

Evolution as a Coexistence Mechanism: Does Genetic Architecture Matter?*

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ABSTRACT: Species sharing a prey or a predator species may go extinct due to exploitative or apparent competition. We examine whether evolution of the shared species acts as a coexistence mechanism and to what extent the answer depends on the genetic architecture underlying trait evolution. In our models of exploitative and apparent competition, the shared species evolves its defense or prey use. Evolving species are either haploid or diploid. A single locus pleiotropically determines prey nutritional quality and predator attack rates. When pleiotropy is sufficiently antagonistic (e.g., nutritional prey are harder to capture), eco-evolutionary assembly culminates in one of two stable states supporting only two species. When pleiotropy is weakly antagonistic or synergistic, assembly is intransitive: species-genotype pairs are cyclically displaced by rare invasions of the missing genotypes or species. This intransitivity allows for coexistence if, along its equilibria, the geometric mean of recovery rates exceeds the geometric mean of loss rates of the rare genotypes or species. By affecting these rates, synergistic pleiotropy can mediate coexistence, while antagonistic pleiotropy does not. For diploid populations experiencing weak antagonistic pleiotropy, super-additive allelic contributions to fitness can mitigate coexistence via an eco-evolutionary storage effect. Density dependence and mutations also promote coexistence. These results highlight how the efficacy of evolution as a coexistence mechanism may depend on the underlying genetic architecture.

Keywords: eco-evolutionary feedbacks, ploidy, storage effect, species coexistence, ecological pleiotropy, mutation.

Introduction

Evolution has produced an immense diversity of species on Earth. When these species share resources or natural enemies, diversity decreases when exploitative competition or apparent competition drives some of them extinct (Holt and Lawton 1993; Grover 1997). For species sharing a common prey or resource (exploitative competition), this species loss may be determined by the R^* rule: the species that suppresses the resource to the lower equilibrium density (R^*) excludes the other species (Volterra 1928; Hsu et al. 1977; Tilman 1982; Grover 1997; Kirk 2002; Miller et al. 2005; Wilson et al. 2007). Species sharing a common predator or pathogen may experience apparent competition—an increase of one species' density that leads to an increase in the predator's density and a corresponding decrease in the other prey species' density (Holt 1977; Holt and Lawton 1993; Holt et al. 1994; Bonsall and Hassell 1997; Chanton and Bonsall 2000; Morris et al. 2004). When predators are at sufficiently high densities, the P^* rule predicts that the prey species supporting the higher-equilibrium predator density (P^*) excludes the other prey species (Holt 1977; Holt and Lawton 1993).

Ecologists have identified a diversity of mechanisms that can maintain diversity and prevent apparent or exploitative competition from excluding species (Chesson 2000). Traditionally, these coexistence mechanisms were considered to be of an ecological nature (Chesson 2000), but an increasing number of studies demonstrate that evolutionary changes in traits occur on sufficiently short timescales to influence ecological dynamics (Strauss et al. 2008; Schoener 2011). Several lines of evidence point to the fact that changes in traits may contribute to species coexistence (Lankau and Strauss 2007; Schreiber et al. 2011; Vasseur et al. 2011; Patel and Schreiber 2015). Plasticity in traits can alter species interactions and increase community stability and coexistence (Vos et al. 2004; Miner et al. 2005). Inducible defenses

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in prey species often increase coexistence with predators (Verschoor et al. 2004; van der Stap et al. 2008; Petrušek et al. 2009). For example, competition between rotifer species led to the exclusion of the less competitive rotifer, but when a shared predator was present, inducible defenses in the less competitive rotifer led to coexistence of species at both trophic levels (van der Stap et al. 2008). Similarly, predators who constantly switch strategies to attack the most abundant or the most palatable prey species increase coexistence relative to predators with a fixed behavior (Křivan 2003).

Just as within-generation changes in traits increase stability and coexistence, so do across-generation changes due to evolution (Lankau 2011). The evolution of defensive or predator-avoidance traits in prey can allow species to find enemy-free space (Jeffries and Lawton 1984). Such trait evolution can increase coexistence between predator and prey (Jones et al. 2009; Fischer et al. 2014; Ikegawa et al. 2015) and alter the stability of predator-prey cycles (Yoshida et al. 2003, 2007; Becks et al. 2012). For example, populations of intertidal mollusks with strong predator-avoidance strategies in response to predatory sun stars showed increased coexistence with predators in natural communities, relative to prey populations with weaker avoidance strategies (Escobar and Navarrete 2011). In systems with intraguild predation (Patel and Schreiber 2015; Wang et al. 2016) or apparent competition (Schreiber et al. 2011; Schreiber and Patel 2015), intraspecific variation or evolution of predator traits can also stabilize communities and lead to species coexistence.

However, it is not well understood how different genetic architectures of evolving traits may affect the role that eco-evolutionary feedbacks play in facilitating species coexistence (Yamamichi and Ellner 2016). Most studies to date have focused on the effects of genetic architecture on purely evolutionary dynamics. In particular, components of the genetic architecture of traits, such as species ploidy, patterns of dominance, pleiotropy, and the distribution of mutational effects, are predicted to affect how species evolve (Hansen 2006). For example, diploid species tend to have greater genetic variation by virtue of more mutations but also tend to be less efficient in responding to selection (Otto and Gerstein 2008). In addition, theory suggests that traits influenced by multiple loci or multiple alleles make trait dynamics more prone to cycles or even chaos (Seeger and Antonovics 1988; Kopp and Gavrillets 2006). While the role of genetic architecture on evolutionary dynamics has been explored, the ecological consequences at the community level due to eco-evolutionary feedbacks remain unexplored. Work on predator-prey coevolution suggests that these consequences may be substantial (Doebeli 1997; Yamamichi and Ellner 2016). For example, predator extinction is more likely when there is dominance at a single diploid locus for a prey trait (Yamamichi and Ellner 2016) and when the number of loci that contribute to the predator trait is much greater

than the number of loci contributing to the prey trait (Doebeli 1997).

Here we explore the role of eco-evolutionary feedbacks and genetic architecture on mediating coexistence for species sharing a common prey or predator species. We fuse classical ecological models of exploitative and apparent competition with classical population-genetic models accounting for haploid and diploid genetics, pleiotropy, dominance, and mutation. In these models, pleiotropy occurs ecologically through the simultaneous effects of genes on the attack rate of predators and the nutritional benefit of captured prey. Dominance arises in whether a single copy of an allele is sufficient to defend against a particular predator species or sufficient to effectively attack a particular prey species. We conduct a mathematical analysis that identifies when coexistence of all species and genotypes occurs in the sense of permanence (Hofbauer and Sigmund 1998). We also numerically explore to what extent this coexistence occurs via a Red Queen dynamic, converges to a stable eco-evolutionary state, or is limited by the rate of mutations.

