Network structure embracing mutualism–antagonism continuums increases community robustness

Article · October 2017

DOI: 10.1038/s41559-017-0320-6

Alicia Montesinos-Navarro
Spanish National Research Council

Fernando Hiraldo
Spanish National Research Council

José L Tella
Estación Biológica de Doñana

nature ecology & evolution
ARTICLES
DOI: 10.1038/s41559-017-0320-6

Network structure embracing mutualism–antagonism continuums increases community robustness

Alicia Montesinos-Navarro[1*], Fernando Hiraldo[2], José L. Tella[2] and Guillermo Blanco[3]

Theory predicts that contrasting properties of mutualistic and antagonistic networks differentially promote community resilience to species loss. However, the outcome of most ecological interactions falls within a continuum between mutualism and antagonism, and we ignore the extent to which this interactions' continuum might influence community stability. Using a large data set of interactions, we compared co-extinction cascades that either consider or ignore the mix of beneficial and detrimental actions that parrots exert on plants. When the antagonism–mutualism continuum was considered, a combination of the properties that separately enhance community stability in ecological networks emerged. This combination of properties led to an overall increase of the parrot community robustness to face plant species loss. Our results highlight that the conditional outcomes of interactions can influence the structure of ecological networks, thus affecting our predictions of community stability against eventual changes.

The dynamics of ecological systems are influenced by the outcomes of biotic interactions, which usually fall within antagonistic–mutualistic continuums[1–4]. The ultimate outcome of a biotic interaction might range from beneficial to progressively detrimental when it is considered from a cost/benefit perspective[1,5]. The context-dependency of interaction outcomes has been previously revised considering the influence of indirect effects through the presence of intermediary species. This has been approached by assessing the different effects of plant mutualists and enemies[6], or single and multiple mutualists[7], on plant performance. In addition, also the sign and magnitude of species interactions such as competition, mutualisms and predation can be context-dependent[8]. However, despite its potentially strong influence on the structure and functioning of ecological systems[1,9–12], the implications of considering antagonistic–mutualistic continuums in the robustness of an ecological network remain largely unknown.

Interactions between plant resources and animal services, such as pollination or seed dispersal, provide well-known examples of ecological processes that can fall along an antagonistic-mutualistic continuum. Animals involved in these interactions have primarily been considered as fully mutualistic pollinators and endozoochorous seed dispersers[13]. However, pollinators or dispersers that increase their own benefit by robbing nectar or consuming seeds (cheaters) may still contribute to pollination and dispersal[14]. Similarly, most seed and flower predators also pollinate and disperse seeds[12,15–17], and this duality can imply opposing selective forces on plant populations and communities[3].

Ecological networks have arisen as a powerful tool to explore complex biotic interaction patterns. Until recently, network ecology has been limited to describe mono-layered ecological systems (for example, addressing only one type of interaction: trophic, competitive or mutualistic), despite the need to introduce realism in these studies by considering multiple layers of complexity. Currently, the development of theory and tools to approach dynamics in multilayer networks (for example, to consider multiple types of interactions at a time) are blooming in other scientific fields, but there are still few attempts to apply it to ecological systems[18].

The expanding interest in ecological networks has allowed the compilation of enough information to detect common patterns across networks, showing that similar properties emerge in several networks independently of the type of guilds involved[19]. Two frequently studied network properties are nestedness and modularity. In nested networks, specialists interact with species that form perfect subsets of the species with which generalists interact. Modularity refers to dense connections among species within a group (or module), but sparse connections across modules[19]. Different patterns can therefore emerge within the same network, and so both nestedness and modularity have been reported, for example, for plant–mycorrhiza[20], seed dispersal[21] and plant pollination[22,23]. Nestedness and modularity are present in all kinds of networks, reflecting either mutualistic or antagonistc interactions. There are examples of modularity in mutualistic interactions, such as with plant pollinators and seed dispersers[21,23], and nestedness in antagonistic ones, such as the diet niche of carnivore species[24]. However, there is some evidence to support that mutualistic and antagonistic interactions might tend to be more nested and modular, respectively. Some studies suggest that mutualistic networks, such plant pollinators and seed dispersers, are highly nested[19,22]. A study has found that the level of nestedness of 14 resource–consumer bipartite graphs were significantly lower than for mutualistic networks (27 plant–disperser and 25 plant–pollinator networks)[22]. Other studies also compared plant–pollinator and plant–herbivores network, concluding that plant–pollinator assemblages exemplify a simple nested pattern, whereas plant–herbivore assemblages illustrate a propensity for compartments, which can also be nested within modules[25].

---

[1]Centro de Investigaciones sobre Desertificación (CSIC-UVEG-GV), Carretera Moncada-Náquera, Km 4.5, 46113 Moncada, Valencia, Spain. [2]Department of Conservation Biology, Estación Biológica de Doñana, CSIC, Americo Vespucio s/n, E-41092 Sevilla, Spain. [3]Department of Evolutionary Ecology, Museo Nacional de Ciencias Naturales, CSIC. José Gutiérrez Abascal 2, 28006 Madrid, Spain. *e-mail: ali.montesinos@gmail.com

Nestedness and modularity have implications for community robustness. In a nested matrix, a set of generalists, either plants or animals, tend to interact also with generalists in the other guild—which results in a few species being involved in many interactions. This interaction pattern allows several ways of maintaining the persistence of the system when some interactions are lost[19]. In addition, specialists tend to interact with generalists that are less dependent on specific interactions, and tend to be more abundant and stable than the former. This asymmetry enhances the persistence of specialists as they rely on stable partners[22], resulting in increased stability in mutualistic networks[26–28]. Regarding modularity, the effect of the network structure on species loss depends on the position of each species in the network[23]. The extinction of species that are densely connected to other species in the same module can result in the disruption of the module due to co-extinction cascades within that module, without affecting other modules. However, in the case of species densely connected across modules, their loss will result in the disruption of the overall network into disconnected modules, without affecting the structure within each module[23]. As network structures presenting a high modularity tend to maximize the number of links within modules, the former scenario is more likely when species loss is random, avoiding cascade effects by retaining the impacts of a perturbation within a module[29,30]. Interestingly, there is some evidence to support that nestedness and modularity in mutualistic and antagonistic networks can have contrasting implications for community stability. Theoretical studies have used a model approach to analyse the relationship between community stability and network structure, showing that contrasting network structures favour stability in mutualistic and antagonistic networks. During simulations of the population dynamics of 34 mutualistic (pollination) and 23 antagonistic (herbivory) networks, some species become extinct before the equilibrium was reached, leading to a high nestedness and low modularity in the case of mutualistic networks, and the opposite pattern (low nestedness and high modularity) in the case of antagonistic networks[31]. This might be related to a potential enhancement of robustness due to (1) a link-dense core of interactions (nestednes) in mutualistic networks, and (2) isolated groups of antagonistic interactions, resulting in a contention effect in antagonistic networks.

Research focusing on how conditional outcomes of interactions result in the emergence of specific properties in the structure of ecological networks can contribute to understanding the ultimate effects of this ecological variation on community robustness. An attempt to merge conditional interaction outcomes in a bipartite network has been made for effective pollination and cheating, usually considering these processes separately[10] (but see ref. [12]). However, this approach is rare for other plant-resource–animal interactions (such as granivorous, herbivorous and generalist plant consumers). Nowadays it is possible to combine networks with different interaction types, and analyse them as multilayer networks[18,32]. However, we are unaware of any attempt to integrate this approach into ecological networks to assess its implications on community robustness.

