



COEVOLUTION AND THE ARCHITECTURE OF MUTUALISTIC NETWORKS

Scott L. Nuismer,^{1,2} Pedro Jordano,³ and Jordi Bascompte³

¹Department of Biological Sciences & Institute for Bioinformatics and Evolutionary Studies, University of Idaho, Moscow, ID 83844

²E-mail: snuismer@uidaho.edu

³Integrative Ecology Group, Estación Biológica de Doñana, CSIC E-41080, Sevilla, Spain

Received May 18, 2012

Accepted August 15, 2012

Data Archived: Dryad doi:10.5061/dryad.tk400

Although coevolution is widely recognized as an important evolutionary process for pairs of reciprocally specialized species, its importance within species-rich communities of generalized species has been questioned. Here we develop and analyze mathematical models of mutualistic communities, such as those between plants and pollinators or plants and seed-dispersers to evaluate the importance of coevolutionary selection within complex communities. Our analyses reveal that coevolutionary selection can drive significant changes in trait distributions with important consequences for the network structure of mutualistic communities. One such consequence is greater connectance caused by an almost invariable increase in the rate of mutualistic interaction within the community. Another important consequence is altered patterns of nestedness. Specifically, interactions mediated by a mechanism of phenotype matching tend to be antinested when coevolutionary selection is weak and even more strongly antinested as increasing coevolutionary selection favors the emergence of reciprocal specialization. In contrast, interactions mediated by a mechanism of phenotype differences tend to be nested when coevolutionary selection is weak, but less nested as increasing coevolutionary selection favors greater levels of generalization in both plants and animals. Taken together, our results show that coevolutionary selection can be an important force within mutualistic communities, driving changes in trait distributions, interaction rates, and even network structure.

KEY WORDS: Dispersal, mutualism, network structure, nestedness, pollination.

Coevolution has been demonstrated to be an important force shaping the evolution and ecology of tightly interacting pairs of species. For instance, theoretical studies suggest that interactions generating intense coevolutionary selection can favor the evolution of sexual reproduction under some circumstances (Otto and Nuismer 2004; Agrawal 2006; Salathe et al. 2008; Lively 2010) and even modest levels of coevolutionary selection can favor transitions between ploidy levels (Nuismer and Otto 2004), levels of local adaptation (Gandon et al. 1996; Lively et al. 2004; Gandon and Nuismer 2009), or patterns of mate choice (Nuismer et al. 2008). In addition to contributing to such evolutionary transitions, both theoretical and experimental studies suggest that coevolution shapes predator–prey and epidemiologi-

cal dynamics (Abrams 2000; Burdon and Thrall 2000). Together, this body of work clearly demonstrates that when pairs of species interact tightly and persistently, coevolution is a potent ecological and evolutionary force.

Although the importance of coevolution in tightly specialized pairwise interactions is widely recognized, its significance for species-rich communities, which include more generalized interactions—such as those between plants and their pollinators or seed dispersers—is much debated. In short, this debate centers on the extent to which coevolution between individual pairs of species remains important and influential when any given species likely interacts with many other species, each of which may impose conflicting selection pressures (Hougenieztman and

Rausher 1994; Iwao and Rausher 1997; Stinchcombe and Rausher 2001; Strauss and Irwin 2004). In the face of so many potentially conflicting selection pressures it is often argued that pairwise coevolution becomes unimportant and species interactions evolve through only a diffuse mechanism (Iwao and Rausher 1997). A resolution to this debate has been slow in coming primarily because studying coevolution within complex multispecific communities of generalized species is a formidable empirical and theoretical challenge.

Recently, significant strides have been made in better understanding the structure, function, and evolutionary origin of highly diversified communities of mutualists by estimating summary statistics that describe the patterns of interaction among community members and the distribution of phenotypes characterizing interacting species. This approach has revealed that mutualistic communities of plants and their pollinators or seed dispersers show repeated and predictable patterns. Specifically, such communities tend to be nested such that the more specialized pollinator or disperser species interact with the most generalized plant species and vice versa (Bascompte et al. 2003; Bascompte and Jordano 2007). Put differently, within a nested community the most specialized partners (animals or plants) interact only with proper subsets of those partner species interacting with the most generalized ones. In addition, the traits of the species within these communities tend to be convergent, such that both animal and plant species have more similar phenotypes for traits relevant to mutualistic interactions than expected by chance (Bascompte and Jordano 2007). Finally, traits of interacting species tend to be complementary meaning that those species within the community that do interact with one another have similar phenotypic values for the traits involved in the mutualistic interaction (Bascompte and Jordano 2007). Although it is generally thought that these patterns are generated by a combination of species abundances, trait distributions, and phylogenetic history (Guimarães et al. 2007; Rezende et al. 2007; Santamaría and Rodríguez-Gironés 2007; Bluthgen et al. 2008; Krishna et al. 2008; Verdú and Valiente-Banuet 2010; Fontaine et al. 2011), it is also possible they are the product of coevolution (Thompson 2005; Guimarães et al. 2011).

Only one previous study has explored how coevolution shapes these commonly observed properties of mutualistic communities (Guimarães et al. 2011). In this study, coevolutionary models were built upon a scaffold defined by patterns of interaction observed within real mutualistic communities. This study revealed that coevolution plays an important role within mutualistic communities by increasing levels of trait complementarity and convergence; a result previously predicted by Kiestler et al. (1984) and by verbal arguments (Thompson 2005). Specifically, Guimarães et al. (2011) showed that although pairwise coevolu-

tion represents only a small fraction of total evolutionary change, it has pervasive influences on levels of trait complementarity and convergence. Because this study assumed a fixed network structure, however, a key question remains unanswered: does coevolutionary selection itself drive changes in the network structure of mutualistic communities?

In an effort to address this gap in our understanding, we develop and analyze a very general quantitative genetic model that allows the network structure of mutualistic communities to itself evolve and coevolve. Specifically, we use our model to address the following questions: (1) Does coevolutionary selection increase the connectance and overall interaction rate of mutualistic communities? (2) Under what conditions does coevolutionary selection promote the convergence and matching of traits mediating mutualistic interactions? (3) Does coevolutionary selection alter levels of nestedness within mutualistic communities?

The General Model

We model the evolution and coevolution of N_A animal and N_P plant species living in sympatry. Each animal species i has a fixed population size of $n_{A,i}$, and each individual is characterized by a single phenotype y . Similarly, each plant species i has a fixed population size $n_{P,i}$, and each individual is characterized by a single phenotype z . Individuals encounter one another at random and individual fitness is assumed to depend on the abiotic environment and mutualistic interactions.

Specifically, we assume that the fitness of an individual of animal species i with phenotype y is given by

$$W_{A,i}(y) = \exp[-\gamma_A(y - \theta_{A,i})^2](1 + \xi_{A,i}\pi(y, z)), \quad (1a)$$

and that the fitness of an individual of plant species i with phenotype z is given by

$$W_{P,i}(z) = \exp[-\gamma_P(z - \theta_{P,i})^2](1 + \xi_{P,i}\pi(y, z)). \quad (1b)$$

The first term in (1) measures the reduction in fitness caused by deviating from the optimal phenotype favored by the abiotic environment for animal species i ($\theta_{A,i}$) and for plant species i ($\theta_{P,i}$), with larger values of γ indicating a greater sensitivity of fitness to deviations from the optimum. The second term in (1) captures the fitness benefit accrued by encountering and successfully interacting with a mutualistic individual with phenotype z (for animals) or y (for plants). Specifically, if the individuals interact successfully (which occurs with probability π), the fitness of the focal individual is increased by $\xi_{j,i}$.

Whether an encounter between an individual animal and plant leads to a successful interaction depends on the phenotypes (y and z) of the interacting individuals. We consider two possible functional relationships between the traits of the

interacting species. The first functional relationship, which we refer to as the “phenotype matching” model (e.g., Nuismer et al. 2005; Kopp and Gavrillets 2006), assumes that the probability of successful interaction decreases with increasing distance between the phenotypes of the interacting individuals such that

$$\pi = \exp[-\alpha(y - z)^2]. \tag{2a}$$

This model corresponds to a scenario where successful interaction depends on the match between animal and plant trait as could be the case for plant and animal phenology in both dispersal and pollination mutualisms (Jordano et al. 2003; Olesen et al. 2010; Campbell et al. 2011) or proboscis and corolla lengths in some pollination mutualisms (Agosta and Janzen 2005; Santamaría and Rodríguez-Gironés 2007; Stang et al. 2007). The second functional relationship, which we refer to as the “phenotype differences” model (e.g., Nuismer et al. 2007), is a generalized version of what is often referred to as the “threshold model” in the ecological literature and assumes the probability of successful interaction decreases as the phenotype of the plant individual increases relative to the phenotype of the animal individual such that

$$\pi = 1/(1 + \exp[-\alpha(y - z)]) \tag{2b}$$

This model corresponds to a scenario where successful interaction depends on the degree to which the animal trait surpasses that of the plant trait as might be the case for fruit and beak size in a dispersal mutualism (Lambert 1989; da Silva and Tabarelli 2000) or proboscis and corolla length in some pollination mutualisms (Inouye 1980; Borrell 2007; Anderson and Johnson 2009; Anderson et al. 2010). These two models (matching and differences) correspond to the unidirectional and bidirectional axes of vulnerability recognized by Abrams (2000) for predator–prey interactions.

Together, the fitness functions (1) and interaction functions (2) determine the probability that individuals survive to maturity. Those individuals that survive are then assumed to mate at random within their species and produce offspring. The next generation is formed by sampling $n_{A,i}$ offspring of animal species i and $n_{P,i}$ offspring of plant species i . Because the detailed genetic assumptions underlying reproduction differ between our analytical approximation and individual based simulations, these details will be explained within the sections devoted to each of these approaches.

Analytical Approximation

To gain analytical insight into the influence of mutualistic co-evolution on community structure, we pursued an approximation to our general model. This approximation requires an important

assumption. Specifically, we will assume that the additive genetic variance for trait y in animal species i has a fixed value $G_{y,i}$, and that for trait z in plant species i a fixed value $G_{z,i}$. With this assumption, and the additional assumption that selection is weak, it is possible to use the classical quantitative genetics equation

$$\Delta \bar{x} = G_x \frac{1}{\bar{W}} \frac{\partial \bar{W}}{\partial \bar{x}}, \tag{3}$$

to predict how the population mean trait values of each species will change as a consequence of selection (Lande 1976; Gavrillets 1997; Nuismer et al. 2010). In equation (3), \bar{x} is the population mean value of trait y (in animals) or trait z (in plants), and \bar{W} is the population mean fitness of the species. To make further progress using equation (3), we must calculate the population mean fitness of each species (\bar{W}) within the community.

