

Character Convergence under Competition for Nutritionally Essential Resources

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ABSTRACT: Resource competition is thought to drive divergence in resource use traits (character displacement) by generating selection favoring individuals able to use resources unavailable to others. However, this picture assumes nutritionally substitutable resources (e.g., different prey species). When species compete for nutritionally essential resources (e.g., different nutrients), theory predicts that selection drives character convergence. We used models of two species competing for two essential resources to address several issues not considered by existing theory. The models incorporated either slow evolutionary change in resource use traits or fast physiological or behavioral change. We report four major results. First, competition always generates character convergence, but differences in resource requirements prevent competitors from evolving identical resource use traits. Second, character convergence promotes coexistence. Competing species always attain resource use traits that allow coexistence, and adaptive trait change stabilizes the ecological equilibrium. In contrast, adaptation in allopatry never preadapts species to coexist in sympatry. Third, feedbacks between ecological dynamics and trait dynamics lead to surprising dynamical trajectories such as transient divergence in resource use traits followed by subsequent convergence. Fourth, under sufficiently slow trait change, ecological dynamics often drive one of the competitors to near extinction, which would prevent realization of long-term character convergence in practice.

Keywords: character convergence, competition, essential resources, quantitative genetics, adaptive dynamics, coexistence.

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Resource competition is common in nature (Schoener 1983; Gurevitch et al. 1992; Harpole and Tilman 2006; Kaplan and Denno 2007). The main evolutionary consequence of resource competition is thought to be character displacement, evolutionary divergence of competing species in resource use traits (reviewed in Schluter 2000; called “divergent character displacement” in Grant 1972). Resource competition generates divergence via frequency-dependent selection. Individuals with common resource use traits will compete intensely with many similar individuals and so have low fitness, while individuals with rare resource use traits will have access to underused resources and so have high fitness (Slatkin 1980; Taper and Case 1992). Many putative examples of character displacement are known, and the overall weight of evidence suggests that resource competition is an important driver of evolutionary diversification and adaptive radiation (Schluter 2000).

However, character displacement is not the only possible evolutionary outcome of resource competition. Abrams (1987a) pointed out that the expectation of character displacement depends crucially on the assumption of competition for nutritionally substitutable resources. Substitutable resources (e.g., different prey species) are those for which increased intake of one resource can always compensate for decreased intake of another (León and Tumpson 1975). Nutritional substitutability allows selection to favor traits that increase the ability to consume resources for which competition is weak but reduce the ability to consume resources for which competition is strong. Most putative examples of character displacement are thought to involve competition for substitutable resources (Schluter 2000). However, many species, particularly plants, algae, and microbes, often compete for nonsubstitutable (essential) resources such as nitrogen and phosphorus (Tilman 1982; Grover 1997; Harpole and Tilman 2007). Competition for essential resources selects for character convergence, not displacement (Abrams 1987a). When resources are essential, fitness depends on the consumption rate of the resource that is consumed at the lowest rate relative to the individual’s nutritional requirements

(León and Tumpson 1975; Grover 1997). Adaptive evolution therefore should alter species' traits so that essential resources are consumed in an optimal ratio matching nutritional requirements, leading to colimitation of fitness by all resources (Tilman 1982; Bloom et al. 1985; Abrams 1987a). Selection for colimitation leads to character convergence (Abrams 1987a).

For instance, consider a consumer species feeding on two essential resources and the evolutionary effect of the arrival of a second consumer species that is a superior competitor for resource 1. The arrival of the second consumer species will reduce the availability of resource 1 in the environment, generating selection on the first consumer species to increase its ability to acquire resource 1 and thereby restore its optimal ratio of resource consumption rates (Abrams 1987a). This represents convergence in resource use traits—the first consumer evolves to become a better competitor for resource 1, making the first consumer more similar in resource use to the second consumer. Abrams (1987a) supported this verbal argument by analyzing a simple model of a single consumer of two essential resources and demonstrating that per capita consumption rates producing colimitation are a CSS (an evolutionarily stable strategy [ESS] that is also an evolutionary attractor). Changes in the CSS per capita consumption rates in response to changes in resource availability imply character convergence when changes in resource availability are assumed to arise from resource consumption by a (nonevolving) competitor.

The pioneering work of Abrams (1987a) identifies the qualitative evolutionary effect of competition for essential resources but leaves important quantitative questions unaddressed. How similar will species become in their resource use traits? How does their evolved degree of similarity depend on their resource requirements and other factors? Can long-term convergence be preceded by transient periods of divergence? Abrams (1987a) also did not address the interplay of ecological and evolutionary dynamics. Ecological and evolutionary dynamics clearly are not independent here: ecological dynamics (resource consumption) determine individual fitnesses, while the subsequent trait evolution feeds back to alter the ecological dynamics by altering the frequency of individuals with different resource use traits. What are the reciprocal effects of ecological and evolutionary dynamics under competition for essential resources? For instance, can adaptive evolution prevent ecological extinction?

Evolutionary character displacement also has analogues on shorter timescales, and character convergence should as well. Many species can adaptively alter their resource use by shifting their behavior, morphology, or physiology ("niche shifts"; Giese 1973; Rhee 1978; Gotham and Rhee 1981; Pacala and Roughgarden 1984; Pfennig and Murphy

2000; Finzi et al. 2007). In general, the optimal resource use traits for a given species should be independent of whether the underlying mechanism of trait change is genetic evolution or phenotypic plasticity, as long as the traits are subject to the same trade-offs in either case (Abrams 1986, 1987a, 1987b). However, genetic evolution and phenotypic plasticity operate on different timescales and so should have different temporal dynamics.

Here we analyze models of adaptive trait change under competition for essential resources. Each model considers two consumers competing for two essential resources, in which both consumers' per capita resource consumption rates can change adaptively. The model can be interpreted as an approximation to standard quantitative genetics models describing slow trait change via genetic evolution (Iwasa et al. 1991; Taper and Case 1992; Abrams et al. 1993) or as a model of rapid trait change via behavioral shifts (Taylor and Day 1997) or rapid genetic evolution. We explore a wide range of relative rates of trait dynamics and ecological dynamics in order to fully understand model behavior. We do not assume any particular answer to the empirical question of how rapid genetic evolution typically is relative to rates of change in population abundances (reviewed in Hairston et al. 2005). We consider alternative models of trait change in appendix A in the online edition of the *American Naturalist*.

The Model

In all of the models, ecological dynamics are described by equations used in previous theoretical work on resource competition (León and Tumpson 1975), with minor modifications:

$$\frac{dR_i}{dt} = D(S_i - R_i) - \sum_j \frac{N_j g_j}{y_{ij}}, \quad (1a)$$

$$\frac{dN_j}{dt} = N_j(g_j - d_j), \quad (1b)$$

where

$$g_j = \min[y_{1j}u_jR_1, y_{2j}(1 - u_j)R_2]. \quad (2)$$

Essential resource i ($i = 1, 2$) has abundance R_i and is supplied in chemostat fashion at flow rate D and inflow concentration S_i . Resources wash out of the system at rate D . Consumer j ($j = 1, 2$) has abundance N_j and experiences density-independent losses at per capita rate d_j . Consumer j grazes on resource i with functional response g_j , parameterized by the per capita resource uptake rates u_j on resource 1 and $1 - u_j$ on resource 2. We assume that consumer j has fixed resource requirements (stoichiom-

etry): the yield coefficient y_{ij} gives the units of consumer j produced from a unit of resource i .

The minimum function in the functional response (eq. [2]) arises in the consumer growth rate (eq. [1b]) because resources are nutritionally essential, and so consumer growth is limited by the resource that the consumer acquires at the lowest rate relative to its requirements. The minimum function in equation (2) also appears in the resource growth rate (eq. [1a]) because we assume that consumer j maintains fixed stoichiometry by consuming the nonlimiting resource at a rate just sufficient to meet its requirements, given its current consumption rate of the limiting resource (León and Tumpson 1975). Our results remain qualitatively unchanged if we instead assume that consumers eat what is available (i.e., the sum in eq. [1a] is replaced by $\sum_j N_j u_j R_1$ for $i = 1$ and by $\sum_j N_j (1 - u_j) R_2$ for $i = 2$) and maintain fixed stoichiometry by excreting excess nonlimiting resource in an unavailable form (results not shown).

We assume constant per capita uptake rates u_j and $1 - u_j$ for the sake of simplicity. Our assumption that consumer j takes up resource 2 at per capita rate $1 - u_j$ enforces a linear trade-off between per capita uptake rates of the two resources. A linear trade-off is the simplest assumption and may be realistic in at least some cases (e.g., in microbes in which the total number of resource uptake proteins may be limited by cell surface area; Aksnes and Egge 1991). Empirical information on trade-off shape is lacking, so we lack an empirical motivation for choosing a particular nonlinear trade-off from the universe of possibilities, and a systematic exploration of various nonlinear trade-offs is beyond the scope of this work. Assigning both consumers the same total per capita uptake rate of 1 ensures that neither consumer is intrinsically superior to the other at resource acquisition.

Without loss of generality, we assume that $y_{11}, y_{22} < 1$ and $y_{21} = y_{12} = 1$, so that consumer j has a lower yield from resource $i = j$ than resource $i \neq j$. Under this assumption, the parameters y_{11} and y_{22} give the ratio of resource requirements for consumers 1 and 2, respectively. Our assumptions on the y_{ij} values also imply interspecific differences in resource requirement ratios, a necessary condition for ecological coexistence (León and Tumpson 1975; Tilman 1982).

