

Interaction Intimacy Affects Structure and Coevolutionary Dynamics in Mutualistic Networks

Paulo R. Guimarães, Jr.,^{1,2,*} Victor Rico-Gray,³
Paulo S. Oliveira,⁴ Thiago J. Izzo,⁵
Sérgio F. dos Reis,⁶ and John N. Thompson⁷

¹Instituto de Física “Gleb Wataghin”

Universidade Estadual de Campinas 6165
Campinas–São Paulo
13083-970

Brazil

²Integrative Ecology Group

Estación Biológica de Doñana
Consejo Superior de Investigaciones Científicas
Apartado 1056
E-41080 Sevilla
Spain

³Departamento de Ecología Aplicada

Instituto de Ecología

AC Apartado 63

Xalapa

Veracruz 91070

México

⁴Departamento de Zoología and

⁵Departamento de Parasitología

Instituto de Biología

Universidade Estadual de Campinas 6109

Campinas–São Paulo

13083-970

Brazil

⁶Biological Dynamics of Forest Fragments Project

Smithsonian Tropical Research Institution

Instituto Nacional de Pesquisas da Amazônia 478

Manaus–Amazonas

69011-970

Brazil

⁷Department of Ecology and Evolutionary Biology

University of California

Santa Cruz, California 95064

Summary

The structure of mutualistic networks provides clues to processes shaping biodiversity [1–10]. Among them, interaction intimacy, the degree of biological association between partners, leads to differences in specialization patterns [4, 11] and might affect network organization [12]. Here, we investigated potential consequences of interaction intimacy for the structure and coevolution of mutualistic networks. From observed processes of selection on mutualistic interactions, it is expected that symbiotic interactions (high-interaction intimacy) will form species-poor networks characterized by compartmentalization [12, 13], whereas nonsymbiotic interactions (low intimacy) will lead to species-rich, nested networks in which there is a core of generalists and specialists often interact with

generalists [3, 5, 7, 12, 14]. We demonstrated an association between interaction intimacy and structure in 19 ant-plant mutualistic networks. Through numerical simulations, we found that network structure of different forms of mutualism affects evolutionary change in distinct ways. Change in one species affects primarily one mutualistic partner in symbiotic interactions but might affect multiple partners in nonsymbiotic interactions. We hypothesize that coevolution in symbiotic interactions is characterized by frequent reciprocal changes between few partners, but coevolution in nonsymbiotic networks might show rare bursts of changes in which many species respond to evolutionary changes in a single species.

Results

Different structural patterns are observed in symbiotic (e.g. ants interacting with myrmecophytes) and nonsymbiotic networks (e.g. ants interacting with fleshy fruits) (Figures 1A and 1B). Nonsymbiotic networks had, on average, four times the number of species found in symbiotic networks (75.2 ± 9.5 versus 18.4 ± 6.5 species, mean \pm SE, $p = 0.0003$, d.f. = 17). The relationship between interaction intimacy and species richness differed between ants and plants. The number of ant species was two times greater in nonsymbiotic than in symbiotic networks (24.2 ± 4.4 versus 10.5 ± 2.9 species, $p = 0.02$, d.f. = 17, Figure 1C), whereas the number of plant species was 6.5 times greater in nonsymbiotic than in symbiotic networks (51.00 ± 6.6 versus 7.85 ± 4.5 species, $p < 0.0001$, d.f. = 17, Figure 1C). As a consequence, plant species dominated nonsymbiotic networks ($69.3\% \pm 0.05\%$ of species) but usually showed species richness similar to that of ants in symbiotic networks (plants are $43.9\% \pm 0.03\%$ of species). Hence, species ratios differed significantly between nonsymbiotic and symbiotic networks ($p = 0.0006$, d.f. = 17).

