

Non-random coextinctions in phylogenetically structured mutualistic networks

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The interactions between plants and their animal pollinators and seed dispersers have moulded much of Earth's biodiversity^{1–3}. Recently, it has been shown that these mutually beneficial interactions form complex networks with a well-defined architecture that may contribute to biodiversity persistence^{4–8}. Little is known, however, about which ecological and evolutionary processes generate these network patterns^{3,9}. Here we use phylogenetic methods^{10,11} to show that the phylogenetic relationships of species predict the number of interactions they exhibit in more than one-third of the networks, and the identity of the species with which they interact in about half of the networks. As a consequence of the phylogenetic effects on interaction patterns, simulated extinction events tend to trigger coextinction cascades of related species. This results in a non-random pruning of the evolutionary tree^{12,13} and a more pronounced loss of taxonomic diversity than expected in the absence of a phylogenetic signal. Our results emphasize how the simultaneous consideration of phylogenetic information and network architecture can contribute to our understanding of the structure and fate of species-rich communities.

Plant and animal species establish mutually beneficial interactions such as pollination and seed dispersal that can form complex networks of dependency. Recent work has characterized the architecture of mutualistic networks, with the ultimate goal of understanding their formation and maintenance and the coevolution of species within them. These networks are very heterogeneous (some species have a much larger number of interactions than expected by chance)⁴, and nested (specialists interact with proper subsets of the species that generalists interact with)⁵, and are built on weak and asymmetric links (for example, if a plant species depends strongly on an animal species, the dependence of the animal on that plant is much weaker)⁶. The next step on the road to understanding these networks is to disentangle the contribution of different evolutionary and ecological processes in generating their patterns^{3,9,14}.

Here we ask to what extent network architecture is associated with species phylogenetic relationships (Fig. 1), and whether coextinction cascades following a species disappearance⁷ involve phylogenetically related (that is, non-randomly sampled) species. The presence of a phylogenetic signal, where patterns of interactions between species can be partly explained by phylogenetic relatedness, would suggest that network patterns are partially dependent on past evolutionary history, and so cannot be exclusively explained by current ecological processes^{14–17}.

We compiled the largest data set of plant–animal mutualistic interactions, comprising 36 plant–pollinator and 23 plant–frugivore mutualistic networks spanning a broad geographic range (data sets are available as Supplementary Information). For each network, we reconstructed the phylogenies of the animals and plants (see Supplementary Methods). We then characterized two components of network architecture. First, we considered the number of interactions

per species, that is, species degree^{4,18}, and its quantitative extension, species strength. The strength of a plant species, for instance, is defined as the sum of dependences or interaction weights of the animal species on that plant⁶. These simple components of network architecture reflect the generalization level of a given species and its quantitative relevance in terms of how other species depend on it. Second, we considered the identity of each species' interactors (Methods). Both the number of interactions per species, and the identity of the species with which they interact have been identified as major determinants of network architecture and robustness^{7,19,20}. With the phylogenies and these components of network structure at hand, we applied phylogenetic statistical tools^{10,11} to characterize the extent to which closely related species tend to have similar patterns of interactions (Fig. 1).