In this study, we aim to include the antagonism–mutualism continuum within a given ecological network. We focused on the traditionally considered antagonistic interactions between parrots (Psittaciformes) and their food plants. Parrots can consume, destroy and waste seeds and flowers of their food plants. However, it has been recently shown that parrots can still provide multiple benefits to the plants on which they feed, such as pollination, primary and secondary seed dispersion, or feeding on invertebrate herbivores and pathogens such as fungi[33–37]. We propose that the network properties enhanced in mutualistic (nestedness) and antagonistic (modularity) networks[19,38] may coexist within a given multilayer network due to the antagonism–mutualism continuum of biotic interactions. Based on previous knowledge, we hypothesize that the mutualistic services provided by parrots to plants will contribute to the nestedness of the multilayer network, while the antagonistic interactions will contribute to modularity. In turn, this can result in an emergent network structure that enhances the robustness of the parrot community. To test our hypothesis, we first split the multilayer network into two sub-networks (by selecting the interactions that involved at least one beneficial or one detrimental ecological function, respectively) and assessed the relative contribution of each sub-network to nestedness and modularity. We then simulated co-extinction cascades and compared parrot community robustness to plant species loss when (1) the network is considered as purely antagonistic, according to the traditional view of plant-parrot interactions, and (2) taking into account the beneficial effects that parrots can exert on plants. Finally, we assessed putative ecological explanations for the observed plant–parrot associations, testing whether plants associated with a given parrot species share functional (growth form), relative abundance (dominance) and historical (endemicity) traits.

Results

Nestedness. Approximately 25% of the potential interactions between plants and parrot species are actually realized, both in the multilayer network and in the two sub-networks (mutualistic and antagonistic) (Table 1). In all three cases, the networks were significantly more nested than expected by chance (Table 1, for all cases $P < 0.001$). However, the relative nestedness in the mutualistic sub-network was twice that of both the antagonistic sub-network and the multilayer network (Table 1). In addition, considering the multilayer network, mutualistic interactions show a significantly lower deduction from perfect nestedness (mean ± SE = 0.0007 ± 0.0001) than antagonistic interactions (0.001 ± 0.0001) ($t = -3.9925$, df = 323.139, $P = 8.097 \times 10^{-5}$), therefore contributing more to the nestedness of the multilayer network.

Modularity. The multilayer network (modularity (with null model confidence interval, CI) of multilayer network $M = 0.393$ (0.386–0.389)) and the antagonistic sub-network ($M = 0.409$ (0.399–0.402)) had a significantly higher modularity than expected by chance, while the mutualistic sub-network was not modular ($M = 0.385$ (0.391–0.395)). The multilayer network revealed four

Table 1 | Descriptive statistics of the three networks and nestedness metrics

				Nestedness			
						Relative	
	Plants	Parrots	*I*	*T*	NODF	*T*	NODF
Multilayer network	108	8	227	55.3	31.0	0.3	0.3
Mutualistic sub-network	55	8	112	70.4	38.9	0.4	0.7
Antagonistic sub-network	107	8	216	57.7	30.2	0.3	0.4

For each of the three networks (multilayer network and mutualistic and antagonistic sub-networks), the following are given: the number of plants species, number of parrot species, number of interactions (I), nestedness calculated as matrix temperature (T); nested overlap and decreasing fill (NODF); relative T, $(T - T_{\text{null model}})/T_{\text{null model}}$ (see the Methods section for details about the null model); and relative NODF $(\text{NODF} - \text{NODF}_{\text{null model}})/\text{NODF}_{\text{null model}}$.

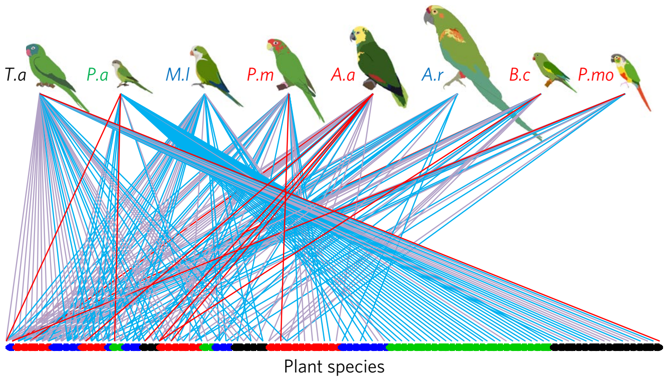

Fig. 1 | Trophic network of parrot species feeding on plant species. The network consists of 8 parrot species (top) and 108 plant species (bottom), but only the names of parrot species are shown (abbreviated; from left to right: *T. acuticaudatus*, *P. aymara*, *M. luchsi*, *P. mitratus*, *A. aestiva*, *A. rubrogenys*, *B. chiriri* and *P. molinae*). The colour of each link (red, blue or purple lines) represents the sign of the interaction: beneficial (red), when parrots are contributing to pollination, dispersing seeds, facilitating mature seeds for secondary dispersers and feeding on noxious organisms of their food plants; antagonistic (blue), when the interaction involves the consumption and destruction of flowers, seeds, bark and other plant structures; or both (purple), when a given parrot species was observed performing either of the two types of function in a given plant species. The colours of the parrot initials and the plants' position in the network (black, green, blue and red) group the species within the same module. The sizes of parrot species are depicted on a similar scale. Credit: parrot drawings, A. Toledo.

modules (Fig. 1). Two modules included only one parrot species (*Thectocercus acuticaudatus* and *Psilopsiagon aymara*, respectively), one module included four species (*Amazona aestiva*, *Petroscirtes mitratus*, *Brotogeris chiriri* and *Pyrrhura molinae*), and one module included two species (*Myiopsitta luchsi* and *Ara rubrogenys*). The module of *P. aymara* has the highest number of plant species (31 species). The module of *A. aestiva*, *P. mitratus*, *B. chiriri* and *P. molinae* and that of *T. acuticaudatus* have a similar number of plant species (28 and 27 species, respectively), and the module of *M. luchsi* and *A. rubrogenys* has the fewest (22 plant species).

Plant traits determining plant–parrot associations. Plant species preferences of *P. aymara* was significantly explained by growth form and dominance (Supplementary Table 1), avoiding trees and plants with low and medium dominance (Fig. 2). *M. luchsi* and *A. rubrogenys* tended to avoid non-endemic plants (Fig. 2 and Supplementary Table 1), and none of the plant traits considered significantly explained the plant species with which *T. acuticaudatus* interacted (Supplementary Table 1). Finally, the growth form and dominance of plants also explained the plant species preferences of *B. chiriri*, *P. molinae*, *A. aestiva* and *P. mitratus* (Supplementary Table 1), which tended to avoid shrubs and species with a medium dominance (Fig. 2).

Parrot community robustness to plant species loss. Our simulations show that, other things being equal, the estimation of the parrot community robustness to the loss of plant species differs when the mutualism–antagonism continuum is considered (removal criteria *c* from Methods), compared to when it is ignored (removal criteria *b* from methods). Simulations considering both mutualistic and antagonistic interactions result in higher estimates of robustness than those considering all interactions as antagonistic, thus ignoring the mutualism–antagonism continuum (Fig. 3). In the first case, the loss of 96% of the plant species is required to lose 50% of the parrot species; meanwhile, the loss of only 19% of the plant species is required when the network is considered purely antagonistic (that is, all the interactions are considered negative) (Fig. 3). The robustness of the parrot community is higher when plant species are removed based on the type of interactions exerted by parrots than when plant species are removed randomly. In the latter case, the removal of 76% of the plant species is required to lose 50% of the parrot species (Fig. 3). Interestingly, the increment in the robustness of the parrot community disappears when the sign of the realized interactions is randomized (Fig. 4). The percentage of species that has to be removed in order to lose half of the parrot species in the community increases with mutualistic nestedness and antagonistic modularity. Thus, randomized matrices with low, medium and high mutualistic nestedness and antagonistic modularity require on average the removal of 39%, 60% and 87% of the plant species, respectively, in order to lose half of the parrot species (Fig. 4). This pattern is consistent across all the thresholds used as extinction criteria (Supplementary Fig. 1), becoming stronger at higher thresholds.

