

Adaptive Dynamics of Competition for Nutritionally Complementary Resources: Character Convergence, Displacement, and Parallelism

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ABSTRACT: Consumers acquire essential nutrients by ingesting the tissues of resource species. When these tissues contain essential nutrients in a suboptimal ratio, consumers may benefit from ingesting a mixture of nutritionally complementary resource species. We investigate the joint ecological and evolutionary consequences of competition for complementary resources, using an adaptive dynamics model of two consumers and two resources that differ in their relative content of two essential nutrients. In the absence of competition, a nutritionally balanced diet rarely maximizes fitness because of the dynamic feedbacks between uptake rate and resource density, whereas in sympatry, nutritionally balanced diets maximize fitness because competing consumers with different nutritional requirements tend to equalize the relative abundances of the two resources. Adaptation from allopatric to sympatric fitness optima can generate character convergence, divergence, and parallel shifts, depending not on the degree of diet overlap but on the match between resource nutrient content and consumer nutrient requirements. Contrary to previous verbal arguments that suggest that character convergence leads to neutral stability, coadaptation of competing consumers always leads to stable coexistence. Furthermore, we show that incorporating costs of consuming or excreting excess nonlimiting nutrients selects for nutritionally balanced diets and so promotes character convergence. This article demonstrates that resource-use overlap has little bearing on coexistence when resources are nutritionally complementary, and it highlights the importance of using mathematical models to infer the stability of ecoevolutionary dynamics.

Keywords: adaptive dynamics, character convergence, complementary resources, stoichiometry, competition, coexistence.

Introduction

Consumers obtain essential nutrients such as N and P from the tissues of the resource species they consume. Different resource species often differ greatly in the ratios of nu-

trients bound in their biomass (Geider and LaRoche 2002), and typically no one resource species will supply essential nutrients in the precise ratio required by a consumer. Provided that resources bracket a consumer's demand ratio, a consumer can obtain a nutritionally balanced diet (one in which the ratio of required essential nutrients is matched in the diet) by eating a mixture of different resource species (Simpson et al. 2009). Resources that bracket a consumer's required ratio of essential nutrients are known as nutritionally complementary or partially substitutable resources (León and Tumpson 1975; Tilman 1982; Abrams 1987c).

When complementary resources are provided ad libitum, empirical work has shown that individuals will modify their feeding behavior to obtain a nutritionally balanced diet (Behmer et al. 2001, 2003). However, if one resource type is rare or driven to rarity by preferential feeding, eating a balanced diet might oblige a consumer to eat only a small amount of food (all of the rare resource, plus just enough of the common resource to balance the diet). In this case it may be optimal (fitness maximizing) for a consumer to eat a large amount of nutritionally unbalanced food and then excrete excess nutrients (postingestion balancing; Anderson et al. 2005; Simpson et al. 2009). For example, zooplankton release a greater fraction of N relative to P when they are fed food with an N/P ratio that is higher than that of their own tissue (Elser and Urabe 1999). Grasshoppers when stressed by predators shift to more carbon-rich food in order to fuel increased metabolism and then excrete excess nitrogen (Hawlena and Schmitz 2010).

The fact that the abundances of complementary resources affect optimal diet choice creates feedbacks between consumer diet and consumer-resource population dynamics. Changes in consumer diet will alter resource abundances, which will then feed back to alter the optimal

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diet. Although nutrient balancing through optimal diet choice has been investigated empirically (Mayntz et al. 2005; Behmer and Joern 2008; Hawlena and Schmitz 2010), the feedbacks generated through resource population dynamics have not. Theoretical work including such feedbacks is limited to two-resource, one-consumer systems (Schreiber and Tobiason 2003).

Optimal diet choice also matters for coexistence. Theory has identified coexistence conditions when consumers compete for complementary resources and consumer diet choices are taken as fixed (León and Tumpson 1975; Hsu et al. 1981). But it seems implausible that coexistence that relies on maladaptive behavior could be sustainable in the long run. Previous models of competition for both nutritionally substitutable resources (e.g., different, nutritionally equivalent prey species) and nutritionally essential resources (e.g., N, water, light) have found that adaptive diet choice by competing consumers promotes ecologically stable coexistence (Lawlor and Maynard Smith 1976; Fox and Vasseur 2008).

Furthermore, even if adaptive diet choice does promote stable coexistence, will it do so via character displacement or convergence? Competition for substitutable resources generally selects for divergence in the optimal diets of competing consumers (character displacement; Lawlor and Maynard Smith 1976; Taper and Case 1992; Schluter 2000). Consumers of substitutable resources can increase their fitness by dropping some resources from their diet in order to feed on alternative resources for which there is less competition. In contrast, competition for essential resources selects for character convergence because consumers cannot increase their fitness by dropping some resources from their diet in favor of (nonexistent) alternatives (Abrams 1987b; Fox and Vasseur 2008). Complementary resources are an intermediate case, one that provides the potential for both character displacement and convergence.

Here we develop a simple model of two adaptive consumers competing for two complementary resources. Our model builds on the competition model of Hsu et al. (1981) by incorporating adaptive adjustment of diet choice on the part of both consumers. Using a combination of analytical and numerical approaches, we identify the conditions under which the two consumers coexist, both with and without adaptive diet choice. We go on to identify the conditions under which interspecific competition generates character convergence, divergence, or parallel shifts in consumer diets, but we argue that these are epiphenomena. Effects of interspecific competition on consumer diets are better understood as depending on the match between consumer nutrient demand and the availability of nutrients in the resource species. The ways in which interspecific competition alters the equilibrium nutrient

availability, and thus optimal consumer diets, are independent of the diet overlap of the competing consumers.

The Model

In this section we develop a simple model incorporating the essential features of competition for complementary resources and adaptive diet choice, and we highlight empirical support for our key assumptions. Even this simple model has rich and complex dynamics, so we rely on a combination of analytical and numerical analyses.

Competition for complementary resources requires that each competitor be able to persist when consuming only one resource type (in the absence of competition). However, each competitor should also be able to increase its fitness by consuming a mixture of different resource types. To meet this constraint, we assume that different resource types contain different ratios of chemical nutrients (as has been reported by Geider and LaRoche 2002) that are nutritionally essential for the growth of each consumer. Consumers also differ in their chemical compositions (Andersen and Hessen 1991) and therefore their requirements for these chemical nutrients. Thus, the nutritional requirements of any consumer can be met by one resource type alone, but a mixed diet can increase fitness by improving nutrient balance. Figure 1 provides a schematic representation of the model.

Ecological Dynamics

Building on the work of Hsu et al. (1981) and Abrams (1987c), we consider competition between two consumers (C_j where $j = 1, 2$) for two resources (R_i where $i = 1, 2$). The resources R_i each contain two chemical nutrients, a and b , that are essential for consumer growth. Consistent with previous work on adaptive diet choice (Abrams 1987c; Fox and Vasseur 2008), we assume that each unit of resource i contains nutrient b relative to nutrient a in the fixed composition ratio

$$\alpha_i = \frac{1 - k_i}{k_i}, \quad (1)$$

where k_i is the proportion of each unit of resource i composed of nutrient a . In nature, many resource species have flexible stoichiometry (Sterner and Elser 2002) and demonstrate seasonal variation in their nutrient content. We assume fixed stoichiometry as a first step to allow evolutionarily stable strategies (ESSs) to emerge. Two resources with identical α_i values would be nutritionally substitutable because of their identical stoichiometry; we therefore require that $\alpha_1 \neq \alpha_2$.

We assume that each unit of consumer j contains the

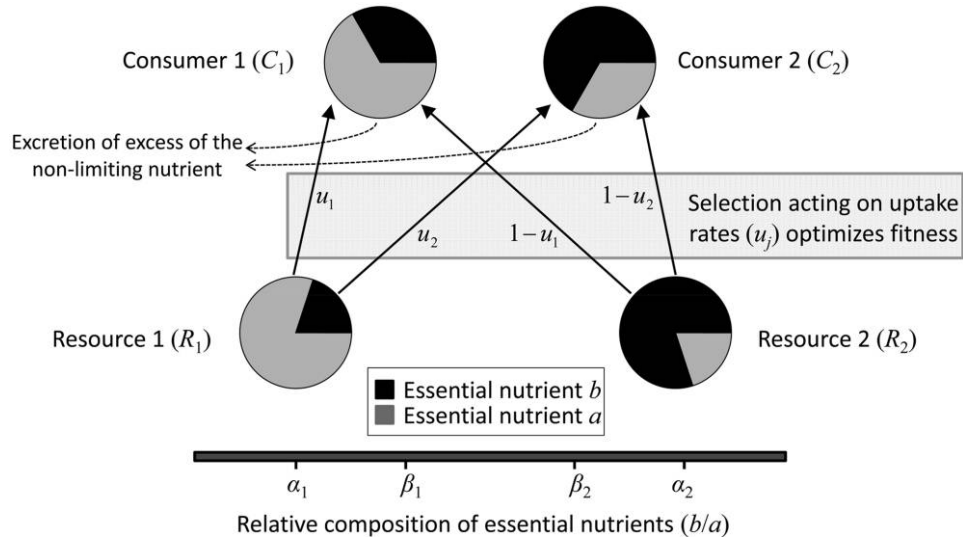


Figure 1: Schematic representation of the ecoevolutionary model of competition for complementary resources. Two nutrients (a and b) are essential for two consumers (C_1 and C_2), but they are available only through the uptake of resources (R_1 and R_2) that differ in their relative compositions of the two nutrients. When the ratio in which a consumer demands nutrients (β_j) is bracketed by the ratios in which they are supplied by the two resources (α_i), resources are complementary. Using an adaptive dynamics model, we investigate how uptake rates (u_j) evolve when two consumers compete for complementary resources.

two essential nutrients in the fixed ratio β_j , which we refer to as the demand ratio. We assume that the two consumers have nonidentical stoichiometry ($\beta_1 \neq \beta_2$), because precisely identical stoichiometries are both empirically implausible and would make stable coexistence of both consumers impossible (León and Tumpson 1975; Hsu et al. 1981). The elemental stoichiometry of many heterotrophs is homeostatic (Sterner and Elser 2002; Persson et al. 2010), and our model applies best to species such as these. Other heterotrophs exhibit stoichiometric differences linked to sex, life stage, season of the year, and other variables. To focus on adaptation of uptake rates, we assume that the demand ratios are evolutionarily inflexible so that consumers cannot reduce their requirements for whatever nutrient is limiting. Although there is some evidence of evolved changes in nutrient demands (e.g., Van Mooy et al. 2009; Vieira-Silva et al. 2010) and genetic variation among individuals for elemental homeostasis (Jeyasingh et al. 2009), fixed-demand ratios have been demonstrated in long-term evolution experiments (Goddard and Bradford 2003; Warbrick-Smith et al. 2006). Incorporating adaptive change in nutrient demand or other physiological complexities such as interactions among nutrients would require more explicit description of physiology and biochemistry (Andersen et al. 2004; Klausmeier et al. 2007, 2008; Behmer 2009), but it is a plausible avenue for further research.

We assume without loss of generality that R_1 is relatively

rich in nutrient a and R_2 is relatively rich in nutrient b (i.e., $\alpha_1 < \alpha_2$). We focus on complementary resources, which means that consumer demand ratios are bracketed by the resource composition ratios such that $\alpha_1 < \beta_j < \alpha_2$. It is therefore possible for each consumer to eat a nutritionally balanced diet (intake ratio of nutrients matching its β_j value) by consuming an appropriate mix of R_1 and R_2 .

