

Eco-Evolutionary Dynamics Enable Coexistence via Neighbor-Dependent Selection

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ABSTRACT: Recent studies suggest that selection can allow coexistence in situations where ecological dynamics lead to competitive exclusion, provided that there is a trade-off between traits optimal for interacting with conspecifics and traits optimal for interacting with heterospecifics. Despite compelling empirical evidence, there is no general framework for elucidating how and when selection will allow coexistence in natural communities. Here we develop such a framework for a mechanism that we term “neighbor-dependent selection.” We show that this mechanism can both augment coexistence when ecological conditions allow for niche partitioning and enable coexistence when ecological conditions lead to competitive exclusion. The novel insight is that when ecological conditions lead to exclusion, neighbor-dependent selection can allow coexistence via cycles driven by an intransitive loop; selection causes one species to be a superior interspecific competitor when it is rare and an inferior interspecific competitor when it is abundant. Our framework predicts the conditions under which selection can enable coexistence, as opposed to merely augmenting it, and elucidates the effects of heritability on the eco-evolutionary feedbacks that drive coexistence. Given increasing evidence that evolution operates on ecological timescales, our approach provides one means for evaluating the role of selection and trait evolution in species coexistence.

Keywords: competition, coexistence, neighbor-dependent selection, intransitive competition, trait evolution.

Introduction

Elucidating the mechanisms that allow species coexistence is one of the most vexing problems in ecology (Gause 1934; Hutchinson 1961). Classical explanations for coexistence focus on niche differences between competitors, including differences in resource use, frequency-dependent interactions with specialist consumers, and species-specific re-

sponses to environmental variability (Chesson 2000). Niche differences allow for stable coexistence by increasing the strength of intraspecific competition relative to interspecific competition. Although theory is unambiguous about how niche differences enable coexistence, empirical demonstrations of such differences among coexisting species in real communities have proven difficult (Silvertown 2004; Adler et al. 2007; Levine and HilleRisLambers 2009; Siepielski and McPeck 2010). This mismatch between theory and data suggests that ecological factors alone may be insufficient to explain coexistence in many natural communities.

Here we investigate the hypothesis that evolutionary processes operating on ecological timescales can provide an alternative mechanism for the stable coexistence of competitors. The influence of evolution on coexistence has a rich history in ecology, exemplified by the large body of work on character displacement (MacArthur and Levins 1967; Taper and Case 1985, 1992; Dayan and Simberloff 2005). Given mounting evidence of feedback loops between ecological and evolutionary processes (Yoshida et al. 2003; Carroll et al. 2007; Duffy and Sivers-Becker 2007; Bell and Gonzalez 2009; Schoener 2011), the latter may be an important and common contributor to coexistence. With character displacement, selection driven by competition drives trait (character) evolution, causing co-occurring species to diverge in niche space. Classic examples involve granivorous species (e.g., kangaroo rats and Darwin's finches; Brown and Lieberman 1973; Grant and Grant 2006). One limitation of character-displacement models, however, is that few species exhibit traits that correspond cleanly to niche differences. Many trait differences between species (e.g., differences in fecundity or resource acquisition ability) simply confer on one species an advantage over another. For example, in a light-limited system, growing taller provides better access to light and, all

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else considered equal, leads to greater growth and fecundity. Although these “fitness differences” (sensu Chesson 2000) in themselves do not lead to character displacement, they are at the heart of an alternative mechanism by which evolutionary and ecological processes interact to maintain species diversity.

The interplay between ecological and evolutionary processes can allow stable coexistence if a species experiences stronger selection on traits involved in interspecific competition when it is rare and stronger selection on traits involved in intraspecific competition when it is abundant. Because selection on competitive traits depends on the identity of neighboring individuals, we term this mechanism “neighbor-dependent selection.” Here we develop a mathematical framework to elucidate how the interplay between competitive dynamics and trait evolution allows stable coexistence via neighbor-dependent selection.

There is strong evidence for neighbor-dependent selection in laboratory experiments as well as field studies. Early experimental work on competition between the housefly and the blowfly demonstrated that evolution could reverse competitive dominance and allow coexistence of species when it would otherwise not have been possible (Pimentel et al. 1965). Here it was suggested that such reversals of competitive dominance are likely because only the rare competitor experiences selection on the traits that make it a better interspecific competitor. More recent work shows that selection can generate long-term coexistence when traits optimal for competing with conspecifics exhibit a trade-off with traits optimal for competing with heterospecifics (Lankau and Strauss 2007; Vellend and Litrico 2008; Lankau 2009). For instance, field studies show that individuals of a mustard species exhibit a trade-off between rapid growth, which is effective in intraspecific competition, and the production of toxic root exudates that directly harm heterospecific competitors (Lankau and Strauss 2007) and also weaken the reciprocal competitive effect of heterospecifics on the mustard (Lankau et al. 2011). When the mustard is abundant relative to its heterospecific competitors (native forbs and grasses), selection favors rapid growth and lower toxin production as a consequence, benefiting the rare heterospecific competitors. Conversely, when the mustard is rare and its competitors are abundant, selection favors high toxin production (and slower growth as a consequence), benefiting the rare mustard. Other examples where trade-offs among competitive abilities can promote coexistence occur in species of *Tribolium* beetles (Park 1962), where intraspecific competition is mainly exploitative and interspecific competition is mainly interference driven.

Neighbor-dependent selection differs from ecological character displacement as follows. In classical character displacement, following the definition of Taper and Case

(1985), the traits involved are potential niche axes along which species could differentiate in response to selection (e.g., beak size; Grant and Grant 2006). In contrast, neighbor-dependent selection involves traits that are not niche axes and cannot allow for coexistence in the absence of evolution; selection enables coexistence because it causes competitive dominance to shift, depending on the relative abundances of species. Thus, selection can transform an ecological scenario with no coexistence (e.g., the mustard wins or loses with traits fixed for inter- or intraspecific competition, respectively) to one where coexistence is possible. This raises the tantalizing possibility that neighbor-dependent selection may enhance diversity in natural communities in which ecological interactions are insufficient to allow coexistence.

Previous theoretical work on neighbor-dependent selection includes an individual-based model parameterized with field data for the mustard-forb community (Lankau 2009) and a more general model involving spatial structure and sexual reproduction (Vellend and Litrico 2008). These studies have found a range of outcomes, including competitive exclusion, stable coexistence, and cycles driven by intransitive competition (Vellend and Litrico 2008; Lankau 2009). What is lacking, however, is a general framework capable of predicting when the interplay between ecological and evolutionary dynamics leads to these different outcomes.

Here we develop a mathematical framework that integrates dynamical models of species interactions with quantitative genetic models of trait evolution. We use this framework to address three important questions: (1) Can evolution allow stable coexistence via neighbor-dependent selection? (2) What types of trade-offs constrain intra- and interspecific competitive interactions under neighbor-dependent selection? (3) How does the rate of evolution influence the nature of ecological dynamics under neighbor-dependent selection? We find that neighbor-dependent selection enables stable coexistence by (1) allowing trait values to evolve to a point where coexistence is possible via ecological mechanisms alone and (2) generating intransitive competitive cycles where coexistence is not possible via ecological mechanisms alone. A number of important characteristics of species' dynamics arise from competitive trade-offs and the rate of evolution.

