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The evolution of niche overlap and competitive differences

Abigail I. Pastore*, György Barabás*, Malyon D. Bimler,
Margaret M. Mayfield & Thomas E. Miller
*Authors contributed equally to the manuscript

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Abstract

Competition can result in evolutionary changes to coexistence between competitors, yet there are no theoretical models that predict how the components of coexistence change during this eco-evolutionary process. We study the evolution of the coexistence components, niche overlap and competitive differences, in a two-species eco-evolutionary model based on consumer-resource interactions and quantitative genetic inheritance. Species evolve along a one-dimensional trait axis that allows for changes in both niche position and species intrinsic growth rates. There are three main results. First, the breadth of the environment has a strong effect on the dynamics, with broader environments leading to reduced niche overlap and enhanced coexistence. Second, coexistence often involves either a reduction in niche overlap while competitive differences stay relatively constant, or vice versa: a change in competitive differences while niche overlap does not change much. Large simultaneous changes in niche overlap and competitive difference often result in one of the species being excluded. Third, provided that the species evolve to a state where they coexist, the final niche overlap and competitive difference values are independent of the system's initial state, though they do depend on the model's parameters. The model suggests that evolution is often a destructive force for coexistence due to evolutionary changes in competitive differences, a finding that expands the paradox of diversity maintenance.

Keywords: competition, eco-evolutionary feedback, equalization, modern coexistence theory, quantitative genetics, stabilization

Introduction

The interplay between evolution and ecological interactions can be a crucial component of the structure and functioning of communities, including the maintenance of species diversity[1,2]. As communities assemble, ecological dynamics filter suites of species within the community based on their interactions with the environment and each other, while simultaneously species change their roles within the community through trait evolution[3]. These feed-backs between ecological and evolutionary processes modify species traits' and can result in changes to the ecological interactions between species and their 'fit' in the community[4], which likely translate into consequences for species coexistence. Therefore, models of species interactions in evolutionarily labile systems may not accurately predict community dynamics unless they have an evolutionary component, as has been demonstrated with predator prey systems[5]. Similarly, species that compete for resources are likely to exhibit feedbacks between ecological processes and evolution[6,7]. This complicates our understanding of coexistence mechanisms because traits mediate both resource use and competitive performance, thus having multiple and possibly conflicting consequences for species coexistence.

Modern coexistence theory describes coexistence between two species by determining the relative magnitude of niche overlap and differences in competitive ability[8–12], with both components capable of responding to different ecological and evolutionary pressures. In this context, niche overlap is the degree to which species share the factors regulating their population growth (such as resources). The competitive difference between species is the difference in how efficiently they can convert resources to population growth in their average environment. Because both niche overlap and competitive differences are moderated by complex processes, they allow many avenues to coexistence. For example, species may coexist because they have differentiated resource use and thus do not significantly interact, or they can coexist with partially overlapping resource use if they are nearly equivalent in their average competitive abilities.

Species coexistence being driven by mechanisms influencing primarily one or the other term could have distinct consequences for the evolutionary trajectory of a community. For example, a community characterized by low niche overlap and small competitive differences will be more resilient to changes in either of these mechanisms than a community with high niche overlap or large competitive differences. As such, initial conditions matter when determining whether evolutionary changes in niche overlap or competitive differences are likely to promote or prevent coexistence. Furthermore, it is unclear how evolution among competitors will change ecological coexistence when evolution can alter both the niche overlap and the competitive ability of a species simultaneously. Germain and colleagues[13,14] hypothesize that niche overlap between species will decrease and competitive differences will increase as a consequence of microevolution, which would have opposing effects on coexistence. Although consensus is growing that both niche overlap and competitive differences structure real communities[15–17], a lack of understanding persists about how evolutionary processes alter when and how niche overlap and competitive differences drive changes in community structure[3,18,19].

Selection acts on the traits that mediate species responses to the environment—not directly on niche overlap or competitive differences, which are derived quantities[12,20]. The dynamics of trait convergence and divergence has been studied extensively in an eco-evolutionary setting before (though mostly theoretically)[6,7,21–23]. This raises the question why these results should be examined and interpreted in light of the niche overlap-competitive difference decomposition of modern coexistence theory in the first place. The reason is that there is no simple relationship between trait convergence or divergence on the one hand, and the probability of coexistence on the other; for example, it is not necessarily true that a greater trait divergence leads to a greater propensity for coexistence, because individuals with extreme traits may suffer from increased mortality or a reduced ability to capture resources. Modern coexistence theory offers one possible way of linking the two, and thus to open the way for formally connecting observed trait patterns with the structure of ecological communities[24,25]. However, although the evolutionary consequences of competition on traits has been studied for decades[6,7,21–23,26,27], there have been no formal investigations of these processes in the context of modern coexistence theory, despite new empirical studies on the matter[28,29].

This body of theoretical work has yet to be interpreted in light of modern coexistence theory. Character divergence in a trait related to resource acquisition (e.g., beak size) is expected to result in decreased niche overlap and subsequently the ability of two species to increase from low density in the presence of the other (i.e., stable coexistence)[26,30,31]. Models of character evolution tend to find that the breadth of resources available in the environment is a major driver of these evolutionary outcomes. For example, when the variance of available resources is small or resources are nonsubstitutable, models often predict trait convergence[32–34], this results in increased overlap in resource utilization which is directly analogous to the Chessonian concept of niche overlap, and have the same implications for coexistence. While previous studies understood that limits to similarity between species depend on the similarity of their carrying capacities (analogous to competitive differences)[26,35,36], this body of work has treated the evolution of carrying capacities only implicitly, without emphasizing its role in shaping coexistence. They also did not ask how niche overlap and competitive differences prior to selection predict these separate components of coexistence after evolution.

In this study, we use a simple model based on previous work[7] to investigate the interactions between ecological and evolutionary dynamics. This model functions like several classic models of trait evolution in competition, combined with quantitative genetic models[6,21–23,37,38], following how niche overlap and competitive differences change as a result of selection on a one-dimensional trait axis under competition and environmental constraint. The model allows for changes in species competitive differences based on position along the trait axis, but additionally assumes that there is some fixed difference in absolute growth potential between the species that is independent of trait value. The relative magnitude of changes in niche overlap and competitive differences in this model determine changes to species interactions (ecological dynamics of the system), depending on variation in available resources in the environment. Ultimately, we address when and how coexistence conditions change as a result of evolution due to competition.

Box 1: Model framework

The eco-evolutionary dynamics of two species i and j are governed by a set of ordinary differential equations which track changes in total population densities N and mean trait values μ of trait z through time (Fig. 1). Changes in both N and μ are governed by population dynamics and quantitative genetic inheritance such that traits determine species interactions, which in turn affect the selection pressures on traits. Species' per capita growth rates are determined by an intrinsic growth rate function in the absence of competition, and a competition kernel. Species i's intrinsic growth rate is parabolic over the trait z and is determined by the maximum growth potential K_i, current distance of the mean trait from the optimal trait value $z = 0$, and the environmental breadth θ: a smaller θ makes the curve of the parabola steeper. Competition between two phenotypes is a decreasing (Gaussian) function of the trait distance between them, with standard deviation proportional to a parameter ω (the competition width). Both species thus experience selection pressure to reach the optimal trait value $z = 0$, as well as pressure to be sufficiently different from the other species to avoid experiencing too much competition.

The model was numerically integrated for 10^6 time units. We varied the three model parameters θ (environmental breadth), ω (competition width), and K_1 (intrinsic growth potential for species 1) as well as initial mean trait values $\mu_1(0)$ and $\mu_2(0)$ for both species (Table 1). Initial and final values of niche overlap ρ and competitive differences κ_1/κ_2 were calculated from the mean trait values of both species and the three model parameters which we varied.

Results

Summary

Our model follows species interacting through an implicit continuum of shared resources, which results in selection on trait values (see Methods, Box 1, and Fig. 1). Evolution of trait values of both species results in changes in niche overlap between species as well as changes in competitive differences, due to Eqs. 7-8 (Fig. 1E). The environmental breadth θ has large effects on the magnitude and direction of the changes in niche overlap and competitive differences, and therefore species coexistence: ultimately, species are more likely to evolve extinction via increased niche overlap in narrow environments, and evolve coexistence by reducing them in broad environments (Fig. 2). Changes in competitive differences tend to result in the eventual extinction and therefore competitive exclusion of one of the species—unless the corresponding change in niche overlap is small (Fig. 3). Finally, an important property of the model is that a fixed combination of the competition width ω, environmental breadth θ, and species 1's growth (dis)advantage K_1 always result in the same final ρ and κ_1/κ_2 values, regardless of the initial trait means $\mu_1(0)$ and $\mu_2(0)$—provided that the species coexist in the final state. Furthermore, altering the parameters changes the final state which species pairs evolve toward along characteristic curves (Fig. 4).

