

Coevolution Slows the Disassembly of Mutualistic Networks

Scott L. Nuismer,^{1,*} Bob Week,² and Marcelo A. Aizen³

1. Department of Biological Sciences, University of Idaho, Moscow, Idaho 83844; 2. Program in Bioinformatics and Computational Biology, University of Idaho, Moscow, Idaho 83844; 3. Laboratorio Ecotono, Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA)–Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional del Comahue, Quintral 1250, 8400 Bariloche, Río Negro, Argentina

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ABSTRACT: Important groups of mutualistic species are threatened worldwide, and identifying factors that make them more or less fragile in the face of disturbance is becoming increasingly critical. Although much research has focused on identifying the ecological factors that favor the stability of communities rich in mutualists, much less has been devoted to understanding the role played by historical and contemporary evolution. Here we develop mathematical models and computer simulations of coevolving mutualistic communities that allow us to explore the importance of coevolution in stabilizing communities against anthropogenic disturbance. Our results demonstrate that communities with a long history of coevolution are substantially more robust to disturbance, losing individual species and interactions at lower rates. In addition, our results identify a novel phenomenon—coevolutionary rescue—that mitigates the impacts of ongoing anthropogenic disturbance by rewiring the network structure of the community in a way that compensates for the extinction of individual species and interactions.

Keywords: coevolutionary rescue, interaction rewiring, evolutionary rescue, mutualism, climate change, eco-evolutionary dynamics.

Introduction

Mutualisms are being disrupted by a wide range of anthropogenic disturbances, including habitat destruction, climate change, invasive species, and increasing use of pesticides and herbicides (Aizen et al. 2008; Aslan et al. 2013; Potts et al. 2016). For instance, recent estimates suggest that about 10% of insect pollinator species in Europe are threatened and that close to 17% of vertebrate pollinator species are threatened worldwide (Potts et al. 2016). In addition to the direct consequences of losing individual species, networks of interacting

mutualists may be vulnerable to secondary extinctions because of the positive feedbacks intrinsic to mutualistic interactions (Biesmeijer et al. 2006; Brodie et al. 2014). These positive feedbacks may predominate among mutualists because, for instance, extinction of a single pollinator species reduces the fitness of the plants it pollinates, increasing their likelihood of extinction. In turn, extinction of these plants may decrease the fitness of other pollinator species that depend on them, thus propagating a continuing chain of extinction. However, these negative cascading effects can be ameliorated by the capacity of many species to “rewire” their interactions by shifting mutualistic partners (Galetti et al. 2013; MacLeod et al. 2016; CaraDonna et al. 2017). Although interaction rewiring can be interpreted as a side effect of the facultative nature of most mutualisms (Kaiser-Bunbury et al. 2010; Burkle and Alarcon 2011), it might also reflect the result of natural selection operating in ecological time (Roels and Kelly 2011; Galetti et al. 2013; Breitung et al. 2015; Gervasi and Schiestl 2017).

Because mutualistic interactions play a fundamental role in natural ecological systems as well as agricultural systems on which humans rely, much work has focused on identifying key factors shaping the stability of mutualistic networks in the face of disturbance. Specifically, studies exploring the network structure of mutualistic interactions (e.g., Thebault and Fontaine 2010; Mougi and Kondoh 2012; Rohr et al. 2014; Vieira and Almeida-Neto 2015; Dattilo et al. 2016; Grilli et al. 2016; Poisot et al. 2016) have revealed that mutualistic networks are frequently nested and modular and are often characterized by asymmetric interactions (Bascompte et al. 2003; Guimarães et al. 2006; Bascompte and Jordano 2007). When the consequences of these network properties have been investigated theoretically, they have been shown to increase the stability of mutualistic communities in some cases (Bascompte et al. 2006; Thebault and Fontaine 2010; Grilli et al. 2016) but not others (Allesina and Tang 2012; Vieira and Almeida-Neto 2015). Even so, as disturbance increases past a critical threshold, mutualistic communities may rapidly disintegrate (Lever et al. 2014).

* Corresponding author; email: snuismer@uidaho.edu.

ORCID: Nuismer, <http://orcid.org/0000-0001-9817-0056>; Week, <http://orcid.org/0000-0001-7687-4757>; Aizen, <http://orcid.org/0000-0001-9079-9749>.

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Although we now have a good understanding of the role ecological network structure plays in mediating the stability of mutualistic interactions, we know very little about the impact of coevolutionary history and contemporary coevolution. This is somewhat surprising given the rapidly expanding recognition that evolution plays a fundamental role in ecological processes (Thompson 1998; Carroll et al. 2007; Fussmann et al. 2007; Kinnison and Hairston 2007; Schoener 2011). For instance, recent work focusing on mutualistic networks has revealed that interactions are phylogenetically structured (Chamberlain et al. 2014a, 2014b; Rohr and Bascompte 2014; Aizen et al. 2016; Ibanez et al. 2016), suggesting that long-term coevolutionary history among groups of species may shape patterns of interaction. Contemporary evolution may also play an important role, as suggested by studies documenting rapid evolutionary change in phenotypic traits relevant for effective mutualism (Bradshaw and Schemske 2003; Whittall and Hodges 2007; Pauw et al. 2009; Galetti et al. 2013). In addition, recent theoretical work has demonstrated that coevolution among mutualists shapes the network structure of interactions (Nuismer et al. 2013) and that network structure may in turn guide coevolutionary dynamics (Guimarães et al. 2011, 2017). Together, these empirical observations suggest that evolution within species—and coevolution among species—may have the potential to reduce the rate of extinction for mutualists subjected to chronic anthropogenic disturbances, such as habitat destruction and climate change.

Here we develop mathematical models and computer simulations that allow us to explore how historical and contemporary coevolution among mutualists influences the persistence of mutualistic networks in the face of habitat destruction and climate change. This work builds on previous modeling that explored the influence of mutualistic coevolution on trait distributions and network structure (Nuismer et al. 2013) by studying distributions of interaction redundancy and integrating explicit feedbacks between coevolution and demography. The inclusion of explicit ecoevolutionary feedbacks in simulated communities allows us to investigate novel questions about the interplay between mutualistic coevolution and the durability of communities in the face of environmental change. Specifically, we use mathematical models and individual-based simulations to answer the following questions: (1) Are communities with a long history of mutualistic coevolution more likely to remain intact? (2) Are communities in which interactions depend on heritable traits that can rapidly coevolve less sensitive to environmental perturbation? (3) Can coevolutionary rescue mitigate the impact of anthropogenic disturbance? Together, our analyses answer these questions in the affirmative, demonstrating that coevolution may play an important role in ameliorating species extinction in the face of large-scale anthropogenic disturbance.