Conceptual Framework

Conditions for Neighbor-Dependent Selection

We consider two species that compete for a limiting resource (e.g., space, nutrients, water, light). As a starting point, we investigate trait evolution in only one of the species and assume that the other species' traits are fixed.

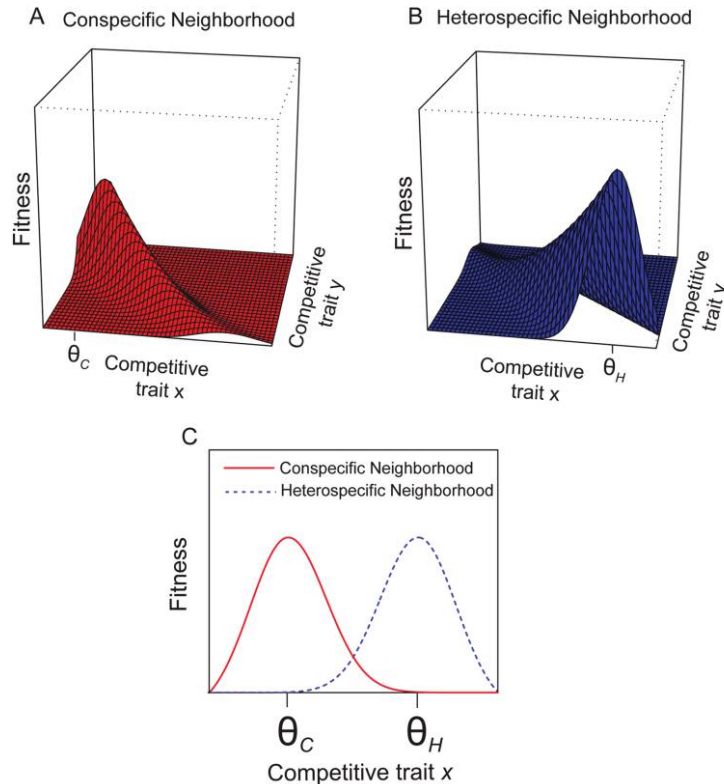


Figure 1: The traits determining optimal fitness in a neighborhood dominated by conspecifics (A) or by heterospecifics (B) exhibit a trade-off, and the optimal point along that trade-off depends on the surrounding neighborhood. An individual surrounded by a monoculture of conspecifics (A) will have optimal fitness at a high value of trait y , which determines conspecific dominance, and a low value of trait x , which determines heterospecific dominance. That same individual will be poorly adapted to a heterospecific neighborhood (B), where high values of trait x and low values of trait y are favored. Given the fitness trade-off, it is sufficient to express conspecific dominance and heterospecific dominance along a single trait x (C); at low values ($x = \theta_C$), individuals are good intraspecific competitors, and at high values ($x = \theta_H$), individuals are good interspecific competitors.

For brevity, we refer to the two species as the “variable species” and the “fixed species.” For neighbor-dependent selection to operate, the following requirements have to be met: (1) a trade-off exists such that the optimal traits for dominance in intraspecific competition preclude dominance in interspecific competition and vice versa, and (2) the traits underlying the trade-off have a genetic basis. It follows from these conditions that along the trade-off surface, the fitness of a given species depends on the relative abundances of conspecific and heterospecific competitors.

To understand how these requirements can be met in natural communities, consider that the variable species has two traits, x and y , that determine dominance in heterospecific and conspecific competition, respectively. These traits are negatively correlated. For example, they could be traits that correspond to growth and defense; energy allocated to defense cannot be allocated to growth. An individual surrounded by a monoculture of conspecifics

will have optimal fitness at a high value of the trait that determines conspecific dominance (y) and a low value of the trait that determines heterospecific dominance (x ; fig. 1A). By contrast, an individual surrounded by a monoculture of heterospecifics will have optimal fitness at a high value of trait x and, because of the trade-off, a low value of trait y (fig. 1B). Given this fitness trade-off between traits x and y , we can simplify the evolutionary analysis by focusing solely on trait x (fig. 1C). Along the trait axis, the optimal value of the trait in heterospecific neighborhoods (θ_H) differs from that in conspecific neighborhoods (θ_C ; fig. 1C).

Model Formulation

We use a Lotka-Volterra competition model to describe the ecological dynamics, following the specific form advocated by Chesson (2000),

$$\begin{aligned}\frac{dN_f}{dt} &= r_f N_f (1 - \bar{\alpha}_{fv}(\bar{x}) N_v - \alpha_{ff} N_f), \\ \frac{dN_v}{dt} &= r_v N_v (1 - \bar{\alpha}_{vf}(\bar{x}) N_f - \bar{\alpha}_{vv}(\bar{x}) N_v),\end{aligned}\quad (1)$$

where N_f and N_v are, respectively, the abundances of the fixed and variable species and r_f and r_v are their respective intrinsic growth rates. We model the competition coefficients as functions of the mean trait value \bar{x} , where $\bar{\alpha}_{ij}(\bar{x})$ is the mean per capita competitive effect of j on i , given the variation in N_v for trait x (see below). The variable species exhibits intraspecific variation in the quantitative trait (x), which governs the competitive effect of an individual with trait x on heterospecifics (α_{fv}) and the competitive effects an individual with trait x experiences from heterospecifics (α_{vf}) and conspecifics (α_{vv}). Consistent with an investment-based trade-off between growth and defense, individuals with a lower α_{vv} also have a weaker effect on conspecifics, because they require fewer resources in order to persist.

We next define the functions describing the dependence of the competition coefficients on trait x , analogous to those in figure 1C. These functions are flexible and can incorporate empirically observed relationships. The only constraints are that they should be continuous, or continuous approximations of discontinuous functions (Fox and Vasseur 2008), and have either a local minimum or a local maximum at some finite value of the quantitative trait. We consider the three competitive coefficients to be Gaussian functions of the quantitative trait x :

$$\begin{aligned}\alpha_{fv}(x) &= c_1 + \exp\left(\frac{-(x - \theta_H)^2}{2\tau^2}\right), \\ \alpha_{vf}(x) &= 1 + c_1 - \exp\left(\frac{-(x - \theta_H)^2}{2\tau^2}\right), \\ \alpha_{vv}(x) &= 1 + c_1 - \delta - (1 - 2\delta) \times \exp\left(\frac{-(x - \theta_C)^2}{2\tau^2}\right).\end{aligned}\quad (2)$$

The intraspecific competition coefficient α_{vv} is an upside-down Gaussian function with width τ that is minimized when $x = \theta_C$ (fig. 2). Minimizing α_{vv} is the optimal strategy for the variable species in conspecific neighborhoods, because it corresponds to the trait value generating the weakest intraspecific competition. The quantity θ_C is therefore the optimal trait value when the environment is dominated by conspecifics (fig. 1C). Interspecific-competition coefficients are modeled in a similar fashion, except that θ_H represents the trait value that maximizes the variable species' competitive effect on the fixed species and minimizes the fixed species' effect on the variable species

