UC Berkeley
UC Berkeley Previously Published Works

Title

Examining the structure of plant-lemur interactions in the face of imperfect knowledge.

Permalink

https://escholarship.org/uc/item/3ks394f5

Journal

Conservation Biology, 39(1)

Authors

Tonos, Jadelys

Papinot, Bastien

Park, Daniel

et al.

Publication Date

2025-02-01

DOI

10.1111/cobi.14323

Peer reviewed

Conservation Biology

CONTRIBUTED PAPER

Examining the structure of plant–lemur interactions in the face of imperfect knowledge

Jadelys Tonos[1] ⓘ | **Bastien Papinot**[2] ⓘ | **Daniel S. Park**[3] ⓘ | **Mihajatiana Raelison**[4] |
Herilantonirina Ramaroson[5] | **Jessica Stubbs**[1] | **Onja H. Razafindratsima**[1] ⓘ

[1]Department of Integrative Biology, University of California, Berkeley, Berkeley, California, USA

[2]Tundra Ecology Lab, Faculty of Life and Environmental Sciences, University of Iceland, Reykjavik, Iceland

[3]Purdue Center for Plant Biology, Purdue University, West Lafayette, Indiana, USA

[4]Ecole Normale Supérieure, University of Antananarivo, Antananarivo, Madagascar

[5]Zootechnic, Veterinary and Fish Research Department (DRZVP), National Research Institute Applied for Rural Development (FOFIFA / CENRADERU), Antananarivo, Madagascar

Correspondence
Jadelys Tonos, Department of Integrative Biology, University of California, Berkeley, Valley Life Science Building, Berkeley, CA 94720, USA.
Email: jmt11@berkeley.edu

Article impact statement: Though lemurs are under substantial extinction threat, data gaps prevent assessment of the impact of lemur loss on plant communities.

Abstract

Biotic interactions, such as plant–animal seed dispersal mutualisms, are essential for ecosystem function. Such interactions are threatened by the possible extinction of the animal partners. Using a data set that includes plant–lemur interactions across Madagascar, we studied the current state of knowledge of these interactions and their structure to determine which plant species are most at risk of losing dispersal services due to the loss of lemurs. We found substantial gaps in understanding of plant–lemur interactions; data were substantially skewed toward a few lemur species and locations. There was also a large gap in knowledge on the interactions of plants and small-bodied or nocturnal lemurs and lemurs outside a few highly studied locations. Of the recorded interactions, a significant portion occurred between lemurs and endemic plants, rather than native or introduced plants. We also found that lemur species tended to primarily consume closely related plant species. Such interaction patterns may indicate the threats to Malagasy endemic plants and highlight how lemur population loss or reductions could affect plant phylogenetic diversity. When examining the impacts of lemur extinction, losing critically endangered species left 164 plant species with no known lemur frugivore partners. Despite phylogenetic patterns in lemur diet, plants for which the only known lemur frugivore is critically endangered were not closely related. These results emphasize the need for further studies to complete our knowledge on these essential interactions and to inform conservation priorities.

KEYWORDS
conservation, extinction, frugivory, mutualism, seed dispersal, tropical

INTRODUCTION

Seed dispersal by animals (zoochory) is fundamental to the reproduction and survival of many plant species and, therefore, to the healthy functioning of ecosystems (Beckman & Sullivan, 2023; Toby Kiers et al., 2010). Zoochory plays a fundamental role in shaping the diversity, structure, composition, and spatial arrangement of plant communities (Razafindratsima & Dunham, 2016; Schupp & Fuentes, 1995) and influences the ability of plant populations to persist through environmental changes (Beckman et al., 2019; Sales et al., 2021; Travis et al., 2013). Unfortunately, as anthropogenic pressures on natural systems

intensify, seed dispersal interactions are at high risk of disruption (Aslan et al., 2013; Bonfim et al., 2023; Tylianakis et al., 2008), which can have cascading impacts on entire ecosystems (Albert et al., 2021; Farwig & Berens, 2012; Heinen et al., 2023; Traveset et al., 2014; Valiente-Banuet et al., 2015).

