

Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance

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The mutualistic interactions between plants and their pollinators or seed dispersers have played a major role in the maintenance of Earth's biodiversity. To investigate how coevolutionary interactions are shaped within species-rich communities, we characterized the architecture of an array of quantitative, mutualistic networks spanning a broad geographic range. These coevolutionary networks are highly asymmetric, so that if a plant species depends strongly on an animal species, the animal depends weakly on the plant. By using a simple dynamical model, we showed that asymmetries inherent in coevolutionary networks may enhance long-term coexistence and facilitate biodiversity maintenance.

It is widely acknowledged that mutualistic interactions have molded biodiversity (1, 2). In the past decade, much has been learned about how communities shape coevolutionary interactions across time and space (3). However, although most studies on coevolution focus on pairs or small groups of species, recent work has highlighted the need to understand how broader networks of species coevolve (4–7). Such knowledge is critical to understanding the persistence and coevolution of highly diverse plant-animal assemblages.

Recent research on the architecture of plant-animal mutualistic networks has been based mostly on qualitative data, assuming that all realized interactions are equally important (Fig. 1A) (5–7). This has precluded a deeper assessment of network structure (8) and strongly limited our understanding of its dynamic implications. To understand how mutualistic networks are organized and how such an organization affects species coexistence, we compiled from published studies and our own work 19 plant-pollinator and 7 plant-frugivore quantitative networks (Fig. 1 and Database S1). These networks range from arctic to tropical ecosystems and illustrate diverse ecological and biogeographical settings. Each network displays information on the mutual dependence or strength between each plant and animal species, mainly measured as the relative frequency of visits (9). Thus, our networks describe ecological interactions, and evolutionary inferences should be made with caution. However, frequency of visits has been shown to be a surrogate for per capita reproductive performance (10). Our results could be more directly related to coevolution when the reproductive success of one species depends directly on visitation frequency. This seems to be the case when there is a high variation of dependences among species (10). Unlike previous studies on food webs

(11–16), for each plant-animal species pair, we have now two estimates of mutual dependence (defined in two adjacency matrices P and A): the dependence d_{ij}^P of plant species i on animal species j (i.e., the fraction of all animal visits coming from this particular animal species) and the dependence d_{ji}^A of animal species j on plant species i (i.e., the fraction of all visits by this animal species going to this particular plant species) (Fig. 1, B and C). Therefore, one can calculate an index of asymmetry for each pairwise interaction (17), depicting the relative dissimilarity between the two mutual dependences (Fig. 1, B and C).

Regardless of the type of mutualism, the frequency distribution of dependences is right-skewed, mostly with weak dependences and a few strong ones (Fig. 2). This is in agreement with previous work on ecological networks (9, 11–16). This heterogeneous distribution is highly significant and cannot be predicted on the basis of an independent association between plants and animals. On the contrary, the distribution of animal visits is highly dependent on plant species ($P < 0.00001$, G-test in all nine communities in which the test can be performed). To illustrate the effect of such weak dependences on community coexistence, we used a mutualistic model (18–21). For the simplest case, there is a positive community steady state (community coexistence) if the following inequality holds (21)

$$\alpha\beta < \frac{ST}{mn}$$

where α and β are the average per capita effects of the animals on the plants, and of the plants on the animals, respectively. Hereafter, such per capita effects are estimated by the mutual dependence values (21). S and T are the average intraspecific competition coefficients of plants and animals, and n and m are the number of plant and animal species, respectively.

As community size increases, the product of mutual dependences has to become smaller for the community to coexist (fig. S1). Two situations fulfill this requirement: (i) either both dependences are weak; or (ii) if one dependence

is strong, the accompanying dependence is very weak (so the product remains small). The dominance of weak dependences (Fig. 2) contributes to situation i. To assess the likelihood of scenario ii, we next look at the asymmetry of mutual dependences.

For each pair of plant species i and animal species j , we calculated the observed asymmetry of mutual dependences using (17). The frequency distribution of asymmetry values is also very skewed, with the bulk of pairwise interactions being highly asymmetric (Fig. 3). The question now is whether dependence pairs are more asymmetric than expected by chance. To answer this question, we calculated a null frequency distribution of asymmetry values to compare with the observed one by means of a χ^2 test. We achieved this by fixing the observed dependence d_{ij}^P of plant species i on animal species j and randomly choosing d_{ji}^A without replacement from the set of all dependences of the animals on the plants in this particular community. This procedure was repeated 10,000 times; the null asymmetry frequency distribution is the average of these replicates.