Effects of environmental breadth

Changes in both niche overlap and competitive differences depend upon the breadth θ of the environment, but the dependence is much stronger for niche overlap (Fig. 2). Niche overlap was more likely to increase in narrow environments and decrease in broader ones. This pattern is shown in Fig. 2 for a fixed competition width of $\omega = 3$, but the same result is obtained for other values as well. This dynamic is driven by the effects of the environmental breadth on intrinsic growth (Eq. 3): all other things equal, species incur smaller decreases in intrinsic growth when diverging from the environmental trait optimum in broader environments. This allows species to be more distant from one another (and thus reduce competition as well as their niche overlap), without losing too much of their potential for population growth by having moved too far from the environmental optimum.

The environmental breadth therefore strongly affects the ability of species to maintain coexistence when evolving. In narrow environments, species often either start out from positions so unfavorable that at least one of them goes extinct, or else they will converge in their traits to the point where coexistence again becomes difficult to maintain. In broad environments however, where there is less penalty for moving away from the environmental optimum, species can diverge farther from one another. This results either in species maintaining a small niche overlap in case they started out that way, or else in being able to evolve away from one another and reduce overlap without losing too much growth potential. All these scenarios are broadly visible in Fig. 3. The vertical strip of high coexistence likelihood around zero niche overlap changes corresponds to the former, and the horizontal strip around zero competitive difference change to the latter case.

Initial conditions and parameter dependence

If one species excludes the other, the dynamical outcome is clear: the winning species, unhindered by interspecific competition, evolves its mean trait to match the environmental optimum at $z = 0$. When species do coexist, there is generally no globally stable state of the dynamics. To give the simplest example: when $K_1 = K_2$, the symmetry of the species as well as of the intrinsic growth

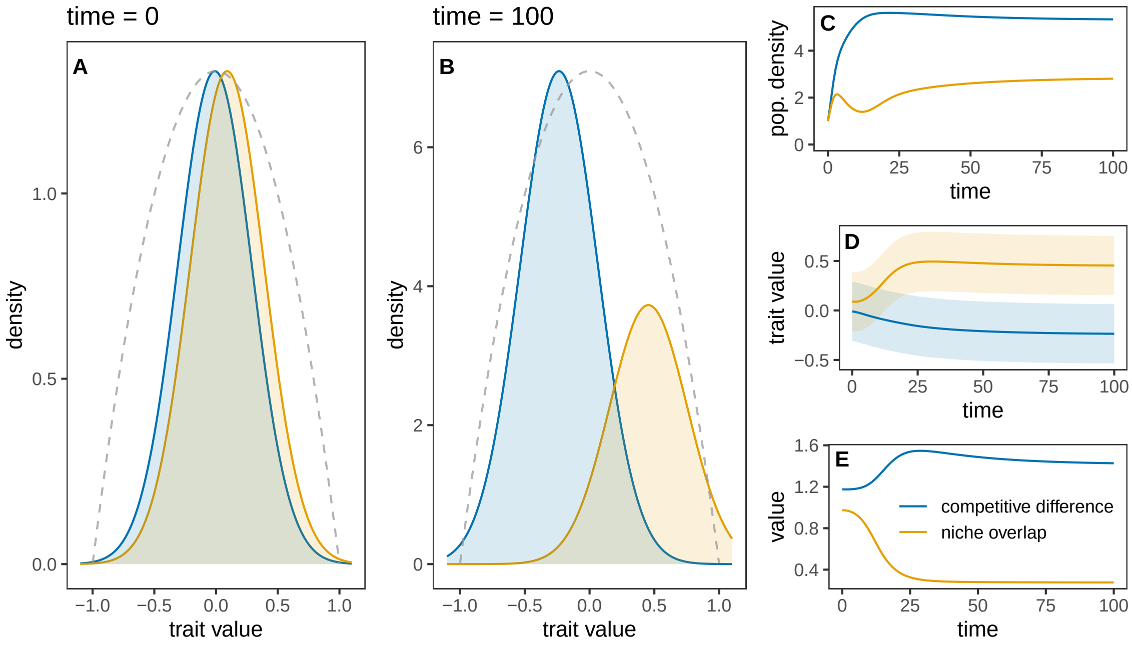

Figure 1: Example of the dynamics generated by the model. A. Initial trait distribution of two species (blue and yellow curves) before any dynamics have taken place. The area under each curve is the total population density of the corresponding species. Each individual phenotype along the abscissa has a normally distributed resource utilization function (not shown); integrating these across the whole trait distribution adds up to the species-level resource utilization curves (Supplementary Information, Eq. S29). The dashed line represents the growth potential of a given phenotype in the absence of competition. B. Trait distribution of two species after eco-evolutionary dynamics have stabilized. C. Change in population density of the two species experiencing ecological and evolutionary dynamics over time. D. The change in mean trait values (solid lines) of the two species as a consequence of evolutionary dynamics; shaded regions show the plus/minus one standard deviation range of their trait distributions. E. Change in competitive difference (blue) and niche overlap (yellow) over time as a consequence of evolution changing species interactions.

function λ_i (Eq. 3) and competition kernel $a(z,z')$ (Eq. 4) means we must have $\mu_1 = -\mu_2$ in the final state—but then, it does not matter whether species 1 is to the left of the optimum and species 2 to the right, or vice versa. The two possible arrangements therefore form two alternative stable states in this case. However, despite this general lack of a global attractor, the derived quantities ρ and κ_1/κ_2 nevertheless do attain values that are independent of initial conditions (Fig. 4).

These stable values depend on the parameters: the competition width ω, the environmental breadth θ, and the growth (dis)advantage K_1 of species 1. Broadly speaking, decreasing the competition width and/or increasing the environmental breadth results in lower final niche overlap (which makes sense, since species now have the space to move farther away from one another without incurring prohibitive growth penalties), while increasing K_1 results in higher final competitive differences between species 1 and 2, changing the attractor's position in ρ-κ space along a characteristic curve. This curve always crosses the $\log(\kappa_1/\kappa_2) = 0$ line when $K_1 = K_2 = 1$. This is because we then recover the symmetric scenario with $\mu_1 = -\mu_2$ mentioned above. By Eq. 8, we then end up with a κ-ratio of 1 and thus a log ratio of 0.

Fig. 5 presents examples of not just the final outcomes, but of the full dynamical trajectories in ρ-κ space. This shows three things. First, the general shape of these trajectories—which are

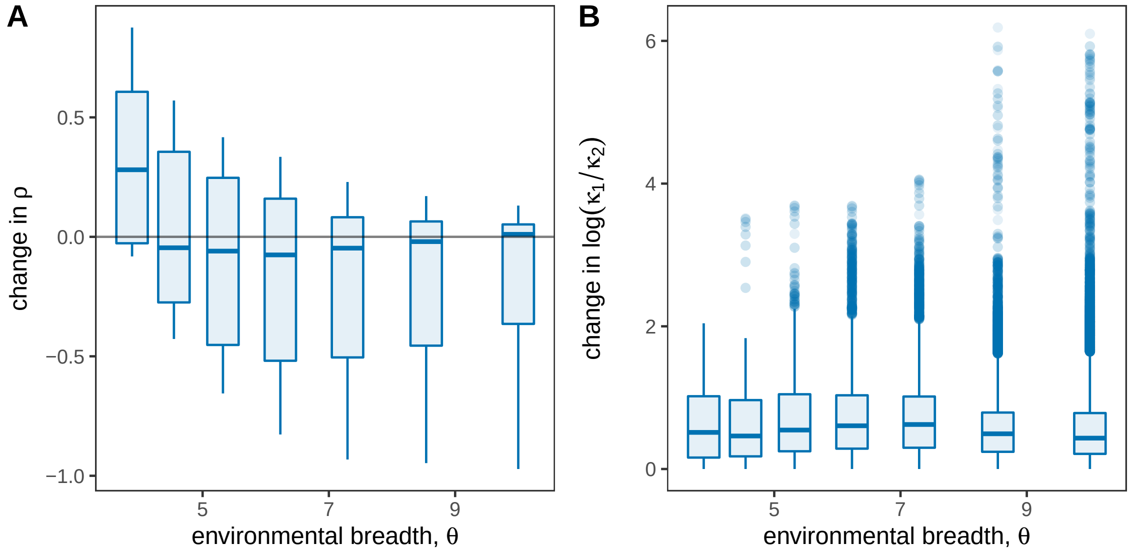

Figure 2: A. The breadth of the resource environment determines how tightly species will pack after trait evolution in response to competition. The change in niche overlap between species indicates whether species are converging (positive change) or diverging (negative change) in resource use. B. Change in log competitive differences indicates whether species are increasing or decreasing in their relative competitive effects. Results are shown for a fixed competition width of $\omega = 3$; variation in the data comes from different initial conditions μ_i and different K_1 values. Interpretation of the box plots: median (horizontal lines), boxes (25% to 75% quartiles), whiskers (ranges), and points (outliers, defined as data falling farther outside the box than 1.5 times the interquartile range).

renditions of graphs such as Fig. 1E, after eliminating the time axis. Second, it shows that the final outcomes are independent of initial conditions; and third, that broader environments or smaller competition widths lead to reduced niche overlap and a higher propensity for species to get rescued evolutionarily when starting out from a state that does not permit coexistence. At the expense of a more detailed exploration of the parameter space, Fig. 5 therefore summarizes our main results.

