

RESEARCH ARTICLE

Drivers and consequences of structure in plant–lemur ecological networks

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Handling Editor: Rafael Raimundo**Abstract**

1. Species interactions shape the diversity and resilience of ecological networks. Plant and animal traits, as well as phylogeny, affect interaction likelihood, driving variation in network structure and tolerance to disturbance.
2. We investigated how traits and phylogenetic effects influenced network-wide interaction probabilities and examined the consequences of extinction on the structure and robustness of ecological networks.
3. We combined both mutualistic and antagonistic interactions of animals (55 species, Infraorder Lemuriformes, Order Primates) and their food plants (590 genera) throughout Madagascar to generate ecological networks. We tested the effects of both lemur and plant traits, biogeographic factors and phylogenetic relatedness on interaction probability in these networks using exponential random graph models. Next, we simulated animal and plant extinction to analyse the effects of extinction on network structure (connectance, nestedness and modularity) and robustness for mutualistic, antagonistic and combined plant–animal networks.
4. Both animal and plant traits affected their interaction probabilities. Large, frugivorous lemurs with a short gestation length, occurring in arid habitats, and with a Least Concern threat level had a high interaction probability in the network, given all other variables. Closely related plants were more likely to interact with the same lemur species than distantly related plants, but closely related lemurs were not more likely to interact with the same plant genus. Simulated lemur extinction tended to increase connectance and modularity, but decrease nestedness and robustness, compared to pre-extinction networks. Networks were more tolerant to plant than lemur extinctions.
5. Lemur–plant interactions were highly trait structured and the loss of both lemurs and plants threatened the tolerance of mutualistic, antagonistic and combined networks to future disturbance.

KEYWORDS

dynamics, food webs, Madagascar, plant–seed disperser, robustness, trophic interaction modification

1 | INTRODUCTION

Species interactions such as seed dispersal, pollination, herbivory and parasitism are essential for maintaining ecological and evolutionary processes. Some interactions (e.g. frugivory resulting in seed dispersal, pollination) are mutualistic, whereas herbivory, seed predation and parasitism are examples of antagonistic interactions. Pairwise species interactions often fall between the mutualism–antagonism continuum and are imbedded within complex ecological networks, involving organisms interacting both directly and indirectly. In plant–animal networks, animal foraging traits such as body size, home range size, seed handling ability and diet influence how animals consume plants (Ong et al., 2022; Rumeu et al., 2020; Schleuning et al., 2011). Plant functional traits such as fruit and seed size also influence interactions (Arroyo-Correa et al., 2021). For example, large-seeded plants are more connected to frugivores than small-seeded plants (Li et al., 2020). The effects of morphological traits on interaction probabilities also depend on ecological contexts (e.g. land use) and phylogenetic relatedness (Fuzessy et al., 2022; Segar et al., 2020). Altered habitat can change species compositions and interaction frequencies (Tylianakis & Morris, 2017), adversely affecting ecosystem services such as carbon sequestration and ecotourism (Keyes et al., 2021; Rogers et al., 2021).

Network analysis facilitates understanding the drivers of plant–animal species interactions at multiple scales, from individuals to populations, communities and ecosystems (Guimarães, 2020). Plant–animal networks are bipartite—consisting of two trophic levels, where interactions (edges) are possible between, but not among, trophic levels. Exponential random graph models (ERGMs) allow us to identify the traits driving global network structure, an advantage over common methods that analyse traits in relation to a single aspect of network structure (e.g. modularity). ERGMs can infer interaction probabilities by simultaneously testing structural and node-level parameters as covariates (Handcock et al., 2020; Hunter et al., 2008). Node-level parameters can include attributes (e.g. traits) and/or dyadic interactions (e.g. phylogenetic distance). ERGMs produce non-biased parameter coefficient estimates when the data are not independent by using random graphs as null models, an improvement over more standard regression approaches. Although widely used in social network analyses, ERGMs have only recently been applied to ecological networks (e.g. Arroyo-Correa et al., 2021; Fuzessy et al., 2022; Tonos et al., 2021). In this study, we extend previous ecological applications of ERGMs that focused on one trophic level, jointly analysing attributes of both trophic levels and incorporating phylogenetic effects to improve our understanding of plant–animal interactions in complex networks.

Plant–animal community tolerance to disturbance depends on network structural characteristics. Here, we focus on three characteristics related to community stability and composition, which are less biased by incomplete sampling than binary metrics (Vizentin-Bugoni et al., 2016): connectance, nestedness and modularity. Connectance, the proportion of observed interactions among potential interactions, is related to community response to environmental

changes such as habitat loss (Fortuna & Bascompte, 2006). The lower connectance typical of disturbed networks can provide robustness to secondary extinctions (Vanbergen et al., 2017; Verdú & Valiente-Banuet, 2008). High modularity, where organisms are more likely to interact with others in their same module than those in other modules, can also stabilize ecological networks (Grilli et al., 2016). The highly nested nature of plant–animal mutualistic networks, whereby the diets of specialists are a subset of generalists' diets, may confer tolerance and facilitate long-term species coexistence (Aizen et al., 2012; Tylianakis et al., 2010). While nestedness may maintain biodiversity and structural stability in mutualistic networks (Bastolla et al., 2009; Rohr et al., 2014; Thébault & Fontaine, 2010), increased nestedness has also been associated with decreased stability in mutualistic networks (Staniczenko et al., 2013; Suweis et al., 2013). Furthermore, unlike independent structural parameters, the number of species interactions determines nestedness in mutualistic systems (Payrató-Borràs et al., 2019). Nevertheless, nestedness is widely related to robustness to disturbance in ecological networks (Mariani et al., 2019).

The effects of network structure on tolerance vary based on network type. Mutualistic bipartite networks consistently demonstrate low connectance (Escribano-Avila et al., 2018) but high modularity and nestedness (Bascompte & Jordano, 2014), whereas antagonistic plant–animal networks tend to be more modular, but less nested (Carretero et al., 2018). High connectance promotes community tolerance in mutualistic plant–animal networks but low connectance confers tolerance in antagonistic networks (Thébault & Fontaine, 2010). Compared to isolated network types, modularity and nestedness have weaker effects on tolerance to perturbations for combined networks, which merge mutualisms and antagonisms in a single framework (Sauve et al., 2014). Furthermore, incorporating the mutualism–antagonism continuum in network analyses increases robustness to species loss (Montesinos-Navarro et al., 2017; Mougi & Kondoh, 2014). Examining the structure of all three network types is important for understanding effects of disturbance on plant and animal communities, especially because animals can interact both mutualistically and antagonistically with the same plant species.