Per capita resource uptake rates can change adaptively via either genetic evolution or phenotypic plasticity. We model trait change as

$$\frac{du_j}{dt} = v_j \frac{\partial(1/N_j)(dN_j/dt)}{\partial u_j}, \quad (3)$$

where rate parameter v_j scales the rate of evolution of

consumer j . The biological interpretation of v_j depends on the model derivation. The quantity $[\partial(1/N_j)(dN_j/dt)]/\partial u_j$ is the slope of the fitness gradient, the partial derivative of the fitness (per capita growth rate) of consumer j with respect to u_j .

There are two ways to derive equation (3) as a model of genetic evolution. First, it can be derived as an approximation to a quantitative genetics model (Iwasa et al. 1991; Taper and Case 1992; Abrams et al. 1993). Quantitative genetics assumes that the trait value of an individual is determined by many loci with small, additive effects, along with a normally distributed environmental deviation, leading to a population phenotypic distribution that is approximately normal on an appropriate measurement scale (Lande 1976, 1982; Taper and Case 1992). Genetic and phenotypic variances are assumed constant (Lande 1982; Taper and Case 1992). Population size is assumed to be sufficiently large that genetic drift can be neglected (Lande 1976). To approximate the underlying quantitative genetics model using equation (3), it is further assumed that the phenotypic variance is small or that the variance is large but that the third- and higher-order derivatives of the fitness function are small (Iwasa et al. 1991; Taper and Case 1992; Abrams et al. 1993). The approximation works best when selection is relatively weak (Lande 1982; Iwasa et al. 1991; Taper and Case 1992; Abrams et al. 1993; Abrams 2005). When equation (3) is interpreted as an approximation to quantitative genetics, v_j is interpreted as the additive genetic variance.

Second, equation (3) can be derived as a deterministic approximation to a stochastic model describing the evolution of a nearly monomorphic asexual lineage in which adaptation occurs via rapid fixation of rare mutations of small effect and the ecological dynamics go to equilibrium between mutation events (Dieckmann and Law 1996). Derived in this fashion, equation (3) has been termed a model of adaptive dynamics (Dieckmann and Law 1996; Abrams 2005). If equation (3) is interpreted as a model of adaptive dynamics in this sense, v_j is proportional to the product of the variance of the mutation distribution and the rate of mutation per birth. Note that equation (3) is an approximation to the evolutionary dynamics of a single population evolving via quantitative genetics but is an approximation to the average evolutionary dynamics of many independent asexual populations evolving via stochastic mutation-limited evolution (Taper and Case 1992; Dieckmann and Law 1996). Derivation of equation (3) as an approximation to a stochastic model of mutation-limited evolution requires the assumption of a separation of timescales between evolutionary dynamics (slow) and ecological dynamics (fast; Dieckmann and Law 1996). Deriving equation (3) as an approximation to quantitative

genetics does not require assumption of a separation of timescales (Taper and Case 1992).

Quantitative genetics is the most generally applicable motivation for equation (3) (Abrams 2005), and we consider equation (3) as an approximation to quantitative genetics when interpreting our model as an evolutionary model. However, the fact that equation (3) can be derived via multiple arguments suggests that it provides a robust description of genetic evolution applicable in a wide range of contexts. For instance, mutation-limited asexual evolution is an empirically reasonable description of many experimental microbial systems (Elena et al. 1996; de Visser et al. 1999; de Visser and Rozen 2005), while quantitative genetics provides a more realistic basis for equation (3) in macroscopic organisms (Lande 1976, 1982).

Of course, the realism of both evolutionary derivations of equation (3) can be questioned on the grounds that adaptive evolution may depend on mutations of large effect (Barton and Polechová 2005). However, currently available empirical information is not sufficient to develop a more realistic evolutionary model that retains generality and tractability. There is a need for models of adaptive evolution that, while possibly unrealistic, are simple enough to be incorporated into general ecological models of interspecific interactions (Abrams 2005). We are not modeling speciation (an issue for which consideration of genetic details is arguably unavoidable), and so sacrificing genetic realism for the sake of general insight is appropriate here.

Equation (3) also can be interpreted as a model of rapid trait change via phenotypic plasticity (Taylor and Day 1997). The derivation assumes that an individual of consumer species j with phenotype u_j has a small probability of changing its phenotype so as to increase its fitness and that this probability is proportional to the fitness gradient at u_j (Taylor and Day 1997). If it is further assumed that the variance in u_j is constant, the rate of change in the mean of u_j is given by equation (3), where v_j is the variance in u_j . This derivation does not assume that u_j is normally distributed.

Equation (3) is difficult to use in numerical integration because the partial derivative is discontinuous:

$$\frac{\partial(1/N_j)(dN_j/dt)}{\partial u_j} = \begin{cases} y_{1j}R_1, y_{2j}R_2(1 - u_j) > y_{1j}R_1u_j & R_1 \text{ limiting} \\ -y_{2j}R_2, y_{2j}R_2(1 - u_j) < y_{1j}R_1u_j & R_2 \text{ limiting} \\ 0, y_{2j}R_2(1 - u_j) = y_{1j}R_1u_j & \text{colimiting} \end{cases} \quad (4)$$

We therefore approximate the discontinuous step function in equation (4) using a sigmoid function, thereby obtaining a continuous approximation to equation (3):

$$\frac{du_j}{dt} = v_j[\phi(x_j, h)(y_{1j}R_1 + y_{2j}R_2) - y_{2j}R_2], \quad (5)$$

where

$$\phi(x_j, h) = 0.5 + \pi^{-1} \tan^{-1}(hx_j), \quad (6a)$$

$$x_j = y_{2j}R_2(1 - u_j) - y_{1j}R_1u_j, \quad (6b)$$

$$h = 10,000. \quad (6c)$$

The sigmoid function $\phi(x_j, h)$ becomes increasingly steep and steplike as the shape parameter h increases, taking on a value of ~ 1 when R_1 is limiting (i.e., $x_j > 0$) and ~ 0 when R_2 is limiting (i.e., $x_j < 0$). We arbitrarily assume $h = 10,000$; our results do not change for larger values of h , and other choices of sigmoid function would give similar results.

Our model is not a quantitatively realistic description of any particular system, but empirical evidence supports many of the underlying assumptions and approximations. Many empirical studies support the assumption of a species-specific optimal ratio in which essential resources must be consumed so as to maximize fitness (Rhee and Gotham 1980; Boersma and Elser 2006; Elser et al. 2006; Behmer and Joern 2008; Lee et al. 2008). Goddard and Bradford (2003) evolved yeast under C or N limitation in chemostats and found that resource requirements are evolutionarily inflexible, at least over a few hundred generations. Comparative studies indicate that resource requirements can evolve over macroevolutionary timescales (Quigg et al. 2003; Strzepek and Harrison 2004), but even long-term macroevolution must have limits. No species can evolve to do without essential resources such as nitrogen, phosphorus, or carbon. And while many organisms have flexible body composition (stoichiometry) that can be adjusted physiologically, this flexibility also has limits and can be captured with models that assume inflexible minimum resource requirements (Klausmeier et al. 2004). The work of Goddard and Bradford (2003) also supports the assumption of an evolutionary trade-off between per capita uptake rates of different resources, although the mechanistic basis of the trade-off is unknown for most species. Results of many studies of plasticity in resource use also are consistent with our assumptions. For instance, Finzi et al. (2007) found that forest trees respond to experimentally increased availability of one essential resource (CO_2) by increasing their uptake of another essential resource (N) but that nitrogen use efficiency (yield) is inflexible. Finally, in the absence of trait change, equations (1) and (2) or similar equations can qualitatively and quantitatively predict the outcome of chemostat experi-

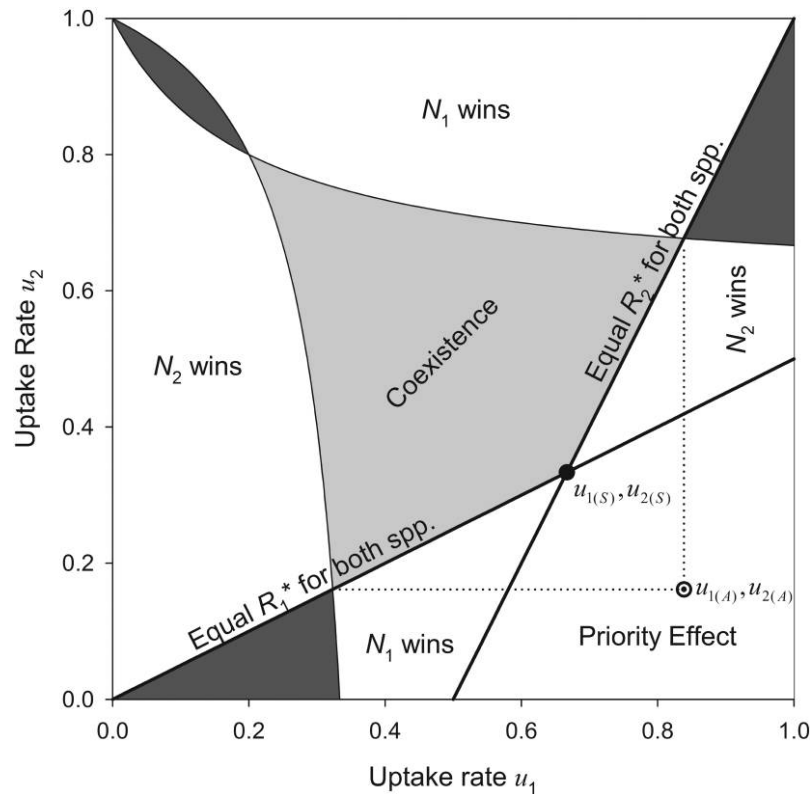


Figure 1: Phase plane for resource uptake rates of consumers 1 (u_1) and 2 (u_2) for a hypothetical illustrative parameter set. Lines divide the plane into regions with different long-term ecological outcomes; black regions are those for which both consumers are washed out. Solid lines indicate u_1 , u_2 combinations that give the two consumers equal R^* values for resources 1 and 2. The intersection of the straight lines defines the sympatric optimum, the trait values toward which adaptation tends to drive the consumers when they are growing together. Also shown are the allopatric optima, the trait values to which adaptation drives the consumers when they are growing alone. Parameter values are $S_1 = S_2 = y_{12} = y_{21} = 1$, $\gamma_{11} = \gamma_{22} = 0.5$, and $D = d_1 = d_2 = 0.1$.

ments in which algae or bacteria compete for two essential resources (Grover 1997).

