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Ecological consequences of intraspecific variation in coevolutionary systems

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Keywords: Coevolution, coexistence, eco-evolutionary dynamics, trait matching, quantitative traits, model, intraspecific variation.

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Abstract

The patterns and outcomes of coevolution are expected to depend on intraspecific trait variation. Various evolutionary factors can change this variation in time. As a result, modeling coevolutionary processes solely in terms of mean trait values may not be sufficient; one may need to study the dynamics of the whole trait distribution. Here, we develop a theoretical framework for studying the effects of evolving intraspecific variation in two-species coevolutionary systems. In particular, we build and study mathematical models of competition, exploiter-victim interactions, and mutualism in which the strength of within- and between-species interactions depends on the difference in continuously varying traits. We use analytical approximations based on the invasion analysis and supplement it with a numerical method. We find that intraspecific variation can be maintained if stabilizing selection is weak in at least one species. When intraspecific variation is maintained, stable coexistence is promoted by small ranges of interspecific interaction in two-species competition and mutualism, and large ranges in exploiter-victim interactions. We show that trait distributions can become multimodal. Our approach and results contribute to the understanding of the ecological consequences of intraspecific variation in coevolutionary systems by exploring its effects on population densities and trait distributions.

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Introduction

Coevolution, that is, reciprocal evolutionary changes in ecologically interacting species, is a major research area where ecology and evolution come together (Futuyma and Slatkin, 1983; Nuismer, 2017; Thompson, 1994). Although coevolution is difficult to demonstrate in natural systems (Janzen, 1980; Nuismer *et al.*, 2010), its importance in nature is well established (Brouat *et al.*, 2001; Clayton *et al.*, 1999; Davies and Brooke, 1988; Soler *et al.*, 2001; Toju and Sota, 2006). Coevolution explains a number of evolutionary phenomena including character displacement in competing species, evolutionary arms race between exploiters and victims, and trait correlation between mutualist partners (Anderson and Johnson, 2008; Benkman *et al.*, 2003; Pfennig and Pfennig, 2009). The geographic mosaic theory of coevolution (GMTC) further highlights the relevance of coevolution by incorporating spatial variation in natural selection and strength of ecological interactions (Thompson, 2005). Through GMTC, coevolution can explain patterns of clinal variation, local adaptation, and stability of mutualisms in the presence of costs (Gavrilets and Michalakis, 2008; Gómez *et al.*, 2009; Gomulkiewicz *et al.*, 2000; Nuismer *et al.*, 2000).

Coevolution is not only a very important process but is also complex due to the intricate relationship between evolutionary and ecological processes. Because of its complexity, there is a strong need for a mathematical theory capturing this relationship. Correspondingly, various population genetics, quantitative genetics, and adaptive dynamics models and methods have been used to study eco-evolutionary dynamics in specific two-species systems: competition (Kremer and Klausmeier, 2017; Leimar *et al.*, 2013; Roughgarden, 1976; Slatkin, 1980; Taper and Case, 1992), mutualism (Akçay, 2016; Ferrière *et al.*, 2002, 2007; Foster and Kokko, 2006), and exploiter-victim interactions (Abrams, 2000; Doebeli, 1997; Fleischer *et al.*, 2018; Gavrilets, 1997; Gavrilets and Michalakis, 2008; Nuismer *et al.*, 2005; Schreiber *et al.*, 2016). Doebeli and Dieckmann (2000); Kopp and Gavrilets (2006); Yoder and Nuismer (2010) modeled all three types of two-species interactions within the same framework. For example, using a weak selection approximation and numerical simulations, Kopp and Gavrilets (2006) studied the dynamics of allele frequencies,

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means, and variances of a trait controlled by several diploid diallelic loci. Yoder and Nuismer (2010) modeled how trait variation in a metapopulation changes due to coevolution using a quantitative genetics approach and an individual-based model. Doebeli and Dieckmann (2000) used the adaptive dynamics approach to study phenotypic diversification due to ecological interactions. They also verified the analytic predictions using individual-based models. These and other similar mathematical models explicated the effects of the eco-evolutionary feedback in coevolution.

Both biological intuition and mathematical models tell us that the time-scales, patterns, and outcomes of coevolution should depend on within-species genetic and phenotypic variation. (Albert *et al.*, 2011; Bolnick *et al.*, 2011; Violle *et al.*, 2012). Genetic and phenotypic variation affects not only evolutionary but also ecological forces and factors including population dynamics, interaction strengths, and community composition (Allen *et al.*, 2018; Austin and Dunlap, 2019; Des Roches *et al.*, 2017; Frankham, 1996; Hausch *et al.*, 2018; Lloyd-Smith *et al.*, 2005; Start, 2019; Start and Gilbert, 2019; Vellend, 2006). These forces can change in time as the level of genetic variation in natural populations is not constant but can change on a much faster ecological time scale (Buckling and Rainey, 2002; Nijhawan *et al.*, 2019; Summers *et al.*, 2003). In particular, man-made events have lead to drastic changes in genetic variation (Jacquemyn *et al.*, 2009; Keller and Largiadèr, 2003; Mitrovski *et al.*, 2008; Smith *et al.*, 1991). Intraspecific variation is also expected to change as a result of coevolutionary processes. Character displacement, the divergence of mean phenotypes of two species in sympatry (Brown and Wilson, 1956; Dayan and Simberloff, 2005; Schulter and McPhail, 1992), is a well-studied example of temporal changes in phenotypes which decreases interspecific competition between the two species. Alternately, interspecific competition can be decreased by phenotypic diversification of one of the species (Abrams and Matsuda, 1994; Dieckmann and Doebeli, 1999; Winkelmann *et al.*, 2014). Overall, the importance of intraspecific variation in eco-evolutionary dynamics is well established. Thus, the description of the coevolutionary processes solely in terms of mean trait values may not be sufficient - one also needs to consider variances and higher-order moments of trait distribution.

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Evolutionary theory has long been concerned with the problem of the maintenance of genetic variation (Barton, 1986; Clarke, 1979; Gavrilets, 2004; Gavrilets and Hastings, 1994b; Lande, 1975; Walsh and Lynch, 2018). There is now a rich variety of models explaining the maintenance of genetic variation by mutation-selection balance, frequency-dependent selection, spatial heterogeneity, *etc*. There is a number of theoretical tools for modeling coevolution of mean trait values. However significantly less efforts have focused on the dynamics of variances. In an early study of the dynamics of genetic variation, Bulmer (1971) used the infinitesimal model which assumes that a quantitative trait is controlled by infinitely many loci with infinitely small effects. In his model, selection builds linkage disequilibrium which changes genetic variation. Using a population genetics model with major loci, Gavrilets and Hastings (1994a, 1995) studied the dynamics of genetic variation under stabilizing selection. Finally, the adaptive dynamics approach has been used to study emergence of genetic polymorphism as a result of evolutionary branching (Dieckmann and Doebeli, 1999; Diekmann, 2004; Geritz *et al.*, 1998; Zu and Wang, 2013). All these methods have to deal with a trade-off between mathematical complexity and biological realism; each of these methods has its own advantages but also shortcomings. For example, Bulmer (1971) and Gavrilets and Hastings (1994a, 1995) ignored population densities, and the assumptions underlying the adaptive dynamics methods prevent one from exploring the changes in genetic variation in detail (Geritz *et al.*, 1998; Waxman and Gavrilets, 2005).

Here we develop an alternative framework for studying the effects of phenotypic variation in coevolution. Our framework is based on earlier single-species theoretical studies capturing both population densities and genetic variation. We apply our approach to three different types of two-species ecological interactions: (i) competition, (ii) exploiter-victim, and (iii) mutualism. For the cases of competition and exploiter-victim interactions, we study the conditions for coexistence, equilibrium trait distributions, and the relationship between the strength of interaction and phenotypic variance. In the case of mutualism, we study the conditions for equilibrium coexistence. Our framework relates stabilizing natural selection, trait-based interactions between coevolving species, phenotypic distributions, and population densities to understand the ecolog-

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ical consequences of intraspecific variation in two-species coevolutionary systems.

Modeling framework

To introduce our approach, we start with the standard logistic model for the dynamics of the population size $N(t)$ in time:

$$\frac{dN(t)}{dt} = rN(t)\left(1 - \frac{N(t)}{K}\right), \tag{1}$$

where r is the population growth rate at low densities and K is the carrying capacity. Here, the population size always approaches K asymptotically. This model implicitly assumes that all individuals are identical (Kot, 2001).

Roughgarden (1972) and Doebeli and Ispolatov (2010) extended this model for the case of heritable intraspecific trait variation. Following their method, we assume that individuals differ with respect to a single continuous trait x. Then the population density $\phi(x,t)$ of trait x at time t changes according to equation

$$\frac{\partial\phi(x,t)}{\partial t} = r\phi(x,t)\left(1 - \frac{\int C(x,y)\phi(y,t)dy}{K(x)}\right). \tag{2}$$

Here r is the growth rate at low densities (assumed to be independent of x), competition kernel $C(x,y)$ measures the effect of competition with individuals with trait y, and function $K(x)$ is the "carrying capacity" for individuals with trait value x. The total population size is given by the integral $N(t) = \int \phi(y,t)dy$. Equation (2) implies that individuals reproduce asexually.