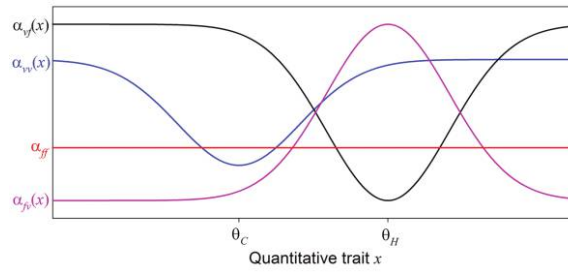


Figure 2: The four competition coefficients $\alpha_{ij}(x)$ as functions of the trait x given by equation (2). When an individual expresses the trait at the level $x = \theta_C$, $\alpha_{vv}(x)$ is minimized and the individual is optimally adapted to competition with conspecifics. When an individual's trait is expressed at the level $x = \theta_H$, $\alpha_{fv}(x)$ is maximized, and the individual is optimally adapted to competition with heterospecifics.

(fig. 2). Although not a requirement for our approach, we assume for simplicity that both of these effects are optimized at the same trait value. The quantity θ_H can therefore be considered the optimal trait value when the community is dominated by heterospecifics (fig. 1C). The constants c_1 and δ determine, respectively, the extreme values and relative rate at which the competition coefficients change with the trait. As the fixed species does not exhibit any trait variation, its intraspecific competition coefficient (α_{ff}) is constant. Although we employ Gaussian functions in equation (2), the results generalize to any set of functions possessing the same critical points that increase (decrease) over the appropriate range of x .

As is typical of quantitative traits, we assume that x is normally distributed, with a mean value \bar{x} and variance σ^2 (Falconer and Mackay 1996). Then, the mean competition coefficients involving the variable species are given by the integrals of the products of equation (2) and the trait distribution function across all trait values,

$$\bar{\alpha}_{ij}(\bar{x}) = \int_{-\infty}^{\infty} \left[\alpha_{ij}(x) \times \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(\frac{-(x - \bar{x})^2}{2\sigma^2}\right) \right] dx, \quad (3)$$

where $\alpha_{ij}(x)$ are as specified by equation (2). Equation (3) can be solved analytically (see the appendix), which allows for straightforward integration of equation (1) to obtain species' abundances under selection and competition. Trait variation allows selection to potentially operate on trait x , and the resulting changes in trait x in turn determine the competition coefficients according to the relationships specified by equation (2). Our approach follows that of Schreiber et al. (2011), who examined trait variation in a model of apparent competition.

We investigate how selection changes the mean trait value (\bar{x}), using the breeder's equation,

$$\frac{d\bar{x}}{dt} = H\sigma^2 \times \frac{\partial(1/N_v)(dN_v/dt)}{\partial\bar{x}} \quad (4)$$

(Falconer and Mackay 1996), where $d\bar{x}/dt$ is the response to selection quantified as the rate of change in the mean trait, H is the heritability of trait x , σ^2 is the variance in trait x , and the remaining factor is the selection differential, given here by the partial derivative of fitness (per capita growth rate) with respect to \bar{x} . We make the simplifying assumption that σ^2 does not respond to the eco-evolutionary dynamics, but investigating this effect requires only a straightforward extension of the current model.

Equation (4) involves a general formulation of trait evolution that can be derived on the basis of quantitative genetics (Taper and Case 1992), stochastic mutation-limited evolution (Dieckmann and Law 1996), and rapid phenotypic change via behavioral plasticity (Taylor and Day 1997). As written, equation (4) forms the backbone of "adaptive dynamics" (sensu Abrams 2005), where the mean trait value changes at a rate proportional to the fitness gradient. When considered in quantitative genetics terms, the product $H \times \sigma^2$ represents the additive genetic variance in the population and the rate at which the mean trait value changes in response to the selection differential. We assume a constant phenotypic variance but vary the rate of evolution by varying the heritability H . The exact expansion of equation (4), given equations (1)–(3), is given in the appendix.

Model Analysis

Because the full model with eco-evolutionary dynamics does not lend itself to analytical results, we used numerical methods to elucidate the interplay between ecological dynamics and selection. We used the "NDSolve" routine in Mathematica (ver. 7) to integrate the model. We initialized simulations by assuming that a small founder population of the fixed species invades a resident population of the variable species, which is adapted to competition with conspecifics ($N_v(0) = 1/\bar{\alpha}_{vv}(\bar{x})$, $N_f(0) = 0.01$, $\bar{x}(0) = \theta_C$). The alternative scenario, which requires the founder population of the variable species to be adapted to competition with heterospecifics, converges to the same outcome (results not shown). An interactive version of the model is provided in a zip file available online.¹

For the analysis of heritability effects, we ran simulations for 50,000 time units and recorded local maximum and minimum densities encountered over the last 5,000 time

units; these long simulations allowed for eco-evolutionary dynamics even when heritability was very low. We set an arbitrary extinction threshold at an abundance level of 0.0001 (approximately 0.01% of the single-species carrying capacities). This threshold allowed us to better understand how heritability, and therefore the pace of evolution in the variable species, is linked to its ability to respond to invasion and, potentially, exclusion by the fixed species. It is important to note that in the absence of an arbitrary extinction threshold, machine precision would still set an extinction threshold for abundances when heritability is very low (and evolution is therefore very slow).

Results

Ecological Constraints on Evolutionary Dynamics

We begin by investigating the effects of the mean trait value (\bar{x}) on ecological dynamics. This is an important starting point because \bar{x} controls the magnitude of competition coefficients and hence the relative strengths of intra- and interspecific competition. We can thus formulate hypotheses about selection-mediated outcomes that we can test with the full eco-evolutionary model. To this end, it is informative to examine how ecological dynamics change with \bar{x} over the region of the trait space between the trait values θ_C and θ_H that maximize fitness in conspecific and heterospecific environments, respectively. We refer to the range of traits bounded by these values as the selection domain. That the two trait optima bound the dynamics of \bar{x} can be understood as follows. From equation (1), when the fixed species is common in the neighborhood of the variable species, the latter's fitness (per capita growth rate) is proportional to $1 - \bar{\alpha}_{vf}(\bar{x})N_f$. Selection on the mean trait value will therefore minimize $\bar{\alpha}_{vf}(\bar{x})$, which occurs when $\bar{x} = \theta_H$. Alternatively, when the fixed species is rare in the neighborhood of the variable species, fitness (per capita growth rate) is proportional to $1 - \bar{\alpha}_{vv}(\bar{x})N_v$. Selection on the mean trait will minimize $\bar{\alpha}_{vv}(\bar{x})$, provided that selection reduces the mean competitive effect of conspecifics on an individual of the variable population.