Discussion

Across multiple ecological processes the outcome of biotic interactions (plant–herbivores, –pollinators, –seed dispersers and –mycorrhiza) depends on the balance between the costs and benefits provided to the partners. Despite the ubiquity of this balance, few studies have assessed its implications in the structure of ecological networks[10,12,32]. Here, for the first time to our knowledge, we approach its effects on community robustness. Our results suggest that the structure of mutualistic and antagonistic interactions can enhance community robustness to the loss of partners, as this enhancement decreases when the structure is progressively disrupted.

The functioning of biotic interactions along antagonism–mutualism continuums is widespread. Interactions with pollinators or mycorrhiza are classic examples in which the plant contribution to its partner is context dependent[39–41]. Thus, plants can avoid mycorrhiza infection when the costs to host mycorrhiza exceed the benefits (under nutrient-rich environments[41]), or provide less reward (nectar sugars) to its pollinators under nutrient-poor conditions[40]. The architecture of ecological networks in some cost/benefit-balanced interactions is similar to that reported in our results. A combination of nestedness and modularity has been reported for example for plant-mycorrhiza[20] and seed dispersal networks considering multiple taxonomic groups of seed dispersers[21]. However, further research is necessary to assess whether the dual nested and modular nature of these networks is due to the relative contribution of mutualistic and antagonistic interactions to different properties of the network structure.

Theoretical studies based on pollination (mutualistic) and herbivory (antagonistic) networks have shown that their stable community compositions tend to be highly nested and lowly modular in the case of mutualistic networks, and the opposite (low nestedness and high modularity) in the case of antagonistic networks[31]. Interestingly, supporting this previous knowledge, our parrot–plant mutualistic sub-network shows twice the value of nestedness than the antagonistic sub-network, and contributes most to the multilayer nestedness, while only antagonistic interactions contribute to the modularity of the multilayer network. It is worth considering that both sub-networks have an unbalanced number of plant (108) and parrot species (8), which implies that the estimates of the network metrics have to be interpreted with caution. However, this unbalance is unlikely to affect the comparison between the two sub-networks, as relative metrics (relative to a null model with the same dimensions) are used for their comparison. In addition, we show that the parrot community robustness to the loss of plant species decreases when mutualistic nestedness and antagonistic modularity decreases. Under our theoretical assumption that the frequency of antagonistic interactions determines plant extinction, the decrease

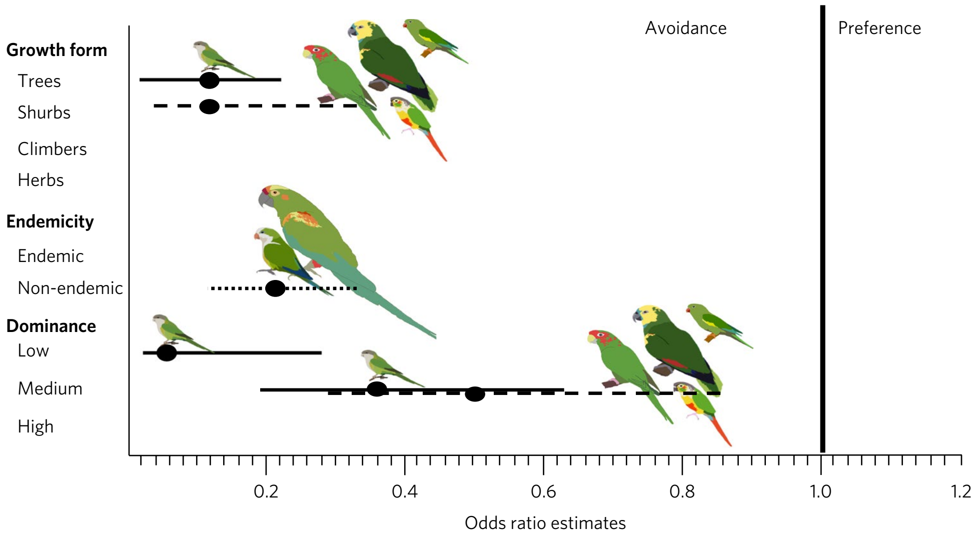

Fig. 2 | Odds ratio estimates and confidence intervals (95%) extracted from the generalized linear models that assess the plant functional traits explaining each module. When the odds ratio estimate is equal to 1, there is an equal probability of being included in a given module, and values above or below 1 indicate a tendency to interact or avoid the plant species in that module, respectively. Only the three modules that were significantly explained by any of the plant functional traits considered are presented: plants interacting with *P. aymara* (solid lines), with *M. luchsi* and *A. rubrogenys* (dotted lines), and with *B. chiriri*, *P. molinae*, *A. aestiva* and *P. mitratus* (dashed lines). Credit: parrot drawings, A. Toledo.

in the community robustness could be interpreted as a result of ignoring the buffering effects of parrot mutualistic interactions on plant extinction. However, this single effect cannot explain the gradual decrease in robustness with a decrease in mutualistic nestedness and antagonistic modularity. This suggests that the differences in robustness are unlikely to be attributed only to the frequency of antagonistic interactions, and that the distribution of mutualistic and antagonistic interactions in the network structure also contributes to those differences. As expected, this pattern is stronger when we increased the threshold established to consider a parrot extinction (when the parrots are more sensitive to plant species loss, becoming extinct with small reductions in their abundance). Our simulations are not designed to accurately predict the processes of co-extinction cascades, as they disregard the myriad of positive and negative biotic interactions or abiotic factors that can also influence the viability of local populations. Instead, this approach intends to show that for a given theoretical scenario, mutualist and antagonistic outcomes can differ in their network structures, which could condition community robustness to species loss.

Nestedness and modularity have opposing effects on the stability of mutualistic and trophic networks[28–30], which could explain their synergistic contribution to community stability when they occur within the same network. On the one hand, nestedness in mutualistic interactions implies that those plant species that receive few mutualistic interactions (specialist) tend to be visited by generalist mutualistic parrots[28]. This can slow down the loss rates of those plant species, considering that generalist parrots will be less prone to disappear as they can use a high diversity of food sources and furthermore enhance the performance of those plants. On the other hand, modularity can retain perturbations in antagonistic networks[29,30]. Modularity in antagonistic parrot–plant interactions indicates that a set of parrots exerts negative effects on a set of plants. Therefore, if negative interactions within a module result in the loss of those plants, only the parrots within that module will be affected.

The central role of parrots in seed dispersal and pollination can be enhanced by their diversity in food exploitation strategies and their mobility. Parrots exploit plants through diverse feeding methods, on multiple plant structures, and in different developmental stages[34,42–44], promoting the dispersal of propagules as an indirect effect of foraging[33–37,43,45]. In addition, they have the capacity to move both seasonally and on a daily basis across large areas, tracking the spatio-temporally variable resources provided by their food plants[46]. They also perform altitudinal movements between valleys of variable exposure and microclimatic conditions[47]. Therefore, the observed high daily and seasonal mobility of parrots (which is also known for our study area[48]) ensures that all plant species are potentially available as food resources for all parrot species, suggesting that the resulting modules did not emerge from potential mismatches between small-scale spatial distributions of parrots and plants.