It is standard and mathematically convenient to use Gaussian functions $C(x,y) = \exp[-(x-y)^2/2\sigma_c^2]$ and $K(x) = K_0 \exp(-x^2/2\sigma_s^2)$. The former function implies that competition decreases with increasing the difference in trait values. The latter function assumes that carrying capacity decreases with deviation from the optimum trait value (which is set to zero without the loss of generality). Parameter σ_c of the competition kernel measures a characteristic *range of competitive interference*: with small σ_c, competition mostly happens between very similar organisms. Parameter σ_s of the carrying capacity measures a characteristic *range of optimal trait values*: with small

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σ_s, stabilizing selection is strong and only individuals with trait values close to the optimum can have high carrying capacity.

In this model, depending on parameter values the population evolves to one of two possible equilibrium states (Doebeli and Ispolatov, 2010). Specifically, if stabilizing selection is relatively strong, i.e. the range of optimal trait values is smaller than the range of competitive interference ($\sigma_s \leq \sigma_c$), the population becomes monomorphic with the optimum trait ($\overline{x} = 0$) and the total equilibrium population density $N^* = K_0$. This outcome is similar to that in the standard logistic model. However, if stabilizing selection is relatively weak (i.e., if $\sigma_s > \sigma_c$), then the equilibrium distribution is Gaussian with the mean at the optimum ($\overline{x} = 0$) and a positive variance $v = \sigma_s^2 - \sigma_c^2$ which increases with decreasing σ_c. That is, if competition between dissimilar individuals is weak, variation can be maintained. The corresponding total equilibrium population density is $N^* = \frac{\sigma_s}{\sigma_c} K_0$ which is always larger than the total population density K_0 at the monomorphic state. That is, maintaining genetic variation leads to larger population densities. Figure (1) illustrates these results.

Below we will generalize this approach for three different two-species models which we will study using analytical approximations and numerical solutions (see the Supplementary Information for details on our numerical method).

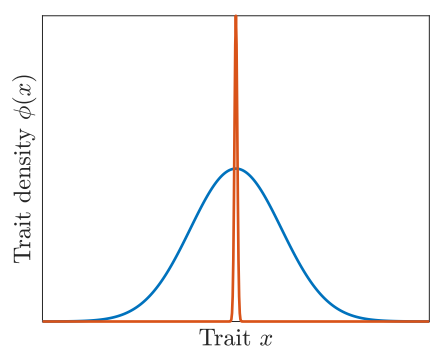

Figure 1: Equilibrium trait distributions in the single-species model. With stronger stabilizing selection ($\sigma_c^2 \geq \sigma_s^2$), the population becomes monomorphic at the optimum trait value $x = 0$ (orange curve). With stronger competition ($\sigma_c^2 < \sigma_s^2$), the equilibrium trait distribution is Gaussian with a positive variance $v = \sigma_s^2 - \sigma_c^2$ (blue curve).

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Two-species competition

The standard Lotka-Volterra competition model describes the dynamics of two competing species with densities N_1 and N_2:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + \alpha_{12} N_2}{K_1}\right), \tag{3a}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{\alpha_{21} N_1 + N_2}{K_2}\right). \tag{3b}$$

Here, for species i ($i = 1, 2$), r_i is the growth rate at low densities, K_i is the carrying capacity in the absence of the competing species, and parameters α_{12} and α_{21} represent the strength of between-species competition relative to that within species. In this model, the necessary and sufficient condition for coexistence is that within-species competition is stronger than between species competition for both species: $\alpha_{12} K_2 / K_1 < 1$ and $\alpha_{21} K_1 / K_2 < 1$. If the condition is satisfied in one species (say $\alpha_{12} K_2 / K_1 < 1$) and not satisfied in the other species (so that $\alpha_{21} K_1 / K_2 \geq 1$) then the first species survives and the second species goes extinct. We then say that the first species *1* is a stronger competitor and species 2 is a weaker competitor. If $\alpha_{12} K_2 / K_1 \geq 1$ and $\alpha_{21} K_1 / K_2 \geq 1$, then one species survives and the other becomes extinct based on initial conditions.

We extend the Lotka-Volterra competition model to individuals differing in continuous traits x in the first species and y in the second species by adapting the single species approach described above:

$$\frac{\partial \phi_1(x,t)}{\partial t} = r_1 \phi_1(x,t) \left(1 - \frac{\int C_{11}(x,z)\phi_1(z,t)dz + \alpha_{12} \int C_{12}(x,z)\phi_2(z,t)dz}{\kappa_1(x)}\right), \tag{4a}$$

$$\frac{\partial \phi_2(y,t)}{\partial t} = r_2 \phi_2(y,t) \left(1 - \frac{\alpha_{21} \int C_{21}(y,z)\phi_1(z,t)dz + \int C_{22}(y,z)\phi_2(z,t)dz}{\kappa_2(y)}\right). \tag{4b}$$

Here ϕ_i, r_i and κ_i are the population density of the trait, the intrinsic growth rate, and carrying capacity for species i, and C_{ij} are the corresponding competition kernels. As above, we assume that carrying capacity, intraspecific competition, and interspecific competition kernel functions are Gaussian: $\kappa_i(z) = K_i \exp(-(z-\theta_i)^2/2\sigma_{si}^2)$, $C_{ii}(x,y) = \exp(-(x-y)^2/2\sigma_{ci}^2)$, and $C_{ij}(x,y) = \exp(-(x-y)^2/2\sigma_{cij}^2)$ respectively. Here θ_i, σ_{ci}, and σ_{si} are the optimum trait value, the range

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of within-species competitive interference, and the range of optimal trait values for species i, σ_{c12} and σ_{c21} measure the ranges of between-species competitive interference, whereas α_{12} and α_{21} measure the strength of interspecific competition due to trait-independent between-species differences.

Results

To find sufficient conditions for coexistence we used mutual invasibility analysis (Armstrong and McGehee, 1980; Geritz *et al.*, 1998). The idea underlying this method is that the two species will coexist only if each of them can invade a resident population of the other species at equilibrium. For example, in the Lotka-Volterra competition model described above, species 2 can invade a resident population of species 1 at equilibrium ($N_1 = K_1$) from low population density ($N_2 \approx 0$) only when $\frac{dN_2}{dt} > 0$. This gives the invasion criterion for species 2: $\alpha_{21}K_1/K_2 < 1$. Invasion criteria are sufficient conditions for coexistence since they guarantee neither species can go extinct.

Assume first that the resident population is monomorphic which is the case if stabilizing selection is sufficiently strong ($\sigma_{sj} \leq \sigma_{cj}$). Then the invasion criterion for the invader species i is identical to that in the standard Lotka-Volterra competition model:

$$\alpha_{ij}\frac{K_j}{K_i} < 1 \tag{5a}$$

(see Appendix A for details). Assume next that the resident population is polymorphic which is the case if $\sigma_{sj} \geq \sigma_{cj}$. From the single-species model, the variance of a polymorphic resident population is $v_j = \sigma_{sj}^2 - \sigma_{cj}^2$ and population size is $N_j^* = K_j\sigma_{sj}/\sigma_{cj}$. In this case, if stabilizing selection in the invader is weak enough ($\sigma_{si}^2 \geq v_j + \sigma_{cij}^2$), it will invade always. Otherwise, invasion happens whenever

$$\alpha_{ij}\frac{N_j^*}{K_i} < \sqrt{1 + \frac{v_j}{\sigma_{cij}^2}}\ \exp\left(\frac{\delta^2}{2(v_j + \sigma_{cij}^2 - \sigma_{si}^2)}\right). \tag{5b}$$

where $\delta = |\theta_i - \theta_j|$ is the difference between the optimum trait values. Note that increasing the difference in the optimum trait values δ, decreasing the strength of stabilizing selection in the invader (i.e., increasing σ_{si}), or decreasing the range of between-species competitive interference

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σ_{cij} always increases the right-hand side of equation (5b) and, thus, makes invasion easier. If $\delta = 0$, increasing the ratio v_j/σ_{cij}^2, i.e. decreasing the range of between-species competitive interference relative to the phenotypic variance in the resident species, makes invasion easier. Figure (2) illustrates our analytical results.