Results and Discussion

Equilibrium Results

The model reaches equilibrium when consumer abundances, resource levels, and trait values are all unchanging. It is possible to solve analytically for the values of u_i at equilibrium, both for a single consumer species growing alone in allopatry and for the two consumers growing together in sympatry (app. B in the online edition of the *American Naturalist*). In both the one- and two-species cases, the equilibrium is unique, given our assumptions about species' resource requirements (app. B). The equilibrium for a single species growing in allopatry is globally stable (app. B; Abrams 1987a). The stability of the equilibrium for two species growing in sympatry depends on

whether there is a strict separation of timescales between trait dynamics and ecological dynamics.

It is also possible to solve analytically for the values of u_i that would, in the absence of trait change, lead to any given ecological outcome (coexistence, competitive exclusion of one species by the other independent of initial abundances, exclusion of one species or the other depending on initial abundances, washout of both species; fig. 1; app. B). Knowledge of the ecological dynamics that would occur for any given fixed values of u_i aids interpretation of feedbacks between ecological dynamics and trait dynamics.

Our analytical results reveal that competition for essential resources selects for character convergence: the optimal uptake rates of the two consumers are always more similar in sympatry than in allopatry (app. B; fig. 1). This result confirms and extends the argument of Abrams (1987a), who considered a single consumer evolving in response to competition from a nonevolving competitor. To under-

stand character convergence, it is useful to consider the zero net growth isoclines (ZNGIs) of the two consumers and how these isoclines vary as a function of trait values. The ZNGI for consumer j defines the break-even levels of resources R_1 and R_2 , at which consumer per capita growth rate is 0. The ZNGI for consumer j is a right-angle curve because the resources are nutritionally essential (fig. 2A; León and Tumpson 1975). The break-even level of R_1 for consumer j is a decreasing function of u_j , while the break-even level of R_2 for consumer j is a decreasing function of $1 - u_j$. The value of u_j therefore defines the position of the corner of consumer j 's ZNGI along a continuous, negatively sloped trade-off curve (fig. 2A). In the long term,

a single consumer growing alone in allopatry attains an optimal value of u_j (denoted $u_{j(A)}$) that causes it to be colimited by both resources (app. B; Tilman 1982; Abrams 1987a; Klausmeier et al. 2007). The trade-off curve is species specific; different consumers have different resource requirements and so attain different $u_{j(A)}$ when growing in allopatry (fig. 2B). However, the optimal u_j values in sympatry ($u_{j(S)}$) will always be more similar than the optimal u_j values in allopatry. To see why, consider a case in which two consumers that have evolved optimal traits in allopatry come into secondary contact (fig. 2B). The equilibrium resource levels will be defined by the point at which the two consumers' ZNGIs cross, given the consumers' current

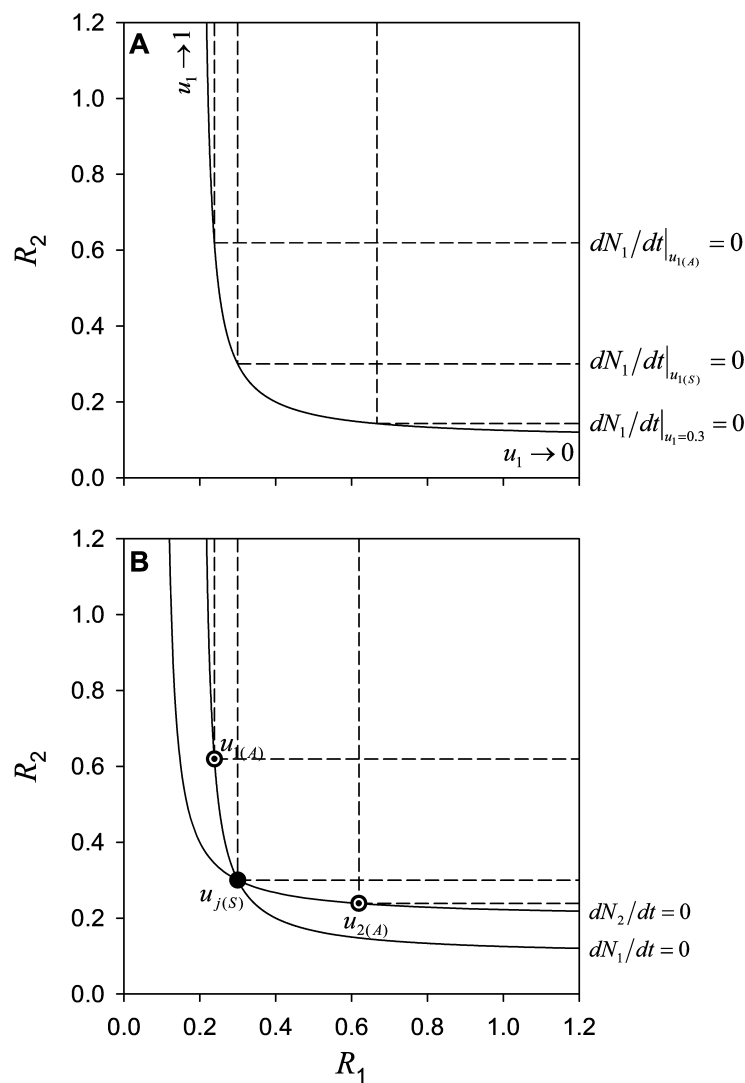


Figure 2: A, Three zero net growth isoclines (ZNGIs; dashed lines) for consumer 1 shown in the resource phase plane; each ZNGI corresponds to a different value of the uptake rate u_1 . Under adaptive trait change, the corners of these ZNGIs form a curved line, which represents the adaptive ZNGI for consumer 1. B, When the adaptive ZNGIs for consumers 1 and 2 are plotted together, their intersection determines the sympatric optimum.

allopatrically adapted trait values (fig. 2B). Consumer 2 reduces R_2 below the level to which consumer 1 is preadapted. In response, consumer 1 can increase its fitness by increasing its uptake rate of R_2 , shifting its ZNGI down and to the right along its trade-off curve. Conversely, consumer 1 reduces R_1 below the level to which consumer 2 is preadapted, so consumer 2 can increase its fitness by increasing its uptake rate of R_1 , thereby shifting its ZNGI up and to the left. Both consumers' ZNGIs will continue shifting in this fashion as long as the intersection of their ZNGIs remains above and to the right of the point where the trade-off curves cross (fig. 2B). Eventually, both ZNGI corners shift to the point where the two trade-off curves cross. At this point, the two consumers' ZNGIs coincide, and both consumers are colimited (app. B; fig. 2B). The per capita uptake rates that produce coincident ZNGIs in sympatry therefore represent an optimum because neither consumer can increase its fitness by shifting its per capita uptake rates (app. B).

However, the two consumers do not have identical optimal per capita uptake rates in sympatry because they differ in resource requirements (app. B). In order for coexisting consumers with different resource requirements to both be colimited, they must have different per capita resource uptake rates (León and Tumpson 1975).

The optimal u_i values in sympatry always lie on the boundary of the set of values that would permit stable ecological coexistence in the absence of trait change (app. B; fig. 1). This is because consumers evolve resource use traits that cause them to become colimited. The interior of the space of u_i values permitting ecological coexistence comprises those combinations of u_i values that cause each consumer to be limited by a different resource (León and Tumpson 1975; Tilman 1982; Grover 1997). The boundary of the space of u_i values permitting ecological coexistence necessarily is defined by those combinations of u_i values that cause at least one consumer to be colimited by both resources, with a unique combination of u_i values at which both consumers are colimited. The optimal resource use traits of competing consumers will fall on the edge of coexistence in any model of competition for essential resources in which consumers are strictly resource limited, colimitation maximizes fitness, and other traits take on fixed values.

The above adaptive argument explains why the optimal consumer traits are always more similar (but nonidentical) at the sympatric optimum than at the allopatric optimum. However, it does not address the stability of the sympatric optimum and so does not address whether the sympatric optimum would actually be attained in practice. Next we address stability of the sympatric optimum.

Model Dynamics under a Strict Separation of Timescales

The stability of the sympatric equilibrium depends on the rate of trait change relative to the rate of ecological dynamics. In the limiting case of a strict separation of timescales, so that ecological dynamics always go to equilibrium before any trait change can occur, the system never attains the sympatric optimum unless the initial trait values are within the region of u_1, u_2 space permitting stable ecological coexistence in the absence of trait change. If the initial trait values are outside this region, competitive exclusion will occur before any trait change can occur, and the system will subsequently evolve to the allopatric optimum of the winning species. Further, even if the initial trait values, species abundances, and resource levels place the system in ecological equilibrium at the sympatric optimum, the ecological equilibrium will be neutrally stable under a strict separation of timescales. This is because the sympatric optimum falls on the boundary of the set of u_i values permitting stable ecological coexistence.