For pollination, only seven out of 19 communities (36.8%) showed a frequency distribution of asymmetry values that deviates significantly from the null frequency distribution (46.1% when considering only networks with at least 100 pairs). For seed dispersal, only one out of seven communities (14.3%) showed a frequency distribution of asymmetry values that deviates significantly from the null frequency distribution (20.0% when considering only networks with at least 100 pairs). These results show that in the bulk of the cases, the frequency distribution of asymmetry values originates exclusively from the skewed distribution of dependences. That is, most communities show mutual dependences that are asymmetric, but no more asymmetric than what we would expect by chance, given the distribution of dependence values.

Because strong interactions have the potential to destabilize ecological networks (16, 18, 22–24), we repeated the above calculations considering only dependence pairs in which at least one value is larger than or equal to 0.5 (other threshold values do not significantly affect our results). The fraction of large pollination networks (at least 100 pairs) with a frequency distribution of asymmetry significantly departing from expectation increased to 87.5% (seven out of eight communities). Similarly, for seed dispersal, the three largest communities ($n \geq 20$ pairs) also have frequency distributions of asymmetry values significantly departing from random (100%). Overall, these results suggest that there are constraints in the combination of strong mutual dependence values. Next, from the significant comparisons, we explored which intervals of asymmetry contribute to significance.

Asymmetry values range from 0 to 1 (Fig. 3). Within this range, some values may be over-

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represented and some underrepresented, relative to random expectation (again comparing the null frequency distribution with the observed frequency distribution by using a χ^2 probability distribution). We found that the first half of the range (low to moderate asymmetry) is significantly underrepresented ($P = 3.81 \times 10^{-6}$ for pollination and $P = 0.0156$ for seed dispersal; binomial test). This underrepresentation of low asymmetry values implies that a strong dependence value for one of the partners in the mutualistic interaction tends to be accompanied by a weak dependence value of the other partner. That is, two strong interactions tend to be avoided in a pair, which agrees with the analytic prediction (scenario ii).

Our above analysis of mutual dependences, however, is based on isolated analysis of pairwise interactions and thus provides only limited information on the complexity of the whole mutualistic network (25). For example, how does the pattern of skewed dependences and strong asymmetries scale up to account for properties at the community level? A more meaningful measure of network complexity is provided by the concept of species strength (25). The strength of an animal species, for example, is defined as the sum of dependences of the plants relying on this animal. It is a measure of the importance of this animal from the perspective of the plant set (Fig. 1, D and E). This measure is a quantitative extension of the species degree, which is the number of interactions per species in qualitative networks (5). Previous work showed that mutualistic networks are highly heterogeneous (i.e., the bulk of species have a few interactions, but a few species have many more interactions than expected by chance) (5). Next, we considered how this result stands when quantitative information is considered.

In all but one case, there is a significant positive relationship between species strength and species degree (Fig. 4). To explore deviations from linearity, we performed a quadratic regression and tested for the significance of the quadratic term. The quadratic term is significant in 35 out of the 52 cases (for each community, we looked at both plants and animals independently). This fraction increases to 24 out of 30 cases when considering only communities with at least 30 species. That is, species strength increases faster than species degree (Fig. 4), a pattern previously found for the worldwide airport network, but not for the scientific collaboration network (25). The strength of highly connected species is even higher than expected based on their degree, because specialists tend to interact exclusively with the most generalized species (6, 7) and so depend completely on them. Thus, specialists contribute disproportionately to increase the overall strength of the generalists they depend on.

Overall, previous results based on qualitative networks (i.e., their high heterogeneity in the number of links per species) (5) are confirmed

Fig. 1. A network approach to plant-animal mutualisms. **(A)** Example of a community of plants and their seed dispersers in Cazorla, SE Spain (see Database S1 for references and data sets). Green circles represent plant species and red squares represent animal species. A plant and an animal interact if there is a qualitative link between them. **(B and C)** Each of the above plant-animal interactions is described by two weighted links (arrows) depicting the relative dependence of the plant on the animal (green arrow) and the animal on the plant (red arrow). The asymmetry of the pairwise interaction is proportional to the difference between the thickness of both arrows. Here we show a symmetric **(B)** and an asymmetric **(C)** example. **(D and E)** A species degree is the number of interactions it has with the other set. Species strength is the quantitative extension of species degree, and can be defined as the sum of dependences of the animals on the plant **(D)** and the plants on the animal **(E)**. Although the degree is four in both **(D)** and **(E)**, the strength of the animal **(E)** is higher than that of the plant **(D)**.