Models and Methods

To explore the roles of ecological and genetic structures on eco-evolutionary coexistence mechanisms, we study four models with two ecological and two genetic structures (fig. 1). The ecological structures correspond to two classical ecolog-

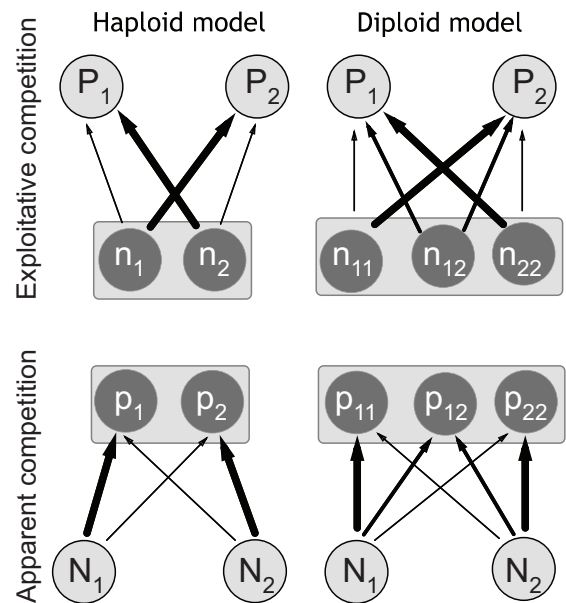


Figure 1: Schematics for the exploitative competition (*top*) and apparent competition (*bottom*) models. Circles correspond to the evolving genotypes (in dark gray) and the nonevolving species (in light gray). Solid black arrows correspond to feeding links, with the width of the arrow representing the magnitude of the corresponding per capita attack rates.

ical modules: exploitative and apparent competition. In the exploitative competition module, two predator species (which may be herbivores, predators, parasites, or pathogens) share a common prey (which may be plants, herbivores, or hosts). In the apparent competition module, two prey species share a common predator but do not interact directly. We use Lotka-Volterra equations to model the ecological dynamics in both modules.

For both ecological modules, the shared species can evolve. Specifically, the shared prey's defense against predation evolves in the exploitative competition module, and the shared predator's resource use evolves in the apparent competition module. We model this evolution with both haploid and diploid genetics. For both genetic structures, we assume that only the interspecific interactions drive selection. This assumption allows us to focus on how the countervailing selection pressures from other species in and of themselves influence the eco-evolutionary dynamics. Selection occurs at a single locus with two alleles, A_1 and A_2 , where allele A_i provides the best adaptive response to species i . For the diploid model, individuals randomly mate, and heterozygote individuals are assumed to have intermediate phenotypes. We also investigate how mutation between alleles influences coexistence.

The Exploitative Competition Module

The exploitative competition model consists of two predatory species with densities P_1 and P_2 and a common evolving prey. For the haploid version of the model, n_i is the density of prey genotype A_i . For the diploid version, n_{ij} is the density of prey genotype A_iA_j , and $n_i = 2n_{ii} + n_{i2}$ is the density of A_i alleles. The total prey density is $N = n_1 + n_2$ for the haploid model and $N = n_{11} + n_{12} + n_{22} = (n_1 + n_2)/2$ for the diploid model. Prey individuals live in one of K habitable sites in the landscape, for example, germination sites, territories, and nesting or breeding sites. All prey genotypes produce offspring at a rate b of which a fraction $1 - N/K$ survive. All prey individuals die at rate d .

The prey genotype pleiotropically affects both the prey's defense against the predators and its nutritional value. Hence, the predator's attack rates and conversion efficiencies—that is, how much reproductive benefit the predator receives from each prey consumed—depend on the prey genotype: a_i^{ℓ} and c_i^{ℓ} , respectively, are the attack rate and conversion efficiency of predator ℓ on haploid prey genotype A_i , and a_{ij}^{ℓ} and c_{ij}^{ℓ} , respectively, are the attack rate and conversion efficiency of predator ℓ on diploid prey genotype A_iA_j . Since conversion efficiencies do not directly affect the prey fitness, selection only directly acts on the defensive trait of the prey. Individuals of predator ℓ die at rate δ_{ℓ} . Under these

assumptions, the haploid dynamics are governed by

$$\begin{aligned}\frac{dn_1}{dt} &= n_1(b(1 - N/K) - d - a_1^1P_1 - a_1^2P_2), \\ \frac{dn_2}{dt} &= n_2(b(1 - N/K) - d - a_2^1P_1 - a_2^2P_2), \\ \frac{dP_1}{dt} &= P_1(c_1^1a_1^1n_1 + c_2^1a_2^1n_2 - \delta_1), \\ \frac{dP_2}{dt} &= P_2(c_1^2a_1^2n_1 + c_2^2a_2^2n_2 - \delta_2).\end{aligned}\tag{1}$$

For the diploid model, we define $x_{ij} = n_{ij}/N$ as the frequency of prey genotype A_iA_j . If individual prey mate randomly and the prey have a one-to-one sex ratio, then the diploid dynamics satisfy

$$\begin{aligned}\frac{dn_{11}}{dt} &= bN((x_{11})^2 + x_{11}x_{12} + (x_{12})^2/4)(1 - N/K) \\ &\quad - dn_{11} - a_{11}^1n_{11}P_1 - a_{11}^2n_{11}P_2, \\ \frac{dn_{22}}{dt} &= bN((x_{22})^2 + x_{22}x_{12} + (x_{12})^2/4)(1 - N/K) \\ &\quad - dn_{22} - a_{22}^1n_{22}P_1 - a_{22}^2n_{22}P_2, \\ \frac{dn_{12}}{dt} &= bN(x_{11}x_{12} + 2x_{11}x_{22} + x_{22}x_{12} \\ &\quad + (x_{12})^2/2)(1 - N/K) - dn_{12} - a_{12}^1n_{12}P_1 \\ &\quad - a_{12}^2n_{12}P_2, \\ \frac{dP_1}{dt} &= P_1(c_{11}^1a_{11}^1n_{11} + c_{12}^1a_{12}^1n_{12} + c_{22}^1a_{22}^1n_{22} - \delta_1), \\ \frac{dP_2}{dt} &= P_2(c_{11}^2a_{11}^2n_{11} + c_{12}^2a_{12}^2n_{12} + c_{22}^2a_{22}^2n_{22} - \delta_2).\end{aligned}\tag{2}$$

We also analyze models accounting for mutations of probability μ for each of the alleles. These modified equations are presented in appendix A (apps. A, B are available online).

Apparent Competition Model

The apparent competition model consists of two prey species with densities N_1 and N_2 and a common evolving predator species. Prey species i exhibits logistic dynamics $dN_i/dt = r_iN_i(1 - N_i/K_i)$ in the absence of the predator, where r_i is the intrinsic growth rate and K_i is the carrying capacity. The predator genotypes affect their attack rates and conversion efficiencies with respect to the prey species: a_i^{ℓ} and c_i^{ℓ} , respectively, are the attack rate and conversion efficiency of the haploid predator i on prey ℓ , and a_{ij}^{ℓ} and c_{ij}^{ℓ} , respectively, are the attack rate and conversion efficiency of the diploid predator genotype A_iA_j on prey ℓ . Since both affect predator fitness, selection directly acts on both the attack rate and conversion efficiency traits. Individuals of predator i die at rate δ_i . Equations for the haploid and diploid models are presented in appendix B.

Methods

Our analyses begin with examining the eco-evolutionary assembly dynamics. That is, we identify which subcommunities of species and genotypes coexist and how invasions by missing genotypes or species change the ecological or genetic structure of the community. In particular, we analyze subsystems consisting of either three species with only one genotype of the shared species or two species with all genotypes of the shared species. For each of these subcommunities, we find that the missing species (or allele) can either invade and displace the other species (or allele) or fail to invade. Proofs of these assertions are in the appendixes.