If the competitive ability of the fixed species is such that it excludes the variable species over the entire selection domain, or vice versa, then selection cannot prevent competitive exclusion. Therefore, we focus on the situation where the variable species wins in interspecific competition when trait x is optimized for heterospecific environments ($x = \theta_H$) and loses when trait x is optimized for conspecific environments ($x = \theta_C$). We take these two boundary conditions, where the outcome of competition is defined, as the starting point for our model. Without loss of generality, we assume that $\theta_C < \theta_H$.

¹ Code that appears in the *American Naturalist* has not been peer-reviewed, nor does the journal provide support.

Phase-plane analysis, which entails plotting the zero-net-growth isoclines (ZNGIs) in the N_v , N_f plane, is useful in illustrating the ecological dynamics at each endpoint of the selection domain (fig. 3). When $\bar{x} = \theta_C$, the variable species is optimally adapted to competition with conspecifics but susceptible to invasion and subsequent exclusion by the fixed species. The ZNGIs must therefore be nonintersecting in the N_v , N_f plane, and the only stable equilibrium is the fixed species at its carrying capacity (fig. 3a). When $\bar{x} = \theta_H$, the variable species is optimally adapted to competition with heterospecifics and can invade and exclude the fixed species. The ZNGIs are again nonintersecting in the N_v , N_f plane, but now the only stable equilibrium has the variable species at its carrying capacity (fig. 3e). The key point is that there is a reversal of competitive dominance between one trait endpoint and the other. This means that the two ZNGIs must cross at some intermediate value of \bar{x} . Such a crossing is possible only if the trait mean evolves in response to shifts in relative abundance. Contingent on how the trait (\bar{x}) influences competition, different ecological outcomes are possible when the trait evolves away from the endpoints of the selection domain.

With this information in hand, we are able to generate hypotheses about possible evolutionary outcomes. Given

that the ecological dynamics at the trait extremes involve exclusion of the fixed species ($\bar{x} = \theta_H$) or the variable species ($\bar{x} = \theta_C$), only three ecological outcomes are possible over the range of intermediate trait values (fig. 3b–3d): coexistence at a stable equilibrium, neutrality, or a priority effect (where each species can exclude the other, depending on species' initial densities). Which of these outcomes ensues depends on how changes in the mean trait \bar{x} influence the relative positions of the species' ZNGI intercepts on the N_f and N_v axes of the phase plot. We denote the mean trait value at which the N_f intercepts cross ($1/\alpha_{ff} = 1/\alpha_{vf}$) \bar{x}_f and the value at which the N_v intercepts cross ($1/\alpha_{fv} = 1/\alpha_{vv}$) \bar{x}_v . Now we can characterize the three outcomes at intermediate trait values: (1) when the fitness functions are such that $\bar{x}_f < \bar{x}_v$, the outcome is coexistence at a stable equilibrium (figs. 3b, 4); (2) when the fitness functions are such that $\bar{x}_f > \bar{x}_v$, the outcome is a priority effect (fig. 3d); and (3) in the singular case when $\bar{x}_f = \bar{x}_v$, the species are competitively equivalent, and the outcome is neutral coexistence (fig. 3c). Importantly, the precise way in which the competition coefficients change with the mean trait \bar{x} determines whether intermediate trait values will favor coexistence at a stable equilibrium, priority effects, or neutrality.

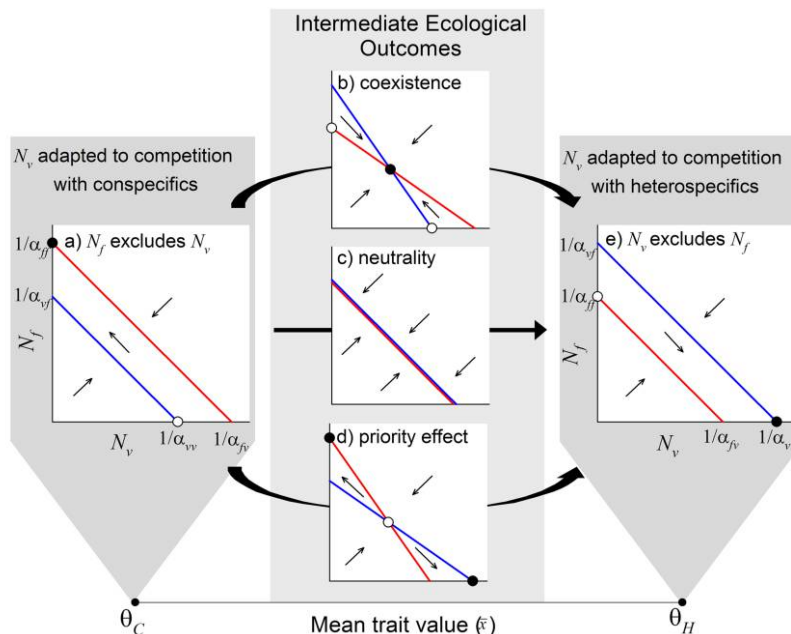


Figure 3: Three ecological outcomes are possible at intermediate values of the mean trait \bar{x} when the variable and fixed species are, respectively, excluded at the boundaries of the selection domain (a and e). In order for the outcome to transition from a to e, both the horizontal and vertical intercepts of the zero-net-growth isoclines must change their relative positions. Depending on which set of intercepts (horizontal or vertical) changes first, three different ecological outcomes are possible at intermediate trait values: coexistence at a stable equilibrium (b), neutral dynamics (c), or a priority effect (d). Blue (red) lines denote the zero-net-growth isoclines of the variable (fixed) species. Filled circles represent stable ecological equilibrium points; open circles represent unstable ecological equilibrium points.

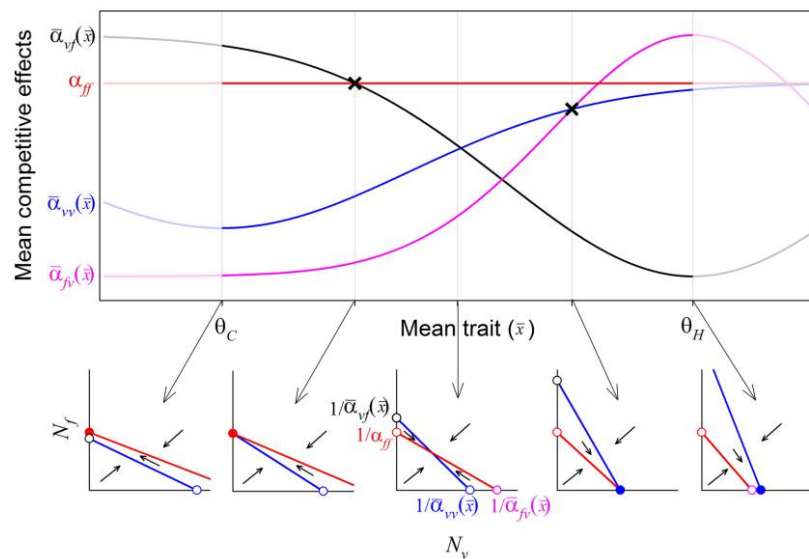


Figure 4: Mean competitive effects as functions of the mean trait \bar{x} , given by equation (3), and the zero-net-growth isoclines for the variable (N_v) and fixed (N_f) species at five important values of the mean trait. When $\bar{x} = \theta_c$, the fixed species can invade and exclude the variable species. When $\bar{x} = \theta_H$, the variable species can invade and exclude the fixed species. When $\bar{x} < \bar{x}_v$ (as shown in this example), an intermediate region of stable coexistence occurs in the selection domain. Intercepts on the lower panels are color-coded to match the curves in the upper panel.