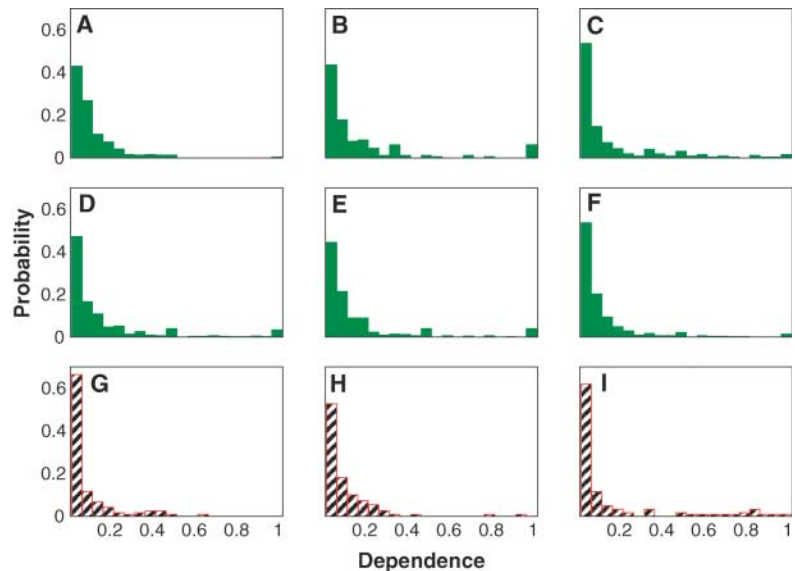
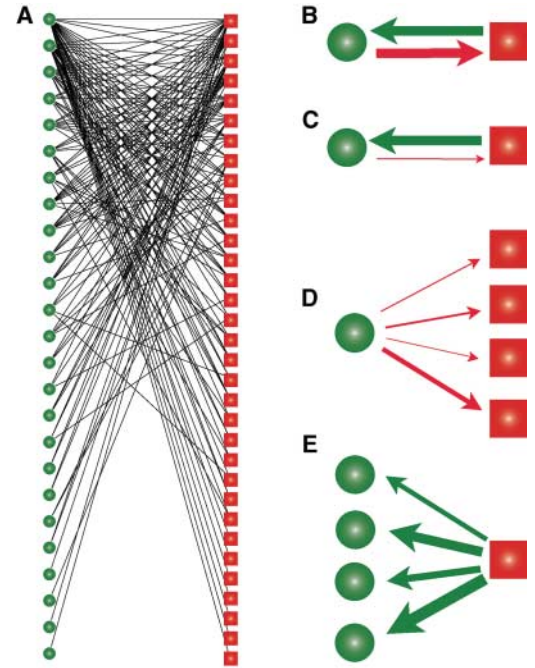


Fig. 2. Frequency distributions of dependence values within a mutualistic community. Green solid histograms **(A to F)** represent dependences of plants on pollinators, and red dashed histograms **(G to I)** represent dependences of seed dispersers on plants. See Database S1 for references and data sets.

by our analysis of quantitative networks. Second, previous work (i.e., asymmetry at the species level) (6, 7) provides a mechanistic explanation for some of the new results presented here as the higher-than-expected strength of generalist species. However, our results go a step further, because we show here that asymmetry is also a property at the link level based on species-specific mutual dependences.

Our results suggest that the architecture of quantitative mutualistic networks is characterized by the low number of strong dependences,

their asymmetry, and the high heterogeneity in species strength, all of which may promote community coexistence. Community coexistence, in turn, may favor the long-term persistence of reciprocal selective forces required for the coevolution of these species-rich assemblages (2, 3). By considering mutualistic networks as coevolved structures rather than as diffuse multi-specific interactions, we can better understand how these networks develop (3). There are two forces that, acting in combination, may lead to networks with the reported architecture: coevolu-

