the extent of competition among resources increases. However, the magnitude of decrease in the convergent niche width is less than 20% even at  $\sigma_\alpha = 0.38$  (Fig. 2.3b). It also shows that  $\hat{y}$  also becomes narrower along with larger  $c$  as reported in the previous study.

Although both factors affect the convergent niche width, their interaction seems to be limited as shown in Fig. 2.3. Relative reduction of  $\hat{y}$  due to  $\sigma_\alpha$  is not greatly affected by the value of  $c$ . This suggests that these two factors operate more or less independently of one other.

Once evolution leads the population near the convergent phenotypes, there are two events that can follow. First, no further phenotypic change occurs in the population. This occurs when the convergent stable phenotype is also evolutionary stable. Second, the phenotype of population diverges. This occurs when the convergent stable phenotype is not evolutionary stable. In order to determine evolutionary stability of the convergent stable phenotypes, we evaluate the second order partial derivatives of the invasion fitness function evaluated at a convergent stable point  $(\hat{x}, \hat{y})$ . Let  $H$  be a Hessian matrix, whose elements are the second order partial derivatives of  $f$ :

$$H = \left( \begin{array}{cc} \frac{\partial^2 f}{\partial u, u} & \frac{\partial^2 f}{\partial u, v} \\ \frac{\partial^2 f}{\partial v, u} & \frac{\partial^2 f}{\partial v, v} \end{array} \right) \Bigg|_{u=\hat{x}, v=\hat{y}} = \begin{pmatrix} h_1 & h_2 \\ h_3 & h_4 \end{pmatrix} \quad (2.17)$$

The mixed partial derivatives,  $h_2$  and  $h_3$ , always vanish independent of  $c$  and  $\sigma_\alpha$ . The convergent stable point is evolutionary unstable if the product of  $h_1$  and  $h_4$  is negative. Fig. 2.4a shows that  $h_1$  is positive as either  $c$  or  $\sigma_\alpha$  increases, and Fig. 2.4b shows that  $h_4$  remains negative again independent of  $c$  and  $\sigma_\alpha$ . The magnitudes of  $h_1$  and  $h_4$  increases as either  $c$  or  $\sigma_\alpha$  becomes large. Therefore, the convergent stable strategy becomes more evolutionarily unstable with larger  $c$  or  $\sigma_\alpha$ . However,  $\sigma_\alpha$  does

not have strong effect on  $h_1$  and  $h_4$  unless  $c$  is sufficiently large (Figs. 2.4a and 2.4b).

I additionally perform a set of individual-based simulations to test how inter-phenotypic competition affects phenotypic evolution of the consumers. The simulations are implemented following Appendix 3 of Ackermann and Doebeli (2004). Each simulation is initiated with 200 consumers. Their niche position and width are normally distributed with mean -2.5 and 0.5, respectively, and with standard deviation 0.1 for both the position and width. At each reproductive event, a mutation occurs with probability 0.01. Deviation of a mutant phenotype from a parental phenotype is normally distributed with mean equivalent to parental phenotype and with standard deviation 0.01. Mutations in the niche position and width occur independent of each other. The simulations run for 20,000 generations. Ecological parameters of models are chosen to match those used in Ackermann and Doebeli (2004), so my results are directly comparable to theirs. I explore a combination of two values each of a bias toward generalists,  $c = \{0, 0.4\}$ , and the strength of resource competition,  $\sigma_\alpha = \{0, 0.2\}$ . A thousand runs are performed with different random seed for each of four combinations of  $c$  and  $\sigma_\alpha$ . Due to stochastic nature of my simulation algorithm, the number of distinct phenotypic clusters in niche position at the end of simulations differ considerably. Numbers of clusters at the end of simulations are summarized in Fig. 2.5. Fig. 2.6 shows sample evolutionary trajectories obtained from some runs.