The Model

We study a community of mutualists consisting of two interacting guilds, X and Y. For simplicity, we will consistently refer to guild X as plants and to guild Y as animals. We assume that there are N_x plant species within the community, each of which has an effective population size of $n_{x,i}$ individuals. Similarly, we assume that there are N_y animal species, each of which has an effective population size $n_{y,i}$. We assume that individuals encounter one another at random and that the probability of exchanging fitness benefits (e.g., pollen is transferred, nectar is consumed, seeds are dispersed) depends on a single key trait, x , in the plant (e.g., corolla depth, flowering date, seed size) and a single key trait, y , in the animal (e.g., proboscis length, emergence date, beak depth). Specifically, we assume that random encounters lead to the exchange of fitness benefits with a probability, P , given by

$$P = \exp[-\alpha(x - y)^2], \quad (1)$$

where the parameter α determines how sensitive the outcome of interactions is to the difference between plant and animal traits. When a successful interaction occurs, we assume that it increases plant fitness by an amount ξ_x and animal fitness by an amount ξ_y . We assume that all plant species are obligate outcrossers and that all animal species rely on plants exclusively for a critical resource (e.g., nectar, pollen, fruit) such that a plant or animal that fails to interact successfully with at least one individual has a fitness equal to zero. These assumptions lead to the following expressions for expected biotic fitness: in plant species i ,

$$W_{B,X,i} = \sum_{j=1}^{N_y} \sum_{k=1}^{n_{y,j}} \varphi \xi_x \exp[-\alpha(x - y_{j,k})^2], \quad (2a)$$

and within animal species i ,

$$W_{B,Y,i} = \sum_{j=1}^{N_x} \sum_{k=1}^{n_{x,j}} \varphi \xi_y \exp[-\alpha(x_{j,k} - y)^2], \quad (2b)$$

where each individual animal can visit a fraction, φ , of all plants within the community and the summations are carried out over all individuals (n) and species (N) in the interacting guild.

In addition to species interactions, we assume that both plants and animals experience stabilizing selection toward some optimal phenotype. Although our model does not specify the source of this stabilizing selection, we will refer to it as “abiotic” to separate it from selection imposed by “biotic” interactions between plants and animals. Specifically, we assume that the abiotic fitness of an individual plant of species i with phenotype x is given by

$$W_{A,X,i} = \exp[-\gamma_x(x - \theta_{x,i})^2], \quad (3a)$$

and the abiotic fitness of an individual animal of species i with phenotype y is given by

$$W_{A,Y,i} = \exp[-\gamma_Y(y - \theta_{Y,i})^2], \quad (3b)$$

where the parameters γ_X and γ_Y measure the intensity of stabilizing selection and the parameters $\theta_{X,i}$ and $\theta_{Y,i}$ measure the (species-specific) optimal phenotypes in plants and animals, respectively. Ultimately, the total fitness of individual plants ($W_{T,X}$) and animals ($W_{T,Y}$) is assumed to depend on the product of their biotic and abiotic fitness such that

$$W_{T,X,i} = \sum_{j=1}^{N_Y} \sum_{k=1}^{n_{Y,j}} \varphi \xi_X \exp[-\alpha(x - y_{j,k})^2] \exp[-\gamma_X(x - \theta_{X,i})^2], \quad (4a)$$

$$W_{T,Y,i} = \sum_{j=1}^{N_X} \sum_{k=1}^{n_{X,j}} \varphi \xi_Y \exp[-\alpha(x_{j,k} - y)^2] \exp[-\gamma_Y(y - \theta_{Y,i})^2]. \quad (4b)$$

We study this general model using two complementary approaches. First, we develop analytical approximations that assume that selection is weak, that additive genetic variances are fixed, and that coevolution does not interact with population abundance. The goal of these analytical approximations is to gain general insights into the role coevolution plays in stabilizing mutualistic networks and buffering them against future disturbance. Second, we develop and analyze individual-based simulations that allow for strong selection and eco-evolutionary feedbacks between population sizes and coevolution. We use these simulations to evaluate the predictions made by our analytical approximations when communities are confronted with habitat destruction or climate change.

Analytical Approximations

To gain general insights into the role coevolution may play in buffering mutualistic networks against disturbance, we first develop a simplified analytical approximation that ignores feedbacks between demography and evolution. In addition to ignoring eco-evolutionary feedbacks, our analytical approximation rests on the following key assumptions: (1) weak abiotic and biotic selection, (2) fixed additive genetic variance, and (3) Gaussian trait distributions within species. These assumptions allow us to use well-studied quantitative genetic equations (Lande 1976) to investigate the influence of coevolution on the interaction rates among species within the community (Nuismer et al. 2013).

Coevolution Drives the Convergence of Mutualistic Traits

We begin our investigation by predicting how the population mean phenotypes of plant and animal species change

in response to coevolution. Using standard quantitative genetic approaches, results derived in appendix A (apps. A–C are available online) show that the population mean phenotype of plant species i , \bar{x}_i , in the next generation is

$$\bar{x}'_i = \bar{x}_i + 2\gamma_X G_X(\theta_{X,i} - \bar{x}_i) + 2\alpha G_X(\mu_{\bar{y}} - \bar{x}_i) + \delta_{X,i}, \quad (5a)$$

and the population mean phenotype of animal species i , \bar{y}_i , in the next generation is

$$\bar{y}'_i = \bar{y}_i + 2\gamma_Y G_Y(\theta_{Y,i} - \bar{y}_i) + 2\alpha G_Y(\mu_{\bar{x}} - \bar{y}_i) + \delta_{Y,i}, \quad (5b)$$

where G_X and G_Y are the additive genetic variances for plant and animal species, respectively, and $\delta_{X,i}$ and $\delta_{Y,i}$ are random fluctuations in mean phenotype arising in plant species i and animal species i through random genetic drift, respectively. The terms $\mu_{\bar{x}}$ and $\mu_{\bar{y}}$ are the expected values of population mean phenotypes taken across plant and animal species, respectively, and measure, for example, the average corolla depth across all plant species and the average proboscis length across all animal species. Although it is possible to study coevolution within small communities of mutualists using equations (5) directly, this becomes increasingly cumbersome as the number of species increases.

To study large mutualistic networks with many species of plants and animals, a more practical approach is to study how the distribution of trait means evolves within plants and animals (Nuismer et al. 2013). Specifically, results derived in appendix B show that the distribution of trait means among all plants in the next generation can be approximated by recursions for three statistical moments:

$$\mu'_{\bar{x}} = \mu_{\bar{x}} + 2G_X(\gamma_X(\bar{\theta}_X - \mu_{\bar{x}}) + \alpha(\mu_{\bar{y}} - \mu_{\bar{x}})), \quad (6a)$$

$$V'_{\bar{x}} = V_{\bar{x}}(1 - 4G_X(\alpha + \gamma_X)) + 4\gamma_X G_X C_{\bar{x},\theta_X} + \frac{G_X}{\bar{n}_X}, \quad (6b)$$

$$C'_{\bar{x},\theta_X} = C_{\bar{x},\theta_X}(1 - 2G_X(\alpha + \gamma_X)) + 2\gamma_X G_X V_{\theta_X}, \quad (6c)$$

where $\mu_{\bar{x}}$ is the expected value of plant trait means, $V_{\bar{x}}$ is the variance among plant trait means, $C_{\bar{x},\theta_X}$ is the covariance between plant trait means and abiotic optima, $\bar{\theta}_X$ is the average phenotype favored by stabilizing selection across all plants, \bar{n}_X is the harmonic mean population size across plant species, and V_{θ_X} is the variance in the phenotypes favored by stabilizing selection among plants. Similarly, the distribution of trait means among all animals in the next generation can be approximated by recursions for the same three moments:

$$\mu'_{\bar{y}} = \mu_{\bar{y}} + 2G_Y(\gamma_Y(\bar{\theta}_Y - \mu_{\bar{y}}) + \alpha(\mu_{\bar{x}} - \mu_{\bar{y}})), \quad (7a)$$

$$V'_{\bar{y}} = V_{\bar{y}}(1 - 4G_Y(\alpha + \gamma_Y)) + 4\gamma_Y G_Y C_{\bar{y},\theta_Y} + \frac{G_Y}{\bar{n}_Y}, \quad (7b)$$

$$C'_{\bar{y},\theta_Y} = C_{\bar{y},\theta_Y}(1 - 2G_Y(\alpha + \gamma_Y)) + 2\gamma_Y G_Y V_{\theta_Y}, \quad (7c)$$

where $\mu_{\bar{y}}$ is the expected value of plant trait means, $V_{\bar{y}}$ is the variance among plant trait means, $C_{\bar{y},\theta_Y}$ is the covariance between plant trait means and abiotic optima, $\bar{\theta}_Y$ is the average phenotype favored by stabilizing selection across all plants, \bar{n}_Y is the harmonic mean population size across plant species, and V_{θ_Y} is the variance in the phenotypes favored by stabilizing selection among plants.

