When Does Coevolution Promote Diversification?

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abstract: Coevolutionary interactions between species are thought to be an important cause of evolutionary diversification. Despite this general belief, little theoretical basis exists for distinguishing between the types of interactions that promote diversification and those types that have no effect or that even restrict it. Using analytical models and simulations of phenotypic evolution across a metapopulation, we show that coevolutionary interactions promote diversification when they impose a cost of phenotype matching, as is the case for competition or host-parasite antagonism. In contrast, classical coevolutionary arms races have no tendency to promote or inhibit diversification, and mutualistic interactions actually restrict diversification. Together with the results of recent phylogenetic and ecological studies, these results suggest that the causes of diversification in many coevolutionary systems may require reassessment.

Keywords: coevolution, diversification, arms race, mutualism, parasite-host interaction, spatial structure.

Introduction

Evolutionary ecologists have long thought that coevolutionary interactions cause interacting clades to diversify over time. This idea dates to Darwin (1859), who focused on the role of competition as an engine of diversification in *The Origin of Species*. After the Modern Synthesis, the importance of coevolution between trophic levels, as well as within them, came to the fore through Grant's (1949) work on the role of pollination systems in plant speciation and Ehrlich and Raven's (1964) seminal study of plant-herbivore interactions. In recent decades, modern phylogenetic methods have allowed empirical assessment of diversification associated with various interactions (Farrell et al. 1991; Hodges and Arnold 1995; Farrell 1998; Sargent 2004; Lengyel et al. 2009). Competitive diversification is a major component of Simpson's (1949, 1953) and Schluter's (2000) theories of adaptive radiation, and Thompson's (1994, 2005) geographic mosaic theory of coevolution holds that most coevolutionary interactions can lead

to diversification when they play out across a metapopulation.

Various studies have linked increased diversification to ecological interactions including mutualism (Kiester et al. 1984; Sargent 2004; Smith et al. 2008), competition (Doebeli and Dieckmann 2000; Calsbeek 2009), predator-prey arms races (Nosil and Crespi 2006; Hanifin et al. 2008; Thompson 2009), and parasite-host coevolution (Farrell 1998; Buckling and Rainey 2002; Summers et al. 2003). These interactions encompass both the complete range of possible interaction outcomes for interacting species and different forms of coevolutionary selection, such as interactions mediated by the difference in the phenotypes of interacting species, as in classic arms-race dynamics (Dawkins and Krebs 1979); the matching of a trait in one species to a trait in another, as in some mutualisms (Pellmyr and Huth 1994); and host-parasite interactions mediated by some form of self-nonself recognition (Ferreira et al. 2004; Lahti 2005).

The general connection between species interactions and diversification is supported by mathematical models (Kiester et al. 1984; Doebeli and Dieckmann 2000; Kopp and Gavrilets 2006), estimates of coevolutionary selection in experimental and natural populations (Buckling and Rainey 2002; Nosil and Crespi 2006), and phylogenetic studies of speciation rates (Hodges and Arnold 1995; Farrell 1998). However, the specific processes by which this wide variety of species interactions may lead to diversification are unclear in many cases, and different lines of evidence are contradictory. For example, one theoretical treatment suggests that pollination mutualisms should cause interacting partners to speciate simultaneously (Kiester et al. 1984), but phylogenetic studies of specific systems implicate pollinator switching as the means by which this interaction can spur diversification, precluding cospeciation (Machado et al. 2005; Whittall and Hodges 2007; Tripp and Manos 2008). In another case, evolutionary cycles generated by classic "arms races" between antagonists are thought to lead to diversification when they occur across spatially structured populations (Thompson 2005; Hanifin et al. 2008); yet, paleontological studies of such interactions find long-term escalation but no increase

in trait variation (Vermeij 1994). Ehrlich and Raven's (1964) original formulation of coevolutionary diversification by plants and insect herbivores proposed that interacting groups diversify in a stepwise fashion: first, plants radiate into enemy-free space created by a novel defensive trait; then, insects diversify after evolving a countermeasure to the new defense. These processes are structured by competition within trophic levels and not the antagonism between them (Ehrlich and Raven 1964; Schluter 2000).

Indeed, recent phylogenetic studies show stepwise, and not simultaneous, diversification of coevolving lineages of plants and insect herbivores (Wheat et al. 2007; McKenna et al. 2009), corroborating ecological studies of plant-pollinator (Armbruster and Muchhala 2009) and plant-herbivore (Janz et al. 2006) interactions and revealing that competition for pollinators or host plants drives diversification. Ricklefs (2010) recently proposed that a more general form of the processes described by Ehrlich and Raven (1964) that occurs in interacting clades of hosts and parasites structures much of the diversity of life on Earth. These results suggest that many coevolutionary interactions formerly thought to accelerate diversification may not actually do so, and they call into question the idea that all species interactions are engines of diversity.

To rigorously identify and compare the causes of diversification in interacting clades, we must evaluate the diversifying effects of competition, mutualism, and antagonism both in comparison with one other and in comparison with the "background" rate of diversification due to genetic drift and spatially variable selection from the abiotic environment (Lande 1992; Thompson 2005). Previous theoretical studies have examined the effect of coevolution on diversification, but these considered only one or a few interaction types and did not account for spatial population structure or compare diversification due to coevolution with that expected from genetic drift and spatially variable abiotic selection (Kiester et al. 1984; Doebeli and Dieckmann 2000; Kopp and Gavrilets 2006; Devaux and Lande 2009).

Here we develop a framework for evaluating and comparing the diversification caused by various coevolutionary interactions by analyzing mathematical models of finite populations of interacting species in spatially variable environments. These analyses allow us to explicitly compare diversification caused by different coevolutionary interactions with that caused by spatially variable abiotic selection and genetic drift alone, to robustly identify interactions that promote diversification.

Methods

In both our analytic and simulation-based models, we approximated evolutionary diversification as the variation in a single phenotypic trait for each of two species interacting across a metapopulation of local populations linked by gene flow. We modeled evolution across a metapopulation so that we could explicitly assess the effects of coevolutionary selection in the face of gene flow, and we compared its effects to those of spatially variable selection from the abiotic environment and random genetic drift. Thus, our model incorporates three major population genetic forces that are expected to alter the effects of coevolutionary selection (Thompson 1999, 2005) but that also shape among-population phenotypic variation on their own (Wright 1952; Lande 1976, 1992). This approach also allowed us to estimate how diversity would evolve across the metapopulation in the absence of coevolution.

Throughout our study, we differentiated between global mean phenotypes for each species, which are taken across the metapopulation, and local mean phenotypes, which are taken for the population at each site within the metapopulation. Our analytic model tracks the global variance in phenotype values for each species as the variance in local mean phenotypes taken across the metapopulation. In contrast, our individual-based simulations are able to track the phenotypes of individuals within each local population, allowing the phenotypic variance of local populations to evolve; but here again, we are primarily concerned with the evolution of the global variance in phenotypes for each species across the entire metapopulation.

In each modeling approach, we considered three kinds of species interactions: mutualism, in which both species benefit from the interaction; antagonism, in which one species benefits at the expense of the other; and competition, in which both species pay a cost for interacting. We considered each of these interaction types to be mediated by either phenotype differences, in which the outcome of the interaction is determined by which species has a greater phenotype value, or phenotype matching, in which the outcome of the interaction is determined by the similarity of the interacting species' phenotype values. This resulted in a total of six interaction types that encompass a wide range of possible species interactions (table 1).

Analytic Model

We modeled two coevolving species whose interaction is mediated by a single quantitative trait z in each. These traits are assumed to be normally distributed, with a constant additive genetic variance G. Within populations, individuals encounter one another at random, and the fitness outcome of encounters depends on the type of ecological interaction (mutualism, competition, or antagonism) and the manner by which the interactions are mediated (phenotype matching vs. phenotype differences).