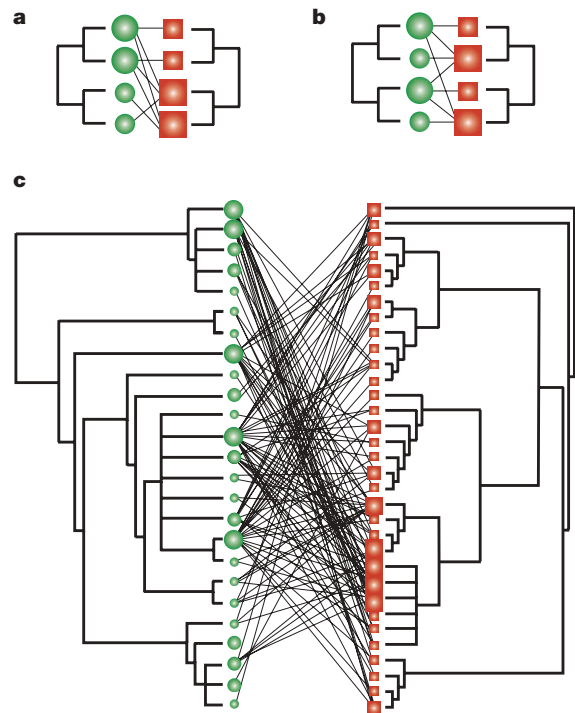


Figure 1 | A phylogenetic approach to mutualistic networks. We test to what extent the architecture of coevolutionary networks is associated with evolutionary history conveyed in the phylogenies of plants and animals. A plant (green circles) and an animal (red squares) are linked if the latter is a pollinator or a seed disperser of the former. Symbol size is proportional to its number of links. **a–c**, Examples where phylogeny accurately predicts the number of interactions (**a**), phylogeny does not predict the number of interactions (**b**), and the real correspondence in one network (**c**) (see NCOR in the Supplementary Methods).

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Randomization tests (see Methods) suggest a significant phylogenetic signal in species degree in 24.8% of the data sets (26 of 105 phylogenies, one-tailed $P < 0.05$; Fig. 2a). Power analyses indicate that these estimates are highly conservative, suggesting that phylogenetic effects may be present in a larger proportion of the communities (Supplementary Figs 1 and 2). Also, the probability of detecting a signal in species degree seems to increase with phylogeny size (for example, 54.5% of the 22 phylogenies with more than 70 species showed significant signal; Supplementary Fig. 1). The negative association between the amount of phylogenetic signal estimated as K and phylogeny size (Fig. 2a) is probably an artefact. Even though the expectation of K is 1 under the null hypothesis of the true phylogeny, its lower bound decreases with the number of species in the phylogeny. Alternatively, Ornstein–Uhlenbeck branch-length transformation methods¹¹ (Methods) supported a significant signal in degree in 36.2% of the phylogenies where analyses converged (25 out of 69). P -values from randomization and branch-length transformation tests were highly positively correlated ($P < 0.001$), indicating that these two tests provide similar results. Thus these results show that phylogenetically related species have a similar number of interactions per species in at least one out of four phylogenies encompassing 39.0% of the networks.

Conversely, significant signal in species strength is present in only 2.6% of the phylogenies according to randomization tests (1 of 38; Fig. 2b), and in 20.8% of the phylogenies where branch-length transformation converged (5 of 24). The amount of phylogenetic signal for species strength was significantly lower than estimates for degree (paired t -test between log-transformed K values, $t_{37} = 1.806$, one-tailed $P = 0.039$; Fig. 2c). In spite of the significant positive correlation between degree and strength⁶, estimates of species strength may be subject to higher levels of uncertainty associated with proximate factors such as species abundance variability, changes associated with phenological sequences, and sampling errors that tend to decrease phylogenetic signal¹¹. This hypothesis could be tested by determining how estimates of species degree and strength vary over time in the same communities, the expectation being that species strength would show larger fluctuations than would degree. Alternatively, one could test whether the signal for strength increases after normalizing by species abundance. Nonetheless, our results suggest that species degree has stronger phylogenetic signal than strength.