Using the mathematical theory of permanence (Hutson and Schmitt 1992; Hofbauer and Sigmund 1998; Hofbauer and Schreiber 2010) in conjunction with our eco-evolutionary assembly analysis, we determine under what conditions all species and genotypes coexist in the sense of permanence. Namely, permanence ensures that there is a positive density that all species and genotypes eventually exceed provided all species and genotypes are initially present. This form of coexistence is robust to large rare perturbations as well as frequent small perturbations (Schreiber 2006). Our analysis, whose details are presented in the appendixes, explicitly characterizes permanence for all four models with and without mutations.

To illustrate the main conclusions of our mathematical analysis, we numerically simulate the models with the *deSolve* package in R (R Core Team 2015). The code for these simulations is available at GitHub (<https://github.com/sebastian-schreiber/eco-evolutionary-coexistence>).

Results for the Exploitative Competition Module

Eco-Evolutionary Assembly

Throughout our analysis of the exploitative competition module, we make three assumptions. First, productivity of the system is sufficiently high to ensure that each predator can persist in the presence of each prey genotype. That is, for all $i, j = 1, 2$, $\hat{n} > \hat{n}_i^j$, where $\hat{n} = K(1 - b/d)$ is the prey equilibrium density in the absence of the predators and \hat{n}_i^j is the density of the homozygous A_i prey genotype for which predator j has a zero per capita growth rate. Following the terminology of Hsu et al. (1978), we call \hat{n}_i^j the break-even density of predator j with respect to the homozygous A_i prey genotype. In terms of the parameters, these break-even densities are $\hat{n}_i^j = \delta_j / (c_i^j a_i^j)$ for the haploid model and

$$\hat{n}_i^j = \frac{\delta_j}{c_{ii}^j a_{ii}^j}$$

for the diploid model. Second, we assume that homozygous prey with allele i are defended against predator i . That is,

$a_1^1 < a_2^1$ and $a_2^2 < a_1^2$ for the haploid model and $a_{11}^1 < a_{22}^1$ and $a_{22}^2 < a_{11}^2$ for the diploid model (widths of arrows in fig. 1). Finally, we assume that heterozygous diploid prey exhibit intermediate defense, that is, $a_{11}^1 \leq a_{12}^1 < a_{22}^1$ and $a_{22}^2 \leq a_{12}^2 < a_{11}^2$. Under these assumptions, if only predator i is in the community, then prey allele A_i always goes to fixation, as it provides the best defense against attack by this predator (app. A).

When only one prey allele is present, say allele A_i , the R^* rule applies (Volterra 1928; Hsu et al. 1978; Tilman 1982): the predator with the lower break-even density \hat{n}_i^j with respect to this homozygous prey genotype excludes the other predator (app. A). More explicitly, if predator 1 has the lower break-even density with respect to prey genotype A_i (i.e., $\hat{n}_1^i < \hat{n}_2^i$), then predator 1 excludes predator 2, and if the inequality is reversed, the opposite outcome occurs.

The relative values of the break-even prey densities \hat{n}_i^j determine three types of eco-evolutionary assembly dynamics (fig. 2). First, if one predator has the lower break-even densities with respect to both homozygous prey, then the assembly dynamics culminate in a community consisting of this predator and the associated defended prey genotype (fig. 2A). Second, if for each homozygous prey, the predator with the lower attack rate has the lower break-even density (i.e., $\hat{n}_1^1 > \hat{n}_2^1$ and $\hat{n}_2^2 > \hat{n}_1^2$), then the eco-evolutionary feedbacks result in an eco-evolutionary bistability (figs. 2B, 3A), in which the stable subcommunities correspond to a predator and the associated defended prey genotype. This outcome occurs only if there is sufficient antagonistic pleiotropy in which the more defended prey genotype for a given predator is more nutritional for that predator. We quantify this pleiotropy using the log ratios of predator conversion efficiencies for undefended to defended prey genotypes. That is,

$$\alpha_1 = \log \frac{c_2^1}{c_1^1} \text{ and } \alpha_2 = \log \frac{c_1^2}{c_2^2} \text{ for the haploid model, and}$$

$$\alpha_1 = \log \frac{c_{22}^1}{c_{11}^1} \text{ and } \alpha_2 = \log \frac{c_{11}^2}{c_{22}^2} \text{ for the diploid model.}$$

When $\alpha_i < 0$, there is antagonistic pleiotropy as predator i produces more offspring when consuming the defended prey genotype than the undefended prey genotype. When $\alpha_i > 0$, there is synergistic pleiotropy as predator i produces fewer offspring when consuming the defended prey genotype. Bistability requires that pleiotropy is sufficiently antagonistic with respect to at least one of the predator species.

Finally, if for each homozygous prey genotype the predator with the higher attack rate has the lower break-even density (i.e., $\hat{n}_1^1 < \hat{n}_2^1$ and $\hat{n}_2^2 < \hat{n}_1^2$), then the eco-evolutionary feedbacks result in intransitive assembly dynamics (fig. 2C): predator 2 can invade the predator 1 prey allele A_1 community and displace predator 1, then prey allele A_2 can invade and fixate, then predator 1 can invade and displace predator 2,

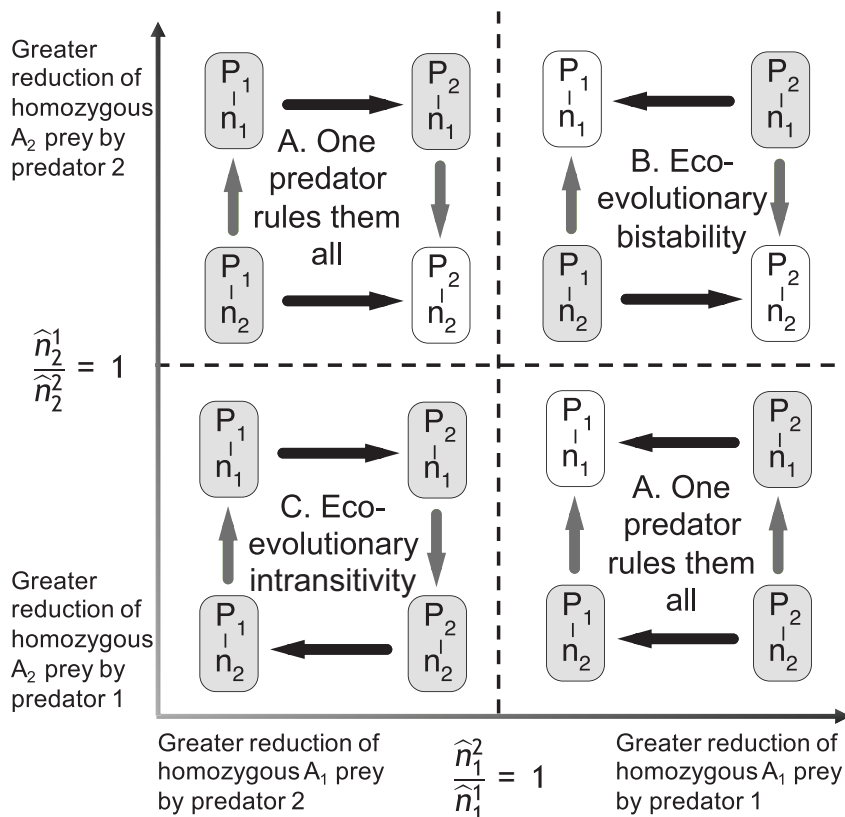


Figure 2: Break-even densities determine eco-evolutionary assembly patterns. The horizontal and vertical axes plot the ratio of break-even densities for the predators with respect to the homozygous prey genotypes. Whether these ratios are greater than 1 or less than 1 determines three types of evolutionary assembly diagrams. In each diagram, rounded boxes correspond to subcommunities, horizontal black arrows correspond to transitions due to predator invasions, and vertical dark gray arrows correspond to transitions due to invasions of prey alleles. Noninvadable communities are white boxes, and invadable communities are light gray boxes. In A, one predator has lower break-even densities with respect to both homozygous prey genotypes. In B, for each homozygous prey genotype, the predator with lower attack rate has the lower break-even density. In C, for each homozygous prey genotype, the predator with higher attack rate has the lower break-even density.