The sympatric equilibrium is globally stable when trait change is sufficiently fast that there is no strict separation of timescales between trait dynamics and ecological dynamics (app. B). Sufficiently fast trait dynamics confer stability on the entire dynamical system and are essential for stable coexistence in sympatry. Note that sufficiently fast trait change is trait change fast enough that ecological dynamics do not go all the way to equilibrium before any trait change can occur. Sufficiently fast trait change in this sense can still be substantially slower than ecological change. The rate of trait change also is known to affect the stability of ecological dynamics in other contexts (e.g., Abrams 2003).

However, even when there is no strict separation of timescales between trait dynamics and ecological dynamics, the relative rates of ecological and trait dynamics strongly affect the transient behavior of the system. Feedbacks between ecological dynamics and trait dynamics become crucial to the transient dynamics of the system in the absence of a strict separation of timescales.

Model Dynamics When There Is No Strict Separation of Timescales

Figure 3A shows a typical trajectory of consumer traits in u_1, u_2 phase space when trait change is slow, although not so slow as to lead to a strict separation of timescales, and figure 3B shows the corresponding ecological population dynamics. Figure 3A, 3B illustrates dynamics that might occur when traits change via genetic evolution and additive genetic variance is low. For purposes of illustration, we consider a case in which consumer traits are at their allopatric optima, as if the two species had evolved allo-

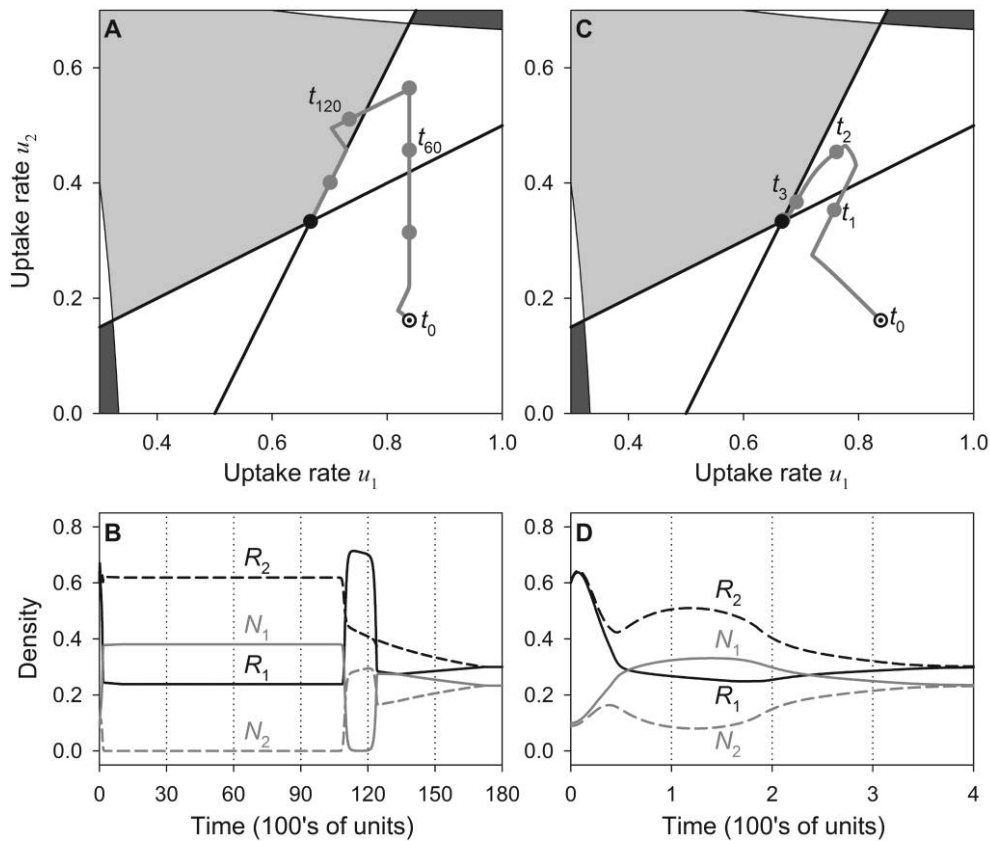


Figure 3: Illustrative model dynamics for high (A, B) and low (C, D) values of rate parameter v_j . A, C, Time courses of trait change in u_1 , u_2 phase space beginning at the consumers' allopatric optima (see fig. 1 for description of the phase space). B, D, Time courses of ecological population dynamics corresponding to A and C, respectively. Densities in B and D are absolute, not relative. Time units are arbitrary but the same in all panels. In A, gray dots indicate trait values at intervals of 3,000 time units, with label t_i indicating time point $100i$. In C, gray dots indicate trait values at intervals of 100 time units, with label t_i indicating time point $100i$. Parameter values are as in figure 1, with $v_1 = v_2 = 0.0002$ (A, B) and $v_1 = v_2 = 0.005$ (C, D). Initial abundances are $R_1(0) = 0.6$, $R_2(0) = 0.6$, $N_1(0) = 0.1$, and $N_2(0) = 0.09$.

patrically and then had come into secondary contact (fig. 3A). The initial position of the system in u_1 , u_2 phase space implies a priority effect that, in the absence of evolution (or in the limit of very slow evolution), would lead to extinction of consumer 2 because of its slightly lower initial abundance in this example. In the very short term, the consumers' resource use traits evolve toward the sympatric optimum. However, the ecological dynamics quickly drive consumer 2 to near extinction, thereby altering resource availability and the direction of trait evolution. The trait values of the initially dominant consumer 1 evolve back toward its allopatric optimum; because consumer 2 is rare, consumer 1 is effectively growing in allopatry. Meanwhile, consumer 2 evolves increased u_2 , and the resulting reduction in consumption pressure on resource 2 allows resource 2 to slowly increase in availability. At approximately time $t = 5,000$, the system enters a region of u_1 , u_2 phase space in which consumer 2 is competitively dominant but

the ecological dynamics do not immediately respond. Instead, at approximately time $t = 9,000$, the rare consumer 2 approaches its optimum trait value for the resource levels set by the currently dominant consumer 1. Adaptive evolution of both species slows to near-zero rates because each species has attained nearly optimal trait values, given the current resource levels. However, these resource levels do not represent an equilibrium. At approximately time $t = 11,000$, the ecological dynamics abruptly respond to the accumulated evolutionary change, with consumer 2 increasing rapidly in abundance at the expense of consumer 1. Such abrupt, lagged responses of ecological populations to gradual directional shifts in model parameters also occur in models of directional environmental change (Abrams 2002). The associated shift in resource levels alters the direction of selection on resource use traits. Consumer 2 now evolves toward its allopatric optimum, while consumer 1 evolves decreased u_1 because this is optimal,

given the resource levels set by the currently dominant consumer 2. The resulting trait evolution drives the system into the region of u_1, u_2 phase space permitting stable coexistence. At approximately time $t = 12,500$, species abundances and resource levels undergo another rapid shift, from dominance by consumer 2 to relatively equal abundance of both consumers. This shift alters the direction of selection. Traits evolve back to the boundary of the region of u_1, u_2 phase space permitting stable coexistence and then evolve along the boundary to the sympatric optimum. The dynamics shown in figure 3A, 3B are typical when trait change is slow and could not have been predicted without a model incorporating both ecological and trait dynamics.

An important feature of the ecological dynamics is transient near extinction (fig. 3B). The fact that many combinations of u_j values lead to exclusion, together with the fact that ecological dynamics are faster than trait dynamics, implies that, for many initial conditions, there will be long transient periods in which one of the two consumers is nearly extinct. Any realistic level of environmental and/or demographic stochasticity would lead to extinction in such cases and prevent the sympatric coexistence equilibrium from being achieved. Transient periods of near extinction are especially long when the species that is initially disfavored in competition also evolves more slowly (results not shown).

The possibility of transient near extinction raises the question of how rapid trait change must be to prevent it. Figure 4 illustrates how the transient minimum density of the initially disfavored consumer in figure 3 varies as a function of the rate parameter v_j . When v_j is low, small changes in v_j make a large difference to this minimum density. Figure 4 can be thought of as quantifying relative extinction risk of the initially disfavored consumer as a function of v_j , assuming that extinction risk scales linearly with minimum density. Figure 4 also could be used to

identify the threshold value of v_j that is too low to prevent extinction in this example, although this would require an assumption about the minimum density below which extinction occurs. Note that the v_j values used in figure 3A, while low, are not so low as to lead to minimum densities close to the threshold of numerical accuracy (2.23×10^{-308} for the Fortran double-precision arithmetic used here).

The transient minimum density of the initially disfavored consumer also depends on initial conditions: systems with initial trait values farther from the sympatric optimum attain lower transient minimum densities. In particular, when initial trait values are assumed to fall at their allopatric optima (as in cases of secondary contact such as fig. 3), transient minimum densities will decrease as the distance in u_1, u_2 phase space between the allopatric and sympatric optima increases (fig. C1 in the online edition of the *American Naturalist*). This distance depends on consumers' resource requirements (y_{ij} values). For the special case of mirror image consumers (as in fig. 3), the greatest difference between the allopatric and sympatric optima occurs at intermediate values of $y_{11} = y_{22}$. When consumers have very similar resource ratio requirements, allopatric and sympatric optima are similar because interspecific competition has little effect on the relative abundance of the two resources. When consumers have contrasting, extreme resource ratio requirements, each consumer's optimum consumption rates in allopatry will be strongly skewed toward the resource it requires most, and interspecific competition will shift these optima only slightly. As resource ratio requirements are pushed to further extremes, the shaded coexistence region in figure 1 disappears and the sympatric optimum lies in a region of ecologically unstable parameter space. At the (unrealistic) limit in which each consumer requires only one of the two resources ($y_{11}, y_{22} \rightarrow 0$), interspecific competition would vanish and would not affect the optimum u_j .