Depending on the shapes of functions governing the dependence of competition coefficients on the mean trait, it is possible for multiple intermediate ecological outcomes to occur within the selection domain (e.g., a region favoring stable coexistence bracketing a region of exclusion). For simplicity, we restrict our analysis to a set of functions (eq. [2]) that allow each pair of intercepts to cross only once in the selection domain, ensuring that only one type of intermediate ecological outcome is possible for any given parameter set; that is, provided that α_{ff} is constant and $0 \leq \delta \leq 0.5$, each pair of intercepts can cross only once in the trait space. This constraint allows us to forego an analysis of parameter sensitivity; as all parameterizations of equation (2) must lead to one of the possible intermediate outcomes, our depicted results for each outcome provide a general set. Also note that in order to satisfy the reversal of the competitive dominance at the boundary conditions, $\bar{\alpha}_{vf}(\bar{x})$ must decrease below α_{ff} over the selection domain (and because of the trade-off, $\bar{\alpha}_{vv}(\bar{x})$ must increase), and $\bar{\alpha}_{fv}(\bar{x})$ must increase faster than $\bar{\alpha}_{vv}(\bar{x})$ (fig. 4).

Eco-Evolutionary Dynamics Resulting from Neighbor-Dependent Selection

Figure 5 illustrates the ecological evolutionary dynamics at values of α_{ff} that generate, from top to bottom, (1)

coexistence at a stable equilibrium, (2) neutral dynamics, and (3) priority effects at fixed intermediate values of the mean trait \bar{x} . In all cases, the fixed species successfully invades the variable species, and as the variable species becomes rare, selection increases the value of the mean trait in the direction of the heterospecific optimum.

As we hypothesized, the nature of ecological dynamics at intermediate trait values influences the eco-evolutionary dynamics of the system. For instance, when the intermediate ecological outcome is coexistence at a stable equilibrium, the mean trait converges to an optimum value within this intermediate region that is evolutionarily stable (fig. 5a–5c). When the intermediate ecological outcome is neutrality or a priority effect, the trait does not converge to an optimum value but oscillates across a range that allows both species periods of higher relative fitness (fig. 5d–5i). In both cases, neighbor-dependent selection enables stable coexistence by generating a stable limit cycle, where none was apparent in the absence of selection, in which the two species and the mean trait oscillate (fig. 5e, 5h). Regardless of whether the underlying ecological dynamic is neutrality or a priority effect, the system converges to the stable limit cycle (fig. A1).

The cyclic dynamics generated when a priority effect is present (fig. 5h, 5i) are a form of intransitive competition occurring between two species, as predicted by Lankau

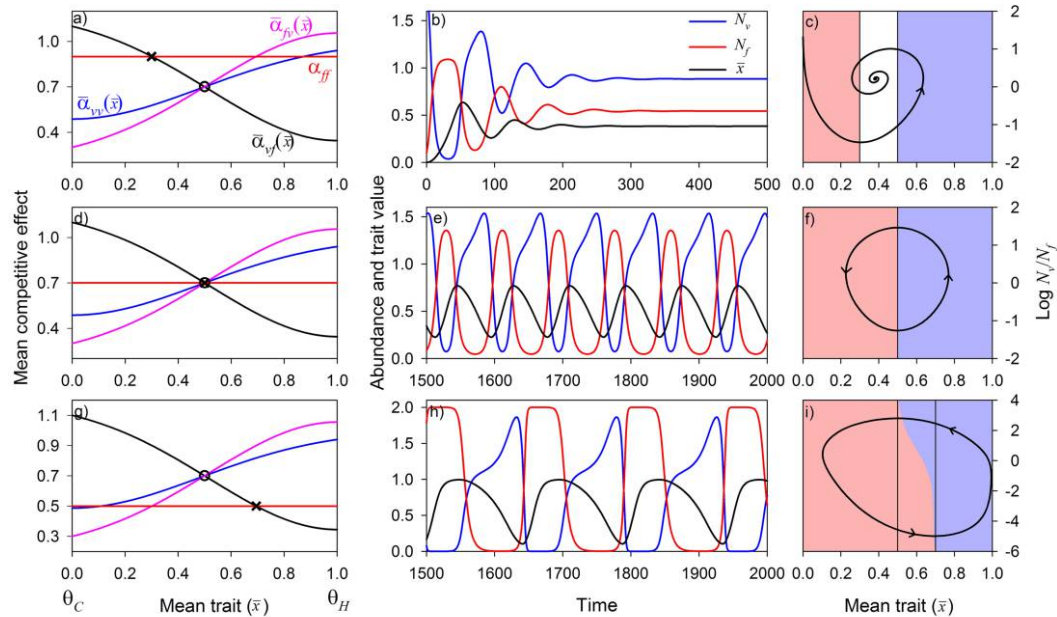


Figure 5: Competition coefficients (a, d, g), dynamics (b, e, h), and the shape of the attractor (c, f, i) produced by the model under the three scenarios given in figure 3. In a–c, a range of values of the mean trait generates an ecologically stable equilibrium (provided that heritability is low); simulation of the model shows that selection leads to an evolutionarily stable strategy in this range. In d–f, only a single value of the mean trait generates a neutrally stable ecological equilibrium; simulation of the model shows that selection stabilizes coexistence by generating stable limit cycles. In g–i, a range of values of the mean trait generates an ecological priority effect; simulation of the model shows that selection stabilizes coexistence by generating cycles in the mean trait that span this unstable range. Color-coding (in c, f, and i) shows the winner of competition when the mean trait value is fixed; this depends on abundances in the priority-effect region of i. Note that we generate the three intermediate ecological outcomes by altering only the constant α_{ff} . Parameter values are $r_v = r_f = 1$, $\theta_C = 0$, $\theta_H = 1$, $\tau = 0.412715$, $\sigma = 0.25$, $c_1 = \delta = 0.2$, $H = 0.3$, and $\alpha_{ff} = 0.9$ (a), 0.7 (b), or 0.5 (c). The value of τ was specifically chosen so that x_v was fixed at $\bar{x} = 0.5$. An interactive version of this figure is available online.

and Strauss (2007) and demonstrated theoretically by Velend and Litrico (2008). Coexistence via intransitive competition typically requires at least three species in order to form the nonhierarchical competitive loop (Gilpin 1975; Jackson and Buss 1975; May and Leonard 1975). However, if selection leads to alterations in relative fitness, then the variable species is effectively two different species, allowing the two-species system to mimic three-species intransitive competition. In analogy to the common game of rock-paper-scissors, the variable species adapted to heterospecific competition wins against the fixed species, the fixed species wins against the variable species adapted to conspecific competition, and the variable species adapted to conspecific competition wins over individuals of the same species adapted to heterospecific competition.