Discussion

Recent work in coexistence theory has noted that a complete picture of competition should consider evolutionary changes in both niche overlap and competitive differences[13,24,39]. Moreover, it is often assumed that evolution is a mechanism that will facilitate the maintenance of diverse species assemblages, but there is scant evidence for this. Not only are there few unequivocal examples of ecological character displacement[27,40], there are also no explicit theoretical models that predict how changes in niche overlap and changes in competitive differences jointly mediate the eco-evolutionary feedbacks involved in determining coexistence outcomes. We analyzed a model that demonstrates how selection on trait values results in changes in both niche overlap and competitive differences between species. We found that environmental breadth has a strong influence on evolutionary patterns, which result in more competitive exclusion in narrow environments, and larger changes in niche overlap in broad environments resulting in more coexistence (Fig. 2). Large simultaneous changes in niche overlap and competitive differences tended to be characteristic of unstable, transient dynamics (Fig. 3). In systems where the final outcome is stable coexistence, the final values of niche

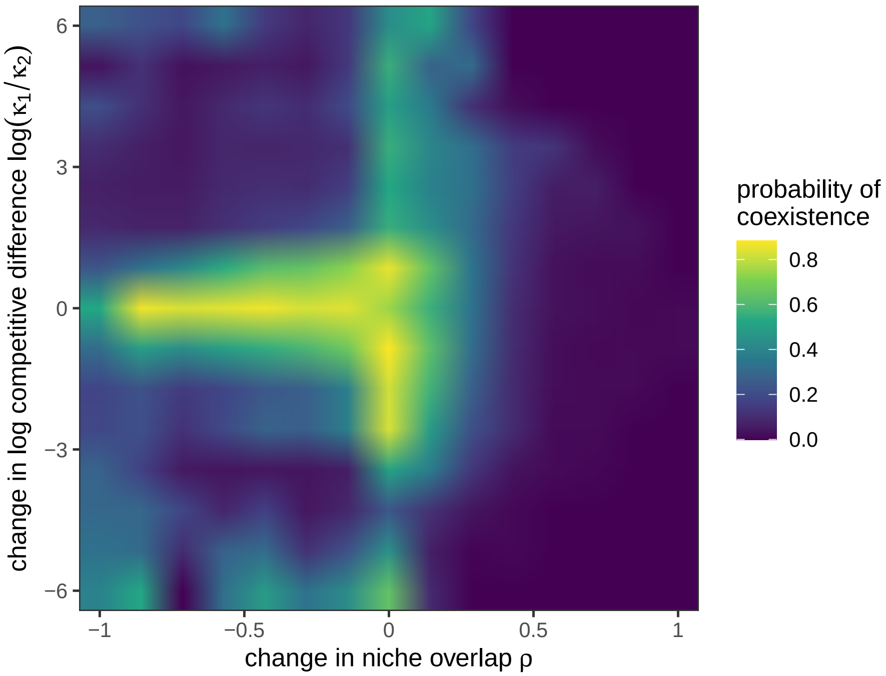

Figure 3: Heat map of the total change in niche overlap (abscissa) and the log competitive differences (ordinate) between the initial and final community states, showing the likelihood that the given observed change led to coexistence (colors, with warmer tones corresponding to higher probabilities). Variation in the data comes from different initial conditions for μ_i, as well as different ω, θ, and K_1 values (Table 1). Overall, coexistence is more likely when the change in competitive difference is small—unless the change in niche overlap is itself small.

overlap and competitive differences were independent of initial conditions. They instead depended only on the parameters, leading to characteristic curves of attraction in coexistence space (Fig. 4).

Our model is similar to ones used in adaptive dynamics to illustrate the influence of frequency-dependent fitness landscapes over eco-evolutionary outcomes[41], with evolutionary branching being one of the main phenomena of interest. Our quantitative genetics-based approach is very similar, with three important differences. First, adaptive dynamics operates with a strict separation of ecological and evolutionary time scales, while our model does not (Fig. 1 illustrates how the dynamics of population densities and trait means unfold on the same time scale). Second, species are assumed monomorphic in adaptive dynamics, whereas in our case they have a finite σ width. Intraspecific variation is thus built into our approach. Third, the characteristic evolutionary branching of adaptive dynamics does not happen here: the underlying multilocus genetics that ensures the normality of the trait distribution also prevents the species from splitting into two daughter species. The impossibility of evolutionary branching is a natural outcome if we assume sexual populations and strictly random mating: this restores the normal shape of the trait distribution even in the face of disruptive selection, preventing speciation[42].

Considering changes in niche overlap and competitive differences separately disentangles the subtlety of how differences in competitive abilities interact with niche overlap in evolutionary models to result in stable coexistence[26]. Importantly, we are only likely to be able to detect how evolution interfaces with these processes to drive stable coexistence[13] because signals of evolution that result in

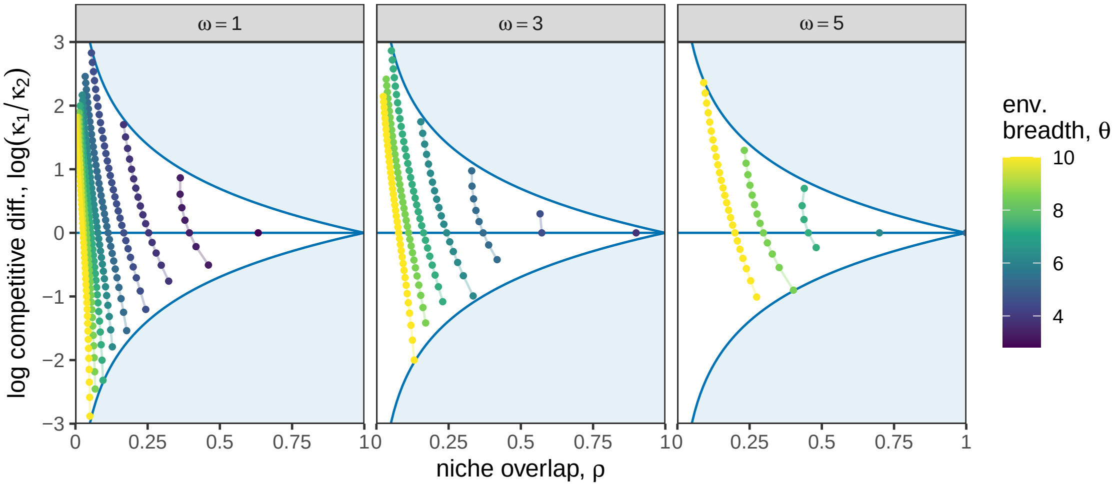

Figure 4: Coexistence at eco-evolutionary equilibria, represented in the space spanned by niche overlap ρ (abscissa) and log competitive difference $\log(\kappa_1/\kappa_2)$ (ordinate). White/blue regions show where coexistence is possible/not possible. Stable combinations of ρ and κ_1/κ_2 depend on the competition width ω (panels), the width of the environment θ (colors), and the growth (dis)advantage K_1 of species 1. They are, however, independent of initial conditions: for given values of ω, θ, and K_1, the same final state is reached regardless of $\mu_1(0)$ and $\mu_2(0)$. Points belonging to the same value of θ are connected by lines; moving upwards along these lines correspond to increasing K_1 while holding other parameters constant. Species are more likely to evolve to coexist in environments with a larger environmental niche breadth (yellow) and species evolve tighter packing in narrower environments (indigo). Competition width similarly constrains how tightly species pack, with larger competition widths resulting in less space for coexisting pairs.

unstable species interactions will likely be erased by extinction[29]. In the classic evolution literature, species equivalence is involved in setting species' carrying capacities, which is well-known to play an important role in driving coexistence (especially in tightly packed environments); this concept is now known as synonymous with the idea of competitive differences[8,9]. Unsurprisingly, our results are consistent with long-held theoretical expectations that there is a limit to how similar species in a community can be, with the degree of similarity being a function of the difference in growth potential or carrying capacities[43,44]. Somewhat counter-intuitively, this limit becomes smaller with increasing constraints on the community from the environment[32,35,36]. This is because species will diverge in traits until selection due to competition balances selection toward the environmental optimum. Our model goes further and allows for the investigation of how competitive differences evolve in response to evolution between species. In fact, we see the role of changing competitive differences to be quite important in narrow environments, allowing for the evolution of competitive exclusion (Fig. 5), which is often ignored because it is difficult to observe.

Since recent work has found that functional traits are often more correlated with competitive differences than niche overlap, the relationships among traits, niche overlap, and competitive differences are currently unclear[45,46]. While multiple experimental[47–50] and phylogenetic[51–53] examples exist that show species' traits diverging in response to competition, this may not represent character divergence since traits may be more associated with competitive differences than niche overlap. Therefore, it is necessary to directly quantify niche overlap and competitive difference to understand the effects of evolution on coexistence.