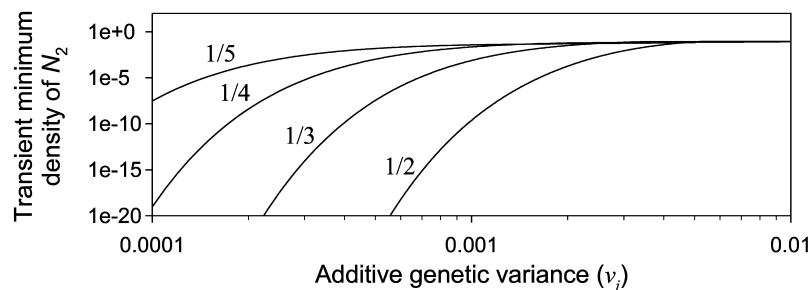


Figure 4: Minimum density encountered on the transient phase from allopatric to sympatric optimum. Four values of yield coefficients $y_{11} = y_{22}$ are depicted in each panel; other parameter values are as in figure 3; N_2 is the initially disfavored competitor. The transient minimum increases as resource requirements become more differentiated (y_{11}, y_{22} decrease from $1/2$ to $1/5$) because the allopatric and sympatric equilibria become closer in phase space (fig. C1 in the online edition of the *American Naturalist*).

Figure 3C shows a typical trajectory of consumer traits in u_1, u_2 phase space for a faster rate of trait change, such as might be produced by phenotypic plasticity or rapid genetic evolution, and figure 3D shows the corresponding ecological population dynamics. Figure 3A, 3B and figure 3C, 3D differ only in the rate parameter v_i . Model dynamics with rapid trait change are qualitatively similar to those with slow trait change but exhibit important quantitative differences. Rapid trait change produces faster convergence to equilibrium (fig. 3B, 3D). Rapid trait change also prevents transient periods of near extinction (fig. 3D). Consumer 2 is initially disfavored in competition, but before it can become too rare, adaptive trait change pushes the system into a region of u_1, u_2 phase space that allows consumer 2 to increase (at approximately time $t = 1,200$; fig. 3C, 3D).

An important and surprising feature of the transient dynamics is nonmonotonic trait change (fig. 3A, 3C). While consumer traits always attain the sympatric optimum in the long term, there generally are transient periods in which consumer traits move away from this optimum rather than toward it. These transient periods occur because of feedback between the ecological and evolutionary dynamics and can include periods of transient evolutionary divergence. For instance, in figure 3A, starting at approximately time $t = 12,500$, there is a transient period during which consumer 1, which has the larger u_p , evolves increased u_i while consumer 2 evolves decreased u_p . The trajectory taken by each competitor's traits always affects and is affected by that of the other, but this coevolutionary dynamic is never unidirectional.

A second surprising feature of the transient dynamics is transient periods in which adaptive trait change promotes competitive exclusion rather than coexistence (e.g., fig. 5). Even when the system has entered (or is initially situated in) a region of trait space permitting ecological coexistence, it can exit this region before reentering (fig. 5).

The direction of trait evolution fluctuates over time in many systems (Bell et al. 1985; Grant and Grant 1995, 2006; Hendry and Kinnison 1999). Fluctuations in the direction of trait evolution often reflect perturbations such as fluctuations in abiotic environmental conditions or invasion by novel species (Grant and Grant 1995, 2006). Our model shows that such fluctuations also can be internally generated by feedbacks between ecological and evolutionary dynamics and can occur even in the absence of perturbations.

The parameter values in figures 1–4 illustrate a special case of two mirror image consumers (i.e., $y_{11} = y_{22}$), but we use this special case purely for clarity of illustration. None of our analytical or numerical results depends on the assumption of mirror image consumers (e.g., fig. 5).

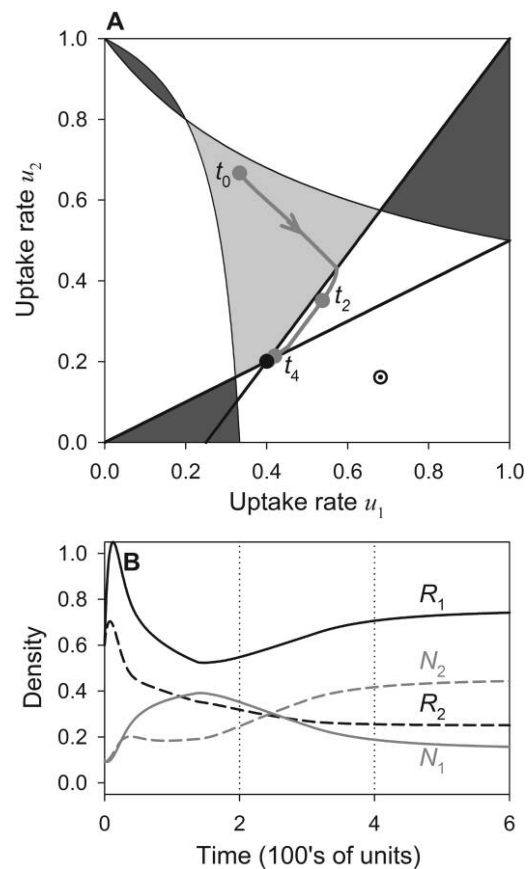


Figure 5: Model dynamics for a parameter set in which consumers are not mirror images in terms of their resource requirements (cf. figs. 1–4). *A*, Initial conditions place the system at an ecologically stable equilibrium that is not an evolutionary equilibrium. The system proceeds to the sympatric optimum by first passing through an ecologically unstable region of phase space. *B*, Time course of ecological population dynamics; densities are absolute, not relative. Parameter values are $S_1 = 1.5$, $S_2 = 1$, $y_{11} = 0.5$, $y_{22} = 0.75$, $D = d_1 = d_2 = 0.15$, and $v_1 = v_2 = 0.002$.

illustrates model dynamics for non-mirror image consumers).

Character Convergence, Displacement, and Coexistence

Character convergence promotes stable ecological coexistence, in the sense that the optimum trait values in allopatry are always located outside the range of values permitting stable ecological coexistence in sympatry (app. B; fig. 1). Even in cases where the optimum trait values in allopatry permit both consumers to have positive equilibrium densities, the equilibrium is unstable, so that in the absence of trait change, one of the two consumers would exclude the other, depending on initial conditions (a pri-

ority effect; app. B). By selecting for character convergence, interspecific competition for essential resources prevents species from attaining extremely different per capita resource uptake rates, which, in our model, lead to priority effects (fig. 1, *lower right*). Trait optimization in allopatry fails to preadapt species for stable coexistence even though our models assume a trade-off in per capita resource uptake rates and assume that species differ in their resource requirements. These trade-offs and differences are necessary but not sufficient for stable coexistence.

This result raises the question of how species that do not share a long coevolutionary history could coexist. This is an important question; species frequently colonize new areas in which they have no previous coevolutionary history with the resident species. The most obvious answer, in the context of our model, is sufficiently fast adaptive trait change in sympatry. However, there are other possibilities not considered by our model. For instance, while newly arrived colonists may lack any coevolutionary history with resident species, they typically have a coevolutionary history with other species similar to the residents, often in similar abiotic environments. Coevolution with species similar to the residents may preadapt newly arrived colonists for coexistence with residents.

Our model contrasts with previous models predicting that competing species will evolve similar resource use traits. Models of competition between two species for substitutable resources can predict character convergence, or at least lack of divergence, but only when the range of available resources is narrow, so that the opportunity for evolutionary diversification is limited (Slatkin 1980; Taper and Case 1992). Competition in these models still favors divergence to the extent permitted by extrinsic limits on resource availability. When many species compete for substitutable resources, initially dissimilar species may exhibit character convergence but only because they are selected to diverge from other species or because they are selected to converge toward trait values that confer intrinsically higher fitness for reasons independent of resource use (MacArthur and Levins 1967; Scheffer and van Nes 2006).

Hubbell and Foster (1986) argued that competing trees should evolve highly convergent traits because all tree species should experience selection favoring the traits best adapted to average forest conditions. Hubbell (2006) formalized this argument in a stochastic numerical model. This argument is incomplete in that it does not account for interspecific variation in resource requirements, which limits the degree of convergence in resource use traits expected in sympatry (Stern and Elser 2002). Hubbell and Foster (1986) and Hubbell (2006) also argued that convergence would lead to ecological dynamics dominated by neutral drift. This argument fails to account for the stabilizing effect of the evolutionary forces that select for

convergence. Adaptive trait change that is sufficiently fast to generate convergence also is sufficiently fast to stabilize the resulting ecological-evolutionary equilibrium, assuming that the current selection pressures consumers experience reflect current consumer and resource abundances.

Future Directions

Empirical evidence for or against character convergence is nearly nonexistent, at least in part because no published empirical study has looked for it. This lack of research is unsurprising. Most species that compete for essential resources lack visually obvious resource use traits. Visual inspection of a plant, an alga, or a microbe reveals little about its ability to acquire essential resources. In contrast, coexisting competitors for substitutable resources often exhibit visually striking differences in morphological resource use traits (e.g., Grant and Grant 2006). It was just such visually obvious trait variation that first motivated the development of the concept of character displacement (Brown and Wilson 1956). Even when there is empirical information on the resource use traits of coexisting competitors for essential resources (e.g., Tilman 1977), it is unclear whether coexisting competitors are more similar in their traits than would have been expected by chance or whether any unexpected similarity is due to evolutionary character convergence. However, the fact that coexisting competitors for essential resources rarely have identical ZNGIs, as predicted by our model, suggests that other factors in addition to those considered in the model govern the realized degree of character convergence in nature (Tilman 1977, 1982; Grover 1997). One promising direction for future work is testing our theoretical predictions using laboratory experiments with rapidly evolving microbes; such studies are already under way (J. W. Fox, unpublished data). These experiments should last as long as possible, in order to distinguish transient dynamics from asymptotic dynamics.