Investigating tolerance to disturbed interactions is critical given global change, which is shifting the synchrony of species interactions, changing ecosystem structure and function (Kharouba et al., 2018; Rogers et al., 2021). For example, disrupting seed dispersal mutualisms may alter forest structure, cause evolutionary cascades in traits and reduce forest carbon storage (Dirzo et al., 2014). Perturbations to interaction networks are particularly concerning for tropical forests which rely heavily on frugivore-mediated seed dispersal and are threatened by habitat degradation, hunting and wildlife trade (Giam, 2017; Rogers et al., 2021; Symes et al., 2018). Understanding of altered interactions is limited because ecological network studies have primarily been conducted in temperate regions and tropical South America (Vizentin-Bugoni et al., 2018); only 9% of tropical frugivore network analyses have been conducted in Africa (Escribano-Avila et al., 2018).

Disturbed interactions are particularly concerning in Madagascar, where anthropogenic pressures threaten 94% of the endemic primates, lemurs (Schwitzer et al., 2014), and 63% of endemic plants (Beech et al., 2021) with extinction. Lemurs—the primary seed dispersers in Madagascar (Razafindratsima, 2014)—have diverse body masses, diets and activity patterns (Herrera, 2017). Through non-random seed dispersal, frugivorous lemurs can spread seeds to favourable microsites and improve plant germination (Razafindratsima, 2014; Razafindratsima & Dunham, 2016). Birds and bats may also disperse seeds on the island, but studies are limited, and only approximately 10% of bird species on Madagascar are frugivorous (del Hoyo et al., 1992; Razafindratsima, 2014). Because of lemurs' critical role in seed dispersal (Albert-Daviaud et al., 2018), local extinction of frugivorous species endangers Madagascar's plants (Albert-Daviaud et al., 2020), 93% of which are endemic (Beech et al., 2021). Lemurs also interact antagonistically with plants by eating their leaves, bark etc. (Steffens, 2020). Many lemurs fluctuate on the mutualism–antagonism continuum, consuming both reproductive and vegetative plant parts. Consequently, understanding the structure of plant–lemur interactions necessitates accounting for mutualisms and antagonisms in a combined framework.

Here, we address a crucial gap in our understanding of animal–plant networks by investigating the drivers and structure of a bipartite ecological network at the national scale. This novel combined network includes both mutualistic (seed dispersal) and antagonistic (herbivorous) interactions. First, we identify the relative effects of traits and phylogeny on network-wide interaction probabilities between lemurs and plants. We predict that a suite of lemur and plant traits, biogeographic factors and phylogenetic effects structure interaction patterns. Second, we assess the effects of simulated extinction on the structure (connectance, nestedness and modularity) and robustness of the mutualistic, antagonistic and combined networks. We expect the extirpation of endangered lemurs and plants from the network to cause decreased connectance, nestedness and robustness to disturbance, but increased modularity.

2 | MATERIALS AND METHODS

2.1 | Data collection

We used plant–lemur interaction data from the *Lemur Food Plant* database (LFP; Steffens, 2020). The LFP consists of 5420 observed interactions between lemur species and their food plants in each study site/forest type, including 56 lemur species and 1026 plant species from 599 genera and 147 families. The LFP only includes consumption interactions, not other interaction types such as lemur-mediated pollination (LFP includes nectivory—1% of observations—but does not specify destructive vs. non-destructive flower consumption—11% of observations). The LFP combined 204 studies focused on animals and with variable methodologies (e.g. observations, captures, faecal analysis), an integrative approach which can improve network analyses (Quintero et al., 2022). We used

interactions between identified lemur species and plant genera for a total of 55 lemur species and 590 plant genera. We analysed plants at the genus level because 42% of plants in the LFP were identified to genus level and trait data are sparse at the species level. We created accumulation curves to evaluate how the number of lemur species, plant genera and unique interactions increased with the number of included studies using the R package *VEGAN* (Oksanen et al., 2019). Although the number of lemur species and plant genera approached an asymptote, the number of interactions did not, indicating interaction incompleteness and warranting careful results interpretation (Figure S1). Nevertheless, the LFP represents the most comprehensive plant–lemur interaction network available in the literature.

We divided the LFP into mutualistic (only fruit consumption; 45 lemur species, 379 plant genera) and antagonistic (consumption of leaves, flowers, bark, exudates and/ or nectar; 50 lemur species, 451 plant genera) interactions (Steffens, 2020). Some records of fruit consumption may result in seed predation rather than dispersal. We excluded seeds (2% of observations) in the mutualistic and antagonistic networks because seed consumption could be seed dispersal or, more likely, seed predation.

We compiled trait and phylogenetic data of lemurs (body size, brain size, home range size, gestation length, fruit in diet, seeds in diet, habitat, geographic area, IUCN threat level, taxonomic group, sampling effort, phylogenetic distance) and plants (fruit width, IUCN threat level, endemism, invasion status, agricultural product, taxonomic group, sampling effort and phylogenetic distance) from the literature (Supporting Information, Table S1 for sources and hypotheses). No ethical review nor permits were necessary to compile the published data used in this paper.

2.2 | Data analysis

2.2.1 | Traits that determine connectivity

We transformed the plant–lemur interaction matrix into a binary (unweighted) bipartite network using the R package *NETWORK* (Butts, 2008, 2020) and assigned node-level attributes (traits) to the lemur species and plant genera. We implemented ERGMs using the R package *ERGM* (Handcock et al., 2020; Hunter et al., 2008) to analyse the effect of nodal and network-level attributes on the probability that a given lemur species consumes a given plant genus. The ERGM formula is:

$$P(Y = y|X) = \exp[\theta Tg(y, X)] / k(\theta).$$

Y is the set of all networks of a trophic level and y is a single observation from that level. The numerator of the model represents a generalized linear model-type association between coefficients and observed values, similar to logistic regression. X is the attribute matrix for both trophic levels, θT is the transpose of the coefficient vector for those statistics and $k(\theta)$ is a normalizing constant with probability distribution summing to 1. The vector of network

statistics, $g(y, X)$, includes parameters for node attributes, 'node factors' and 'node match' for categorical data and 'node covariates' for continuous data. 'Node factors' measure the likelihood of forming any interaction given a certain trait value, whereas 'node matches' measure the homophily effects of categorical data (i.e. edge likelihood based on whether the nodes *share the same factor level*). 'Node factors' indicate within-group preference and 'node matches' indicate transitivity—higher interaction probability within a group but without within-group preference.