When species abundances cycle, eco-evolutionary feedbacks can explain the length of time that each species dominates the system (fig. 5e, 5h). At any given time, the direction and strength of selection on the mean trait of the variable species is determined by its relative abundance, which in turn depends on the ecological dynamics gen-

erated by current and previous trait values. When the fixed species is the dominant competitor at θ_C and the variable species is the dominant competitor at θ_H , selection is always weaker when adapting to conspecifics than when adapting to heterospecifics. In conspecific neighborhoods, the selection differential is determined by the gradient of α_{vv} with respect to the trait x , whereas in heterospecific neighborhoods, it is determined by the gradient of α_{vf} . Since the average slope of α_{vf} across the selection domain must be greater than that of α_{vv} in order for our rules for competitive dominance to hold (e.g., fig. 4), selection in conspecific neighborhoods is always weaker (on average) than that in heterospecific neighborhoods. This affords the variable species relatively longer periods of dominance in the intransitive competition cycle, because the slow pace of evolution in conspecific neighborhoods keeps the variable species less vulnerable to the conspecific. This result arises from constraints on the outcomes of competition at the boundaries of the selection domain, but it may not necessarily hold for alternative representations of equation

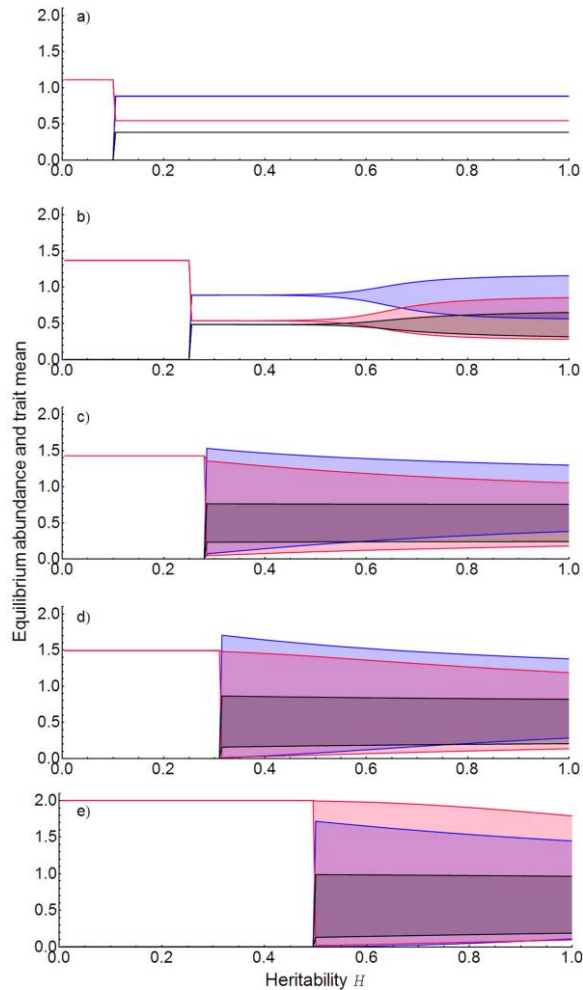


Figure 6: The range of abundances encountered at equilibrium for the variable (blue) and fixed (red) species and the mean trait (black) as a function of the heritability H for five parameter combinations representing a large intermediate coexistence region (a), a small coexistence region (b), a neutral point (c), a small priority-effect region (d), and a large priority-effect region (e). Shaded regions represent cycles between a local maximum and a local minimum. Open regions represent values at which transient extinction of the variable population occurred ($N_i < 0.0001$). Provided that extinction does not occur, heritability has no effect when the intermediate coexistence region is large (a) but can destabilize dynamics if the intermediate coexistence region is small (b). When the intermediate regions do not allow coexistence, increased heritability reduces the amplitude of limit cycles and increases the minimum density encountered by both populations. Parameter values are as in figure 4, but where $\alpha_{if} = 0.9, 0.73, 0.7, 0.67$, and 0.5 in a–e, respectively.

(2) that meet the minimum requirements for our model (see “Conditions for Neighbor-Dependent Selection”).

As the region of the selection domain over which priority effects occur grows, species undergo fluctuations of greater magnitude at equilibrium. By comparison, the sta-

ble limit cycles that occur when the intermediate outcome is neutral exhibit much smaller amplitudes (cf. fig. 5e and 5h). As a result, neither species attains periods of very low abundance. This difference in amplitude arises directly from the length of the trait axis on which selection must act to reverse relative fitness. When the intermediate outcome is neutral, evolution across the point of neutral dynamics immediately reverses relative fitness and leads quickly to a turnover of relative abundance, resulting in a cycle with high frequency (fig. 5e, 5f). When the intermediate outcome is a priority effect, reversal of relative fitness requires the evolution of more extreme trait values, resulting in a cycle with lower frequency (fig. 5h, 5i). This decrease in frequency occurs because evolution of the trait across the region generating a priority effect essentially extends the range of the trait over which the dominant species is favored. For example, when the variable species is adapted to heterospecifics ($x \approx \theta_H$), it is competitively dominant, and x decreases in response to intraspecific competition. As x decreases, the system enters the priority-effect region (when $x = 0.7$; fig. 5i), but because the variable species is much more abundant, the outcome of competition is not reversed until the trait nears the other side of the region ($x \approx 0.5$; fig. 5i). The complementary outcome is observed when the fixed species is dominant and x is increasing. The important point is that increasing the range over which priority effects occur has the additional effect of lengthening periods of relative fitness/dominance, which in turn leads to periods of very low abundance for the maladapted species. Such periods can effectively lead to the extinction of the rare species if one considers the finite nature of real populations. Therefore, spatial subsidies or dispersal from other areas may be necessary for long-term coexistence with this dynamic.

Effects of Heritability

The heritability H represents the proportion of the phenotypic variance σ^2 that can be attributed to genetic variation among individuals. Exploring its influence on neighbor-dependent selection is important because heritability determines the speed of the evolutionary response to the selection differential operating on the trait x . It therefore controls the timescale differential between the ecological and evolutionary dynamics. We investigate the effects of heritability on neighbor-dependent, selection-mediated coexistence by repeating simulations with all three intermediate ecological states but with a range of heritability from 0 to 1.