The first step toward calculating the population mean fitness of each species is to determine the expected fitness of individuals with specific phenotypes. Assuming that individuals encounter one another at random, this is relatively straightforward. Specifically, the expected fitness (\hat{W}) of an individual of animal species i with phenotype y is given by

$$\hat{W}_{A,i}(y) = \exp[-\gamma_A(y - \theta_{A,i})^2] \times \left(\sum_{j=1}^{N_P} f_{P,j} \int (1 + \xi_{A,i} \pi) \Phi_{z,j} dz \right). \tag{4a}$$

and the expected fitness of an individual of plant species i with phenotype z is given by

$$\hat{W}_{P,i}(z) = \exp[-\gamma_P(z - \theta_{P,i})^2] \times \left(\sum_{j=1}^{N_A} f_{A,j} \int (1 + \xi_{P,i} \pi) \Phi_{y,j} dy \right). \tag{4b}$$

In equations (4), the sums are taken over the number of interacting species and weighted by the frequency of each interacting species j , where this frequency is given by $f_{i,j} = n_{i,j} / \sum_{j=1}^{N_i} n_{i,j}$. Weighting by species frequencies captures the fact that encounters with abundant species are more likely than encounters with rare species. The terms $\phi_{z,i}$ or $\phi_{y,i}$ in (4) are the phenotype frequency distributions within species i .

To evaluate the integrals in (4), we assume the sensitivity of fitness to phenotypes is not too strong. Specifically, we assume that the parameters γ and α are of small order ϵ such that terms of $O(\epsilon^2)$ and greater can be ignored (e.g., Nuismer et al. 2010). With this assumption, equations (4) can be readily evaluated (*Mathematica* notebook available upon request) as can the population mean fitness for each animal species

$$\bar{W}_{A,i} = \int \hat{W}_{A,i} \phi_{y,i} dy, \tag{5a}$$

and each plant species

$$\bar{W}_{P,i} = \int \hat{W}_{A,i} \phi_{z,i} dz. \quad (5b)$$

Substituting (5) into (3) and ignoring terms of order $O(\epsilon^2)$ and higher, yields equations for the change in population mean phenotypes for all species within the community (Appendix 1). Surprisingly, these equations reveal that the distribution of species' abundances has no effect on deterministic coevolutionary dynamics of the interacting species, influencing evolution only through its impact on the rate of genetic drift.

The equations for the change in trait means within each species provide a complete description of evolutionary change within communities. However, using even these relatively simple equations to study the evolutionary and coevolutionary dynamics of entire communities requires studying a system of $N_A + N_P$ equations, which is intractable for communities of even modest species richness. Fortunately, the problem can be greatly simplified by making a change of variables from the trait means of the individual species to the statistical moments that describe the distribution of trait means within plants and within animals (Appendix 2). Remarkably, this change of variables reveals that—to leading order—the coevolutionary dynamics of the entire community can be described by recursion equations for only six statistical moments, irrespective of the number of species in the community. Analysis of these statistical moments reveals that mutualistic communities evolve to a stable equilibrium described by relatively simple expressions (Appendix 3). In the following sections, we use these equilibrium expressions to predict how coevolution changes three important properties of mutualistic communities: interaction efficiency, convergence, and complementarity.

INTERACTION EFFICIENCY

Using our assumption that the probability of successful mutualistic interaction does not depend too strongly on the traits of the interacting individuals (α of small order ϵ), it is possible to approximate the proportion of all encounters between plant and animal individuals that result in successful interactions; we term this quantity the “interaction efficiency” of the community. Interaction efficiency is a quantitative measure of community connectance, and these two measures are generally strongly correlated (results not shown). For the matching model, the interaction efficiency is

$$E \approx 1 - \alpha((\bar{Y} - \bar{Z})^2 + V_{\bar{y}} + V_{\bar{z}} + \bar{V}_y + \bar{V}_z) + O(\epsilon^2), \quad (6)$$

where \bar{Y} and \bar{Z} are the expected population mean phenotypes of all animal species and all plant species respectively, $V_{\bar{y}}$ and $V_{\bar{z}}$ are the variance in population mean phenotypes among all animal and plant species respectively, and \bar{V}_y and \bar{V}_z are the expected phenotypic variance within animal species and plant species respectively (Appendix 4). Thus, equation (6) reveals that—for the

matching model—interaction efficiency falls as average animal and plant phenotypes diverge and as phenotypic variation increases both within and among species. Greater insight into the role coevolution plays in shaping the interaction efficiency of mutualistic communities can be obtained by substituting the equilibrium expressions for \bar{Y} , \bar{Z} , $V_{\bar{y}}$, and $V_{\bar{z}}$ found in Appendix 3 into (6). Evaluating the resulting expression numerically shows that increasing the average strength of coevolutionary selection increases the interaction efficiency of the community at equilibrium (Fig. 1A).

For those interactions mediated by phenotypic differences, we find that the interaction efficiency is

$$E = \frac{1}{2} - \frac{\alpha}{4}(\bar{Z}_j - \bar{Y}_i) + O(\epsilon^2). \quad (7)$$

Equation (7) reveals that unlike mutualistic interactions mediated by the matching model, interactions mediated by the phenotypic differences model are independent of the variance within and among species. Instead, interaction efficiency falls as the expected value of plant population mean phenotypes increases relative to the expected value of animal population mean phenotypes. Despite this difference between the specific factors contributing to interaction efficiency in the matching and difference models, substituting the equilibrium expressions for \bar{Y} and \bar{Z} derived in Appendix 3 into (7) demonstrates that mutualistic coevolution mediated by the difference model also invariably increases the interaction efficiency of the community (Fig. 2).

CONVERGENCE

Our analytical approximation can also be used to evaluate how mutualistic coevolution shapes trait convergence within mutualistic communities. Again, assuming that the probability of successful interaction depends only weakly on the traits of the interacting individuals, it is possible to derive approximate expressions for the variance in population mean phenotypes among the subset of animal and plant species that interact with one another. Large values of these variances indicate weak convergence whereas small values of these variances indicate strong convergence. For the matching model, we find that the variance in population mean phenotypes among animal species that successfully interact with plant species is

$$V[\bar{y}'] \approx V_{\bar{y}}(1 - 2\alpha V_{\bar{y}}) + O(\epsilon^2), \quad (8a)$$

and among plant species that successfully interact with animal species is

$$V[\bar{z}'] \approx V_{\bar{z}}(1 - 2\alpha V_{\bar{z}}) + O(\epsilon^2), \quad (8b)$$

where primes indicate values within the bivariate distribution of successfully interacting individuals. Substituting the equilibrium expressions for $V_{\bar{y}}$, and $V_{\bar{z}}$ found in Appendix 3 into (8) reveals

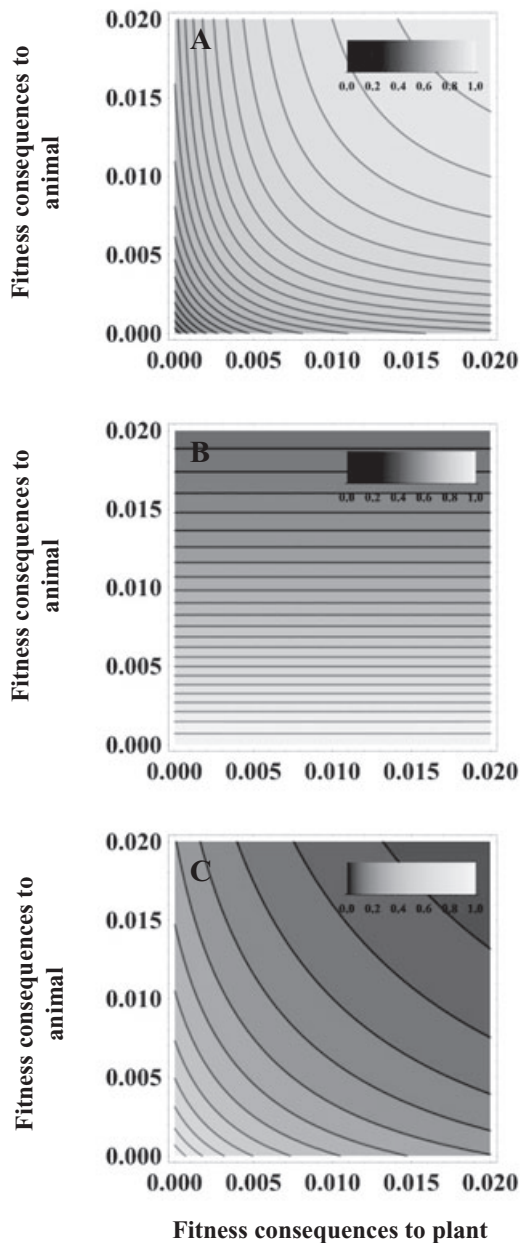


Figure 1. Analytical predictions for equilibrium values of (A) interaction efficiency, (B) convergence, and (C) complementarity for the matching model as a function of the average fitness consequences of interactions for plants and animals. Coevolution is most intense when average fitness consequences are great for both plants and animals. Parameter values: $\alpha = 0.03$, $\gamma_A = 0.005$, $\gamma_P = 0.005$, $V_{\theta_A} = 8$, $V_{\theta_P} = 8$, $n_A = 1000$, and $n_P = 1000$.

two important conclusions. First, the level of convergence in plants and animals is decoupled: changing parameters unique to plant species have no impact on convergence of animal traits and vice versa (Fig. 1B). Second, increasing the strength of coevolutionary selection imposed on animals by plants increases the convergence of animal traits and vice versa (Fig. 1B).

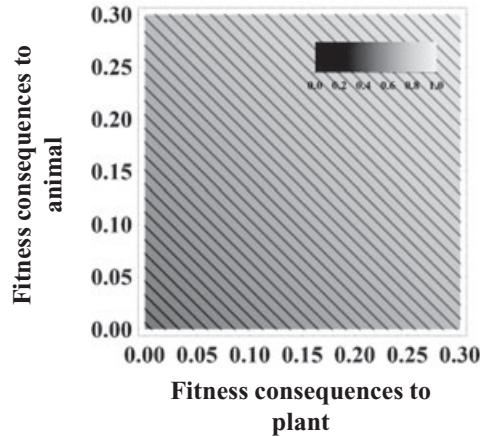


Figure 2. Analytical predictions for equilibrium interaction efficiency for the differences model as a function of the average fitness consequences of interactions for plants and animals. Coevolution is most intense when average fitness consequences are great for both plants and animals. Parameter values are identical to Figure 1.