We tested the effects of lemur traits, plant traits and both on interaction probability using Markov chain Monte Carlo (MCMC) estimation methods. First, we assigned traits to each lemur and plant node and built models for the full network using only the 13 traits with complete coverage among all lemur species or plant genera (body mass, geographic area, fruit diet, seed diet, habitat type, lemur threat level, lemur taxonomic group, lemur sampling effort, plant taxonomic group, wood density, plant agricultural product, plant invasive status, plant sampling effort). We defined citation count (number of data sources in the LFP mentioning a specific lemur-plant interaction) as sampling effort because the variable sampling methodologies among the LFP sources, a pervasive issue in frugivory studies (Quintero et al., 2022), prevent effort standardization. We included the structural parameters 'edge' (interaction probability compared to the random graph, akin to the intercept in a regression) and 'b2concurrent' (captures some of the variance due to many specialized species, accounting for plants with few interactions). We log-transformed body mass, geographic area, gestation length, home range, brain size and fruit width, and transformed all continuous variables to a z-score so coefficients were comparable among variables with different units of measure.

We compared a suite of lemur trait models treating IUCN level, taxonomic group and habitat as either 'node match' or 'node factor' and designated the best model (using the Akaike information criterion, AIC; moving forward, we used AIC values to identify all best models) as the full model. Next, we used a backwards stepwise approach from the lemur full model to determine the best model. We repeated this process for models with plant traits and models combining both lemur and plant traits, ensuring MCMC convergence for all models. We considered plant taxonomic group as 'node match' due to the high number of factor levels. For each final model (lemur traits, plant traits, both), we determined the Monte Carlo maximum likelihood estimate of parameter coefficients.

Next, we created three network subgraphs (subsets of the network with full trait coverage) by removing nodes with missing lemur (gestation length, home range size, brain size), plant (fruit width, IUCN threat level and endemism status) and both lemur and plant trait values. We included all traits (except phylogenetic distance which cannot be evaluated in this application of bipartite ERGMs) as nodal attributes to identify traits that drive interactions but for which we lack complete data. Again, we built lemur, plant and lemur/plant full ERGMs that included categorical traits as node factors or node matches, selected the best full models and determined best final models. We repeated all bipartite models (with both the full

network and the subgraphs with complete trait coverage) with lemurs at the genus level to assess whether taxonomic resolution drives the relative effect sizes of lemur and plant traits.

To analyse phylogenetic effects, we projected the bipartite network into two unipartite networks—(1) lemur network and (2) plant network—using the R package IGRAPH (Csardi & Nepusz, 2006). As opposed to our bipartite network models which demonstrate the probability of a lemur species consuming a plant genus and vice versa, the unipartite network models demonstrate the probability of (1) a lemur species connecting with another lemur species based on a shared plant food genus (lemur unipartite network; lemur nodes, plant edges), and (2) a plant genus interacting with another plant genus based on a shared lemur consumer (plant unipartite network; plant nodes, lemur edges). We rescaled lemur and plant phylogenetic trees to create a unit tree (maximum distance of 1) using the R package GEIGER (Harmon et al., 2008; Pennell et al., 2014), calculated pairwise phylogenetic distances (separate for lemurs and plants) using the R package APE (Paradis & Schliep, Paradis & Schliep, 2019) and included phylogenetic distance as a dyad-level parameter. We tested separate lemur and plant unipartite ERGMs.

2.2.2 | Simulated extinctions

We calculated connectance, nestedness temperature (0 is perfectly nested, 100 is perfectly non-nested), modularity (applying Newman's modularity measure) and robustness of each network type using the R package BIPARTITE (Dormann et al., 2008; Dormann et al., 2009). Robustness values close to one indicate that node removal does not highly affect the network because of redundant interactions, whereas values close to zero indicate a fragile network with less redundancy. To calculate robustness, we iteratively removed nodes from respective trophic levels and calculated the resulting number of nodes in the other trophic level without remaining interactions. We simulated four extinction scenarios: (1) random; (2) based on degree (number of interactions of any given the network), highest to lowest; (3) degree, lowest to highest; and (4) extinction likelihood. We calculated lemur extinction likelihood using the IUCN threat level combined with geographic area because geographic area strongly predicts mammalian extinction risk (Purvis et al., 2000). For example, in the combined network simulations, we removed the critically Endangered lemur with the smallest geographic range (*Propithecus perrieri*) first and the Least Concern lemur with largest geographic range (*Microcebus murinus*) last. Plant extinction likelihood was defined as IUCN threat level, with nodes removed randomly within these levels (geographic ranges for plants are poorly known).

We generated potential post-extinction networks by simulating removal of Endangered and critically Endangered lemur and plant nodes in the three network types (combined, mutualistic and antagonistic; Figure 1). We removed all Endangered and critically Endangered lemurs (combined: 61.8% of all lemurs; mutualistic: 62.2%; antagonistic: 62.0%) from the network, eliminated isolates and recalculated network level statistics (lemur post-extinction