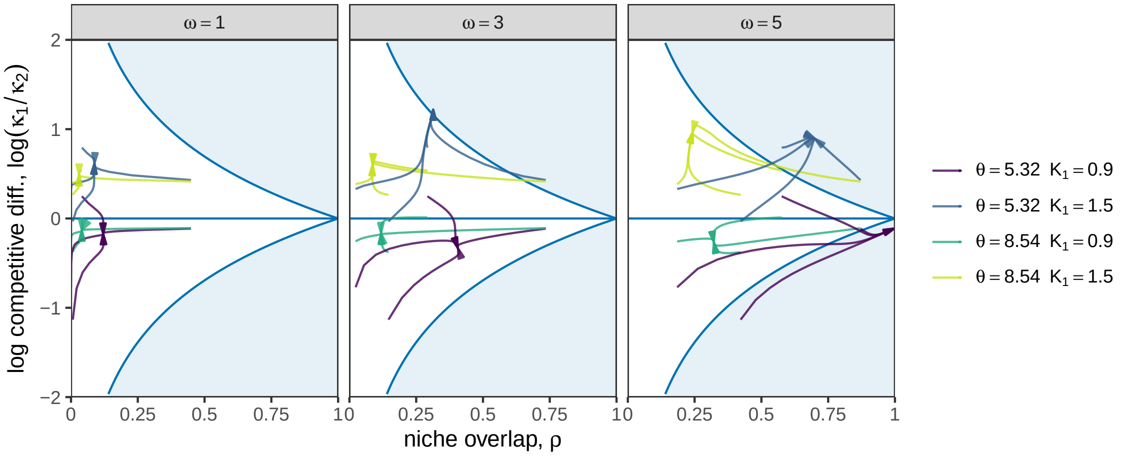

Figure 5: Examples of how niche overlap and competitive differences may change as a result of selection on the trait values of two competitors. White/blue regions show where coexistence is possible/not possible. For each value of the competition width ω (panels), environmental breadth θ, and K_1 (colors), the system is started from four different initial conditions (trajectories). These initial conditions $(\mu_1(0), \mu_2(0))$ were $(1,-3)$, $(1,-1)$, $(4,-3)$, and $(4,-1)$ in each panel. The arrows point to the dynamical endpoint of each trajectory. The final outcomes depend only on the parameters but are always independent of initial conditions. Species are more likely to evolve to coexist in broader environments or with smaller competition widths, and species evolve tighter packing in narrower environments.

Emerging empirical tests of how niche overlap and competitive differences change with evolution have more consistently showed changes in competitive differences than niche overlap. Competing duckweed species, for example, showed no change in niche overlap, but changing competitive differences resulted in a switch in which species was the competitive dominant[29]. In a similar study, competing strains of *Escherichia coli* uniquely showed decreases in niche overlap and idiosyncratic changes in competitive differences[28]. Studies that did not directly calculate niche overlap and fitness differences between species still showed similar patterns to the duckweed study[29]. A study of pitcher plant protists showed that competitive abilities became more equivalent without any changes in niche overlap[54]. Finally, a study of coevolution among a native and invasive grass found increasing competitive effects of the native grass despite no changes in measured traits[14]. While these studies appear inconsistent with past theory, considering the evolution of competitive differences offers some explanation for these results.

Interestingly, the most difficult comparison between model outcomes and empirical systems is the underlying distribution of resources and how the species interact with it. While our model considers a continuous resource gradient, other systems may function differently. For example, because duckweed competes for light, nitrogen and phosphorus, it may be more appropriate to model this system via an eco-evolutionary extension of competition models for essential or at least highly complementary resources[55]. Generalizing the quantities ρ and κ_1/κ_2 to such models is not a straightforward exercise however, because the standard definitions used here and in the literature assume that the underlying ecological model has Lotka–Volterra structure[10,11]. Deriving appropriate niche overlap and competitive difference expressions for models of nonsubstitutable resources ought to be possible, but has not been done as of yet.

In our model, most changes in competitive difference occur under smaller changes of niche overlap; however, large simultaneous changes in both competitive differences and niche overlap are indicative of species that are on a trajectory to competitive exclusion (Fig. 3). Naturally, continued observation of population trajectories would be needed to confirm that evolutionary rescue does not occur. Thus, three[14,29,54] of the four empirical examples above potentially represent evolutionary changes that are degrading pairwise coexistence. Note that our model shows that even when species have minor differences in trait values, substantial differences in competitive ability can arise (Fig. 1).

As with all models, ours is a simplification of reality and should be considered for its conceptual rather than operational value across systems. First, the assumption of a single continuous trait axis corresponding to a continuous resource may not be appropriate for systems with discrete limiting resources. Second, we assume the resource base does not evolve—this may be true for chemostat systems or those with abiotic resources. However, if predators are competing for evolving prey, dynamics may become more complex[56,57], though sometimes their basic character does remain unchanged[37]. Third, we modeled a continuous resource on a single niche axis; the approach presented here is thus relevant only for species interactions that are driven by a single trait (or strongly covarying traits) mapping onto the ability to consume those resources. Higher-dimensional environments with orthogonal traits, however, may have nonadditive effects on evolutionary processes beyond the scope of this model[32,58]. Future work could allow for the evolution of the species-level intrinsic growth potentials K_i (governed by another trait that is more or less independent of the one determining resource utilization), and the evolution of the phenotypic variances σ_i^2. We can, however, make broad hypotheses on how the addition of another trait axis may affect coexistence dynamics. Whilst strongly covarying traits with the same optimum would collapse to one dimension and our results would hold, divergent optima may result in selection trade-offs between the two traits and the emergence of specialists through niche differentiation[7]. Further, strongly orthogonal traits should evolve independently[7,59], and thus may promote coexistence by increasing the possibilities for niche differentiation in ways not possible for a single trait dimension.

Conclusions

Our model of species interacting through shared resources shows that evolution among competitors changes the components of stable coexistence: niche overlap and competitive differences[10]. This work is consistent with classic theory that predicts limiting similarity, but also builds on classic theory to show how competitive abilities of interacting species evolve simultaneously. Interestingly, we find that final competitive differences and niche overlap are independent of initial ones, and depend instead only on model parameters. Therefore, evolutionary stable communities tend to fall on a curve through coexistence space suggesting that competitive abilities and niche overlap will change until species are sufficiently spaced. Ultimately, this model connects the two components of coexistence[8,10] with the dynamics of trait evolution. Selection acts directly on traits, but whether these traits evolve to a state where they can coexist is a question to be answered in terms of coexistence theory. Our results are a step in the direction of linking coexistence to trait patterns[25], and thus they can hopefully contribute to the general program of understanding community structure and organization in terms of a trait-based approach.

Methods

General Framework

We describe the population dynamics and evolutionary changes in a trait value associated with resource acquisition for two competing species, using the framework of previous work[7]. Our goal is to determine how competition between the species and selection on the trait interact to affect the evolutionary stability of coexistence through changes in niche overlap and competitive differences.

The phenotype distribution of species i is given by $p_i(z)$, where z is the phenotype value (Fig. 1A). We assume that all genetic variation influencing an individual's phenotype is additive, that there are no genotype-environment interactions, and that the genetic component of the quantitative trait is determined by a very large number of loci, each having a very small additive effect (the infinitesimal model[60–62]). Under these assumptions, the phenotype distributions $p_i(z)$ are always normal:

$$p_i(z) = \frac{1}{\sigma_i\sqrt{2\pi}} \exp\left(-\frac{(z-\mu_i)^2}{2\sigma_i^2}\right), \tag{1}$$

and the phenotypic variances σ_i^2 do not change in response to selection. This distribution is normalized at any moment of time, so that $p_i(z)$ is the frequency of a trait z in the population.

Both the total population density N_i and mean trait value μ_i of species i change due to population dynamics and quantitative genetic inheritance. The per capita growth rate $r_i(z)$ of species i's phenotype z is derived from MacArthur's consumer-resource model[63,64], and has the following Lotka–Volterra form:

$$r_i(z) = \lambda_i(z) - \sum_{j=1}^{S} N_j \int a(z,z')p_j(z')\,\mathrm{d}z'. \tag{2}$$

See the Supplementary Information for the derivation. The intrinsic growth function $\lambda_i(z)$ has the form

$$\lambda_i(z) = K_i - \frac{z^2}{\theta^2}, \tag{3}$$

which is a quadratic function reaching its maximum growth potential, K_i, at $z = 0$. In the absence of species interactions, $z = 0$ is an optimal trait, and deviating from it leads to reduced intrinsic growth rates; θ measures the width of the growth function. In turn, the competition kernel $a(z,z')$, giving both the intra- and interspecific competitive effect of one unit of abundance of phenotype z' on phenotype z, is a decreasing function of the trait distance between species:

$$a(z,z') = \exp\left(-\frac{(z-z')^2}{\omega^2}\right). \tag{4}$$

Here ω is the competition width, determining the trait distance beyond which competition between two phenotypes is significantly reduced. The forms of both $\lambda_i(z)$ and $a(z,z')$ can also be justified based on the underlying consumer-resource dynamics (Supplementary Information).