For those interactions mediated by phenotypic differences, we find that the variance in population mean phenotypes among animal species observed to interact with plant species is

$$V[\bar{y}'] \approx V_{\bar{y}} + O(\epsilon^2), \tag{8c}$$

and among plant species observed to interact with animal species is

$$V[\bar{z}'] \approx V_{\bar{z}} + O(\epsilon^2), \tag{8d}$$

where primes indicate values within the bivariate distribution of successfully interacting individuals. As with interactions mediated by phenotype matching, substituting the equilibrium expressions for $V_{\bar{y}}$, and $V_{\bar{z}}$ found in Appendix 3 into (8) reveals that convergence in plants and animals is decoupled. In contrast to interactions mediated by phenotype matching, however, levels of convergence are independent of the strength of pairwise coevolutionary selection imposed by the interacting species and are instead solely a function of populations sizes and stabilizing selection: pairwise coevolution plays no role in shaping the convergence of such interactions.

COMPLEMENTARITY

In addition to allowing us to study how coevolution shapes interaction efficiency and convergence, our analytical approximation makes it possible to determine how coevolution changes levels of complementarity between interacting species. Specifically, our approximation allows us to calculate the correlation between the mean phenotypes of those animal and plant species that successfully interact. For interactions mediated by phenotype matching, the correlation between the mean phenotypes of interacting

animals and plants is

$$\rho \approx \frac{2\alpha V_{\bar{y}} V_{\bar{z}}}{\sqrt{V_{\bar{y}}(1-2\alpha V_{\bar{y}})}\sqrt{V_{\bar{z}}(1-2\alpha V_{\bar{z}})}} + O(\epsilon^2). \quad (9a)$$

Substituting the equilibrium expressions for $V_{\bar{y}}$ and $V_{\bar{z}}$ found in Appendix 3 into (9) and evaluating numerically, demonstrates that mutualistic coevolution decreases the correlation between the traits of interacting species whenever interactions are mediated by phenotypic matching (Fig. 1C).

In contrast, for those interactions mediated by phenotypic differences, the correlation between the mean phenotypes of interacting animal and plant species is

$$\rho \approx 0 + O(\epsilon^2). \quad (9b)$$

Thus, equation (9) demonstrates that when interactions are mediated by phenotype differences and the probability of successful interaction is not too sensitive to the traits of interacting individuals, the traits of interacting animal and plant species should be uncorrelated.

In summary, our analytical results predict that coevolution should always increase the interaction efficiency of mutualistic communities irrespective of the underlying mechanism of interaction (i.e., matching vs differences). In contrast, whereas coevolution mediated by phenotype matching increases trait convergence and decreases trait complementarity, coevolution mediated by phenotype differences has no effect on these metrics. Although these analytical results provide valuable insight, they rely on several important assumptions such as fixed additive genetic variance and phenotypes that are not too divergent. Perhaps more importantly, our analytical approach does not allow us to evaluate how coevolution influences nestedness, one of the most commonly studied properties of mutualistic networks (Bascompte et al. 2003; Vázquez et al. 2009; Fortuna et al. 2010; Joppa et al. 2010). For these reasons, we complement our analytical approximations with individual-based simulations that relax the key assumptions of our analytical model and allow nestedness to be easily calculated.

Individual-Based Simulations

Simulations tracked individual animals and plants over a life cycle consisting of (1) abiotic selection, (2) biotic selection, and (3) random mating and reproduction. Abiotic and biotic selections were implemented by calculating the fitness of each individual animal and plant using equations (1–2) under the assumption that η encounters occur between randomly selected animal and plant individuals within each generation. When an encounter occurs, fitness benefits of the mutualism accrue only if the interaction is successful, with success requiring that a randomly drawn number is less than the value of π calculated for the encountering individuals using equation (2). Once the fitness of each individ-

ual animal and plant is calculated, fitness values are transformed into probabilities of survival by dividing individual fitness by the maximum individual fitness within the species. Subsequently, a random number is drawn for each individual and only those individuals with a fitness exceeding this random number survived to the next stage of the life cycle.

Individuals that survive abiotic and biotic selection mate at random within their species and produce offspring. Specifically, for each species, two individuals are selected at random as mates, and an offspring individual is then formed by drawing a random value from a gaussian distribution with a mean equal to the average phenotype of the two parents and a variance equal to 0.05. Mating continues in this way until a new offspring population of size $n_{A,i}$ (for animals) or $n_{P,i}$ (for plants) is assembled; the parental generation then dies. Thus, although population sizes of animal and plant species vary over the life cycle, reproduction always returns each species to its fixed carrying capacity, with the carrying capacity of each species drawn at random from a lognormal distribution (see below).

Simulations were run for both the phenotype matching model and the phenotype differences model, with 635 simulations run with α equal to 0.02 and another 6125 simulations run with α equal to 2.0. The first set of simulations ($\alpha = 0.02$) was performed to evaluate whether our analytical results were robust when our assumption that interactions did not depend too strongly on the phenotypes of interacting individuals held but other assumptions (e.g., fixed additive genetic variance) were violated. This set of simulations used the parameter ranges shown in Table S1. The second set of simulations ($\alpha = 2.0$) was performed to evaluate whether our analytical results remained robust when their assumptions were grossly violated (e.g., interaction outcome strongly dependent on traits, rapidly evolving genetic variance) and to explore how network metrics impossible to calculate with our analytical model (e.g., nestedness) were shaped by coevolution. This second set of simulations used the parameter ranges shown in Table 1. In addition to these simulations—which used randomly selected parameters—we ran numerous individual simulations with deterministically selected parameters for a more thorough exploration of certain cases.

Each simulation run was initiated by setting model parameters and assigning phenotypes to individuals. Phenotypes of individuals were set to the abiotic optimum of their species plus a random perturbation drawn from a uniform distribution on $\{-0.01, 0.01\}$. Each simulation was then run for between 1000 and 2000 generations, with simulated observational experiments of encounters between animals and plants conducted in every generation. Simulated observational experiments recorded the outcome (i.e., whether an interaction was successful or not) of 5000 or 25,000 random encounters between animals and plants; species identities and individual phenotypes were recorded for all successful

Table 1. Parameters used within individual-based simulations.

Parameters	How selected	Distribution
Generations	Fixed at 1000	NA
Sampled	Fixed at 5000	NA
N_A	Fixed at 50	NA
N_P	Fixed at 50	NA
α	Fixed at 2.0	NA
$n_{A,i}$ and $n_{P,i}$	Value selected at random and independently for each species	Lognormal ¹ with mean 7.0 and variance 0.3
$\theta_{A,i}$ and $\theta_{P,i}$	Value selected at random and independently for each species	Gaussian with mean 0 and variance drawn from a uniform distribution on {1.0, 6.0}
γ_A and γ_P	Value selected at random and applied to all species	Uniform with range {0, 0.5}
$\xi_{A,i}$ and $\xi_{P,i}$	Value selected at random and independently for each species	Gaussian ² with mean drawn from a uniform on range {0,1} and variance 0.001

¹Values were truncated at a maximum population size of 29,999 individuals to maintain computational efficiency.

²Values were truncated at a minimum value of 0 because negative values represent antagonistic rather than mutualistic interactions.

interactions. This information was used to calculate network summary statistics such as interaction efficiency, connectance, convergence, complementarity, and nestedness. In the following sections, we use the results of these ≈ 7000 simulations to explore how coevolution shapes the network properties of mutualistic communities.

INTERACTION EFFICIENCY AND CONNECTANCE

For each simulation, we calculated the interaction efficiency of the mutualistic community as well as the more standard index of interaction density, connectance. Specifically, interaction efficiency was calculated as the proportion of random encounters between individuals that resulted in successful interaction (i.e., had fitness consequences) whereas connectance was calculated in the standard way by summing the entries of the binary interaction matrix and dividing this sum by the dimension of the matrix ($N_A \times N_P$). Thus, interaction efficiency measures the overall rate of interaction within the community whereas connectance measures the proportion of possible interactions between animal and plant species within the community that were observed.

Taken together, our simulations confirm our analytical prediction that interaction efficiency increases with the strength of coevolutionary selection. Specifically, when the probability of successful interaction did not depend too strongly on the phenotypes of the interacting individuals ($\alpha = 0.02$), agreement between analytical predictions and simulation results was quantitative (Figs. S1, S2). When the probability of successful interaction was quite sensitive to the phenotypes of the interacting individuals ($\alpha = 2.0$), strongly violating the assumptions of our analytical model, our analytical prediction was still upheld, although in this case agreement with simulations was only qualitative (Fig. 3; first

row). Because most studies focus on connectance rather than interaction efficiency, we also used our simulations to evaluate how connectance changes as a function of the strength of coevolutionary selection. As suggested by our analytical and simulation results for interaction efficiency, connectance also increases as coevolutionary selection becomes more intense (Fig. 3, second row).

CONVERGENCE

In addition to interaction efficiency and connectance, we evaluated the convergence of the mutualistic community by calculating the phenotypic variance of animals and plants that were observed to successfully interact in simulated observational experiments. As described in the analytical results, large variances correspond to weak convergence and small variances to strong convergence. As predicted by our analytical results, in communities where mutualisms are mediated by a mechanism of phenotype matching, increasing the strength of coevolution increases the convergence of the community (Fig. 3; rows 3–4 and Fig. S1). In contrast, for mutualisms mediated by phenotype differences, our analytical prediction that convergence is decoupled from the strength of coevolution only holds when α is small (Fig. S2). When the outcome of interactions depends more strongly on the phenotypes of individuals, our analytical prediction breaks down, and convergence increases with the strength of coevolutionary selection (Fig. 3, rows 3–4).