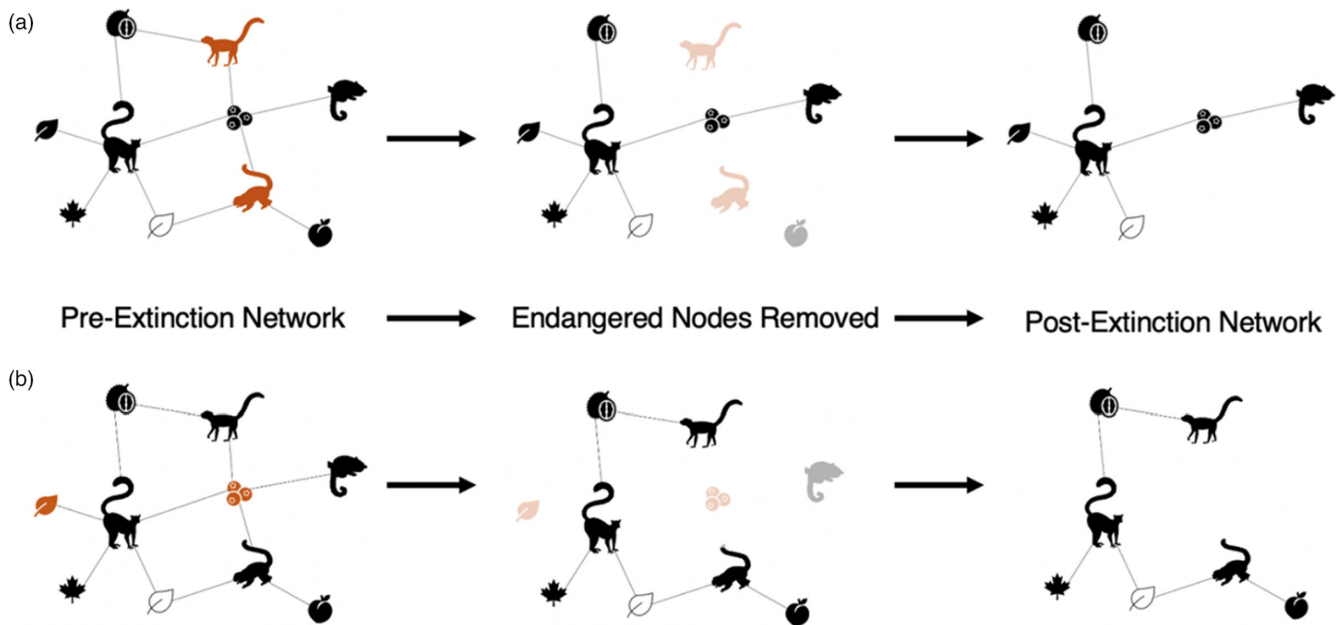


FIGURE 1 Process for generating the potential post-extinction networks for (a) lemurs and (b) plants (conducted for the combined, mutualistic and antagonistic networks). Orange nodes represent Endangered or critically Endangered organisms. Translucent silhouettes indicate isolates removed in the post-extinction network. For the lemur extinction scenarios (a), we identified and removed Endangered and critically Endangered lemurs from the pre-extinction network, resulting in post-extinction networks. Lemur silhouettes from [PhyloPic.org](https://www.phylopic.org/) (credit: Robert Díaz Sibaja, Somkeybjb, Maky, Gabriella Skolar, Rebecca Lewis and unknown artist; <https://creativecommons.org/licenses/by/3.0/>).

network; [Figure 1](#)). We tested for phylogenetic signal in lemur IUCN threat level using 'geiger' (Harmon et al., 2008; Pennell et al., 2014). Because the better model included white noise and not phylogeny, we did not incorporate phylogeny into the simulations. For the plant post-extinction scenarios, we recalculated network statistics after removing all Endangered and critically Endangered plants (combined: 7.6% of all plants; mutualistic: 8.4%; antagonistic: 6.7%; [Figure 1](#)). To compare observed changes in network statistics in the pre-extinction and post-extinction networks, we created a null distribution by randomly removing the *same percentage of nodes* (e.g. 70.9% for combined network lemur extinction) from the network in 100 randomizations and calculated network statistics of each resulting network. To investigate specialization as a potential driver of changes in robustness, we used 'bipartite' (Dormann et al., 2008, 2009) to calculate the average standardized specialization index (d') for lemur species and plant genera in the pre- and post-extinction scenarios for all network types (Strona & Lafferty, 2016a, 2016b).

3 | RESULTS

3.1 | Traits that determine connectivity

Lemurs ranged widely in the number of plant genera with which they interacted (range = 1–207; mean = 47.0; $SD = 45.4$). The most connected lemur species was *Lemur catta*, whereas *Allocebus trichotis*, *Microcebus myoxinus* and *Mirza zaza* were poorly connected. Plants

had lower average degree than lemurs (range = 1–34; mean = 4.4, $SD = 4.9$). *Ficus* spp. was the most connected plant genus.

Including traits from both trophic levels produced better models than only including traits from one level ([Figure 2](#); [Table S2](#)). Our full network model (including all nodes but only traits with full coverage) demonstrated that lemurs that consumed fruit (coef = 1.008, $p < 0.001$) and seeds (coef = 0.514, $p < 0.001$), had large body masses (coef = 0.265, $p = 0.002$) and occupied small geographic areas (coef = -0.191 , $p < 0.001$) interacted with significantly more plant genera than lemurs without those traits ([Figure 2a](#); [Table S2](#)). Compared to lemurs living in arid habitats, lemurs living in wet habitats were less connected (effect = -0.471 , $p < 0.001$). Vulnerable (coef = -1.121 , $p < 0.001$), Endangered (coef = -1.062 , $p < 0.001$) and critically Endangered (coef = -1.071 , $p < 0.001$) lemurs were less connected than Least Concern lemurs. Lemur species in the Lepilemuridae (coef = 1.563, $p < 0.001$) and Lemuridae (effect = 1.517, $p < 0.001$) families were more connected, whereas Daubentoniidae was least connected (base factor). Confamilial plants were more likely to interact with the same lemur species than plants from other families (coef = 0.036, $p < 0.001$; node match), indicating an homophily effect. Our model including a subset of the nodes for which we had complete trait data demonstrated that lemurs with long gestation lengths were less connected than lemurs with short gestation lengths (coef = -1.558 , $p < 0.001$) and that plants with the same IUCN threat level were more likely to interact with the same lemur species than plants with different IUCN threat levels (coef = 0.006, $p = 0.004$; [Figure 2b](#); [Table S3](#)).