Modularity can be driven by a plethora of ecological and historical processes, such as habitat heterogeneity, specificity in biotic interactions, or species home ranges[3,23,25]. The studied plant-parrot network is structured into modules, which seems to emerge from different ecological processes. Although further research is necessary in this regard, the fact that some modules can be explained by the spatial distributions of the interacting species is in agreement with the idea that parrots can play an important role facilitating the establishment of plant species. On the one hand, generalist parrot species with widespread distributions—*B. chiriri*, *P. molinae*, *A. aestiva* and *P. mitratus*[49]—were included in a module together with widely distributed plant species. Several of these plant species, such as *Maclura tictoria*, *Muntingia calabura*, *Ziziphus mistol*, *Erythrina falcata*, *Alnus acuminata*, *Morella chevalieri* and *Handroanthus impetiginosus*, are generalists of humid and temperate environments and have a widespread distribution in the neotropics[50]. However, in the dry biome of the inter-Andean valleys, these species are restricted to microhabitats associated with temporal and permanent flowing water, especially river banks[47]. Parrots might be dispersing seeds of these cosmopolitan plant species across rivers and streams, acting as corridors from adjacent humid biomes. On the other hand, in another module, the two endemic parrot species (*M. luchsi* and *A. rubrogenys*) tend to interact with plant species that are also endemic to the study biome. In a similar way, a strong interaction between endemic species agrees with the idea that endemic plant species can have their dispersal limited by the parrot home ranges with which they interact (endemic parrots, and thus with a small

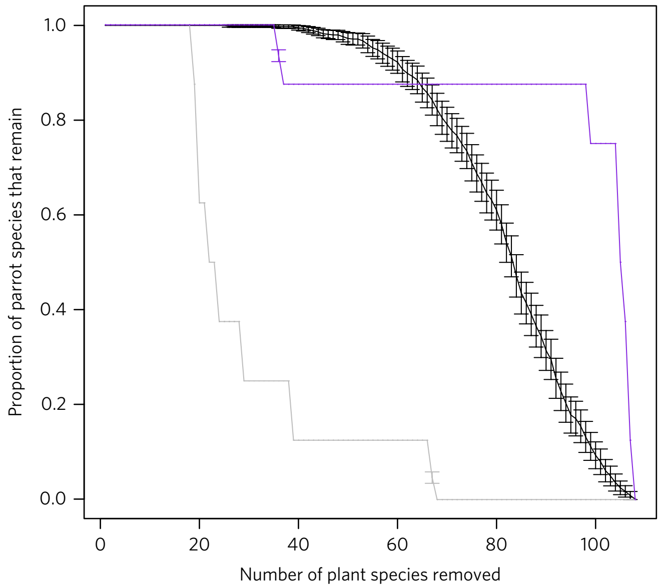

Fig. 3 | Simulations of parrot co-extinction rates triggered by plant species removal based on the observed trophic network. The colour represents the different criteria used for plant species removal. The three criteria are: randomly selecting the plant species to be removed (black); considering all interactions as antagonistic and thus removing first those plant species with a higher number of parrot individuals feeding on them (grey); and weighting the number of parrot individuals by whether they perform mutualistic (multiply by 1), antagonistic (multiply by −1) or both types of interaction (multiply by 0.5) and first removing those plant species with higher numbers of antagonistic interactions with parrot individuals (purple). Error bars correspond to 95% confidence intervals of 100 repetitions of each simulation. A parrot species is considered extinct when less than 20% of its individuals remain in the network.

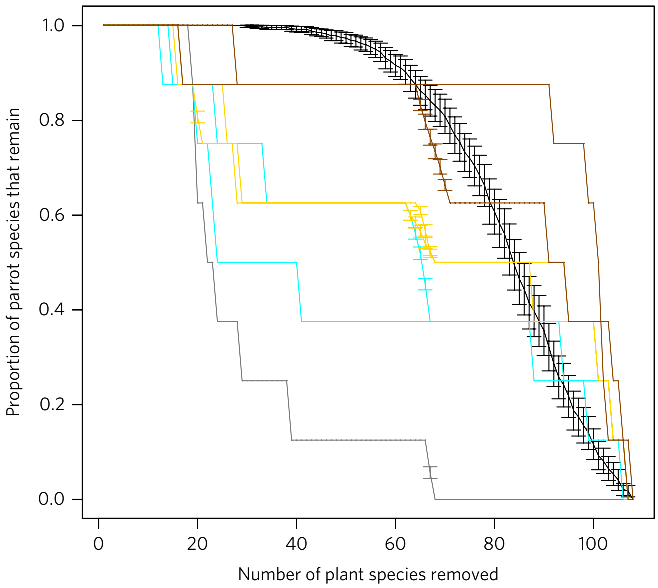

Fig. 4 | Simulations of parrot co-extinction rates triggered by plant species removal. Black and grey points represent the two criteria used for plant species removal (described in Fig. 3), randomly selecting plant species (black) and first removing the plant species with the higher number of parrot individuals feeding on them, considering that all trophic interactions are antagonistic (grey). Blue, yellow and brown points represent simulations in which the multilayer interaction network is maintained but the sign of each interaction has been randomized. The colour represents whether both nestedness of mutualistic interactions and modularity of antagonistic interactions are low (blue), medium (yellow) or high (brown). In all the randomized networks, the nestedness of mutualistic interactions and modularity of antagonistic interactions were similar or lower than in the observed trophic network. Error bars correspond to 95% confidence intervals of 100 repetitions of each simulation. A parrot species is considered extinct when less than 20% of its individuals remain in the network.

distribution). Again, this suggests a relevant role for parrots as important drivers of plant community assemblies. Finally, another module was defined by the habitat preferences of *P. aymara*, the smallest species in the parrot community and the only parrot that forages preferentially on herbs over other growth forms[34].

This study highlights the importance of considering the conditional outcome of interactions for a better understanding of the contribution of biotic interactions to community stability. Antagonism–mutualism continuums in trophic networks could be more common than previously thought, as recent works show that species traditionally considered as pure seed predators may also serve as key seed dispersers[33–37,45]. In addition, not only considering the conditional outcomes of a given interaction type, but also the combined effects of multiple interaction types might be important when trying to assess the robustness of ecological systems. Future attempts to improve the realism of ecological networks might include the conditional outcomes of interactions as a continuum feature, instead of a discrete categorization of interactions into mutualistic or antagonistic. This will require a quantification of the costs and benefits provided to each partner, and could be easily incorporated into the framework proposed here by including appropriate quantitative values for weights in the simulations. In addition, conditional outcomes of biotic interaction can be dynamic, presenting temporal variation or shifting along the ontogeny of the species involved. Further empirical and theoretical research is needed to integrate temporal variation in conditional outcomes of interactions into ecological networks. This study exemplifies how the conditional outcomes of a trophic interaction can be integrated into an ecological network to properly assess the impacts threatening the stability of natural systems.