Our approach could be extended to consider three or more essential resources in order to examine whether nontransitive competitive hierarchies can arise via adaptive trait change. Recent ecological models highlight that nontransitive competitive hierarchies can promote coexistence of many species (Huisman and Weissing 1999; Huisman et al. 2001; Laird and Schamp 2006). In the context of competition for essential resources, a cyclic relationship between consumer competitive ability and consumer stoichiometry can produce nontransitive rock-paper-scissors competitive hierarchy (Huisman and Weissing 1999; Huisman et al. 2001). Such nontransitive hierarchies can lead to nonequilibrium ecological dynamics in which the identities of the dominant competitor and the limiting resource oscillate over time (Huisman and Weissing 1999; Huisman

et al. 2001). It is unclear whether such nontransitive hierarchies could arise and persist when per capita resource uptake rates (and thus competitive abilities) can vary adaptively. It is also unclear how adaptive trait change would affect nonequilibrium ecological dynamics. Sufficiently fast trait change might prevent nonequilibrium dynamics.

Our work focuses on systems in which consumers feed on essential resources that exist separately in the environment rather than packaged within prey items. However, our results may provide insight into cases in which consumers forage on different prey species that vary in their relative content of different essential nutrients. Different prey species comprise nutritionally complementary resources in such cases (Abrams 1987b). Consumers of nutritionally complementary prey must optimize the ratio in which they consume those prey, in order to optimize the ratio in which they obtain the essential resources contained within those prey (Behmer and Joern 2008; Lee et al. 2008). The fact that animal consumers typically can obtain all their essential resources from any single prey species (albeit in suboptimal ratios) suggests that competition might select for either convergence or divergence in resource use in such situations, depending on the relative abundances of the resources. Abrams (1987b) describes the optimal resource use traits for a single consumer of two complementary resources; the extension to the two-consumer case would be an interesting direction for future work.

Future work also should consider the robustness of our results to alternative assumptions. We assume that consumers can adapt to changes in resource availability only by changing their per capita uptake rates. In reality, many species have somewhat flexible resource requirements, which may change adaptively in response to changes in resource availability (Bloom et al. 1985; Sterner and Elser 2002; Klausmeier et al. 2004). Although flexibility in resource requirements always has limits, accounting for flexibility in resource requirements will be necessary for a complete understanding of adaptive trait change in species competing for essential resources. Rates of evolutionary trait change might be temporally variable as well, for instance, because genetic variance likely will change as population size changes and as traits approach an adaptive optimum (Abrams et al. 1993; Barton and Turelli 2004; app. A). We do not consider nutrient recycling, which could have consequences for the identity of the limiting resource and thus for the evolution of resource uptake rates (Daufresne and Hedin 2005). Our model considers only two species, the maximum number that can coexist on two limiting resources at equilibrium in a well-mixed system. It would be interesting to extend our model to consider evolution of essential resource use in many-species systems. Such an extension would have to increase the number of limiting resources or incorporate another

mechanism, such as consumer density dependence, allowing more than two consumers to coexist at equilibrium. The nature of any additional coexistence mechanisms might well affect the results. Mechanisms generating density dependence in consumer per capita growth rates alter the evolutionary effects of competition for substitutable resources (Abrams 1986) and might do the same for essential resources. Our results serve as a baseline case on which alternative models can be built.

The possibility of character convergence has important implications. Competition is thought to be a key driver of evolutionary diversification in animals (Schluter 2000). But insofar as the members of the other kingdoms of life compete for essential resources, they may be diverse despite competition, not because of it. Further theoretical and empirical work should explore the possibility.

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Appendix A from J. W. Fox and D. A. Vasseur, “Character Convergence under Competition for Nutritionally Essential Resources” (Am. Nat., vol. 172, no. 5, p. 000)

Alternative Models of Adaptive Trait Change

Here we illustrate the dynamics of alternative models of adaptive trait change. None of the alternative models alters the position or stability of the equilibria of the model presented in the main text. However, model transient dynamics are somewhat sensitive to how trait change is modeled. All of the alternative models retain the description of ecological dynamics used in the main text (eqq. [1], [2]).

Our first alternative model is a modified version of the model of Klausmeier et al. (2007). We consider a simple case in which consumer j can adjust its u_j values at a constant rate so as to achieve colimitation (maximal fitness):

$$\frac{du_j}{dt} = \begin{cases} c_j u_j, y_{2j} R_2 (1 - u_j) > y_{1j} R_1 u_j & R_1 \text{ limiting} \\ -c_j (1 - u_j), y_{2j} R_2 (1 - u_j) < y_{1j} R_1 u_j & R_2 \text{ limiting} \\ 0, y_{2j} R_2 (1 - u_j) = y_{1j} R_1 u_j & \text{colimiting} \end{cases} \quad (\text{A1})$$

Here, c_j is a constant that scales the rate of change in u_j . In contrast to the model in the main text, the rate of trait change is unrelated to the fitness gradient (cf. eq. [3]). Equation (A1) has the virtue of simplicity and will be empirically appropriate when the rate at which phenotypically plastic consumers can alter their resource use traits is set by constraints independent of the fitness gradient. For instance, in the context of single-celled organisms that acquire resources via uptake proteins on the cell surface, equation (A1) describes the conversion of uptake proteins for resource 1 into uptake proteins for resource 2, and vice versa, via first-order kinetics (Klausmeier et al. 2007; see also Van den Berg et al. 2002). Equation (A1) also describes cases in which phenotypically plastic consumers have only qualitative information about the fitness gradient. When individuals know only the sign of the slope but not the magnitude, they might be expected to adjust their resource use traits at a constant rate so as to increase fitness. The discontinuity of equation (A1) creates problems for numerical integration, so we approximate it with a continuous function:

$$\frac{du_j}{dt} = c_j [-u_j + \phi(x_j, h)], \quad (\text{A2})$$

where $\phi(x_j, h)$ is defined as in equations (6) in the main text.

Model dynamics with trait change described by equation (A2) are qualitatively similar to those of the model used in the main text (fig. A1; cf. fig. 3 in the main text). The only notable difference is that the rate of trait change does not slow when traits near their optimum values, given the current resource levels.

Ma et al. (2003) argue that the rate of trait change du_j/dt should slow as u_j nears the limiting values of the trait’s distribution (here 0 and 1). They envision a population in which individual traits vary little around the population mean and in which the population mean changes as phenotypically plastic individuals sample the fitness consequences of changing their trait values. The rate of sampling should decrease as the population mean approaches the maximum or minimum possible trait value, both because there is less scope for sampling near the end points of the trait distribution and because some fraction of the population will have already reached the limiting value for the trait. To incorporate this assumption, we modify equation (A2) as

$$\frac{du_j}{dt} = V(u_j) [-u_j + \phi(x_j, h)], \quad (\text{A3})$$

where

$$V(u_j) = c_j 2^{2n} u_j^n (1 - u_j)^n. \quad (\text{A4})$$

The parameter $V(u_j)$ is a unimodal function that slows the rate of trait change to 0 at the extreme values $u_j = 0$ and 1. The parameter c_j now represents the maximum rate of trait change, which is realized when $u_j = 0.5$. The parameter n controls the breadth of the function; larger values of n further decrease the rate of trait change at all but the function’s maximum at $u_j = 0.5$ and the end points. Figure A2 shows the dynamics of the model adapted from Ma et al. (2003), using relatively low values of the rate parameter c_j . Similar to the model in the main text (fig. 3A, 3B), consumer 2 initially goes through a transient phase of low density. During this phase, u_1 remains near its allopatric optimum while u_2 increases so that consumer 2 can attain more of its limiting resource, R_1 . This adaptation drives the system into the region of u_1, u_2 phase space where consumer 2 is the superior competitor. Here the competitive superiority combines with its quicker rate of trait change (because u_2 is nearer to 0.5 than is u_1) to produce a phase of low density of consumer 1. The system now moves toward the trait values that are optimal for both species, given the resource levels set by the currently dominant consumer 2. To approach these trait values, the system must enter the region of u_1, u_2 phase space permitting stable coexistence. But now the model’s behavior deviates from that of the model used in the main text. Trait evolution overshoots the sympatric equilibrium just after time $t = 1,500$ because the trait values are such that the currently dominant consumer 2 retains its ability to change its u_j value more rapidly than can consumer 1. However, around time $t = 1,700$, further trait change brings u_1 closer to 0.5 than is u_2 , so that consumer 1 now evolves more rapidly than consumer 2. The ecological dynamics respond to the accumulated trait change, and the system is driven back to the sympatric equilibrium.

Abrams (1999) proposed two other functions that slow the rate of trait change near the extrema of trait values. The first function assumes that the rate changes little over most of the range of trait space but decays rapidly to 0 at the extreme values 0 and 1. Using equation (A3) to model the direction of trait change, we define $V(u_j)$ as

$$V(u_j) = c_j \exp \left\{ \frac{-s}{(u_j - s)[1 - (u_j + s)]} \right\}, \quad (\text{A5})$$

where the shape parameter s is a small, positive constant that ensures that $V(u_j) \approx c_j$ across most of the range of u_j . Abrams (1999) assumed a value $s = 0.001$ for most of his simulations. For our purposes of contrasting the (co)adaptation of consumers in allopatry versus sympatry, this function has a negligible impact on dynamics. At the allopatric optimum, which is the most extreme values of u_j encountered in our simulations, the difference between $V(u_j)$ and a model with constant c_j (eq. [A2]) is less than 1%. This small difference leads to only negligible differences in dynamics.