The dynamics of consumer and resource abundances are described by chemostat dynamics and linear functional responses for simplicity and compatibility with previous models (Hsu et al. 1981; Fox and Vasseur 2008):

$$\frac{dR_1}{dt} = D(S_1 - R_1) - R_1 \sum_j u_j C_j, \quad (2a)$$

$$\frac{dR_2}{dt} = D(S_2 - R_2) - R_2 \sum_j (1 - u_j) C_j, \quad (2b)$$

$$\frac{dC_j}{dt} = C_j[(1 - \delta_j)(g_{aj} + g_{bj}) - d_j]. \quad (2c)$$

Resources are supplied in chemostat fashion, where S_i is the supply concentration and D is the dilution rate. Consumers are washed out of the system at a rate d_j , which we assume for generality to be independent of the chemostat dilution rate D . The total per capita uptake rate of each consumer is fixed at unity, so that neither consumer is intrinsically better than the other at resource

consumption. We implicitly assume that other rate parameters are scaled relative to the total per capita uptake rate. Consumer j allocates its total per capita uptake effort on R_1 and R_2 according to a linear trade-off, so that uptake rates are u_j and $1 - u_j$, respectively. Such a trade-off could occur for many reasons, and in assuming such a trade-off, we follow previous theoretical work on the evolution of resource use under resource competition (e.g., Lawlor and Maynard Smith 1976; Abrams 1987*b*; Fox and Vasseur 2008).

Consumer dynamics depend on the rates at which nutrients a and b are ingested. These rates in turn are given by the functional responses of consumers on their resources. The rates at which nutrients a and b are ingested by consumer j (g_{aj} and g_{bj}) are therefore a combination of those gained from R_1 and R_2 , given the nutrient composition (k_i) and the uptake rates of resources (u_i):

$$g_{aj} = k_1 u_j R_1 + k_2 (1 - u_j) R_2, \quad (3a)$$

$$g_{bj} = (1 - k_1) u_j R_1 + (1 - k_2) (1 - u_j) R_2. \quad (3b)$$

Consumers instantaneously balance their nutrient intake with their nutrient composition by excreting any excess nutrient that cannot be assimilated (due to a paucity of the other nutrient). Herbivores and carnivores are known to engage in such postingestion nutrient balancing (Simpson and Raubenheimer 1996; Rubio et al. 2005; Clissold et al. 2010). The assimilation fraction ($1 - \delta_j$) is equal to 1 when consumer j ingests nutrients in a ratio that matches its demand, $g_{bj}/g_{aj} = \beta_j$. However, when $g_{bj}/g_{aj} > \beta_j$ there is an excess of nutrient b in the diet, equal to $g_{bj} - g_{aj}\beta_j$ that is excreted in a nonusable form at no cost to the consumer. Similarly, when $g_{bj}/g_{aj} < \beta_j$ the excess of nutrient a is excreted in a nonusable form and at no cost. Modeled in this way, the assimilation fraction,

$$1 - \delta_j = 1 - \max\left(\frac{g_{bj} - g_{aj}\beta_j}{g_{aj} + g_{bj}}, \frac{g_{aj} - g_{bj}\beta_j^{-1}}{g_{aj} + g_{bj}}\right), \quad (4)$$

allows consumers to maintain fixed stoichiometry. We assume cost-free excretion of excess nutrients in a nonusable form for tractability, recognizing that in reality, processing and excretion of excess nutrients may not be cost free (Mertz 1981; Raubenheimer et al. 2005) and excreted nutrients typically become available to resource species through decomposition. We evaluate the potential for costly ingestion and excretion of excess nutrients to alter our results in appendix C in the online edition of the *American Naturalist* by incorporating a Type II functional response in our model.

Because nutrients are embedded in different resource types, the ratio of available nutrients (b/a) depends on both the abundances and the compositions of the two

resources. At equilibrium, the ratio of available essential nutrients, which we refer to as the “nutrient supply ratio,” is given by

$$\alpha_s = \frac{(1 - k_1)R_1^* + (1 - k_2)R_2^*}{k_1 R_1^* + k_2 R_2^*}. \quad (5)$$

The nutrient supply ratio is necessarily bounded by the composition ratios of the two resources, $\alpha_1 \leq \alpha_s \leq \alpha_2$. If the composition ratios of resources are reciprocal ($\alpha_1 = 1/\alpha_2$) and resources are equally dense at equilibrium ($R_1^* = R_2^*$), then the nutrient supply ratio equals 1. Resource densities are affected by consumer feeding, and so the equilibrium nutrient supply ratio can be affected by an adaptive change in the uptake rates u_j , a central issue we explore below.

An important feature of the ecology of each consumer is its zero-net-growth isocline (ZNGI), which is defined by those combinations of R_1 and R_2 at which the per capita growth rate of consumer j is 0, given its current u_j value. The consumers’ ZNGIs are convex intersections of two straight lines in the R_1, R_2 plane. As both are expressed as functions of R_1 , the ZNGI’s are given by

$$R_2 = \max\left[\frac{d_j(1 + \beta_j)^{-1} - k_1 u_j R_1}{k_2(1 - u_j)}, \frac{d_j \beta_j(1 + \beta_j)^{-1} - (1 - k_1)u_j R_1}{(1 - k_2)(1 - u_j)}\right], \quad (6)$$

$j \in (1, 2).$

Each line segment denotes limitation by a different nutrient. At the intersection of these lines, nutrient uptake occurs in the same ratio as that demanded by the consumer, and so the consumer is colimited by both nutrients (fig. 2). Adjusting the consumer’s uptake rate shifts the resource levels at which colimitation occurs (fig. 2).

León and Tumpson (1975) and Abrams (1987*b*) state that a consumer feeding on two complementary resources will have a ZNGI that is convex in the R_1, R_2 plane and that crosses both resource axes at positive values. Our ZNGIs satisfy these criteria, using curves that are piecewise linear rather than the smooth curves that are illustrated in standard graphical models of resource competition (e.g., Tilman 1982). Exploring which alternative assumptions would give rise to smooth ZNGIs is beyond the scope of this article.

Evolutionary Dynamics

As in previous work (Fox and Vasseur 2008), we treat the per capita resource uptake rate of consumer j , u_j , as a phenotypic trait that can change adaptively over time. We assume that consumers can adapt to nutrient limitation

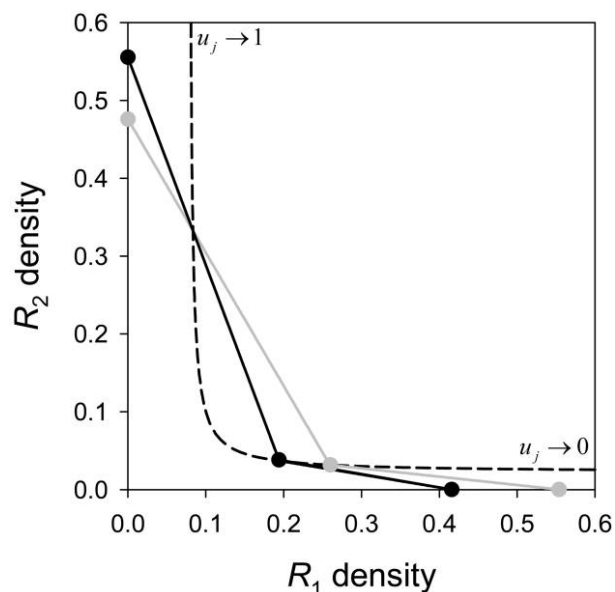


Figure 2: Consumer's zero-net-growth isocline is formed by a convex intersection of two line segments in the R_1 , R_2 phase plane given by equation (5). For comparison, the isocline is shown for two values of u_j ($u_j = 0.4$, solid black line; $u_j = 0.3$, gray line). The intersection of the segments denotes the point where consumers are colimited; this point follows a path through the R_1 , R_2 phase space, which can be found analytically by equating cases of equation (6) (dashed line) and isolating the uptake rate u . Here $\alpha = 0.25$, $\beta = 0.5$, and $d = 0.1$.

only by shifting their diets, and not, for example, by dispersing to seek better food elsewhere (Behmer 2009) or by altering their nutrient requirements. We model trait change using “adaptive dynamics” (Taper and Case 1992; Dieckmann and Law 1996; Abrams 2005):

$$\frac{du_j}{dt} = \nu_j \frac{\partial[(1/C_j)(dC_j/dt)]}{\partial u_j}. \quad (7)$$

The rate parameter ν_j scales the rate of trait change determined by the selection differential (the slope of the fitness gradient in u_j , where fitness is measured as the instantaneous per capita growth rate of consumer j). Equation (7) can be derived in several ways, including as an approximation of a quantitative genetics model (Iwasa et al. 1991; Taper and Case 1992; Abrams et al. 1993; Dieckmann and Law 1996; Taylor and Day 1997; Abrams 2005). This fact suggests that equation (7) provides a robust, widely applicable description of adaptive trait change. The biological interpretation of the rate parameter ν_j and the range of biologically reasonable values of ν_j relative to the other rate parameters in the model depend on the derivation (Dieckmann and Law 1996; Taper and Case 1992; Abrams et al. 1993; Taylor and Day 1997). We rely mainly

on equilibrium solutions of our model, where ν_j has no bearing on our results. We discuss its effect on transient dynamics in appendix B in the online edition of the *American Naturalist*.

Equation (7) is difficult to use in numerical integration because the partial derivative of fitness with respect to the trait u_j is discontinuous. We provide a continuous approximation to equation (7) in appendix B, which is used to integrate the full ecoevolutionary model.

Numerical and Analytical Methods

When necessary, we numerically integrated the model (eqq. [2]–[4] and [B2] in the online edition of the *American Naturalist*) with a fifth-order Runge-Kutta algorithm implemented in the IMSL Math/Stat library, using Intel Fortran, version 10.1. In order to determine the ecological stability of the system at different points in the trait space, we integrated the model in the absence of trait adaptation for 5,000 time steps, initialized at two different vectors of population densities $(R_1, R_2, C_1, C_2) = (0.2, 0.2, 0.1, 1.0)$ and $(0.2, 0.2, 1.0, 0.1)$, and we assumed extinction to have occurred when $C_j < 0.0001$. Visual inspection of the time series ensured that a quantity of 5,000 time steps was sufficient to reach equilibrium (except along bifurcations and in the case of neutrally stable dynamics). We sampled the trait space, using a discrete grid and an adaptive algorithm that improved resolution at the boundaries between different stability regimes. We used Mathematica, version 7, to symbolically compute or verify the trait values generating nutrient colimitation for consumers in allopatry and in sympatry.