When  $c = 0$ , the convergent stable niche width is wide enough for the resources to remain unimodal in the vast majority of runs (Fig. 2.5a with corresponding samples Figs. 2.6a and b) regardless of the extent of resource competition,  $\sigma_\alpha$ . Under this condition, consumers experience very weak frequency-dependent selection on the niche position, and disruptive selection caused by the frequency-dependence cannot force the niche position to diverge.

On the other hand, when the specialists are strongly favored ( $c = 0.4$ ), the convergent niche width  $\hat{y}$  is narrow. Then, frequency-dependent disruptive selection

in the consumers is strong enough to drive the divergence of the niche position. Under this condition, I obtain a wider spectrum of outcomes in simulations. The number of peaks at the end of simulations varies from one to four in both values of  $\sigma_\alpha$ . Although the most frequent outcome, regardless of resource competition, is two peaks at the end of simulations with resource competition ( $\sigma_\alpha = 0.2$ ), higher numbers of runs shows three peaks or more when  $c = 0.2$  (Fig. 2.5b with corresponding samples Fig. 2.6c and d). This illustrates that increased evolutionary instability caused by narrower  $\hat{y}$  of due to resource competition.

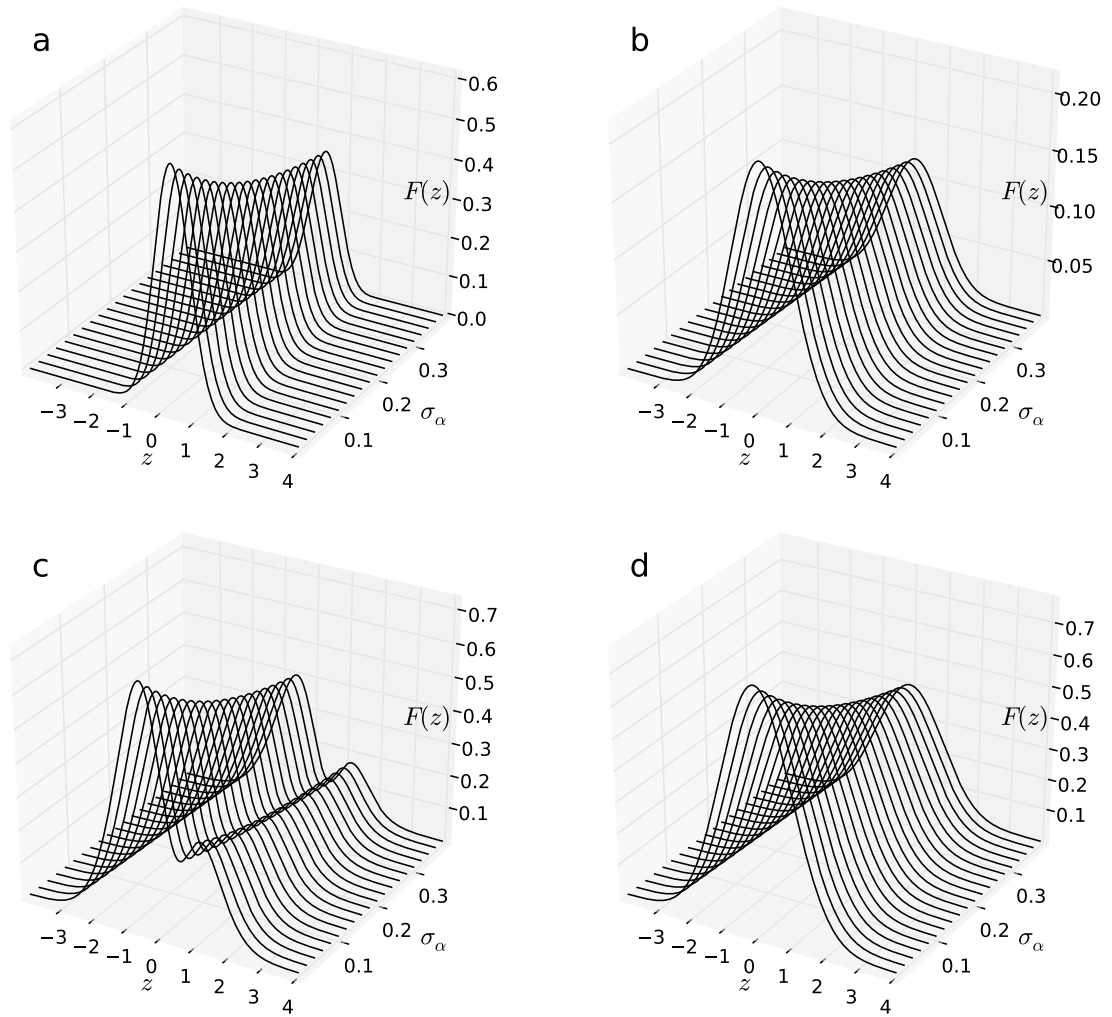


FIGURE 2.2: Examples of predation. Distributions of resources that are eaten by unit density of consumers (**a**, **b**) and equilibrium resource distribution under the presence of consumers (**c**, **d**). The niche position of consumers is 0.5 for all the figures. (**a**, **c**) With a narrow niche width of consumers ( $y = 0.6$ ), and (**b**, **d**) with a broad niche width of consumers ( $y = 1.8$ ). Other parameters are identical to Fig. 2.1.

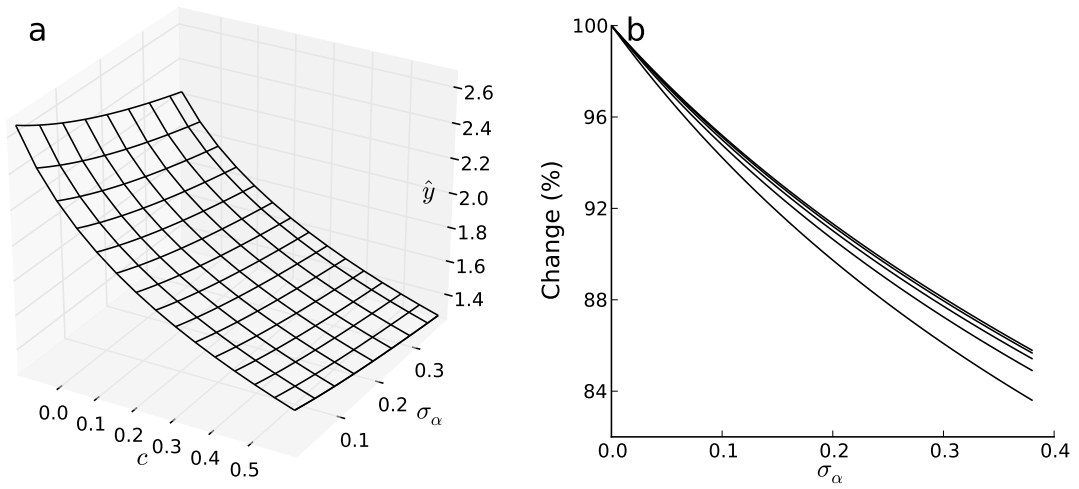


FIGURE 2.3: Convergent stable point for the niche width of consumers. The convergent stable point of the niche position is always at zero; hence, this is not presented. **a.** As a function of competition among resources and the degree of specialist advantage. **b.** The magnitude of decrease due to competition relative to no competition among resources. The bottom line is plotted with  $c = -0.1$ , and  $c$  for other lines are in the increment of 0.1 from bottom to top. The lower-most line is for  $c = -0.1$ . The other lines are for  $c$  increment of 0.1 from the bottom to top. The population parameters used are:  $r = 1$ ,  $\sigma_{K_F} = 1$ ,  $K_{F,0} = 1$ ,  $R = 1$ , and  $m = 0.01$ .