Nonsymbiotic networks were often significantly nested (83.33% of the networks), whereas most symbiotic networks were nonnested (15.38% of the networks were nested; $\chi^2 = 8.44$, $p = 0.004$, d.f. = 17). We also investigated the relative nestedness of the networks, that is, the difference between the observed degree of nestedness and the degree of nestedness predicted for random networks with similar structural properties [3]. After controlling for the degree of nestedness expected by species richness and number of interactions per species, nonsymbiotic networks showed greater values of relative nestedness than symbiotic networks ($p = 0.013$, d.f. = 17, Figure 1D). Greater than 60% of symbiotic networks showed negative relative nestedness ($\chi^2 = 4.83$, $p = 0.028$, d.f. = 17), suggesting symmetric interactions and the existence of isolated subwebs, i.e., isolated groups of interacting species (see Experimental Procedures). In fact, symbiotic networks included three to six isolated subwebs (3.6 ± 0.51 isolated subwebs),

*Correspondence: prguima@ifi.unicamp.br

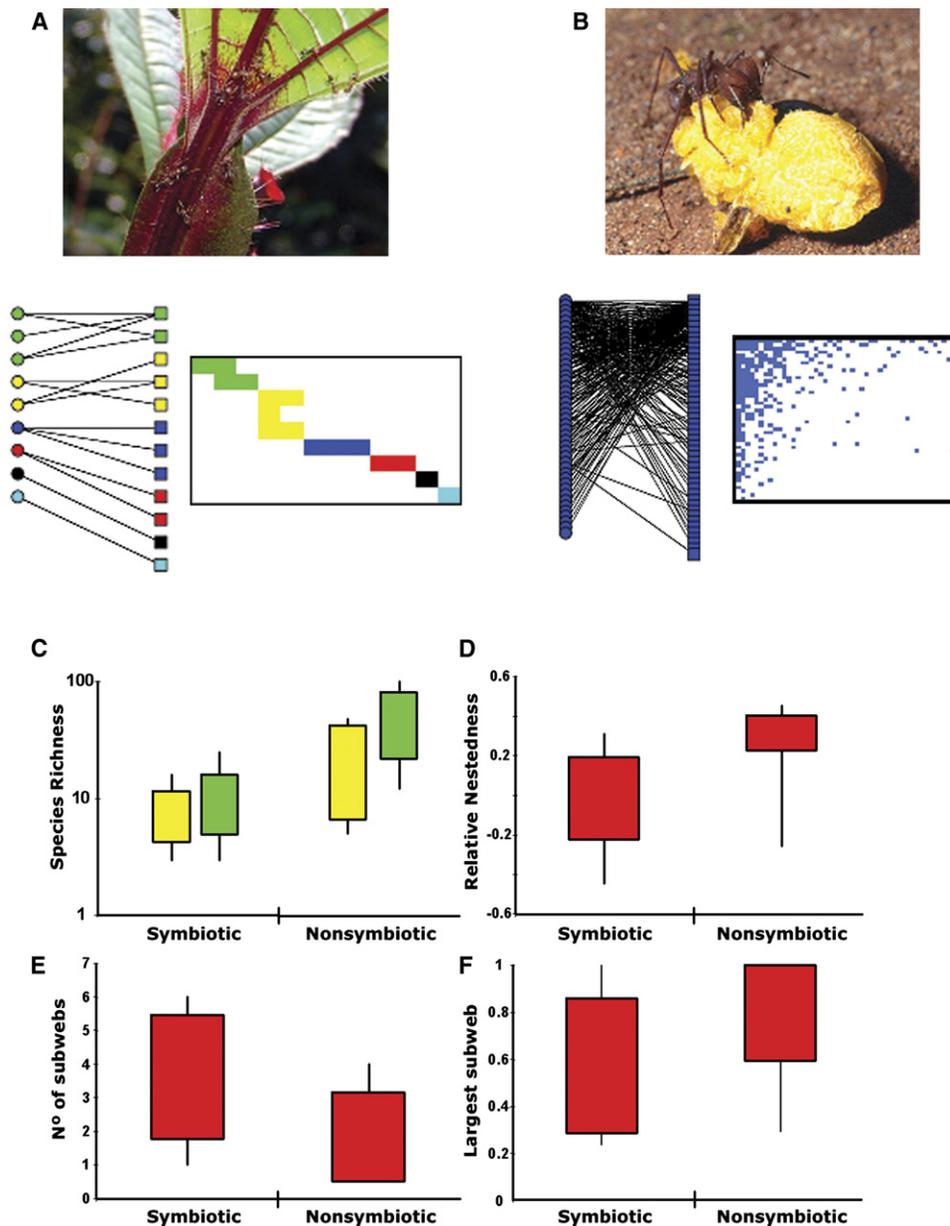


Figure 1. Structure of Symbiotic and Nonsymbiotic Ant-Plant Networks

(A and B) Network representation of two interacting assemblages of ants and plants: (A) the symbiotic interactions between ants and myrmecophytes in an Amazon forest (T.J.L., unpublished data; photo: *Tococa bullifera* [Melastomataceae] hosting in its leaf pouch domatia *Azteca* ants) and (B) the nonsymbiotic interactions between ants and vertebrate-dispersed fruits in a Brazilian forest ([33]; photo: the removal of a fallen arillate seed of the primarily bird-dispersed tree *Copaifera langsdorffii* by a worker of *Atta sexdens*). In the network description, circles and squares represent species, and interactions are depicted as links. Networks can also be described by interaction matrices in which columns represent plant species, rows represent ant species, and colored squares indicate interactions between species. Different colors in the networks and interaction matrices identify isolated groups of species (subwebs).