With the species- and phenotype-specific per capita growth rates given, the dynamics of population densities and mean trait values are governed by[7]

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i \int r_i(z)p_i(z)\,\mathrm{d}z, \tag{5}$$

$$\frac{\mathrm{d}\mu_i}{\mathrm{d}t} = h_i^2 \int (z-\mu_i)r_i(z)p_i(z)\,\mathrm{d}z, \tag{6}$$

where h_i^2 is the heritability of the trait for species i. Eq. 5 gives the change in population densities by multiplying the density at each trait value by the local growth, and adding them up (integrating) for all possible trait values. Eq. 6 is a continuous-time version of the breeder's equation[59,65], giving the rate of change of species' mean trait values by adding up the local selection pressures at all points along the phenotype axis.

Given the per capita growth rates $r_i(z)$ and the parameters of species' phenotype distributions, Eqs. 5-6 convert their purely ecological interactions into eco-evolutionary dynamics. Traits affect species interactions, which in turn affect the selection pressures on traits. Thus, there is constant feedback between the ecological and evolutionary dynamics. The final outcome is determined by some compromise between being as close to the optimal trait value at $z = 0$ as possible, while being sufficiently different from the competitor species to avoid experiencing too much competition. Sometimes the selection pressure to evolve $\mu_i = 0$ is so strong that species evolve equivalent mean traits despite competition[37]; note, however, that evolving identical mean traits does not imply that the converged species actually coexist. In fact, unless parameters are specially chosen, the expected outcome is that the better competitor will outcompete the other species in the converged state[38].

The standard way of obtaining the niche overlap ρ and competitive differences κ_1/κ_2 is through the parameters of a Lotka–Volterra competition model[11]. The particular definitions are motivated by MacArthur's consumer-resource model[63,64] which is also the basis for our model. While ρ and κ_1/κ_2 can be expressed in full generality (Supplementary Information), here we assume equal phenotypic variances across the species ($\sigma_1^2 = \sigma_2^2 = \sigma^2$), leading to the simpler

$$\rho = \exp\left(-\frac{(\mu_1-\mu_2)^2}{\omega^2+4\sigma^2}\right), \tag{7}$$

$$\frac{\kappa_1}{\kappa_2} = \frac{K_1\theta^2-\mu_1^2-\sigma^2}{K_2\theta^2-\mu_2^2-\sigma^2}. \tag{8}$$

As seen, both quantities are functions of species' trait means μ_i, which are undergoing evolution. Niche overlap and competitive differences therefore also evolve. Moreover, they do not evolve independently, but exhibit an interdependence pattern[20], depending on how μ_1 and μ_2 change with time.

Model analysis

We analyzed the model by numerically integrating Eqs. 5 and 6 for 10^6 units of time, which was more than sufficient to achieve convergence in all cases. In parameterizing the model, we restricted our analyses to species having equal intraspecific standard deviations: $\sigma_1 = \sigma_2 = \sigma$. Since σ, ω, θ, and μ_i are measured in units of the trait z whose evolution we study, we set $\sigma = 1$ without loss of generality. This way, the quantities above are all measured in comparison to σ (see Table 1 for a summary of the meaning and values of all model parameters). When $\theta = 1$, the width of the environment matches the intraspecific trait variation $\sigma = 1$ in both species. This results in high constraints in the ability for species to differentiate in their resource use, and therefore acts as a strong selective force toward the environmental optimum. Therefore, the environmental breadth θ is inversely related to the selection strength due to environmental constraints.

Our numerical experiments varied the three model parameters θ, ω, and K_1, plus the two initial conditions $\mu_1(0)$ and $\mu_2(0)$, in a fully factorial way (Table 1). For each simulation, we recorded the initial and final values of the niche overlap ρ and competitive difference κ_1/κ_2. These are determined from Eqs. 7-8, given the trait means μ_i and parameters ω, θ, and K_i. While here we assume the

Quantity	Value	Description
z		trait value
N_i		species i's density
μ_i		species i's mean phenotype
$p_i(z)$	Eq. (1)	phenotype distribution
$r_i(z)$	Eq. (2)	per capita growth of species i's phenotype z
$\lambda_i(z)$	Eq. (3)	intrinsic growth of species i's phenotype z
$a(z,z')$	Eq. (4)	competitive effect of phenotype z' on z
ρ	Eq. (7)	niche overlap
κ_1/κ_2	Eq. (8)	competitive difference
ω	0.5, 1, 3, or 5	competition width
θ	0.5 to 10, in 20 steps*	environmental breadth
K_1	0.2 to 5, in 51 steps*	species 1's intrinsic growth potential
K_2	1	species 2's intrinsic growth potential
σ_i	1	species i's phenotypic standard deviation
h_i^2	0.1	species i's trait heritability
$N_i(0)$	1	species i's initial density
$\mu_i(0)$	-10 to 10, in 41 steps**	species i's initial trait mean

*Linearly spaced on the natural log scale

**Cases where $\mu_1(0) > \mu_2(0)$ were discarded without loss of generality, since they are equivalent to the scenario where the trait means are swapped and the species relabelled.

Table 1: Table of parameters, their values, and their descriptions.

two species have an equal $\sigma = 1$, this assumption can be freely relaxed in an interactive application we have developed, available at `https://github.com/aipastore/CoexistenceTheory`. This application allows one to adjust all model parameters and obtain plots like Fig. 1. It therefore allows users to explore a broader spectrum of possible parameterizations than we present here.

Data and Code Accessibility The Shiny App and code to replicate our analyses are available at `https://github.com/aipastore/CoexistenceTheory`

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References

[1] Marjorie G. Weber, Catherine E. Wagner, Rebecca J. Best, Luke J. Harmon, and Blake Matthews. Evolution in a community context: on integrating ecological interactions and macroevolution. *Trends in Ecology and Evolution*, 32(4):291–304, 2017.

[2] Casey P. TerHorst, P.C. Zee, K.D. Heath, T.E. Miller, A.I. Pastore, S. Patel, S.J. Schreiber, M.J. Wade, and M.R. Walsh. Evolution in a community context: Trait responses to multiple species interactions. *American Naturalist*, 191(3):368–380, 2018.

[3] Mark Vellend. Conceptual synthesis in community ecology. *The Quarterly review of biology*, 85(2):183–206, 2010.

[4] D. M. Post and E. P. Palkovacs. Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1523):1629–1640, 2009.

[5] Teppo Hiltunen, Nelson G Hairston, Giles Hooker, Laura E Jones, and Stephen P Ellner. A newly discovered role of evolution in previously published consumer-resource dynamics. *Ecology letters*, 17(8):915–23, aug 2014.

[6] David A Vasseur, Priyanga Amarasekare, Volker H W Rudolf, and Jonathan M Levine. Eco-evolutionary dynamics enable coexistence via neighbor-dependent selection, 2011.

[7] György Barabás and Rafael D'Andrea. The effect of intraspecific variation and heritability on community pattern and robustness. *Ecology Letters*, 19(8):977–986, 2016.

[8] Peter Chesson. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31(May):343–366, 2000.

[9] Peter B. Adler, Janneke HilleRislambers, and Jonathan M. Levine. A niche for neutrality. *Ecology Letters*, 10(2):95–104, 2007.

[10] Peter Chesson. Species competition and predation. In *Ecological Systems*, chapter 13, pages 223–256. Springer, New York, 2013.

[11] Peter Chesson. Updates on mechanisms of maintenance of species diversity. *Journal of Ecology*, 106(5):1773–1794, 2018.

[12] György Barabás, Rafael D'Andrea, and Simon Maccracken Stump. Chesson's coexistence theory. *Ecological Monographs*, 2018.

[13] Rachel M. Germain, Jennifer L. Williams, Dolph Schluter, and Amy L. Angert. Moving character displacement beyond characters using contemporary coexistence theory. *Trends in Ecology and Evolution*, 33(2):74–84, 2018.

[14] R. M. Germain, D. Srivastava, and A. L. Angert. Evolution of an inferior competitor increases resistance to biological invasion. *Nature Ecology and Evolution*, 4:419–425, 2020.

[15] Peter B. Adler, Stephen P. Ellner, and Jonathan M. Levine. Coexistence of perennial plants: an embarrassment of niches. *Ecology Letters*, 13:1019–1029, 2010.

[16] Malyon D. Bimler, Daniel B. Stouffer, H. R. Lai, and Margaret M. Mayfield. Accurate predictions of coexistence in natural systems require the inclusion of facilitative interactions and environmental dependency. *Journal of Ecology*, 106(5):1839–1852, 2018.

[17] Claire E. Wainwright, Janneke HilleRisLambers, Hao R. Lai, Xingwen Loy, and Margaret M. Mayfield. Distinct responses of niche and fitness differences to water availability underlie variable coexistence outcomes in semi-arid annual plant communities. *Journal of Ecology*, 107:293–306, 2018.

[18] S P Hubbell. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, 2001.

[19] Mathew A. Leibold and Mark A. McPeek. Coexistence of the niche and neutral perspectives in community ecology, 2006.