The second function proposed by Abrams (1999) is derived from quantitative genetics and assumes that the u_j are S-shaped functions of some polygenic trait (x). This function is

$$V(u_j) = v_j \{[\gamma u_j(1 - u_j)]\}^2, \quad (\text{A6})$$

where v_j is the additive genetic variance of x (as in eq. [3] in the main text) and γ is a scaling coefficient, chosen by Abrams (1999) such that $V(u_j) = v_j$ at equilibrium. This function is very similar to that proposed by Ma et al. (2003; eq. [A4]), albeit different in height at the peak and with slightly different curvature. Given the similarities in shape, this function generates the same qualitative behavior as the model of Ma et al. (2003) when inserted into equation (A3) in place of equation (A4), only for different values of the scaling parameters c_j and v_j (fig. A2).

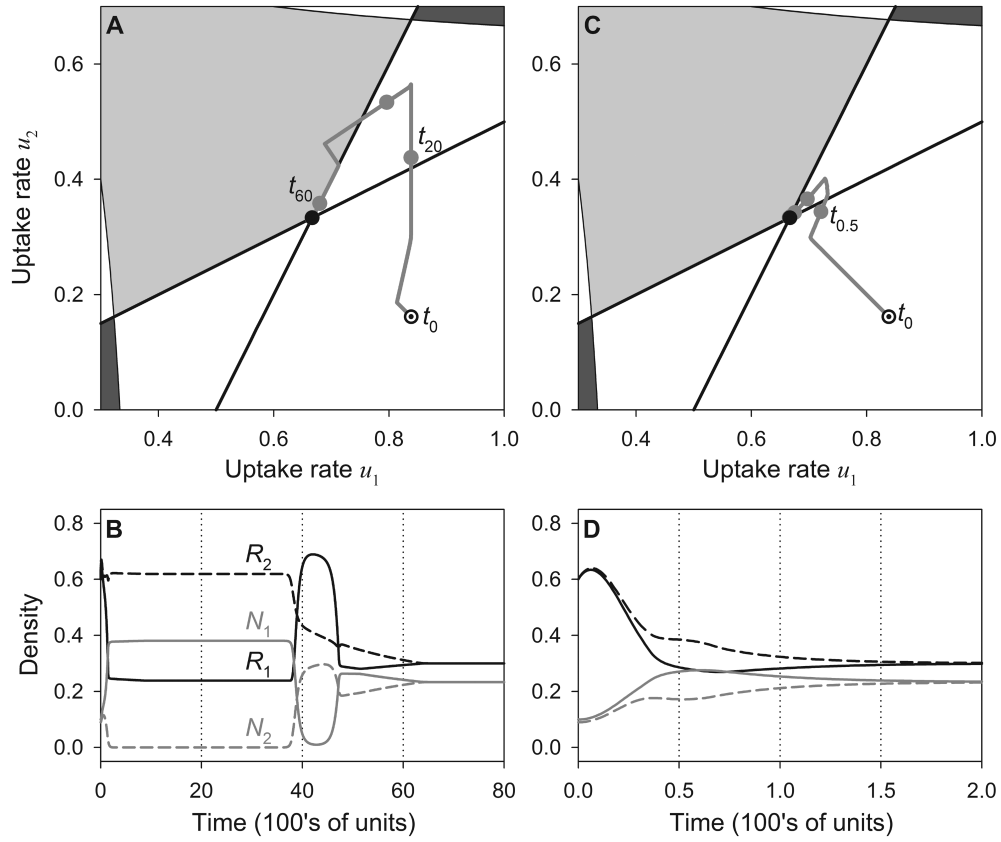


Figure A1: Dynamics of the trait change model adapted from Klausmeier et al. (2007) for slow (A, B) and fast (C, D) rates of trait change. Upper panels show trait dynamics in u_1, u_2 phase space beginning at the consumers’ allopatric optima; lower panels show the corresponding ecological dynamics. Time units are arbitrary but consistent with those in other figures. Densities in B and D are absolute, not relative. Parameter values are $c_j = 0.0002$ (A, B) and $c_j = 0.005$ (C, D), the same as the values of v_j used in the corresponding panels in figure 3 in the main text. Other parameters and initial conditions are as in figure 3 in the main text.

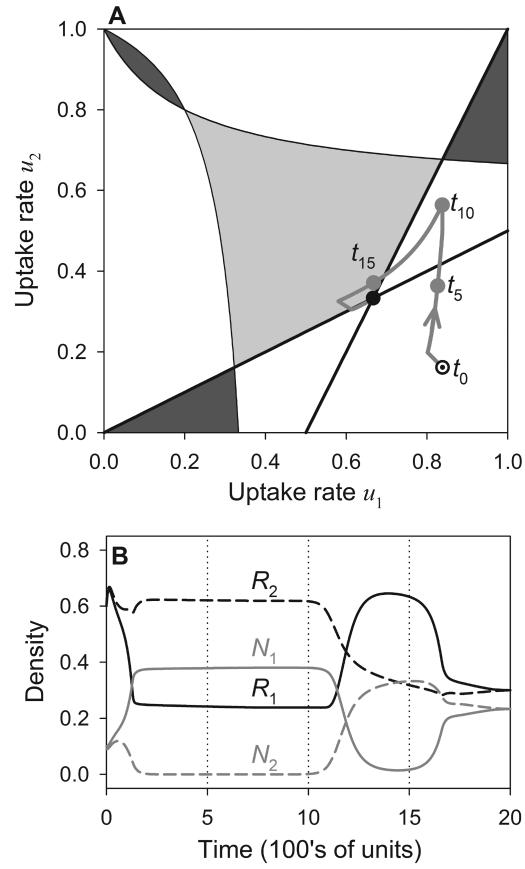


Figure A2: Time courses (A) of the trait change model adapted from Ma et al. (2003) in u_1 , u_2 phase space beginning at the consumers' allopatric optima. See figure 1 for description of the phase space. B, Ecological population dynamics. Densities in B are absolute, not relative. Time units are arbitrary but consistent with those in other figures. Parameter values are $c_j = 0.001$ and $n = 2$; other parameter values and initial conditions are as in figure 3 in the main text.

Appendix B from J. W. Fox and D. A. Vasseur, “Character Convergence under Competition for Nutritionally Essential Resources” (Am. Nat., vol. 172, no. 5, p. 000)

Analytical Results

Ecological Dynamics of Competitors for Essential Resources

First let us consider the ecological dynamics of the system (eqq. [1], [2]) in the absence of evolution ($v_j = 0$) or phenotypic plasticity ($c_j = 0$). The zero net growth isocline (ZNGI) for consumer j is the set of resource densities where $dN_j/dt = 0$. The ZNGIs are “corners,” each composed of a vertical and a horizontal line in the R_1, R_2 phase space. In allopatry, the positions of these vertical and horizontal lines along the R_1 and R_2 axes denote the equilibrium densities of R_1 and R_2 when they are the limiting resources for consumer j . The equilibrium density of R_i when limiting for N_j (here denoted $R_{i(N_j)}^*$) can be found by solving equation (1b) at equilibrium:

$$R_{1(N_1)}^* = \frac{d_1}{y_{11}u_1}, \quad (\text{B1a})$$

$$R_{2(N_1)}^* = \frac{d_1}{y_{21}(1 - u_1)}, \quad (\text{B1b})$$

$$R_{1(N_2)}^* = \frac{d_2}{y_{12}u_2}, \quad (\text{B1c})$$

$$R_{2(N_2)}^* = \frac{d_2}{y_{22}(1 - u_2)}. \quad (\text{B1d})$$

Feasibility of a two-consumer equilibrium requires that the ZNGIs intersect in the R_1, R_2 phase space (León and Tumpson 1975). By necessity, this means that either

$$R_{1(N_1)}^* \geq R_{1(N_2)}^*, \quad (\text{B2a})$$

$$R_{2(N_2)}^* \geq R_{2(N_1)}^* \quad (\text{B2b})$$

or the opposing condition (which has the signs reversed) must be met. Because the two cases provide symmetric results, we will consider only the case defined in equations (B2). By substituting the equilibrium densities from equations (B1) into equations (B2), we can solve for the limits of consumer uptake rates that will allow feasibility of a two-species equilibrium:

$$u_1 \leq \frac{d_1 y_{12}}{d_2 y_{11}} u_2, \quad (\text{B3a})$$

$$u_2 \geq 1 - \frac{d_2 y_{21}}{d_1 y_{22}} (1 - u_1). \quad (\text{B3b})$$

The pair of per capita uptake rates u_1, u_2 that lies on the boundaries of the conditions in equations (B3) defines the unique case where $R_{1(N_1)}^* = R_{1(N_2)}^*$ and $R_{2(N_1)}^* = R_{2(N_2)}^*$. This unique pair of per capita uptake rates allows both consumers to attain colimitation. If only condition (B3a) is violated, consumer 1 will set a lower R^* for both

resources, thereby competitively excluding consumer 2 (and vice versa). If conditions (B3a) and (B3b) both are violated, the outcome of competition depends on initial conditions (a priority effect).