(C–F) The differences between the structure of symbiotic and nonsymbiotic networks can be characterized by distinct metrics (upper and lower edges of boxes indicate mean + SD and mean – SD, respectively). (C) Ant (yellow) and plant (green) species richness, (D) relative nestedness, a measure of nestedness independent of species richness, richness ratio between ants and plants and ecological specialization (see [Experimental Procedures](#) for further details) are shown. Positive values indicate the existence of asymmetric specialization and a generalist core, whereas negative values are associated with symmetric interactions and isolated groups of species, (E) number of isolated subwebs, and (F) the proportion of the total species richness observed in the largest isolated subweb. Photo credits are as follows: G. Machado (A) and P.S. Oliveira (B). All networks were drawn with Pajek [34].

whereas nonsymbiotic networks included only one or two isolated subwebs (1.83 ± 0.54 isolated subwebs, $p = 0.034$, d.f. = 17, [Figure 1E](#)). Accordingly, the largest isolated subweb in symbiotic networks was often composed of half the interacting species ($57.1\% \pm 0.08\%$

species), whereas nonsymbiotic networks are often dominated by a single giant subweb that includes almost all species ($87.7\% \pm 0.12\%$ species, $p = 0.027$, d.f. = 17, [Figure 1F](#)). Our second set of analyses designed to partially control for sampling biases led to

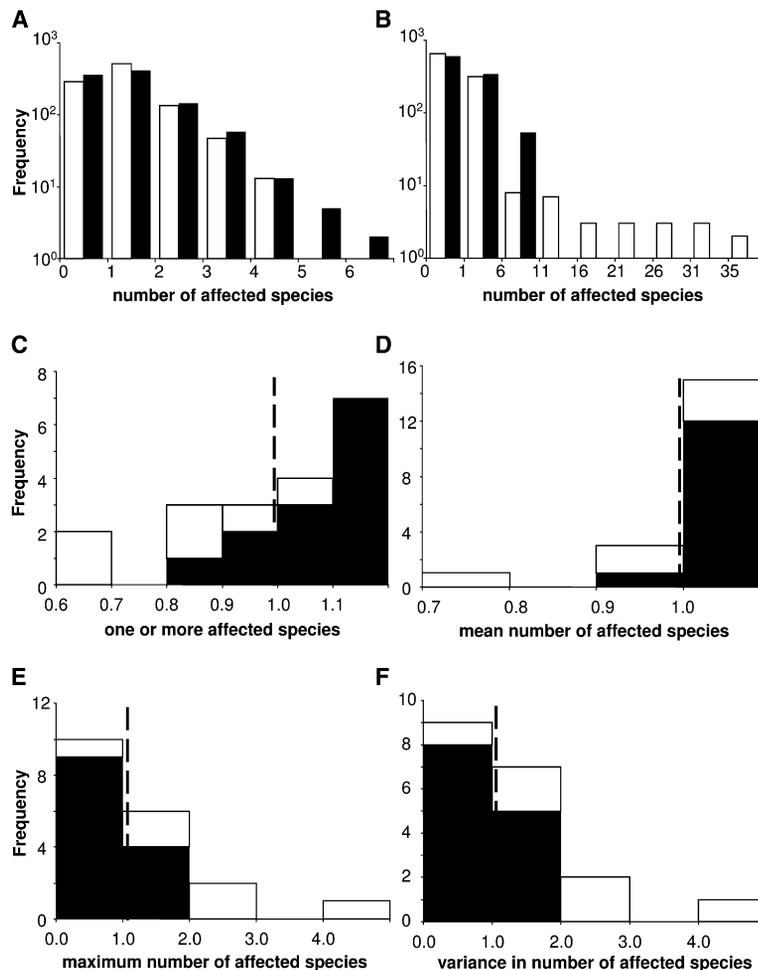


Figure 2. Simulated Coevolutionary Dynamics in Symbiotic, Nonsymbiotic, and Random Networks

(A and B) Differences between real (white columns) and random (black) networks in the number of affected species after the change of a mutualistic partner ($n = 1000$ simulations); (A) shows a symbiotic, ant-myrmecophyte network (Amazon forest, Brazil; T.J.I., unpublished data), and (B) shows a nonsymbiotic, ant-extrafloral nectar-producing plants network (La Mancha, [5]).