Methods

Study system. The study was conducted in the tropical dry forest biome of the inter-Andean valleys of Bolivia, on the eastern slopes of the central Andes, a small region ranging from 900 to 3500 m.a.s.l. (details previously published[34,48]). The climate ranges from dry to semi-arid with rainfall (200–650 mm) concentrated in the austral summer, and the habitat is a tropical dry forest with multiple valleys and a high proportion of vegetal endemisms[47,51,52]. Eight parrot species regularly inhabit this biome[34], including two endemic species (*Ara rubrogenys*, *Myiopsitta luchsi*). The remaining species (*Thectocercus acuticaudatus*, *Pyrrhura molinae, Psittacara mitratus*, *Psilopsiagon aymara*, *Brotogeris chiriri*, *Amazona aestiva*) are also present year-round but show a much wider distribution throughout several neotropical ecosystems[49,53]. Two other parrot species not breeding in the dry forest (*Pionus maximiliani* and *Psittacara leucopthalmus*) were rarely observed at the eastern border of the study area[34] moving from adjacent humid biomes[49,53], and thus were not considered in this study. Other large-bodied recognized frugivores able to ingest or transport relatively large (>5 mm diameter) seeds by other methods (for example, monkeys, trogons, toucans and cotingas) were not present in the ecosystem, while facultative frugivores (such as the greater grison, *Galictis vittata* and crab-eating fox, *Cerdocyon thous*) and scatter-hoarding rodents (such as the common yellow-toothed cavy, *Galea musteloides*) occurred at comparatively much lower abundances[54].

Field sampling. Fieldwork was conducted during eight surveys in 2011–2013, four in the rainy season and four in the dry season. All collected data was observational and fieldwork was conducted in public-free areas, so it did not require permits. Parrots were located during roadside surveys, driving slowly (20–40 km h^{-1}) over 6,823 km of unpaved roads, involving 153 days of fieldwork by 2–5 people (401 person-days overall). When parrots were located, stops were made to record their numbers and foraging behaviour. We recorded foraging activities of ~1,350 flocks comprising >22,000 individuals, and noted the consumed part of each plant species exploited (>100 species of 38 families) (details previously published[34]).

We conducted vegetation surveys throughout the study area to categorize the relative abundance (dominance) of the woody plants by means of an index with three levels, defined as: (1) relict presence implying very low dominance; (2) a medium dominance derived from local distribution and abundance; and (3) a high dominance derived from an overall high abundance and widespread distribution. We categorized plants exploited by parrots into four major growth forms: trees, shrubs, climbers and herbs (see ref. [34] for details and additional variables), and as endemic or not endemic in the studied biome according to the literature[47,51,52].

Mutualistic and antagonistic interactions. We considered that a parrot–plant interaction occurred when the parrot was observed eating any part of the given plant species, including their pests[34], with the help of binoculars and telescopes (10× and 20–60× magnification, respectively) to avoid disturbing their foraging behaviours. During foraging observations, we recorded the consumed part of each plant species, in the case of fruits noting whether parrots consumed pulp of ripe or unripe fruits and/or the seeds, and whether they drop entire fruits or seeds beneath the food plant or eventually dispersed the fruit (Fig. 5a–f). Whenever we had doubts about the plant species or the parts of the plant eaten by parrots (such as the seeds or pulp of a given fruit), after conducting the foraging observations we walked underneath the plant in which the observation was made in order to confirm which parts of the plant were the parrots eating and wasting (Fig. 5g). In the case of noxious invertebrates, we collected samples to identify them up to the family level.

During observations, we noted that a single foraging flock of parrots may interact in different ways with a single food plant. For example, in many instances some individuals consumed seeds (predation), some others dropped entire fruits or seeds (facilitating secondary dispersal), and others flew carrying fruits with the beak (primary dispersal). These different antagonistic and mutualistic interactions were simultaneously performed by different individuals or sequentially by the same individual. Moreover, the dense canopy of trees often made it difficult to simultaneously observe the foraging behaviour of all flocking individuals. Therefore, we could not accurately determine the number of parrot individuals involved in each plant–parrot interaction. We thus relied on qualitative rather than on quantitative data for network structure analyses: after pooling all foraging observations of a given parrot species on a given plant species, we recorded whether they included mutualistic interactions, antagonistic interactions, or both. We then considered the presence/absence of each interaction type (antagonistic and mutualistic) for each interacting parrot–plant species.

Briefly, antagonistic interactions included the consumption and destruction of flowers, seeds, leaves, bark and other plant structures, while beneficial interactions included feeding on nectar and pollen (thus contributing to pollination), dispersing seeds, facilitating mature seeds for secondary dispersers (such as birds, small mammals and ants), and feeding on noxious organisms of their food plants[34]. Regarding seed dispersal, we only considered parrots departing from food plants with entire ripe fruits or mature seeds in the beak and subsequently dropping the item in flight or at another distant perch (external dispersal or stomatochory). Although we also observed parrots eating pulp of some fruits containing tiny seeds (Fig. 5b) that could be dispersed after gut passage (internal dispersal or endozoochory), we did not consider this potential mutualistic interaction since we did not search for the presence of viable seeds in parrot faeces. However, as previously shown, some plant species dispersed through endozoochory (as seeds) can also be dispersed through stomatochory (as ripe fruits) by parrots[35].

The qualitative information described above on plant–parrot interactions was used to build a multilayer network, including both antagonistic and mutualistic interactions, and two sub-networks, selecting only the interactions in which at least one of the ecological functions reported was beneficial (mutualistic sub-network) or detrimental (antagonistic sub-network), respectively (Fig. 1). This implies that interactions in which a parrot species provides both beneficial and detrimental ecological functions to a plant species will be represented in both sub-networks.

Analyses summary. First, we used presence/absence data of each interaction type to assess nestedness and modularity in the multilayer network and mutualistic and antagonistic sub-networks, as the information regarding the exact number of parrot individuals performing each interaction type is lacking. Second, we explored the plant characteristics that explain plant–parrot associations, by testing which traits are shared across plant species within modules. Finally, we used a simulation approach to assess whether considering or ignoring the mutualism–antagonism continuum in plant–parrot interactions can result in different estimates of the parrot community robustness to plant species loss. The simulations comprised two phases, and in both we used quantitative data on the number of individual parrots observed interacting with a given plant species (without discerning the type of interaction). In the first phase, we propose three scenarios: (1) plant species get extinct randomly (our reference scenario); and in the other two scenarios, the order in which plant species are extinct is determined by the abundance of antagonistic interactions that parrots exert on each plant species, distinguishing between (2) when all plant–parrot interactions are considered antagonistic, as traditionally thought, and (3) when interactions are considered as mutualistic or antagonistic based on specific behaviour (the mutualism–antagonism continuum is considered). In the second phase, we assessed whether differences in the robustness can be attributed to the nestedness of the mutualistic sub-network, and modularity of the antagonistic sub-network. To do so, we randomized our multilayer network and selected those randomizations in which the nestedness of the mutualistic sub-network and modularity of the antagonistic sub-network were simultaneously high, medium and low. Then, we used the selected matrices to perform the same simulations explained in the first phase, expecting that if these network properties influence the differences in the parrot community robustness, the values of those

Fig. 5 | Pictures of various antagonistic and mutualistic interactions recorded during fieldwork. a, *Thectocercus acuticaudatus* predating a seed. **b**, *Myiopsitta luchsi* feeding on a fleshy fruit. **c**, *Psittacara mitratus* feeding on sprouts of leaves. **d**, *Brotogeris chiriri* feeding on flowers. **e**, *Myiopsitta luchsi* dropping a fruit containing an intact seed, thus facilitating secondary dispersal by terrestrial fauna. **f**, *Ara rubrogenys* dispersing an ear of corn (although this cultivated plant was not considered in this study, it illustrates the large size of fruits that can be dispersed by parrots). **g**, We recovered the food wasted by parrots from beneath the food plants, to confirm whether they were consuming ripe or unripe fruits, pulp and/or seeds, and whether they dropped intact ripe fruits or seeds that could be available for secondary dispersers. Pictures show the detail with which foraging parrots were observed with binoculars (×10 magnification), while insets show details observed by using telescopes (×20–60 magnification). Credit: **a**–**e**,**g**, M. de la Riva, CSIC; **f**, J. L. Tella, CSIC.

estimates should change gradually across the randomizations in which those network properties were high, medium and low. This will tease apart whether the differences in the parrot community robustness are only due to the frequency of antagonistic interactions on each plant species, or instead, the structure of the two sub-networks also contributes to explaining those differences.