Previous analyses of a similar model (Nuismer et al. 2013) and results derived in appendix B demonstrate that coevolution among mutualist species leads to trait convergence at equilibrium. Specifically, as the strength of coevolutionary selection increases, the average trait values of plants and animals draw closer to one another, and variation in trait values among plants and animals is reduced (fig. 1). To investigate how rapidly this trait convergence occurs, we iterated the recursion equations (4). These numerical investigations demonstrate that coevolution can cause convergence of trait values over as few as tens of generations, particularly when additive genetic variation for the key traits mediating interactions between plants and animals is substantial. Although mutualistic coevolution favors trait convergence, such convergence never goes to completion as long as stabilizing selection exists for diverse optima. Thus, our model qualitatively captures the fact that other forces, such as reproductive character displacement, may act in opposition to mutualistic convergence. In the next section, we explore how trait convergence influences the distribution of species interactions within the community and its potential consequences for the stability of mutualistic networks in the face of ecological disturbance.

Coevolution Increases Interaction Redundancy

To better understand how trait convergence caused by coevolution influences the ecological structure of mutualistic networks, we developed predictions for the compatibility distribution in plants and in animals. The compatibility distribution, $f_i(C)$, defines the frequency of species in guild i capable of interacting with a proportion of individuals C in the opposing guild. We focus on this distribution because it quantifies the extent of functional redundancy within plants and animals and thus how sensitive a given community is likely to be to an environmental disturbance. Specifically, communities in which compatibility distributions of plants and animals have a high mean and low variance should be less sensitive to the loss of individual species because most species are able to interact successfully with more than one other species.

We derived solutions for the compatibility distribution of plants and animals under the assumption that trait means followed Gaussian distributions within the community and that the outcome of interactions did not depend too strongly on the traits of individuals (app. C). With these assumptions,

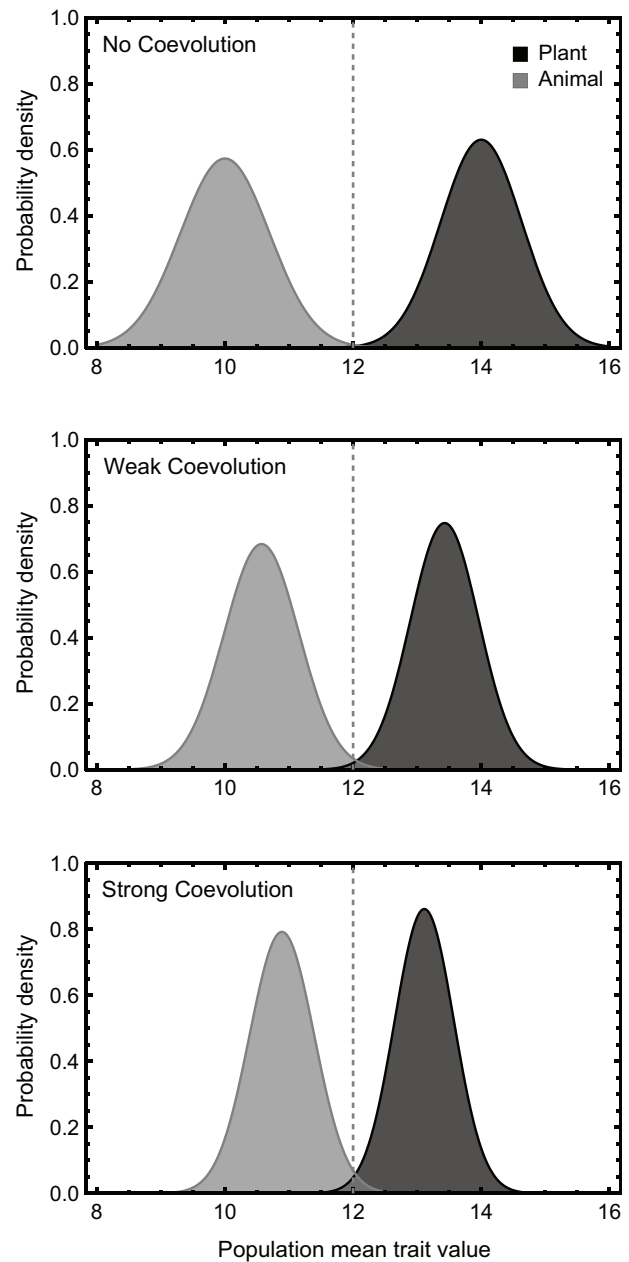


Figure 1: Trait convergence in response to coevolution of different strengths. Each panel shows the equilibrium probability density of species within the community that have a particular population mean trait value (app. B; eqq. [7]–[12]), with plant species depicted by the dark gray distribution and animal species by the light gray distribution. The top panel shows a case in which coevolution is absent and evolution occurs in response to stabilizing selection and random genetic drift alone, the middle panel shows a case in which coevolution is weak ($\alpha = 0.01$), and the bottom panel shows a case in which coevolution is moderately strong ($\alpha = 0.02$). Remaining parameters were $\gamma_X = 0.05$, $\gamma_Y = 0.05$, $\bar{\theta}_X = 14.0$, $\bar{\theta}_Y = 10.0$, $V_{\theta_X} = 0.35$, $V_{\theta_Y} = 0.45$, $\bar{n}_X = 100$, and $\bar{n}_Y = 150$.

it is possible to show that the compatibility distribution for plants is given by

$$f_x(C) = \frac{\left(\exp\left(-\frac{(\sqrt{\alpha(1-C-\alpha(V_x+V_y+V_{\bar{y}})})+\alpha(\mu_{\bar{x}}-\mu_{\bar{y}}))^2}{2\alpha^2 V_{\bar{y}}}\right) + \exp\left(-\frac{(\sqrt{\alpha(1-C-\alpha(V_x+V_y+V_{\bar{y}})})-\alpha(\mu_{\bar{x}}-\mu_{\bar{y}}))^2}{2\alpha^2 V_{\bar{x}}}\right) \right)}{2\sqrt{2\pi}\sqrt{V_{\bar{x}}}\sqrt{\alpha(1-C-\alpha(V_x+V_y+V_{\bar{y}}))}} \quad (8a)$$

and the compatibility distribution for animals is given by

$$f_y(C) = \frac{\left(\exp\left(-\frac{(\sqrt{\alpha(1-C-\alpha(V_y+V_x+V_{\bar{x}})})+\alpha(\mu_{\bar{y}}-\mu_{\bar{x}}))^2}{2\alpha^2 V_{\bar{y}}}\right) + \exp\left(-\frac{(\sqrt{\alpha(1-C-\alpha(V_y+V_x+V_{\bar{x}})})-\alpha(\mu_{\bar{y}}-\mu_{\bar{x}}))^2}{2\alpha^2 V_{\bar{x}}}\right) \right)}{2\sqrt{2\pi}\sqrt{V_{\bar{y}}}\sqrt{\alpha(1-C-\alpha(V_y+V_x+V_{\bar{x}}))}} \quad (8b)$$

where V_x and V_y are the phenotypic variance within plant and animal species, respectively. A combination of inspection and numerical investigation of equations (8) reveals two important points. First, as the average trait values of plant and animal species draw closer to one another, the compatibility distribution shifts to the right and narrows. Second, as the variance of trait values across plant and animal species de-

creases, the compatibility distribution narrows. Because we know from previous work (Guimarães et al. 2011; Nuismer et al. 2013) and the results of the previous section that mutualistic coevolution causes trait convergence, these results suggest that coevolution will cause the compatibility distribution to shift rightward and narrow. Biologically speaking, this suggests that coevolution will increase interaction redundancy within the community by promoting generalization.