(C–F) Standardized metrics describing simulated coevolutionary dynamics in symbiotic (black) and nonsymbiotic (white) networks (see [Experimental Procedures](#) for further details). For all metrics, if the network has a random structure, the expected value is equal to one (dashed line). (C) shows the number of simulations in which at least one species is affected, (D) shows the mean number of affected species, (E) shows the maximum number of affected species, and (F) shows variance in the number of affected species.

similar results (see [Supplemental Data](#) available with this article online).

Numerical simulations suggested distinct coevolutionary dynamics for symbiotic and nonsymbiotic networks. The number of simulations in which at least one mutualistic partner was affected by a change in a randomly selected species was more than 1.5 times greater in symbiotic than in nonsymbiotic networks ($68.32\% \pm 13.34\%$ versus $40.1\% \pm 5.2\%$ simulations, $p = 0.001$, d.f. = 17). The mean number of affected species in symbiotic networks was slightly greater than in nonsymbiotic networks (1.01 ± 0.44 versus 0.93 ± 0.09 species, $p = 0.008$, d.f. = 17). The maximum number of affected species was four times larger in nonsymbiotic than in symbiotic networks (16.00 ± 10.99 versus 4.38 ± 2.18 species, $p = 0.006$, d.f. = 17). In addition, the number of species affected in the simulations was four times more variable in nonsymbiotic than in symbiotic networks (variances: 4.36 ± 3.27 versus 1.06 ± 0.78 , $p = 0.006$, d.f. = 17).

We assessed whether other effects of structure beyond differences in number of species and interactions explain the coevolutionary dynamics by comparing the simulation results between real and random networks with the same number of ants, plants, and interactions. These comparisons suggested that the nonrandom structure of symbiotic and nonsymbiotic networks affects

coevolutionary dynamics in distinct ways (Figures 2A and 2B). The number of simulations in which at least one mutualistic partner was affected by change in another species was greater in symbiotic networks than in their random counterparts. In contrast, the number of simulations in which at least one species was affected was greater in random networks than in nonsymbiotic networks (Figure 2C, $p = 0.003$, d.f. = 17). The difference between real and random networks in the mean number of affected species did not vary between symbiotic and nonsymbiotic networks (Figure 2D, $p = 0.1$, d.f. = 17). On the other hand, the maximum number of affected species in symbiotic networks was often lower than observed in random networks, whereas in nonsymbiotic networks, the maximum number of affected species was two times greater than in random networks (Figure 2E, $p = 0.003$, d.f. = 17). Similarly, simulations in symbiotic networks were often less variable in the number of affected species, whereas in nonsymbiotic networks, the variance in the number of affected species was twice as high as in random networks (Figure 2F, $p = 0.004$, d.f. = 17). Overall, the simulations suggested that evolutionary change in one species differs between symbiotic and nonsymbiotic in the likelihood of coevolutionary response, the maximum number of species that undergo a coevolutionary response, and the variance in the number of species participating in the coevolutionary response.

Discussion

Our results corroborate predictions from coevolutionary theory [12, 15] and suggest that symbiotic and nonsymbiotic ant-plant interactions differ fundamentally in the patterns of interaction found within networks. In their seminal paper on ant-plant networks, Fonseca and Ganade [13] showed that groups of ants are more likely to interact with certain groups of plants in an ant-myrmecophyte community, a feature called compartmentalization [9]. Here, we demonstrate that compartmentalization is a general feature of symbiotic ant-plant networks. In addition, symbiotic networks are not nested at the community level, although these networks might show nestedness at regional scale [8]. At the community level, symbiotic networks are often characterized by several completely isolated groups of species (subwebs) with symmetric patterns of interactions among interacting species (Figure 2). Other compartmentalized plant-animal networks often show an interaction path between compartments and, consequently, no isolated subweb (e.g., Figure 3B from [9], Table 1 from [16]). Therefore, the observed degree of compartmentalization in symbiotic ant-plant networks is extreme.