Results

Ecological Dynamics in the Absence of Adaptive Trait Change

To interpret the effects of adaptive trait change, it is useful to first consider the ecological dynamics (eqq. [2]–[4]) in the absence of trait change (u_j fixed). These dynamics are rich. Assuming that both resources are available (i.e., $S_i > 0$), as many as six equilibria can exist for a given parameter set. These correspond to a trivial equilibrium where both consumers are absent, two equilibria where one of the consumers is absent, and between one and three equilibria for which both consumers coexist (fig. 3). In addition, there is a unique set of uptake rates that causes both branches of the consumer ZNGIs to be overlaid in the phase space, leading to neutrally stable dynamics. These uptake rates occur only when both consumers are strongly maladapted (outside the range we discuss below),

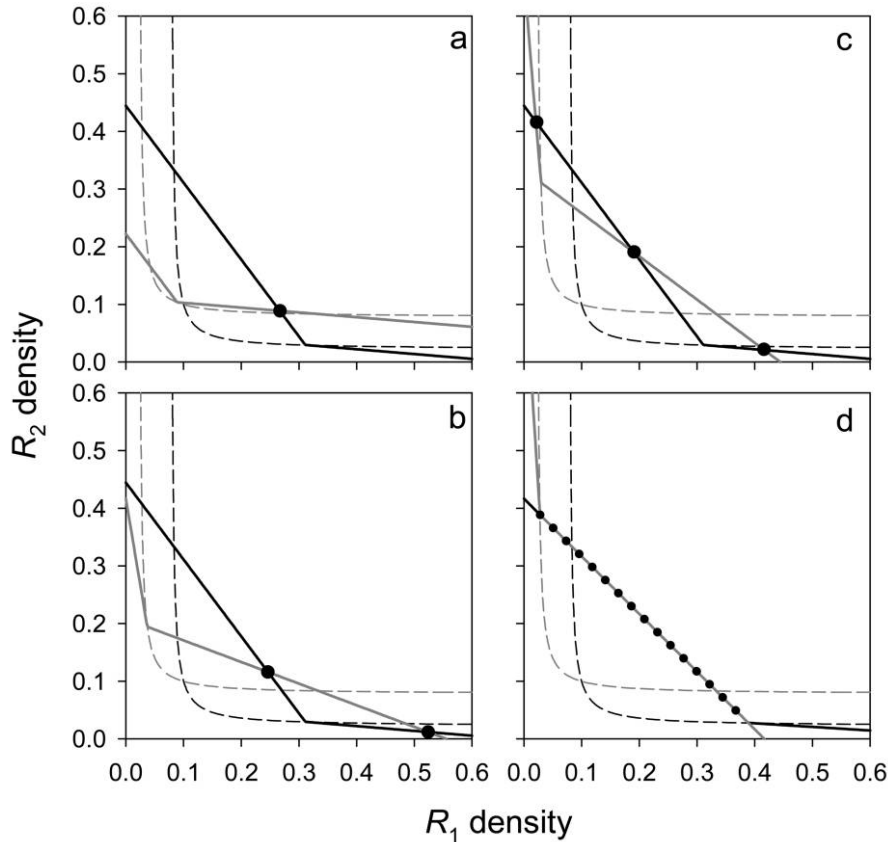


Figure 3: Equilibrium resource densities occur at the intersection between the zero-net-growth isoclines of consumer 1 (black lines) and consumer 2 (gray lines). In *a*, there is only a single intersection (circle); however, varying uptake rates (u_i) can generate two (*b*), three (*c*), or a linear set of equilibria (*d*; diagonal line) in the positive-valued resource phase space. Dashed lines trace the set of colimitation points for each consumer. Here $\alpha_1 = 0.25$, $\alpha_2 = 4.0$, $\beta_1 = 0.5$, $\beta_2 = 2.0$, and $d = 0.1$, and $(u_1, u_2) = (0.25, 0.25)$, $(0.25, 0.6)$, $(0.25, 0.75)$, and $(0.2, 0.8)$ in *a–d*, respectively.

and we therefore do not further examine cases of neutral stability arising from overlaid ZNGIs.

The feasibility of an equilibrium at which consumers coexist requires only that the consumer ZNGIs intersect in the R_1, R_2 plane. The conditions determining stability of this equilibrium are complex, as stable coexistence can arise when consumers are limited by the same nutrient but are specialized on different resources, or when they are limited by different nutrients but are specialized on the same resource. Given this complexity and that the eigenvalues of this system are not analytically solvable, we determined the outcome of competition as a function of per capita resource uptake rates u_1 and u_2 , using numerical methods and holding other parameters fixed.

Figure 4 shows the outcome of ecological competition for a pair of consumers whose nutrient demand ratios are similar but reciprocal about the nutrient supply ratio such that $1/\beta_2 = \beta_1 < \alpha_s < \beta_2$ (we consider this symmetric case

purely for clarity of illustration). We show an extension of this figure in appendix B, which includes representative ZNGIs for each of the distinct regions.

There are three distinct regions of the trait space in which consumers always coexist at equilibrium. In the upper-left and lower-right areas of the u_1, u_2 plane, consumers coexist because they differ in their resource use; each is relatively specialized on a different resource. In the upper-left region, consumers specialize on the resource with the nutrient composition that least reflects their demand, resulting in strong nutrient limitation (C_1 is *a* limited and C_2 is *b* limited). In the lower-right region, consumers specialize on the resource with the composition that most reflects their demand, so that C_1 is *b* limited and C_2 is *a* limited. In the central coexistence region, consumers do not strongly differentiate their resource use but are limited by different nutrients for most (but not all) combinations of u_1 and u_2 .

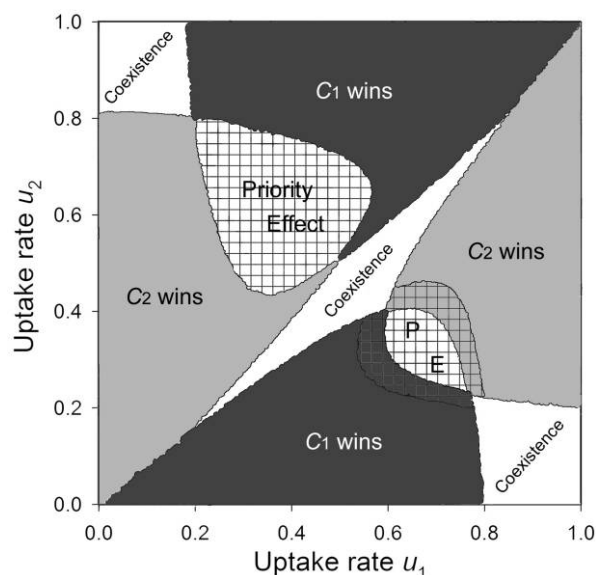


Figure 4: Ecological outcome of competition in trait space and zero-net-growth isoclines for the 11 regions. In the white regions, coexistence is stable. In the black (gray) regions, consumer 1 (consumer 2) excludes the other consumer. In the hatched regions, exclusion of one competitor occurs via a priority effect. In the shaded hatched region, a priority effect selects between exclusion of one consumer and coexistence. Ecological outcomes were determined numerically by simulating the model for 5,000 time steps, using two different initial conditions, $(C_1, C_2) = (0.1, 1.0)$ and $(1.0, 0.1)$, and numerically discovering transitions between the regions. Precisely at $u_1, u_2 = 0.2, 0.8$, the dynamics are neutrally stable (as in fig. 2d). Other parameters are as follows: $\alpha_1 = 0.25$, $\alpha_2 = 4.0$, $\beta_1 = 1/1.2$, $\beta_2 = 1.2$, $d_i = 0.1$, $S_1 = S_2 = 1$, $D = 0.1$, $R_1(0) = R_2(0) = 0.2$.

Competitive exclusion occurs over much of the u_1, u_2 phase space. Such outcomes typically arise when the sole intersection of consumer ZNGIs is located on the same branch for both consumers. In such cases, the intersection denotes a point where both consumers are limited by the same nutrient, and the better competitor for that nutrient wins (R^* rule; Tilman 1982).

Priority effects occur whenever the ZNGIs cross multiple times in the R_1, R_2 phase space. These priority effects can be separated into three distinct classes. In the hatched regions of figure 4, consumer ZNGIs intersect three times but none of these equilibria are stable. Rather, one consumer will always exclude the other, depending on initial conditions. In the shaded hatched region of figure 4, initial conditions determine whether stable coexistence or exclusion of one consumer will occur.

As the demand ratios of consumers (β_i) become increasingly different (but still satisfy $\alpha_1 < \beta_1 < \alpha_2 < \beta_2 < \alpha_2$), the amount of trait space resulting in coexistence grows relative to space generating exclusion and priority

effects. The two regions of competitive exclusion in the lower right of the trait space recede, and the central and lower-right coexistence regions join in a single large region (see figs. B3–B5 in the online edition of the *American Naturalist* for examples). Mathematically, this occurs because intersections between different branches of the consumer ZNGIs become relatively more likely, increasing the likelihood that consumers are limited by different nutrients regardless of their specialization on resource types. Moreover, as the consumer demand ratios become increasingly different, the conditions for stable coexistence nearly match those found under competition for essential resources: each consumer must ingest proportionately more of the resource that limits its growth rate (León and Tumpson 1975; Tilman 1982). The more different the consumer demand ratios are, the greater the range of u_i values consistent with this coexistence condition (Tilman 1982).

Adaptive Dynamics of an Allopatric Consumer

Below we summarize the conditions under which single-nutrient limitation (i.e., an unbalanced diet) and colimitation (a balanced diet) are optimal for a single consumer of two complementary resources (for derivation, see app. A in the online edition of the *American Naturalist*). Abrams (1987c) previously derived these conditions, treating resource densities as parameters. We place these conditions in the context of a dynamical model in which resource densities are state variables, thereby obtaining an expression for the optimal diet defined solely in terms of resource supply concentrations, resource composition ratios, and consumer demand ratios (app. A). Figure 5 illustrates our analytical results for an arbitrarily chosen set of parameter values.

Colimitation maximizes fitness only when the consumer's demand ratio is sufficiently near to the nutrient supply ratio (fig. 5). As the consumer's demand ratio and nutrient supply ratio become more mismatched, colimitation becomes suboptimal. This change occurs because a colimited consumer feeds on its preferred resource at a high per capita rate, reducing the density of this resource to such an extent that shifting the uptake rates toward the more abundant but less profitable (on a per unit basis) resource actually increases fitness. In shifting its uptake rates toward the less profitable but more abundant resource, the consumer becomes limited by one nutrient and therefore excretes excess amounts of the other. It can be shown that the uptake rate corresponding to the ESS occurs when the abundance of the limiting nutrient is equally distributed across the two resources (app. A). Whenever colimitation requires uptake rates u_i that are greater than (less than) those optimized under a -limited (b -limited) conditions, the a -limited (b -limited) ESS is also

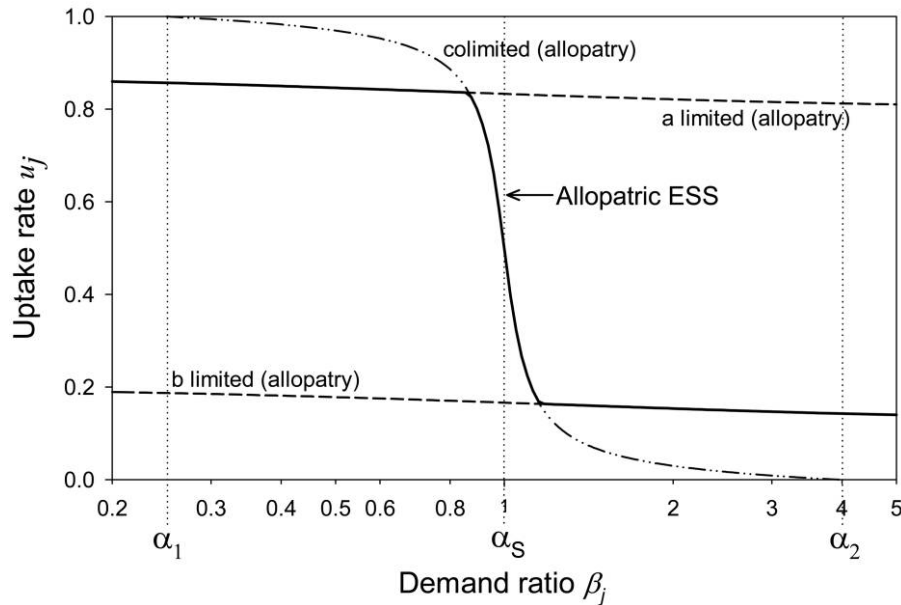


Figure 5: Trait values leading to the evolutionarily stable strategy (ESS) for a single consumer (allopatry) are given as a function of the demand ratio (β) by the solid black line. The allopatric ESS follows the curve defining nutrient colimitation only when the demand ratio is sufficiently near to the supply ratio (α_s). When colimitation requires a more extreme uptake rate than an a -limited or b -limited state, adaptation selects a nutrient-limited ESS. Nutrient-limited states are favored over colimitation because of the dynamic renewal of resources; colimitation by extreme specialization on a single resource leads to reduced density of that resource and release of the other resource from consumption pressure. Parameter values are as follows: $\alpha_1 = 0.25$, $\alpha_2 = 4.0$, $d_j = 0.1$, $S_1 = S_2 = 1$, $D = 0.1$.

the convergent stable strategy for a single consumer growing in allopatry. Whenever colimitation requires uptake rates which are intermediate between the a -limited and b -limited ESSs, the colimited state is the convergent stable strategy for a single consumer growing in allopatry (fig. 5).