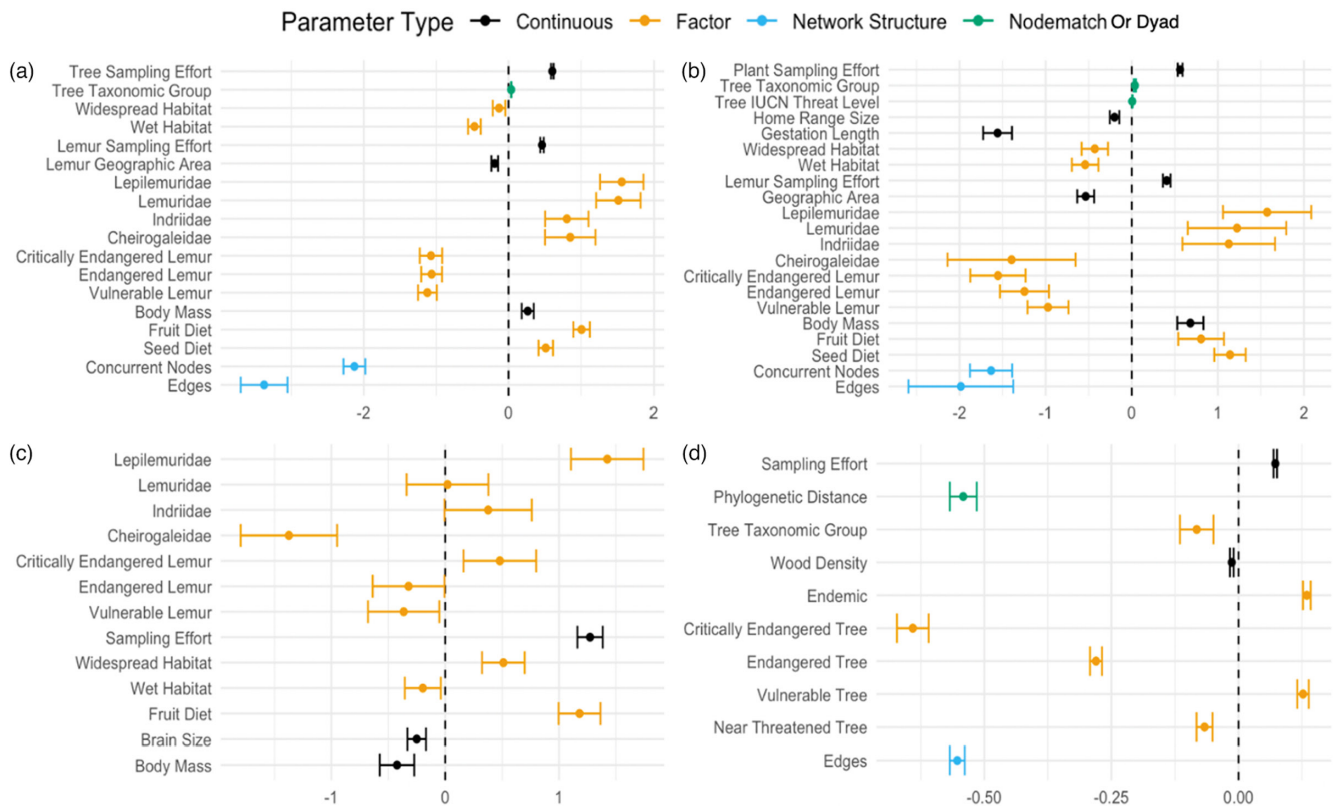


FIGURE 2 ERGM coefficient plots for the (a) full combined bipartite network, including only traits with complete coverage, (b) subgraph of the combined bipartite network, considering all traits, (c) unipartite lemur network and (d) unipartite plant network. Points represent coefficients and error bars represent standard error. Colours correspond to parameter types: Blue = network structure, black = continuous, yellow = factor, green = nodematch or dyad.

Lemur phylogenetic distance was not included in the best unipartite model. However, compared to the base factor Daubentoniidae, lemurs in the family Cheirogaleidae were less likely to share plant food species with other Cheirogaleidae lemurs (coef = -1.373 , $p = 0.001$). Lemurs in Lepilemuridae were more likely to interact with the same plants than lemurs in other families (coef = 1.423 , $p < 0.001$). Lemurs were more likely to share food plants with other lemurs if they had smaller brains (coef = -0.251 , $p = 0.002$) and body masses (coef = -0.423 , $p = 0.005$), ate fruit (coef = 1.180 , $p < 0.001$) and occurred in widespread habitats compared to only arid habitats (coef = 0.511 , $p < 0.006$; [Figure 2c](#); [Table S4](#)). Plants were more likely to share lemur consumers with other plant genera if they were endemic (coef = 0.134 , $p < 0.001$) and if they had lower wood densities (coef = -0.013 , $p < 0.001$). Compared to genera of Least Concern, vulnerable plants were more likely to share lemur consumers (coef = 0.127 , $p < 0.001$), whereas Endangered (coef = 0.280 , $p < 0.001$) and critically Endangered plant genera were less likely (coef = -0.640 , $p < 0.001$). Plant genera with small phylogenetic distances (i.e. closely related) were more likely to interact with the same lemur species than distantly related plant genera (coef = -0.541 , $p < 0.001$; [Figure 2d](#); [Table S5](#)). Given the effect of phylogenetic distance, confamilial plants were slightly less likely to share lemur consumers than plants in different families (coef = -0.082 , $p = 0.013$).

3.2 | Simulated extinctions

Network structural parameters were relatively consistent among the combined, mutualistic and antagonistic pre-extinction networks, but antagonistic networks were more modular and less connected than combined or mutualistic networks, especially after simulated extinction ([Figure 3](#); [Tables S6–S8](#)). All network types were sparse, with connectance values of 0.08 (combined), 0.09 (mutualistic) and 0.06 (antagonistic; [Figure 3a](#); [Tables S6–S8](#)). Compared to the null models of random extinction, connectance and nestedness temperatures were lower in the lemur pre-extinction scenarios for all three network types and higher in the plant post-extinction scenarios for the mutualistic and antagonistic network types ([Figure 3a,b](#); [Tables S6–S8](#)). Modularity significantly increased with lemur extinction in the combined and mutualistic network types ([Figure 3c](#); [Tables S6–S8](#)). Modularity decreased with plant extinction in the antagonistic network.

Networks were more robust to the simulated extinction of plants than lemurs ([Figures 4 and 5](#); [Tables S6–S8](#)). As expected, robustness tended to be lowest when we removed lemurs in order of highest to lowest degree, and highest when we removed lemurs in order of lowest to highest degree. The ‘extinction likelihood’ scenario produced a level of robustness similar to random extinction ([Figure 4](#); [Tables S6–S8](#)). Overall, robustness to lemur extinctions