Symmetric specialization and sympatric isolation among subwebs probably result from coadaptations within symbiotic interactions. For example, myrmecophytes are known to have several different structures that filter out colonization by many ant species. These structures include the shape of the prostoma in African *Leonardoxa africana* [17] and wax barriers on the Asian *Macaranga* species [18]. The chemical location of host plants by specialized ant queens [19] might also be an important mechanism for maintaining the isolation of subwebs. In these cases, plant-specific ant queens are the most efficient in finding and colonizing their respective myrmecophyte, and some plants can be chemically “invisible” to ants from other subwebs. Therefore, the restrictive lifestyles of symbiotic ants and plants not only lead to species-poor networks (this study) and higher specialization [4] but also actually create, within a single ecological community, groups of interacting ant and plant species that are totally isolated from one another.

The existence of isolated subwebs has profound consequences for coevolutionary processes acting on a symbiotic network because there is no direct interaction path for an evolutionary change occurring in a species from a particular subweb to propagate through species in other subwebs. In fact, the maximum number of species affected by a change in a mutualistic partner in our numerical simulations was usually lower for symbiotic than for random networks with similar number of interactions. This result suggests that the structure of symbiotic interactions constrains large coevolutionary cascades, and it implies that each subweb might show distinct and predominantly independent coevolutionary dynamics. In addition, our simulations suggest that the structure of symbiotic networks facilitates the response of a species to changes in its mutualistic partner, therefore promoting reciprocal evolutionary changes between interacting species within the subwebs. Thus, we hypothesize that coevolution in symbiotic networks

is characterized by frequent reciprocal changes between few partners.

Nonsymbiotic networks, in contrast, form species-rich highly nested networks, with no evidence of compartmentalization at the community level; a lack of such evidence supports the view that the structure of coevolutionary processes might be different in nonsymbiotic and symbiotic networks. In a nonsymbiotic interaction, each individual has the opportunity to interact with multiple individuals of different species during its lifetime. In this case, coevolution favors the convergence of traits among species within the community (e.g., similar functionality of extrafloral nectaries in phylogenetically nonrelated plants), thereby maximizing the probability that a mutualistic interaction occurs [12]. As a consequence, nonsymbiotic networks are characterized by higher generalism [4]. The core of generalist species might act as a coevolutionary vortex, collecting additional species into the network as species continue to coevolve through convergence on a set of traits on both sides of the interaction. The new species introduce new selective pressures to the species that are already part of the network and that affect and are being affected by the generalist core. The generalist core might provide a stable resource and set of traits that might allow the emergence of species specialized to interact with one or a few species at the core of the network, leading to nestedness [3, 12]. In addition, nestedness might be reinforced by filters or barriers that constrain the occurrence of interactions [2, 20] (e.g. large ponerine ants disperse small- and medium-sized seeds, but small myrmicine ants usually disperse only small seeds [21]) and higher extinction rates for specialists that interact with other specialists [22]. Interestingly, although ant and plant species numbers are both greater in nonsymbiotic networks than in symbiotic networks, the increase in species richness is 3-fold greater for plants than for ants. We hypothesize that the higher diversity of plants in tropical communities allows the domination of plant species in the nonsymbiotic networks. In contrast, symbiotic networks are usually dominated by ants [4, 13].

Our simulations indicate that the structure of nonsymbiotic networks is less likely to allow coevolutionary changes than the structure of symbiotic or random networks. However, our results demonstrate that there are both direct and indirect pathways for coevolution in nonsymbiotic networks because there are usually no isolated subwebs. This network structure therefore allows for the possibility, as a working hypothesis, that the generalist core drives the evolution of the entire system [12, 23]. In this context, our simulations suggest that the number of species affected by an event of evolutionary change is extremely variable, and there is a small but nonnegligible probability that dozens of species respond to a change in a single species. These events of large coevolutionary change might occur as an evolutionary response to shifts in some relevant biological aspect of a very generalist species (e.g., changes in foraging behavior in an abundant ant species). Therefore, we should expect that the coevolutionary process in nonsymbiotic networks will be characterized by rare bursts of change in which many species respond to evolutionary changes in a single species.