To formalize our predictions for the influence of coevolution on the compatibility distribution, we substituted the equilibrium solutions for trait means and variances into equations (8) and compared the resulting distribution across various coevolutionary scenarios. As coevolution becomes an increasingly potent force within the community, the compatibility distribution shifts rightward and narrows, confirming an increase in interaction redundancy arising from coevolution (fig. 2). To gain further insight into the timescale over which coevolution shifts the compatibility distribution, we iterated equations (5) for a range of parameter combinations and calculated the compatibility distribution in each generation. The results of these numerical investigations demonstrate that coevolution can drive substantial shifts in the compatibility distribution over very short timescales (e.g., tens of generations), particularly when substantial genetic variation is available for the key traits mediating mutualistic interactions.

Together, the results of our analytical approximation suggest that coevolution increases the redundancy of mutualistic interactions. Because communities showing greater levels of

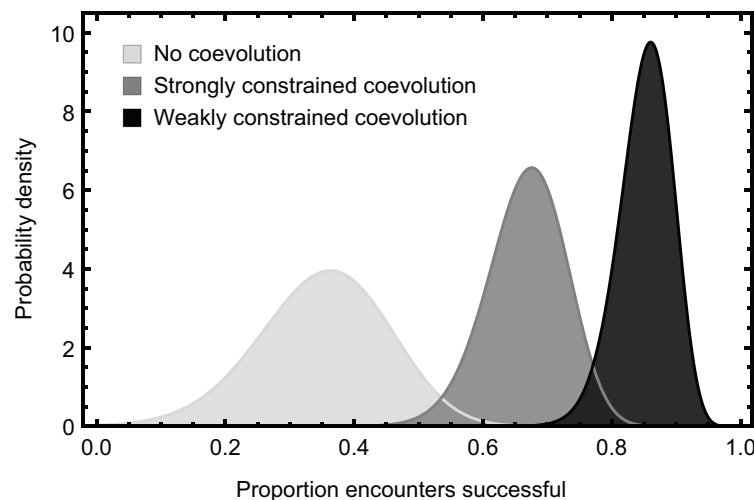


Figure 2: Equilibrium plant compatibility distribution (eq. [8a]) for scenarios in which coevolution is absent (light gray), present but strongly constrained (gray), and present with only weak constraint (dark gray). As the importance of coevolution increases, the compatibility distribution narrows and shifts to the right, indicating that an increasing number of plant species are able to interact with a wide range of animals. Parameters for the light gray and gray distributions were $\alpha = 0.01$, $\gamma_x = 0.05$, $\gamma_y = 0.05$, $\bar{\theta}_x = 15.0$, $\bar{\theta}_y = 7.0$, $V_{\theta_x} = 0.35$, $V_{\theta_y} = 0.45$, $\check{n}_x = 100$, and $\check{n}_y = 150$. Parameters for the dark gray distribution were $\alpha = 0.02$, $\gamma_x = 0.02$, $\gamma_y = 0.02$, $\bar{\theta}_x = 15.0$, $\bar{\theta}_y = 7.0$, $V_{\theta_x} = 0.35$, $V_{\theta_y} = 0.45$, $\check{n}_x = 100$, and $\check{n}_y = 150$.

interaction redundancy may be less sensitive to the loss of individual species, these results suggest that communities with a long history of mutualistic coevolution may be more robust to environmental disturbance than communities in which coevolution has played an insignificant historical role. In the next section, we investigate whether this prediction holds when key assumptions of our analytical approximation are relaxed and simulated communities are confronted with realistic ecological disturbance.

Individual-Based Simulations

To evaluate the robustness of our analytical predictions, we developed individual-based simulations that relaxed key assumptions and allowed us to study the consequences of coevolution for the fate of mutualistic networks confronted with environmental disturbance. Specifically, our simulation approach freed us from the assumptions of normally distributed traits and weak selection, explicitly integrated demography, and allowed us to study how coevolution influences the response of mutualistic networks to habitat destruction and climate change. Simulations followed individual plants and animals over a life cycle consisting of (1) stabilizing selection toward species-specific phenotypic optima, (2) interspecific interactions among plants and animals, and (3) random mating, reproduction, and population regulation. Populations were assumed to be well mixed, with all plants and animals present as a well-defined community occupying a single geographic location. The details of each phase of the life cycle are described in the following sections.

Stabilizing selection. In each generation, stabilizing selection was imposed by assigning each individual an abiotic fitness using expression (2). The phenotypic optima, θ , favored by stabilizing selection were species specific and assumed to be phylogenetically structured. Specifically, at the beginning of each simulation run a phylogenetic tree was generated for animals and plants using a pure birth process ($b = 1 \times 10^{-5}$). The phenotypic optima were then evolved on the phylogenetic tree following a model of Brownian motion where the value of θ within each lineage was changed by an amount drawn from a normal distribution with mean 0 and variance equal to $5b/N$, where N is the number of species in the guild. The result of this process is a community with diverse phenotypic optima that inhibit mutualistic convergence.

Interspecific interactions. The number of plants an animal could visit in any given generation was assumed to be density dependent, as might be the case if animals are capable of searching only a finite amount of territory. Specifically, over a single generation, animals visited a number of plants drawn from a Poisson distribution with mean equal to twice the proportion of habitat occupied by plants. Thus, if all plant species were at carrying capacity, each animal would visit, on average, two individual plants. If instead all plant species

were at half carrying capacity, each animal would be capable of visiting only one plant, on average. After drawing the number of plants an animal would visit, the identity of the visited plants was drawn at random. For each visit, the probability that the interaction was successful (i.e., increased fitness) was determined by drawing a random variable and asking if it exceeded the threshold given by equation (1). Thus, a plant and animal with similar phenotypes were more likely to interact successfully than a plant and animal with dissimilar phenotypes. If a successful interaction occurred, the biotic component of plant fitness was incremented by an amount (ξ_x), and the biotic component of animal fitness was incremented by an amount (ξ_y).