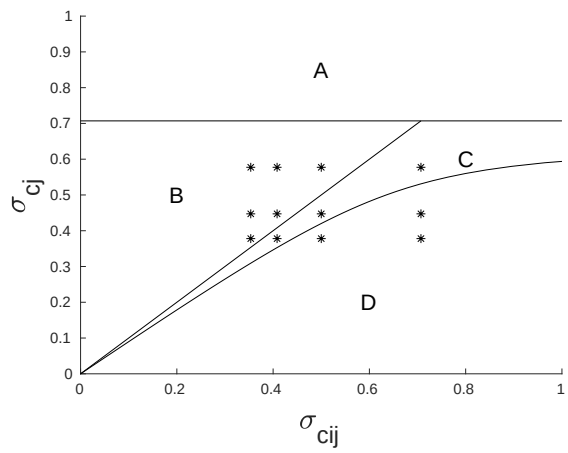

Figure 2: Conditions for invasion as a function of the ranges of between-species σ_{cij} and within-species σ_{cj} competitive interference. In region A, $\sigma_{cj} > \sigma_{sj}$, the resident is monomorphic, and the invasion condition is based on inequality (5a). The line separating regions B and C is based on whether stabilizing selection on the invader is sufficiently weak to guarantee invasion ($\sigma_{si}^2 \geq v_j + \sigma_{cij}^2$ in region B). In region B, invasion is guaranteed for any choice of α_{ij}. Inequality (5b) determines the boundary between region C and D. It is satisfied in region C and not satisfied in region D. The black dots corresponds to the parameter choice for the numerical simulations illustrated in figure (3) below. Other parameters: $\sigma_{sj} = 0.71, \delta = 0, \alpha_{ij} = 0.9$.

The invasion analysis provides only sufficient conditions for coexistence and does not tell anything about the equilibrium distributions of traits. Therefore we supplement it with a numerical study of the model dynamics for different combinations of parameters and initial conditions using an adaptive finite difference method (see Appendix B, also Doebeli (2011)). We describe our results next. In all cases considered, the system evolves to an equilibrium. If only one species survives, the equilibrium trait distribution matches the one predicted by equation (2).

At a coexistence equilibrium with both species polymorphic there are three possibilities: (i) both species are unimodal, (ii) one species is unimodal and another bimodal, or (iii) both species

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are bimodal. These outcomes are illustrated in figure (3). The values of parameters σ_{cij} and σ_{cj} used in these graphs are marked by dots in figure (2). Assuming that species 2 can invade a resident population of species 1 (i.e. that inequality (5b) holds for $i = 2, j = 1$), parameters relevant for species 1's invasion may lie in one of the regions A-C. In region B, species 1 is bimodal if the range of within-species competitive interference in species 2 is large and unimodal otherwise. Species 2 is bimodal only if the range of within-species competitive interference in species 2 is intermediate. In region A and C, both species are unimodal.

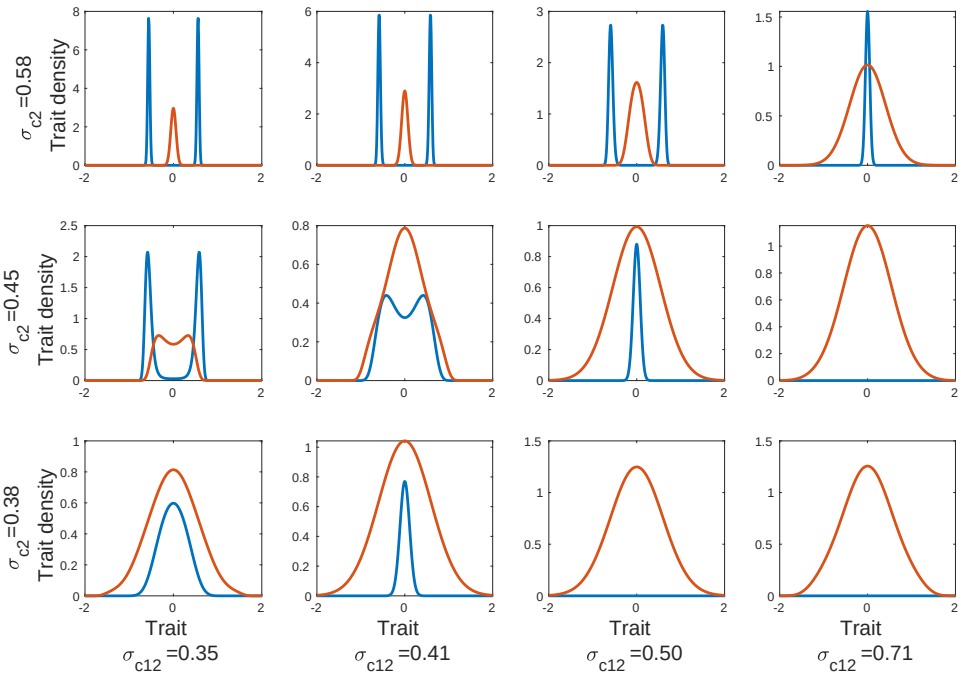

Figure 3: Equilibrium trait distributions of species 1 (blue) and species 2 (orange) from numerical simulations for parameters values σ_{cij} and σ_{cj} marked by dots in figure (2). Identical initial phenotypic distributions $\phi(z) = 0.1e^{-10z^2}$. For all the simulations, $\alpha_{12} = 0.9, \alpha_{21} = 0.8, \sigma_{c1} = 0.71, \sigma_{c21} = 0.71, \sigma_{s1} = 0.71, \sigma_{s2} = 0.71, \delta = 0, r_1 = 1, r_2 = 1, K_1 = 1, K_2 = 1$.

In the single species model, the equilibrium population size and variance decrease with the range of within-species competitive interaction σ_{ci} (see above). To explore the effects of σ_{ci} in the case of two coexisting species, we varied σ_{c2} assuming that parameters for species 1 are in regions B or C, and for species 2 in region A of figure (2). Figure (4) shows the equilibrium variance and

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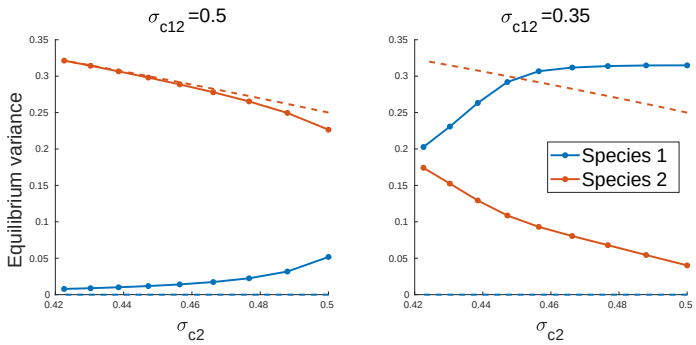
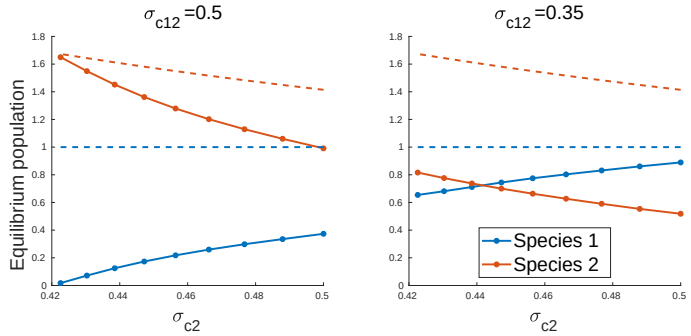
population when the both species coexist (solid lines) and the analytical solution of the single-species model (dotted line). We find that the equilibrium variance of species 2 decreases with σ_{c2} and is always smaller when the other species is present. Equilibrium variances of the two species are inversely related. Similarly, the equilibrium population size of species 2 decreases with σ_{c2} whereas that of species 1 increases with σ_{c2}. Equilibrium population sizes of both the species are lower than their respective single-species equilibrium.



(a)



(b)

Figure 4: Effect of the range of within-species competitive interference σ_{c2} on the equilibrium variance and population sizes of the two species. The dotted lines are based on the equilibrium of the single-species model and the solid lines are based on numerical solutions of the two-species model with identical initial phenotypic distributions $\phi(z) = 0.1\exp(-10z^2)$. The left and right panels correspond to coexistence in region C and B in figure (2), respectively. Other parameters: $\alpha_{12} = 0.9, \alpha_{21} = 0.8, \sigma_{c1} = 0.71, \sigma_{c21} = 0.71, \sigma_{s1} = 0.71, \sigma_{s2} = 0.71, \delta = 0, r_1 = 1, r_2 = 1, K_1 = 1, K_2 = 1$.

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Exploiter-victim interactions

Here we consider exploiter-victim interactions such as between a predator and a prey or a parasite and a host (Clayton *et al.*, 1999; Davies and Brooke, 1988; Gavrilets, 1997; Soler *et al.*, 2001; Toju and Sota, 2006). Writing the population density of the victim species as $N_1(t)$ and that of the exploiter species as $N_2(t)$, and assuming that the exploiter has an obligate relationship with the victim, we start with the model

$$\frac{dN_1}{dt} = \alpha N_1 \left(1 - \frac{N_1}{K_1}\right) - \zeta N_2 N_1, \tag{6a}$$

$$\frac{dN_2}{dt} = \beta N_1 N_2 - \gamma N_2 \left(1 + \frac{N_2}{K_2}\right). \tag{6b}$$

Here, the intrinsic growth rate of the victim is α, the intrinsic death rate of the exploiter is γ, β and ζ are the exploiter birth rate and victim death rate due to exploitation, K_1 and K_2 are characteristic population densities. This is a generalization of the classical Lotka (1920) model to which we have added a quadratic death rate term due to within-species competition. [This change also allows one to avoid structural instability inherent in the Lotka-Volterra model (Kot, 2001). We recover the Lotka-Volterra model in the limit of large K_1 and K_2.]