We emphasize that the results reported here, as in any comparative study of ecological networks [24], should be viewed as preliminary because we analyzed empirical data that differed in several methodological procedures. However, after we partially controlled for some sampling biases, the results remained qualitatively similar. Of course, the differences observed among symbiotic and nonsymbiotic networks might not be only a result of differences in interaction intimacy. The structure of each mutualistic network also results from a complex interplay among biogeography [25], differences in abundance among species [7, 9], and the evolutionary history of interacting species [9, 10]. For example, a nested structure might be generated by differences in abundance among interacting species [9], although recent studies suggest that abundance only partially explains nestedness ([26] and A. Krishna, P.R.G., P. Jordano, and J. Bascompte, unpublished data).

Our results open new avenues for future research by suggesting specific patterns through which interaction intimacy affects the structure and dynamics of ecological networks. In addition, the simulations of coevolution introduced here to the study of mutualistic networks might be a useful approach for investigating the unanticipated consequences of network structure to coevolutionary dynamics. Future studies are now needed on how interaction intimacy affects network structure and dynamics in other forms of interaction, so that the generality of the patterns described here could be tested. Other potential comparisons include those between insects that feed as grazers (e.g., some grasshoppers) and those that feed as parasites by completing development on a single host-plant individual (e.g., many caterpillars); or interactions between plants and free-living pollinators, such as hummingbirds and bees, as compared with pollinating floral parasites such as fig wasps and yucca moths. In addition, our coevolutionary model assumes that network structure is fixed. We therefore also suggest that in the future, the implications of speciation and the emergence of new interactions to coevolutionary dynamics of mutualistic networks should be explored. For example, on the basis of complex network theory [27], we should expect that the emergence of a few new species or interactions might lead to profound changes in symbiotic networks, connecting the structure and, consequently, the coevolutionary dynamics of previously isolated subwebs. In contrast, we should expect that new species or interactions will not affect qualitatively the dynamics of nonsymbiotic networks. Finally, recent studies emphasize the relevance of network structure to maintenance of biodiversity [6, 10, 28], and future studies should also explore the consequences to the extinction dynamics of symbiotic and nonsymbiotic networks.

For now, we have evidence that interaction intimacy at least partially shapes community-level patterns of interactions in symbiotic and nonsymbiotic networks involving dozens of ant and plant species, leading to distinct structures that might markedly affect coevolutionary dynamics within these networks. These results imply that multispecific interactions might not simply coevolve through diffuse coevolution with little internal structure. Rather, different forms of interaction tend to evolve toward different network structures, and the problem to

solve is how, and the extent to which, reciprocal evolutionary change might contribute to the repeated patterns found within these mutualistic networks.

Experimental Procedures

Dataset

Our dataset included 19 networks compiled from the literature or derived from our own fieldwork. Although there is a continuum of interaction intimacies across ecological interactions [11], our networks can be divided into two groups on the basis of strong differences in interaction intimacy: symbiotic networks (high-interaction intimacy, $n = 13$), such as long-term, ant-mycorrhizal mutualisms (Figure 1A), in which ants provide defense against plant's natural enemies, and nonsymbiotic networks (low-interaction intimacy, $n = 6$), such as short-term interactions of seed dispersal (Figure 1B) and nectar-mediated facultative mutualisms [4]. See [Supplemental Data](#) for additional details about the dataset, the biology of ant-plant mutualisms, and interaction intimacy.

Metrics and Statistical Analyses

We first characterized species richness (number of species) of each network and searched for differences among symbiotic and nonsymbiotic networks. We tested for differences in the mean species richness of the two types of interactions by conducting two-independent samples randomization test [29] (10,000 randomizations).

We determined whether nestedness is more frequently observed in nonsymbiotic than in symbiotic networks by defining the degree of nestedness, N , as $N = (100 - T)/100$, in which T is the matrix temperature, with values ranging from 0–100, yielding a value of N that varies between 0 (perfectly nonnested) to 1 (perfectly nested). Additional details about N and T are provided elsewhere [3, 5]. Some degree of nestedness is expected from the basic structure of networks, with the baseline expectation varying with variables such as species richness, the ratio between animal and plant species richness, the total number of interactions, and the variation in the number of interactions among the species [3, 5]. Here, we controlled for the effects of all the above network metrics by using a null model in which the probability that an ant i interacts with a plant j depends on the observed number of interactions of both species, such that $p(r_{ij} = 1) = 0.5[(k_i/P) + (k_j/A)]$, in which k is the number of interactions observed for the species [3]. Each network was compared with 1000 replicates generated by the null model. The p value was defined as the probability of a null-model replicate being equally or more nested than the observed network. All nestedness analyses were performed with ANINHADO [30]. We used a χ^2 test to investigate whether the frequency of significantly nested networks is higher in nonsymbiotic than symbiotic interactions.