Random mating, reproduction, and population regulation. For simplicity, we assumed that both plants and animals were hermaphroditic and mated at random. The number of offspring produced by each individual was drawn at random from a Poisson distribution with mean equal to the individual's total fitness. Total fitness was calculated as the product of abiotic and biotic fitness components and capped at a maximum possible value of 10 to capture limits on maximum possible reproductive output (e.g., total number of ovules). Offspring phenotypes were determined by selecting a random father (independent of fitness) and assigning an offspring phenotype, z_o , using

$$z_o = \bar{z} + h^2 \left(\frac{z_m + z_p}{2} - \bar{z} \right) + \omega, \quad (9)$$

where \bar{z} is the mean phenotype of the parental generation, h^2 is the heritability, $(z_m + z_p)/2$ is the average phenotypic value of the parents, and ω is a random variable drawn from a Gaussian distribution with mean 0 and variance equal to 0.01. Once all individuals within all species completed reproduction, offspring were selected at random and placed into their species-specific "habitat," with the habitat of each species having a carrying capacity drawn from a lognormal distribution at the beginning of the simulation. If the habitat of the randomly selected offspring was full but other species-specific habitats were not, one of the alternative habitats with vacancies was selected at random. The probability that an offspring successfully established in an alternate habitat was equal to 0.2 in simulation results we report, but modest changes in this value had no qualitative impact on the results. Large increases in this value, however, make coexistence among species within a guild increasingly unlikely—a result that is not surprising since it corresponds to reduced niche differentiation. Thus, our simulation assumes that each species has a unique habitat in which it performs better than all other species within its guild but that each species can occupy and survive in any other vacant habitat with some reduced probability. This mode of population regulation allows for coexistence through niche differentiation as well as for extinction and subsequent range expansion by surviving species.

Each simulation run began by drawing key parameters at random from the values shown in table 1 and drawing initial phenotypes for all individuals at random from Gaussian distributions with mean equal to the species-specific optimal phenotype, θ , and variance equal to 0.01. The resulting community of plants and animals was then allowed to coevolve for 10, 100, or 300 generations prior to initiation of the disturbance regime. We refer to this initial phase of the simulation as “establishment.” After the establishment phase, we initiated a disturbance regime corresponding to either habitat destruction or climate change. All simulations considered communities initially composed of 80 plant and 80 animal species.

Habitat destruction. To model habitat destruction, we destroyed between 10% and 90% of the total habitat over the course of 50 generations by randomly reducing the carrying capacity of each species in each generation. The expected per-generation reduction in habitat differed across species and was drawn at random at the beginning of the simulation such that the impact of habitat destruction was greater for some species than for others. After the habitat destruction phase completed, we calculated the number of remaining plant and animal species as well the number of unique interactions that were observed to occur. We then compared these numbers to those prior to habitat destruction to calculate the proportion of remaining animals species, plant species, and unique interactions. Results of initial simulations exploring the impact of the extent of habitat destruction revealed that the sensitivity of communities to habitat destruction depends heavily on the potential for coevolution. Specifically, in cases in which the traits mediating plant-animal interactions were not her-

itable, such that coevolution could not occur, species and their interactions were lost rapidly as levels of habitat destruction surpassed 40% (fig. 3, gray region). In cases in which plant traits were heritable but animal traits were not (unilateral evolution), the rate of loss in species and their interactions was more mild (fig. 3, yellow region). In contrast, if the traits of both plants and animals were heritable, such that coevolution could occur, species and their interactions were lost much more slowly than the previous two cases (fig. 3, red region). In addition to identifying an important role for heritability, our simulations demonstrated that the duration of coevolution prior to habitat destruction played an important role. Specifically, long-established communities with an extensive history of coevolution (i.e., hundreds of generations) were less sensitive to habitat destruction than were communities with only a brief (i.e., tens of generations) history of coevolution (fig. 4).

Climate change. To model climate change, we reduced the optimal phenotype of each species, θ , by a randomly selected amount in each generation. Our motivation for this regime arises from a scenario in which the traits mediating the interaction are flowering or fruiting phenology and the timing of pollinator or disperser activity. For such traits, the optimal trait value is likely to shift directionally with climate change as, for instance, warming leads to earlier snowmelt and reductions in soil water availability later in the season. We recognize, however, that this is only one of many ways climate change could influence mutualistic interactions and that our model applies more generally to any scenario in which environmental change generates sustained directional modification of phenotypic optima. At the beginning of each simulation run, we set the per-generation rate of climate change to a value C , which ranged from 0.002 (slow climate change) to 0.022 (rapid climate change). Once climate change began in a simulation, it continued for 50 generations such that the total amount of climate change that occurred in a simulation ranged between 0.1 and 1.1. Heterogeneity among species in their sensitivity to climate change was incorporated by assuming the per-generation rate of climate change for species i was equal to

$$C_i = -\varepsilon C, \quad (10)$$

where ε is a random variable drawn from a uniform distribution on $\{0.5, 1.5\}$. Finally, temporal stochasticity in the change in the optimal phenotype caused by climate change was captured by reducing the optimal phenotype of each species, i , by an amount equal to

$$\Delta\theta_i = -\varepsilon C_i \quad (11)$$

in each of the final 50 generations, where ε is a random variable drawn from a uniform distribution on $\{0.9, 1.1\}$. Much like the simulations exploring habitat destruction, climate change simulations revealed that communities in which traits

Table 1: Parameters used in simulations

Parameter	Method	Value/range
α	Fixed	1, 5, 10
ξ_x	Random	Drawn from a normal distribution on (5.0, .5)
ξ_y	Random	Drawn from a normal distribution on (5.0, .5)
γ_x	Random	Drawn from a uniform distribution on (1.0, 3.0)
γ_y	Random	Drawn from a uniform distribution on (1.0, 3.0)
k_x	Random	Drawn from a lognormal distribution on (6.5, .3)
k_y	Random	Drawn from a lognormal distribution on (6.5, .3)
θ_x	Random	Birth tree
θ_y	Random	Birth tree
h_x^2	Random	Drawn from a uniform distribution on ($h_x^2 \pm .1$)
h_y^2	Random	Drawn from a uniform distribution on ($h_y^2 \pm .1$)

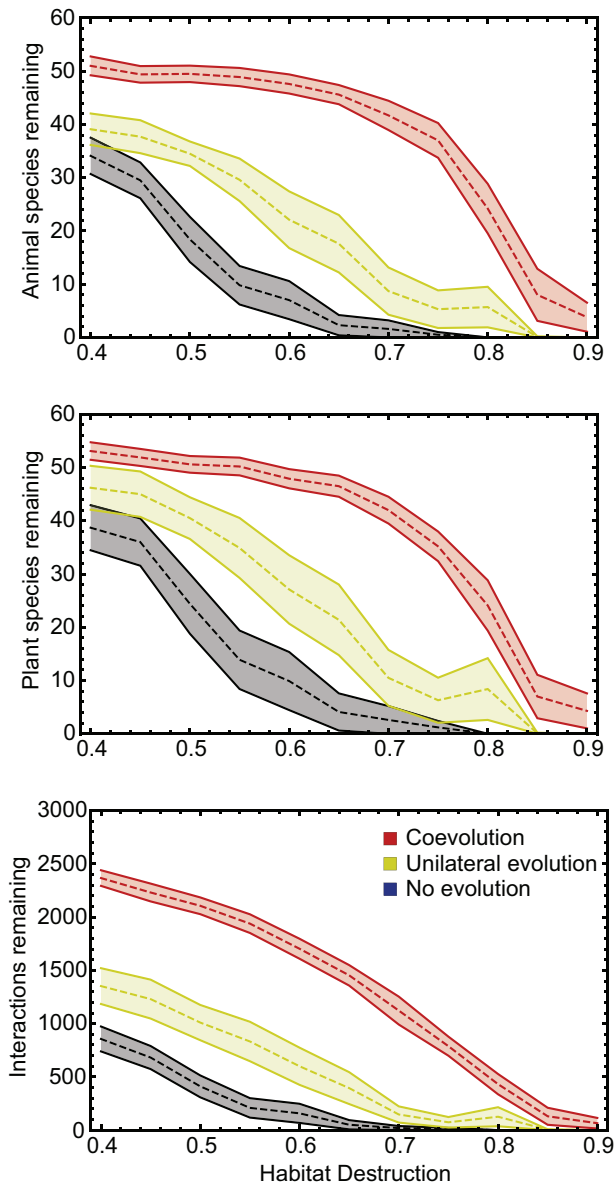


Figure 3: Number of animal species (*top*), plant species (*middle*), and unique interactions (*bottom*) remaining as a function of the proportion of habitat destroyed for scenarios in which evolution is absent (gray band), only one species evolves (yellow band), and both species coevolve (red band). For each level of habitat destruction, 10 replicate simulations were run, each of which had background parameters drawn at random from the ranges shown in table 1. The dashed line of each color represents the mean of replicate simulations, and the shaded region represents the SE.