Interestingly, adaptation in allopatry always “preadapts” consumers of complementary resources to coexist in sympatry (e.g., fig. 4; app. B). This result reflects the fact that the conditions for coexistence are relatively loose under competition for complementary resources. Coexistence can occur independently of the relative rates at which the consumers take up the two resources, because of the complex interplay of nutrient limitation and resource specialization. In contrast, adaptation in allopatry never preadapts consumers of essential resources to coexist in sympatry (Fox and Vasseur 2008).

Adaptive Dynamics of Two Consumers in Sympatry: ESS Diets and Coexistence

In sympatry, resource densities and therefore nutrient availabilities are set by the densities and traits of both consumers. Considering only ecological dynamics, it is possible for two consumers with any combination of non-

identical demand ratios to coexist stably, given an appropriate choice of uptake rates (e.g., fig. 4; app. B). However, when two consumers have demand ratios that fall either both above or both below the nutrient supply ratio (α_s), the ESS will always exclude the consumer whose demand ratio is most different from the nutrient supply ratio. Competitive exclusion occurs because both consumers become limited by a single nutrient as their uptake rates adapt. The consumer that can make the best use of the nonlimiting nutrient will reduce the availability of the limiting nutrient to the greatest extent, thereby excluding its competitor in a manner consistent with R^* theory (Tilman 1982).

Coexistence in sympatry at an ESS therefore requires that consumers’ demand ratios fall on opposite sides of the nutrient supply ratio (α_s), and so we assume without loss of generality that $\alpha_1 < \beta_1 < \alpha_s < \beta_2 < \alpha_2$. In contrast to the allopatric case, adaptive consumers coexisting in sympatry are always nutrient colimited at equilibrium. To understand why, recall that in allopatry, each consumer’s uptake rates adapt so as to achieve colimitation, unless doing so would drive the preferred resource to low density relative to the other resource. In sympatry, two consumers with demand ratios that bracket the nutrient supply ratio complement one another. Each consumer prefers a dif-

ferent resource, so that neither resource is driven to very low density relative to the other at equilibrium.

The trait values yielding colimitation of adaptive consumers in sympatry can be solved for analytically (app. A). Although it is not necessary to assume equal death rates, this assumption ($d_1 = d_2$) simplifies the solution for uptake rates at the sympatric nutrient-colimited equilibrium to

$$u_{i(s)} = \frac{1 - k_2(1 + \beta_j)}{(k_1 - k_2)(1 + \beta_j)}. \quad (8)$$

Numerical simulation demonstrates that this trait value is the evolutionarily and convergent stable strategy when $\alpha_1 < \beta_1 < \alpha_s < \beta_2 < \alpha_2$ (app. B).

For the parameters used herein, the sympatric ESS always falls inside a region of parameter space permitting stable ecological coexistence (fig. 4; app. B). Although an analytical solution is not feasible, numerical analysis of the dominant eigenvalue of the community matrix suggests that this result is robust for all parameterizations where both consumers can persist in allopatry (results not shown). This contrasts somewhat with the case of competition for essential resources, in which the sympatric optimum trait values always fall on the boundary of the region of parameter space permitting ecologically stable coexistence (although coadaptation stabilizes the resulting dynamics; Fox and Vasseur 2008). Coadaptation of competitors for complementary resources (e.g., herbivores) therefore seems more likely to promote stable coexistence than does coadaptation of competitors for essential resources (e.g., primary producers; Abrams 1987b).

Our model predicts that the consumers' relative abundances in sympatry reflect their relative proximity to the nutrient supply ratio (app. B). A consumer whose demand ratio more closely reflects the nutrient supply ratio will reach a higher equilibrium density than one whose demand ratio is more different, yet the two will coexist. This suggests that competitive dominance among herbivores in nature may reflect a closer association between the demand and supply of nutrients in common herbivores relative to rare ones. Our model provides a scenario in which rare species can coexist with common species in an ecologically stable fashion. This prediction could be tested with data on the relative abundances and stoichiometries of coexisting herbivores and plants (e.g., Behmer and Joern 2008).

*Adaptive Dynamics of Two Consumers in Sympatry:
Character Displacement, Convergence,
and Parallel Shifts*

Character displacement, convergence, and parallel shifts all arise naturally in the context of our simple model under

different demand ratios of the consumers when consumers adapted to allopatric conditions are forced into sympatry. Notably, these situations do not depend on additional biological complexities such as consumer density dependence (Abrams 1987a).

When consumer demand ratios are both close to the nutrient supply ratio, and therefore close to one another, adaptive trait change in sympatry leads to character convergence (fig. 6). Convergence occurs because consumers must balance their uptake rates to cope with the reduction in the density of the resource that least matches their demand but that best matches and is preferred by the other consumer. Each must adapt to gain a larger share of their competitor's preferred resource, and so adaptation yields character convergence. Of course, the transient ecological and evolutionary dynamics can be complex and can include temporary changes in the direction of selection (see app. B), but the ultimate equilibrium outcome is character convergence. In this case, competition for complementary resources has the same effect on consumer traits as competition for nutritionally essential resources (Abrams 1987b; Fox and Vasseur 2008). Resource competition leads to character convergence when it is adaptive for consumers to be colimited in both allopatry and sympatry.

When consumers' demand ratios are far from the supply ratio and each is closely matched to the composition of a particular resource, coadaptation in sympatry generates character displacement (fig. 6). The pattern arises because the allopatric optima represent nutrient-limited states where consumers ingest their preferred resource at a lower rate than is required to achieve colimitation because less preferred resources are abundant. In sympatry, consumers drive down the abundance of these less preferred resources, and the benefit of ingesting a nutrient-limited diet is lost. Fitness increases when ingestion rates diverge toward colimited states (fig. 6). In this case, competition for complementary resources has the same effect on consumer traits as competition for nutritionally substitutable resources (Lawlor and Maynard Smith 1976). However, character displacement in the case considered here arises for different reasons. Under competition for substitutable resources, nutrient limitation or colimitation is nonexistent; instead, consumers diverge to gain access to resources that are underutilized on a per capita basis, thereby increasing their total resource uptake rate.

In the case where the nutrient demands of consumers are sufficiently asymmetric about the nutrient supply ratio (one is close to the nutrient supply ratio, and the other is far from it), coadaptation in sympatry causes both consumers' uptake rates to change in the same direction (fig. 6). For brevity, we refer to this as "parallel" adaptation, even though the uptake rates generally do not change in strictly parallel fashion. Such parallel character shifts do

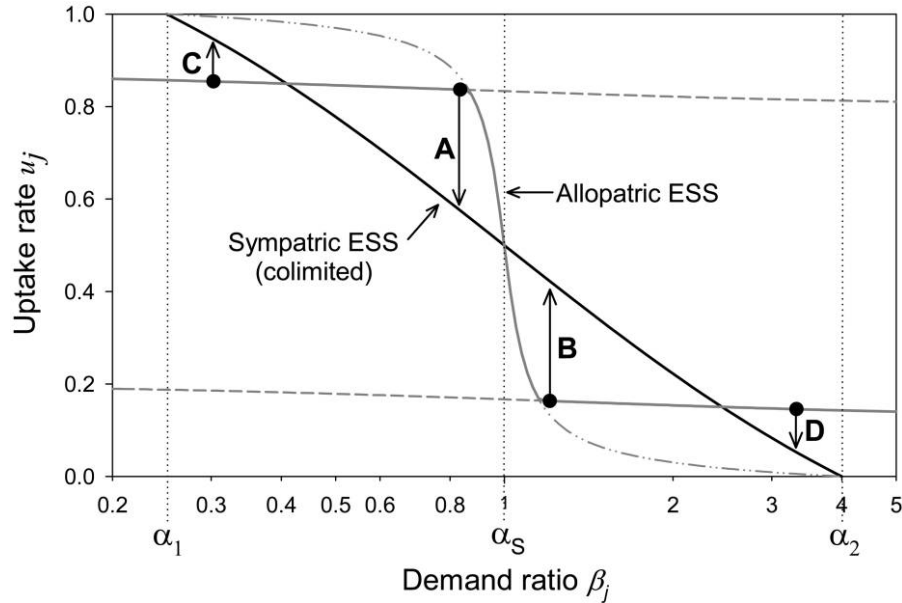


Figure 6: Trait values at the sympatric and allopatric evolutionarily stable strategies (ESSs), as a function of the demand ratio (β), are given by the solid black line and the gray line, respectively. Preadaptation to allopatric conditions leads to three possible relative directions of trait adaptation in sympatry: consumers with demand ratios corresponding to A and B demonstrate trait convergence, C and D represent trait divergence, and A and D (and C and B) represent parallel trait shifts. Pairings A and C and B and D are ecologically unstable at their evolutionary optimum because both consumers have demand ratios on the same side of the supply ratio (α_s); the more proximate consumer to the supply ratio will exclude the other as adaptation occurs. Exemplary transient dynamics are shown in appendix B in the online edition of the *American Naturalist*. Parameter values are as follows: $\alpha_1 = 0.25$, $\alpha_2 = 4.0$, $d_1 = d_2 = 0.1$, $S_1 = S_2 = 1$, $D = 0.1$.

not occur in otherwise similar models of competition for essential or substitutable resources (Lawlor and Maynard Smith 1976; Abrams 1987b; Fox and Vasseur 2008).

Transient Ecoevolutionary Dynamics

The results presented so far describe stable equilibrium behavior. However, recent empirical studies reveal the ability of sufficiently rapid adaptive evolution to alter ecological dynamics (Yoshida et al. 2003; Carroll et al. 2007; Duffy and Sivars-Becker 2007), suggesting that transient dynamics may be complicated by ecoevolutionary feedbacks. In appendix B, we illustrate the transient dynamics of the full model for cases of convergent, divergent, and parallel evolution of competitors from their allopatric optima.

Two key points emerge from our numerical explorations of transient dynamics. First, adaptive trait change often exhibits temporary reversals in direction for one or both consumers (similar to models of competition for essential resources; Fox and Vasseur 2008). Second, even though adaptation ultimately favors stable coexistence in our model, the transient dynamics can be characterized by long periods of near extinction in one or both consumers (app. B). In nature, demographic and environmental stochas-

ticity would likely convert these near extinctions to actual extinctions. Rapid adaptation reduces or eliminates near extinctions by causing the system to quickly adapt through regions to trait space leading to priority effects or competitive exclusion. This suggests that rapid trait changes via behavioral shifts or mediated by substantial genetic variation may be more conducive to ecological coexistence.