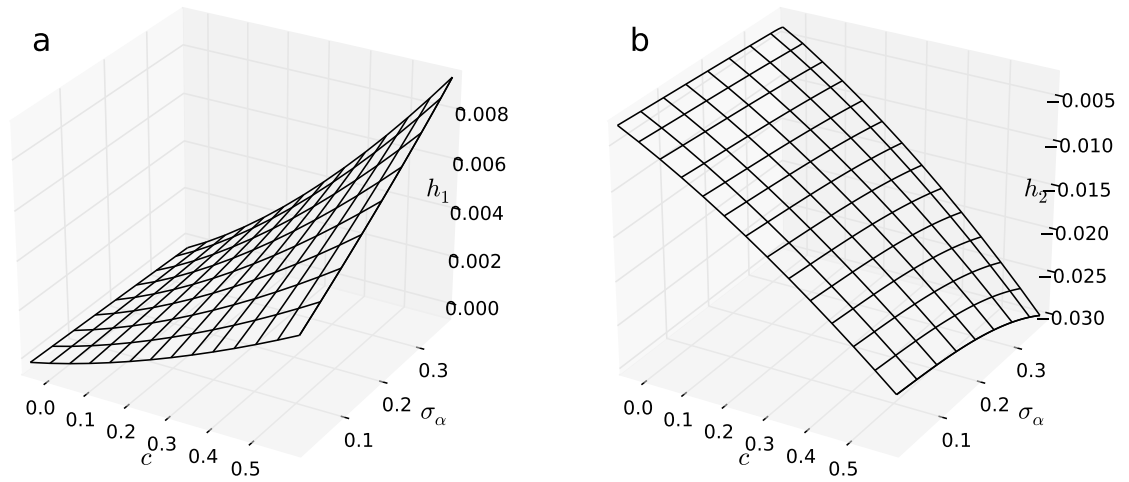


FIGURE 2.4: Second order partial derivatives of invasion fitness in terms of  $u$  ( $h_1$  in **a**) and  $v$  ( $h_2$  in **b**) evaluated at the convergent stable point. The convergent stable niche position is zero, and the niche width is presented in Fig. 2.3. If the extent of competition among resources  $\sigma_\alpha$  and the degree of specialist advantage are both zero,  $h_1 = 0$ . Mixed derivatives in terms of  $u$  and  $v$ ,  $h_2$  and  $h_3$ , are not shown, because these derivatives are always zero regardless of  $c$  and  $\sigma_\alpha$ . Parameter values are identical to those in Fig. 2.3.