COMPLEMENTARITY

Our analytical results predict that mutualisms mediated by phenotype matching will exhibit positive complementarity, but that complementarity will decrease as coevolutionary selection increases. In contrast, our analytical results predict that

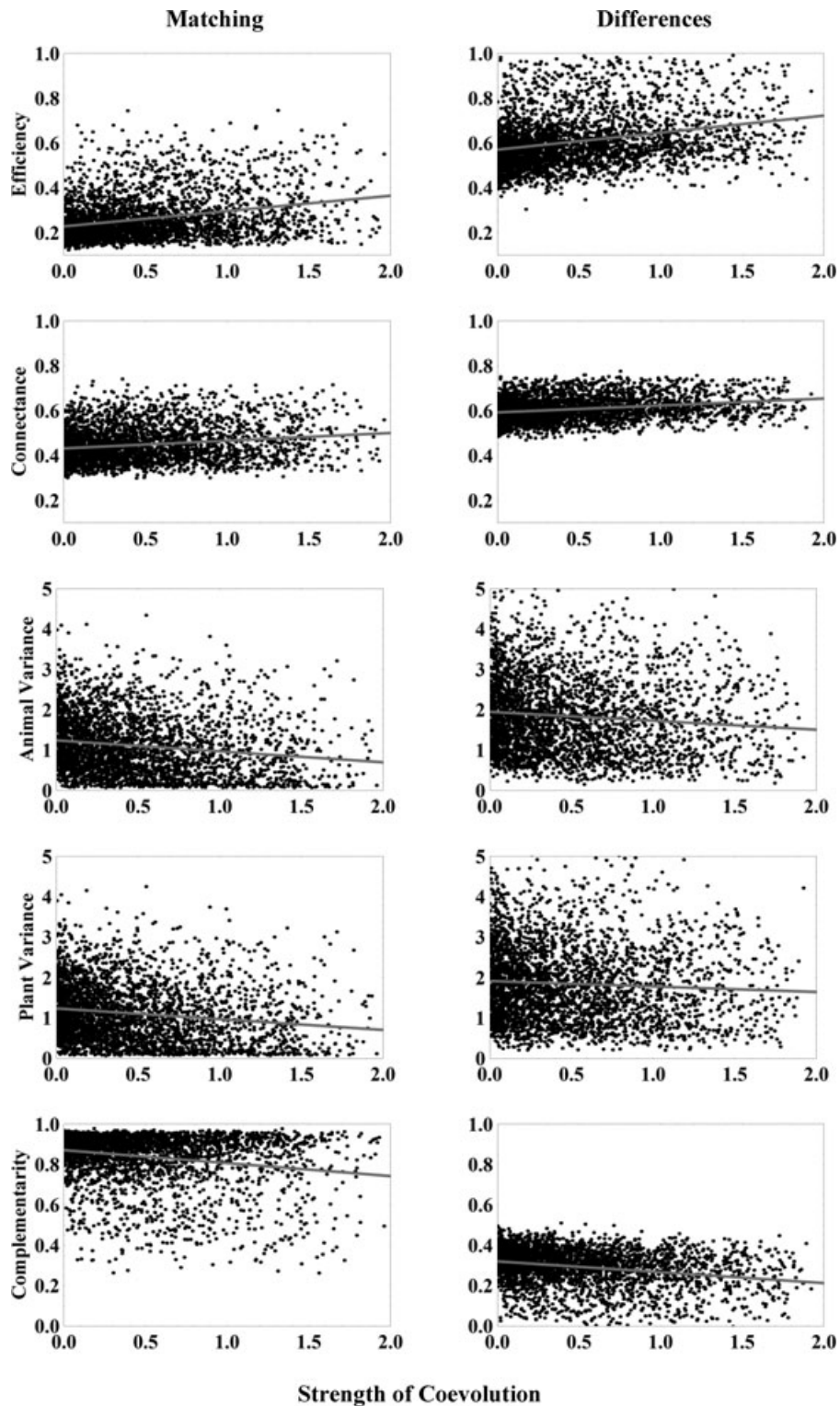


Figure 3. The relationship between the average strength of coevolutionary selection ($\alpha \times \xi_A \times \xi_P$) and various network metrics calculated in generation 1000 for the 6125 simulations run using the parameter values described in Table 1. Each point represents the result of a single simulation run and the gray line is the best-fit linear model. The left-hand column shows results for the matching model and the right-hand column results for the differences model.

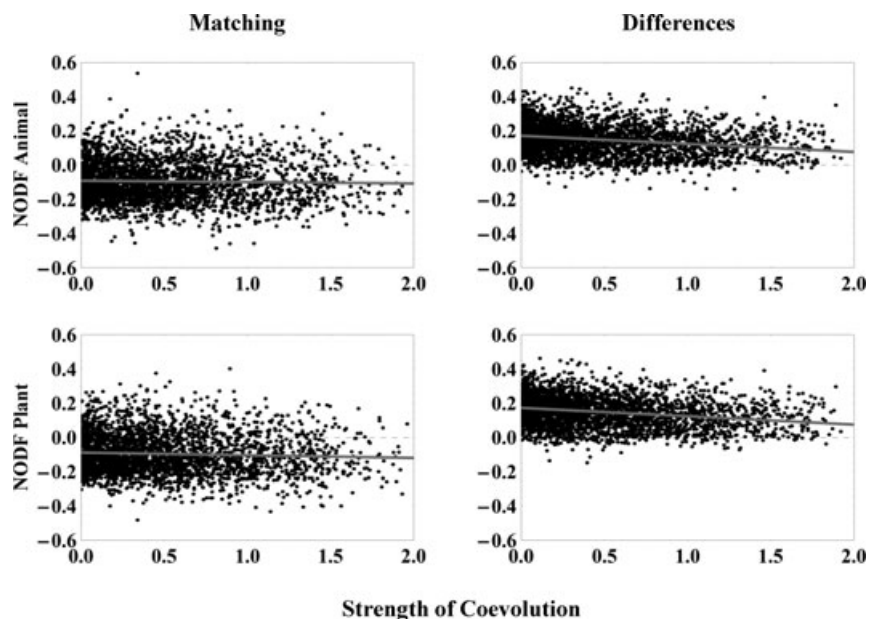


Figure 4. The relationship between the average strength of coevolutionary selection ($\alpha \times \xi_A \times \xi_P$) and nestedness calculated in generation 1000 for the 6125 simulations run using the parameter values described in Table 1. Each point represents the result of a single simulation run and the gray line is the best-fit linear model. The left-hand column shows results for the matching model and the right-hand column results for the differences model.

mutualisms mediated by phenotype differences will not exhibit complementarity, no matter what the strength of coevolutionary selection.

To explore the robustness of this prediction, we evaluated how coevolution shaped complementarity for our simulated observational experiments by calculating the correlation between traits of interacting animals and plants. When interactions depended only weakly on phenotypes ($\alpha = 0.02$), our analytical results were supported for both the matching and differences models (Figs. S1, S2). In contrast, as phenotypes became increasingly important to the outcome of interactions, our analytical predictions broke down for the phenotype differences model. Specifically, when α became large ($\alpha = 2.0$), mutualistic communities mediated by phenotype differences exhibited positive levels of complementarity that decreased as the strength of coevolution increased (Fig. 3, row 5). Although our analytical prediction breaks down for the phenotype differences model, our overall qualitative predictions remain intact: complementarity is stronger for interactions mediated by phenotype matching than those mediated by phenotype differences and decreases as mutualistic coevolution becomes stronger.

NESTEDNESS

Finally, we used our simulation results to explore how coevolution shapes the nested structure of mutualistic communities. Specifically, we quantified nestedness for our simulations by calculating the nestedness metric based on overlap and decreasing

fill (NODF) metric (Almeida-Neto et al. 2008) for the binary interaction matrices generated through simulated observational experiments. Raw NODF scores were corrected by subtracting the average NODF score of 100 randomized interaction matrices and then dividing by the average NODF score of the randomized interaction matrices (Bascompte et al. 2003). Each randomization was performed by generating a new matrix that maintained the observed connectance, but assigned 1's at random with a probability proportional to the product of the interacting species abundances. This randomization procedure corrects observed nestedness scores for contributions made by lognormal species abundance distributions, and thus isolates only the contributions made by coevolved distributions of trait values in animals and plants.

Our analyses of simulated data revealed that corrected NODF scores for interactions mediated by phenotype matching tend to be negative whereas corrected NODF scores for interactions mediated by phenotypic differences tend to be positive (Fig. 4). In addition, our simulations revealed that coevolution tends to decrease nestedness for interactions mediated by both phenotype matching and phenotype differences (Fig. 4). Specifically, a significant negative relationship exists between the strength of coevolutionary selection and NODF for both models, although this relationship is generally weaker for the phenotype matching model than the phenotype differences model. Greater insight into the role mutualistic coevolution plays in driving patterns of nestedness can be gained by plotting nestedness values as a function of time.

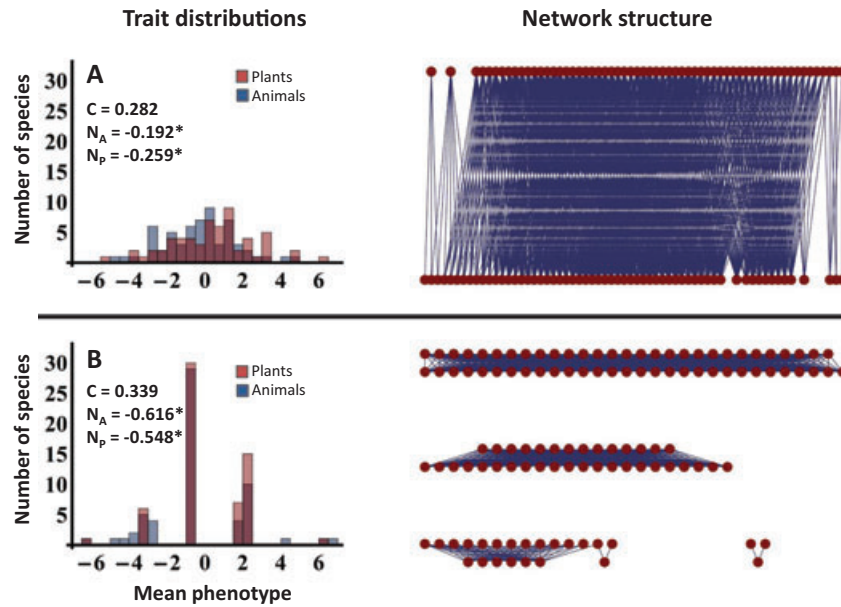


Figure 5. The distribution of mean phenotypes among species (left-hand panels) and the network topology (right-hand panels) for a community of 60 animal species and 60 plant species where interactions are mediated by phenotype matching. The top panels derive from simulations conducted with weak coevolutionary selection ($\xi_A = 0.1$, $\xi_P = 0.1$) whereas the bottom panels derive from simulations conducted with strong coevolutionary selection ($\xi_A = 0.9$, $\xi_P = 0.9$). The connectance and corrected NODF scores for each community are indicated by C , N_A , and N_P within each panel. Corrected NODF scores in the top 2.5% or bottom 2.5% of the null distribution are indicated by asterisks. Trait distributions and network topology were assessed during the final generation of the simulations ($G = 500$). Population sizes of animal and plant species were drawn from a lognormal distribution with mean 7.0 and variance 0.3 other parameters were: $\alpha = 10.0$, $\gamma_A = 0.02$, $\gamma_P = 0.02$, $V_{\theta_A} = 5$, $V_{\theta_P} = 5$, $V_{\xi_A} = 0.001$, and $V_{\xi_P} = 0.001$. Network topology and statistics were calculated from a sample of 36,000 interactions observed during generation 500.