Including Costly Ingestion of an Unbalanced Diet

Ingesting an unbalanced diet and excreting excess nutrients without cost is an unlikely assumption in nature. Costs may be associated with investment and maintenance of excretory structures, the energy required to process and transport excreta, or the opportunity cost of time spent ingesting nutrients that have no benefit to growth. In appendix C we explore the third effect by incorporating a saturating Type II functional response in our model. We summarize the main results here.

Assuming that handling times are equal for all consumer-resource pairs, increasing handling time influences only the ESS of consumers in allopatry; because consumers ingest a nutritionally balanced diet in sympatry, there is no opportunity cost to be paid. As handling time

increases, it becomes unfavorable for consumers in allopatry to ingest a nutritionally unbalanced diet (fig. C1 in the online edition of the *American Naturalist*). Once the costs of ingesting an unbalanced diet reach a critical threshold, competition for complementary resources generates only character convergence, and not character displacement or parallel shifts.

Fitness costs associated with investment and maintenance of excretory structures and the processing and transport of excreta would likely promote character convergence as well. These costs select for colimitation, especially if they increase with the amount of nonlimiting nutrient to be excreted. Character convergence is the rule whenever it is adaptive for consumers to be colimited in both allopatry and sympatry (Abrams 1987b, Fox and Vasseur 2008; this study).

Discussion

Empirical Evidence

Our model assumptions apply best to competing herbivores (e.g., Behmer and Joern 2008). Unfortunately, empirical evidence regarding character displacement in herbivores, or character convergence or parallel shifts in any species, is scarce (reviewed in Schluter 2000). It is unclear whether this paucity of empirical evidence for character convergence or parallel shifts reflects reality or merely a lack of studies seeking these phenomena. As with classic examples of character displacement, species-poor islands and islandlike habitats would be promising places to look for comparative evidence of character convergence and parallel shifts among herbivores.

Our model also suggests new directions for experimental research. Many diet-choice experiments show that insect herbivores can choose nutritionally balanced mixtures of complementary plant resources (Behmer 2009), and several studies show that nutritionally balanced diets maximize fitness, all else being equal (e.g., Behmer and Joern 2008; Lee et al. 2008). Some studies also examine the negative fitness consequences of forcing insect herbivores to adopt a nutritionally imbalanced diet, with consideration for why herbivores might prefer one imbalanced diet over another (Simpson et al. 2004; Lee et al. 2008). However, we are aware of no diet choice studies that allow consumers to reduce resource availability (possibly even to zero) so as to test whether herbivores ever decline the opportunity to consume a balanced diet in favor of consuming a larger amount of imbalanced food and whether doing so maximizes herbivore fitness. Ritchie and Tilman (1993) allowed caged grasshoppers to forage on a mixture of plants in both the presence and the absence of a competing grasshopper species. They found that grasshoppers competed

for food and altered their diets in the presence of other species, with some species pairs exhibiting character convergence. However, it is unclear whether the plant resources were nutritionally complementary, and so the results of Ritchie and Tilman (1993) are difficult to interpret in light of our model.

We know of no study reporting the sort of complex transient ecological and trait dynamics predicted by our model for many parameter combinations. Reports of adaptive evolutionary fluctuations in species' trait values come from predator-prey systems with cyclic ecological dynamics (Yoshida et al. 2003) or from systems with fluctuating abiotic conditions (Grant and Grant 2006). Many field and laboratory observations report monotonic directional evolution (e.g., Hunt et al. 2008; Barrick et al. 2009), likely because these studies consider evolution toward a fixed optimum whereas in our model the optimum trait values change over time because of changes in the species abundances. It would be interesting to try to test our model predictions with experimental evolution of consumers with short generation times.

One challenge in applying our model to natural systems is that our model considers only two consumers and two resources. Work on models of competition for substitutable resources suggests that many-consumer, many-resource systems can exhibit behavior that could not have been predicted from consideration of two-consumer, two-resource systems (Scheffer and van Nes 2006). Work on many-consumer systems is urgently needed to provide a guide for empirical work. For instance, Behmer and Joern (2008) show that five of seven coexisting grasshopper species differ from one another in their demand ratios for two macronutrients (protein and carbohydrate). Behmer and Joern (2008) suggest that the degree of differentiation in nutrient demand should determine how strongly herbivores compete for plant resources. Our results for two competitors support this intuition: as the demand ratios of consumers diverge, the fraction of the trait space allowing coexistence increases. However, given our model framework, the pattern of demand ratios found by Behmer and Joern (2008) is insufficient to explain stable coexistence when resources are dynamic and reach limiting densities (given that the number of coexisting species exceeds the number of limiting nutrients). Further work is necessary to identify the precise coexistence conditions for more than two competitors for complementary resources.

Our approach assumes that only two nutrients matter for the dynamics of consumers and resources, and it ignores the contributions made by other nonlimiting nutrients to resource and consumer biomass. Provided that the proportion of resource biomass consisting of other nonlimiting nutrients is equal in both resources, this assumption has no effect on model dynamics. If resources

differ in their proportions of other nonlimiting resources, optimal uptake rates will shift to reflect the absolute availability of limiting nutrients in the two resources. Explicitly considering the contribution of more than two nutrient types provides the potential for additional consumers to coexist at equilibrium. One complication that arises in the context of many-consumer, many-resource models is that resources that are complementary for one consumer can be substitutable for another consumer. In the two-consumer, two-resource case, this situation leads to competitive exclusion with or without adaptive trait change, but we suspect that it might not do so in a multiple-consumer, multiple-resource system.

Conclusion: Character Shifts as Epiphenomena

Our results, together with those of others (Abrams 1987*b*; Fox and Vasseur 2008), show that the whole concept of “resource-use overlap” is useful only in the context of competition for substitutable resources. In the case of substitutable resources, an individual consumer that reduces its resource-use overlap with other individuals gains fitness because it focuses its foraging effort on resources for which there is little competition (i.e., resources that are in high abundance on a per consumer basis). However, in the cases of complementary or essential resources, limitation by their nutrient content must be taken into account (Abrams 1987*b*; Fox and Vasseur 2008; this study). For example, we have shown that when nutrients limit growth (as opposed to limiting resource densities themselves), reducing resource overlap via character divergence rarely provides access to more of the limiting nutrient. Fitness is therefore disconnected from resource-use overlap and depends instead on gaining access to the limiting nutrients contained in resources (see also Abrams 1990). When competition is for complementary or essential resources, resource-use overlap between consumers is an epiphenomenon, and considering resource-use overlap does not aid in understanding how resource competition translates into selection pressure on resource-use traits.

A further reason for regarding character displacement, convergence, and parallel shifts as epiphenomena when competition is for nonsubstitutable resources is the fact that they have no effect on the stability of coexistence. The simplest theoretical models predict that coadaptation of competitors always leads to stable coexistence, even when coadaptation leads to character convergence (Lawlor and Maynard Smith 1976; Fox and Vasseur 2008; this study). This conclusion contrasts with previous verbal arguments claiming that character convergence leads to neutrally stable dynamics (Hubbell and Foster 1986), as well as with “competition” models, where selection is actually imposed by external abiotic conditions rather than by re-

source levels (Hubbell 2006). It is essential to explicitly model consumer and resource dynamics and the feedbacks between trait change and ecological change in order to correctly derive the effects of resource competition on competitor traits and system stability.

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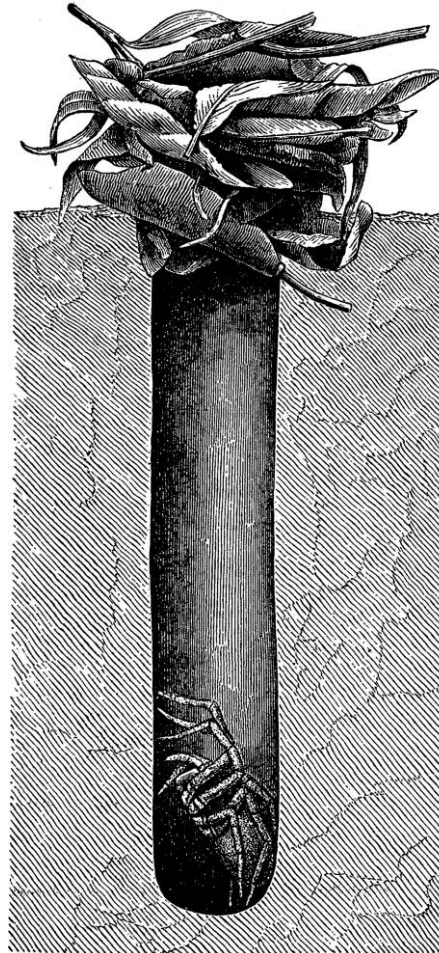
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Lycosa. “The holes were from six to eight inches deep and lined with a delicate web.... Before opening the holes we sounded them with straws and tried to provoke the spiders to come out, but they took no notice of it.” From “The *Lycosa* at Home” by J. H. Emerton (*American Naturalist*, 1871, 4:664–665).

Appendix A from D. A. Vasseur and J. W. Fox, “Adaptive Dynamics of Competition for Nutritionally Complementary Resources: Character Convergence, Displacement, and Parallelism” (Am. Nat., vol. 178, no. 4, p. 000)

Derivations of the Allopatric and Sympatric Evolutionarily Stable Strategies

The Single-Species Evolutionarily Stable Strategy

Abrams (1987c) derived the conditions at which a single consumer will evolve to be colimited, or single-nutrient limited, when growing on two complementary resources (what he called “complementarily substitutable”). We reiterate those conditions here, using the formalism of our model (eqq. [1]–[3]).