When the model is parameterized to include a large intermediate region of coexistence at a stable equilibrium, heritability has little effect on the equilibrium outcomes (fig. 6a). Over most of the range of H , the trait value

Table 1: Key requirements for and predictions about neighbor-dependent selection (NDS), given three possible intermediate ecological outcomes

Relative strengths of competition	Ecological outcome (species interactions)	Evolutionary outcome (trait evolution)	Effects of heritability
$\bar{x}_i < \bar{x}_j$: intraspecific > interspecific for both species	Stable coexistence	Trait converges to evolutionarily stable strategy when adaptation is slow; NDS leads trait to ecologically stable coexistence	Increasing heritability introduces stable limit cycles as a result of evolutionary overcompensation
$\bar{x}_i = \bar{x}_j$: species competitively equivalent	Neutral equilibrium	Stable limit cycles; NDS stabilizes coexistence	Increasing heritability reduces the amplitude of stable limit cycles
$\bar{x}_i > \bar{x}_j$: interspecific > intraspecific for both species	Priority effect	Stable limit cycles; NDS stabilizes coexistence	Increasing heritability reduces the amplitude of stable limit cycles

converges to a stable equilibrium within the coexistence region. However, when heritability is near 0, the variable species cannot adapt quickly enough to avoid exclusion during the initial transient phase after the fixed species invades. When the intermediate coexistence region is small (fig. 6b), a larger heritability is required to overcome exclusion of the variable species during the initial transient phase, because the trait value necessary for reinvasion by the variable species is at a greater distance along the trait axis. Furthermore, as heritability increases from intermediate to high values, the system undergoes a Hopf bifurcation and no longer converges to an evolutionarily stable strategy but exhibits regular stable limit cycles (fig. 6b). These cycles occur because of evolutionary overcompensation. Rather than converging to 0, the selection differential remains large in magnitude as the trait value passes through the coexistence region, because the ecological dynamics do not have adequate time to respond and thereby weaken the selection differential. The outcome is still stable coexistence, albeit on a stable limit cycle that fails to converge on the evolutionarily stable strategy but rather continually overcompensates, resulting in consistent overshooting and undershooting of the stable equilibrium.

When the ecological dynamics involve stable limit cycles (fig. 6c–6e), the minimum amount of heritability needed to prevent the initial exclusion of the variable species is even greater than that in the case where species' abundances converge to a stable equilibrium (fig. 6a, 6b). This occurs because the magnitude of trait change required to prevent exclusion increases but the rate at which selection alters the mean trait is unchanged. In the absence of a stable ecological outcome at intermediate trait values, coexistence occurs via the intransitive cycles mediated by selection on the mean trait value of the variable species. Consequently, the destabilizing effects of overcompensatory selection that accompany high heritability are less important than the benefit of shortened boom and bust

periods with high H . Increasing heritability leads to a quicker turnover of species' dominance and a shorter cycle period. The shorter period reduces the amplitude of cycles and bounds their densities farther above 0 (fig. 6c–6e). Although we often find extinctions within the range of heritabilities commonly found in nature (0.2–0.4), other parameters, including the trait variance σ^2 , affect the rate of trait evolution; the qualitative effect of heritability is a robust feature of our model, but the ranges over which it produces extinctions and persistence have no particular biological relevance.

Discussion

Our model demonstrates that neighbor-dependent selection operating on a quantitative trait in one species can allow stable coexistence of two competitors by (1) causing trait values to evolve to a stage where stable coexistence is possible via ecological mechanisms alone and (2) generating intransitive competitive cycles where stable coexistence is not possible via ecological mechanisms alone (summarized in table 1). In the latter case, adaptive evolution prevents competitive exclusion by ensuring that each species experiences periods of greater relative fitness, during which intraspecific competition is stronger than interspecific competition.

That eco-evolutionary dynamics can allow the coexistence of species that cannot coexist via ecological processes alone is a particularly noteworthy result. Our model shows that this scenario emerges only when the intermediate ecological outcome is a priority effect. Under these conditions, no fixed trait value for the variable species allows long-term coexistence via purely ecological mechanisms, and coexistence is made possible by subjecting the trait to neighbor-dependent selection. By contrast, when the intermediate ecological state is coexistence at a stable equilibrium, a range of fixed trait values allow stable coexis-

tence via ecological mechanisms alone: weaker interspecific competition relative to intraspecific competition. Thus, if the fixed trait value falls within this range, neighbor-dependent selection is not essential for stable coexistence, and niche-based mechanisms are likely important for governing coexistence at the evolutionarily stable trait value. Nonetheless, the trait of the variable species can initially lie outside the range suitable for coexistence, and under these conditions, selection will be critical for driving the trait toward the region of stable coexistence. This scenario is particularly likely if only a small trait range gives an intermediate ecological outcome of coexistence.

A second key finding is that heritability, which governs the rate of selection, can have varied effects on species coexistence, depending on the outcome of competition at intermediate trait values. When the intermediate ecological outcome is stable coexistence, increasing heritability can destabilize dynamics and generate cycles; when the intermediate region is neutrally stable or unstable, increasing heritability can reduce the amplitude of intransitive cycles by shortening the cycle period and therefore the periods of maladaptation (summarized in table 1). This result might also provide insight into the role that phenotypic plasticity can play in influencing coexistence. Under the assumption that trait changes achieved through phenotypic plasticity are analogous to rapid selection in our model, our framework and results could be interpreted as demonstrating the influence of plasticity on coexistence.

Intransitive competition has been suggested as a means of coexistence where a lack of niche differentiation ensures that coexistence at a stable equilibrium is not possible (Gilpin 1975; May and Leonard 1975; Laird and Schamp 2006). Recently, Huisman and Weissing (2001) showed that competition for essential abiotic resources can lead to intransitive cycles and heteroclinic cycles. The latter mimic intransitive competition in their patterns of species replacement but are impermanent, leading to lower and lower species abundances over time. The dynamics observed in our model of neighbor-dependent selection lack the properties of heteroclinic cycles; however, when the rate of evolution is relatively slow or the magnitude of trait change required to reverse relative fitness is large, neighbor-dependent selection can cause one or both species to decline to unsustainably low abundances. In such cases, long-term coexistence may be sustained if immigration provides a constant source of genetically variable individuals. This may be a realistic consideration, given that neighborhood effects may be localized relative to the ranges of many species.

Our broader framework yields insight into the mechanisms by which neighbor-dependent selection leads to coexistence. Previous studies have found different types of dynamics emerging from this type of mechanism. Lankau

(2009) used field measurements from his mustard system to parameterize an individual-based model with asexual reproduction of 11 genotypes varying in their toxin production. Despite expectations that intransitive cycles should emerge in this system (Lankau and Strauss 2007; Lankau 2009), only stable equilibria were found. Viewed in the context of our findings, this suggests that the field-informed parameters favored stable coexistence at intermediate trait values. Indeed, the parameters suggested that independent of selection, species are more limited by conspecific than by heterospecific competitors. In contrast, Vellend and Litrico (2008), also motivated by the mustard system of Lankau and Strauss (2007), found only cyclical equilibria. Our analysis suggests that these cycles could result either from neighbor-dependent selection with a priority effect at intermediate trait values or from the overcompensatory effects of selection driven by high heritability when intermediate ecological dynamics are stable.

The key requirement of neighbor-dependent selection, the trade-off between traits that determine intra- and interspecific competitive ability, is likely to be met in a wide variety of competitive systems (Pimentel et al. 1965; Pease 1984; Lankau and Strauss 2007). Aquatic plants exhibit a trade-off between nitrogen and phosphorus uptake (Linhart 1988) that directly affects their competitive ability. Such trade-offs should also arise from the allocation constraints driving growth-defense trade-offs in plants (Van Dam and Baldwin 1998; Marak et al. 2003; Lankau and Strauss 2007) or the growth-predation risk trade-offs observed in many animal prey species (Brodin and Johansson 2004). Here, species that are less vulnerable to herbivores or predators are competitively superior in their presence but competitively inferior when they are lacking, generating the same fluctuation in competitive dominance that we report here as necessary for neighbor-dependent selection.