Table 1: Six types of species interactions considered in this study and examples of each

Interaction type, selective regime	Example
Mutualism (both species benefit):	
Phenotype differences	Long-tongued pollinators and nectar-spurred flowers (i.e., "Darwin's race"; Whittall and Hodges 2007; Anderson and Johnson 2008)
Phenotype matching	Obligate pollination mutualism (Pellmyr 2003)
Antagonism (one species benefits, one is harmed):	
Phenotype differences	Predator-prey arms races (Dawkins and Krebs 1979; Brodie et al. 2002)
Phenotype matching	Brood parasitism (Lahti 2005; Yang et al. 2010)
Competition (both species are harmed):	
Phenotype differences	Allelopathy (Bais et al. 2003)
Phenotype matching	Competitive exclusion (Rummel and Roughgarden 1985; Devaux and Lande 2009)

Under phenotype matching, the fitness outcome of the interaction depends on how closely a trait in one species matches a trait in the other species, regardless of the relative values of the traits. For example, the ovipositors of pollinating yucca moths must be long enough to penetrate their host plants' ovary walls but not so long as to risk triggering a selective floral abortion mechanism that kills flowers receiving too many moth eggs (Pellmyr 2003; Smith et al. 2009). Similarly, brood parasites' eggs are selected for visual similarity to their hosts' eggs, so that the parasite eggs are not recognized and ejected from the nest, and hosts' eggs are selected to be visually dissimilar to those of their parasites, for the inverse reason (Lahti and Lahti 2002; Lahti 2005). Finally, ecological competitors, such as co-occurring species of *Anolis* lizards (Calsbeek and Smith 2007; Calsbeek 2009; Losos 2009) or Galápagos finches (Grant and Grant 2008), are generally thought to maximize their fitness when their phenotypes are more dissimilar from those of their competitors. We captured the natural selection arising from such interactions by modeling the fitness outcome for an individual of species i encountering an individual of species j as

$$w_{\text{bio}}(z_i, z_j) = \kappa_i + \xi_{Mi} e^{-\alpha_i(z_i - z_j)^2}. \tag{1}$$

The term α_i measures the sensitivity of the interaction outcome to the phenotypes of the interacting species, ξ_{Mi} measures the cost or benefit to species i caused by a successful interaction, and κ_i is the fitness of species i in the absence of the interaction.

Under phenotype differences, a species maximizes its coevolutionary fitness by having a greater phenotype value, regardless of the phenotype value of the other interacting species. This form of selection describes classic arms races, such as those between plants producing toxic defensive chemicals and herbivores tolerating or detoxifying those chemicals (Zangerl and Berenbaum 2005) or those between prey producing armor or chemical defenses and predators that must penetrate or tolerate those defenses

(Vermeij 1994; Hanifin et al. 2008). However, phenotype differences may also describe mutualism, as in pollination relationships in which a pollinator extracts more benefit from a plant if its tongue is longer than the plant's nectar tube (e.g., Anderson and Johnson 2008) or interactions among plants that use allelopathic chemicals to exclude competitors (Bais et al. 2003). For interactions of this form, we modeled the fitness outcome of an encounter as

$$w_{\text{bio}}(z_i, z_j) = \kappa_i + \frac{\xi_{Ei}}{1 + e^{-\alpha_i(z_i - z_j)}}. \tag{2}$$

Here the term ξ_{Ei} is the benefit species i receives from successful interaction, and other parameters are as in equation (1). The fitness functions described by equations (1) and (2) are illustrated in figure 1.

In addition to interactions between species, the total fitness for an individual of species i depends on the difference between the individual's phenotype value z_i and some optimal value θ_i that is determined by the abiotic environment, such that the total fitness of an individual is given by

$$w_{\text{total}}(z_i, z_j) = e^{-\gamma_i(z_i - \theta_i)^2} w_{\text{bio}}(z_i, z_j), \tag{3}$$

where γ_i is the strength of stabilizing selection toward the abiotic optimum and $w_{\text{bio}}(z_i, z_j)$ takes the form of equation (1) or equation (2) depending on the nature of the interaction between species i and j. Accounting for abiotic selection in this way allowed us to model cases where there is a cost of escalating traits (e.g., Hanifin et al. 2008). Equations (1)–(3) are sufficiently general to model most forms of ecological interaction mediated by a mechanism of phenotype matching or phenotype differences.

The change in population-mean phenotypes caused by natural selection following the fitness function in equation (3) is replicated across a metapopulation of finite local populations linked by gene flow under a "propagule pool" model, which we used for its mathematical simplicity. By

Possible biotic fitness functions

Interaction costly   **Interaction beneficial**
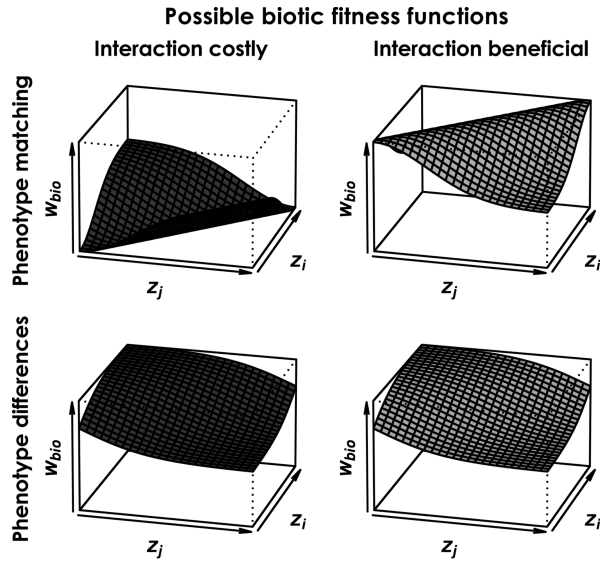
Figure 1: Fitness functions described by equations (1) and (2). Surface plots illustrate the relationship between species phenotype values z_i and z_j and the biological component of fitness w_{bio} for species i when the interaction is costly (*left column*) or beneficial (*right column*) to species i, and under interactions mediated by phenotype matching (*top row*) or by phenotype differences (*bottom row*). In all panels, z_i and z_j are between 0 and 1, $\kappa_i = \kappa_j = 1$, $\xi_{Mi} = \xi_{Ei} = \xi_{Mj} = \xi_{Ej} = 0.1$, and $\alpha = 5$.

assuming weak selection, low rates of gene flow, a weakly variable abiotic environment, and fixed additive genetic variance, we can completely describe the evolutionary dynamics of the metapopulation by following only the changes in the global mean phenotype value of each species over the entire metapopulation, the global variance of each species' population mean phenotype across the entire metapopulation, and the global covariance between the local population mean phenotype values of the two species at each site across the entire metapopulation. We assumed that each generation involves (1) movement among sites, (2) biotic and abiotic selection, and (3) sampling of a finite number of individuals to form the next generation. Each stage of the life cycle is described in detail below.

Movement among Sites. Movement among sites in the metapopulation was implemented as a propagule pool model, such that every site contributes a fraction of its population m_i as emigrants to a global propagule pool and receives the same number of immigrants from the pool. Following movement, the local mean phenotype of species i is

$$\bar{z}_i' = (1 - m_i)\bar{z}_i + m_i \overline{Z}_i, \tag{4}$$

where $\overline{Z}_i$ is the global mean phenotype of species i across the entire metapopulation.