Under limitation by nutrient a , the rate of ingestion of nutrient b relative to that of a exceeds the demand such that $g_b/g_a > \beta$. Then the optimal uptake rate occurs when the total amount of nutrient a is equally distributed across resources (Abrams 1987c) such that

$$k_1 R_1 - k_2 R_2 = 0. \quad (\text{A1})$$

In the opposing case, where nutrient b is limiting such that $g_b/g_a < \beta$,

$$(1 - k_1)R_1 - (1 - k_2)R_2 = 0 \quad (\text{A2})$$

yields the optimal uptake rate. Substituting these equations respectively into the a - and b -limited branches of the consumer isoclines (eq. [6]) yields expressions for the equilibrium density of resources R_1 and R_2 under nutrient a and nutrient b limitation, which we denote with additional subscripts:

$$\begin{aligned} R_{1(a)} &= \frac{d}{k_1(1 + \beta)}, \\ R_{1(b)} &= \frac{d\beta}{(1 - k_1)(1 + \beta)}, \\ R_{2(a)} &= \frac{d}{k_2(1 + \beta)}, \\ R_{2(b)} &= \frac{d\beta}{(1 - k_2)(1 + \beta)}. \end{aligned} \quad (\text{A3})$$

From equation (2), we also find that at equilibrium, $R_1 = DS_1/(uC + D)$ and $R_2 = DS_2/[(1 - u)C + D]$ (for the sake of simplicity we have dropped the subscripts from the consumer’s parameters in the allopatric calculations). Equating these expressions with those in equation (A3) under nutrient a limitation yields two expressions for the equilibrium consumer density, which can be combined to solve for the optimal uptake rate under limitation of a :

$$u_{(a)} = \frac{S_1 k_1 (1 + \beta) - d}{S_1 k_1 (1 + \beta) + S_2 k_2 (1 + \beta) - 2d}. \quad (\text{A4a})$$

Similar logic yields the optimal uptake rate under b limitation:

$$u_{(b)} = \frac{S_1 (1 - k_1) (1 + \beta) - d\beta}{S_1 (1 - k_1) (1 + \beta) + S_2 (1 - k_2) (1 + \beta) - 2d\beta}. \quad (\text{A4b})$$

In addition to the single-nutrient-limited states, colimitation by both nutrients can occur. Arbitrarily assuming

that each unit of resource 1 has an excess of nutrient a and each unit of resource 2 has an excess of nutrient b relative to the requirements of the consumer (such that $\alpha_1 < \beta < \alpha_2$) yields the following requirements for colimitation of a single consumer (Abrams 1987c):

$$\begin{aligned} k_1 R_1 - k_2 R_2 &< 0, \\ (1 - k_1) R_1 - (1 - k_2) R_2 &> 0. \end{aligned} \quad (\text{A5})$$

Simply stated, colimitation will occur when there is a relatively larger total amount of nutrient a bound in R_2 and a relatively larger amount of nutrient b bound in R_1 . Colimitation implies that the ratio of ingested nutrients matches the demand $g_b/g_a = \beta$, which can be expanded with equation (3) to yield

$$\beta[k_1 u R_1 + k_2(1 - u) R_2] = (1 - k_1) u R_1 + (1 - k_2)(1 - u) R_2, \quad (\text{A6})$$

and that assimilation efficiency is unity ($\delta = 0$), which yields the expression (from eq. [2a]) $g_a + g_b - d = 0$ when C is at equilibrium. As above, this expression and equation (A6) can be used to solve the equilibrium consumer density. When equated, and after some rearrangement, these yield an expression of the optimal uptake rate under nutrient colimitation:

$$u_{(C)} = \frac{2d\eta_1\eta_2 - (1 + \beta)(k_1 - k_2)(S_1\eta_1 + S_2\eta_2) + \sqrt{4d^2\eta_1^2\eta_2^2 + (1 + \beta)^2(k_1 - k_2)^2(S_1\eta_1 + S_2\eta_2)^2}}{2(1 + \beta)(k_2 - k_1)(S_1\eta_1 + S_2\eta_2)}, \quad (\text{A7})$$

where $\eta_1 = \beta k_1 + k_1 - 1$ and $\eta_2 = \beta k_2 + k_2 - 1$. This expression produces the S -shaped function of $\log(\beta)$ shown in figures 5 and 6. Note that the domain of this function is bounded by the resource composition ratio. When the consumer demand ratio equals the composition ratio of one of the two resources, colimitation requires that the other resource be dropped from the diet.

The Evolutionarily Stable Strategy for Two Consumers and Two Resources

Numerical simulation of the model shows that whenever consumer demand ratios β_j fall on opposite sides of the supply ratio α_s (eq. [5]) and within the range of resource composition ratios (α_1, α_2), adaptation of the uptake rates leads to an ecologically stable equilibrium where both consumers are colimited by uptake of nutrients a and b . The trait values yielding colimitation can be solved analytically because of a notable invariance in the loci of the colimitation points in the u_1, u_2 phase space. We can show this clearly by assuming colimitation of both consumers and setting $dN_1/dt = 0$ and $dN_2/dt = 0$. This yields a linear system of two equations and two unknowns (R_1, R_2):

$$u_j R_1 + (1 - u_j) R_2 = d_j, \quad (\text{A8})$$

where $j = 1, 2$. Solving for R_1 and R_2 , we find the following equilibrium resource densities:

$$\begin{aligned} R_{1(s)}^* &= \frac{d_1(1 - u_2) - d_2(1 - u_1)}{u_1 - u_2}, \\ R_{2(s)}^* &= \frac{d_1 u_2 - d_2 u_1}{u_2 - u_1}. \end{aligned} \quad (\text{A9})$$

When equal rates of consumer death are assumed, that is, $d = d_1 = d_2$, the solution simplifies to $R_{1(s)} = R_{2(s)} = d$. Equation (A9) shows that when both consumers are colimited, their demand ratios (β_j) have no impact on equilibrium resource densities. This notable invariance arises because demand ratios and equilibrium consumer densities are compensatory; consumers that have demand ratios that are nearer to the supply ratio obtain higher equilibrium densities than do those with demand ratios further from the supply ratio (see app. B; fig. B5).

Given these constraints on the equilibrium resource densities, we can solve for the values of uptake rates u_j that occur at the sympatric optimum by substituting $R_{1(s)}$ and $R_{2(s)}$ into the equations for colimitation ($g_{bj}/g_{aj} = \beta_j$ for $j = 1, 2$). When consumer death rates are nonidentical, the solutions for the optimum uptake rates in sympatry $u_{j(s)}$ are obtainable but so complicated that they are analytically uninformative. However, assuming

equal rates of consumer death ($d_1 = d_2$), the solution for optimal uptake rates at the sympatric colimited equilibrium simplify to

$$u_{j(s)} = \frac{1 - k_2(1 + \beta_j)}{(k_1 - k_2)(1 + \beta_j)}. \quad (\text{A10})$$

Appendix B from D. A. Vasseur and J. W. Fox, “Adaptive Dynamics of Competition for Nutritionally Complementary Resources: Character Convergence, Displacement, and Parallelism” (Am. Nat., vol. 178, no. 4, p. 000)

Transient Dynamics of the Coupled Ecoevolutionary Model

In order to integrate the full ecoevolutionary model, we must first replace equation (7), which is difficult to use in numerical integration because of the discontinuity in the selection differential, with a continuous approximation. First, by expanding the selection differential from equation (7), we find

$$\frac{\partial[(1/C_j)(dC_j/dt)]}{\partial u_j} = \begin{cases} \frac{(1 + \beta_j)\partial g_{aj}}{\partial u_j}, \frac{g_{bj}}{g_{aj}} > \beta_j & \text{when nutrient } a \text{ is limiting,} \\ \frac{(1 + 1/\beta_j)\partial g_{bj}}{\partial u_j}, \frac{g_{bj}}{g_{aj}} < \beta_j & \text{when nutrient } b \text{ is limiting,} \\ 0, \frac{g_{bj}}{g_{aj}} = \beta_j & \text{when colimited.} \end{cases} \quad (\text{B1})$$

As has been done in previous work (Klausmeier et al. 2007; Fox and Vasseur 2008), we approximate the discontinuous function (8), using a steep continuous sigmoid function:

$$\frac{du_j}{dt} = v_j \left(\phi(x_j, h) \left(\frac{(1 + \beta_j)\partial g_{aj}}{\partial u_j} - \frac{[1 + (1/\beta_j)]\partial g_{bj}}{\partial u_j} \right) + \frac{[1 + (1/\beta_j)]\partial g_{bj}}{\partial u_j} \right), \quad (\text{B2})$$

where $\phi(x_j, h) = 0.5 + \pi^{-1} \tan^{-1}(h \times x_j)$, $x_j = g_{bj} - g_{aj}\beta_j$, $\partial g_{aj}/\partial u_j = k_1 R_1 - k_2 R_2$, $\partial g_{bj}/\partial u_j = (1 - k_1)R_1 - (1 - k_2)R_2$, and $h = 1,000,000$. Given this large value of h , the function $\phi(\cdot)$ resolves to a value of 1 for nearly all positive values of x_j and 0 for nearly all negative values of x_j . This makes equation (B2) a very close approximation of the discontinuous equation (B1).

With this modified version of the trait-change model, we conduct a series of in silico common garden experiments by initiating numerical simulations of the two-consumer, two-resource model at the optimal trait values derived for single consumers (allopatry). Traits (consumer uptake rates) vary according to equation (B2), which in turn generates feedback between the ecological and the evolutionary dynamics. This feedback depends in large part on the stability of the underlying ecological system. Figure B1 shows the ecological outcome of competition in the trait space, along with representative consumer zero-net-growth isoclines for each region. Figures B2–B5 show the results of these experiments for the different combinations of consumer demand ratios (β_j) noted in figure 6 of the main text. Each of these figures consists of two parts. In part *a*, the temporal dynamics of the consumer uptake rates in the u_1, u_2 trait space are superimposed over the trait space, where shaded regions indicate different outcomes of ecological competition (in the absence of trait change). In part *b*, the temporal dynamics of resources and consumers are shown. Because the rate of evolutionary change is slow relative to the rate of ecological change, competitive outcomes are important for determining the direction and rates of trait changes. In each of these experiments, consumer C_1 is afforded a slight advantage in initial density (+1%) so that priority effects can be observed.

Figure B1 shows the ecoevolutionary trajectory of the system when two consumers evolve from the allopatric conditions labeled *A* and *B* in figure 6. These conditions correspond to consumers that have nutrient demand ratios that are reciprocal and near to the nutrient supply ratio (α_s). Initially, the two consumers coexist through strong partitioning of their resource use. Adaptation causes their uptake rates to converge, and they enter a

region of trait space where priority effects occur (fig. B2, *gray area*). The initial advantage afforded to C_1 allows it to grow while C_2 declines. However, as C_2 is gradually excluded from the system, C_1 adapts toward its allopatric optimum while the rare consumer C_2 adapts to the resource densities set by C_1 . This change in direction in the trait space forces the system across another region of coexistence and eventually into a region where C_1 is gradually excluded. These adaptive transitions continue until the system becomes sufficiently near to the adaptive fixed point (fig. B1). Increasing rates of adaptation (ν_j) lessen the amplitude and number of these adaptive transitions encountered along the evolutionary transient, whereas slowing the rates of adaptation increases their amplitude and number (results not shown). Surprisingly, in the transient approach to the sympatric optimum, it is the consumer whose initial density is higher (C_1) that reaches the lowest density along the ecoevolutionary transient (fig. B2).

As the consumer demand ratios move further from the supply ratio, the evolutionary transient leading from the allopatric optimum to the sympatric optimum becomes more stable. This occurs because of changes in the ecological stability of the trait space; the regions of competitive exclusion in the lower-right triangular area of figure B1 recede toward the axes, eventually bridging the central and lower regions of ecologically stable trait space. This allows character convergence to occur along an ecologically stable evolutionary transient (fig. B3).

When each consumer's demand ratio more closely reflects the composition ratio of a particular resource, adaptation from allopatric conditions generates trait divergence (fig. B4). Trait divergence leads to increased specialization of both consumers at the sympatric optimum. Single-nutrient limitation is not, favored as it is in allopatry under strongly skewed demand ratios due to exploitation of the second resource by the second consumer. The adaptive transient generated by combining consumers with demand ratios corresponding to points C and D in figure 6 is stable over the entire range of traits encountered during adaptation. Furthermore, all cases of trait divergence in this model produce adaptive transients that are ecologically stable (results not shown).

In the case where the nutrient demands of consumers are not reciprocal but are opposed in value relative to the nutrient supply ratio, there is potential for parallel trait evolution from allopatric conditions and combinations of consumers that may match a "well-adapted" consumer to a "maladapted" consumer (as measured by the difference between the allopatric and sympatric optima in trait space). Formulating the experiment in such a manner removes the symmetry from the competitive outcomes in trait space; however, the ecoevolutionary transient dynamics for parallel trait adaptation from allopatric conditions (corresponding to points A and D in fig. 6) are again confined within ecologically stable trait space (fig. B5). Because of the lack of symmetry in consumer nutrient-demand ratios, the equilibrium consumer densities obtained at the sympatric optimum reflect the suitability of consumers' nutrient demands to that supplied by the resources.