Investigation of many such time courses shows that initially, and prior to any coevolution, interactions mediated by phenotype matching tend to be antinested (corrected NODF < 0) whereas interactions mediated by phenotype differences tend to be positively nested (corrected NODF > 0). As coevolution proceeds over time, however, nestedness decreases.

To further explore why mutualistic coevolution reduces the nested structure of communities in some cases, we studied how the topology of network graphs describing the interaction matrix derived from simulated observational experiments was influenced by the strength of coevolutionary selection. When interactions are mediated by phenotype matching and coevolutionary selection is weak, communities tend to be less nested than expected by chance (antinested), with significant levels of reciprocal specialization between groups of species with similar trait values (Fig. 5A). As coevolutionary selection becomes stronger, however, mutualistic coevolution can break the community into discrete groups of reciprocally interacting plants and animals (compartments) generating even stronger antinested structure (Fig. 5B). Interestingly, this increase in compartmentalization is accompanied by increasing connectance generated by the coevolution of very high levels of interaction within individual compartments.

In contrast, when interactions are mediated by phenotype differences and coevolutionary selection is weak, network topologies are more nested than expected by chance with specialized species interacting primarily with more generalized species (Fig. 6A). This nested pattern emerges simply because the phenotype differences model allows individual animals with large trait values to interact with a larger range of plant species than those animals with small trait values. Similarly, plant species with small trait values can interact with a larger range of animal species than can plants with large trait values. When coevolutionary selection is relatively weak, plant and animal trait values exhibit substantial variation in trait values (Fig. 6A, left panel) and it is this variation that produces the nested pattern. As coevolutionary selection becomes stronger, however, the nested pattern of mutualistic networks is eroded, resulting in communities that may exhibit only a weakly nested structure or even an antinested structure (Fig. 6B). Strong coevolutionary selection erodes the nested structure of such communities because it favors plants and animals with generalized traits (i.e., plants with small traits and animals with large traits)—given sufficiently strong coevolutionary selection, trait variation is reduced to the point where all species have an approximately equal chance of interacting with any other species (Fig. 6B).

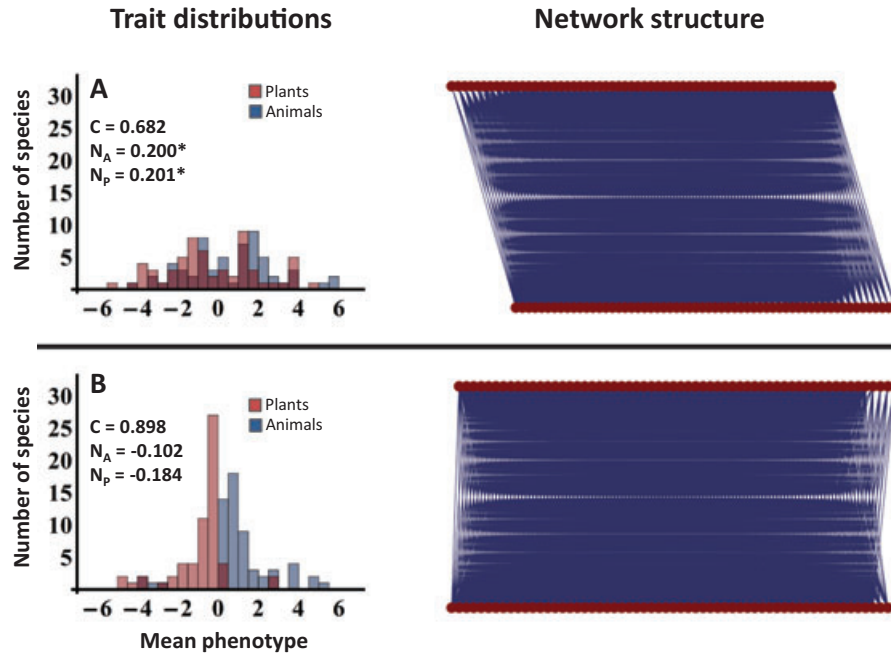


Figure 6. The distribution of species mean phenotypes (left-hand panels) and the network topology (right-hand panels) for a community of 60 animal species and 60 plant species where interactions are mediated by phenotype differences. The top panels derive from simulations conducted with weak coevolutionary selection ($\bar{\xi}_A = 0.1, \bar{\xi}_P = 0.1$) whereas the bottom panels derive from simulations conducted with strong coevolutionary selection ($\bar{\xi}_A = 0.9, \bar{\xi}_P = 0.9$). The connectance and corrected NODF scores for each community are indicated by C , N_A , and N_P within each panel. Corrected NODF scores in the top 2.5% or bottom 2.5% of the null distribution are indicated by asterisks. Trait distributions and network topology were assessed during the final generation of the simulations ($G = 500$). Population sizes of animal and plant species were drawn from a lognormal distribution with mean 7.0 and variance 0.3 other parameters were: $\alpha = 10.0$, $\gamma_A = 0.02$, $\gamma_P = 0.02$, $V_{\theta_A} = 5$, $V_{\theta_P} = 5$, $V_{\xi_A} = 0.001$, and $V_{\xi_P} = 0.001$. Network topology and statistics were calculated from a sample of 36,000 interactions observed during generation 500.

Discussion

Our analyses reveal that coevolutionary selection can be a powerful force, even in large, complex communities. Specifically, our results show that coevolutionary selection drives changes in network structure, distributions of traits, and even the pattern of interactions within the community itself. That coevolutionary selection has such strong effects in our model is surprising for two reasons. First, each species in our model encounters all other species at random, and thus has the potential to interact with many other species within each generation. Second, we assume the probability that individuals interact depends on only a single “key” trait such as phenology or body size. As a consequence, our model makes trade-offs across interactions with multiple species inevitable, virtually guaranteeing that each species experiences extreme patterns of conflicting selection pressure. Thus, even though our model explicitly integrates two of the factors frequently used as arguments for why coevolution should be irrelevant in large communities of generalists (Hougenieztman and Rausher 1994; Rausher 1996; Iwao and Rausher 1997; Stinchcombe and Rausher 2001), as with other recent studies (e.g., Wade 2003, 2007; Guimarães

et al. 2011), our results show the contrary: coevolution matters, and it matters a lot.

In addition to demonstrating that coevolution can be important even in species-rich communities of generalists, our results show that coevolution shapes properties of mutualistic networks. Specifically, our results show that mutualistic coevolution almost invariably increases the connectance of communities. Given the importance of connectance for community stability (Dunne et al. 2002), this general result suggests that those communities with a long history of mutualistic coevolution may be more stable to perturbation than those lacking a long history of coevolutionary interaction. Our results also demonstrate that coevolution influences patterns of specialization within complex communities, which has important consequences for nestedness. When interactions are mediated by a mechanism of phenotype matching, intense coevolutionary selection can promote increased levels of reciprocal specialization by breaking an initially generalized community into independent modules containing variable numbers of species (e.g., Fig. 5B). In contrast, when interactions are mediated

by a mechanism of phenotype differences, coevolution can cause initially nested communities to evolve toward a state of extreme generalization where all species tend to interact equally with all others and specialists are quite rare (e.g., Fig. 6B).

The differences we observe across models suggest that communities where interactions are mediated primarily by a mechanism of phenotype matching should tend to be more specialized and less nested than those communities where interactions are mediated primarily by a mechanism of phenotype differences. Comparing our simulated values of nestedness with values calculated from previously compiled mutualistic networks (Fortuna et al. 2010) is intriguing in this context. Specifically, within our simulated data, the average raw value of NODF for communities mediated by matching is $\{53.79 \pm 11.82\}$, whereas the average value for communities mediated by differences is $\{84.19 \pm 3.30\}$. These values agree well with raw values of NODF calculated for seed dispersal $\{55.28 \pm 18.49\}$ and pollination $\{70.04 \pm 14.32\}$ mutualisms, respectively. Although this comparison offers tantalizing hints that different mechanism may be involved in these different types of mutualisms, it is premature to draw any firm conclusions based on this crude comparison of raw NODF scores.

Our results provide interesting predictions for how traits should be distributed within mutualistic communities. When interactions are mediated by a mechanism of trait matching and coevolutionary selection is weak or absent, trait values in animal and plant species should be highly variable (nonconvergent) and traits of interacting animal and plants species should be positively correlated (pairwise complementary). As coevolutionary selection intensifies, however, variation in the trait values of animal and plant species is reduced (convergence) and correlations between traits of interacting species are weakened (low pairwise complementarity). This occurs because as trait variation is reduced within animals and plants, traits play a less significant role in determining whether any two species interact, simply because all species within a guild tend to have similar trait values and thus become equally likely to interact with any other species. In contrast, when mutualistic interactions are mediated by a mechanism of phenotype differences, the intensity of coevolutionary selection has no impact on levels of traits variation within animals and plants and only a relatively weak influence on correlations between traits of interacting species.