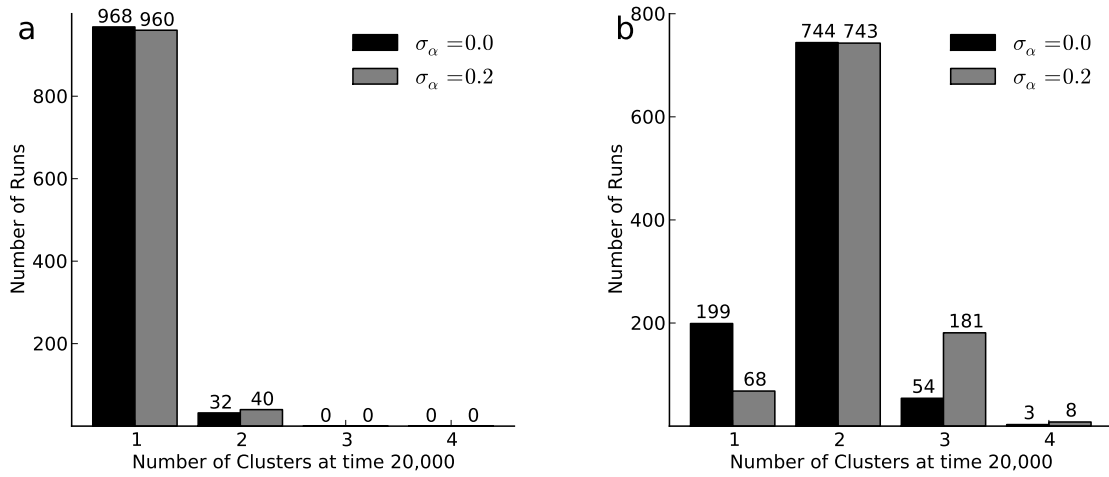


FIGURE 2.5: Number of phenotypic clusters at the end of 20,000 generations in each simulations. In order to avoid an observation bias, information telling if a run is with or without resource competition is concealed. Then, the results from both cases are pooled and randomly shuffled. I visually inspect the result to assign the number of phenotypic clusters to each result. After the assignment is done, the identity of each result is revealed, and the results are tallied to generate this figure. (a) when  $c = 0$  and (b) when  $c = 0.4$ . In both cases, the black bar represents  $\sigma_\alpha = 0$  and the gray bar represents  $\sigma_\alpha = 0.2$ . The model parameters are selected to match those used in Ackermann and Doebeli (2004). Parameters:  $K_{F,0} = 12$ ,  $\sigma_{K_F} = 1$ ,  $r = 144$ ,  $R = 0.2$ , and  $m = 0.4$ .

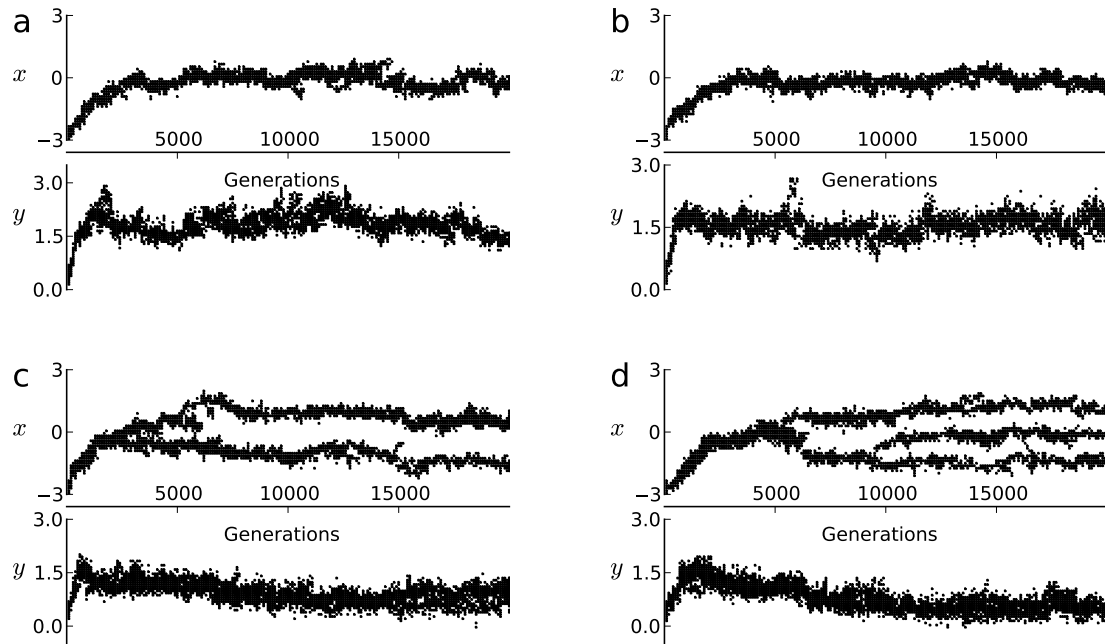


FIGURE 2.6: Sample evolutionary trajectories of the niche position  $x$  and width  $y$  in the consumers from individual-based simulations. (**a** and **b**) There is no cost to either generalists or specialists ( $c = 0$ ). Diversification does not occur if resources do not compete ( $\sigma_\alpha = 0$  in **a**) or if resources compete ( $\sigma_\alpha = 0.2$  in **b**). (**c** and **d**) There are costs to generalists ( $c = 0.4$ ). Parameter values are the same as Fig. 2.5. Although the trajectories with two and three peaks at the end of simulations are presented in **c** and **d**, respectively, these are by no means the only outcomes observed in 1,000 replicated simulations. One to four peaks are observed in both  $\sigma_\alpha$  when  $c = 0.4$ . See Fig. 2.5 for detail.