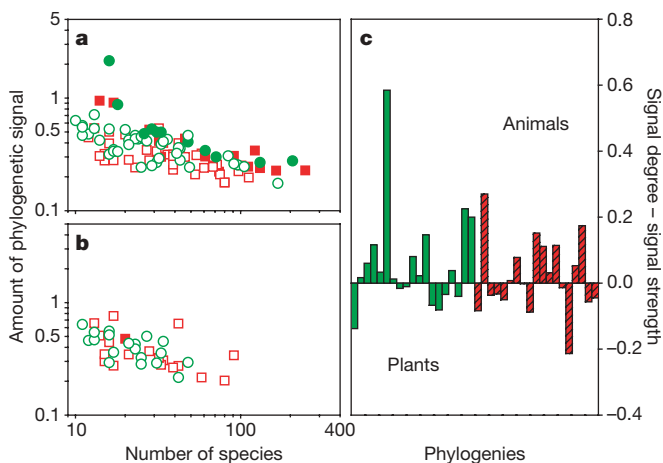


Figure 2 | Magnitude of phylogenetic signal on the number and strength of mutualistic interactions. Relationship between the magnitude of phylogenetic signal K and phylogeny size, estimated for species degree (a), and strength (b). Each data point represents a phylogeny: green circles for plants and red squares for animals. Solid symbols indicate statistically significant phylogenetic signals. c, Comparison of phylogenetic signal for species degree and strength. Green and dashed red bars correspond to plants and animals, respectively. Estimates obtained for degree were significantly higher.

Turning now to our second component of network architecture—which species interacts with which—we tested whether phylogenetic relatedness correlates with ecological similarity. The ecological similarity of any two species is defined as the number of species with which they both interact divided by the total number of species with which they interact (Methods). Phylogenetic and ecological distance matrices are positively and significantly correlated in 42.7% of the phylogenies (44 of 103, one-tailed Mantel test, $P < 0.05$). This means that phylogenetically related species tend to interact with a similar set of species. To determine whether this result is a consequence of the phylogenetic signal in degree reported above, we repeated these tests, controlling for differences in the number of interactions per species (partial Mantel test, see Methods). The results remained qualitatively similar. Partial Mantel correlations are significant in 46.6% of the phylogenies, supporting the idea that phylogeny is associated with the identity of the species' interactors after controlling for degree.

The association between phylogenetic resemblance and ecological similarity tends to be more common among animals: 60.8% of Mantel correlations between ecological and phylogenetic distance matrices were significant for animals, whereas 25.0% were significant for plants (Fig. 3). In addition, comparison of the Mantel coefficients Z for plants and animals indicated that animal phylogenies were more strongly associated with species interaction patterns than were plant phylogenies (paired t -test between log-transformed values, $t_{43} = 3.218$, one-tailed $P = 0.001$; Fig. 3). Further, these results are robust even when the number of animal and plant species is statistically controlled (analysis of covariance, ANCOVA, $F_{1,100} = 10.16$, $P = 0.02$). Results from partial Mantel tests controlling for degree were qualitatively similar (paired t -test, $t_{43} = 2.576$, one-tailed $P = 0.014$). It would be interesting to investigate multiple alternative hypotheses, such as differences in mobility and evolvability^{21–23}, to determine the cause of this difference.

Although network structure seems significantly more associated with animal phylogenies, structure may be driven by the evolutionary history of both plants and animals (7 of 44 communities), only plants or only animals (3 and 21 communities, respectively), or neither plants nor animals (the remaining 13 communities). This highlights the large variability across networks, indicated by the residual variation of K or Z after controlling for phylogeny size (Figs 2 and 3; Supplementary Table 1). Part of this variability is related to the taxonomic diversity of the plant lineages, though apparently not to the diversity of frugivores (fruit-eaters) or pollinators according to

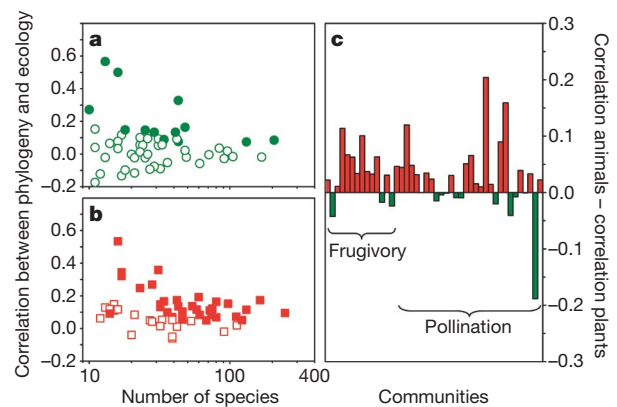


Figure 3 | Correlation between ecological similarity and phylogenetic relatedness. Results of regular Mantel tests correlating phylogenetic and ecological distance matrices plotted against phylogeny size, obtained for plants (a) and animals (b). Each data point corresponds to a phylogeny, and a solid symbol indicates a statistically significant correlation. c, Comparison between Mantel Z estimates obtained separately for plants and animals composing each network. Communities where interaction patterns are more associated with animal phylogenies are depicted in red; those more associated with plants in green. The phylogenetic structure of animals correlates significantly better with interaction matrices than that of plants.