The predictions our model makes for trait distributions within animals and plants, and among interacting species, refine previous verbal arguments (Thompson 2005) and model predictions (Guimarães et al. 2011). Whereas previous work predicted mutualistic coevolution should favor trait convergence (reduced trait variation within animals and plants) and trait complementarity (positive correlations among traits of interacting species), our results suggest that this need not always be the case. Specifically, our results show that when interactions are mediated by a mech-

anism of phenotypic differences, rather than the mechanism of phenotype matching assumed in previous work and verbal arguments, convergence and complementarity are unlikely to evolve. This result is important because phenotype differences are likely a common mechanism mediating mutualistic interactions within natural communities of pollinators and dispersers. Second, and more technically, the study of Guimarães et al. (2011) measured complementarity using the quantity $-\log(\tau)$ where τ is the mean pairwise difference between animals and plants. As long as animals and plants have similar trait values, this measure indicates high levels of complementarity even if there is no variability in trait values within either animals or plants. In contrast, we have used a more traditional product moment correlation to measure complementarity. Consequently, if there is no trait variability within animals or plants, complementarity is zero even if the trait values of animals and plants are perfectly matched. Which of these measures is the more useful measure of complementarity is unclear and likely depends on the particular question being addressed.

Although our results are, in many respects, quite general, they do rely on several important assumptions. Perhaps the most obvious of these is that the population density of each species is returned to its individual carrying capacity at the end of each generation. This assumption allowed us to maintain species abundance distributions that were distributed lognormally as observed in natural communities (Hubbell 2001), but also precluded dynamic feedbacks between demography and evolution. Because lognormal distributions are known to have important consequences for patterns of nestedness (Bluthgen et al. 2008; Krishna et al. 2008), we felt it was useful to fix this property of the community. Another potentially important assumption of our models is that interactions between all animals and plants depend on a single “key” trait. Although clearly an oversimplification, this assumption may be appropriate for communities where a single trait such as phenology or body size plays a dominant role in shaping the likelihood of interactions (Levey 1987; Stang et al. 2006). However, it might be unrealistic for highly diversified mutualisms where selective pressures of different pollinator or seed dispersers “target” different plant traits (Gómez et al. 2011). Finally, we assumed that evolution resulted only from the combined action of drift, abiotic selection toward some optimum trait value, and selection imposed by mutualistic interactions. Consequently, our results ignore potentially important consequences of selection generated by competitive or reproductive interactions within animals or within plants (Johnson and Steiner 2000; Fenster et al. 2004) and ignore the potentially important influence of gene flow from other communities (Thompson 2005).

In summary, our results show that coevolution can have important consequences for the structure and function of highly diverse and species-rich communities of mutualists. Thus, our

results do not support claims that coevolution is ineffectual or unimportant in species-rich communities characterized by generalized interactions (Hougenieztman and Rausher 1994; Iwao and Rausher 1997; Stinchcombe and Rausher 2001; Strauss and Irwin 2004). At the same time, however, our results show that the specific consequences of coevolution for community structure and function depend on the particular mechanism of coevolution that predominates (matching vs differences) as well as its overall strength. Thus, attempts to implicate coevolution or demonstrate its importance in the wild using network metrics or other summary statistics are likely to be challenging. Furthermore, there are many reasons other than coevolution for communities to be nested or to exhibit trait complementarity or convergence (Santamaría and Rodríguez-Gironés 2007; Bluthgen et al. 2008; Krishna et al. 2008). Only by fusing more sophisticated data sets that include quantitative rates of interaction and estimates for the fitness consequences of individual interactions with model based statistics (e.g., Bertorelle et al. 2010; Beaumont 2010; Csillery et al. 2010) will it likely be possible to robustly infer anything about the coevolutionary process within natural communities of mutualists.

ACKNOWLEDGMENTS

We thank J. N. Thompson, D. Stouffer, P. R. Guimarães Jr., N. Loeuille, and F. Jabot for helpful comments on earlier versions of this manuscript and M. A. Fortuna for generous help with network analyses. Funding was provided by National Science Foundation grants DEB 1118947 and DMS 0540392 to SLN, Spanish Ministry of Science to PJ, and by the European Science Foundation Advanced Grant to JB.

LITERATURE CITED

- Abrams, P. A. 2000. The evolution of predator-prey interactions: theory and evidence. *Ann. Rev. Ecol. Syst.* 31:79–105.
- Agosta, S. J., and D. H. Janzen. 2005. Body size distributions of large Costa Rican dry forest moths and the underlying relationship between plant and pollinator morphology. *Oikos* 108:183–193.
- Agrawal, A. F. 2006. Similarity selection and the evolution of sex: revisiting the red queen. *PLOS Biol.* 4:1364–1371.
- Almeida-Neto, M., P. Guimarães, P. R. Guimarães, R. D. Loyola, and W. Ulrich. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117:1227–1239.
- Anderson, B., and S. D. Johnson. 2009. Geographical covariation and local convergence of flower depth in a guild of fly-pollinated plants. *New Phytol.* 182:533–540.
- Anderson, B., J. S. Terblanche, and A. G. Ellis. 2010. Predictable patterns of trait mismatches between interacting plants and insects. *BMC Evol. Biol.* 10:204.
- Bascompte, J., and P. Jordano. 2007. Plant-animal mutualistic networks the architecture of biodiversity. *Ann. Rev. Ecol. Syst.* 38: 567–593.
- Bascompte, J., P. Jordano, C. J. Melian, and J. M. Olesen. 2003. The nested assembly of plant-animal mutualistic networks. *Proc. Natl. Acad. Sci. USA* 100:9383–9387.
- Beaumont, M. A. 2010. Approximate Bayesian computation in evolution and ecology. *Ann. Rev. Ecol. Syst.* 41:379–406.
- Bertorelle, G., A. Benazzo, and S. Mona. 2010. ABC as a flexible framework to estimate demography over space and time: some cons, many pros. *Mol. Ecol.* 19:2609–2625.
- Bluthgen, N., J. Frund, D. P. Vazquez, and F. Menzel. 2008. What do interaction network metrics tell us about specialization and biological traits? *Ecology* 89:3387–3399.
- Borrell, B. J. 2007. Scaling of nectar foraging in orchid bees. *Am. Nat.* 169:569–580.
- Burdon, J. J., and P. H. Thrall. 2000. Coevolution at multiple spatial scales: *Linum marginale*-*Melampsora lini*—from the individual to the species. *Evol. Ecol.* 14:261–281.
- Campbell, C., S. Yang, R. Albert, and K. Shea. 2011. A network model for plant-pollinator community assembly. *Proc. Natl. Acad. Sci. USA* 108:197–202.
- Csillery, K., M. G. B. Blum, O. E. Gaggiotti, and O. Francois. 2010. Approximate Bayesian Computation (ABC) in practice. *Trends Ecol. Evol.* 25:410–418.
- da Silva, J. M. C., and M. Tabarelli. 2000. Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature* 404:72–74.
- Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.* 5:558–567.
- Fenster, C. B., W. S. Armbruster, P. Wilson, M. R. Dudash, and J. D. Thomson. 2004. Pollination syndromes and floral specialization. *Ann. Rev. Ecol. Syst.* 35:375–403.
- Fontaine, C., P. R. Guimarães, S. Kefi, N. Loeuille, J. Memmott, W. H. van der Putten, F. J. F. van Veen, and E. Thebault. 2011. The ecological and evolutionary implications of merging different types of networks. *Ecol. Lett.* 14:1170–1181.
- Fortuna, M. A., D. B. Stouffer, J. M. Olesen, P. Jordano, D. Mouillot, B. R. Krasnov, R. Poulin, and J. Bascompte. 2010. Nestedness versus modularity in ecological networks: two sides of the same coin? *J. Anim. Ecol.* 79:811–817.
- Gandon, S., and S. L. Nuismer. 2009. Interactions between genetic drift, gene flow, and selection mosaics drive parasite local adaptation. *Am. Nat.* 173:212–224.
- Gandon, S., Y. Capowiez, Y. Dubois, Y. Michalakis, and I. Olivieri. 1996. Local adaptation and gene-for-gene coevolution in a metapopulation model. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 263:1003–1009.
- Gavrilets, S. 1997. Coevolutionary chase in exploiter-victim systems with polygenic characters. *J. Theor. Biol.* 186:527–534.
- Gómez, J. M., F. Perfectti, and P. Jordano. 2011. The functional consequences of mutualistic network architecture. *Plos One* 6(1):e16143.
- Guimarães, P. R., P. Jordano, and J. N. Thompson. 2011. Evolution and coevolution in mutualistic networks. *Ecol. Lett.* 14:877–885.
- Guimarães, P. R., V. Rico-Gray, P. S. Oliveira, T. J. Izzo, S. F. dos Reis, and J. N. Thompson. 2007. Interaction intimacy affects structure and coevolutionary dynamics in mutualistic networks. *Curr. Biol.* 17:1797–1803.
- Hougenieztman, D., and M. D. Rausher. 1994. Interactions between Herbivorous insects and plant-insect coevolution. *Am. Nat.* 143:677–697.
- Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton Univ. Press, Princeton, NJ.
- Inouye, D. W. 1980. The effect of proboscis and corolla tube lengths on patterns and rates of flower visitation by bumblebees. *Oecologia* 45:197–201.
- Iwao, K., and M. D. Rausher. 1997. Evolution of plant resistance to multiple herbivores: quantifying diffuse coevolution. *Am. Nat.* 149: 316–335.
- Johnson, S. D., and K. E. Steiner. 2000. Generalization versus specialization in plant pollination systems. *Trends Ecol. Evol.* 15:140–143.