Selection. Individual fitness functions are described in equations (1)–(3). Assuming that additive genetic variance G_i is constant, the mean phenotype in each local population of species i following natural selection is

$$\bar{z}_i'' = \bar{z}_i' + G_i \frac{1}{\overline{W}_{\text{total}}} \frac{\partial \overline{W}_{\text{total}}}{\partial \bar{z}_i}, \tag{5}$$

where $\overline{W}_{\text{total}}$ is the local population mean fitness and is equal to the expectation of equation (3) taken over the distributions of phenotypes in species i and species j. In order to produce an analytically tractable expression for $\bar{z}_i''$, we assumed that selection is weak (γ_i and α_i are of order ε). Ignoring all terms $O(\varepsilon^2)$ and higher shows that the local population mean phenotype following selection and movement is

$$\bar{z}_i'' = \bar{z}_i' + 2G_i\left[\gamma_i(\theta_i - \bar{z}_i') + \frac{\alpha_i\xi_{Mi}}{1 + \xi_{Mi}}(\bar{z}_i' - \bar{z}_j')\right] \tag{6a}$$

for the case of phenotype matching described by equation (1) but

$$\bar{z}_i'' = \bar{z}_i' + 2G_i\left[\gamma_i(\theta_i - \bar{z}_i') + \frac{\alpha_i\xi_{Ei}}{4(2 + \xi_{Ei})}\right] \tag{6b}$$

for the case of phenotype differences described by equation (2).

Genetic Drift. Finally, the effect of genetic drift on the local population mean phenotype was incorporated by sampling n_i individuals independently from each local population of species i to form the next generation (Lande 1976). In each local population of species i, then, the mean phenotype after this sampling step is

$$\bar{z}_i''' = \bar{z}_i'' + \zeta_i, \tag{7}$$

where ζ_i is a random variable with a mean of 0 and variance equal to G_i/n_i, where n_i is the local effective population size of species i.

Evolution of Global Phenotypic Mean, Variances, and Covariance. Although it is possible in principle to study how coevolution shapes diversification by directly analyzing equations (1)–(7) for some number of individual sites, this approach is tractable for only a very small number of sites. Thus, in order to make analytical progress, we de-

rived expressions for evolutionary change in the statistical moments that describe the multivariate distribution of population mean phenotypes for both species across the entire metapopulation. Because our goal is to understand diversification, we are particularly interested in understanding how the global variance of population mean phenotypes evolves.

We began by calculating the global mean phenotype for each species taken over the entire metapopulation in the next generation:

$$\overline{Z}_i' = \mathrm{E}[\bar{z}_i'''].\tag{8}$$

Here, $\mathrm{E}[\bullet]$ denotes an expectation of the quantity in brackets taken over the metapopulation. Next, we calculated the global phenotypic variance for each species in the next generation:

$$\sigma_{\bar{z}_i}^{2'} = \mathrm{E}[(\bar{z}_i''' - \overline{Z}_i')^2].\tag{9}$$

Finally, we calculated the covariance of the local population mean phenotypes of the interacting species in the next generation:

$$\sigma_{\bar{z}_i\bar{z}_j}' = \mathrm{E}[(\bar{z}_i''' - \overline{Z}_i')(\bar{z}_j''' - \overline{Z}_j')].\tag{10}$$

Together, equations (8)–(10) completely describe the global evolutionary dynamics of the metapopulation subject to the assumptions described above.

Although equations (8)–(10) are too complex to offer useful insight in this form, if we assume that the rate of movement m_i and the global variance of the abiotic optimum θ_i are both small (order ε), we can obtain analytically tractable expressions for the per-generation change in the statistical moments that describe the metapopulation (Nuismer et al. 2010). In fact, it is possible to completely describe the evolution of the global phenotypic variances and covariance without referring to the grand mean phenotype of either species. Because we are interested in the evolution of diversity, for which the global phenotypic variance is a convenient index, we proceeded using only the closed system of three equations describing the change in global phenotypic variance for each species i:

$$\Delta\sigma_{\bar{z}_i}^2 = \frac{G_i}{n_i} + 4G_i[S_{Mi}(\sigma_{\bar{z}_i\bar{z}_j} - \sigma_{\bar{z}_i}^2) - \gamma_i\sigma_{\bar{z}_i}^2] - 2m_i\sigma_{\bar{z}_i}^2,\tag{11a}$$

and the change in the covariance between the two species' local phenotypes:

$$\Delta\sigma_{\bar{z}_i\bar{z}_j} = \sigma_{\bar{z}_i\bar{z}_j}[2G_i(S_{Mi} + \gamma_i) + 2G_j(S_{Mj} + \gamma_j)]$$
$$- 2(G_j\sigma_{\bar{z}_i}^2 S_{Mj} + G_i\sigma_{\bar{z}_j}^2 S_{Mi}),\tag{11b}$$

where the terms S_{Mi} and S_{Mj} are equal to $\alpha_i\xi_{Mi}/(1 + \xi_{Mi})$ and $\alpha_j\xi_{Mj}/(1 + \xi_{Mj})$, respectively, and measure the strength of selection caused by interactions mediated by phenotype matching. Because equations (11a) and (11b) have no equivalent term for the strength of selection caused by interactions mediated by phenotype differences, an important conclusion is revealed: coevolutionary interactions mediated by phenotype differences do not alter the evolution of global phenotypic variance. Instead, the evolution of global phenotypic variance is identical to the noncoevolutionary case and is thus described by the expression

$$\Delta\sigma_{\bar{z}_i}^2 = \frac{G_i}{n_i} - 4G_i\gamma_i\sigma_{\bar{z}_i}^2 - 2m_i\sigma_{\bar{z}_i}^2.\tag{12}$$

Expression (12) is simply a special case of equation (11a) with $S_{Mi} = 0$ (i.e., with no selection for phenotype matching).

Comparing Diversification due to Different Interactions. To compare the propensity of different coevolutionary interactions to promote phenotypic diversification (i.e., to increase global phenotypic variance), we solved for the equilibrium of the closed three-equation system (11a) and (11b), which is presented and analyzed in the appendix. To determine what effect coevolution has on diversification, we examined the ratio of the equilibrium global variance under coevolution (eq. [A1]) to that under only drift and structured abiotic selection (eq. [A1] with $S_{Mi} = 0$). This ratio is always equal to 1 for interactions mediated by phenotype differences because, as noted above, interactions mediated by phenotype differences have no impact on the global phenotypic variance. When coevolution is mediated by phenotype matching, however, the relative equilibrium variance is greater than 1 whenever $\xi_{Mi} < 0$ and less than 1 whenever $\xi_{Mi} > 0$ (fig. 2). That is, matching coevolution increases the global equilibrium variance of a species whenever it experiences a cost of closer phenotype matching (as would be the case for the host or the prey in an antagonistic interaction or for both species in a competitive interaction), but it decreases the global equilibrium variance of a species whenever it experiences a benefit of closer matching (as would be the case for both species in a mutualistic interaction or for the parasite/predator in an antagonistic interaction). Interestingly, while the cost or benefit of interaction to the focal species strongly shapes the effect of coevolution on diversification, the cost or benefit of interaction to the other species has little impact (fig. 2).
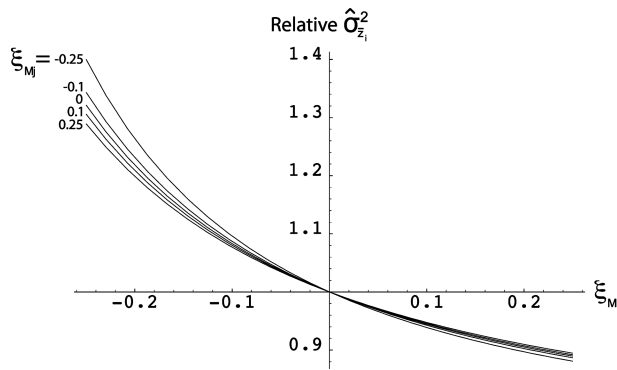
Figure 2: Relative equilibrium global phenotypic variance under matching coevolution relative to the cost/benefit of interaction for species i, ξ_{Mi}. The relative equilibrium variance is greater than 1 (i.e., matching coevolution increases equilibrium variance) whenever $\xi_{Mi} < 0$, that is, whenever closer trait matching imposes a cost on the focal species. When $\xi_{Mi} > 0$ and the focal species benefits from closer trait matching, coevolution acts to reduce among-population phenotypic variance. The value of the cost/benefit of interaction for species j, ξ_{Mj}, only slightly alters the shape of this relationship. (Other parameter values are as follows: $\alpha_i = \alpha_j = 0.01$, $\gamma_i = \gamma_j = 0.01$, $m_i = m_j = 0.01$, $G_i = G_j = 1$, and $n_i = n_j = 1,000$.)