In this model, both species coexist at an asymptotically stable equilibrium if

$$\frac{\beta K_1}{\gamma} > 1. \tag{7}$$

The numerator of the above ratio is the growth rate of the exploiter when the victim is at carrying capacity (i.e., $N_1 = K_1$) and the denominator is the exploiter's death rate at low densities. The corresponding equilibrium densities are $N_1^* = \gamma K_1 \frac{\alpha + \zeta K_2}{\alpha\gamma + \beta\zeta K_1 K_2}$ and $N_2^* = \alpha K_2 \frac{\beta K_1 - \gamma}{\alpha\gamma + \beta\zeta K_1 K_2}$. If the inequality above is reversed, only the victim species survives. This model does not lead to exploiter-victim cycles.

We extend the above model to individuals differing in continuous traits x in the victim and y in exploiter:

$$\frac{\partial \phi_1(x,t)}{\partial t} = \alpha \phi_1(x,t) \left(1 - \frac{\int C_1(x,z)\phi_1(z,t)dz}{\kappa_1(x)}\right) - \zeta \phi_1(x,t) \int D(x,z)\phi_2(z,t)dz, \tag{8a}$$

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$$\frac{\partial \phi_2(y,t)}{\partial t} = \beta\phi_2(y,t)\int D(y,z)\phi_1(z,t)dz - \gamma\phi_2(y,t)\left(1 + \frac{\int C_2(y,z)\phi_2(z,t)dz}{\kappa_2(y)}\right). \tag{8b}$$

Here $\phi_1(x,t)$ and $\phi_2(y,t)$ are the corresponding densities of the traits, and parameters α, β, γ and ζ have the same meaning as above. Similar to the competition model with continuous traits, we assume that selection and within-species competition kernels are Gaussian: $\kappa_i(z) = K_i \exp(-(z-\theta_i)^2/2\sigma_{si}^2)$ and $C_i(x,y) = \exp(-(x-y)^2/2\sigma_{ci}^2)$, where parameters θ_i, σ_{ci}^2 and σ_{si}^2 have the same meaning as before. Assuming that exploiter-victim interactions are based on trait matching (Gavrilets, 1997; Yoder and Nuismer, 2010), the exploitation kernel can be modelled as a Gaussian function: $D(x,y) = \exp(-(x-y)^2/2\sigma_d^2)$, where σ_d^2 measures the *range of exploitative interactions*. For example, with small σ_d^2 the exploiter can utilize only victims with very similar trait values.

Results

Using the invasibility analysis, for the exploiter to coexist with the victim, it should be able to grow from small densities. Consider first the case where stabilizing selection in the victim is strong ($\sigma_{c1} \geq \sigma_{s1}$). In this case, the victim is monomorphic and the sufficient conditions for coexistence is identical to the coexistence condition from the model with no individual variation (inequality (7)). In contrast, if $\sigma_{c1} < \sigma_{s1}$, the victim is polymorphic with equilibrium variance $v_1 = \sigma_{s1}^2 - \sigma_{c1}^2$ and equilibrium population size $N_1^* = K_1\sigma_{s1}/\sigma_{c1}$ in the victim-only model. In this case, the sufficient condition for a successful invasion of the exploiter (and thus for coexistence) is

$$\frac{\beta N_1^*}{\gamma} > \sqrt{1 + \frac{v_1}{\sigma_d^2}}. \tag{9}$$

In particular, this shows that increasing the range of exploitative interactions σ_d simplifies survival of the exploiter.

We did not observe any non-equilibrium dynamics in numerical simulations. The equilibrium trait distribution of the victim matched the single-species equilibrium when the exploiter did not

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survive. Figure (5) illustrates trait distributions when the species coexist. The distributions are unimodal if the exploiter death rate (γ) is large. If it is small, the victim diversifies around the exploiter to survive. [This situation was dubbed the Burridan's Ass regime in Gavrilets and Waxman (2002).] If stabilizing selection in the victim (σ_{c1}) is weak, the diversification in the victim can be followed by that in the exploiter (top right graph in figure (5)).

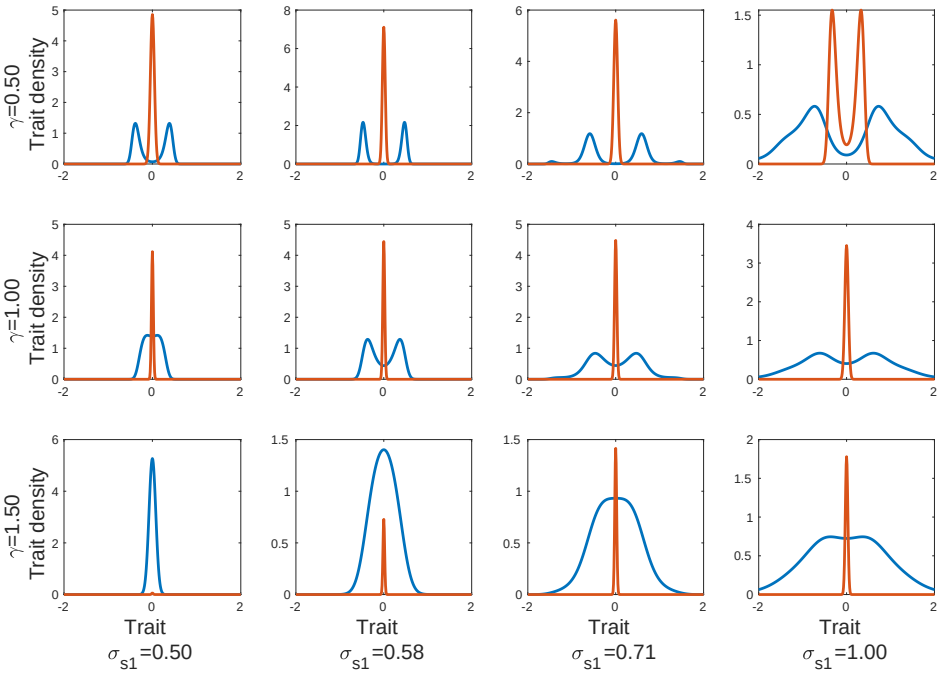

Figure 5: Examples of equilibrium trait distributions of the exploiter (orange) and victim (blue) from numerical simulations with identical initial trait distributions $\phi(z) = 0.1\exp(-10z^2)$. Other parameters: $\alpha = 1, \beta = 1.5, \zeta = 1, \sigma_{c1} = 0.5, \sigma_{c2} = 0.71, \sigma_d = 0.71, \delta = 0, K_1 = 1, K_2 = 1$.

The equilibrium variance in both species increases with the strength of competition among victims (figure (6)). The exploiter's variance is smaller than that in the victim even when the exploiter trait distribution is bimodal ($\sigma_{s1} = 1, \gamma = 0.5$ in figure (5)). Figure (6) also shows that if the exploiter survives, the victim's variance is larger and the population size is smaller than the equilibrium values of the victim-only model.

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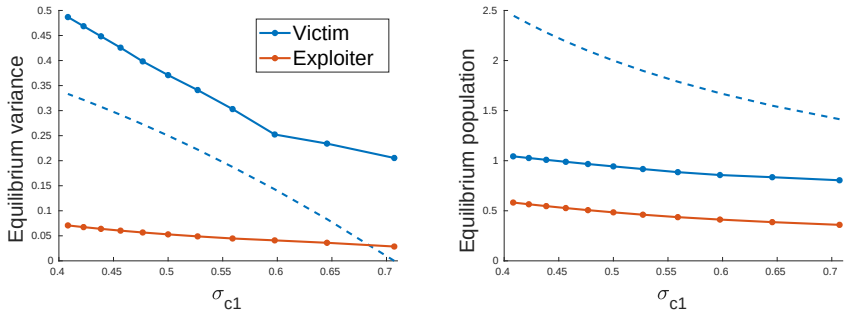

(a) (b)

Figure 6: The equilibrium variances and population sizes of both species when the exploiter survives. The dotted line is the equilibrium variance of the victim in the single-species model and the solid lines are numerical simulations using identical phenotypic distribution for the victim and exploiter ($\phi(z) = 0.1\exp(-10z^2)$). Other parameters: $\alpha = 1, \beta = 2, \zeta = 1, \gamma = 1, \sigma_{c2} = 0.32, \sigma_{s1} = 0.71, \sigma_{s2} = 0.71, \delta = 0, K_1 = 1, K_2 = 1$.