- Joppa, L. N., J. M. Montoya, R. Sole, J. Sanderson, and S. L. Pimm. 2010. On nestedness in ecological networks. *Evol. Ecol. Res.* 12:35–46.
- Jordano, P., J. Bascompte, and J. M. Olesen. 2003. Invariant properties in coevolutionary networks of plant-animal interactions. *Ecol. Lett.* 6:69–81.
- Kiester, A. R., R. Lande, and D. W. Schemske. 1984. Models of coevolution and speciation in plants and their pollinators. *Am. Nat.* 124:220–243.
- Kopp, M., and S. Gavrillets. 2006. Multilocus genetics and the coevolution of quantitative traits. *Evolution* 60:1321–1336.
- Krishna, A., P. R. Guimarães, P. Jordano, and J. Bascompte. 2008. A neutral-niche theory of nestedness in mutualistic networks. *Oikos* 117:1609–1618.
- Lambert, F. 1989. Fig-eating by birds in a malaysian lowland rain-forest. *J. Trop. Ecol.* 5:401–412.
- Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30:314–334.
- Levey, D. J. 1987. Seed size and fruit-handling techniques of avian frugivores. *Am. Nat.* 129:471–485.
- Lively, C. M. 2010. A Review of Red Queen Models for the persistence of obligate sexual reproduction. *J. Hered.* 101:S13–S20.
- Lively, C. M., M. E. Dybdahl, J. Jokela, E. E. Osnas, and L. E. Delph. 2004. Host sex and local adaptation by parasites in a snail-trematode interaction. *Am. Nat.* 164:S6–S18.
- Nuismer, S. L., and S. P. Otto. 2004. Host-parasite interactions and the evolution of ploidy. *Proc. Natl. Acad. Sci. USA* 101:11036–11039.
- Nuismer, S. L., M. Doebeli, and D. Browning. 2005. The coevolutionary dynamics of antagonistic interactions mediated by quantitative traits with evolving variances. *Evolution* 59:2073–2082.
- Nuismer, S. L., S. P. Otto, and F. Blanquart. 2008. When do host-parasite interactions drive the evolution of non-random mating? *Ecol. Lett.* 11:937–946.
- Nuismer, S. L., R. Gomulkiewicz, and B. J. Ridenhour. 2010. When is correlation coevolution? *Am. Nat.* 175:525–537.
- Nuismer, S. L., B. J. Ridenhour, and B. P. Oswald. 2007. Antagonistic coevolution mediated by phenotypic differences between quantitative traits. *Evolution* 61:1823–1834.
- Olesen, J. M., J. Bascompte, Y. L. Dupont, H. Elberling, C. Rasmussen, and P. Jordano. 2010. Missing and forbidden links in mutualistic networks. *Proc. R. Soc. B Biol. Sci.* 278:725–732.
- Otto, S. P., and S. L. Nuismer. 2004. Species interactions and the evolution of sex. *Science* 304:1018–1020.
- Rausher, M. D. 1996. Genetic analysis of coevolution between plants and their natural enemies. *Trends Genet.* 12:212–217.
- Rezende, E. L., P. Jordano, and J. Bascompte. 2007. Effects of phenotypic complementarity and phylogeny on the nested structure of mutualistic networks. *Oikos* 116:1919–1929.
- Salathe, M., R. D. Kouyos, and S. Bonhoeffer. 2008. The state of affairs in the kingdom of the Red Queen. *Trends Ecol. Evol.* 23:439–445.
- Santamaría, L., and M. A. Rodríguez-Gironés. 2007. Linkage rules for plant-pollinator networks: trait complementarity or exploitation barriers? *PLOS Biol.* 5:354–362.
- Stang, M., P. G. L. Klinkhamer, and E. van der Meijden. 2006. Size constraints and flower abundance determine the number of interactions in a plant-flower visitor web. *Oikos* 112:111–121.
- . 2007. Asymmetric specialization and extinction risk in plant-flower visitor webs: a matter of morphology or abundance? *Oecologia* 151:442–453.
- Stinchcombe, J. R., and M. D. Rausher. 2001. Diffuse selection on resistance to deer herbivory in the ivyleaf morning glory, *Ipomoea hederacea*. *Am. Nat.* 158:376–388.
- Strauss, S. Y., and R. E. Irwin. 2004. Ecological and evolutionary consequences of multispecies plant-animal interactions. *Ann. Rev. Ecol. Evol. Syst.* 35:435–466.
- Thompson, J. N. 2005. The geographic mosaic of coevolution. Univ. of Chicago Press, Chicago, IL.
- Vázquez, D. P., N. P. Chacoff, and L. Cagnolo. 2009. Evaluating multiple determinants of the structure of plant-animal mutualistic networks. *Ecology* 90:2039–2046.
- Verdú, M., and A. Valiente-Banuet. 2010. The relative contribution of abundance and phylogeny to the structure of plant facilitation networks. *Oikos* 120:1351–1356.
- Wade, M. J. 2003. Community genetics and species interactions. *Ecology* 84:583–585.
- . 2007. The co-evolutionary genetics of ecological communities. *Nat. Rev. Genet.* 8:185–195.

Associate Editor: T. Craig

Appendix 1

EQUATIONS FOR THE CHANGE IN TRAIT MEANS OF ANIMAL AND PLANT SPECIES

Matching model

For the matching model, we find that the change in the mean phenotype of animal species i is

$$\Delta \bar{y}_i = G_{A,i}(\psi_A(\theta_{A,i} - \bar{y}_i) + S_{A,i}(\bar{Z} - y_i)) + \delta_{A,i}, \quad (\text{A1})$$

and the change in the mean phenotype of plant species i is

$$\Delta \bar{z}_i = G_{P,i}(\psi_P(\theta_{P,i} - \bar{z}_i) + S_{P,i}(\bar{Y} - z_i)) + \delta_{P,i}, \quad (\text{A2})$$

where the expected value of animal population mean phenotypes is $\bar{Y} = \sum_{j=1}^{N_A} f_{A,j} \bar{y}_j$ and plant mean phenotypes is $\bar{Z} = \sum_{j=1}^{N_P} f_{P,j} \bar{z}_j$. The compound parameters $\psi_i = 2\gamma_i$ and $S_{i,j} = \frac{2\alpha\xi_{i,j}}{(1+\xi_{i,j})}$ measure the strength of stabilizing abiotic selection, and the strength of selection caused by mutualistic interactions, respectively. Finally, the term $\delta_{i,j}$ measures the change to the population mean phenotype caused by genetic drift and is a random variable with mean zero and variance $G_{i,j}/n_{i,j}$.

Phenotype differences/threshold model

For the phenotype differences model, we find that the change in the mean phenotype of animal species i is

$$\Delta \bar{y}_i = G_{A,i}(\psi_A(\theta_{A,i} - \bar{y}_i) - S_{A,i}) + \delta_{A,i}, \quad (\text{A3})$$

and the change in the mean phenotype of plant species i is

$$\Delta \bar{z}_i = G_{P,i}(\psi_P(\theta_{P,i} - \bar{z}_i) + S_{P,i}) + \delta_{P,i}, \quad (\text{A4})$$

where all parameter are as defined for the matching model with the exception of $S_{i,j}$, which takes the value $\frac{\alpha\xi_{i,j}}{2(2+\xi_{i,j})}$ for the phenotype differences model.

Appendix 2

EQUATIONS FOR THE CHANGE IN THE DISTRIBUTION OF TRAIT MEANS WITHIN ANIMALS AND PLANTS

Remarkably, making only the additional assumptions that species mean trait values do not become too divergent, the strength of abiotic selection (ψ) is equal across species within guilds, and that additive genetic variance is equal across guilds, our results show that the evolution of the distributions describing plant and animal species mean trait values can be completely described using recursions for only six moments irrespective of the number of species in the community

Matching model

The evolutionary dynamics of communities where mutualisms are mediated by trait matching are completely described by the following set of six recursion equations, each of which describes the change in a statistical moment, which occurs over a single generation:

$$\Delta \bar{Y} = G_A(\bar{S}_A(\bar{Z} - \bar{Y}) + \psi_A(\bar{\theta}_A - \bar{Y})), \quad (\text{A5})$$

$$\Delta \bar{Z} = G_P(\bar{S}_P(\bar{Y} - \bar{Z}) + \psi_P(\bar{\theta}_P - \bar{Z})), \quad (\text{A6})$$

$$\Delta V_{\bar{y}} = 2G_A(\psi_A C[\bar{y}, \theta_A] - (\bar{S}_A + \psi_A)V_{\bar{y}}) + \frac{G_A}{\bar{n}_A}, \quad (\text{A7})$$

$$\Delta V_{\bar{z}} = 2G_P(\psi_P C[\bar{z}, \theta_P] - (\bar{S}_P + \psi_P)V_{\bar{z}}) + \frac{G_P}{\bar{n}_P}, \quad (\text{A8})$$

$$\Delta C[\bar{y}, \theta_A] = G_A(\psi_A V_{\theta_A} - (\bar{S}_A + \psi_A)C[\bar{y}, \theta_A]), \quad (\text{A9})$$

$$\Delta C[\bar{z}, \theta_P] = G_P(\psi_P V_{\theta_P} - (\bar{S}_P + \psi_P)C[\bar{z}, \theta_P]), \quad (\text{A10})$$

where $V_{\bar{y}}$ and $V_{\bar{z}}$ are the variance among animal and plant species mean trait values, respectively, V_{θ_A} and V_{θ_P} are the variance among animal and plant phenotypic optima, respectively, \bar{S}_A and \bar{S}_P are the expected values of the parameter $S_{i,j}$ for animals and plants, respectively, \bar{n}_A and \bar{n}_P are the harmonic means of animal and plant population sizes, and $C[\bar{y}, \theta_A]$ and $C[\bar{z}, \theta_P]$ are the covariance between species mean trait values and phenotypic optima favored by stabilizing selection in animals and plants, respectively.

Phenotype differences/threshold model

The evolutionary dynamics of communities where mutualisms are mediated by phenotype differences are completely described by the following set of six recursion equations, each of which describes the change in a statistical moment, which occurs over a

single generation:

$$\Delta \bar{Y} = G_A(\bar{S}_A + \psi_A(\bar{\theta}_A - \bar{Y})), \quad (\text{A11})$$

$$\Delta \bar{Z} = G_P(-\bar{S}_P + \psi_P(\bar{\theta}_P - \bar{Z})), \quad (\text{A12})$$

$$\Delta V_{\bar{y}} = 2G_A\psi_A(C[\bar{y}, \theta_A] - V_{\bar{y}}) + \frac{G_A}{\bar{n}_A}, \quad (\text{A13})$$

$$\Delta V_{\bar{z}} = 2G_P\psi_P(C[\bar{z}, \theta_P] - V_{\bar{z}}) + \frac{G_P}{\bar{n}_P}, \quad (\text{A14})$$

$$\Delta C[\bar{y}, \theta_A] = G_Z\psi_A(V_{\theta_A} - C[\bar{y}, \theta_A]), \quad (\text{A15})$$

$$\Delta C[\bar{z}, \theta_P] = G_P\psi_P(V_{\theta_P} - C[\bar{z}, \theta_P]). \quad (\text{A16})$$