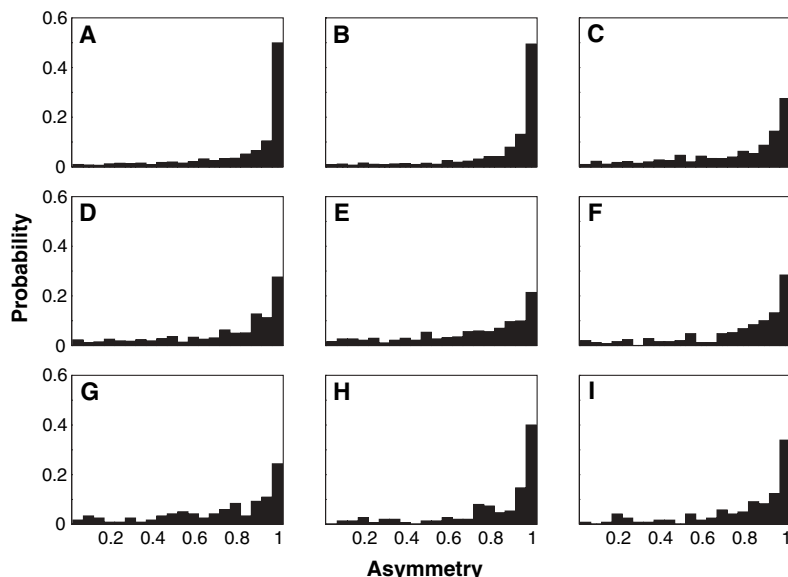


Fig. 3. Frequency distributions of asymmetry values of mutual dependences within a mutualistic community. (A to F) Plant-pollinator communities. (G to I) Plant seed-disperser communities. See Database S1 for references and data sets.

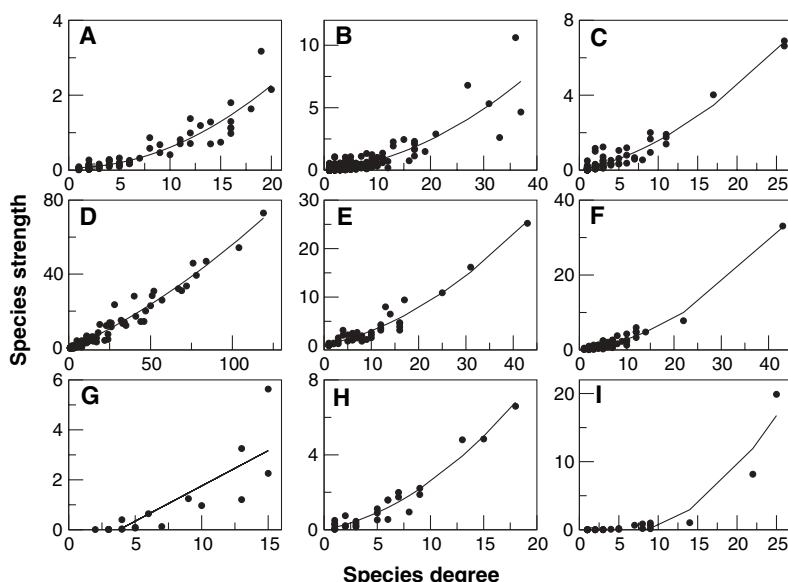


Fig. 4. Relationship between the number of interactions per species (degree) and its quantitative extension, species strength. (A to C) Pollinator species in plant-pollinator communities. (D to F) Plant species in plant-pollinator communities. (G and H) Animal species in plant seed-disperser communities. (I) Plants in a plant seed-disperser community. A quadratic regression is represented when the quadratic term is significant; otherwise a linear regression is plotted (G). As noted, in all cases but (G), species strength increases faster than species degree. See Database S1 for references and data sets.

tionary complementarity and coevolutionary convergence (3). Pairwise interactions build up on complementary traits of the plants and the animals (e.g., corolla and pollinator tongue lengths), whereas the convergence of traits allows other species to attach to the network as this evolves (e.g., convergence in fruit traits among plants dispersed by birds rather than mammals) (3). These forces differ from those shaping antagonistic interactions such as coevolutionary alter-

nation (i.e., selection favoring herbivores attacking less defended plants) (2, 3). Thus, one could predict differences in the architecture of mutualistic and antagonistic networks. Other types of biological interactions also show high asymmetry values. For example, a large fraction of competitive interactions are asymmetric, especially in the marine intertidal (26, 27). Our results highlight the importance of asymmetric interactions in mutualistic networks. Asym-

metry seems to be the key to both their diversity and coexistence. Whether asymmetry extends to other types of complex networks remains to be seen.

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- The asymmetry of a pairwise mutualistic interaction is estimated as follows: $AS(i, j) = |d_{ij}^p - d_{ji}^p| / \max(d_{ij}^p, d_{ji}^p)$, where d_{ij}^p and d_{ji}^p are the relative dependences of plant species i on animal species j and of animal species j on plant species i , respectively; $\max(d_{ij}^p, d_{ji}^p)$ refers to the maximum value between d_{ij}^p and d_{ji}^p . Related measures of asymmetry are highly correlated to this equation, so results are insensitive to the particular asymmetry measure used.
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Materials and Methods

Fig. S1

Database S1

References

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