Mutualism

In this section we consider mutualistic interactions where both species benefit from the interaction (Bronstein, 2015). We start with a classical mutualism model (Gause and Witt, 1935; Kostitzin, 1939) describing the dynamics of a pair of mutualistic partners with densities N_1 and N_2:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} + B_1 N_2\right), \tag{10a}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2} + B_2 N_2\right). \tag{10b}$$

Here, the mutualistic benefit for species i is denoted by B_i and the carrying capacity is denoted by K_i. A stable equilibrium exists if and only if $B_1 B_2 K_1 K_2 < 1$. At this equilibrium, the population size of species i is $K_i \left(\frac{1+B_i K_j}{1-B_i B_j K_i K_j}\right)$. If the above inequality does not hold, both species grow to infinite sizes. This unbounded growth is sometimes referred to as the "orgy of beneficial mutualism" (May, 1981).

Allowing for individual differences in continuous traits x in the first species and y in the second species, the corresponding dynamics of the mutualistic system are described by equations

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$$\frac{\partial \phi_1(x,t)}{\partial t} = \phi_1(x,t)\left(r_1 - \frac{\int C_1(x,z)\phi_1(z,t)dz}{\kappa_1(x)} + B_1 \int M_1(x,z)\phi_2(z,t)dz\right), \tag{11a}$$

$$\frac{\partial \phi_2(y,t)}{\partial t} = \phi_2(y,t)\left(r_2 - \frac{\int C_2(y,z)\phi_2(z,t)dz}{\kappa_2(y)} + B_2 \int M_2(y,z)\phi_1(z,t)dz\right). \tag{11b}$$

Here ϕ_i, r_i, and κ_i represent the population density of the trait, the intrinsic growth rate, carrying capacity for species i, and C_i are the corresponding competition kernels. Similar to the other models, we assume carrying capacity and competition kernel functions are Gaussian: $\kappa_i(z) = K_{i,0}\exp(-(z-\theta_i)^2/2\sigma_{si}^2)$ and $C_i(x,y) = \exp(-(x-y)^2/2\sigma_{ci}^2)$. Assuming that mutualism is based on trait matching (Brouat *et al.*, 2001; Yoder and Nuismer, 2010), the mutualism kernel M_i can be modelled by a Gaussian function: $M_i(x,y) = \exp(-(x-y)^2/2\sigma_{mi}^2)$, where σ_{mi} measures the *range of mutualistic interactions*, *i.e.* range of phenotypes over which an individual receives mutualistic benefits. Parameters B_i represent mutualistic benefits due to other trait independent factors.

Results

Similar to the case of no intraspecific variation, in this model the two species either reach an equilibrium with finite population sizes or grow to infinite populations due a positive feedback of mutualistic benefits. To find the conditions for the population to reach an equilibrium, an approach similar to the invasion analysis does not work. Instead we first find upper bounds for the time series of population sizes of the two species, and then determine conditions for the upper bound to converge. This gives us the necessary conditions for stable coexistence (see Appendix A for details).

Our results are as follows. If stabilizing selection is sufficiently strong ($\sigma_{ci} \geq \sigma_{si}$) in both species, then both species are monomorphic and the necessary condition for an equilibrium is identical to that in the model with no intraspecific variation:

$$B_1 B_2 K_1 K_2 < 1. \tag{12a}$$

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If stabilizing selection is strong in only one of the species (say, 2nd), then the necessary condition for an equilibrium is

$$B_1 B_2 N_1^* K_2 < \sqrt{1 + \frac{v_1}{\sigma_{m2}^2}}. \tag{12b}$$

Here $N_i^* = K_i \sigma_{si} / \sigma_{ci}$ and $v_i = \sigma_{si}^2 - \sigma_{ci}^2$ are the equilibrium population size and variance of the single-species model for species 1. This shows that if stabilizing selection is strong in one of the species, an equilibrium is easier to achieve when the range of mutualistic interactions (σ_{m2}) is small.

Finally, if stabilizing selection is weak in both species, then the necessary condition for an equilibrium is

$$B_1 B_2 N_1^* N_2^* < \sqrt{\left(1 + \frac{v_1}{\sigma_{m2}^2}\right)\left(1 + \frac{v_2}{\sigma_{m1}^2}\right)}. \tag{12c}$$

In contrast to the case of strong stabilizing selection in only one of the species, here an equilibrium is easier to achieve when the range of mutualistic benefits is small in either of the two species. Overall, if variation is maintained (i one of both species), it is less likely that their population growth would be unbounded.

Numerical exploration of the model revealed two types of polymorphic equilibrium trait distributions: (i) a unimodal (figure (7(a))), or (ii) a multimodal (figure (7(b))). In the multimodal case, there is one large peak and two smaller peaks (figure (7(b))) or one large and one small peak. The latter case is observed when δ is large and the former when δ is small. These additional smaller peaks exist because with large range of within-species competition σ_{ci}, mutualistic benefits do not decrease as quickly as competitive costs (decrease in growth rate due to competition) for traits farther away from the mean of the distribution.

We also found that as the range of within-species competition decreases, the equilibrium variance increases (figure 7(a)). Figure (8) show that the equilibrium variance increases with smaller range of within-species competition irrespective of the range of within-species competition in the other species. Also, the equilibrium variance is always smaller than the equilibrium variance of the single-species model. In comparison to the single-species model, the equilibrium populations

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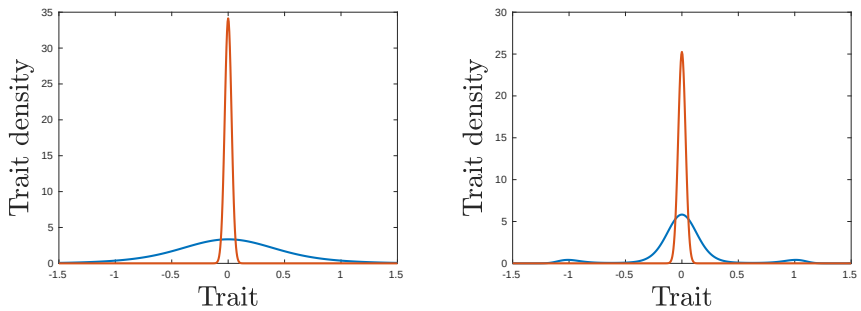
are higher when the mutualist partner is present. The equilibrium population becomes larger as the range of within-species competition in either species decreases.



(a) (b)

Figure 7: Common equilibrium trait distributions of mutualists. (a) $\sigma_{c1} = 0.35$ and (b) $\sigma_{c1} = 0.53$. Species 1 (blue) and mutualist 2 (orange); identical initial trait distributions, other parameters $\phi(z) = 0.1\exp(-10z^2)$ with $r_1 = 1, r_2 = 1, B_1 = 0.5, B_2 = 0.5, \sigma_{c2} = 0.71, \sigma_{s1} = 0.71, \sigma_{s2} = 0.71, \sigma_{m1} = 0.71, \sigma_{m2} = 0.71, \delta = 0, K_1 = 1, K_2 = 1$. For $\delta > 0$, the mean of the distributions will shift but the shape remains the same.

Discussion

Although the dynamic patterns of between-species interactions are expected to strongly depend on intraspecific variation, how exactly ecological and evolutionary processes interact is still largely an open question. Here we approached this question theoretically using three simple two-species models describing competition, exploiter-victim interaction, and mutualism. In our models, individuals differ with respect to a single quantitative character which controls both within- and between-species density-dependent interactions and, simultaneously, is subject to stabilizing natural selection. We analysed conditions for species coexistence, equilibrium population densities as well as the characteristics of trait distributions observed at equilibrium.

For intraspecific variation to be important, it needs to be maintained. Our results show that without mutation, intraspecific variation is lost if stabilizing selection is strong enough, specifically, if the range of optimal traits values is narrower than the range of within-species

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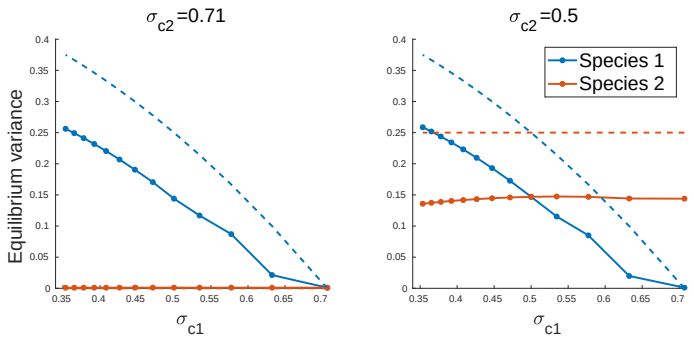
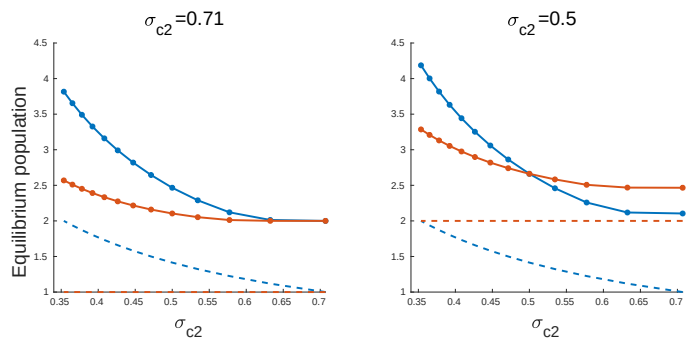


(a)



(b)

Figure 8: Effect of the range of within-species competitive interference on equilibrium variance and population of the mutualists. The dotted lines show the equilibrium of a single-species model and the solid lines are based on the numerical solution of the two species model with initial phenotypic distributions $\phi(z) = 0.1e^{-10z^2}$. Other parameters: $r_1 = 1, r_2 = 1, \sigma_{s1} = 0.71, \sigma_{s2} = 0.71, \sigma_{m1} = 0.71, \sigma_{m2} = 0.71, B_1 = 0.5, B_2 = 0.5, \delta = 0$.

competitive interference ($\sigma_s < \sigma_c$). In this case, the outcomes of population dynamics are the same as predicted by standard ecological models neglecting intraspecific variation. The condition $\sigma_s < \sigma_c$ for the loss of intraspecific variation is the same as the one in single-species models (Doebeli and Ispolatov, 2010; Roughgarden, 1972). Intraspecific variation can be maintained if stabilizing selection is weak enough in at least one species of the pair. In the discussion below, we assume that this is the case.