The negative correlation between intra- and interspecific competitive abilities is also key to selection's stabilizing effects on coexistence in character-displacement models. However, the key difference between character displacement and neighbor-dependent selection is that in the former, the correlation itself evolves; as sympatric species diverge in niche space, the correlation becomes more negative. By contrast, with neighbor-dependent selection the negative correlation is a fixed constraint on the system (as in fig. 2), driven, presumably, by allocation-based trade-offs operating at the individual level. Selection in sympatry does not change the inverse correlation itself; only the optimal location along the trade-off is under selection.

While empirical studies indicate that trade-offs between intra- and interspecific competition are common (Linhart 1988; Van Dam and Baldwin 1998; Marak et al. 2003; Brodin and Johansson 2004; Lankau and Strauss 2007),

the strength of this trade-off has rarely been quantified empirically. We suggest that this could easily be tested experimentally, especially in plants where the fitness of clones from a range of genotypes could be quantified when exposed to intra- and interspecific competition. Whether a measured trade-off indicates neighbor-dependent selection or character displacement could be further determined by quantifying the trade-off between sympatry and allopatry. Only with character displacement is the correlation expected to be stronger in sympatry than in allopatry; the latter is common in definitions of character displacement (Taper and Case 1985; Grant and Grant 2006). By contrast, if the correlation is unchanged, it may drive neighbor-dependent selection.

In conclusion, our mathematical framework shows that an effective means for understanding and predicting eco-evolutionary dynamics involves exploring how ecological outcomes change with focal traits. This approach is particularly promising in investigations of the effect of selection on competitive interactions in more complex communities. A logical extension of our model is to investigate neighbor-dependent selection in the coevolutionary dynamics of two competing species. Such a scenario requires a more complete understanding of the ways in which different species' traits may interact when governing interspecific competition. The addition of a second trait axis

may simply increase the potential for stable ecological coexistence, in which case our analysis suggests that selection will lead the system to this outcome. The fact that our model of only one species subjected to selection still captures the full range of possible ecological dynamics between two species raises the important question of whether coevolution leads to situations where selection is necessary for coexistence or whether selection merely augments ecologically mediated coexistence. Investigating these and related issues is an important future direction.

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APPENDIX

Exact Solutions to Equations (3) and (4)

Equation (3)

The mean competitive effects $\bar{\alpha}_{ij}(\bar{x})$, given the mean trait value \bar{x} , are given by equation (3). Solving the integral for each effect yields

$$\begin{aligned}\bar{\alpha}_{vv}(\bar{x}) &= 1 + c_1 - \delta - (1 - 2\delta) \times \left(\frac{\tau}{\sqrt{\tau^2 + \sigma^2}} \right) \exp\left(\frac{-(\bar{x} - \theta_C)^2}{2\tau^2 + 2\sigma^2} \right), \\ \bar{\alpha}_{vf}(\bar{x}) &= 1 + c_1 - \left(\frac{\tau}{\sqrt{\tau^2 + \sigma^2}} \right) \exp\left(\frac{-(\bar{x} - \theta_H)^2}{2\tau^2 + 2\sigma^2} \right), \\ \bar{\alpha}_{fv}(\bar{x}) &= c_1 + \left(\frac{\tau}{\sqrt{\tau^2 + \sigma^2}} \right) \exp\left(\frac{-(\bar{x} - \theta_H)^2}{2\tau^2 + 2\sigma^2} \right).\end{aligned}\tag{A1}$$

Equation (4)

The rate of change of the mean trait is given by equation (4). The second factor in this equation is the selection differential, which can be solved to yield an exact expression for equation (4). Substituting the expressions from equation (A1) into equation (1) and computing the partial derivative yields

$$\frac{\partial(dN_v/N_v dt)}{\partial \bar{x}} = r_v \tau (\sigma^2 + \tau^2)^{-3/2} \{ N_f (\theta_H - \bar{x}) e^{[-(\bar{x} - \theta_H)^2 / 2(\sigma^2 + \tau^2)]} + N_v (1 - 2\delta) (\theta_C - \bar{x}) e^{[-(\bar{x} - \theta_C)^2 / 2(\sigma^2 + \tau^2)]} \}.\tag{A2}$$

When N_v is rare, the direction of selection is determined entirely by $\theta_H - \bar{x}$, and when N_f is rare, the direction of selection is determined entirely by $\theta_C - \bar{x}$. In both cases, selection will generate convergence to the optimum value. Together, the absolute distance between optima, the variance in competitive effect τ^2 , and the intraspecific variance σ^2 determine the selection gradient; too little variance relative to $|\theta_C - \theta_H|$ makes selection weak when x is not proximate to θ_C or θ_H , whereas too much variance flattens the selection differential across the entire domain of x . The additional factor in the second term of the final equation, $1 - 2\delta$, appears because of the boundary constraints in our model. It ensures that adaptation in conspecific neighborhoods always occurs more slowly than adaptation in heterospecific neighborhoods.

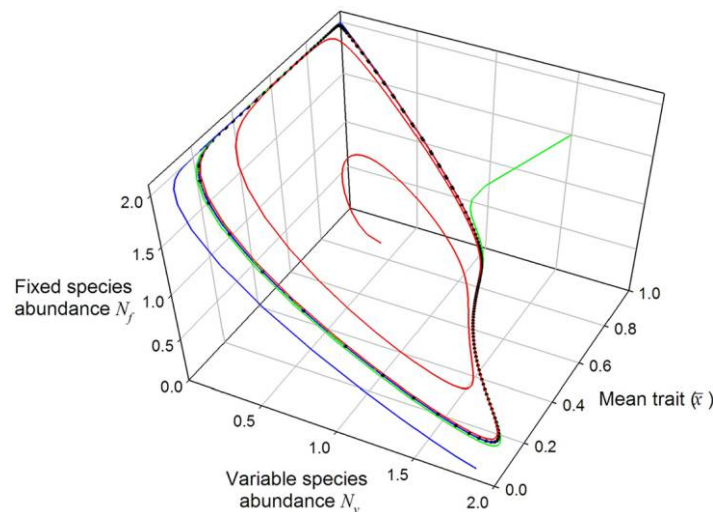


Figure A1: Dynamics of the model eco-evolutionary model when the intermediate ecological outcome is neutral. When selection is modeled in concert with ecologically neutral competition, the equilibrium changes to a stable limit cycle (dotted black line). This cycle is globally attractive in the positive-valued phase space; we show three solution trajectories (green, red, and blue lines) that converge to the stable limit cycle from different initial points in the phase space. Parameter values are $r_v = r_f = 1$, $\theta_C = 0$, $\theta_H = 1$, $\tau = 0.412715$, $\sigma = 0.25$, $c_1 = \delta = 0.2$, $H = 0.3$, and $\alpha_H = 0.7$.

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