and finally prey allele A_1 can invade and fixate. This outcome occurs for weakly antagonistic to synergistic pleiotropy.

Coexistence

Coexistence of the predators and the prey genotypes, in the sense of permanence, is possible only for the intransitive assembly dynamics. Whether coexistence occurs depends on whether this intransitivity (a cycle between the four subcommunity equilibria) is unstable or stable. When the intransitivity is unstable (fig. 3B), all genotypes and predator species remain bounded away from extinction and may approach an equilibrium (left panel of fig. 3B) or exhibit long-term oscillatory behavior (right panel of fig. 3B). When the intransitivity is stable, the eco-evolutionary dynamics exhibit increasingly extreme oscillatory dynamics as the community cycles between four eco-evolutionary states domi-

nated by one predator species and one prey allele (fig. 3C). From one oscillation to the next, the time spent in each of these states increases, and the frequencies of the rare species and genotypes at each state decrease exponentially fast. Ultimately, for populations of finite size, this leads to the extinction of a predator species and a prey allele. In appendix A, we derive an explicit condition for coexistence for both models. This condition is summarized graphically in figure 4. Before stating the general form of this condition, we consider the special case of a highly productive system, that is, when K is large.

Highly Productive Systems. For highly productive systems, coexistence for the haploid model occurs if and only if the average pleiotropy is synergistic:

$$\frac{\alpha_1 + \alpha_2}{2} > 0. \quad (3)$$

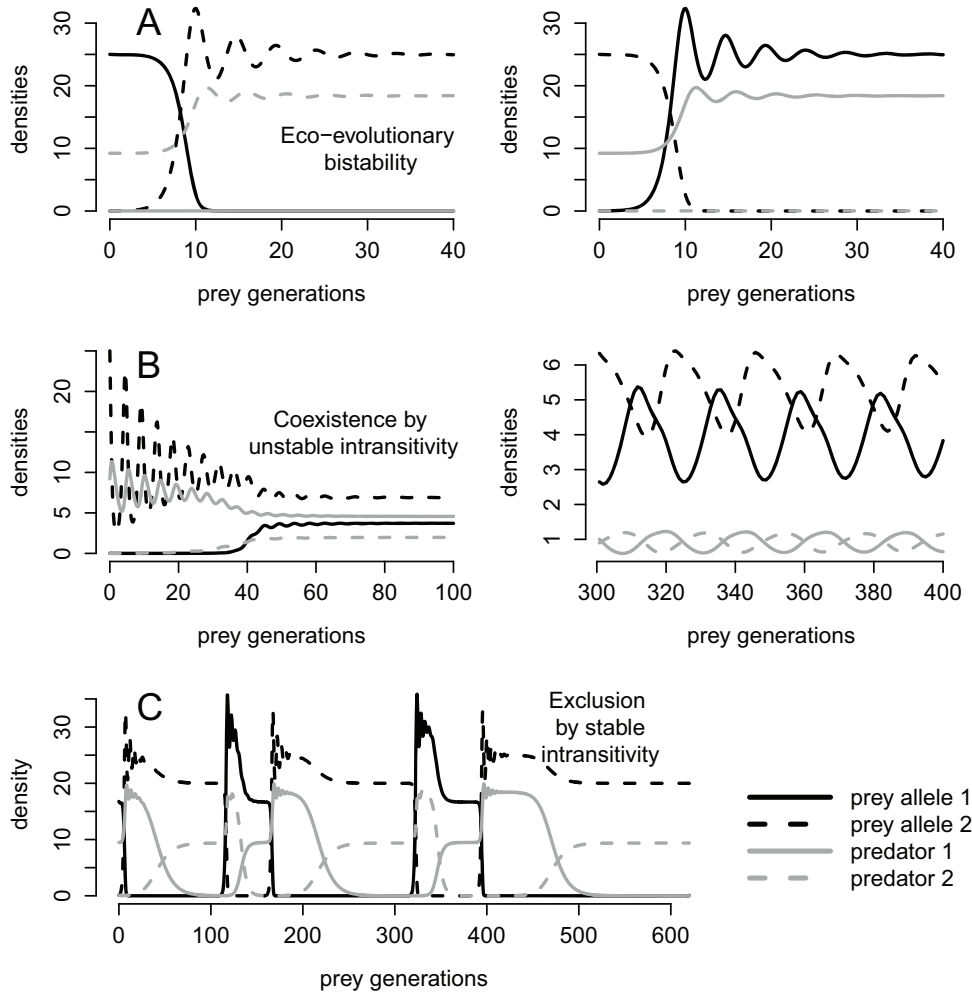


Figure 3: Eco-evolutionary outcomes for the diploid exploitative competition module. Predator densities are in black, while densities of prey alleles are in gray. In A, an eco-evolutionary bistability: different initial conditions lead to different stable equilibria. In B, two dynamics of an unstable intransitivity: equilibrium and oscillatory coexistence on the left and right, respectively. In C, the dynamics of a stable intransitivity: densities of each species and genotype approach 0 in a cyclic fashion.

In other words, if the defended genotypes are less nutritional on average, then all the species and genotypes coexist at a stable equilibrium or nonequilibrium attractor (fig. 3B). Conversely, if the defended genotype is more nutritional on average, then the community is extinction prone: ultimately, one predator is excluded and the prey allele least defended to this predator is lost (fig. 3C). In figure 4, this condition corresponds to the positive half of the pleiotropy axis.

To state the coexistence condition for the diploid model, we need the following metric of the dominance of the defense alleles:

$$\beta_1 = \log \left(\frac{a_{22}^1 - a_{12}^1}{a_{12}^1 - a_{11}^1} \right), \text{ and } \beta_2 = \log \left(\frac{a_{11}^2 - a_{12}^2}{a_{12}^2 - a_{22}^2} \right).$$

If $\beta_i = -\infty$, then the attack rate of predator i on the heterozygote is the same as its attack rate on the undefended genotype ($a_{12}^i = a_{jj}^i$ with $j \neq i$). Hence, in this case, the defensive allele i is recessive: only individuals with both copies of the defensive allele are defended against predator i . Alternatively, if $\beta_i = \infty$, then allele i is dominant: one copy ensures defense against predator i . If $\beta_1 > 0$ and $\beta_2 > 0$, then the more beneficial allele is dominant with respect to defense against each predator (Rose 1982; Curtsinger et al. 1994). In particular, if $\beta_1 = \beta_2 = \infty$, then the alleles are codominant: heterozygotes are fully defended against both predator species. If $\beta_i = 0$, then the alleles contribute additively to defense against predator i , that is, the attack rate a_{12}^i on heterozygotes is at the midpoint $(a_{11}^i + a_{22}^i)/2$ of attack rates of the homozygotes.