several regression models (Methods). One plausible explanation for this result is that flower or fruit morphology is variable across the taxonomic groups examined, whereas phenotypic variation for frugivores and insects is more relevant at other taxonomic levels. Partitioning the phenotypic variance across taxonomic groups may address this hypothesis, and also clarify the mechanisms by which evolutionary history translates into patterns of interactions.

We have shown that phylogenetically related species tend to have similar roles in the network of interactions in almost half of the communities studied here. These effects are not a reflection of differences between major taxonomic groups only, because they also appear at finer scales of the phylogenies (Supplementary Fig. 3). In light of this, we tested whether simulated coextinctions⁷ involve taxonomically related species more often than expected by chance for cascades of identical size (Methods). This would result in a non-random pruning of the evolutionary tree^{12,13}. Simulations show that the rate of taxonomic diversity loss is higher than expected in the

absence of phylogenetic signal (Fig. 4). Although these effects may seem quantitatively small (partly owing to the averaging nature of the index), they can actually encompass the extinction of entire families or higher taxonomic groups from the community. The overall reduction in taxonomic diversity holds across communities, so that values falling below the null expectation are significantly more frequent than those above it ($\chi^2 = 50.7$, degrees of freedom, d.f. = 1, $P < 0.0001$; Fig. 4). Moreover, the contribution of phylogeny to species patterns of interaction correlates with the magnitude of taxonomic diversity loss across communities ($P < 0.05$ for parametric and non-parametric correlations; Fig. 4c). Therefore, communities in which species interactions have a strong phylogenetic component are more prone to have closely related species going coextinct following an extinction event. We conclude that the interaction between network and phylogenetic structures can ultimately result in non-random coextinction patterns.

Plant–animal mutualisms form heterogeneous, nested networks built on weak and asymmetric links among species, which may facilitate long-term species persistence^{6,7}. Our results provide evidence for the role of phylogenetic relationship as one determinant factor shaping these patterns: phylogeny partly accounts for species' propensities to interact in more than one-third of the networks, and the identity of the species with which they interact in about half of the networks. From a theoretical point of view, our results warrant the inclusion of evolutionary history into mechanistic models of network formation and maintenance²⁴. From a conservation perspective, our results show that cascading effects of coextinction may spread across taxonomically related species, further increasing the erosion of taxonomic diversity.

METHODS SUMMARY

The amount of phylogenetic signal in degree and strength was quantified with the K statistic, which is the fraction of the amount of signal of the real data set over that expected, assuming brownian motion and the same tree topology. Significance of phylogenetic signal was tested with randomization and branch-length transformation methods¹¹.

We used Mantel tests to compare phylogenetic distance matrices with matrices of ecological distance. Phylogenetic distance between pairs of plants (or animals) was estimated as the expected covariance of the trait between the two species^{11,25}. Ecological distance was calculated as $1 - S$, where S is the Jaccard index of similarity²⁶. We also performed partial Mantel tests controlling for the absolute difference in degree between two species.