mediating interactions are heritable, allowing for coevolution, are able to tolerate a much greater extent of climate change than communities in which heritability is present in only plant species or absent altogether (fig. 5). In contrast to simulations of habitat destruction, however, simulations of

climate change showed that the duration of coevolution had little impact on the sensitivity of communities to climate change (fig. 6). This result suggests that the influence of coevolution on the response of a community to climate change must arise primarily from contemporary coevolution rather than the historical impact of coevolution on community struc-

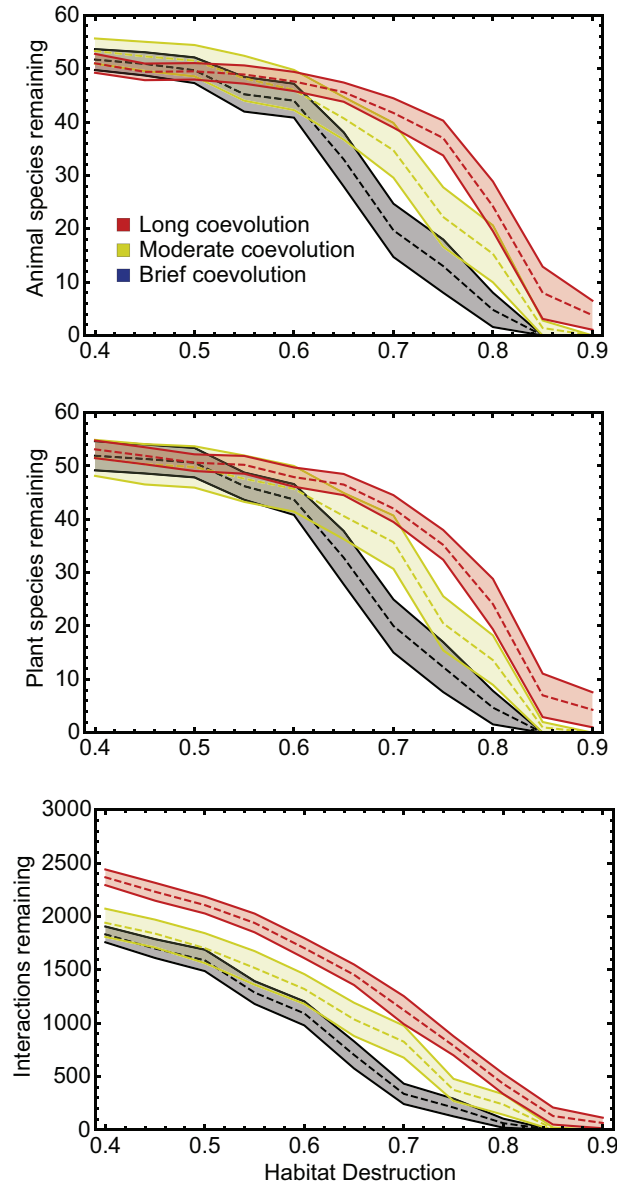


Figure 4: Number of animal species (*top*), plant species (*middle*), and unique interactions (*bottom*) remaining as a function of the amount of climate change for scenarios in which evolution is absent (gray band), only one species evolves (yellow band), and both species coevolve (red band). For each level of climate change, 10 replicate simulations were run, each of which had background parameters drawn at random from the ranges shown in table 1. The dashed line of each color represents the mean of replicate simulations, and the shaded region represents the SE.

ture. In the next section, we confirm this suggestion and demonstrate that a process of “coevolutionary rescue” facilitates the persistence of mutualistic communities in the face of rapid environmental deterioration.

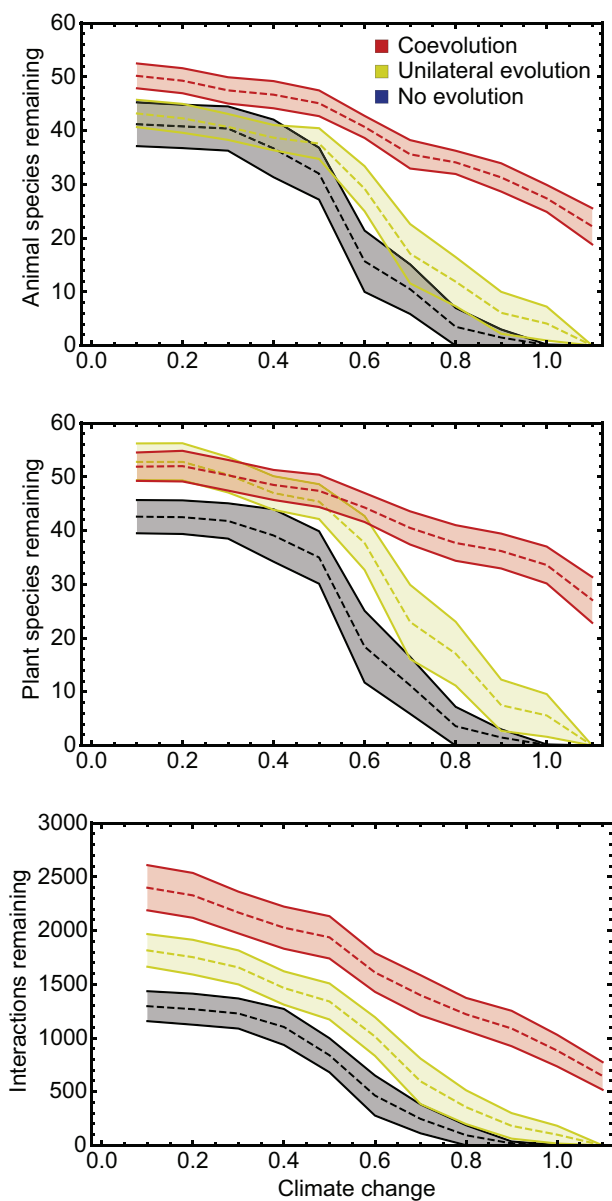


Figure 5: Number of animal species (*top*), plant species (*middle*), and unique interactions (*bottom*) remaining as a function of the proportion of habitat destroyed for scenarios in which coevolution occurred only briefly prior to the initiation of disturbance (gray band), coevolution occurred for a modest period of time prior to the initiation of disturbance (yellow band), and coevolution occurred for a substantial period of time prior to the initiation of disturbance (red band). For each level of habitat destruction, 10 replicate simulations were run, each of which had background parameters drawn at random from the ranges shown in table 1. The dashed line of each color represents the mean of replicate simulations, and the shaded region represents the SE.