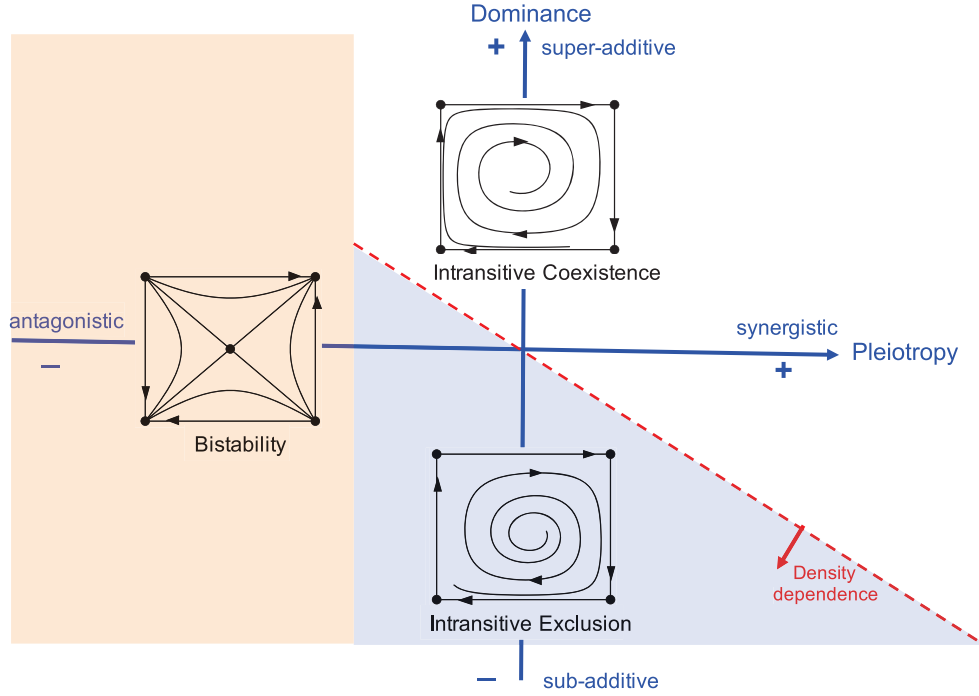


Figure 4: Dependency of eco-evolutionary outcomes on the mean pleiotropy and mean dominance of the defensive alleles in the diploid exploitative competition model. When pleiotropy is sufficiently antagonistic (orange region), the eco-evolutionary dynamics are bistable. When pleiotropy is more synergistic, there is an eco-evolutionary intransitivity. This intransitivity allows for coexistence if the sum of the mean pleiotropy and the mean dominance is positive (white region). Exclusion occurs otherwise (blue region). Density dependence in the prey increases the region of coexistence (red arrow).

Coexistence for the diploid model occurs if and only if

$$\frac{\alpha_1 + \alpha_2}{2} + \frac{\beta_1 + \beta_2}{2} > 0. \quad (4)$$

In other words, the sum of the mean pleiotropy and the mean dominance must be positive for coexistence to occur (unshaded region in fig. 4). In the special case that the allelic contributions are additive (i.e., $\beta_1 = \beta_2 = 0$), the diploid coexistence criterion (4) reduces to the haploid criterion (3). When the allelic contributions are nonadditive, diploidy can either facilitate or inhibit coexistence. Facilitation is greatest when the alleles are codominant with respect to predator defense. Inhibition is greatest when both alleles are recessive with respect to predator defense.

The General Condition for All Levels of Productivity. At lower productivity levels, the coexistence condition involves density-dependent correction factors. We present these correction factors and the general coexistence condition for the diploid model; the haploid coexistence condition corresponds to the coexistence condition for diploids with additive genetics. The density-dependent correction factors are given by

$$\gamma_1 = \log \frac{a_{22}^1 \hat{p}_{22}^1}{a_{11}^1 \hat{p}_{11}^1} = \log \frac{b(1 - \hat{n}_{22}^1/K) - d}{b(1 - \hat{n}_{11}^1/K) - d}, \text{ and}$$

$$\gamma_2 = \log \frac{a_{11}^2 \hat{p}_{11}^2}{a_{22}^2 \hat{p}_{22}^2} = \log \frac{b(1 - \hat{n}_{11}^2/K) - d}{b(1 - \hat{n}_{22}^2/K) - d}.$$

Namely, for the subsystems with predator i , γ_i is the log ratio of the equilibrium predation rate on a population of undefended prey to the equilibrium predation rate on a population of defended prey. The equivalence between $b(1 - \hat{n}_{ii}^j/K) - d$ and $a_{ii}^j \hat{p}_{ii}^j$ follows from the prey per capita growth rates equaling 0 at equilibria. As coexistence is possible only with the intransitive eco-evolutionary assembly dynamics (i.e., $\hat{n}_{11}^1 > \hat{n}_{11}^2$ and $\hat{n}_{22}^2 > \hat{n}_{22}^1$), these density-dependent correction factors γ_i are always positive. Furthermore, the correction factors γ_i are decreasing functions of K and in the limit of high productivity approach a value of 0.

The general coexistence condition for the diploid model with the density-dependent correction factors γ_i is

$$\frac{\alpha_1 + \alpha_2}{2} + \frac{\beta_1 + \beta_2}{2} + \frac{\gamma_1 + \gamma_2}{2} > 0. \quad (5)$$

Hence, density dependence always makes coexistence more likely (red lines in fig. 4). An important special case occurs when the predator conversion efficiencies are equal among all prey genotypes (i.e., $\alpha_1 = \alpha_2 = 0$). When this occurs and the prey genetics are additive (i.e., $\beta_1 = \beta_2 = 0$), the coexistence criterion is always satisfied due to the density-dependent correction factor.

Figure 5 illustrates several of our analytical results numerically. As predicted by our analysis for additive genetics, coexistence occurs for synergistic pleiotropy and mildly antagonistic pleiotropy due to prey density dependence (fig. 5A). Exclusion through a stable intransitivity occurs with intermediate antagonistic pleiotropy, and exclusion through a bistability occurs with strong antagonistic pleiotropy. Alternatively, even if there is antagonistic pleiotropy, coexistence occurs if there is on average sufficiently strong dominance in the defensive alleles, and intransitive exclusion occurs otherwise (fig. 5B). Finally, prey density dependence (low K) can

promote coexistence provided the prey carrying capacity K is sufficiently high to support both predators (fig. 5C).

Mutation-Limited Coexistence. When there is a positive mutation probability $\mu > 0$ and an eco-evolutionary intransitivity, the species always coexist (app. A). However, when exclusion occurs without mutation, the coexistence is mutation limited in the sense that the populations exhibit oscillations where the minimal densities of each species and genotype are on the order of the mutation probability (fig. A1; figs. A1, B1 are available online).