[20] C. Song, G. Barabás, and S. Saavedra. On the consequences of the interdependence of stabilizing and equalizing mechanisms. *American Naturalist*, 194:627–639, 2019.

[21] M. L. Taper and T. J. Case. Quantitative genetic models for the coevolution of character displacement. *Ecology*, 66:355–371, 1985.

[22] M. L. Taper and T. J. Case. Models of character displacement and the theoretical robustness of taxon cycles. *Evolution*, 46:317–333, 1992.

[23] Sebastian J. Schreiber, Reinhard Bürger, and Daniel I. Bolnick. The community effects of phenotypic and genetic variation within a predator population. *Ecology*, 92(8):1582–1593, 2011.

[24] Richard A Lankau. Rapid evolutionary change and the coexistence of species. *Annual Review of Ecology, Evolution, and Systematics*, 42(1):335–354, dec 2011.

[25] R. D'Andrea and A. Ostling. Challenges in linking trait patterns to niche differentiation. *Oikos*, 125:1369–1385, 2016.

[26] Peter A. Abrams. The theory of limiting similarity. *Annual Review of Ecology and Systematics*, 14:359–376, 1983.

[27] Yoel E. Stuart and Jonathan B. Losos. Ecological character displacement: Glass half full or half empty? *Trends in Ecology and Evolution*, 28(7):402–408, 2013.

[28] Lin Zhao, Quan Guo Zhang, and Da Yong Zhang. Evolution alters ecological mechanisms of coexistence in experimental microcosms. *Functional Ecology*, 30(8):1440–1446, 2016.

[29] Simon P. Hart, Martin M. Turcotte, and Jonathan M. Levine. Effects of rapid evolution on species coexistence. *Proceedings of the National Academy of Sciences of the United States of America*, 116(6):2112–2117, 2019.

[30] Montogemery Slatkin. Ecological character displacement. *Ecology*, 61(1):163–177, 1980.

[31] John D Rummel and Joan D Roughgarden. A theory of faunal buildup for competition communities. *Evolution*, 39(5):1009–1033, 1985.

[32] Robert MacArthur and Richard Levins. The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, 101(921):377–385, 1967.

[33] Peter A. Abrams. Alternative models of character displacement and niche shift. I. Adaptive shifts in resource use when there is competition for nutritionally nonsubstitutable resources. *Evolution*, 41:651–661, 1987.

[34] Casey P. TerHorst, Thomas E. Miller, and Eric Powell. When can competition for resources lead to ecological equivalence? *Evolutionary Ecology Research*, 12(7):843–854, 2010.

[35] Robert M. May. Stability in multispecies community models. *Mathematical Biosciences*, 12:59–79, 1971.

[36] Robert M. May. Will a large complex system be stable? *Nature*, 238:413–414, 1972.

[37] M. A. McPeek. Limiting similarity? the ecological dynamics of natural selection among resources and consumers caused by both apparent and resource competition. *American Naturalist*, 193:E92–E115, 2019.

[38] L. Pásztor, G. Barabás, and G. Meszéna. Competitive exclusion and evolution: convergence almost never produces ecologically equivalent species. *American Naturalist*, 2020.

[39] Margaret M. Mayfield and Jonathan M. Levine. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, 13:377–385, 2010.

[40] J. H. Connell. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, 35:131–138, 1980.

[41] A. Vukics, J. Asbóth, and G. Meszéna. Speciation in multidimensional evolutionary space. *Physical Review E*, 68:041903, 2003.

[42] U. Dieckmann and M. Doebeli. On the origin of species by sympatric speciation. *Nature*, 400:354–357, 1999.

[43] R. M. May. *Stability and complexity in model ecosystems*. Princeton University Press, Princeton, 1973.

[44] G. Meszéna, M. Gyllenberg, L. Pásztor, and J. A. J. Metz. Competitive exclusion and limiting similarity: a unified theory. theoretical population biology. *Theoretical population biology*, 69:68–87, 2006.

[45] Oscar Godoy, Nathan J B Kraft, and Jonathan M. Levine. Phylogenetic relatedness and the determinants of competitive outcomes. *Ecology Letters*, 17(7):836–844, 2014.

[46] Nathan J.B. Kraft, Oscar Godoy, and Jonathan M. Levine. Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences of the United States of America*, 112:797–802, 2015.

[47] Lisa M Bono, Catharine L Gensel, David W Pfennig, and Christina L Burch. Competition and the origins of novelty: Experimental evolution of niche-width expansion in a virus. *Biology letters*, 9(1):2012.0616, 2013.

[48] Y E Stuart, T S Campbell, P A Hohenlohe, R G Reynolds, L J Revell, and J B Losos. Rapid evolution of a native species following invasion by a congener. *Science*, 346(6208):463–466, 2014.

[49] Debra Zuppinger-Dingley, Bernhard Schmid, Jana S Petermann, Varuna Yadav, Gerlinde B De Deyn, and Dan F B Flynn. Selection for niche differentiation in plant communities increases biodiversity effects. *Nature*, 515(7525):108–111, 2014.

[50] Crystal N. Ellis, Charles C. Traverse, Leslie Mayo-Smith, Sean W. Buskirk, and Vaughn S. Cooper. Character displacement and the evolution of niche complementarity in a model biofilm community. *Evolution*, 69(2):283–293, 2015.

[51] Megan L. Peterson, Kevin J. Rice, and Jason P. Sexton. Niche partitioning between close relatives suggests trade-offs between adaptation to local environments and competition. *Ecology and Evolution*, 3(3):512–522, 2013.

[52] Ingi Agnarsson, Nicholas J Gotelli, Agostini D, and Matjaz Kuntner. Limited role of character displacement in the coexistence of congeneric Anelosimus spiders in a Madagascan montane forest. *Ecography*, 39(8):743–753, 2016.

[53] Cene Fišer, R Luštrik, S Sarbu, JF Flot, and P Trontelj. Morphological evolution of coexisting amphipod species pairs from sulfidic caves suggests competitive interactions and character displacement, but no environmental filtering and convergence. *PloS one*, 10(4):e0123535, 2015.

[54] Thomas E Miller, Emma R Moran, and Casey P TerHorst. Rethinking niche evolution: experiments with natural communities of Protozoa in pitcher plants. *The American Naturalist*, 184(2):277–283, aug 2014.

[55] D. Tilman. *Resource Competition and Community Structure*. Princeton, New York, USA, 1982.

[56] Peter A. Abrams. The evolution of predator-prey interactions: Theory and evidence. *Annual Review of Ecology and Systematics*, 31:79–105, 2000.

[57] Nelson G. Hairston, Stephen P. Ellner, Monica A. Geber, Takehito Yoshida, and Jennifer A. Fox. Rapid evolution and the convergence of ecological and evolutionary time. *Ecology Letters*, 8(10):1114–1127, 2005.

[58] Daniel S. Falster, Åke Brännström, Mark Westoby, and Ulf Dieckmann. Multitrait successional forest dynamics enable diverse competitive coexistence. *Proceedings of the National Academy of Sciences*, 114(13):E2719–E2728, 2017.

[59] Russell Lande and Stevan J. Arnold. The measurement of selection on correlated characters. *Evolution*, 37(6):1210–1226, 1983.

[60] M. G. Bulmer. *The mathematical theory of quantitative genetics*. Clarendon Press, Oxford, UK, 1980.

[61] N. H. Barton, A. M. Etheridge, and A. Véber. The infinitesimal model: Definition, derivation, and implications. *Theoretical Population Biology*, 118:50–73, 2017.

[62] M. Turelli. Commentary: Fisher's infinitesimal model: A story for the ages. *Theoretical Population Biology*, 118:46–49, 2017.

[63] R. H. MacArthur. Species packing and competitive equilibria for many species. *Theoretical Population Biology*, 1:1–11, 1970.

[64] P. Chesson. MacArthur's consumer-resource model. *Theoretical Population Biology*, 37:26–38, 1990.

[65] D. S. Falconer. *Introduction to Quantitative Genetics*. Longman, London, UK, 1981.

The evolution of niche overlap and competitive differences Supplementary Material

Abigail I. Pastore, György Barabás, Malyon D. Bimler,
Margaret M. Mayfield & Thomas E. Miller

General framework

Let there be S competing species. Individuals possess a quantitative trait z affecting their ecological performance. Each species is characterized by a population density N_i and trait distribution $p_i(z)$; $N_i p_i(z)\mathrm{d}z$ is the population density of species i's individuals whose phenotype values fall between z and $z + \mathrm{d}z$.