Consider first between-species competition. In classical ecological models of competition, there are three possible outcomes: the extinction of a weaker competitor and persistence of a stronger competitor, survival of one species or another depending on initial densities, or coex-

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istence. With intraspecific variation maintained, these three possible outcomes are still possible but the conditions for them to be observed depend on parameters characterizing ranges of interference. In particular, small ranges of between-species interference (σ_{cij}) make coexistence a more likely outcome. When the species coexist, their equilibrium trait distribution can be unimodal for both species, bimodal for both species, or unimodal for one species and bimodal for the other. The weaker competitor (based on ecological model) has a bimodal distribution when the range of between-species competition is large, and unimodal otherwise. The strong competitor has a unimodal trait distribution when the range of between-species competition is small or large, and a bimodal distribution for a narrow range of intermediate values.

Second, in classical ecological models of exploiter-victim interactions there are two possible outcomes: the victim species survives and the exploiter is extinct, or coexistence. These outcomes are also possible if within-species variation is maintained. In general, large ranges of exploitative interactions (σ_d) promotes survival of the exploiter. When the species coexist, their equilibrium trait distributions can be both unimodal, both bimodal, or unimodal in one species and bimodal in the other. When the exploiter's death rate (γ) is high, both the exploiter and victim have unimodal trait distributions at the coexistence equilibrium. When the exploiter's death rate is low, the victim diversifies and its equilibrium trait distribution is bimodal. If stabilizing selection in the victim is weak, its trait distribution becomes bimodal which can be followed by the evolution of bimodality in the exploiter. Third, in classical ecological models of mutualism there are two possible outcomes: the two species coexist at finite population sizes, or both species grow indefinitely due to non-diminishing mutualistic benefits. With intraspecific variation maintained, small range of mutualistic interactions (σ_m) promotes coexistence at finite sizes. The equilibrium trait distribution is typically unimodal, but can become multimodal (with two or three peaks) if stabilizing selection is strong enough. In this case, only one of the peaks has a high trait density, while other peak(s) have a much smaller trait density.

In single-species models allowing for heritable intraspecific variation (such as given by equation (2)), the appearance of bimodal trait distributions or evolutionary branching require a non-

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Gaussian competition kernel, e.g. an asymmetric (Kisdi, 1999) or a platykurtic (Doebeli and Ispolatov, 2010). In contrast, our coevolutionary models show that species interactions could lead to bimodal trait distribution even for Gaussian competition and interaction functions. In our competition model, the equilibrium trait variances are smaller than those in the corresponding single-species model. For the exploiter-victim interaction, the equilibrium trait variance of the exploiter is always much smaller than that in the victim. In comparison to the single-species model, the victim always has a higher variance in presence of the exploiter. In the case of mutualism, equilibrium trait variances are smaller for both mutualist species compared to those in the corresponding single-species model. Overall, we find that coevolutionary interactions lead to smaller trait variances except for the victims in exploiter-victim interactions.

Both theoretical and empirical studies have explored the ecological consequences of intraspecific variation (Austin and Dunlap, 2019; Breza *et al.*, 2012; Des Roches *et al.*, 2017; Frankham, 1996; Gavrilets, 1997; Hart *et al.*, 2016; Lichstein *et al.*, 2007; Start, 2019; Start and Gilbert, 2019). However only few earlier theoretical studies allowed for within-species variation to evolve (Kopp and Gavrilets, 2006; Nuismer *et al.*, 2005). An interesting consequence of heritable trait variation is character displacement when between-species competition is reduced due to the divergence of mean phenotypes (Brown and Wilson, 1956; Dayan and Simberloff, 2005; Schulter and McPhail, 1992). Our results suggest competition can also be reduced due to an increase in phenotypic variances, or when the distributions become multimodal.

Our models show that the relationship between the range of optimum traits (which depends on the strength of stabilizing selection) and the ranges of within- and between-species interactions is an important determinant of coevolutionary dynamics. In general, a larger range of optimum traits relative to the range of within-species interactions leads to the maintenance of trait variation which in turn allows for competitors to coexist, exploiters to survive, and mutualists to reach a stable equilibrium. Increased evolutionary flexibility allowed for by intraspecific variation potentially offers a way to reconcile differences in empirical observations, some of which shows that intraspecific variation promotes coexistence (Clark, 2010; Fricke *et al.*, 2019; Jung *et al.*,

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2010), while others suggest that it restricts it (Hausch *et al.*, 2018). The coexistence conditions we have derived extend coexistence theory (Barabás *et al.*, 2018; Chesson, 2000; Ellner *et al.*, 2019) by including the effect of heritable intraspecific variation, stabilizing selection, and trait-dependent competition. Our models also demonstrate that with heritable intraspecific variation maintained, the strength of trait-based interactions can change through time.

Cyclical dynamics in exploiter-victim interactions have been of great interest in ecological (Lotka, 1920; Turchin, 2003) and evolutionary (Gavrilets, 1997; Kopp and Gavrilets, 2006; Nuismer and Doebeli, 2004; Nuismer *et al.*, 2005) models. However cycling was not possible in our basic model (equations (6)) and we did not observe it in our extension of that model for the case of within-species variation. We note that Nuismer *et al.* (2005) investigated a range of evolutionary models of victim-exploiter type and concluded that cycling happens only under certain conditions.

Our results show that exploiter-victim interactions and competition can lead to bimodal trait distributions. Such distributions can emerge via the process of evolutionary branching (Geritz *et al.*, 1998) and can potentially lead to speciation. Doebeli and Dieckmann (2000) studied coevolutionary interaction between an exploiter and a victim using adaptive dynamics, and found that a large range of exploitative interaction and weak stabilizing selection in the victim can lead to evolutionary branching in exploiters. We find similar relationships between the range of exploitative interaction, the strength of stabilizing selection in the victim, and bimodality of the exploiter's trait distribution when the exploiter's death rate is high. Yoder and Nuismer (2010) studied phenotypic diversification in a metapopulation. They found that in coevolutionary interactions where fitness of at least one species is reduced when its traits match the other species, phenotypic diversity is higher compared to diversification by spatially variable selection without coevolution. We find that such costly trait matching leads to a higher trait variance in the victim, but can lead to a lower variance for a competitor. This is due to one of the competitor diversifying around the other competitor (*i.e.* bimodal distribution with the modes on either side of the mean trait of the other species), and competing from both directions of the mean trait value of

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the other species (see figure (3), $\sigma_{c2} = 0.58, \sigma_{c12} = 0.35$).

The main limitations to our approach in terms of biological realism are that we ignored mutation and sexual reproduction. Including mutation would make it easier to maintain intraspecific variation at low levels but is not expected to significantly change our results. For analytical convenience, we assumed clonal reproduction in all our models neglecting the homogenizing force of sexual reproduction. Earlier theoretical studies of coevolution find that genetic details can lead to novel dynamics (Kopp and Gavrilets, 2006; Nuismer and Doebeli, 2004; Nuismer *et al.*, 2005). Some of the effects we observed (e.g., bimodal trait distributions) may be an artifact of our simplifying assumptions. Future work should focus on extending these models to sexually reproducing populations. The analytical conditions we have found are only sufficient (but not necessary) in the case of competition and exploiter-victim interaction, and necessary (but not sufficient) in the case of mutualism.

Our work adds to the toolkit of theoretical studies of coevolution a numerical approach (described in the SI) for modeling the dynamics of population densities and phenotypic distributions under different two-species interactions. We have also developed a novel application of the invasion analysis (Armstrong and McGehee, 1980), and derived an approximate analytical condition for existence of a stable coexistence equilibrium for mutualists (Appendix A). Our methods allowed us to obtain analytical results without the common assumption of weak selection in coevolutionary models (Gavrilets, 1997; Nuismer and Doebeli, 2004). Overall, our approach allows us to understand better the role of heritable trait variation in coevolutionary systems, which is the first step towards achieving a better understanding of the implications of heritable trait variation in evolutionary community ecology (McPeek, 2017).