Results for the Apparent Competition Module

Our analysis of the apparent competition module makes three assumptions. First, productivity of the system is sufficiently high (i.e., $K_i \gg 1$ for $i = 1, 2$) to ensure that the

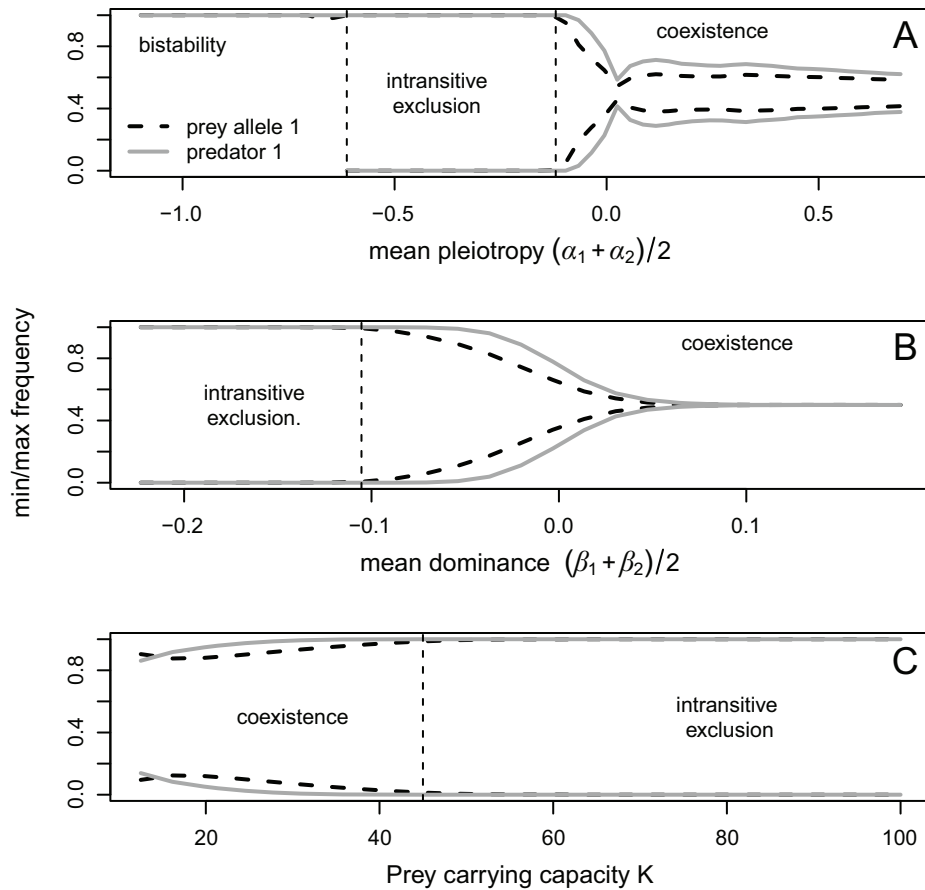


Figure 5: Long-term minimum and maximum frequencies as a function of the mean pleiotropy (A), the mean dominance (B), and the prey carrying capacity (C). In A and C, the genetics are additive. In B and C, there is no pleiotropy. In C, both predator species fail to persist when $K \leq 12.5$. Parameter values: $b = 1$, $d = 0.2$, $\delta_1 = \delta_2 = 0.1$, $c_{11}^2 = c_{22}^1 = 0.2$, $a_{11}^1 = a_{22}^1 = 0.08$, and $a_{11}^2 = a_{22}^2 = 0.04$. In A, $c_{11}^1 = c_{22}^2$ varies between 0 and 0.6, $K = 400$, and $a_{12}^i = (a_{11}^i + a_{22}^i)/2$. In B, $c_{ij}^l = 0.2$ for all i, j, ℓ , and $K = 400$. In C, $c_{ij}^l = 0.2$ for all i, j, ℓ , and $a_{12}^i = (a_{11}^i + a_{22}^i)/2$.

P^* rule holds (Holt and Lawton 1993). Without this assumption, the prey species can coexist, as predator densities remain too low to cause exclusion. Second, we assume that predator allele i is most adapted to exploiting prey i . That is, $c_1^1 a_1^1 > c_1^2 a_1^2$ and $c_2^2 a_2^2 > c_2^1 a_2^1$ for the haploid model and $c_1^{11} a_1^{11} > c_1^{22} a_1^{22}$ and $c_2^{22} a_2^{22} > c_2^{11} a_2^{11}$ for the diploid model. Finally, for the diploid model, the heterozygous individuals have intermediate phenotypes, that is, $c_1^{11} a_1^{11} \geq c_1^{12} a_1^{12} > c_1^{22} a_1^{22}$ and $c_2^{22} a_2^{22} \geq c_2^{12} a_2^{12} > c_2^{11} a_2^{11}$. The analysis for this module is presented in appendix B.

Under these assumptions, if only prey species i is present, then predator allele A_i goes to fixation, as it has the lower break-even density with respect to prey i ($\hat{N}_i^i = \delta / (c_i^i a_i^i)$ for the diploid model and $\hat{N}_i^i = \delta / (c_i^i a_i^i)$ for the haploid model). Alternatively, when only one predator allele is present, say allele A_i , the prey that can support a larger equilibrium density of this predator genotype excludes the other prey species. As in the exploitative competition model, there are three types of eco-evolutionary assembly diagrams (fig. B1). First, if one prey species supports higher equilibrium densities of both homozygous predator genotypes than the other prey species, then eco-evolutionary assembly always culminates in a community consisting of this prey species and the predator allele specialized on this prey species (fig. 2A). Second, if each prey species supports a higher equilibrium density of the predator genotype least adapted to it, then the assembly dynamics exhibit a bistability (fig. 2B). This outcome is possible only if there is some antagonistic pleiotropy in the sense that a predator genotype adapted to capturing one prey species receives more nutritional reward for capturing individuals of the other species. As in the exploitative competition model, we quantify this pleiotropy with the log ratio of the conversion efficiency of the least-adapted predator genotype to the most-adapted predator genotype with respect to prey i :

$$\alpha_1 = \log \frac{c_1^2}{c_1^1} \text{ and } \alpha_2 = \log \frac{c_2^1}{c_2^2} \text{ for haploids, and}$$

$$\alpha_1 = \log \frac{c_1^{22}}{c_1^{11}} \text{ and } \alpha_2 = \log \frac{c_2^{11}}{c_2^{22}} \text{ for diploids.}$$

Synergistic pleiotropy occurs when $\alpha_i > 0$. Finally, the eco-evolutionary assembly dynamics are intransitive when each prey species supports a higher equilibrium density of the predator genotype most adapted to it (fig. 2C). This outcome occurs when pleiotropy is weakly antagonistic or synergistic.

Coexistence is possible only in the case of intransitive eco-evolutionary assembly dynamics and, for the diploid model, depends on the dominance of allele A_i :

$$\beta_i = \log \frac{|c_i^{jj} a_i^{jj} - c_i^{12} a_i^{12}|}{|c_i^{ii} a_i^{ii} - c_i^{12} a_i^{12}|}.$$

As before, $\beta_i = -\infty, 0, \infty$ corresponds to when the A_i allele is recessive, additive, and dominant, respectively. For the diploid model, coexistence occurs only if

$$\frac{\alpha_1 + \alpha_2}{2} + \frac{\beta_1 + \beta_2}{2} > 0. \tag{6}$$

In other words, the sum of the mean pleiotropy and the mean dominance of the predator alleles is positive. For the haploid model, the coexistence condition coincides with additive genetics case for the diploid model: $(\alpha_1 + \alpha_2)/2 > 0$.