The loss or decline of vertebrate populations worldwide (Dirzo et al., 2014) may leave many plant species without some of the essential seed dispersal services they rely on (Lamperty & Brosi, 2022). For plant species, populations, and communities, this can mean impaired regeneration (Albert et al., 2021; Traveset et al., 2012), decreased connectivity (Pérez-Méndez et al., 2018), altered genetic diversity (da Silva Carvalho et al., 2016), and shifting plant traits (Albert et al., 2020; Galetti et al., 2013). When a plant's seed dispersers are lost and there is no functional

---

Jadelys Tonos and Bastien Papinot contributed equally to this work.

alternative (Heinen et al., 2023), the plant may be extirpated or go extinct (Federman et al., 2016; Janzen, 2001; Meehan et al., 2002). The high stakes involved in the loss of frugivorous species call for swift conservation actions focused on the protection of such ecological interactions (Heinen et al., 2020). To support this conservation work, interaction structures in vulnerable habitats need to be described and vulnerable interactions and gaps in knowledge need to be identified.

The impacts of disperser loss may be particularly pronounced for island ecosystems. In insular ecosystems, where fewer frugivores exist, interactions may be highly asymmetric because many plant species rely on a few disperser species (Schleuning et al., 2014). This characteristic asymmetry, and a comparative lack of redundancy (McConkey & Drake, 2015), leaves these ecosystems vulnerable to the loss of functions that are not easily replaced. This risk is exacerbated by the isolated nature of islands, which can reduce opportunities for the immigration of novel seed dispersers that could compensate for the lost dispersal services (Fricke et al., 2018). This means that the type of interaction rewiring that can maintain interaction stability in other systems (Mubamba et al., 2022; Timóteo et al., 2016) may be less likely for island interaction networks. As a result, entire island mutualism networks could face ecological instability when seed-dispersing species decrease in abundance or are extirpated (Fricke et al., 2018; Schleuning et al., 2014).

This scenario of ecological instability in the face of disperser loss may be the case for Madagascar's highly diverse ecosystems, an island with immense plant diversity and endemism relying on a relatively small frugivore community (Albert-Daviaud et al., 2018; Razafindratsima et al., 2023). Lemurs, Madagascar's unique primates, play a crucial role in the dispersal of many endemic plants in the island's diverse forests (Razafindratsima & Dunham, 2014; Razafindratsima et al., 2023). With a depauperate frugivore community (Goodman & Ganzhorn, 1997), which includes relatively few bird frugivores and 3 frugivorous bats (Razafindratsima et al., 2023), lemurs seem to undertake the bulk of seed dispersal services in the island (Albert-Daviaud et al., 2018). Their foraging and seed-handling behavior lead to improved dispersal outcomes for many plants species (Mertl-Millhollen et al., 2011; Ramananjato et al., 2020; Razafindratsima & Dunham, 2015; Razafindratsima & Martinez, 2012), many of which can only be dispersed by lemurs as the largest frugivores in the ecosystem (Albert-Daviaud et al., 2020). Unfortunately, these key frugivores are highly threatened (Dunham, 2008; Morelli et al., 2020; Schwitzer et al., 2014); 96% of 110 lemur species are under threat of extinction (IUCN, 2020). The loss of these animal seed dispersers could have debilitating impacts on their natural communities (Dirzo et al., 2014; Razafindratsima, Sato, et al., 2018), threatening the functioning of the ecosystem and its ability to provide vital goods and services for many living organisms and Malagasy communities.