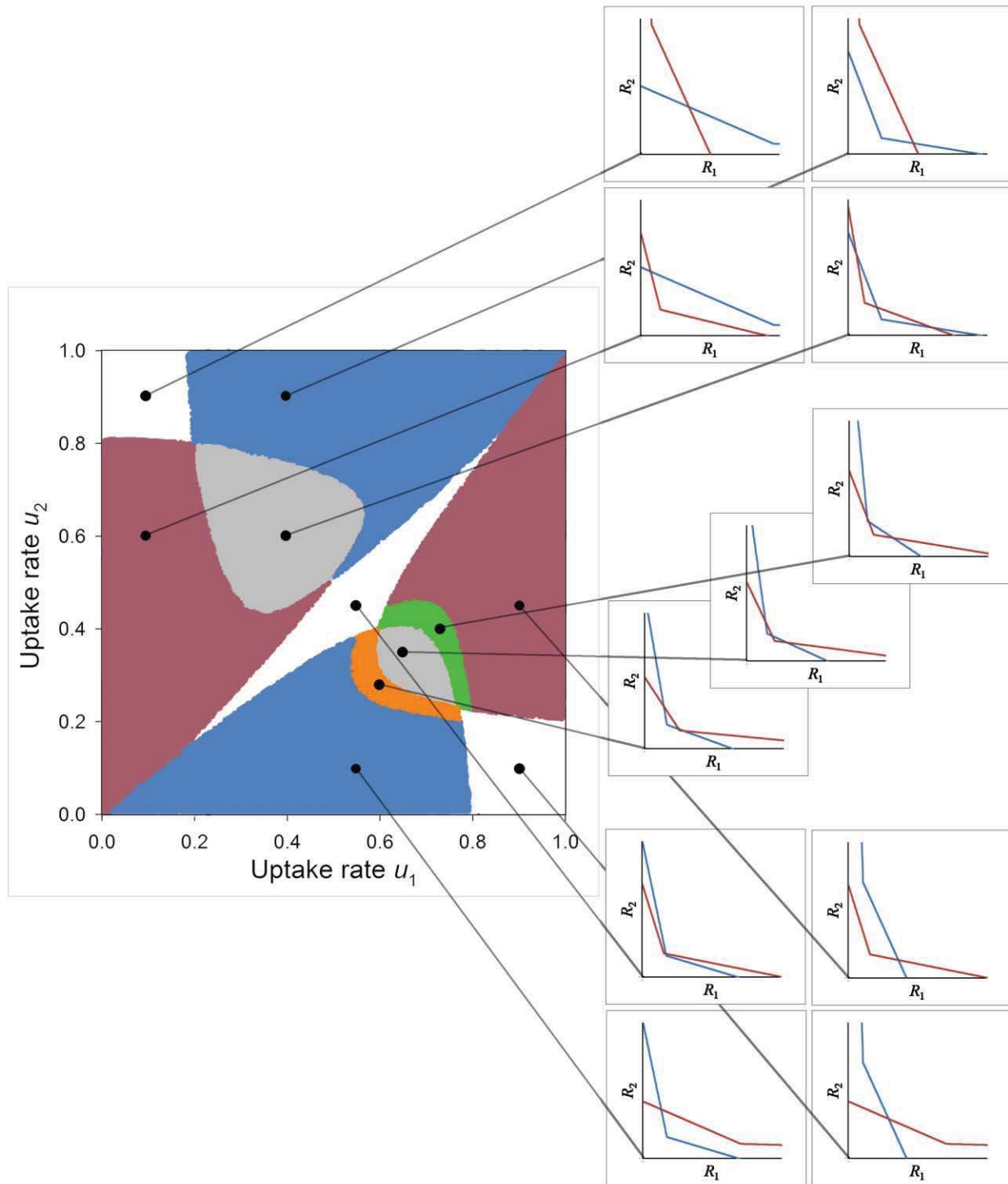


Figure B1: Ecological outcome of competition in trait space and zero-net-growth isoclines (ZNGIs) for the 11 regions. In the white regions, coexistence is stable. In the blue (red) regions, consumer 1 (2) excludes the other consumer. In the gray regions, exclusion of one competitor occurs via a priority effect. In the orange (green) region, a priority effect selects between exclusion of consumer 2 (1) and coexistence. The inset panels show the orientation of consumer ZNGIs for each of the 11 regions. Ecological outcomes were determined numerically by simulating the model for 5,000 time steps, using two different initial

conditions, $(C_1, C_2) = (0.1, 1.0)$ and $(1.0, 0.1)$. Precisely at $u_1, u_2 = 0.2, 0.8$, the dynamics are neutrally stable (as in fig. 3d). Other parameters were $\alpha_1 = 0.25$, $\alpha_2 = 4.0$, $\beta_1 = 1/1.2$, $\beta_2 = 1.2$, $d_j = 0.1$, $S_1 = B_1 = 1$, $D = 0.1$, $R_1(0) = R_2(0) = 0.2$.

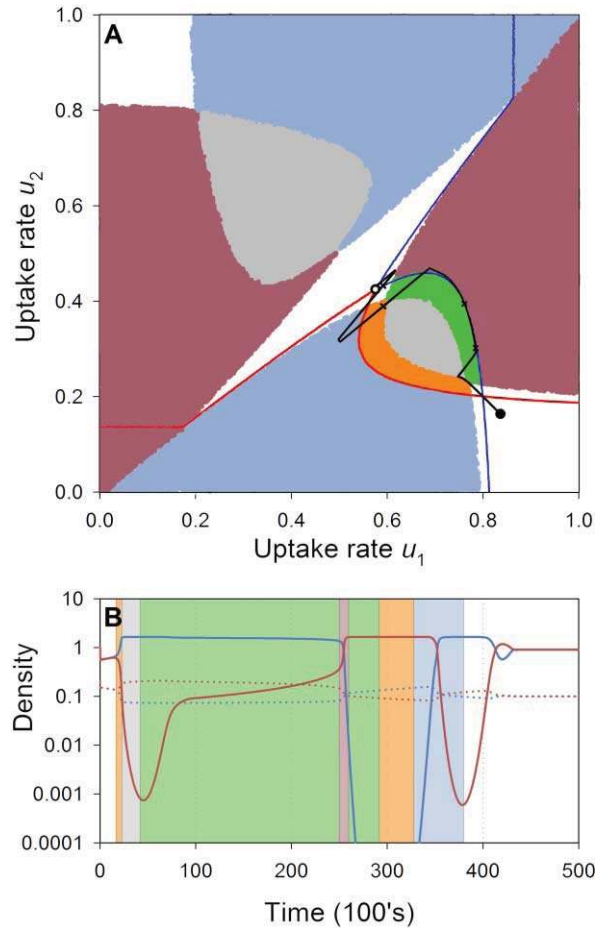


Figure B2: Adaptation of two consumers from their allopatric optima generates trait convergence but leads the system through trait space that is ecologically unstable. *A*, Outcome of competition in the trait space: in blue (red) regions, C_1 (C_2) excludes the other consumer; in the gray region, exclusion of one competitor occurs via a priority effect; in the orange (green) region, a priority effect selects between exclusion of C_2 (C_1) and coexistence; and in the white region, stable coexistence occurs. Precisely at $u_1, u_2 = 0.2, 0.8$, the dynamics are neutrally stable (as in fig. 3d). The blue (red) lines trace the points in phase space where C_1 (C_2) is colimited. The temporal dynamics of traits (overlaid on *A*, beginning from the solid black point) and population densities (*B*) are shown, with the background color corresponding to the region of trait space occupied at each time (C_1 is indicated by a solid blue line; C_2 , a solid red line; R_1 , a dashed blue line; R_2 , a dashed red line). Initial densities were $R_1(0) = R_2(0) = 0.2$; $C_1(0) = 1.0$; $C_2(0) = 0.99$. Other parameters are $\alpha_1 = 0.25$, $\alpha_2 = 4.0$, $\beta_1 = 1/1.2$, $\beta_2 = 1.2$, $d_j = 0.1$, $S_1 = B_1 = 1$, $D = 0.1$, and $\nu = 0.0002$.

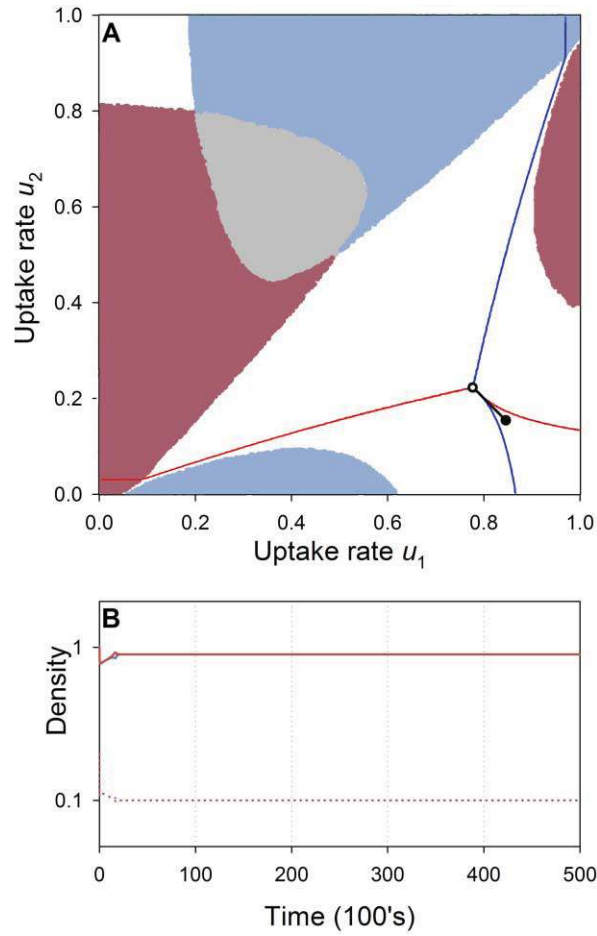


Figure B3: Adaptation of two consumers from their allopatric optima generating trait convergence. Here consumer demand ratios are less proximate to the supply ratio than in figure B1. *A*, Outcome of competition in the trait space (color coding is described in fig. B1). The temporal dynamics of traits (overlaid on *A*, beginning from the solid point at $t = 0$) and population densities (*B*) are shown, with the background color corresponding to the region of trait space occupied at each time. Initial densities were $R_1(0) = R_2(0) = 0.2$; $C_1(0) = 1.0$; $C_2(0) = 0.99$. Other parameters are $\alpha_1 = 0.25$, $\alpha_2 = 4.0$, $\beta_1 = 1/2$, $\beta_2 = 2$, $d_j = 0.1$, $S_1 = B_1 = 1$, $D = 0.1$, $\nu = 0.0002$.