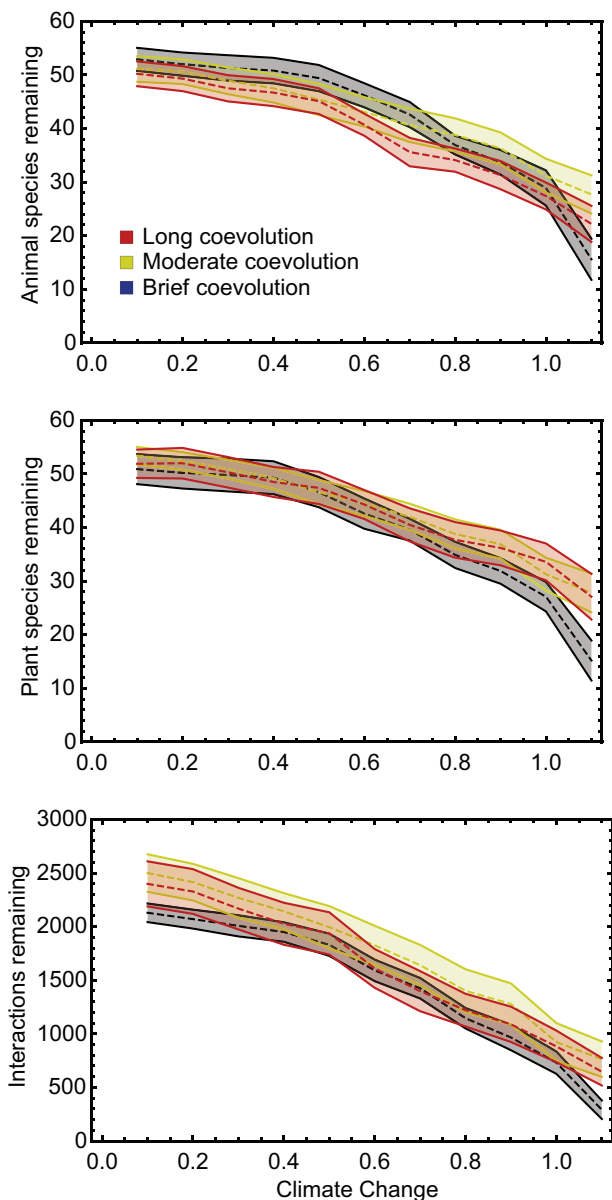


Figure 6: Number of animal species (*top*), plant species (*middle*), and unique interactions (*bottom*) remaining as a function of the amount of climate change for scenarios in which coevolution occurred only briefly prior to the initiation of environmental change (gray band), coevolution occurred for a modest period of time prior to the initiation of environmental change (yellow band), and coevolution occurred for a substantial period of time prior to the initiation of environmental change (red band). For each level of climate change, 10 replicate simulations were run, each of which had background parameters drawn at random from the ranges shown in table 1. The dashed line of each color represents the mean of replicate simulations, and the shaded region represents the SE.

Coevolutionary Rescue

So far, our results have shown that mutualistic networks can be buffered from environmental change through a combina-

tion of historical (prior to environmental change) and contemporary (during environmental change) coevolution. In this section, we attempt to isolate the impact of contemporary coevolution by studying an additional set of simulations that compared the fate of communities that were allowed to coevolve after the initiation of disturbance with the fate of those that were not. Specifically, for 10 randomly generated phylogenetic histories we assembled communities of mutualists and let them interact for 100 generations. During this first 100 generations, the trait mediating the interactions was not heritable, precluding any historical impact of coevolution on community structure. After this initial 100 generations, we began to impose disturbance in the form of habitat destruction or climate change, as previously described. We then compared the trajectory of extinction for communities in which the trait mediating interactions was heritable in both guilds (allowing for coevolution after the initial 100 generations) with that for communities in which the trait was heritable in only one of the two guilds (allowing for unilateral evolution after the initial 100 generations) and with that for communities in which the trait was not heritable in either guild (no evolution for the entire simulation). Thus, we were able to isolate the impact of contemporary coevolution on the extinction of individual species and of interactions. The results of these simulations demonstrate that contemporary coevolution can have very strong buffering effects on communities by substantially slowing the rate at which species and interactions are lost (fig. 7). Although this process of coevolutionary rescue slows the disintegration of mutualistic networks, it cannot prevent it altogether if disturbance continues unabated.

Discussion

Our results demonstrate that a history of coevolution promotes the persistence of mutualistic networks in the face of disturbance. Specifically, under simulated habitat destruction and climate change, communities with a substantial history of coevolution lose species—and the interactions between them—more slowly than communities in which coevolution has been historically weak or absent. Mathematical analyses of quantitative genetic approximations show that the driving force behind the stabilizing impact of coevolution is trait convergence and the increased levels of interaction redundancy it provides. Simply put, a long history of coevolution drives traits of mutualists together in ways that increase generalization and reduce the specialization that makes species sensitive to the loss of mutualistic partners and communities susceptible to cascades of extinction (Stang et al. 2007; Brodie et al. 2014; Lever et al. 2014).

Our results make two novel, testable predictions about the characteristics of mutualistic networks and how these characteristics influence robustness to anthropogenic disturbance.

First, our results suggest that long-established communities of mutualists will have had greater opportunities for coevolution and will thus demonstrate greater levels of trait convergence, interaction redundancy (generality), and network connectance. Second, communities in which interactions depend on traits that are highly heritable will have been—and will continue to be—more coevolutionarily responsive and thus more robust to environmental change. Although we are unaware of any existing data that can be used to test these predictions explicitly, collecting the relevant data is feasible and would substantially improve our understanding of the roles coevolution and evolution play in shaping the structure and function of communities. For instance, the prediction that long-established communities with extensive opportunities for coevolution should show greater levels of trait convergence, interaction redundancy, and network connectance could be tested using islands of different ages (e.g., Traveset et al. 2016) or communities occupying habitats with different histories of ecological disturbance (e.g., time since glacial recession, volcanic eruption, or wildfire). It might also be possible to test these predictions, for instance, by studying changes in the network properties of microbiomes as a function of host age or at larger temporal and geographic scales by comparing temperate with tropical networks or networks located along a latitudinal gradient. Although more challenging, it is also possible to estimate heritabilities for key traits mediating mutualistic interactions, such as corolla depth and proboscis length or flowering phenology and emergence time. Because estimating heritabilities requires extensive trait measurements and a known pedigree, however, direct estimation of heritability is unlikely to be feasible for all—or even a sizable fraction of—species within complex mutualistic networks. The amount of phenotypic variation within species could, however, serve as a useful proxy (Cheverud 1988).