The phenotype distributions are normal with mean μ_i and variance σ_i^2:

$$p_i(z) = \frac{1}{\sigma_i\sqrt{2\pi}} \exp\left(-\frac{(z-\mu_i)^2}{2\sigma_i^2}\right). \tag{S1}$$

This distribution is normalized, so

$$\int p_i(z)\,\mathrm{d}z = 1 \tag{S2}$$

at any moment of time. If we assume purely additive genetic variance, random mating, and equal sex ratios, then the phenotypic variance σ_i^2 is the sum of the (additive) genetic variance $\sigma_{G,i}^2$ and the environmental variance $\sigma_{E,i}^2$:

$$\sigma_i^2 = \sigma_{G,i}^2 + \sigma_{E,i}^2. \tag{S3}$$

The ratio of genetic to total phenotypic variance is the heritability h_i^2:

$$h_i^2 = \frac{\sigma_{G,i}^2}{\sigma_i^2}. \tag{S4}$$

The equations governing eco-evolutionary dynamics take the per capita growth rate $r_i(z)$ of species i's phenotype z, and express the change in population densities and species trait means via

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i \int r_i(z) p_i(z)\,\mathrm{d}z, \tag{S5}$$

$$\frac{\mathrm{d}\mu_i}{\mathrm{d}t} = h_i^2 \int (z-\mu_i) r_i(z) p_i(z)\,\mathrm{d}z \tag{S6}$$

(Barabás and D'Andrea 2016). This framework is a continuous-time version of classical quantitative genetic recursion models (Roughgarden 1979, Schreiber et al. 2011, Taper and Case 1985, 1992, Vasseur et al. 2011), derived using the infinitesimal model of quantitative genetics (Barton et al. 2017, Bulmer 1980, Turelli 2017) and the breeder's equation (Falconer 1981) in the weak selection limit (Bürger 2011). Given a set of arbitrary species- and phenotype-specific per capita growth rates $r_i(z)$ and the parameters of species' phenotype distributions, Eqs. S5-S6 convert the ecological dynamics prescribed by these growth rates into eco-evolutionary dynamics.

Consumer-resource dynamics

Let us consider a gradient of abiotic resources, with $R(y)$ being the availability of resources with quality y along the gradient. Consumer species feed on these resources. Each individual is characterized by a phenotype, z, which is more or less well suited for consuming resources of various quality y. This suitedness is given by $u(z,y)$, the degree to which an individual of phenotype z can utilize resource y. The per capita growth rate of individuals with phenotype z is proportional to their total resource consumption, and to a species- and phenotype-specific mortality rate $m_i(z)$:

$$r_i(z) = \int u(z,y)R(y)\,\mathrm{d}y - m_i(z) \tag{S7}$$

(MacArthur 1970), where $r_i(z)$ is the per capita growth rate of individuals of species i with phenotype z. Formally, the limits of integration extend from minus to plus infinity, with the understanding that while resources cannot extend forever, the utilization function $u(z,y)$ is confined to a finite region and so the integral's contribution from outside this region becomes negligible.

The abiotic resources are assumed to operate on a fast time scale compared to the population dynamics (MacArthur 1970), and are therefore always in a state of quasi-equilibrium:

$$R(y) = R_0(y) - \sum_{j=1}^{S} \int u(y,z')N_j p_j(z')\,\mathrm{d}z', \tag{S8}$$

where $R_0(y)$ is the saturation concentration of resource y in the absence of consumption, S is the number of consumer species, and $N_j p_j(z')$ is the fraction of species j's individuals that have phenotype z'. The fact that resource depletion is weighted by the same function, $u(z,y)$, as population growth in Eq. S7 expresses the assumption that the benefit an individual gains from resource y is proportional to its consumption of the same resource.

Substituting Eq. S8 into Eq. S7 yields

$$r_i(z) = \int u(z,y)\left(R_0(y) - \sum_{j=1}^{S} \int u(y,z')N_j p_j(z')\,\mathrm{d}z'\right)\mathrm{d}y - m_i. \tag{S9}$$

Rearranging, we get

$$r_i(z) = \underbrace{\left(\int u(z,y)R_0(y)\,\mathrm{d}y - m_i\right)}_{\lambda_i(z)} - \sum_{j=1}^{S} \int \underbrace{\left(\int u(z,y)u(y,z')\,\mathrm{d}y\right)}_{a(z,z')} N_j p_j(z')\,\mathrm{d}z', \tag{S10}$$

which has the form of Lotka–Volterra growth with intrinsic rates $\lambda_i(z)$ and competition kernel $a(z,z')$:

$$r_i(z) = \lambda_i(z) - \sum_{j=1}^{S} N_j \int a(z,z')p_j(z')\,\mathrm{d}z'. \tag{S11}$$

Assigning parameters to this model, the resource utilization curve $u(z,y)$ is a Gaussian function of the difference between consumer phenotype z and resource quality y:

$$u(z,y) = \sqrt{\frac{2}{\omega\sqrt{\pi}}}\exp\left(-2\frac{(z-y)^2}{\omega^2}\right). \tag{S12}$$

Thus, $z = y$ is the trait providing the best match for consuming resource y. The prefactor in front of the exponent was introduced for convenience, because the competition kernel $a(z,z')$ between phenotypes z and z' now reads

$$a(z,z') = \int u(z,y)u(y,z')\,\mathrm{d}y = \frac{2}{\omega\sqrt{\pi}}\int \exp\left(-2\frac{(z-y)^2+(y-z')^2}{\omega^2}\right)\mathrm{d}y = \exp\left(-\frac{(z-z')^2}{\omega^2}\right). \tag{S13}$$

In turn, we assume that each resource saturates at the same level without consumption:

$$R_0(y) = A\sqrt{\frac{1}{\omega\sqrt{\pi}}}, \tag{S14}$$

where A is a constant proportional to the growth rate achieved by a phenotype when resource availability is maximal, and the subsequent factor was again introduced for convenience:

$$\int u(z,y)R_0(y)\,\mathrm{d}y = A\sqrt{\frac{2}{\omega^2\pi}}\int \exp\left(-2\frac{(z-y)^2}{\omega^2}\right)\mathrm{d}y = A. \tag{S15}$$

The mortalities $m_i(z)$ are parameterized as

$$m_i(z) = M_i + z^2/\theta^2, \tag{S16}$$

where M_i is a constant describing a species-specific intrinsic mortality. Mortality is thus minimal for phenotype $z = 0$, and increases quadratically as one moves away from this optimum. Further, this increase is faster for smaller values of the environmental breadth θ. Using Eqs. S15 and S16, we now obtain the intrinsic rate $\lambda_i(z)$:

$$\lambda_i(z) = \int u(z,y)R_0(y)\,\mathrm{d}y - m_i = A - M_i - \frac{z^2}{\theta^2}. \tag{S17}$$

Introducing $K_i = A - M_i$,

$$\lambda_i(z) = K_i - \frac{z^2}{\theta^2}. \tag{S18}$$

An alternative parameterization

The above parameterization assumes a constant resource availability R_0 regardless of resource quality, plus quadratically increasing mortality rates as one moves away from $z = 0$. These assumptions are by no means forced. Here we present a very similar, alternative parameterization where it is resource availability that decreases quadratically. This expresses the natural assumption that resources of extreme quality (e.g., extremely large or small ones) are not available to the same extent as resources with more average quality.

First, we implement a naive version of this parameterization. We choose the resource availabilities to be

$$R_0(y) = \sqrt{\frac{1}{\omega\sqrt{\pi}}}\left(A - \frac{y^2}{\theta^2}\right), \tag{S19}$$

which is quadratically decreasing, and the multiplying factor at the front was chosen for future convenience. (This function is unbiological, because it allows resource availabilities to be negative. This is why our choice is naive. We fix this problem below.) In turn, let the mortalities be

$$m_i = M_i + \frac{\omega^2/4}{\theta^2}, \tag{S20}$$

where M_i is species-specific. Note the lack of trait-dependence in these mortalities. Still assuming Gaussian resource utilization functions (Eq. S12), we can calculate $\lambda_i(z)$ from Eq. S17 by explicitly evaluating the integral:

$$\lambda_i(z) = \int u(z,y) R_0(y)\,\mathrm{d}y - m_i = A - M_i - \frac{z^2}{\theta^2}, \tag{S21}$$

which after defining $K_i = A - M_i$, is identical to the form in Eq. S18 we had before. Thus, the same equations are derived from two different interpretations of the parameters: one where mortalities are trait-dependent and resource availabilities are constant, and one where resource availabilities are trait-dependent but mortalities are (species-specific) constants.

To correct for the unbiological assumption of negative resource availabilities, we can introduce a cutoff which prevents the function from dropping below zero. A modification of Eq. S19 in this way can be written

$$R_0(y) = \sqrt{\frac{1}{\omega\sqrt{\pi}}} \max\left[A - \frac{y^2}{\theta^2}, 0\right], \tag{S22}$$

where $\max(\cdot)$ is the maximum function. Calculating $\lambda_i(z)$ from Eq. S17 again, we get a more complicated expression than before:

$$\begin{aligned}\lambda_i(z) &= \int u(z,y) R_0(y)\,\mathrm{d}y - m_i \\ &= \frac{\omega^2 + 4z^2 - 4A\theta^2}{8\theta^2}\left[\operatorname{erf}\left(\frac{\sqrt{2}\left(z - \sqrt{A}\theta\right)}{\omega}\right) - \operatorname{erf}\left(\frac{\sqrt{2}\left(\sqrt{A}\theta + z\right)}{\omega}\right)\right] \\ &+ \frac{\omega}{\theta^2\sqrt{2\pi}}\exp\left(-\frac{2\left(A\theta^2 + z^2\right)}{\omega^2}\right)\left[z\sinh\left(\frac{4\sqrt{A}\theta z}{\omega^2}\right) + \sqrt{A}\theta\cosh\left(\frac{4\sqrt{A}\theta z}{\omega^2}\right)\right] - m_i.\end{aligned} \tag{S23}$$

While the expression is complicated, it is conceptually the same as before, in Eq. S21; it just accounts for the sharp cutoff of $R_0(y)$ at $\pm\theta$.