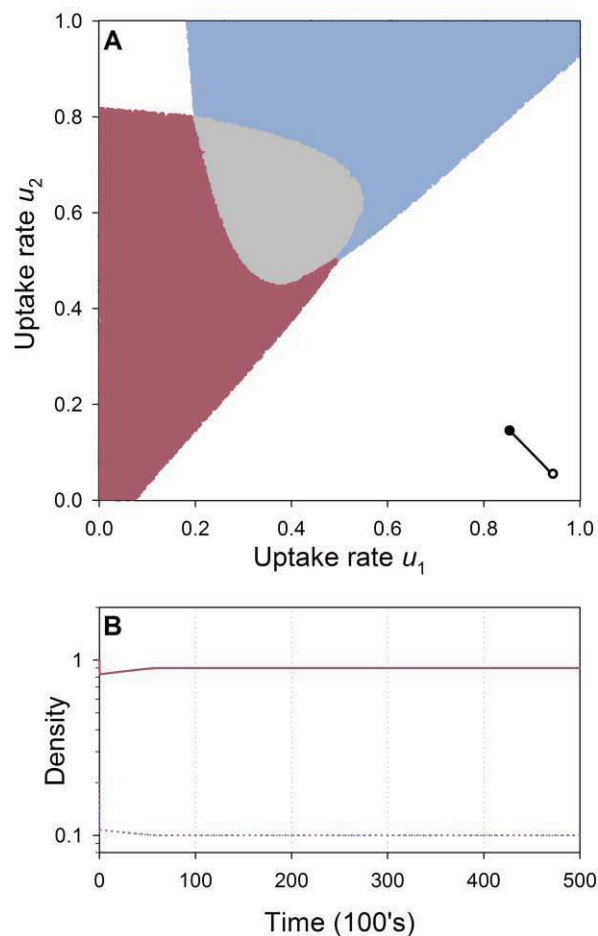


Figure B4: Adaptation of two consumers from their allopatric optima generating trait divergence. *A*, Outcome of competition in the trait space (color coding is described in fig. B1). The temporal dynamics of traits (overlaid on *A*, beginning from the solid point at $t = 0$) and population densities (*B*) are shown, with the background color corresponding to the region of trait space occupied at each time. Initial densities were $R_1(0) = R_2(0) = 0.2$; $C_1(0) = 1.0$; $C_2(0) = 0.99$. Other parameters are $\alpha_1 = 0.25$, $\alpha_2 = 4.0$, $\beta_1 = 1/3.3$, $\beta_2 = 3.3$, $d_j = 0.1$, $S_1 = B1 = 1$, $D = 0.1$, $\nu = 0.0002$.

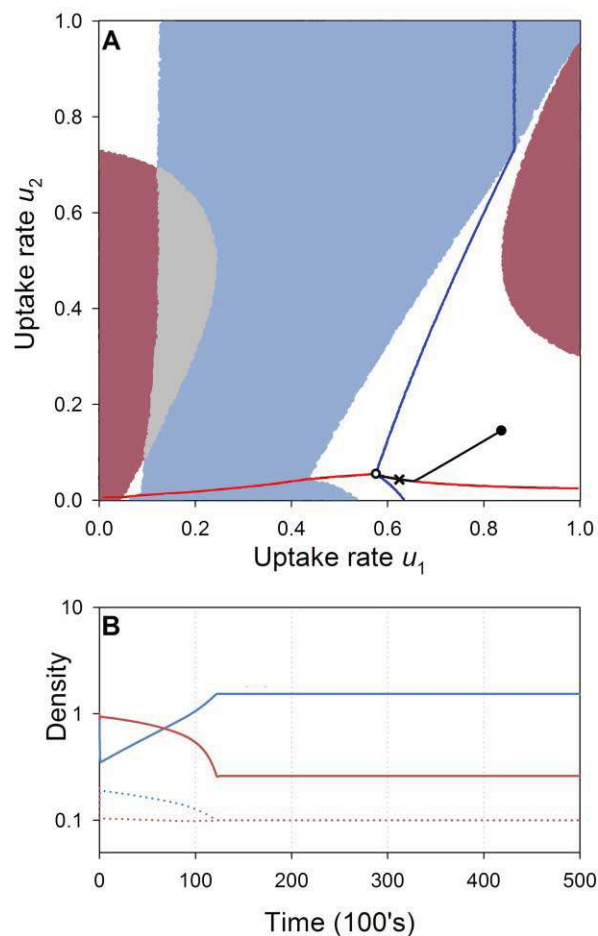


Figure B5: Adaptation of two consumers from their allopatric optima generating parallel trait evolution. *A*, Outcome of competition in the trait space (color coding is described in fig. B1). The temporal dynamics of traits (overlaid on *A*, beginning from the solid point at $t = 0$) and population densities (*B*) are shown, with the background color corresponding to the region of trait space occupied at each time. Initial densities were $R_1(0) = R_2(0) = 0.2$; $C_1(0) = 1.0$; $C_2(0) = 0.99$. Other parameters are $\alpha_1 = 0.25$, $\alpha_2 = 4.0$, $\beta_1 = 1/1.2$, $\beta_2 = 3.3$, $d_j = 0.1$, $S_1 = B_1 = 1$, $D = 0.1$, $\nu = 0.0002$.

Appendix C from D. A. Vasseur and J. W. Fox, “Adaptive Dynamics of Competition for Nutritionally Complementary Resources: Character Convergence, Displacement, and Parallelism” (Am. Nat., vol. 178, no. 4, p. 000)

Costly Ingestion of Excess Nutrients

Here we evaluate the effect of costly ingestion and excretion of excess nutrients in the diets of consumers. Such costs can be incurred in multiple ways. For example, the costs of excreting excess nutrients can directly impact a species’ growth rate because of the expenditure of energy and resources for the transport, packaging, and ultimate excretion of excess nutrients. Alternatively, ingestion of excess nutrients can incur an opportunity cost; time spent handling nutrients that will later be excreted, with no extracted benefit, reduces the amount of time in which an individual can spend handling those nutrients that are limiting growth. We investigate such an opportunity cost but argue that the ultimate effect it has on character shifts is likely similar for all such costs.

When we reformulate our model of competition for complementary resources to include a multispecies Type II functional response, the model becomes

$$\begin{aligned}\frac{dR_1}{dt} &= D(S_1 - R_1) - \sum_j \frac{u_j R_1 C_j}{1 + u_j t_h R_1 + (1 - u_j) t_h R_2}, \\ \frac{dR_2}{dt} &= D(S_2 - R_2) - \sum_j \frac{(1 - u_j) R_2 C_j}{1 + u_j t_h R_1 + (1 - u_j) t_h R_2}, \\ \frac{dC_j}{dt} &= C_j [(1 - \delta_j)(g_{aj} + g_{bj}) - d_j],\end{aligned}\tag{C1}$$

where

$$\begin{aligned}g_{aj} &= \frac{k_1 u_j R_1 + k_2 (1 - u_j) R_2}{1 + u_j t_h R_1 + (1 - u_j) t_h R_2}, \\ g_{bj} &= \frac{(1 - k_1) u_j R_1 + (1 - k_2) (1 - u_j) R_2}{1 + u_j t_h R_1 + (1 - u_j) t_h R_2}.\end{aligned}\tag{C2}$$

This model adds one parameter to the original formulation, the handling time t_h , which we assume is equivalent for all combinations of consumer and resource pairs. Notably, when $t_h = 0$, the model reverts to the version in the main text.

The solution for the evolutionarily stable strategy (ESS) in sympatry can be found using the same process outlined above for the model with a linear functional response. Again, provided that consumers’ demands lie on opposite sides of the nutrient supply ratio (α_s), two consumers should evolve to be nutrient colimited; therefore, $\delta_j = 0$. Setting $dN_j/dt = 0$ and assuming that $d_1 = d_2 = d$, we find the steady-state densities:

$$R_j^* = \frac{d}{1 - u_1 t_h d - u_2 t_h d}.\tag{C3}$$

Substituting these expressions into $g_{bj}/g_{aj} = \beta_j$ from equation (C2) yields the solution for uptake rates at the sympatric ESS:

$$u_{j(s)} = \frac{1 - k_2(1 + \beta_j)}{(k_1 - k_2)(1 + \beta_j)},\tag{C4}$$

which is identical to those rates for the model with linear functional responses. Although the uptake rates that consumers evolve in sympatry is independent of handling time, their equilibrium densities are altered. As handling time increases, consumer densities decrease because of the reduction in their ability to capture resources.

The opportunity cost of handling time is most important in allopatry, where we have shown that it can be optimal for consumers to ingest a nutritionally unbalanced diet when there is no cost of doing so. Unfortunately, solving the allopatric ESS is not analytically possible, so we resort to numerical simulation of this problem. Figure C1 shows the allopatric ESSs for four different handling times, determined by integrating the model for 5,000 time steps in the presence of one consumer. As handling time increases, the “flat” areas of the allopatric ESS corresponding to limitation by a single nutrient disappear because the costs of ingesting an unbalanced diet are too high. As t_h increases further, the allopatric ESS approaches the sympatric ESS because consumer densities decline and resources are no longer driven to low densities by consumer foraging. Most notably, character convergence becomes the only possibility as the costs of ingesting excess nutrients increase; when the costs of handling time are large enough ($t_h \geq 2$), the allopatric ESS will always produce more extreme uptake rates than the sympatric ESS, leading to character convergence in sympatry.

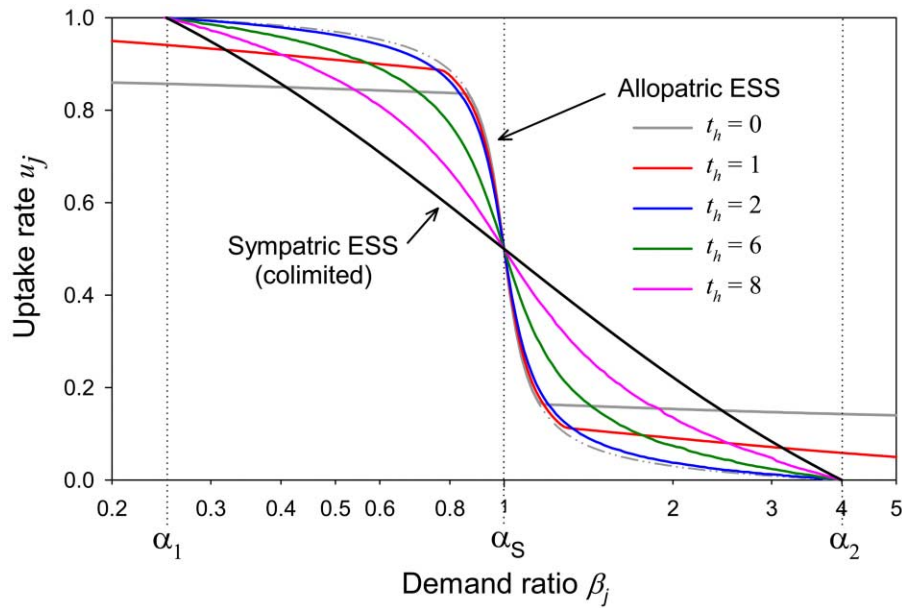


Figure C1: Trait values at the sympatric and allopatric evolutionarily stable strategies (ESSs), as a function of the demand ratio (β), across a gradient of handling times (t_h) using a Type II multispecies functional response. When the handling time equals 0, the result is equivalent to that shown in the main text for a linear functional response. As handling time increases, the “flat” areas of the allopatric ESS, which correspond to limitation by a single nutrient, disappear because the costs of ingesting an unbalanced diet are too high. As t_h increases further, the allopatric ESS approaches the sympatric ESS because consumer densities decline and resources are no longer driven to low densities by consumer foraging. Most notably, character convergence becomes the only possibility as the costs of ingesting excess nutrients grow. Parameter values are $\alpha_1 = 0.25$, $\alpha_2 = 4.0$, $d_1 = d_2 = 0.1$, $S_1 = B_1 = 1$, $D = 0.1$.