Appendix 3

EQUILIBRIUM SOLUTIONS FOR THE DISTRIBUTION OF TRAIT MEANS

Matching model equilibrium

The equilibrium distribution of trait means describing communities where mutualisms are mediated by trait matching is completely described by the following set of six equations:

$$\hat{Y} = \frac{\bar{S}_A\bar{\theta}_P\psi_P + \bar{\theta}_A\psi_A(\bar{S}_P + \psi_P)}{\bar{S}_P\psi_A + (\bar{S}_A + \psi_A)\psi_P}, \quad (\text{A17})$$

$$\hat{Z} = \frac{\bar{S}_P\bar{\theta}_A\psi_A + \bar{\theta}_P\psi_P(\bar{S}_A + \psi_A)}{\bar{S}_A\psi_P + (\bar{S}_P + \psi_P)\psi_A}, \quad (\text{A18})$$

$$\hat{V}_{\bar{y}} = \frac{\bar{S}_A + \psi_A + 2\psi_A^2\bar{n}_A V_{\theta_A}}{2\bar{n}_A(\bar{S}_A + \psi_A)^2}, \quad (\text{A19})$$

$$\hat{V}_{\bar{z}} = \frac{\bar{S}_P + \psi_P + 2\psi_P^2\bar{n}_P V_{\theta_P}}{2\bar{n}_P(\bar{S}_P + \psi_P)^2}, \quad (\text{A20})$$

$$\hat{C}[\bar{y}, \theta_A] = \frac{\psi_A}{\bar{S}_A + \psi_A} V_{\theta_A}, \quad (\text{A21})$$

$$\hat{C}[\bar{z}, \theta_P] = \frac{\psi_P}{\bar{S}_P + \psi_P} V_{\theta_P}. \quad (\text{A22})$$

Phenotype differences/threshold model equilibrium

The equilibrium distribution of trait means describing communities where mutualisms are mediated by phenotype differences is completely described by the following set of six equations:

$$\hat{Y} = \bar{\theta}_A + \frac{\bar{S}_A}{\psi_A}, \quad (\text{A23})$$

$$\hat{Z} = \bar{\theta}_P - \frac{\bar{S}_P}{\psi_P}, \quad (\text{A24})$$

$$\hat{V}_{\bar{y}} = \frac{\psi_A + 2\psi_A^2 \bar{n}_A V_{\theta_A}}{2\bar{n}_A \psi_A^2}, \quad (\text{A25})$$

$$\hat{V}_{\bar{z}} = \frac{\psi_P + 2\psi_P^2 \bar{n}_P V_{\theta_P}}{2\bar{n}_P \psi_P^2}, \quad (\text{A26})$$

$$\hat{C}[\bar{y}, \theta_A] = V_{\theta_A}, \quad (\text{A27})$$

$$\hat{C}[\bar{z}, \theta_P] = V_{\theta_P}. \quad (\text{A28})$$

Appendix 4

DERIVATION FOR THE BIVARIATE DISTRIBUTION DESCRIBING INTERACTING PAIRS OF INDIVIDUALS

Our goal in this section is to derive the expected correlation, or complementarity, between the traits of plants and pollinators that successfully interact. Thus, we must derive formulae for the variances and covariance of the bivariate distribution describing the mean trait values of interacting plant and animal species. This goal is facilitated by assuming that levels of phenotypic variance within species are small and that the distributions of trait means within guilds are Gaussian.

We begin by calculating the probability that an animal species with mean phenotype \bar{y} and a plant species with mean phenotype \bar{z} encounter one another and interact successfully. This probability is equivalent to the frequency of interacting pairs of species with traits y and z in the multivariate distribution describing successful interactions:

$$f'(\bar{y}, \bar{z}) = f(\bar{y})f(\bar{z})\frac{\pi(\bar{y}, \bar{z})}{\bar{\pi}}. \quad (\text{A29})$$

In (A1), $f(\bar{y})$ is the frequency of animal species with mean trait value \bar{y} , $f(\bar{z})$ is the frequency of plant species with mean trait value \bar{z} , $\pi(\bar{y}, \bar{z})$ is the probability of successful interaction between two species with trait values \bar{y} and \bar{z} , and $\bar{\pi}$ is the expected probability of successful interactions taken over all plant and animal species. Thus, $\bar{\pi}$ also defines the interaction efficiency of the plant–animal network.

To calculate the correlation between traits of interacting species, we must also calculate the frequency of animal species with mean phenotype \bar{y} and plant species with mean phenotype \bar{z} within the bivariate distribution describing interacting pairs of species. These frequencies are given by

$$f'(\bar{y}) = f(\bar{y})E_{\bar{z}}\left[\frac{\pi(\bar{y}, \bar{z})}{\bar{\pi}}\right], \quad (\text{A30})$$

$$f'(\bar{z}) = f(\bar{z})E_{\bar{y}}\left[\frac{\pi(\bar{y}, \bar{z})}{\bar{\pi}}\right], \quad (\text{A31})$$

where all parameters and variables are as defined for (A1). Equations (A1–A3) can now be used to calculate the expected values of y and z , the variances of y and z , and the covariance

between y and z in the multivariate distribution describing interacting pairs of species. From this information the correlation between traits of interacting species can be easily calculated.

Matching model

For the matching model, the means, variances, and covariance of the multivariate distribution describing pairs of successfully interacting species are

$$E[\bar{y}'] = E[f'(\bar{y}) \cdot \bar{y}] = 2\alpha\bar{Z}V_{\bar{y}} - \bar{Y}(-1 + 2\alpha V_{\bar{y}} + \alpha V_{\bar{z}}), \quad (\text{A32})$$

$$E[\bar{z}'] = E[f'(\bar{z}) \cdot \bar{z}] = 2\alpha\bar{Y}V_{\bar{z}} - \bar{Z}(-1 + \alpha V_{\bar{y}} + 2\alpha V_{\bar{z}}), \quad (\text{A33})$$

$$V[\bar{y}'] = E[f'(\bar{y}) \cdot (\bar{y} - E[\bar{y}'])^2] = V_{\bar{y}}(1 - 2\alpha V_{\bar{y}}), \quad (\text{A34})$$

$$V[\bar{z}'] = E[f'(\bar{z}) \cdot (\bar{z} - E[\bar{z}'])^2] = V_{\bar{z}}(1 - 2\alpha V_{\bar{z}}), \quad (\text{A35})$$

$$\text{Cov}[\bar{y}, \bar{z}] = E[f'(\bar{y}) \cdot f'(\bar{z}) \cdot (\bar{y} - E[\bar{y}']) (\bar{z} - E[\bar{z}'])] = 2\alpha V_{\bar{y}} V_{\bar{z}}. \quad (\text{A36})$$

where $E[\bullet]$ indicates an expectation, $V[\bullet]$ indicates a variance, and $f'(\bullet)$ is a frequency among paired individuals. Thus, the correlation between traits of interacting species is given by

$$\rho = \frac{2\alpha V_{\bar{y}} V_{\bar{z}}}{\sqrt{V_{\bar{y}}(1 - 2\alpha V_{\bar{y}})}\sqrt{V_{\bar{z}}(1 - 2\alpha V_{\bar{z}})}}. \quad (\text{A37})$$

Phenotype differences/threshold model

For the phenotype differences model, the means, variances, and covariance of the multivariate distribution describing pairs of interacting species are

$$E[\bar{y}'] = E[f'(\bar{y}) \cdot \bar{y}] = \bar{Y} + \frac{\alpha V_{\bar{y}}}{2}, \quad (\text{A38})$$

$$E[\bar{z}'] = E[f'(\bar{z}) \cdot \bar{z}] = \bar{Z} - \frac{\alpha V_{\bar{z}}}{2}, \quad (\text{A39})$$

$$V[\bar{y}'] = E[f'(\bar{y}) \cdot (\bar{y} - E[\bar{y}'])^2] = V_{\bar{y}}, \quad (\text{A40})$$

$$V[\bar{z}'] = E[f'(\bar{z}) \cdot (\bar{z} - E[\bar{z}'])^2] = V_{\bar{z}}, \quad (\text{A41})$$

$$\text{Cov}[\bar{y}, \bar{z}] = E[f'(\bar{y}) \cdot f'(\bar{z}) \cdot (\bar{y} - E[\bar{y}']) (\bar{z} - E[\bar{z}'])] = 0. \quad (\text{A42})$$

Thus, the correlation between traits of interacting species is given by

$$\rho = 0. \quad (\text{A43})$$

Appendix 5

DERIVATION FOR THE INTERACTION EFFICIENCY OF THE ANIMAL-PLANT NETWORK

Here we derive the expected interaction efficiency of the mutualistic network for interactions mediated by the matching model and interactions mediated by the phenotype differences model. Because we have assumed that each plant individual (not species) interacts with only a single animal individual each generation, the interaction efficiency of the mutualistic network is simply the expected probability of interaction:

$$E = \sum_{i=1}^{N_Y} \sum_{j=1}^{N_Z} \left(f_{A,i} f_{P,j} \int \int \pi(y, z) \phi_{y,i} \phi_{z,j} dy dz \right). \quad (\text{A44})$$

Matching model

Evaluating the integrals in (A1) for the matching model under the assumption that α is small results in

$$E = \sum_{i=1}^{N_Y} \sum_{j=1}^{N_Z} (f_{A,i} f_{P,j} (1 - \alpha((\bar{y}_i - \bar{z}_j)^2 + V_{y,i} + V_{z,j}))), \quad (\text{A45})$$

where $V_{y,i}$ and $V_{z,j}$ are the phenotypic variances within animal species i and plant species j , respectively. Evaluating the sums in (A2) results in our final simplification:

$$E = 1 - \alpha((\bar{Y}_A - \bar{Z}_P)^2 + V_{\bar{y}} + V_{\bar{z}} + \bar{V}_y + \bar{V}_z), \quad (\text{A46})$$

where \bar{V}_y and \bar{V}_z are the expected phenotypic variance within animal and plant species, respectively.

Phenotype differences/threshold model

Evaluating the integrals in (A1) for the phenotype differences model under the assumption that α is small results in

$$E = \sum_{i=1}^{N_Y} \sum_{j=1}^{N_Z} (f_{A,i} f_{P,j} \left(\frac{1}{2} - \frac{\alpha}{4} (\bar{z}_j - \bar{y}_i) \right)). \quad (\text{A47})$$

Evaluating the sums in (A4) results in our final simplification:

$$E = \frac{1}{2} - \frac{\alpha}{4} (\bar{Z}_P - \bar{Y}_A). \quad (\text{A48})$$

Supporting Information

The following supporting information is available for this article:

Figure S1. Plots of analytical predictions for network metrics at equilibrium versus their values calculated from simulations for the matching model.

Figure S2. Plots of analytical predictions for network metrics at equilibrium versus their values calculated from simulations for the differences model.

Table S1. Parameters for individual-based simulations.

Supporting Information may be found in the online version of this article.

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.