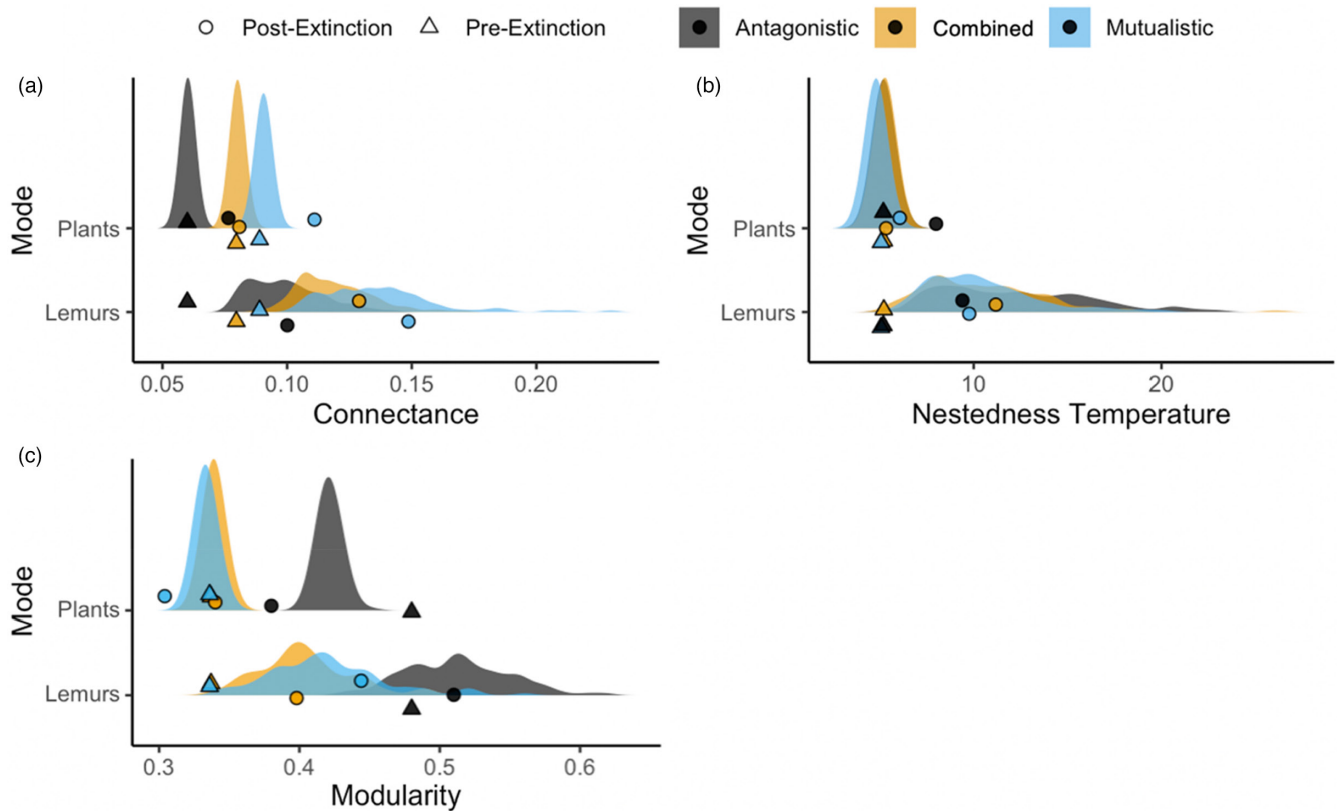


FIGURE 3 Network structural parameters for lemur and plant trophic levels for the combined, mutualistic and antagonistic networks. Points denote structure values in the pre-extinction and post-extinction networks. Density plots demonstrate extinction null models. Points are vertically jittered (height = 0.2) to avoid overlap.

was consistent among network types, but robustness to plant extinction tended to be lower in the mutualistic than the combined and antagonistic networks (Figure 5; Tables S6–S8). For all network types, robustness (random scenario) was higher in the pre-extinction networks than the lemur extinction null model (Figure 5; Tables S6–S8). Robustness in degree high–low extinction scenarios was also higher than in the extinction null models for the combined and mutualistic networks. In the antagonistic network, robustness was only marginally higher in the pre-extinction network than in the lemur null extinction model for the degree low–high scenario. On average, lemurs were less specialized post-extinction ($d_{\text{combined}} = 2.427$, $d_{\text{mutualistic}} = 2.420$, $d_{\text{antagonistic}} = 2.526$) than pre-extinction ($d_{\text{combined}} = 2.529$, $d_{\text{mutualistic}} = 2.600$, $d_{\text{antagonistic}} = 2.820$; Table S11). Plants also tended to be less specialized post-extinction ($d_{\text{combined}} = 1.776$, $d_{\text{mutualistic}} = 1.301$, $d_{\text{antagonistic}} = 1.7340$) than pre-extinction ($d_{\text{combined}} = 2.423$, $d_{\text{mutualistic}} = 2.121$, $d_{\text{antagonistic}} = 2.560$).

4 | DISCUSSION

4.1 | Traits that determine connectivity

Throughout Madagascar, both lemur and plant traits (morphological, dietary and evolutionary) were critical in determining plant–lemur interactions. Similar to frugivory networks in South America (Silva

et al., 2016; Vidal et al., 2014), large lemurs were more connected than small species. Frugivorous and granivorous animals consumed more plant genera than folivores, consistent with previous work (e.g. Ong et al., 2022). Frugivorous lemur species exhibit a generalist, flexible feeding ecology, perhaps an adaptation to fruit scarcity (Donati et al., 2011; Wright, 1999). Lemurs tended to share food plants with species in their same habitats, likely because bioclimatic variables shape the geographic distribution of plant taxonomic and functional groups (Engemann et al., 2016). Lemurs in dry habitats interacted with more plant genera than lemurs in wet habitats; they likely eat a greater variety of plants in response to strong seasonal shifts in dry forests (Sato et al., 2016). Unlike other studies in which more endangered animal species contributed most to network organization (e.g. Vidal et al., 2014), Least Concern lemurs were significantly more connected than other lemur species. The effect of IUCN level could be due to the relatively small, fragmented geographic ranges of Endangered lemurs (Donati et al., 2011; Schübler et al., 2018) or sampling bias. Rare species interactions, which may be ecologically important even if infrequent (Guimarães, 2020), could be under-represented in the LFP. Although combining multiple methods and sources is important for filling gaps and reducing sampling bias in ecological networks, a standardized method for measuring effort in seed dispersal studies is needed (Quintero et al., 2022).