Discussion

Empirical studies and theory have demonstrated that species sharing a prey species or a predator species may be driven to extinction due to the negative indirect effects of exploitative or apparent competition (Volterra 1928; MacArthur 1972; Holt 1977; Hsu et al. 1977, 1978; Tilman 1982; Holt and Lawton 1993; Bonsall and Hassell 1997; Wilson et al. 2007). Our analysis demonstrates that evolution of the shared species can mitigate these negative indirect effects and as a consequence simultaneously facilitate species coexistence and maintain genetic polymorphisms. This requires trade-offs in the ability to defend against multiple predators or the ability to attack multiple prey. While such trade-offs are common in nature (Schluter and Grant 1984; Norton 1991; Sih et al. 1998; Svanbäck and Eklöv 2003; Bolnick and Smith 2004), whether they lead to eco-evolutionary feedbacks promoting diversity critically depends on the genetic architecture underlying these trade-offs. Our analysis reveals that pleiotropy, ploidy, dominance, and mutation rates influence how the communities assemble, whether all species and genotypes coexist, and whether this coexistence occurs at a stable equilibrium.

Synergistic Pleiotropy Promotes Coexistence

Ecological pleiotropy occurs when a single trait or gene influences multiple components of the ecological dynamics (Strauss and Irwin 2004; DeLong 2017). In our models, this pleiotropy arises from the simultaneous effects of alleles on the rates at which different predators capture individual prey and the nutritional quality of the captured prey to different predators. For example, body size can simultaneously affect both capture rate and nutritional quality. When larger prey provide more nutrition and are easier to capture (e.g., increased visibility of prey; Brooks and Dodson 1965), the ecological pleiotropy is synergistic (McGee et al. 2016). Smaller body sizes make evolving prey harder to capture and may decrease predator number due to providing lower nutritional rewards. In contrast, when larger prey provide greater nutritional rewards but are more difficult to capture (e.g., by gape-limited fish, birds, or zooplankton predators; Gliwicz and

Umana 1994; Persson et al. 1996; Janzen et al. 2000), the ecological pleiotropy is antagonistic (Paaby and Rockman 2013). Larger body size of an evolving prey lowers attack rates but may increase predator numbers by providing greater nutritional rewards.

Ecological pleiotropy determines how the community structure changes due to rare introductions of missing species or genotypes. If the ecological pleiotropy is sufficiently antagonistic ($\alpha_i < 0$), the eco-evolutionary assembly dynamics culminate in one of two stable states, depending on the initial community state. Each stable state consists of one nonevolving species and the genotype of the evolving species best adapted to interacting with this species. For example, in the exploitative competition module, antagonistic pleiotropy allows the predator to suppress defended prey genotypes to a lower equilibrium abundance than the other predator species, and this prevents the invasion of the other predator courtesy of the R^* rule (Tilman 1982). In contrast, if the ecological pleiotropy is synergistic ($\alpha_i < 0$), nonexistent, or weakly antagonistic, then the eco-evolutionary assembly is intransitive: species-genotype pairs get successively displaced in a cyclic fashion due to rare invasions of the missing genotypes or species. Intransitivities in assembly have been observed in ecological models of interacting competitors (May and Leonard 1975; Yodzis 1978; Allesina and Levine 2011) and coevolutionary models of victim-exploiter interactions (Seger and Antonovics 1988; Gavrilets and Hastings 1998; Kopp and Gavrilets 2006). Unlike these models, the intransitivities in our models stem from an interdigitation of ecological displacements and selective sweeps of more adapted genotypes. This type of interdigitation has been observed in the empirical work of Lankau and Strauss (2007) on genotypes of *Brassica nigra* that produce different levels of sinigrin (an allelochemical that kills mycorrhizal fungi that are beneficial to other plant species). *Brassica nigra* genotypes with high sinigrin concentrations are able to invade diverse communities of other plant species, but patches of high-sinigrin *B. nigra* can be invaded by low-sinigrin *B. nigra* genotypes that grow quickly because they do not invest energy in costly sinigrin production. These low-sinigrin patches are easily invaded by other plant species, resulting in the same type of eco-evo intransitivity that we observe in our model.

When the eco-evolutionary assembly dynamics are intransitive, coexistence or the loss of multiple species and genotypes may occur. Which outcome occurs depends on the per capita growth rates of the species and genotypes when they are rare in the community. Unlike classical coexistence theory (Chesson 2000), positive per capita growth rates of each species or genotype when rare (mutual inviability) is not required for coexistence. Indeed, the intransitive assembly in our models is governed by equilibria supporting one genotype and one nonevolving species. At these

equilibria, one of the missing species or genotypes has a negative per capita growth rate while the other has a positive per capita growth rate. The absolute value of the negative per capita growth rate (the loss rate) determines how quickly one rare genotype or species decreases, while the positive per capita growth rate (the recovery rate) determines how quickly the other rare species or genotype increases. Coexistence requires that the geometric mean of the recovery rates is greater than the geometric mean of the loss rates for the equilibria along this intransitivity (apps. A, B; Hofbauer and Sigmund 1998). Why geometric means? Heuristically, in the initial phase of community establishment, each species and genotype experiences a fluctuating environment as the composition of the community changes from one equilibrium to the next. The geometric means capture the average rate at which species or genotypes increase or are lost as the community composition fluctuates. Coexistence occurs when the recovery rates dominate over the loss rates. Hence, coexistence is promoted by mechanisms that either increase recovery rates or decrease loss rates.

Synergistic pleiotropy simultaneously increases the recovery rates and decreases the loss rates and hence can promote coexistence. For example, in the exploitative competition module, when the community is dominated by one predator and the defended prey genotype, synergistic pleiotropy reduces the density of this predator and thereby decreases selection against the undefended genotype. Synergistic pleiotropy also limits the predator's ability to suppress the density of this genotype and thereby increases the recovery rate of the other predator. Antagonistic pleiotropy has the opposite effects and consequently tends to disrupt coexistence. Density dependence can mitigate the effects of antagonistic pleiotropy. For example, in the exploitative competition module, density dependence in the evolving prey simultaneously decreases loss rates and increases recovery rates. This mitigation allows for an eco-evolutionary counterpart to the paradox of enrichment (Rosenzweig 1971): increasing the carrying capacity of the prey destabilizes the intransitivity, and one species and one genotype are lost (fig. 5C).