In addition to demonstrating the importance of historical coevolution, our results identify an important role for contemporary and rapid coevolution. Specifically, as environmental disturbance begins to drive individual species and interactions to extinction, coevolution adjusts the network structure of the community to buffer it against further losses of species and interactions. This process of coevolutionary rescue slows the disintegration of mutualistic networks, particularly when interactions are mediated by highly heritable traits. Our observation that the adaptive rewiring caused by coevolution slows the disassembly of mutualistic networks contrasts with recent work on antagonistic networks (Gilljam et al. 2015), where adaptive rewiring has been shown to reduce stability in some cases. This difference between mutualistic and antagonistic networks likely arises because the alignment of mutualistic partners' interests leads to rewiring that benefits both partners simultaneously. Although coevolutionary rescue can substantially slow the disassembly of mutualistic networks, it cannot save them if habitat destruc-

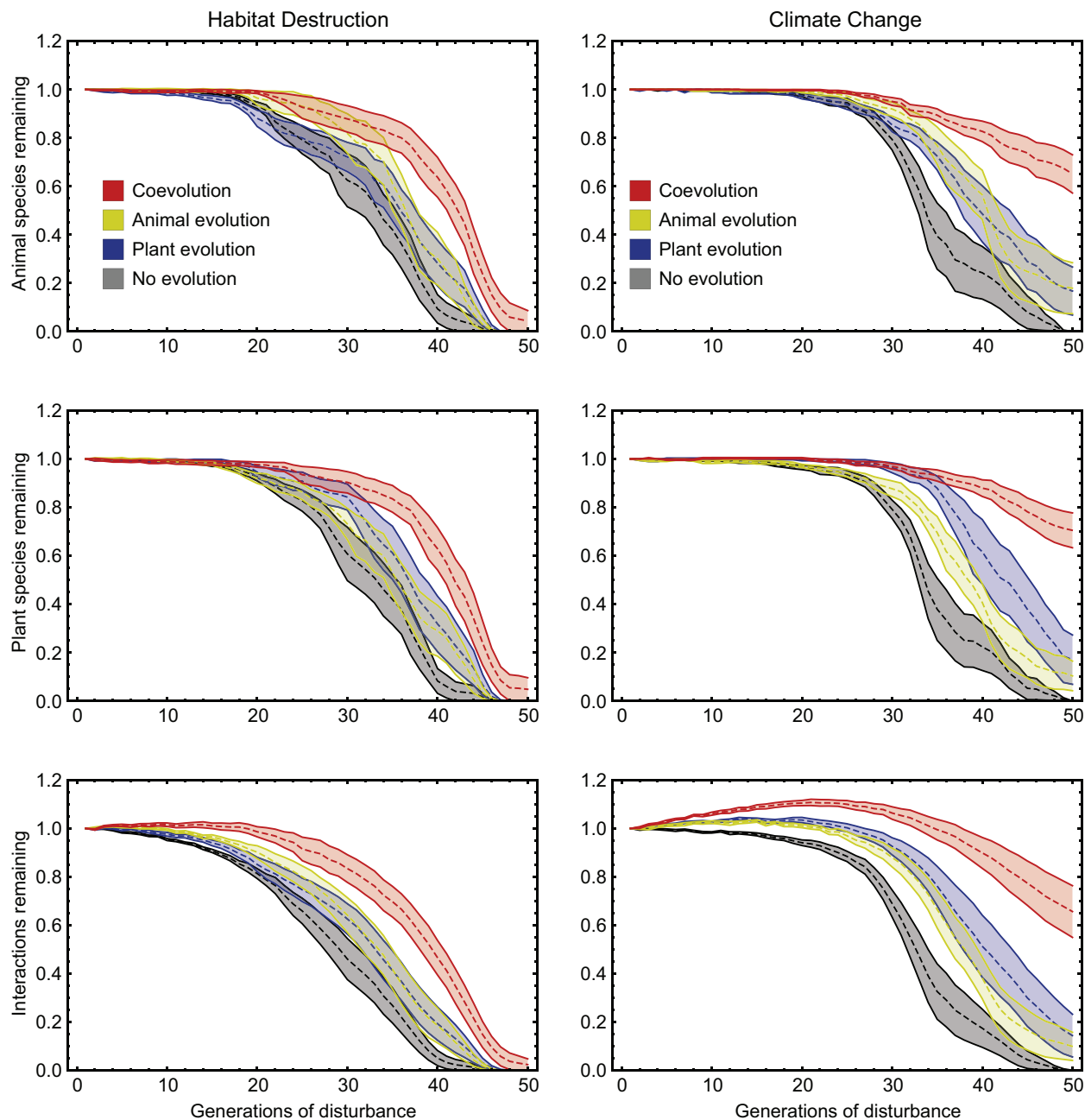


Figure 7: Impact of coevolutionary rescue (red) on the disassembly of mutualistic communities impacted by habitat destruction (*left column*) and climate change (*right column*). Each panel shows the proportion of animal species (*top row*), plant species (*middle row*), and unique interactions (*bottom row*) remaining as a function of the number of generations of anthropogenic disturbance endured. The red dashed line shows the average value of simulations in which coevolutionary rescue operates, and the red region indicates variability across the 10 simulation runs as a single SE. The yellow and blue dashed lines show the average value for simulations in which evolution is unilateral, and the corresponding shaded regions denote a single SE. The gray dashed line shows the average value of simulations in which neither species evolves, and the gray region denotes a single SE.

tion or climate change continues indefinitely and at a sufficiently high rate.

Although the models and simulations studied here are quite general and suggest a robust role for coevolution in

stabilizing mutualistic networks, they do depend on several key assumptions that may influence the quantitative impact of coevolution. For instance, our models assume that interactions among mutualists are all mediated by a single key

trait pair, such as corolla depth and proboscis length or flowering phenology and emergence time. In real communities, however, interactions may depend on a suite of different traits that define a multidimensional space of trait matching (Gilman et al. 2012; Debarre et al. 2014). Although the presence of multiple traits should not qualitatively alter our results, it could slow or reduce trait convergence via genetic correlations and thus lessen the stabilizing impact of historical coevolution and the scope for coevolutionary rescue. Another important assumption of our models is the constant and steady availability of additive genetic variation. Because our analytical results assume a fixed level of additive genetic variance and our simulations assume a constant influx of genetic variance, coevolution can proceed efficiently and produce extensive and sustained phenotypic change. Including models with more realistic genetic architectures would allow additive genetic variation to evolve and place limits on the rate and extent of phenotypic coevolution (Nuismer et al. 2005; Nuismer 2017). In some cases, such genetic constraints could reduce the stabilizing impact of historical coevolution and the scope for coevolutionary rescue. Finally, our assumption that all species are obligate outcrossers may magnify the fragility of mutualistic networks by eliminating self-fertilization as a mechanism buffering species from loss of mutualistic partners, a mechanism that is surely of significant importance in real plant-pollinator networks.

Together, our results demonstrate that coevolution can play an important historical and contemporary role in stabilizing communities against anthropogenic disturbance. The extent to which coevolution matters in real communities, however, depends on the temporal stability of community composition and the degree to which interactions among mutualists depend on heritable traits. Future studies that address these fundamental issues will help further our understanding of the importance of coevolution and its scope for slowing the disassembly of mutualistic networks.

Acknowledgments

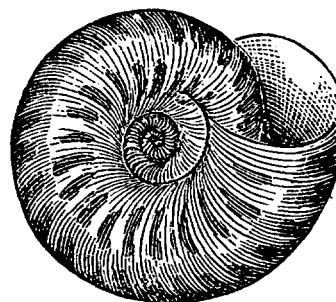
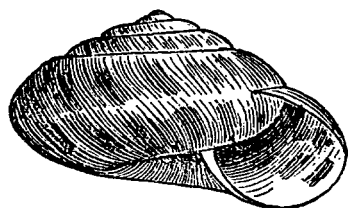
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“*HELIX ALTERNATA* Say. . . . Whorls six in full-grown shells. In young specimens the shell is carinated, that is, the outer whorl is keeled or angulated, instead of rounded.” From “The Land Snails of New England” by Edward S. Morse (*The American Naturalist*, 1867, 1:186–188).