Nestedness. We estimated nestedness using two metrics: temperature index[55] and nested overlap and decreasing fill (NODF)[56]. To assess the significance of observed metrics, we randomized the interaction matrices 1,000 times using the null model II[22] and obtain the frequency distribution of the metrics expected by chance, which we compared with the values observed. Null model II constrains the dimensions of the matrix and a given probability of each cell of being occupied. This probability is the arithmetic mean of the connection probability between the focal plant and parrot species. Therefore, only asymmetric distribution of interactions can result in deviations from the null model[57]. Both nested overlap and decreasing fill values depend on the dimensions of the interaction matrix, and therefore, a relative nestedness measure is necessary for comparison among networks. We calculated the relative NODF as $(\mathrm{NODF}_{\mathrm{observed}} - \mathrm{NODF}_{\mathrm{null\ model}})/\mathrm{NODF}_{\mathrm{null\ model}}$, where $\mathrm{NODF}_{\mathrm{observed}}$ is the nestedness of the observed matrix, and $\mathrm{NODF}_{\mathrm{null\ model}}$ is the average nestedness of the 1,000 random replicates. The described approach has been previously used in other studies to characterize network nestedness[20]. Nestedness metrics are influenced by the order of rows and columns in the matrix. To make our results comparable with previous studies, rows and columns were ordered by interaction abundance before the calculation of nestedness with the software ANINHADO[58].
We evaluated the contribution of beneficial and antagonistic interactions to the multilayer network nestedness in two ways. First, we separately calculated the nestedness of the mutualistic and antagonistic sub-networks, and compared them. Secondly, following previous work[59], we calculated the contribution of each interaction to departure from perfect nestedness (that is, the proportional deduction from NODF; the lower the value, the higher the contribution to nestedness), and then used a Student's *t*-test for assessing whether mutualistic interactions show a significantly lower deduction from NODF than antagonistic interactions.

Modularity. To assess the contribution of mutualistic and antagonistic interactions to modularity, we calculated and compared modularity in the multilayer network and in the mutualistic and antagonistic sub-networks. We calculated modularity based on presence/absence data. We used the simulated annealing method to calculate modularity, which has been suggested to be the most appropriate choice for small networks like ours (116 nodes), since it gives the more accurate partitions[60–62]. Although module identification using simulated annealing is possible for bipartite networks[63], the convenience of using algorithms for unipartite or bipartite networks depends on the question addressed, as they give slightly different information. In the later, the algorithm identifies groups of nodes with similar outgoing connections and groups of nodes with similar incoming connections (groups of plants (or parrots) that interact with the same parrots (or plants))[63]. Meanwhile, the identification of modules for unipartite networks is more direct, as it is based on selecting groups of species that show more interactions between them than across modules. In this case, although a node could be potentially connected to every other node in a unipartite framework, the realized interactions used as our input only include interactions across guilds (and not within plants or parrots). Therefore, this approximation has been previously suggested as a better option than the bipartite approach, even for plant–animal networks, if the question approached implies finding highly connected groups of plants and animals[23,64]. Thus, we used a simulated annealing optimization approach for unipartite networks to detect the groups of species (combining plant and parrots) that maximized modularity (the proportion of links within versus between modules)[61,65]. We used the following parameters for the simulated annealing search: number of randomizations = 100, iteration factor = 1 and cooling factor = 0.99. Considering the heuristic nature of the process, we performed 10 runs of the algorithm to assess the variation in the results. When the modularity was significant, the variation in the estimate of modularity was negligible (range: 0.39 to 0.41; average SE < 0.002). For further analyses, we used the modularity associated with the module species composition that was exactly the same across the 10 runs, and for which this occurred most frequently across the 100 runs. We tested for modularity significance by comparing the observed modularity with a null model based on 100 random graphs[62]. We calculated modularity and its significance using the software Netcarto[61,62,65].

Plant traits determining plant–parrot associations. We assessed the plant species' traits explaining the associations between plants and parrots by exploring which traits were shared across plant species within each module. We characterized plant species based on ecological factors related to plant functional traits (growth form: climbers, herbs, shrubs and trees), plant dominance in the community (low, medium or high), and endemicity (endemic to the studied biome or not). We used generalized linear models (GLMs) with a binomial distribution to search for ecological factors explaining the probability of plant species membership to each of the modules. We built three models per module with each factor as the only explanatory variable, and used chi-square tests to assess their significance by comparing them with a model including only an intercept (null). We then extracted the odds ratio for each level of the factor and their 95% CIs as an estimate of the magnitude of the effect[66]. When the odds ratio estimate is equal to 1, there is an equal probability of being included in a given module (the parrots in the module prefer plants with that given trait (>1)) or not (avoid them (<1)). The effect of a given trait significantly affects the membership of a species within a module when 1 is not within the 95% CI of the odds ratio estimate. Analyses were performed using the 'base' package in the software R version 3.2.2[67].

Parrot community robustness to plant species loss. We performed co-extinction simulations to estimate the robustness of the parrot community to the removal of the plant species on which they feed. In co-extinction simulations based on presence/absence data, a species is considered extinct when all its trophic resources have been removed from the network. However, this can lead to an underestimation of co-extinction rates, as species can become extinct below a critical threshold of availability of its trophic resources[68]. We therefore used quantitative networks, considering the individuals of each parrot species feeding on each plant species as a proxy for interaction frequency. To simulate a quantitative scenario, we calculated the dependence d_{ij} of the parrot species *i* on the plant species *j* (the proportion of the total number of individuals of species *i* feeding on the plant species *j*)[69]. Following previous work[70], we considered a parrot species extinct when the sum of its dependences across the remaining plant species was lower than a particular threshold, ranging from 0 (all its trophic resources are extinct, that is, presence/absence interaction networks) to 0.8 (when the remaining resources hold less than 80% of parrot individuals). Given that the patterns obtained were similar across all thresholds and stronger in more sensible scenarios (Supplementary Fig. 1), only those using a representative threshold of 0.2 are shown.

All the simulations were done in the multilayer network. We removed one plant species at a time, pursuing the following three aims linked with different removal criteria: (1) to obtain a null reference regarding the network robustness, (2) to assess the network robustness ignoring that some interactions can be mutualistic, and (3) to assess the network robustness considering that some interactions can be mutualistic, antagonistic, or both (Fig. 1). Each aim was respectively pursued by (1) randomly selecting the plant species to be removed next, (2) considering all interactions as antagonistic, removing plant species with increasing antagonistic interactions (weighted by the number of parrot individuals), and (3) considering that interactions can be mutualistic, antagonistic or both by multiplying its number of parrot individuals by 1, −1 or 0.5 respectively, summing up, and removing the plant species with the lowest values first (increasing antagonistic interactions).
As with any theoretical exercise, our approach makes strong assumptions to provide a theoretical scenario in which the combined effects of mutualistic and antagonistic sub-networks on community robustness can be explored.
This approach assumes that the plant species that will first become extinct are those on which parrots exert more negative effects, and that a parrot species will disappear when the plant species on which it feeds had become extinct.
This is an oversimplification of the ecological system, as parrots might change their interaction patterns with plants (rewiring) depending on the temporal variation of the relative abundances of plant species, and the persistence of plants can also be regulated by other factors besides their interactions with parrots. However, our approach does not aim to represent realistically and accurately co-extinction cascades; instead, it should be interpreted as an exercise to assess whether, other things being equal, the estimation of community robustness differs when the mutualism–antagonism continuum is considered versus ignored.