Individual-Based Simulations

We evaluated the robustness of our analytic predictions using individual-based simulations in which individuals of two species interacted across a metapopulation of sites linked by the movement of individuals. The simulations tracked the phenotypes of every individual in the metapopulation, allowing us to relax key assumptions of the analytical model and study the dynamics of diversification under nonequilibrium conditions, strong selection, high rates of gene flow, significant levels of spatial abiotic variability, and evolving additive genetic variances. We simulated each interaction type listed in table 1, as well as the evolution of the two species without coevolutionary selection, to provide a null expectation for the amount of diversification caused by spatially variable abiotic selection and genetic drift alone.

The simulations tracked evolution within N finite local populations for each species. Local population sizes of the two species were determined by a spatially homogenous local carrying capacity K, which is drawn at random from a uniform distribution $\{300 < K < 2,000\}$ at the beginning of each simulation run. Individuals were assumed to be hermaphroditic and were characterized by a single phenotype value z. In each simulated generation, individuals (1) mate and produce offspring, (2) migrate among local populations in the metapopulation, (3) experience selection arising from the similarity of their phenotype to the local abiotic optimum value θ_i, and (4) interact with a randomly drawn individual from the local population of the other species, with fitness consequences being determined by the nature of the interaction being modeled and the phenotypes of the interacting individuals.

Mating and Reproduction. Hermaphroditic reproduction was conducted at each site by randomly drawing a pair of individuals from the local population of each species and then generating a single offspring whose phenotype is equal to the average of the two parents' phenotypes plus a randomly generated variable to account for segregation variance. This allowed additive genetic variance to evolve without using more computationally intensive explicit genetic models. (Initial comparison of results from these genetically implicit simulations with those of genetically explicit multilocus simulations demonstrated qualitatively identical predictions.) This procedure was repeated, drawing new pairs of parents from the local parental population with replacement, until the number of offspring reached the local carrying capacity, K. The offspring then replaced the local parental population of each species.

Movement among Sites. Following mating and reproduction, individuals move between populations. Movement was simulated by moving individuals of each species from their local populations into a migrant pool at rate m; individuals within the migrant pool were then distributed back into randomly selected local populations until each local population reaches its premovement size, n.

Abiotic Selection. To simulate selection from the abiotic environment, each individual was assigned a probability of survival that was determined by the squared difference between its phenotype and the local abiotic optimum as provided in equation (3) above. Individuals survive if a randomly selected number is less than their survival probability, but they die otherwise. This procedure has the effect of selecting individuals with phenotypes that are closer to the optimal trait value, but in a nondeterministic fashion.

Biotic Interaction and Selection. To simulate coevolutionary interactions in each local population, pairs of individuals were drawn at random and without replacement from each species' population, and then they were assigned probabilities of survival determined by their relative phenotype values: following equation (1) if the interaction is based on phenotype matching and following equation (2) if it is based on phenotype differences. Pairs of individuals were drawn, and they interacted until all of the individuals in the species with a smaller local population size had interacted. Unpaired individuals then died if they belonged to a species that benefits from the interaction (as in the case of parasites in host-parasite antagonism or either part-

Table 2: Parameter values used for individual-based solution runs

Parameter	Value or distribution	
	For distributions (fig. 3)	For time series (figs. 4 and 5)
Number of sites, N	50	100
Individuals per population, K	U(300, 2,000)	1,000
Strength of abiotic selection, γ	U(.005, 1)	.2
Strength of biotic selection, α	U(1, 10)	4
Cost/benefit of biotic interaction, ξ	U(.01, 5)	.25
Probability of movement between sites, m	U(0, .01)	.0001
Mean local abiotic optimum, $\bar{\theta}$	U(.4, .6)	.5
Variance of local abiotic optimum, σ_θ^2	U(0, 1)	.1
Correlation between species's abiotic optima, ρ_θ	U($-$.1, .1)	0

Note: U(x, y) indicates that, for each new simulation run, a parameter was drawn at random from a uniform distribution with minimum x and maximum y.

ner in a mutualism), but they survived if they belonged to a species that suffers a cost from the interaction (hosts in host-parasite antagonism or either species under competition). Individuals who survived were retained to form the parental population for the next generation.

Abiotic optima for each species, θ_i, were assigned to each of N population sites by drawing a pair of random variables from a bivariate Gaussian distribution with mean $\bar{\theta}_i$, variances $\sigma_{\theta_i}^2$, and correlation ρ_{θ_i}. Initial populations were created by populating each site with n individuals whose phenotypes were equal to the local optimum value favored by stabilizing selection, $\bar{\theta}_i$, plus a random deviation drawn from a uniform distribution. Selecting initial phenotypes in this way minimized the chances that a local population would become extinct before it could adapt to local environmental conditions.

We ran 1,000 simulations of each interaction type listed in table 1 according to the parameters provided in table 2. Simulations were run for 1,000 generations, starting with 200 generations of "burn-in" when the strength of selection was gradually ramped up to the values shown in table 2. Starting simulations with initially weak selection allows populations to gradually adapt to local conditions, thus minimizing the probability of extinction. Local and global population phenotype means and variances for each species were written to text files as the simulations proceeded. At the end of each simulation run, the mean value of the phenotypic trait z for each species in each of the N populations was recorded. As a standard for comparison, we also ran 1,000 simulations without coevolutionary selection.

Results

The qualitative results of the analytic model are listed in table 3. Compared with the "background" rate of diversification caused by drift and abiotic selection, we found that interactions mediated by phenotype differences have

no effect on diversification and that interactions mediated by phenotype matching inhibit diversification in species that benefit from closer matching. Only species that experience a cost of closer phenotype matching experience increased diversification as a result of coevolution.

One apparently counterintuitive consequence of this is that, under antagonism mediated by phenotype matching, we found that the global phenotypic variance of the exploiter, which benefits from closer matching, should decrease even as the global phenotypic variance of its victim, which experiences a cost of closer matching, increases (table 3). This is a consequence of the weak selection conditions we assume for the analytic model. Under weak selection, the distributions of local mean phenotypes remain unimodal. So long as the distribution of victims' local mean phenotypes remains unimodal, local exploiter populations on average evolve toward the global mean phenotype of their victims even as they track local populations. This average movement toward the victims' global mean phenotype results in reduced global phenotypic variance for the exploiter. When we are able to relax the assumption of weak selection, as in our individual-based simulations, the victim can evolve a bimodal distribution of local mean phenotypes; after that point, the exploiter population evolves greater global phenotypic variance than it would in the absence of coevolution.

Table 3: Effects of ecological interactions on phenotypic diversification

Interaction type	Phenotype differences		Phenotype matching	
	Species 1	Species 2	Species 1	Species 2
Mutualism	0	0	−	−
Antagonism	0	0	+	−
Competition	0	0	+	+

Note: Values indicate whether different ecological interactions promote (plus sign), restrict (minus sign), or have no effect on (0) phenotypic diversification relative to drift and spatially variable selection alone.

Results from the simulations are presented in figure 3, which illustrates the distribution of global phenotypic variance values found in the final generation of 1,000 replicate simulations for each interaction type, and in figure 4, which illustrates changes in the global phenotypic variation over time in one simulation of each interaction type. These results demonstrate that the qualitative conclusions of the analytical model are quite robust. Although coevolutionary interactions mediated by phenotype differences lead to more extreme mean phenotypes (fig. 4, *left column*), they do not alter the global variance in phenotypes relative to the noncoevolutionary case (fig. 3, *left column*). When interactions are mediated by phenotype matching, coevolution enhances diversification only for competitors and victim species in antagonisms; coevolution inhibits diversification for mutualistic interactions and exploiter species in antagonisms (fig. 3, *right column*).