# 3

## Discussion

I investigated how competition among resources affects phenotypic evolution of consumers. The consumers are under frequency-dependent selection for shared resources. I focused on two traits that related to resource acquisition: niche position, the easiest type of resources to prey upon, and niche width, a range of resources they can prey upon. My model is closely based on Ackermann and Doebeli (2004), but differs in a simple but important manner; the resources are allowed to compete among themselves.

In the previous model, each resource phenotype was assumed to be independent, and, as a consequence, resources did not compete if their phenotypes were different. Therefore, the presence of a phenotype did not affect the population regulation of other phenotypes. This assumption may be appropriate if the resources are abiotic, however, resources are likely to interact with other resources in some degree if resources are biotic. The interaction can be competitive, mutual, or of any other different forms. Here, I focused on competitive interactions for its reputed importance in population regulation (Schoener, 1983; Sih et al., 1985; Chase et al., 2002). The competition can arise if subsistence of biotic resources depends on acquisition

of limited energy and nutrients; essentially the same reason consumers compete.

There is reason to suspect that such interactions within resources affect the evolution of consumers, because the shape of competition function in the consumers is critically important in determining if divergence of the niche position occurs (Doebeli et al., 2007; Baptestini et al., 2009; Pigolotti et al., 2010). The shape of the function in turn depends on the shape of resource distribution. Therefore, any interaction at the resource level can affect evolutionary outcome of consumers if the interactions alter the shape of the resource distribution. I found that competition among resources indeed affected the phenotypic evolution of consumers in a couple of ways. First, the convergent stable niche width becomes narrower, which leaves some of resource phenotypes to be underexploited, and other phenotypes over-exploited by specialist consumers. This pattern leads to the second point; the evolutionary instability of the convergent stable strategy increases. Mutant consumers that can exploit those underutilized phenotypes can outcompete and usurp residents.

A prominent feature of consumer phenotypic evolution is unaffected by resource competition at the resource level. The competition does not influence a condition that determined if the niche position diverges. Ackermann and Doebeli (2004) showed that the divergence of the niche position occurred when having a broader niche width was associated with less efficient foraging. This condition held true even when resources competition was considered.

What resource competition changes is how the consumer niche position evolves when the condition for divergence is satisfied. As numerical computation of increased evolutionary instability and individual-based simulations showed, the niche position became more susceptible to divergence with resource competition. In fact, I found that the second round of divergence can occur when the costs to generalists and the strength of competition among resources are both high. More than one round of diversification was also observed in the previous study, but it was observed only with

very large costs to generalists. My finding suggests that resource competition may cause higher consumer diversity without invoking extreme preference of specialists over generalists.

In a coevolutionary model of consumer-resource interaction, Ripa et al. (2009) showed that consumers became more diverse when resources competed weakly. Although this finding contrasts with mine, the difference can be attributed to how I envisioned resource distribution. In our model, resources were continuously distributed over the entire phenotypic space, and the main effect of competition is to reduce the resource population density. However, this competition alone does not promote the formation of multimodal resource distribution. In their model, however, resources were discretely distributed. Then, the strength of competition determines how tightly resources can be packed. Consumers, in turn, were able to specialize on those phenotypes. Therefore, the resource phenotypes effectively acted as distinct niches, and weaker competition provides more niches. Real biological situations are probably somewhat in between these two extreme formulations. Additional study is needed to reconcile these contrasting observations.

Universality of my findings awaits confirmation from additional analyses. It is especially important to examine how different forms of resource carrying capacity affects the evolution of consumers. Nevertheless, I hope that my results demonstrates enough to show that interactions occurring at lower trophic level can affect evolution in a focal population in a systematic fashion as long as the interactions alter the resource distribution in systematic ways. Therefore, understanding of phenotypic evolution may sometimes require far more information than that of the focal population.

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