Acknowledgements

We thank E. Derryberry, J. Day, D. Tverskoi, B. Fitzpatrick, and J. Bailey for comments and suggestions. Supported by the Office of Naval Research grant W911NF-17-1-0150, the National

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Institute for Mathematical and Biological Synthesis through NSF Award #EF-0830858, and by the University of Tennessee, Knoxville.

Appendix A: Analytical solution

Competition

Based on mutual invasibility analysis, we can derive conditions for each species to grow from low density in a population of the other species. In the absence of the species 1, species 2 will reach the equilibrium of the one species model (equation (2)). If $\sigma_{s2}^2 > \sigma_{c2}^2$, the trait distribution at the single-species equilibrium will be $\phi_2^*(y) = \frac{\sigma_{s2}}{\sigma_{c2}} \frac{K_2}{\sqrt{2\pi(\sigma_{s2}^2 - \sigma_{c22}^2)}} \exp\left(-\frac{(y-\theta_2)^2}{2(\sigma_{s2}^2 - \sigma_{c2}^2)}\right)$. Else, it would be a delta function at θ_2. Invasion criteria for species 1 in that case turns out to be identical to the population dynamics model (*i.e.*, $\alpha_{12} < K_1/K_2$).

For species i to coexist with species j, atleast individuals of some trait x needs to survive when $\phi_1(x) \approx 0$ and $\phi_2(y) = \phi_1^*(y)$. From equation (4),

$$\phi_1(x)\left(1 - \frac{\alpha_{12}\int \exp\left(-\frac{(x-z)^2}{2\sigma_{c12}^2}\right)\phi_2^*(z)dz}{K_1 e^{-\frac{(x-\theta_1)^2}{2\sigma_{s1}^2}}}\right) > 0$$

$$\Rightarrow f(x) = \alpha_{12}\frac{\sigma_{s2}}{\sigma_{c2}}\frac{\sigma_{c12}}{\sqrt{\sigma_{s2}^2 - \sigma_{c2}^2 + \sigma_{c12}^2}}\frac{K_2}{K_1}\exp\left(\frac{(x-\theta_1)^2}{2\sigma_{s1}^2} - \frac{(x-\theta_2)^2}{2(\sigma_{s2}^2 - \sigma_{c2}^2 + \sigma_{c12}^2)}\right) < 1$$

If $\sigma_{c2}^2 - \sigma_{c12}^2 \geq \sigma_{s2}^2 - \sigma_{s1}^2$ (inequality $\mathcal{A}$), then $\lim_{x\to\pm\infty} f(x) = 0$ and the inequality holds for some x. Else, $\lim_{x\to\pm\infty} f(x) = \infty$ and the condition holds only if $\min f(x) < 1$. This gives the invasion criteria for species 1,

$$\alpha_{12}\frac{\sigma_{s2}}{\sigma_{c2}}\frac{\sigma_{c12}}{\sqrt{\sigma_{s2}^2 - \sigma_{s2}^2 + \sigma_{c12}^2}}\frac{K_2}{K_1}\exp\left(-\frac{(\theta_1-\theta_2)^2}{2((\sigma_{s2}^2 - \sigma_{s1}^2) - (\sigma_{c2}^2 - \sigma_{c12}^2))}\right) < 1 \tag{A1}$$

Since the system is symmetric, a similar analysis yields the invasion criteria for species 2.

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Exploiter-victim

For exploiter to coexist with the victim, the exploiter should be able to grow from low density in a population of victim. In the absence of the exploiter and strong competition among victims ($\sigma_{s1}^2 > \sigma_{c1}^2$), the victim trait distribution will be $\phi_1^*(x) = \frac{\sigma_{s1}}{\sigma_{c1}} \frac{K_1}{\sqrt{2\pi(\sigma_{s1}^2 - \sigma_{c1}^2)}} \exp\left(-\frac{(x-\theta_1)^2}{2(\sigma_{s1}^2 - \sigma_{c1}^2)}\right)$. From equation (8), the condition for coexistence is,

$$\left(\beta \int \exp\left(-\frac{(y-z)^2}{2\sigma_d^2}\right) \phi_1^*(z) dz\right) - \gamma > 0,$$

$$\Rightarrow \frac{\beta K_1 \sigma_{s1} \sigma_d}{\sigma_{c1}\sqrt{\sigma_{s1}^2 - \sigma_{c1}^2 + \sigma_d^2}} \exp\left(-\frac{(y-\delta)^2}{2(\sigma_{s1}^2 - \sigma_{c1}^2 + \sigma_d^2)}\right) > \gamma.$$

This is a Gaussian function. Therefore for some trait y of the exploiter to coexist with the victim, the maximum value of the function should satisfy the condition. This gives the sufficient conditions for coexistence,

$$\frac{\beta K_1 \sigma_{s1} \sigma_d}{\sigma_{c1}\sqrt{\sigma_{s1}^2 - \sigma_{c1}^2 + \sigma_d^2}} > \gamma. \tag{A2}$$

equation (A2) is the sufficient condition for coexistence when intraspecific variation is allowed to change over time, and intraspecific competition in victim is stronger than the stabilizing selection acting on them ($\sigma_{s1}^2 > \sigma_{c1}^2$). If $\sigma_{s1}^2 \leq \sigma_{c1}^2$, then the sufficient condition for coexistence is $\beta > \gamma$ which is identical to the model with no intraspecific variation.

Mutualism

To obtain conditions for the two species to exist at finite population sizes at equilibrium, we find a sequence of trait distributions for species 1 and species 2 which is the upper bound for the dynamics. The equilibrium population will be finite only if the sequence of population sizes obtained from the sequence of trait distributions converges. If $\phi_1(x,0) \approx 0$ and $\phi_2(y,0) \approx 0$, $\phi_1(x,\tau)$ will be smaller than its one species equilibrium trait distribution. Assume $\sigma_{si}^2 > \sigma_{ci}^2$.

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Then, for some small τ_1,

$$\phi_1(x,\tau_1) \leq \frac{r_1 K_1 \sigma_{s1}}{\sigma_{c1}\sqrt{2\pi(\sigma_{s1}^2-\sigma_{c1}^2)}} \exp\left(-\frac{(x-\theta_1)^2}{2(\sigma_{s1}^2-\sigma_{c1}^2)}\right) = f_{1,1}(x).$$

Mutualistic benefit for species 2 at time τ is bounded by

$$\begin{aligned} B_2 \int \exp\left(-\frac{(y-z)^2}{2\sigma_{m2}^2}\right) f_{1,1}(z)dz &= \frac{B_2 r_1 K_1 \sigma_{s1}\sigma_{m2}}{\sigma_{c1}\sqrt{\sigma_{s1}^2-\sigma_{c1}^2+\sigma_{m2}^2}} \exp\left(-\frac{(y-\theta_1)^2}{2(\sigma_{s1}^2-\sigma_{c1}^2+\sigma_{m2}^2)}\right) \\ &\leq \frac{B_2 K_1 \sigma_{s1}\sigma_{m2}}{\sigma_{c1}\sqrt{\sigma_{s1}^2-\sigma_{c1}^2+\sigma_{m2}^2}} r_1 \end{aligned}$$

Therefore for $\tau_i < \tau_{i+1}$,

$$\phi_2(y,\tau_2) \leq \left(r_2 + \frac{B_2 K_1 \sigma_{s1}\sigma_{m2}}{\sigma_{c1}\sqrt{\sigma_{s1}^2-\sigma_{c1}^2+\sigma_{m2}^2}} r_1\right) \frac{K_2 \sigma_{s2}}{\sigma_{c2}\sqrt{2\pi(\sigma_{s2}^2-\sigma_{c2}^2)}} \exp\left(-\frac{(y-\theta_2)^2}{2(\sigma_{s2}^2-\sigma_{c2}^2)}\right) = f_{2,1}(y),$$

$$\begin{aligned} \phi_1(x,\tau_3) \leq \Bigg(r_1 + \frac{B_1 K_2 \sigma_{s2}\sigma_{m2}}{\sigma_{c2}\sqrt{\sigma_{s2}^2-\sigma_{c2}^2+\sigma_{m2}^2}} \left(r_2 + \frac{B_2 K_1 \sigma_{s1}\sigma_{m2}}{\sigma_{c1}\sqrt{\sigma_{s1}^2-\sigma_{c1}^2+\sigma_{m2}^2}} r_1\right)\Bigg) \\ \frac{K_1 \sigma_{s1}}{\sigma_{c1}\sqrt{2\pi(\sigma_{s1}^2-\sigma_{c1}^2)}} \exp\left(-\frac{(x-\theta_1)^2}{2(\sigma_{s1}^2-\sigma_{c1}^2)}\right) = f_{1,2}(x), \end{aligned}$$