Despite the integral ecological role of these frugivores, understanding of their interactions with plant species across Madagascar is far from complete. Understanding how lemurs interact with plants of different native status or phylogenetic relatedness, for example, can help us assess how the risk of lemur loss is distributed among Madagascar's fruiting plants. If threatened lemurs interact primarily with a subset of closely related plant species, lemur extinctions may reduce the abundance and even trigger coextinction cascades of closely related species (Rezende et al., 2007), with drastic negative impacts on plant diversity. The ability to assess what is at risk, prepare for losses, and plan ecologically sound interventions, thus, relies on a comprehensive understanding of these plant–lemur interactions. We sought to contribute to such understanding by assessing the structure of plant–lemur interactions based on current data and highlighting the gaps that need to be addressed for a full assessment of lemur seed-dispersal mutualisms. Based on a data set of trophic interactions between plants and lemurs, encompassing the entire island of Madagascar (1687 plant species, 153 plant species known only by Malagasy vernacular names, 59 lemur species from 73 locations spanning a broad geographic range of different ecosystems), we characterized patterns of plant–lemur frugivory interactions and examined the data gaps that can prevent a full assessment of the effect of lemur species loss on the island's ecosystems. With this data set, we sought to answer the following questions: What are the gaps in knowledge that must be addressed to gain a comprehensive understanding of plant–lemur interactions in Madagascar? How are plant–lemur interactions structured in terms of plant native status and phylogenetic relatedness? Which plant species might be most vulnerable to the loss of critically endangered lemurs? Is the loss of critically endangered lemur species most likely to affect closely related plant species?

METHODS

Data set

We created a data set on the plant species consumed by lemurs with data from published journal articles, book chapters, dissertations, theses, masters equivalent theses from Madagascar (master 2, DEA, and CAPEN), and unpublished reports. We cross-referenced our data set with a newly established data set of lemur food plants by Steffens (2020) to add articles we did not have in our original data set and to correct species names. Our final data set included the following variables: lemur species, plant species consumed by each lemur species, plant part exploited by lemurs (i.e., fruits, seeds, leaves, flowers, nectar, exudates, or bark), native status of each plant species (i.e., endemic native, nonendemic native, or non-native introduced) based on the distribution in the Plants Of the World online database (http://www.plantsoftheworldonline.org/), the site where the original research took place, forest type, and the International Union for Conservation of Nature (IUCN) status of each lemur species (https://www.iucnredlist.org/). For plant species referred to only by vernacular names in the original source, we searched for its scientific name in other publications from the same study site. We cleaned and standardized the taxonomic nomenclature and synonyms of each plant species
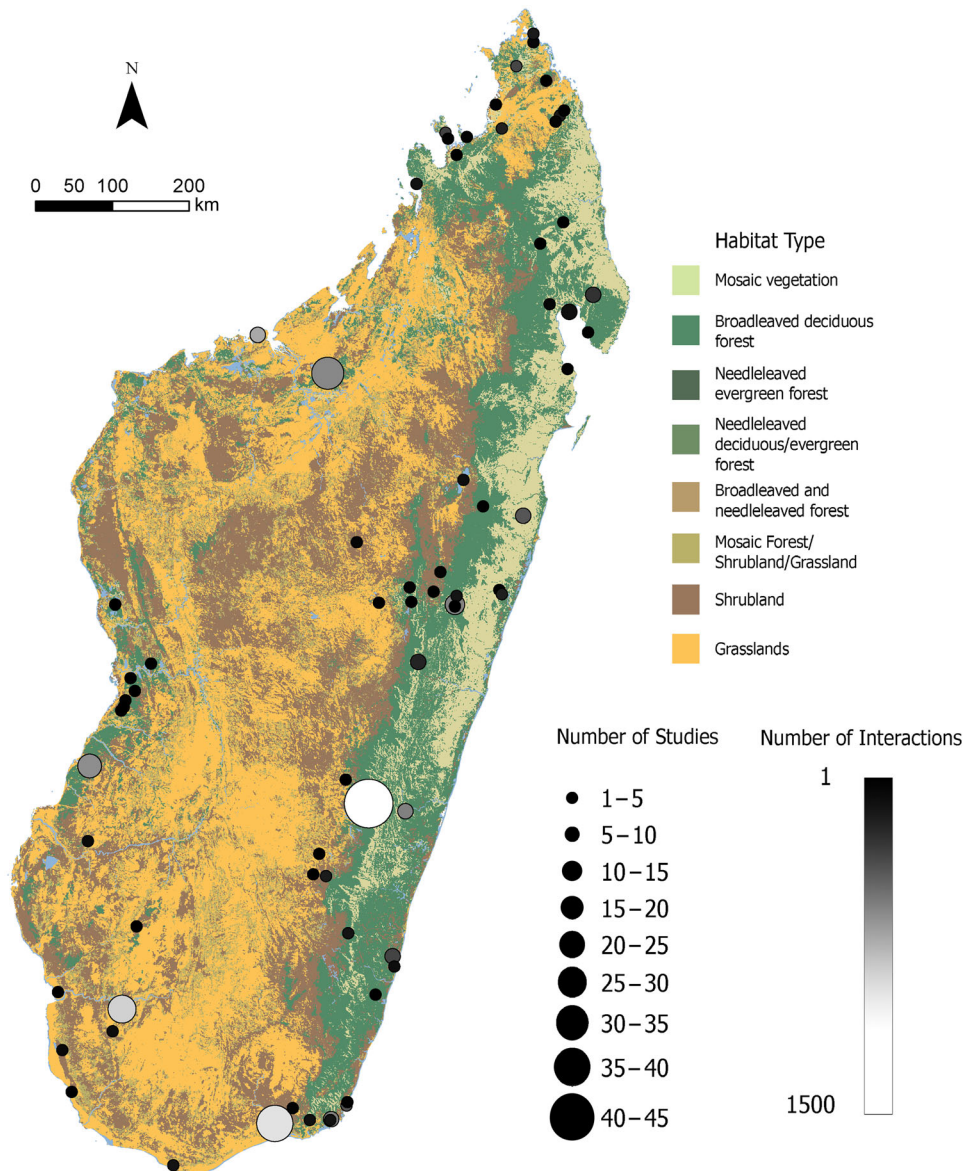
FIGURE 1 Location of sites in our data set on plant–lemur interactions in Madagascar and the number of studies (size) and number of plant–lemur interactions recorded in each study.