Eco-evolutionary consumer-resource dynamics

We now convert the ecological model of Eq. S11 into an eco-evolutionary one, using Eqs. S5-S6:

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i\left[\int \lambda_i(z) p_i(z)\,\mathrm{d}z - \sum_{j=1}^{S} N_j \iint p_i(z) a(z,z') p_j(z')\,\mathrm{d}z'\,\mathrm{d}z\right], \tag{S24}$$

$$\frac{\mathrm{d}\mu_i}{\mathrm{d}t} = h_i^2\left[\int (z-\mu_i)\lambda_i(z) p_i(z)\,\mathrm{d}z - \sum_{j=1}^{S} N_j \iint (z-\mu_i) p_i(z) a(z,z') p_j(z')\,\mathrm{d}z'\,\mathrm{d}z\right]. \tag{S25}$$

Introducing the simplifying notations

$$b_i = \int \lambda_i(z) p_i(z)\,\mathrm{d}z, \tag{S26}$$

$$\alpha_{ij} = \iint p_i(z) a(z,z') p_j(z')\,\mathrm{d}z'\,\mathrm{d}z, \tag{S27}$$

$$g_i = \int (z-\mu_i)\lambda_i(z) p_i(z)\,\mathrm{d}z, \tag{S28}$$

$$\beta_{ij} = \iint (z-\mu_i) p_i(z) a(z,z') p_j(z')\,\mathrm{d}z'\,\mathrm{d}z, \tag{S29}$$

Eqs. S24 and S25 can be written as

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i\left(b_i - \sum_{j=1}^{S} \alpha_{ij}N_j\right), \tag{S30}$$

$$\frac{\mathrm{d}\mu_i}{\mathrm{d}t} = h_i^2\left(g_i - \sum_{j=1}^{S} \beta_{ij}N_j\right). \tag{S31}$$

The newly introduced quantities can be explicitly evaluated. We first calculate b_i and g_i by writing Eq. S18 into Eqs. S26 and S28, and integrating:

$$b_i = \int\left(K_i - \frac{z^2}{\theta^2}\right)p_i(z)\,\mathrm{d}z = K_i - \frac{\mu_i^2+\sigma_i^2}{\theta^2}, \tag{S32}$$

$$g_i = \int(z-\mu_i)\left(K_i - \frac{z^2}{\theta^2}\right)p_i(z)\,\mathrm{d}z = -\frac{2\mu_i\sigma_i^2}{\theta^2}. \tag{S33}$$

To obtain α_{ij} and β_{ij}, we substitute Eq. S13 into Eqs. S27-S29 and integrate:

$$\alpha_{ij} = \iint p_i(z)a(z,z')p_j(z')\,\mathrm{d}z'\,\mathrm{d}z = \sqrt{\frac{\omega^2}{\omega^2+2\sigma_i^2+2\sigma_j^2}}\exp\left(-\frac{(\mu_i-\mu_j)^2}{\omega^2+2\sigma_i^2+2\sigma_j^2}\right), \tag{S34}$$

$$\beta_{ij} = \iint (z-\mu_i)p_i(z)a(z,z')p_j(z')\,\mathrm{d}z'\,\mathrm{d}z = \frac{-2\omega\sigma_i^2(\mu_i-\mu_j)}{(\omega^2+2\sigma_i^2+2\sigma_j^2)^{3/2}}\exp\left(-\frac{(\mu_i-\mu_j)^2}{\omega^2+2\sigma_i^2+2\sigma_j^2}\right). \tag{S35}$$

Niche overlap and fitness ratio

The Lotka–Volterra model reads

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = N_i\left(b_i - \sum_{j=1}^{S} \alpha_{ij}N_j\right), \tag{S36}$$

where N_i is species i's population density, t is time, S the number of species, b_i is i's intrinsic growth rate, and α_{ij} is the competitive effect of species j on i. For $S=2$ competing species, the niche overlap ρ and fitness ratio κ_1/κ_2 are given by

$$\rho = \sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}}, \tag{S37}$$

$$\frac{\kappa_1}{\kappa_2} = \frac{b_1}{b_2}\sqrt{\frac{\alpha_{21}\alpha_{22}}{\alpha_{12}\alpha_{11}}} \tag{S38}$$

(Chesson 2018). Eq. S36 is equivalent to Eq. S30, the equation governing population densities in the eco-evolutionary consumer-resource model. This means we can use the above definitions of ρ and κ_1/κ_2 to calculate niche overlap and the fitness ratio in our model, at any moment of time. Substituting Eqs. S32 and S34 into Eqs. S37-S38, we get

$$\rho = \exp\left(-\frac{(\mu_1-\mu_2)^2}{\omega^2+2\sigma_1^2+2\sigma_2^2}\right)\left(\frac{(\omega^2+4\sigma_1^2)(\omega^2+4\sigma_2^2)}{(\omega^2+2\sigma_1^2+2\sigma_2^2)^2}\right)^{1/4}, \tag{S39}$$

$$\frac{\kappa_1}{\kappa_2} = \frac{K_1\theta^2-\mu_1^2-\sigma_1^2}{K_2\theta^2-\mu_2^2-\sigma_2^2}\left(\frac{\omega^2+4\sigma_1^2}{\omega^2+4\sigma_2^2}\right)^{1/4}. \tag{S40}$$

In the special case when $\alpha_{ij} = \alpha_{ji}$ (symmetric competition coefficients), the fitness ratio simplifies to

$$\frac{\kappa_1}{\kappa_2} = \frac{b_1}{b_2}\sqrt{\frac{\alpha_{22}}{\alpha_{11}}}, \tag{S41}$$

from which the individual κ_i value of species i can be consistently defined:

$$\kappa_i = \frac{b_i}{\sqrt{\alpha_{ii}}}. \tag{S42}$$

In our model, which has symmetric competition coefficients (Eq. S34), we have

$$\kappa_i = \left(\frac{\omega^2 + 4\sigma_i^2}{\omega^2}\right)^{1/4}\left(K_i - \frac{\mu_i^2 + \sigma_i^2}{\theta^2}\right). \tag{S43}$$

If the two intraspecific trait variances are equal ($\sigma_1^2 = \sigma_2^2 = \sigma^2$), then further simplification is available, with Eqs. S39-S40 simplifying to

$$\rho = \exp\left(-\frac{(\mu_1 - \mu_2)^2}{\omega^2 + 4\sigma^2}\right), \tag{S44}$$

$$\frac{\kappa_1}{\kappa_2} = \frac{K_1\theta^2 - \mu_1^2 - \sigma^2}{K_2\theta^2 - \mu_2^2 - \sigma^2}. \tag{S45}$$

References

Barabás, G., D'Andrea, R., 2016. The effect of intraspecific variation and heritability on community pattern and robustness. Ecology Letters 19 (8), 977–986.

Barton, N. H., Etheridge, A. M., Véber, A., 2017. The infinitesimal model: Definition, derivation, and implications. Theoretical Population Biology 118, 50–73.

Bulmer, M. G., 1980. The mathematical theory of quantitative genetics. Clarendon Press, Oxford, UK.

Bürger, R., 2011. Some mathematical models in evolutionary genetics. In: FACC Chalub, Rodrigues, J. F. (Eds.), The Mathematics of Darwins Legacy. Birkhäuser, Basel, Germany, pp. 67–89.

Chesson, P., 2018. Updates on mechanisms of maintenance of species diversity. Journal of Ecology 106 (5), 1773–1794.

Falconer, D. S., 1981. Introduction to Quantitative Genetics. Longman, London, UK.

MacArthur, R. H., 1970. Species packing and competitive equilibria for many species. Theoretical Population Biology 1, 1–11.

Roughgarden, J., 1979. Theory of Population Genetics and Evolutionary Ecology: an Introduction. Macmillan, New York, USA.

Schreiber, S. J., Bürger, R., Bolnick, D. I., 2011. The community effects of phenotypic and genetic variation within a predator population. Ecology 92 (8), 1582–1593.

Taper, M. L., Case, T. J., 1985. Quantitative genetic models for the coevolution of character displacement. Ecology 66, 355–371.

Taper, M. L., Case, T. J., 1992. Models of character displacement and the theoretical robustness of taxon cycles. Evolution 46, 317–333.

Turelli, M., 2017. Commentary: Fisher's infinitesimal model: A story for the ages. Theoretical Population Biology 118, 46–49.

Vasseur, D. A., Amarasekare, P., Rudolf, V. H. W., Levine, J. M., 2011. Eco-evolutionary dynamics enable coexistence via neighbor-dependent selection.

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