Because the results shown in figure 3 consider only the among-population variance present in the final generation and pool results across many different parameter combinations, we ran additional simulations for specific parameter combinations and recorded the evolution of trait means over time (e.g., fig. 4). These simulations also revealed that all interaction types approach an equilibrium level of diversification quite rapidly (within 100 generations), where the effects of coevolution on the global variance are counterbalanced by abiotic selection and gene flow (fig. 4). Even at this equilibrium level of diversity, however, the local mean phenotypes of individual populations may be highly dynamic, suggesting that strong local coevolutionary dynamics are poor predictors of species-wide evolutionary trajectories.

Although these simulations generally confirmed the results of our analytical approximation and pooled simulations, they revealed that under very strong coevolutionary selection, our analytic predictions for exploiter species in antagonistic interactions mediated by phenotype matching may break down. Specifically, under such conditions, the victim species evolves a bimodal distribution of local mean phenotypes, which can cause the exploiter species to evolve greater diversity than it would in the absence of coevolution, even approaching bimodality itself (fig. 5).

Discussion

Our analytic and simulation results demonstrate that the effect of coevolution on diversification depends strongly on the ecological form of the interaction and the phenotypic mechanism that mediates it. Specifically, we find that although interactions mediated by phenotype differences may generate evolutionary trends toward more extreme phenotypes (Vermeij 1994), they do not increase phenotypic diversity (fig. 3). In contrast, we find that in-

teractions mediated by phenotype matching may promote diversification for those species harmed by matching. Those species that experience a benefit from closer trait matching actually diversify less than they would in the absence of coevolution (fig. 3). An exception to this result is the case of exploiters that are selected to match their victims: our simulations revealed that under very strong coevolutionary selection, exploiters may evolve greater phenotypic diversity as their victims do so (fig. 5).

Our analysis is the first to examine coevolutionary diversification across a metapopulation in a range of ecological interactions mediated by different possible fitness functions and to explicitly compare diversification due to coevolution with that arising from genetic drift and spatially structured abiotic selection alone. However, our results are largely consistent with previous work examining one or a few of the interactions we model. For instance, modeling the evolution of multilocus quantitative trait variation in coevolving mutualists, competitors, or antagonists, Kopp and Gavrilets (2006) found that variation within a single population evolves much as we have shown for variation across a metapopulation. Similarly, Devaux and Lande (2009) found that competition for generalist pollinators could promote divergence in flowering time and reproductive isolation within a population of animal-pollinated plants.

Kiester et al. (1984) modeled a matching mutualism (with specific reference to obligate pollination mutualism) and found that selection for phenotype matching constrains the mutualists to remain on an adaptive ridge. They concluded that this should allow isolated populations of mutualists to evolve away from one another because of drift, sexual selection, or selection from the abiotic environment (Kiester et al. 1984). Our model, which explicitly incorporates effects of drift and stabilizing abiotic selection, demonstrates that the constraints of matching mutualisms can actually act against these diversifying forces.