Plant traits were also important drivers of interactions. Although plants with animal-dispersed seeds tend to have higher wood

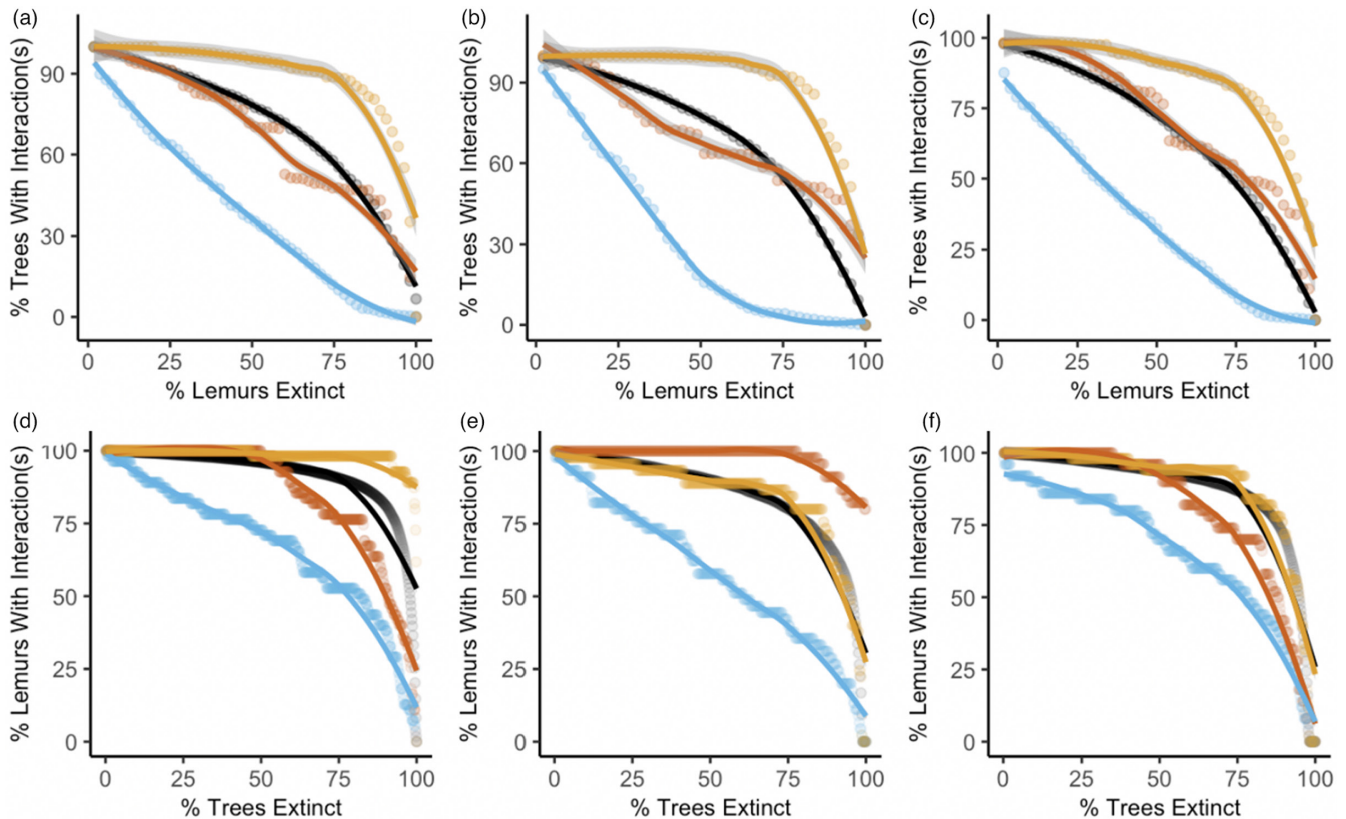


FIGURE 4 Relationship between simulated extinction of one trophic level to the proportion of nodes in the other trophic level with remaining interactions in the combined (a, d) mutualistic (b, e) and antagonistic (c, f) networks. Colours correspond to extinction scenario: Black = random, blue = degree high to low, yellow = degree low to high and red = extinction likelihood. Lines show Loess smoothing best fits and grey outlines represent the 95% confidence intervals.

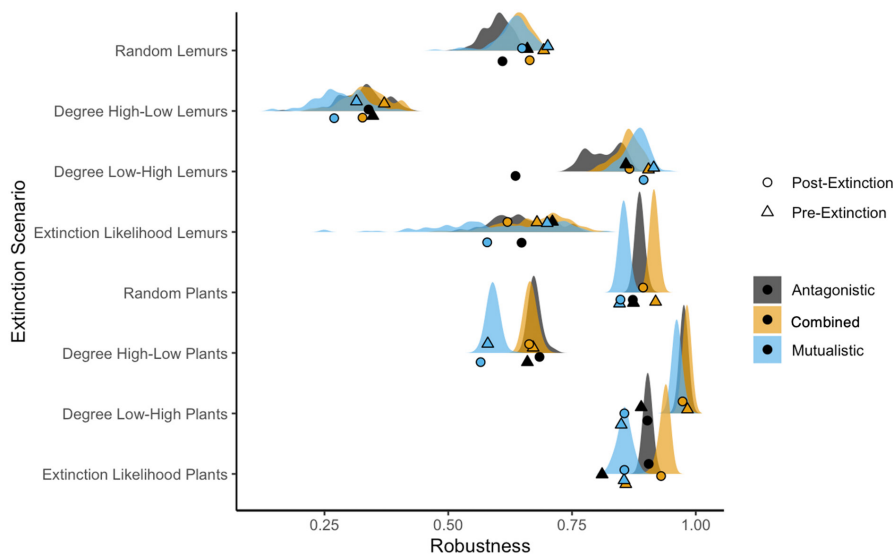


FIGURE 5 Robustness ridge plot under the four extinction scenarios for lemurs and plants. Density plots show the null distribution of robustness. Points denote robustness values in the pre-extinction and post-extinction networks. Points are vertically jittered (height = 0.2) to avoid overlap.

densities in other ecosystems (e.g. Bello et al., 2015), in this study, wood density did not affect connectivity. However, plants were less likely to share lemur consumers if they had higher wood densities. Furthermore, contrary to our expectations (Li et al., 2020), fruit width did not affect lemur–plant interaction probability, perhaps because of poor trait data. Additionally, rather than intrinsic functional traits, plant–lemur interactions may be driven by extrinsic

factors (e.g. plant richness, Tonos et al., 2021). Effects of plant traits on connectivity were smaller than lemur traits, possibly because we did not include feeding preference traits (e.g. fruit colour, odour, nutritional content) due to sparse data availability. The lack of plant taxonomic and trait data available for tropical ecosystems (Cornwell et al., 2019) presents a challenge for ecological network studies, especially in areas with high endemism such as Madagascar. Because

parameter effect sizes were also lower for plants than lemurs at the genus level (Tables S9 and S10), we did not find evidence to support that analysing lemurs and plants at different taxonomic levels drove the differences in effect sizes between lemur and plant traits. However, analysing lemurs at the species level led to different results (Tables S9 and S10), suggesting that our results for plant genera cannot be extrapolated to patterns among plant species, and emphasizing the need for species-level plant trait and interaction data in future studies.