Species removal simulations started from the most specialized to the most generalized species⁷. After an extinction cascade, we calculated the community taxonomic diversity as the average taxonomic distance between species²⁷. Path length weights between species increased the more distantly related they were taxonomically (that is, species of the same genus have a distance of 1 whereas species from different genera within the same family have a distance of 2, and so on). Thus, the higher the index, the more diverse the community. To calculate the decrease of taxonomic diversity of the real community with respect to the expected decrease in the absence of phylogenetic signal, we replicated the coextinction cascade 1,000 times after randomizing the taxonomic affiliation of species going coextinct. The taxonomic diversity relative to the null expectation was the ratio between real and null values, and the significance was estimated by counting how often the real value fell below the randomization results. The average rate of taxonomic loss per community was calculated as the slope of a linear regression with an intercept forced through 1.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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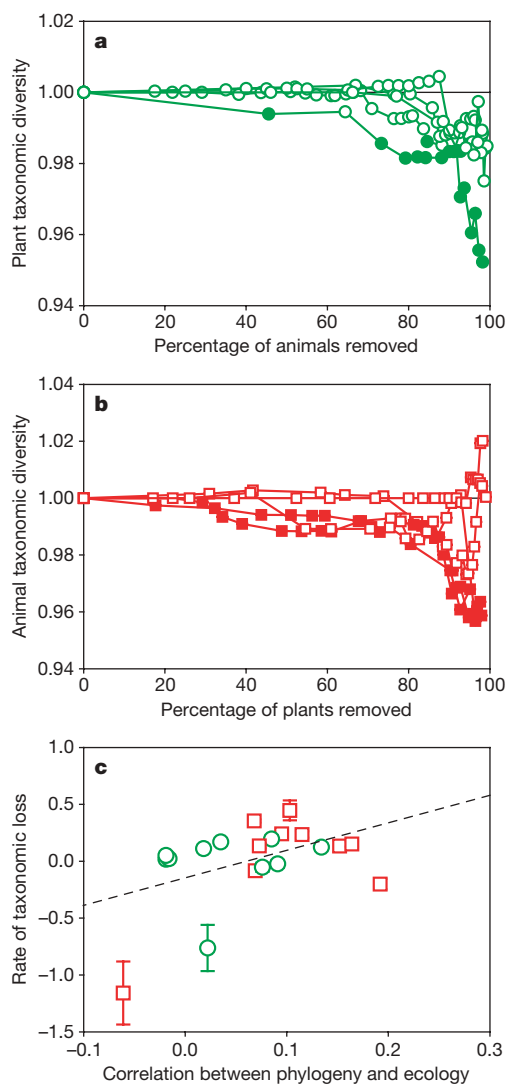


Figure 4 | Phylogenetic resemblance induces a higher loss of taxonomic diversity after species extinctions. Taxonomic diversity of plants (a) and animals (b) of five communities as a function of the number of extinct species, removed from most specialized to most generalized. Each symbol represents the removal step leading to the next generalization level. Taxonomic diversity is the ratio between indexes from the real communities over randomization results removing phylogenetic effects. Full symbols indicate taxonomic losses below 95% of the null model. **c**, Average (\pm s.e.m.) rate of taxonomic loss of ten communities regressed against the magnitude of phylogenetic effects.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions E.L.R. performed all the analysis and compiled the phylogenies jointly with J.E.L. P.R.G. performed the extinction simulations. P.J. and J.B. designed the study and compiled the interaction matrices. E.L.R. and J.B. wrote a first version of the manuscript, and all authors contributed to the final draft.

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METHODS

Database. We compiled 59 qualitative mutualistic networks (36 plant–pollinator and 23 plant–frugivore webs) describing the presence or absence of interactions. The data set encompasses Mediterranean, tropical, temperate, subtropical and Arctic communities from all continents except mainland Asia and Antarctica. Of these networks, 22 (9 for pollination and 13 for frugivory) are quantitative, describing the strength of each interaction or pairwise dependence (see data sets in Supplementary Information). From these networks, we calculated species degree and species strength for plants and animals separately, and recorded the taxonomic affiliation of species forming each community.

Phylogenies. We assembled one animal and one plant phylogeny for each community. Phylogenies are based primarily on molecular data, with a few species included according to taxonomic information (Supplementary Methods). Phylogenies with less than ten species or with too many unresolved nodes were not included in analyses. This resulted in 105 phylogenies for the following groups: 35 insect phylogenies (Class Insecta; all pollinators), 18 bird phylogenies (Class Aves; all frugivores), and 52 angiosperm phylogenies (Infraphylum Angiospermae; 33 belonging to plant–pollinator and 19 to plant–frugivore networks).