Models following the adaptive dynamics framework have generally found increased diversification (evolutionary branching) in competitive (e.g., Dieckmann and Doebeli 1999; Bolnick 2006) or antagonistic (e.g., Calcagno et al. 2010) interactions, although few have explicitly compared different kinds of species interaction. Doebeli and Dieckmann (2000) compared competition, antagonistic interactions, and mutualism and found that all three could promote evolutionary branching, including simultaneous branching for mutualists as predicted by Kiester et al. (1984). This result for mutualism would seem to contrast with our findings, but branching in Doebeli and Dieckmann's (2000) model of mutualism is driven by selection for resource optima that differ for each interacting species, resulting in one population that is entirely dependent on the benefits of the mutualism (e.g., nectar rewards) and a
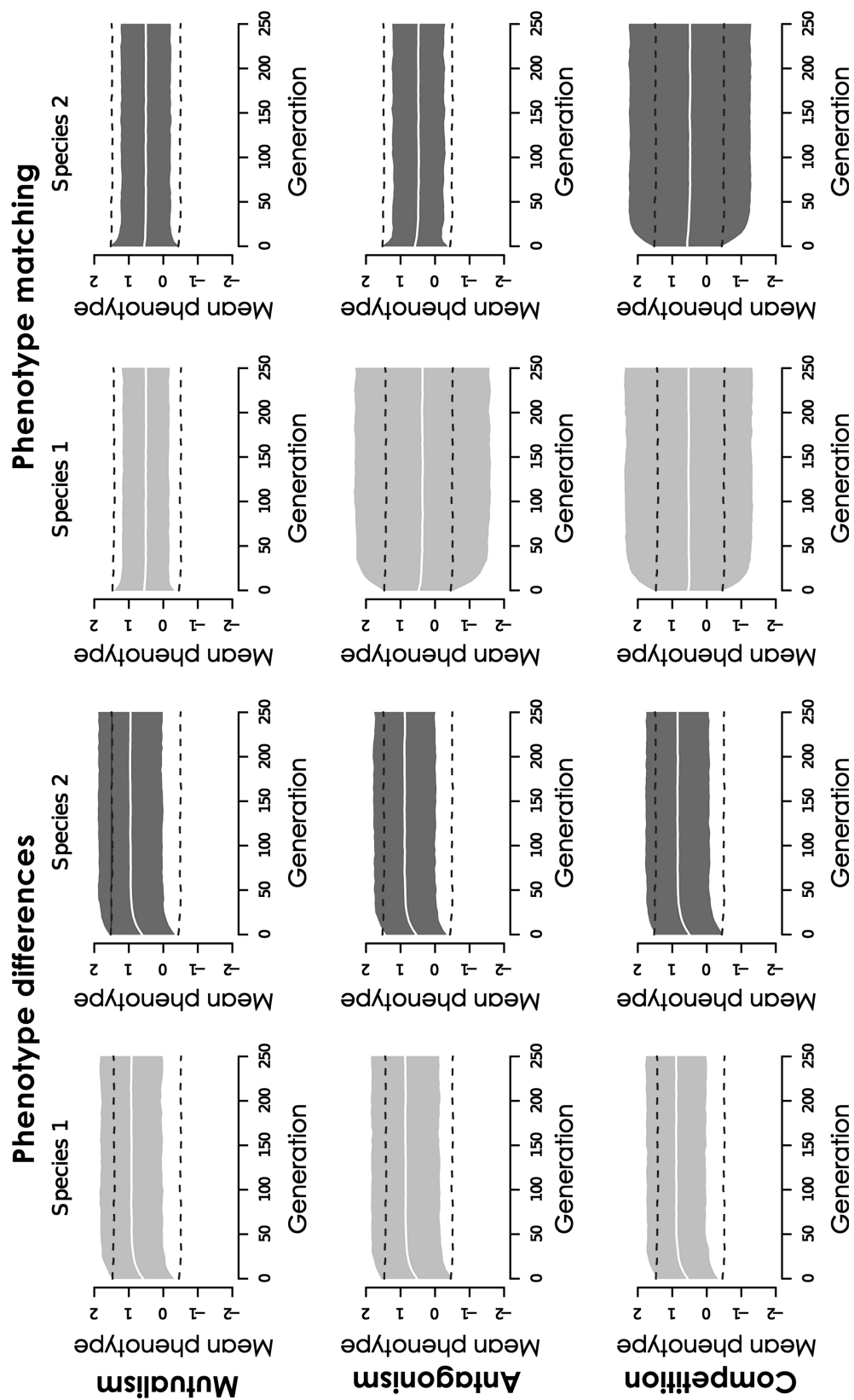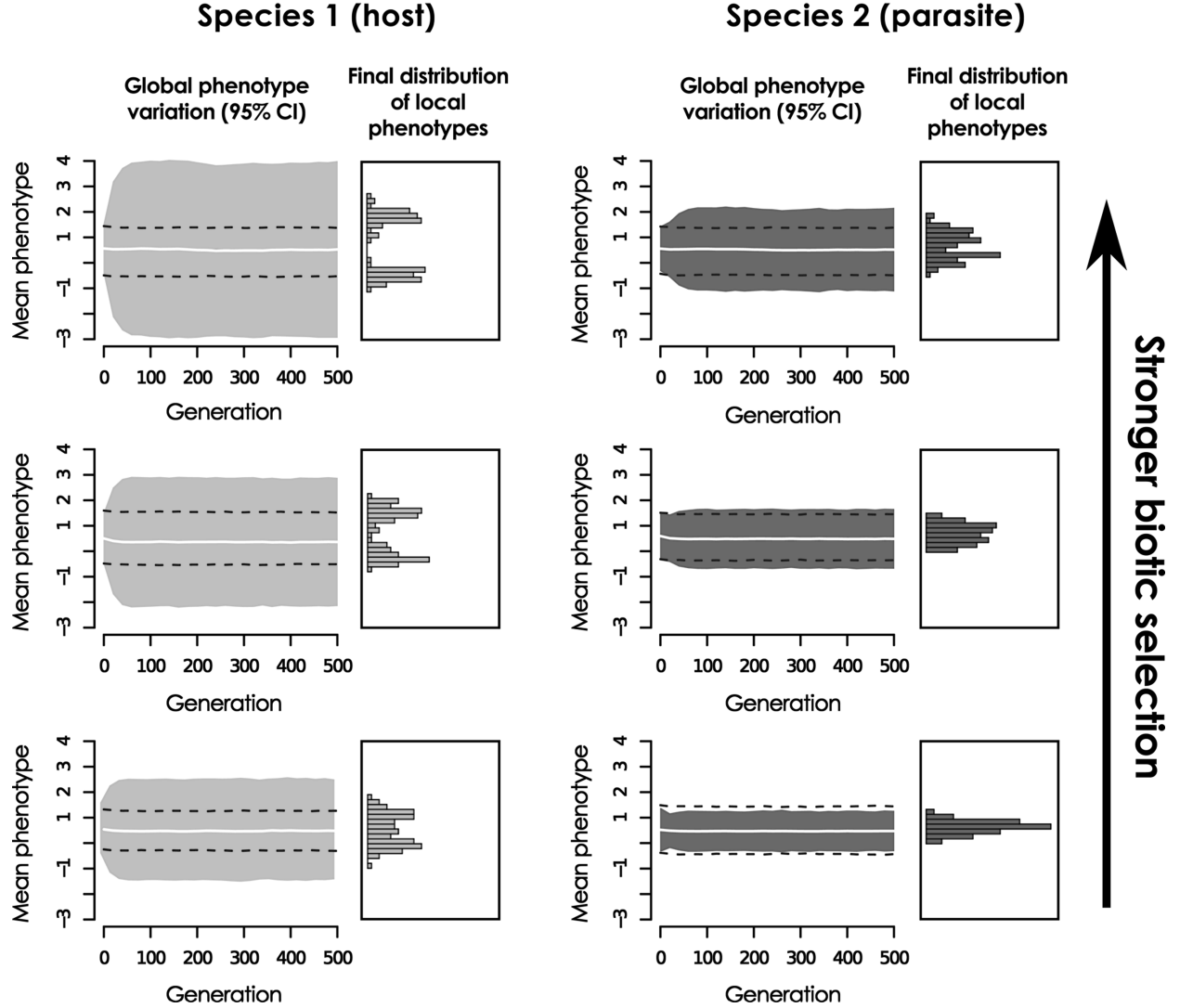
Final global phenotypic variance
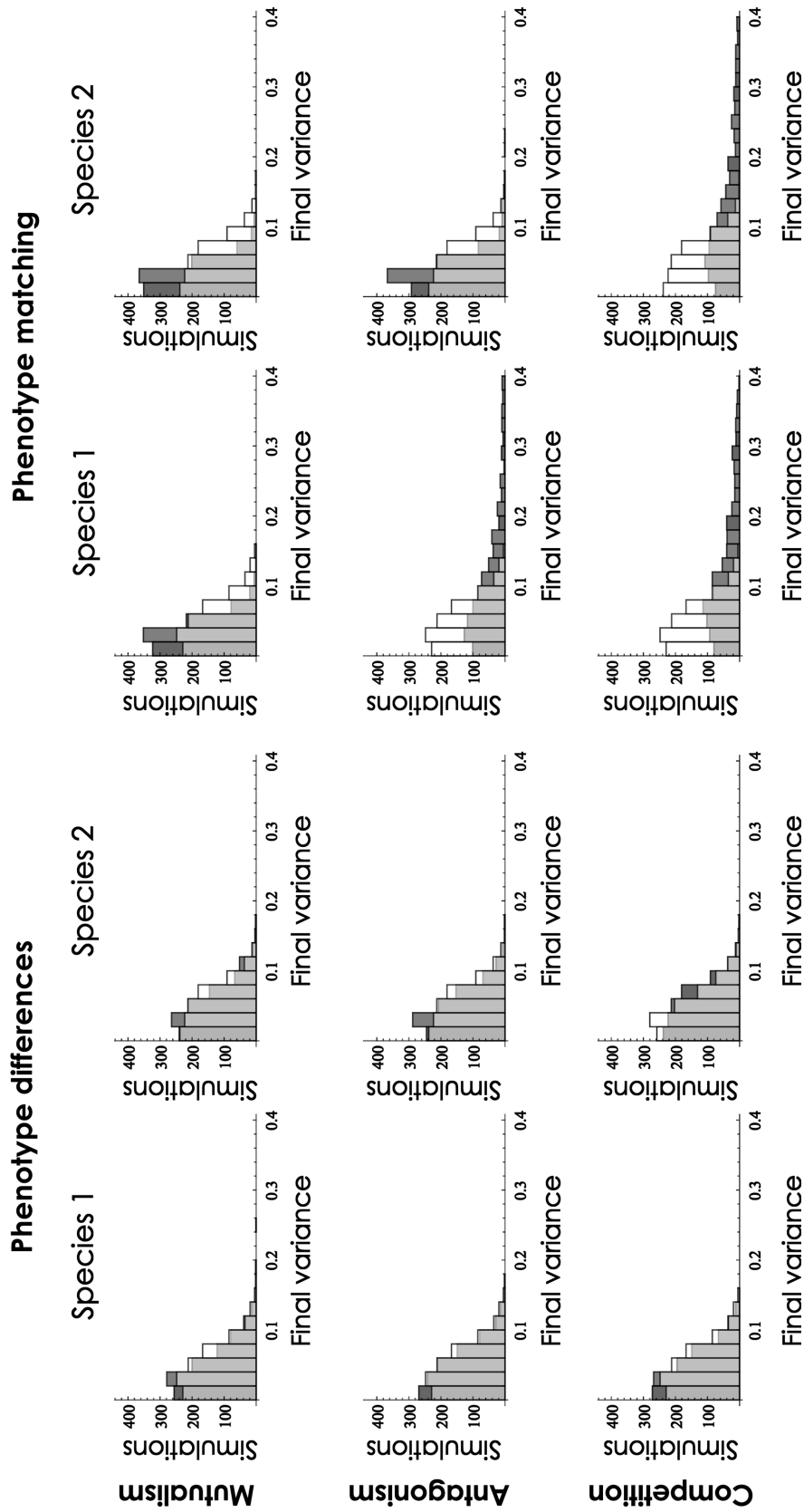
Figure 3: Distribution of final global phenotypic variance under different species interactions. For each of the six interaction types simulated, the distribution of final global phenotypic variance (i.e., diversity) of each species (*dark gray*) is overlaid with the distribution of final global phenotypic variances resulting from evolution without species interactions (*light gray*) for comparison. For each interaction type and a scenario where coevolutionary selection was absent, 1,000 replicate simulations were run for 1,000 generations under the parameters given in table 2, well past the point at which global phenotypic variation stabilized (see fig. 4). All interactions mediated by phenotype differences resulted in similar diversity to evolution without coevolutionary selection. Interactions mediated by phenotype matching reduced diversity in species that received a benefit of closer matching (both species, matching mutualism; species 1, matching mutualism; species 1, matching antagonism) but increased diversity for species that experienced a cost of closer matching (species 2, matching antagonism; both species, matching competition).