$$\begin{aligned} \phi_2(y,\tau_4) \leq \Bigg(r_2 + \frac{B_2 K_1 \sigma_{s1}\sigma_{m2}}{\sigma_{c1}\sqrt{\sigma_{s1}^2-\sigma_{c1}^2+\sigma_{m2}^2}} \Bigg(r_1 + \frac{B_1 K_2 \sigma_{s2}\sigma_{m2}}{\sigma_{c2}\sqrt{\sigma_{s2}^2-\sigma_{c2}^2+\sigma_{m2}^2}} \Bigg(r_2 + \dots \\ \dots \frac{B_2 K_1 \sigma_{s1}\sigma_{m2}}{\sigma_{c1}\sqrt{\sigma_{s1}^2-\sigma_{c1}^2+\sigma_{m2}^2}} r_1\Bigg)\Bigg)\Bigg) \frac{K_2 \sigma_{s2}}{\sigma_{c2}\sqrt{2\pi(\sigma_{s2}^2-\sigma_{c2}^2)}} \exp\left(-\frac{(y-\theta_2)^2}{2(\sigma_{s2}^2-\sigma_{c2}^2)}\right) = f_{2,2}(y), \end{aligned}$$

$$\begin{aligned} \phi_1(x,\tau_5) \leq \Bigg(r_1 + \frac{B_1 K_2 \sigma_{s2}\sigma_{m2}}{\sigma_{c2}\sqrt{\sigma_{s2}^2-\sigma_{c2}^2+\sigma_{m2}^2}} \Bigg(r_2 + \frac{B_2 K_1 \sigma_{s1}\sigma_{m2}}{\sigma_{c1}\sqrt{\sigma_{s1}^2-\sigma_{c1}^2+\sigma_{m2}^2}} \Bigg(r_1 + \dots \\ \dots \frac{B_1 K_2 \sigma_{s2}\sigma_{m2}}{\sigma_{c2}\sqrt{\sigma_{s2}^2-\sigma_{c2}^2+\sigma_{m2}^2}} \left(r_2 + \frac{B_2 K_1 \sigma_{s1}\sigma_{m2}}{\sigma_{c1}\sqrt{\sigma_{s1}^2-\sigma_{c1}^2+\sigma_{m2}^2}} r_1\right)\Bigg)\Bigg)\Bigg) \frac{K_1 \sigma_{s1} \exp\left(-\frac{(x-\theta_1)^2}{2(\sigma_{s1}^2-\sigma_{c1}^2)}\right)}{\sigma_{c1}\sqrt{2\pi(\sigma_{s1}^2-\sigma_{c1}^2)}} \\ = f_{1,3}(x), \end{aligned}$$

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The time series of population sizes of the two species are bounded by the sequences $N_{1,i} = \int f_{1,i}(x)dx$ and $N_{2,i} = \int f_{2,i}(y)dy$ respectively. From the sequence of trait distributions, we can infer that

$$N_{1,1} = \frac{\sigma_{s1}}{\sigma_{c1}} K_1 r_1,$$

$$N_{1,i} = \frac{\sigma_{s1}}{\sigma_{c1}} K_1 \left(r_1 + \frac{B_1 K_2 \sigma_{s2} \sigma_{m2}}{\sigma_{c2}\sqrt{\sigma_{s2}^2 - \sigma_{c2}^2 + \sigma_{m2}^2}} \left(r_2 + \frac{B_2 K_1 \sigma_{s1} \sigma_{m2}}{\sigma_{c1}\sqrt{\sigma_{s1}^2 - \sigma_{c1}^2 + \sigma_{m2}^2}} \frac{\sigma_{c1}}{\sigma_{s1}} \frac{N_{1,i-1}}{K_1} \right) \right), \forall i \geq 2.$$

The equilibrium population size is finite only if these sequences converge. Real-valued sequences converge if and only if they are Cauchy.

$$N_{1,i} - N_{1,i-1} = \frac{\sigma_{s1}}{\sigma_{c1}} K_1 \left(r_1 + \frac{B_1 K_2 \sigma_{s2} \sigma_{m2}}{\sigma_{c2}\sqrt{\sigma_{s2}^2 - \sigma_{c2}^2 + \sigma_{m2}^2}} r_2 + \dots \right.$$
$$\left. \dots \left(\frac{B_1 B_2 K_1 K_2 \sigma_{s1} \sigma_{s2} \sigma_{m1} \sigma_{m2}}{\sigma_{c1}\sigma_{c2}\sqrt{(\sigma_{s1}^2 - \sigma_{c1}^2 + \sigma_{m2}^2)(\sigma_{s2}^2 - \sigma_{c2}^2 + \sigma_{m1}^2)}} - 1 \right) \frac{\sigma_{c1}}{\sigma_{s1}} \frac{N_{1,i-1}}{K_1} \right).$$

Since $N_{1,i}$ is an increasing sequence, for it to be Cauchy,

$$\frac{B_1 B_2 K_1 K_2 \sigma_{s1} \sigma_{s2} \sigma_{m1} \sigma_{m2}}{\sigma_{c1}\sigma_{c2}\sqrt{(\sigma_{s1}^2 - \sigma_{c1}^2 + \sigma_{m2}^2)(\sigma_{s2}^2 - \sigma_{c2}^2 + \sigma_{m1}^2)}} < 1 \tag{A3}$$

The condition for convergence of $N_{2,i}$ is identical. Equation (A3) is a necessary condition for the equilibrium population of the two species to be finite.

Appendix B: Numerical Method

We solved our dynamic equations using a finite difference method (Doebeli, 2011; Kreyszig *et al.*, 2011; Simmons and Krantz, 2007). Specifically, we first truncate the phenotype space to a finite interval $[-\lambda, \lambda]$. λ needs to be chosen such that ϕ and $\frac{\partial \phi}{\partial \tau}$ are small. Second, we partition the truncated phenotype space into intervals of length l. This gives a partition of size $N = 2\lceil \lambda / l \rceil$. We can now discretise the dynamic equations. For example, in the two species competition model (4),

$$\frac{\partial \phi_1(x_i, \tau)}{\partial \tau} \approx r_1 \phi_1(x_i, \tau) \left(1 - \frac{\int C_{11}(x_i, z)\phi_1(z, \tau)dz + \alpha_{12} \int C_{12}(x_i, z)\phi_2(z, \tau)dz}{\kappa_1(x_i)} \right), \tag{A4a}$$

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$$\frac{\partial \phi_2(y_i,\tau)}{\partial \tau} \approx r_2 \phi_2(y_i,\tau)\left(1 - \frac{\alpha_{21}\int C_{21}(y_i,z)\phi_1(z,\tau)dz + \int C_{22}(y_i,z)\phi_2(z,\tau)dz}{\kappa_2(y_i)}\right). \tag{A4b}$$

Here, the integrals are over $[-\lambda,\lambda]$ and $1 \leq i \leq N$. Finally, the integrals can be computed using trapezoidal rule over the same partition and the derivatives can be approximated using the Euler forward method. This leads to the iterative equations:

$$\phi_{1,\tau+\Delta}(x_i) \approx \phi_{1,\tau}(x_i)\Bigg(1 + r_1\Delta - \frac{r_1 l\Delta}{2\kappa_2(x_i)}\sum_{k=1}^{N-1}\Big(C_{11}(x_i,z_k)\phi_{1,\tau}(z_k) + C_{11}(x_i,z_{k+1})\phi_{1,\tau}(z_{k+1}) + \alpha_{12}\Big(C_{12}(x_i,z_k)\phi_{2,\tau}(z_k) + C_{12}(x_i,z_{k+1})\phi_{2,\tau}(z_{k+1})\Big)\Big)\Bigg), \tag{A5a}$$

$$\phi_{2,\tau+\Delta}(y_i) \approx \phi_{2,\tau}(y_i)\Bigg(1 + r_2\Delta - \frac{r_2 l\Delta}{2\kappa_2(y_i)}\sum_{k=1}^{N-1}\Big(\alpha_{21}\Big(C_{21}(y_i,z_k)\phi_{1,\tau}(z_k) + C_{21}(x_i,z_{k+1})\phi_{1,\tau}(z_{k+1})\Big) + C_{22}(y_i,z_k)\phi_{2,\tau}(z_k) + C_{22}(y_i,z_{k+1})\phi_{2,\tau}(z_{k+1})\Big)\Bigg). \tag{A5b}$$

For small Δ and l, these equations converge. Numerical convergence can be made faster by using adaptive time steps. This is achieved by halving the time steps and reiterating one step whenever population densities becomes negative. Time steps can also be occasionally doubled if population densities remains positive over several time steps.

Setting $\alpha_{12} = \alpha_{21} = 0$ reduces the two-species competition model to two independent single-species model (equation (2)). We then confirmed that the equilibrium phenotypic distribution we obtain using the numerical method matches the analytical solution of the single-species model for different parameter choices.

This same method was applied to the exploiter-victim and mutualism models.

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