Phylogenetic statistical methods. We tested for the presence of phylogenetic signal on species degree and strength with randomization and branch-length-transformation tests¹¹. These methods test whether species attributes are significantly associated with phylogeny, using randomization or maximum-likelihood procedures. Branch-length transformation tests were performed assuming the Ornstein–Uhlenbeck model of stabilizing selection and a model in which character evolution can accelerate or decelerate (ACDC)¹¹. Because ACDC models did not converge in most cases, here we discuss results from the Ornstein–Uhlenbeck model (all analyses are included in Supplementary Material for completeness). Although these techniques provide similar information about the presence of a phylogenetic signal, applying both methods can be useful in determining how robust our results are and in overcoming limitations inherent to each statistical test (Supplementary Figs 1 and 2). The amount of phylogenetic signal was quantified with the *K* statistic (Fig. 2), which is the fraction of the amount of signal of the real data set over that expected, assuming brownian motion and the same tree topology.

We used Mantel tests to compare phylogenetic distance matrices with matrices of ecological distances between species. Phylogenetic distance between pairs of plants (or animals) was estimated as the expected covariance of the trait between the two species^{11,25}. Ecological distance was calculated as $1 - S$, where *S* is the Jaccard index of similarity obtained from qualitative interaction matrices²⁶. The similarity between two species *i* and *j* is defined as $S(i, j) = a/(a + b + c)$, where *a*, *b* and *c* represent the number of shared interacting

species, the number of interactions specific to species *i*, and the number of interactions exclusive to species *j*, respectively.

Because differences in degree affect Jaccard estimates, we also performed partial Mantel tests controlling for degree (the pairwise distance in degree was calculated as the absolute difference in degree between two species; Supplementary Methods). Hence, this partial test can discern whether phylogeny strictly affects the species with which species interact, independently of the total number of interactions of each species. When necessary, estimates were log-transformed to improve normality (or log-value + 1 for statistics varying between –1 and 1, as Mantel's *Z*).

According to regression models controlling for phylogeny size, community size, and number of interactions, phylogenetic signal was similar for frugivory and pollination networks ($P > 0.28$ for *K* and for Mantel's regular and partial *Z*), hence results were pooled.

Taxonomic diversity and coextinction simulations. As a surrogate for phylogenetic diversity, we estimated taxonomic diversity of plants and animals in the largest available phylogenies (23 plant and 27 pollinator phylogenies with more than 30 species, and 15 bird phylogenies with more than 15 species; see Supplementary Methods). The mean taxonomic distance between all species was employed as an index of taxonomic diversity²⁷ in subsequent regressions.

Extinction cascades were simulated for the ten largest communities (all having more than 40 animal and plant species) with available taxonomic affiliation, following ref. 7. After one species is removed, species left without any interaction go coextinct. Species removal started from the most specialized (least-linked) to the most generalized (most-linked) species, which was proposed as a more plausible extinction sequence because specialist species tend to be less abundant than generalists^{4,7,8}. In spite of several assumptions implicit in the model (for example, all plants require animals for reproduction, and species cannot adapt to new resources), this approach provides the first reasonable attempt to study coextinction patterns in phylogenetically structured networks⁷. Although these assumptions may affect the total number of species going extinct⁷, our comparisons involve coextinction cascades of the same size, with and without phylogenetic signal.

After an extinction cascade, we calculated the decrease of taxonomic diversity of the real community respect to the expected decrease in the absence of phylogenetic signal. This was done by replicating the coextinction cascade after randomizing the taxonomic affiliation of species going coextinct (that is, nodes remain unchanged but their 'name tags' are shuffled). This null model removes effects of phylogenetic relatedness¹¹ controlling for network structure and species number. The relative taxonomic diversity is the ratio between real and null values, and the average rate of taxonomic loss per community is the slope of a linear regression with an intercept forced through 1 (that is, real values and the null expectation are equal when no species are removed).