810

95% C.I. of local mean phenotypes over time

Figure 4: Evolution of global phenotypic variance under different species interactions. For each of the six interaction types considered, the shaded areas indicate the 95% confidence interval around the global mean phenotype (*white lines*) for species 1 (*light gray*) and species 2 (*dark gray*) over 250 generations of simulated coevolution under the parameters given in table 2. Dashed black lines indicate the 95% confidence interval of the global mean phenotype under evolution without coevolutionary selection. Interactions mediated by phenotype differences result in increased local and global mean phenotype values but no substantial change in global phenotypic variation (*left column*). Interactions mediated by trait matching lead to no change in the global mean phenotype, but they reduce the global phenotypic variation in species that benefit from closer matching and increase variation in species that experience a cost of closer matching.

Strength of biotic selection and equlibrium variance in matching antagonism

Species 1 (host)

Global phenotype variation (95% CI)   Final distribution of local phenotypes

Species 2 (parasite)

Global phenotype variation (95% CI)   Final distribution of local phenotypes

Stronger biotic selection

Figure 5: Evolution of global phenotypic variation in matching antagonism under varying strengths of coevolutionary selection. As in figure 2, shaded areas indicate 95% CIs of local mean phenotypes over time under the coevolutionary interaction and dotted lines indicated 95% CIs of local mean phenotypes in the absence of coevolution. Boxes to the right of each time series display histograms of the local mean phenotypes for each species in the final generation of the simulation. For all other interaction types, the qualitative predictions of the analytic model are robust to strong coevolutionary selection (high α and ξ); however, in antagonistic interactions mediated by phenotype matching, strong coevolutionary selection can cause species 1 (the "host") to evolve a bimodal distribution of local mean phenotypes, causing species 2 (the "parasite") to evolve to an equilibrium variation that is greater than that achieved in the absence of coevolution. Simulation parameters are as in table 2 for all three cases shown, except that the strength of coevolutionary selection increases from the bottom to the top: $\alpha_i = \alpha_j = 4$, $\xi_{Mi} = -0.2$, $\xi_{Mj} = 0.2$ (*bottom*); $\alpha_i = \alpha_j = 7$, $\xi_{Mi} = -0.35$, $\xi_{Mj} = 0.35$ (*middle*); $\alpha_i = \alpha_j = 10$, $\xi_{Mi} = -0.5$, $\xi_{Mj} = 0.5$ (*top*).

second population that is reliant on some external food resource.

When Does Coevolution Not Promote Diversification?

Our results suggest that several types of coevolutionary interaction that have been associated with diversification may not, in themselves, be capable of promoting diversity. Most broadly, we find that all types of interaction mediated by phenotype differences, such as predator-prey arms races (Dawkins and Krebs 1979) or a "Darwin's race" between plants and pollinators (Whittall and Hodges 2007), do not generate increased diversity even though they do drive trends toward more extreme phenotype values at both the local level and across the metapopulation. This is consistent with the results of empirical studies that have generally found that diversification in such systems is not driven by the selection generated by the interaction per se. For instance, floral diversity in the genus *Aquilegia* is better explained by rapid adaptation of the plants' nectar spurs to pollinator tongue length following pollinator shifts than by gradual and sustained arms-race dynamics (Whittall and Hodges 2007). Similarly, plant production of secondary defensive chemicals has been shown to increase over phylogenetic (Agrawal et al. 2009) and ecological (Zangerl et al. 2008) timescales, but diversification of specialist herbivores in such systems seems to have begun after diversification of their host plants was substantially underway (e.g., Wheat et al. 2007), which is not consistent with the hypothesis that diversification is driven by coevolutionary selection. In such systems, it has been argued that coevolution driven by phenotype differences has generated phenotype matching between local populations of the interacting species (e.g., Nattero and Cocucci 2007; Anderson and Johnson 2008, but see Nuismer et al. 2010), but trait matching driven by coevolution need not imply increased diversity across the species as a whole.

We also find that coevolution should act to slow diversification in species under selection to match the phenotypic traits of other species. This applies both to many forms of mutualism, and, perhaps more surprisingly, to parasites selected to match their hosts (fig. 4). The former case is supported by recent studies of phenotype matching in yuccas and yucca moths that found that these mutualists are so strongly matched at the species level that there remains little variation in matching among local populations within species (Godsoe et al. 2008, 2010). However, mutualism has also been proposed to create diversification via the evolution of nonmutualistic "cheater" phenotypes (Pellmyr and Leebens-Mack 2000; Law et al. 2001; Ferriere et al. 2007). Because our model does not consider such evolutionary changes to the fundamental fitness outcomes of the interaction (i.e., from a benefit of closer phenotype matching to a cost), it cannot directly address the conditions under which the evolution of cheating may promote diversification in these systems.

In contrast, the finding that coevolution may restrict the diversification of exploiters selected to match their victims' phenotypes is somewhat counterintuitive, but it is explained by the parameter space under consideration. Under weak coevolutionary selection, as is assumed in our analytic model, the victim's distribution of population mean phenotypes remains unimodal even as its variance increases, so that the average exploiter population evolves toward the victim's global mean phenotype. This results in reduced global phenotypic variance for the exploiter (table 3; fig. 4). However, as we discuss below, this result breaks down under stronger coevolutionary selection.

When Does Coevolution Promote Diversification?

Divergence in the face of gene flow is thought to become easier as selection acts on more independent traits (Nosil et al. 2009; Doebeli and Ispolatov 2010). This suggests that our model, in which a single trait evolves under selection from both the biotic and abiotic environments, may be quite conservative in its estimation of conditions permitting divergence. Even under such restrictive circumstances, however, we find that some coevolutionary interactions can promote increased phenotypic diversity.

Specifically, our model finds that interactions that impose a cost of phenotype matching should increase diversity. Interactions of this sort include parasites evading hosts' immune systems, hosts avoiding egg mimicry by brood parasites, and competitors excluding each other from particular regions of niche space. All of these specific interactions have been implicated in diversification. Avian brood parasitism has indeed been shown to maintain diversity in egg coloration within natural host populations (Lahti 2005; Yang et al. 2010), although it has not been implicated in increased rates of host speciation. Selection by host immune system recognition is thought to maintain antigenic diversity in malaria parasites (Ferreira et al. 2004), and it has apparently resulted in intrahost speciation in at least one case (Pérez-Tris et al. 2007). Finally, competitive exclusion has been widely demonstrated to select for increased resource-use diversity in experimental microbial systems (Kassen 2009), and it is implicated in the classic adaptive radiations of freshwater sticklebacks (Svanbäck and Bolnick 2007), Darwin's finches (Grant and Grant 2006, 2008), and Caribbean *Anolis* lizards (Losos 2009), among many other systems.

Although we generally found that exploiters that are selected to match their victims' phenotypes should diversify more slowly than they would in the absence of coevolutionary selection (table 3; fig. 3), our exploration of

parameter space with the individual-based simulations found that under very strong coevolutionary selection, the distribution of the victims' local mean phenotypes becomes bimodal, causing the exploiter to evolve greater global phenotypic variance than it would in the absence of coevolution (fig. 5). Interestingly, this closely parallels the result of a recent survey of egg-color variation in a single population of passerine songbirds and the common cuckoos who parasitize their nests: the host population has evolved strongly dimorphic egg coloration, and the cuckoos have evolved similarly dimorphic eggs, but the differentiation within the cuckoo population is not as strong as that within the host population (Yang et al. 2010). Increased rates of speciation in brood-parasitic cuckoo lineages (Krüger et al. 2009) may therefore be explained by strong selection to match host eggs and avoid egg eviction, as well as by brood parasites competing for available host species.