Comparisons to Earlier Ecological Theory

In the case of the haploid model, these results parallel findings from earlier ecological studies of consumer species competing for resources (León and Tumpson 1975; Tilman 1980; Leibold 1996; Schreiber and Rittenhouse 2004). In all of these earlier studies, the same necessary condition for coexistence was found. Namely, each predator species has a lower break-even density than the other predator with respect to one of the prey species. When this occurs, there is a coexistence equilibrium at which "each species is limited only by one resource which is different from that limiting the other species" (León

and Tumpson 1975, 194). This condition is not sufficient for coexistence, however, when the resources can be driven extinct via apparent competition. Instead, this classical coexistence condition is sufficient only to ensure that there is an intransitivity in the assembly dynamics. Schreiber and Ritzenhouse (2004) studied these intransitive dynamics for ecological models of two competing prey species that are exploited by two predator species. They found that for highly productive systems (i.e., weak density dependence in the prey), “coexistence required the predators convert their preferred prey at least as efficiently their less preferred prey,” that is, required synergistic pleiotropy if one views the two prey species as two prey genotypes. Our results extend this result by showing that density dependence always has a positive effect on coexistence. Hence, density dependence can mitigate coexistence even if the predators convert their preferred prey less efficiently than their less preferred prey.

Dominance of Defensive Alleles Promotes Coexistence

Our analysis highlights that the inefficacy of selection for diploid populations compared to haploid populations can stabilize communities through a genetic storage effect. As rare alleles are masked in heterozygotes of diploid populations (Otto and Gerstein 2008; Gerstein and Otto 2009), recovery rates (respectively, loss rates) of rare alleles are lower (respectively, higher) in diploid populations than in haploid populations. The net effect of this selective inefficacy on coexistence depends on the dominance of the alleles, that is, whether allelic contributions to defense or resource use are superadditive or subadditive. For the exploitative competition module, superadditivity in prey fitness occurs when the per capita attack rate of a predator on heterozygous genotypes is lower than the average per capita attack rate on homozygous genotypes. That is, the heterozygotes are better defended than the average homozygous genotype. Superadditivity with respect to both predators is caused by a beneficial reversal of dominance: when a single locus contributes to two aspects of fitness (in this case, defense against two different predators), the more advantageous allele is dominant (Rose 1982; Curtsinger et al. 1994). Superadditivity ensures that the stabilizing effects of reduced loss rates outweigh the destabilizing effects of reduced recovery rates. These reduced loss rates help store alleles during periods in which they do not provide a fitness benefit, such as defense against a particular predator—an eco-evolutionary analog of the storage effect (Chesson and Warner 1981; Chesson 1994). A related stabilizing mechanism exists for maintaining genetic polymorphisms in fluctuating environments (Gillespie and Langley 1974; Gillespie 1978). Gillespie’s (1978) SAS-CFF model demonstrates that superadditivity for heterozygote fitness (the concave fitness function

[CFF]) in a stochastic environment increases the geometric mean of fitness (the stochastic additive scale [SAS]) of heterozygotes via Jensen’s inequality (Jensen 1906; Ruel and Ayres 1999), and thereby, heterozygotes persist and allelic diversity is maintained.

When synergistic pleiotropy or superadditivity of heterozygotes is sufficiently strong, our simulations suggest that species coexistence occurs at a stable equilibrium. At this equilibrium, eco-evolutionary feedbacks minimize fitness differences among the nonevolving species. For example, in the exploitative competition module, the prey genotypic frequencies at the coexistence equilibrium are such that both predator species in isolation have equal break-even densities (Hsu et al. 1978). Thus, eco-evolutionary feedbacks equalize the fitness differences of the competing predators (Chesson 2000; Lankau 2011). This equalization, in and of itself, allows only for neutral coexistence in which small levels of demographic or environmental stochasticity can result in species loss (Chesson 1988; Adler et al. 2007). Evolution, however, stabilizes coexistence by favoring whichever species becomes less common (Lankau 2011). While these results highlight an important ecological feature of the coexistence equilibrium, we have not studied the genetic features of this equilibrium. However, we can gain some insights from Wilson and Turelli (1986), who studied the evolution of resource use for a diploid consumer population with two implicitly defined resources. As in our model, resource use is determined by two alleles at a single locus, and there is a trade-off between using one resource and using the other resource. They found that superadditive contributions of alleles to resource uptake lead to a stable polymorphic equilibrium at which heterozygotes are the most fit (overdominance), while subadditive contributions can result in a stable polymorphic equilibrium with heterozygote disadvantage (underdominance). As their model does not explicitly account for resource dynamics or ecological pleiotropy, it remains to be seen whether their conclusions extend to our model and what role, if any, ecological pleiotropy plays in determining the relative fitness of heterozygotes at polymorphic equilibria.

Mutational Rescue

When antagonistic pleiotropy or subadditivity of heterozygotes are barriers to coexistence, mutations can serve as a stabilizing mechanism by rescuing alleles that otherwise would be lost. However, this rescue effect permits only a fragile form of oscillatory coexistence. That is, our simulations suggest that the densities of the nonevolving species and the frequencies of genotypes repeatedly reach levels proportional to the mutation rates and consequently may lead to permanent loss of the nonevolving species via demographic stochasticity. This mutation-limited form of coex-

istence was observed in two-species coevolutionary models of host-parasites (Seger and Antonovics 1988) and mimicry (Gavrilets and Hastings 1998). In both of these earlier studies, both species were evolving at a single diallelic locus, and the authors numerically showed that in cases where one allele in each species was lost with no mutation, low mutation enabled cycles in allele frequencies close to fixation of alternating alleles. Our work provides an analytic demonstration of mutation as a coexistence mechanism.

Future Challenges and Opportunities

Our results highlight several opportunities for empirical and theoretical work. Although there is considerable work examining how a single trait affects multiple components of species interactions, much of it has not invoked the term ecological pleiotropy (reviewed in Strauss and Irwin 2004). Thus, it is unclear whether ecological pleiotropy is synergistic or antagonistic in previous work. When ecological pleiotropy is sufficiently antagonistic, it creates an eco-evolutionary mismatch, in which the predator against which prey are most defended is also the predator that suppresses them to the lowest density. This eco-evolutionary mismatch disrupts the opportunity for eco-evolutionary feedbacks to facilitate coexistence. Knowing the prevalence of synergistic versus antagonistic ecological pleiotropy in natural communities would provide greater knowledge of the extent to which eco-evo feedbacks affect species diversity. Additionally, we have shown that superadditive selection on traits by multiple species can lead to a genetic storage effect. However, few studies have measured nonadditive selection, although data likely exist to do so in many different systems (terHorst et al. 2015). Finally, our models assumed that the evolutionary dynamics are governed by two alleles at a single locus. However, multiple loci likely determine the traits that govern interactions with multiple species; accounting for multiple loci has the potential to change eco-evolutionary dynamics by altering the capacity for species to respond to selection pressures (Seger and Antonovics 1988; Doebeli 1997; Kopp and Gavrilets 2006). Understanding how this additional genetic complexity, which allows for recombination and epistasis, influences our conclusions remains to be tested.

Concluding Remarks

Our results show that eco-evolutionary feedbacks can act as a coexistence mechanism and that the strength of this mechanism depends on underlying genetics. Synergistic pleiotropy, density dependence, diploidy with dominance of the better-adapted allele, and mutation can act as stabilizing mechanisms. Stabilization occurs either by increasing the rate at which rare genotypes or species recover or by slowing the rate at which rare species or genotypes are lost and thereby al-

lowing sufficient time for other eco-evolutionary feedbacks to rescue these at-risk species or genotypes. The extent to which these genetic details influence the stability of natural communities, which are inherently more complex ecologically and genetically, remains to be seen.

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