Feasibility of a two-consumer equilibrium does not imply ecological coexistence unless the equilibrium is stable. The two-consumer equilibrium is stable provided that each consumer ingests a larger fraction of the net rate of supply of its limiting resource (that for which it has the larger R^* compared with the other consumer) than of its competitor’s limiting resource (León and Tumpson 1975). Given our assumption in equations (B2), stable coexistence of two consumers requires that

$$\frac{g_1/y_{11}}{S_1 - R_{1(N_1)}^*} > \frac{g_1/y_{21}}{S_2 - R_{2(N_2)}^*}, \quad (\text{B4a})$$

$$\frac{g_2/y_{22}}{S_2 - R_{2(N_2)}^*} > \frac{g_2/y_{12}}{S_1 - R_{1(N_1)}^*}. \quad (\text{B4b})$$

Substitution of $R_{1(N_1)}^*$ and $R_{1(N_2)}^*$ into equations (B4) gives the requirements for the stability of the two-consumer equilibrium in the u_{11}, u_{12} phase space:

$$u_1 > \frac{d_1 y_{12}}{y_{11}\{y_{12}S_1 - y_{22}S_2 + [d_2/(1 - u_2)]\}}, \quad (\text{B5a})$$

$$u_2 < 1 - \frac{d_2 y_{21}}{y_{22}[y_{21}S_2 - y_{11}S_1 + (d_1/u_1)]}. \quad (\text{B5b})$$

Together, the conditions in equations (B3) and (B5) enclose the region of stable two-species coexistence in the u_1, u_2 phase space (see fig. 1 in the main text).

Note that the optimum u_j values in sympatry lie on the boundary of the coexistence region. Accordingly, in the absence of adaptive trait change, the ecological dynamics of coexisting species would exhibit neutral stability if species’ traits were fixed at the sympatric optimum.

Adaptive Dynamics of Competitors for Essential Resources

In the case of one consumer species feeding on a pair of resources, adaptive trait change (due to genetic evolution or phenotypic plasticity) will maximize consumer fitness by generating colimitation of consumer growth. Under colimitation, the ratio in which the resources are required by consumer j (y_{1j}/y_{2j}) will match the ratio in which resources are consumed (Abrams 1987a). The same is true for two competing consumers in sympatry; however, in this case, adaptation must respond to resource densities that are influenced by both consumers.

The boundaries of the inequalities (B3) define lines in the u_{11}, u_{12} phase space at which consumers 1 and 2 are colimited. The intersection of these lines defines the unique sympatric optimum where both consumers achieve colimitation. In the u_1, u_2 phase space, this sympatric optimum, $\mu_{j(S)}$, is

$$u_{1(S)} = \frac{y_{12}(d_1 y_{22} - d_2 y_{21})}{d_2(y_{11} y_{22} - y_{12} y_{21})}, \quad (\text{B6a})$$

$$u_{2(S)} = \frac{y_{11}(d_1 y_{22} - d_2 y_{21})}{d_1(y_{11} y_{22} - y_{12} y_{21})}. \quad (\text{B6b})$$

For comparison with the sympatric optimum, it is useful to define the optimum in allopatry, $\mu_{j(A)}$. When consumer 1 exists in the absence of consumer 2, we find, by setting $dR_i/dt = 0$ and equating expressions for N_1^* , that

$$\frac{y_{11}}{g_1} D(S_1 - R_{1(N_1)}^*) = \frac{y_{21}}{g_1} D(S_2 - R_{2(N_1)}^*). \quad (\text{B7})$$

If we substitute $R_{1(N_1)}^*$ and $R_{2(N_1)}^*$ from equations (B1), expression (B7) leads to the quadratic equation

$$Xu_{1(A)}^2 - (X + 2)u_{1(A)} + 1 = 0, \quad (\text{B8})$$

where $X = (y_{11}S_1 - y_{21}S_2)/d_1$. This equation has two real roots but only one ever lies in the domain of feasible parameter space (fig. B1):

$$u_{1(A)} = \frac{X + 2 - \sqrt{X^2 + 4}}{2X}. \quad (\text{B9})$$

Following the same logical progression, it can be shown that when consumer 2 exists in allopatry, the optimum per capita uptake rate is

$$u_{2(A)} = \frac{Y - 2 + \sqrt{Y^2 + 4}}{2Y}, \quad (\text{B10})$$

where $Y = (y_{22}S_2 - y_{12}S_1)/d_2$.

We wish to know whether it is possible for the two consumers, when preadapted to allopatric conditions, to coexist in sympatry. Because the conditions for the existence of a two-consumer equilibrium (eqq. [B2]) always have positive slope in the u_1, u_2 phase space, the intersections of these conditions and the stability boundaries (eqq. [B4]) represent the most extreme values of u_1 and u_2 that permit stable coexistence (see fig. 1). Solving for the intersection of equations (B2b) and (B4b), we find

$$1 - \frac{d_2 y_{21}(1 - u_1)}{d_1 y_{22}} < 1 - \frac{d_2 y_{21}}{y_{22}[y_{21}S_2 - y_{11}S_1 + (d_1/u_1)]}. \quad (\text{B11})$$

Some simplification yields

$$\frac{y_{21}S_2 - y_{11}S_1}{d_1} > \frac{1}{1 - u_1} - \frac{1}{u_1}, \quad (\text{B12})$$

and substitution of X from equation (B8) yields

$$Xu_1^2 - (X + 2)u_1 + 1 > 0. \quad (\text{B13})$$

The inequality (B13) takes the same form as the solution of the allopatric optimum (eq. [B8]); however, the allopatric optimum can never satisfy the stability criterion for sympatry (eq. [B13]).

Thus, consumers N_1 and N_2 can never be preadapted for stable coexistence by adaptation to allopatric conditions; rather, stable coexistence in sympatry requires $\mu_1 < \mu_{1(A)}$ (fig. B1). Furthermore, the sympatric evolutionary optimum, which lies on the boundary of the region of stable coexistence, is subject to the same constraint: $\mu_{1(S)} < \mu_{1(A)}$. A similar logical progression can be used to arrive at this condition as it applies to the second consumer, $\mu_{2(S)} > \mu_{2(A)}$. Given our assumption in equations (B2), a condition for stable coexistence at the sympatric evolutionary optimum can be written

$$\mu_{1(A)} > \mu_{1(S)} > \mu_{2(S)} > \mu_{2(A)}. \quad (\text{B14})$$

Thus, for stable sympatric coexistence at the sympatric optimum, consumer traits must converge from their allopatric optima toward more intermediate values.

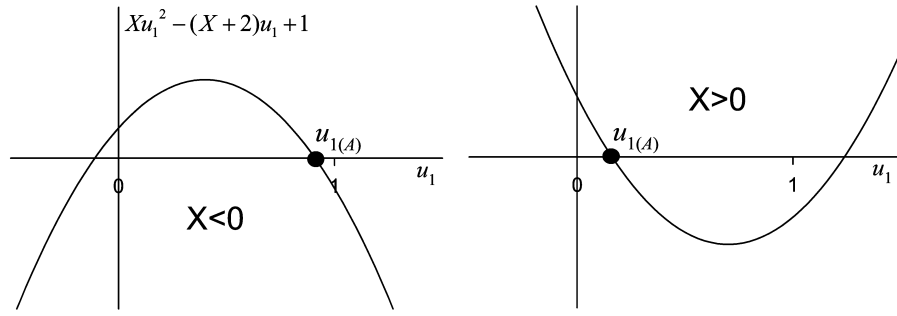


Figure B1: Parabola generated by $y = X\mu_1^2 - (X + 2D)\mu_1 + 1$ for $X < 0$ and $X > 0$. The root of this equation, which falls in the interval $(0, 1)$, is the allopatric optimum ($\mu_{1(A)}$). In sympatry, stable coexistence requires that $y < 0$; this occurs only in the feasible parameter space ($0 \leq \mu_1 \leq 1$) when $\mu_{1(S)} < \mu_{1(A)}$.

Appendix C from J. W. Fox and D. A. Vasseur, “Character Convergence under Competition for Nutritionally Essential Resources” (Am. Nat., vol. 172, no. 5, p. 000)

Plot of Transient Minimum Density of the Initially Disfavored Consumer

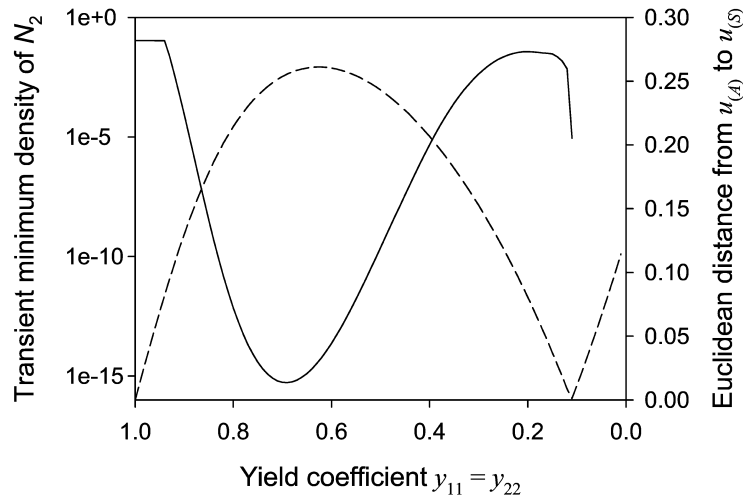


Figure C1: Transient minimum density of N_2 (*solid line*) for the evolutionary model across a range of symmetric yield coefficients, given the parameter values from figure 3 in the main text. Overlaid is the Euclidean distance from the allopatric to the sympatric optimum in u_1, u_2 phase space (*dashed line*). As parameters dictate a larger distance between the allopatric and sympatric optima, adaptation requires increased time and results in lower transient densities.