Conclusions

By modeling two species that are coevolving across a metapopulation and are subject to the noncoevolutionary forces of spatially structured abiotic selection and genetic drift, we have attempted to rigorously identify specific types of species interaction that are able to promote phenotypic diversification in the face of gene flow. Although we do not explicitly model speciation, ecological differentiation can be a major contributor to reproductive isolation (Coyne and Orr 2004; Nosil et al. 2005; Schluter 2009), and increased phenotypic diversity is therefore widely considered to be a first step toward adaptive radiation (Darwin 1859; Schluter 2000; Thompson 2005; Gavrilets and Losos 2009; Yoder et al. 2010). Even if ecological speciation rarely contributes to evolutionary diversification (Coyne and Orr 2004), interactions that promote phenotypic diversity can provide more variation to be subdivided by allopatric speciation, leading to more diverse descendent taxa (Futuyma 1987).

Our analytic model and individual-based simulations of evolution suggest that coevolution can indeed promote diversification when species interactions impose a cost of closer phenotype matching, as in the cases of hosts evading parasites or competitors excluding each other from specific regions of niche space. Our results also suggest that there are many coevolutionary interactions that may not promote diversification, as in the case of interactions mediated by phenotype differences, or that even restrict it, as in the case of interactions in which species benefit from closer phenotype matching. Increased rates of diversification in species engaged in such interactions must therefore be explained by processes in addition to coevolutionary selection. These results may help to explain why recent empirical studies of plant-herbivore (Janz et al. 2006; Wheat et al. 2007; McKenna et al. 2009) and pollination (Armbruster and Muchhala 2009) interactions have suggested that competition within trophic guilds, rather than antagonistic or mutualistic interactions between them, has driven their diversification. Our model suggests that the causes underlying many other putative cases of coevolutionary diversification may require reassessment.

APPENDIX

Equilibria for the Analytic Model

The equilibrium of the closed system describing the evolution of among-population phenotypic variance for each species ($\hat{\sigma}_{z_i}^2$) and the covariance of the two species phenotypes across the entire metapopulation ($\hat{\sigma}_{\bar{z}_i, \bar{z}_j}$) is given by

$$\hat{\sigma}_{z_i}^2 = \frac{\nu_j R_{Mi}^2 + \nu_j\{-4R_{Mi}R_{Mj} + (m_j + 2R_{Tj})[m_i + m_j + 2(R_{Ti} + R_{Tj})]\}}{2[m_i + m_j + 2(R_{Ti} + R_{Tj})][-4R_{Mi}R_{Mj} + (m_i + 2R_{Ti}) + (m_j + 2R_{Tj})]}, \tag{A1}$$

$$\hat{\sigma}_{\bar{z}_i, \bar{z}_j} = \frac{\nu_j R_{Mi} + (m_i + 2R_{Ti}) + \nu_i R_{Mj}(m_j + 2R_{Tj})}{2[m_i + m_j + 2(R_{Ti} + R_{Tj})][-4R_{Mi}R_{Mj} + (m_i + 2R_{Ti}) + (m_j + 2R_{Tj})]}, \tag{A2}$$

where $\nu_i = G_i/n_i$, $R_{Mi} = G_i S_{Mi}$, $R_{Ai} = G_i \gamma_i$, and $R_{Ti} = R_{Mi} + R_{Ai}$.

Stability of the Equilibrium

The eigenvalues of the Jacobian matrix generated from the variance-covariance recursion equations (eqq. [11a] and [11b] in main text) and the equilibria are

$$\lambda_1 = -[2(R_{Ti} + R_{Tj}) + m_i + m_j], \tag{A3}$$

$$\lambda_2 = -[2(R_{Ti} + R_{Tj}) + m_i + m_j] + \sqrt{[2(R_{Ti} - R_{Tj}) + m_i - m_j]^2 + 16R_{Mi}R_{Mj}}, \tag{A4}$$

$$\lambda_3 = -[2(R_{Ti} + R_{Tj}) + m_i + m_j] - \sqrt{[2(R_{Ti} - R_{Tj}) + m_i - m_j]^2 + 16R_{Mi}R_{Mj}}. \tag{A5}$$

Assuming that all evolutionary forces are weak allows us to analyze the stability of the system of discrete recursions as a continuous time system. Examination of the leading eigenvalue, λ_2, reveals that the system is stable only when $2(R_{Ti} + R_{Tj}) + m_i + m_j > 0$ and when

$$[2(R_{Ti} + R_{Tj}) + m_i + m_j]^2 \geq [2(R_{Ti} - R_{Tj}) + m_i - m_j]^2 + 16R_{Mi}R_{Mj},$$

$$(m_i + 2R_{Mi} + 2R_{Ai})(m_j + 2R_{Mj} + 2R_{Aj}) \geq 4R_{Mi}R_{Mj},$$

$$2R_{Mi}(m_j + 2R_{Aj}) + 2R_{Mj}(m_i + 2R_{Ai}) + (m_i + 2R_{Ai})(m_j + 2R_{Aj}) \geq 0,$$

$$\frac{2R_{Mi}}{m_i + 2R_{Ai}} + \frac{2R_{Mj}}{m_j + 2R_{Aj}} \geq -1. \tag{A6}$$

The system will oscillate when

$$[2(R_{Ti} - R_{Tj}) + m_i - m_j]^2 + 16R_{Mi}R_{Mj} < 0. \tag{A7}$$

Thus, coevolutionary cycles are not possible in interactions mediated by phenotype differences, matching mutualism, or matching competition because $16R_{Mi}R_{Mj} \geq 0$ for these interactions. In contrast, antagonistic interactions mediated by phenotype matching may generate coevolutionary cycles any time $16R_{Mi}R_{Mj} < 0$.

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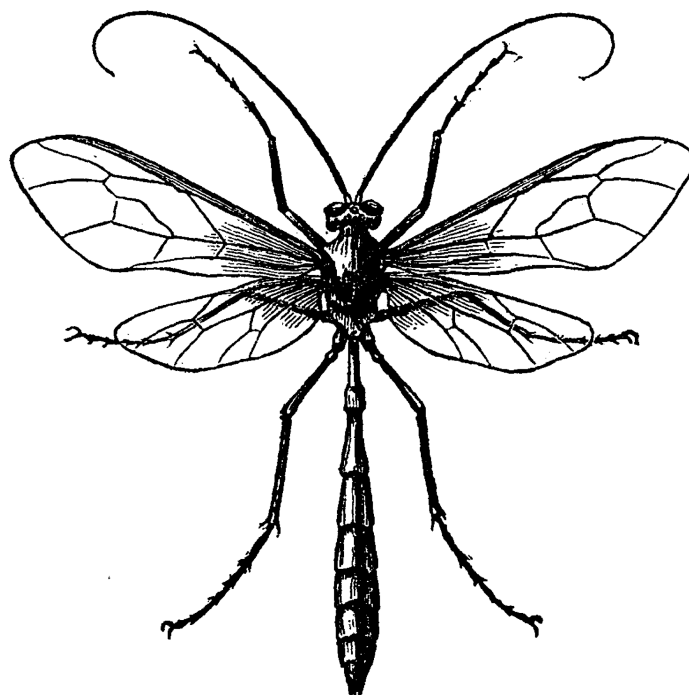
Ophion macrurum Linn., Ichneumon parasite of the silk worm. From "The American Silk Worm" by L. Trouvelot (*American Naturalist*, 1867, 1: 85–94).