To specifically assess the effect of the structure of mutualistic and antagonistic interactions, we generated 100 matrices randomizing the weights assigned to each interaction within the realized interactions, thus maintaining the multilayer network structure (the same realized interactions). We then selected matrices resulting in low, medium and high values of both nestedness of mutualistic interactions and modularity of antagonistic interactions. To select the matrices from the 100 randomizations we repeated the analyses previously described for the observed matrix, extracting the value of nestedness of mutualistic interactions and modularity of antagonistic interactions in each of the 100 randomized matrices. Finally, we selected two matrices in which both nestedness and modularity values were within the first quartile of the 100 randomizations (low), within the second and third (medium), and within the forth quantile (high).

Each simulation was repeated 100 times to obtain the 95% CI of the number of parrot species lost after each plant species removal. In most of the simulations, except for that involving random removal of the plant species (removal criteria), the order in which plant species were removed (that is, plants with increasing antagonistic interactions) did not usually change across the 100 repetitions, thus resulting in a constant value (and 0 CI) across the 100 repetitions.

Data availability. All data generated or analysed during this study are included in the Supplementary Information.

Received: 17 July 2016; Accepted: 16 August 2017;
[redacted]

References

1. Bronstein, J. L. Conditional outcomes in mutualistic interactions. *Trends Ecol. Evol.* **9**, 214–217 (1994).
2. Thompson, J. N. *The Coevolutionary Process* (Univ. Chicago Press, Chicago, 1994).
3. Thompson, J. N. *The Geographic Mosaic of Coevolution* (Univ. Chicago Press, Chicago, 2005).
4. Bascompte, J. & Jordano, P. *Mutualistic Networks* (Princeton Univ. Press, Princeton, 2014).
5. Shantz, A., Lemoine, N. & Burkepile, D. Nutrient loading alters the performance of key nutrient exchange mutualisms. *Ecol. Lett.* **19**, 20–28 (2016).
6. Morris, W. F. et al. Direct and interactive effects of enemies and mutualists on plant performance: a meta-analysis. *Ecology* **88**, 1021–1029 (2007).
7. Larimer, A. L., Bever, J. D. & Clay, K. The interactive effects of plant microbial symbionts: a review and meta-analysis. *Symbiosis* **51**, 139–148 (2010).
8. Chamberlain, S. A., Bronstein, J. L. & Rudgers, J. A. How context dependent are species interactions? *Ecol. Lett.* **17**, 881–890 (2014).
9. Blanco, G., Tella, J. L., Potti, J. & Baz, A. Feather mites on birds: costs of parasitism or conditional outcomes? *J. Avian Biol.* **32**, 271–274 (2001).
10. Maruyama, P. K., Vizentin-Bugoni, J., Dalsgaard, B., Sazima, I. & Sazima, M. Nectar robbery by a hermit hummingbird: association to floral phenotype and its influence on flowers and network structure. *Oecologia* **178**, 783–793 (2015).
11. Mougi, A. & Kondoh, M. Diversity of interaction types and ecological community stability. *Science* **337**, 349–351 (2012).
12. Yoshikawa, T. & Isagi, Y. Determination of temperate bird-flower interactions as entangled mutualistic and antagonistic sub-networks: characterization at the network and species levels. *J. Anim. Ecol.* **83**, 651–660 (2014).
13. Fleming, T. H. & Kress, W. J. *The Ornaments of Life: Coevolution and Conservation in the Tropics* (Univ. Chicago Press, Chicago, 2013).
14. Heleno, R. H., Olesen, J. M., Nogales, M., Vargas, P. & Traveset, A. Seed dispersal networks in the Galápagos and the consequences of alien plant invasions. *Proc. R. Soc. B* **280**, 20122112 (2013).
15. Bronstein, J. L. in *Insect–Plant Interactions* Vol. IV (ed. Bernays, E. A.) 1–44 (CRC Press, Boca Raton, 1992).
16. Norconk, M. A., Grafton, B. W. & Conklin-Brittain, N. L. Seed dispersal by neotropical seed predators. *Am. J. Primatol.* **45**, 103–126 (1998).
17. Vander Wall, S. B., Kuhn, K. M. & Beck, M. J. Seed removal, seed predation, and secondary dispersal. *Ecology* **86**, 801–806 (2005).
18. Pilosof, S., Porter, M. A., Pascual, M. & Kéfi, S. The multilayer nature of ecological networks. *Nat. Ecol. Evol.* **1**, 0101 (2017).
19. Bascompte, J. & Jordano, P. Plant-animal mutualistic networks: the architecture of biodiversity. *Annu. Rev. Ecol. Evol. S.* **38**, 567–593 (2007).
20. Montesinos-Navarro, A., Segarra-Moragues, J. G., Valiente-Banuet, A. & Verdú, M. The network structure of plant-arbuscular mycorrhizal fungi. *New Phytol.* **194**, 536–547 (2012).
21. Donatti, C. I. et al. Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. *Ecol. Lett.* **14**, 773–781 (2011).
22. Bascompte, J., Jordano, P., Melián, C. J. & Olesen, J. M. The nested assembly of plant-animal mutualistic networks. *Proc. Natl Acad. Sci. USA* **100**, 9383–9387 (2003).
23. Olesen, J. M., Bascompte, J., Dupont, Y. L. & Jordano, P. The modularity of pollination networks. *Proc. Natl Acad. Sci. USA* **104**, 19891–19896 (2007).
24. Sinclair, A., Mduma, S. & Brashares, J. S. Patterns of predation in a diverse predator-prey system. *Nature* **425**, 288–290 (2003).
25. Lewinsohn, T. M., Inácio Prado, P., Jordano, P., Bascompte, J. & Olesen, J. M. Structure in plant–animal interaction assemblages. *Oikos* **113**, 174–184 (2006).
26. Memmott, J., Waser, N. M. & Price, M. V. Tolerance of pollination networks to species extinctions. *Proc. R. Soc. Lond. B* **271**, 2605–2611 (2004).
27. Burgos, E. et al. Why nestedness in mutualistic networks? *J. Theor. Biol.* **249**, 307–313 (2007).
28. Okuyama, T. & Holland, J. N. Network structural properties mediate the stability of mutualistic communities. *Ecol. Lett.* **11**, 208–216 (2008).
29. Krause, A. E., Frank, K. A., Mason, D. M., Ulanowicz, R. E. & Taylor, W. W. Compartments revealed in food-web structure. *Nature* **426**, 282–285 (2003).
30. Teng, J. & McCann, K. S. Dynamics of compartmented and reticulate food webs in relation to energetic flows. *Am. Nat.* **164**, 85–100 (2004).
31. Thébault, E. & Fontaine, C. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* **329**, 853–856 (2010).
32. Genrich, C. M., Mello, M. A., Silveira, F. A., Bronstein, J. L. & Paglia, A. P. Duality of interaction outcomes in a plant-frugivore multilayer network. *Oikos* **126**, 361–368 (2017).
33. Young, L. M., Kelly, D. & Nelson, X. J. Alpine flora may depend on declining frugivorous parrot for seed dispersal. *Biol. Conserv.* **147**, 133–142 (2012).
34. Blanco, G., Hiraldo, F., Rojas, A., Dénes, F. V. & Tella, J. L. Parrots as key multilinkers in ecosystem structure and functioning. *Ecol. Evol.* **5**, 4141–4160 (2015).
35. Blanco, G. et al. Internal seed dispersal by parrots: an overview of a neglected mutualism. *PeerJ* **4**, e1688 (2016).
36. Tella, J. L. et al. Parrots as overlooked seed dispersers. *Front. Ecol. Environ.* **13**, 338–339 (2015).
37. Baños-Villalba, A. et al. Seed dispersal by macaws shapes the landscape of an Amazonian ecosystem. *Sci. Rep.* **7**, 7373 (2017).
38. Fontaine, C. et al. The ecological and evolutionary implications of merging different types of networks. *Ecol. Lett.* **14**, 1170–1181 (2011).
39. Johnson, N., Graham, J. & Smith, F. Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytol.* **135**, 575–585 (1997).
40. Hoover, S. E. et al. Warming, CO_2, and nitrogen deposition interactively affect a plant-pollinator mutualism. *Ecol. Lett.* **15**, 227–234 (2012).
41. Koide, R. The nature of growth depressions in sunflower caused by vesicular-arbuscular mycorrhizal infection. *New Phytol.* **99**, 449–462 (1985).
42. Ragusa-Netto, J. & Fecchio, A. Plant food resources and the diet of a parrot community in a gallery forest of the southern Pantanal (Brazil). *Braz. J. Biol.* **66**, 1021–32 (2006).
43. Gleiser, G. et al. The southernmost parakeet might be enhancing pollination of a dioecious ancient conifer. *Ecology* http://dx.doi.org/10.1002/ecy.1938 (2017).
44. Lee, A. T. et al. Diet and geophagy across a western Amazonian parrot assemblage. *Biotropica* **46**, 322–330 (2014).
45. Tella, J. L. et al. Endangered plant-parrot mutualisms: seed tolerance to predation makes parrots pervasive dispersers of the Parana pine. *Sci. Rep.* **6**, 31709 (2016).
46. Toft, C. A. & Wright, T. F. *Parrots of the Wild: A Natural History of the World's Most Captivating Birds* (Univ. California Press, Berkeley, 2015).
47. Navarro, G. & Maldonado, M. *Geografía ecológica de Bolivia: Vegetación y ambientes acuáticos* (Centro de Ecología Simón I. Patiño, Cochabamba, 2002).
48. Tella, J. L., Rojas, A., Carrete, M. & Hiraldo, F. Simple assessments of age and spatial population structure can aid conservation of poorly known species. *Biol. Conserv.* **167**, 425–434 (2013).
49. Forshaw, J. M. *Parrots of the World: An Identification Guide* (Princeton Univ. Press, Princeton, 2006).
50. *The Plant List Version 1.1*. (accessed 1 January 2013); http://www.theplantlist.org/
51. López, R. P. Diversidad florística y endemismo de los valles secos bolivianos. *Ecol. Bolivia* **38**, 27–60 (2003).
52. Atahuachi-Burgos, M. et al. *La guía"Darwin" de las flores de los valles bolivianos* (Darwin Initiative, Le Paz, 2005).
53. Juniper, A. & Parr, M. *Parrots: A Guide to the Parrots of the World* (Christopher Helm, London, 2010).
54. Anderson, S. H., Kelly, D., Ladley, J. J., Molloy, S. & Terry, J. Cascading effects of bird functional extinction reduce pollination and plant density. *Science* **331**, 1068–1071 (2011).
55. Atmar, W. & Patterson, B. D. The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* **96**, 373–382 (1993).
56. Almeida-Neto, M., Guimaraes, P., Guimarães, P. R., Loyola, R. D. & Ulrich, W. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* **117**, 1227–1239 (2008).
57. Vacher, C., Piou, D. & Desprez-Loustau, M.-L. Architecture of an antagonistic tree/fungus network: the asymmetric influence of past evolutionary history. *PLoS ONE* **3**, e1740 (2008).
58. Guimarães, P. R. & Guimarães, P. Improving the analyses of nestedness for large sets of matrices. *Environ. Modell. Softw.* **21**, 1512–1513 (2006).
59. Joppa, L. N. & Williams, R. The influence of single elements on nested community structure. *Methods Ecol. Evol.* **2**, 541–549 (2011).
60. Danon, L., Diaz-Guilera, A., Duch, J. & Arenas, A. Comparing community structure identification. *J. Stat. Mech. Theory Exp.* **2005**, P09008 (2005).
61. Guimerà, R. & Amaral, L. A. N. Cartography of complex networks: modules and universal roles. *J. Stat. Mech. Theory Exp.* **2005**, P02001 (2005).
62. Guimerà, R., Sales-Pardo, M. & Amaral, L. A. N. Modularity from fluctuations in random graphs and complex networks. *Phys. Rev. E* **70**, 025101 (2004).
63. Guimerà, R., Sales-Pardo, M. & Amaral, L. A. N. Module identification in bipartite and directed networks. *Phys. Rev. E* **76**, 036102 (2007).
64. Fortuna, M. A. et al. Nestedness versus modularity in ecological networks: two sides of the same coin? *J. Anim. Ecol.* **79**, 811–817 (2010).
65. Guimerà, R. & Amaral, L. A. N. Functional cartography of complex metabolic networks. *Nature* **433**, 895–900 (2005).
66. Nakagawa, S. & Cuthill, I. C. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol. Rev.* **82**, 591–605 (2007).
67. R Core Team *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna, 2014).