We controlled the effects of the above network metrics and allowed across-network comparisons by using relative nestedness [3], defined as $N^* = (N - N_R)/N_R$, in which N is the degree of nestedness observed for the real network and N_R is the average value of nestedness for null model replicates. Positive values indicate that the network shows asymmetrical specialization and a generalist core, whereas negative values of relative nestedness might be associated with symmetric patterns of interactions and the existence of compartments. Because nestedness analysis is not an adequate method to test for the existence of nonnested patterns [31], we investigated the degree of compartmentalization of ant-plant networks through searching for isolated subwebs. Two species are part of the same isolated subweb or component if there is a direct or indirect interaction path between them [32]. Therefore, a network that contains two subwebs is formed by a totally isolated group of species. We recorded the number of isolated subwebs in each ecological community and the number of species that form the largest isolated subweb. We evaluated whether symbiotic and nonsymbiotic networks differ in their mean relative nestedness, number of isolated subwebs, and the proportion of species of the largest isolated subweb by using a two-independent samples randomization test ($n = 10000$ randomizations).

Simulating Coevolutionary Dynamics

Coevolution implies reciprocal change in interacting species. Within the simplest pairwise cases, evolutionary change in one species

directly favors an evolutionary response in the other species. As the number of interacting species increases, the number of species affected by evolution in any one species also increases. Evolution in one species might affect the evolution of one or more of its interacting partners, and reciprocally, the evolution of different network structures might subsequently affect the evolution of individual species. We therefore explored a model in which evolutionary change did not necessarily involve the same two species. We explored how different network structures influenced the number of species affected by each round of evolutionary change. To simulate coevolutionary changes, we first assumed that a randomly selected species i evolves some biological attribute that might affect its interactions with other species in the network (e.g., food preferences, activity patterns, nectar composition, and domatia architecture). For simplicity, all species have the same probability of being selected. Second, we assumed that there is a probability c_j that a species j that interacts with species i will also evolve some biological attribute in response to the change in species i , thereby simulating evolution in very general terms. We assumed that the probability of coevolutionary response is $C_j = 1/k_j$, and therefore it is more likely that a specialist species evolves in response to a change in a mutualistic partner than a more generalist species. To simplify the analysis, we assumed that no new interaction or species appear in the network during the simulations.

We performed 1000 simulations for each ant-plant network, and in each simulation, we recorded the number of affected species, that is, the species that evolves in response to a change in a randomly selected species i . We recorded (1) the number of simulations in which there was no affected species, defined as a measurement of robustness of the network against coevolutionary change, (2) the mean and maximum number of affected species, defined as measures of the potential impact of coevolutionary change in the networks analyzed, and (3) the variance in number of affected species, defined as a measure of the variation within coevolutionary change.

We tested whether the symbiotic and nonsymbiotic networks differed in the mean values of the above metrics. Differences between the two types of network might be a result of differences in species richness, the number of interactions, or the structural patterns (e.g., degree of nestedness or the existence of isolated subwebs). We investigated the role of different structural patterns in simulated coevolutionary dynamics by performing an additional set of simulations using random networks with the same number of plants, ants, and interactions as that observed in real networks ($n = 1000$ networks in which the probability of any ant-plant pair interacts is constant). To allow across-network comparisons, we used $d_o = d_o/d_R$, in which d_o is the value observed for a given metric (e.g., mean number of affected species) in simulations with real networks, d_R is the average value of the same metric for simulations with random networks, and d_o is a standardized value for the metric, after controlling for the effects of species richness and the number of interactions. We tested whether symbiotic and nonsymbiotic networks differed in their mean values for standardized and nonstandardized metrics by using a two-independent samples randomization test [29] ($n = 10,000$ randomizations).

Supplemental Data

Additional Experimental Procedures, two figures, and two tables are available at <http://www.current-biology.com/cgi/content/full/17/20/DC1/>.

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