Evolutionary history was also important for structuring plant–lemur interactions. Confamilial plants were more likely to share interactions with lemur species than plants in different families, possibly due to shared functional traits or underlying coevolutionary processes (Chapman, 1995). Unlike other networks (e.g. Schleuning et al., 2011), animal phylogenetic proximity did not predict plant–lemur interaction likelihood. Although confamilial lemurs were more likely to share food trees than lemurs in different families, closely related lemur species may have not interacted with similar plants because they tend not to co-occur biogeographically (Herrera, 2017). Plant genera were more likely to be connected via shared lemur consumers if they were more closely related phylogenetically, likely because of traits shaped by evolutionary history (Vázquez et al., 2009). Future empirical studies should improve models by considering other drivers of network structure, such as seasonality, phenology and conservation status/land use (Encinas-Viso et al., 2012; Fuzessy et al., 2022; Takemoto et al., 2014).

4.2 | Network structure and simulated extinctions

Simulated lemur and plant extinctions altered network structure. Our combined lemur–plant network was sparser (connectance = 0.80) than other plant–animal networks in tropical South America (connectance = 0.1 ± 0.0) or the palaeotropics (connectance = 0.3 ± 0.1 ; Escribano-Avila et al., 2018), possibly because the data in this study were a literature compilation. Contrary to our prediction that connectance would decrease with extinction (Vanbergen et al., 2017; Verdú & Valiente-Banuet, 2008), connectance tended to increase when we simulated extinction. This is likely because connectance is scale dependent in mutualistic networks (Olesen et al., 2006). However, because the null models are the same size as the post-extinction networks, it is still notable that mutualistic and antagonistic network connectance was significantly higher in the plant post-extinction scenarios compared to the null models (Figure 3, Tables S7 and S8). Although ecological network complexity increases with geographic area, per-species link distribution remains constant, highlighting the conservation of network organization at different spatial scales (Galiana et al., 2022). Therefore, because high connectance promotes community tolerance to perturbations in mutualistic, but not antagonistic, plant–animal networks (Thébault & Fontaine, 2010), the high connectivity of our national-scale mutualistic compared to antagonistic network may confer tolerance.

The lower nestedness of our post-extinction network may decrease tolerance to disturbances (Aizen et al., 2012), whereas the higher modularity post-lemur extinction may confer mutualistic and combined network stability (Grilli et al., 2016). Besides network structure, other factors such as lemur and plant mutualistic strategies could drive community stability (Fricke et al., 2017). Nevertheless, our research reveals that animal and plant extinctions threatened mutualistic, antagonistic and combined network structure.

For all network types, robustness to random lemur extinction was consistent with robustness levels in other tropical networks (Escribano-Avila et al., 2018). Robustness tended to decrease post-extinction, highlighting potential threats to lemurs and plants. Although robustness was similar among network types, the high robustness of combined networks indicated the importance of interaction complexity in community stability (Mougi & Kondoh, 2014). Conservation of Madagascar's lemurs and plants is contingent upon mutualistic and antagonistic interactions, as lemurs are important frugivores and/or folivores. Our networks had similar robustness under the 'extinction likelihood' and random extinction scenarios, likely because generalist lemurs were not at a disproportionately high extinction risk. Lemur and plant specialization decreased post-extinction, indicating a higher extinction risk for specialists than for generalists. Food plant redundancies might promote higher robustness to plant simulated extinctions compared to lemurs (Memmott et al., 2004). Many lemurs have both mutualistic and antagonistic interactions with plants, potentially driving benefits for the post-extinction scenario plants that are well connected mutualistically but poorly connected antagonistically. Combining mutualisms and antagonisms in a multilayer network could improve future robustness estimates (Montesinos-Navarro et al., 2017). Additionally, future analyses should include other lemur–plant interaction types such as pollination.

Trophic rewiring could mitigate the consequences of interaction loss on extinction cascades and increase network robustness (Vizentin-Bugoni et al., 2020). Alternatively, rewiring could exacerbate the effects of species loss on ecological networks (Gilljam et al., 2015). If lemurs surviving extinction events favour plant species with higher interaction frequencies, post-extinction rewiring could lead to interaction deficits rather than compensation (Fricke et al., 2018). Rewiring induced by lemur extirpation could have cascading ecological consequences such as decreased plant population persistence and connectivity (Rogers et al., 2021) and altered plant functional trait compositions (Kurten et al., 2015). Frugivore extinctions might also reduce evolutionarily distinct interactions (Emer et al., 2019), prevent plant gene flow (Browne & Karubian, 2018) and cause rapid plant trait evolution (Galetti et al., 2013). However, size matching may limit lemur–plant rewiring. Adaptive network frameworks, a critical area for future research, may improve understanding of the mechanisms and consequences of many Malagasy plants persisting without available lemur dispersers, while disperser extinction threatens other species (Albert-Daviaud et al., 2020).

5 | CONCLUSIONS

Collectively, these results highlight that both plant and lemur traits and evolutionary history affected the structure of lemur–plant networks, and that community stability depended on the nature of extinction scenarios. Dietary redundancy of lemurs likely conferred network stability, such that interactions were lost more slowly when plants are removed from the network than lemurs. The consequences of lemur–plant interaction loss could be even greater for ecosystem functions such as seed dispersal than network structure (Donoso et al., 2020). Future research must investigate adaptive lemur–plant networks at the local scale and account for interaction consequences (i.e. plant recruitment and lemur nutritional outcomes; González-Castro et al., 2022). Further lemur and plant extinctions may have cascading ecosystem effects, highlighting the need to conserve both mutualistic and antagonistic interactions.

AUTHORS' CONTRIBUTIONS

C.D. and J.P.H. conceived the idea and designed the methodology. C.D. conducted analyses and led the writing of the manuscript. Both authors contributed critically to drafts and approved the final version for publication.

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CONFLICT OF INTEREST

We report no conflict of interest.

DATA AVAILABILITY STATEMENT

Data on lemur–plant interactions which were already published are cited in this submission, as noted in the Materials and Methods. Newly compiled trait data and code are accessible via the Zenodo repository <https://doi.org/10.5281/zenodo.6813285> (DeSisto, Camille, & Herrera, James, DeSisto & Herrera, 2022).

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