68. Amarasekare, P. Spatial dynamics of mutualistic interactions. *J. Anim. Ecol.* **73**, 128–142 (2004).
69. Bascompte, J., Jordano, P. & Olesen, J. M. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* **312**, 431–433 (2006).
70. Valiente-Banuet, A. & Verdú, M. Human impacts on multiple ecological networks act synergistically to drive ecosystem collapse. *Front. Ecol. Environ.* **11**, 408–413 (2013).

Acknowledgements

We thank M. de la Riva, A. Rojas, E. Pacifico, H. Garrido, A. Requejo, I. Vera, R. Rojas, J. Paca, G. Flores, S. Huici, E. Yucra and D. Alberto for fieldwork assistance, and A. Toledo for making the parrot drawings. M. de la Riva gave permission to publish his photographs in this article. M. Verdú greatly helped to improve the manuscript. Funding was provided by Zoo de Barcelona and Biorena (January 2011), Junta de Andalucía (PAI RNM107 to J.L.T. and F.H., April–September 2011), Fundación Biodiversidad (2012–2013), and a Severo Ochoa 'microproyecto' award (to F.H.). A.M.-N. was supported by a Juan de la Cierva-Incorporación postdoctoral contract from the Spanish Ministerio de Economía y Competitividad (IJCI-2015-23498).

Author contributions

G.B., J.L.T., F.H. and A.M.-N. designed the study. G.B., J.L.T. and F.H. compiled the data, A.M.-N. performed the analyses, G.B. and A.M.N. wrote the first draft of the manuscript and all the authors contributed substantially to improving the manuscript.

Competing interests

The authors have no competing financial interests.

Additional information

Supplementary information is available for this paper at doi:10.1038/s41559-017-0320-6.

Reprints and permissions information is available at www.nature.com/reprints.

Correspondence and requests for materials should be addressed to A.M.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.