with the Taxonomic Name Resolution Service 5.0 (https://tnrs.biendata.org/).

The complete data set comprised 8934 records of plant–lemur interactions (Appendix S1) from 295 sources (Appendix S2) published from 1962 to 2018. These data were collected from 1956 to 2016 at 73 field sites across Madagascar that encompassed diverse ecosystems (i.e., humid forest, dry forest, littoral forest, wetland, gallery forest, mangrove, and riverine forest) (Figure 1). The data set contained records on 59 lemur species that consumed 1687 known vascular plant species (658 genera, 148 families), of which 99.23% were angiosperms, 0.24% gymnosperms, and 0.53% pteridophytes. One hundred and fifty-three plant species lacked scientific names but were identified by local names. The data set contained 4939 unique plant–lemur interactions. Due to our interest in seed disper-

sal, we focused on frugivorous interactions as a proxy for the role of lemur species as seed dispersers. Our frugivory network contained 52 lemur species that consumed the fruits of 1157 known flowering plant species across Madagascar. Of these lemur species, 94.23% are listed as threatened (IUCN, 2020): 19 species Critically Endangered (CR), 12 Endangered (EN), and 18 Vulnerable (VU).

Structure of plant–lemur interactions

To fully assess the potential impact of frugivore loss, in the context of current knowledge, we examined the distribution of studies and frugivory interactions across ecosystems, lemur, and plant species in Madagascar. We looked at the number

of studies per site and per lemur species, and the impact of these studies on the number of recorded frugivory interactions. We then examined the relationship between lemur activity pattern and body size (data from Razafindratsima, Yacoby, et al. (2018) and Razafindratsima et al. (2019)) and the number of studies undertaken on each species. We also estimated the complete species richness of fruiting plant partners for each lemur species and created species accumulation curves with the "specaccum" and "specpool" functions in R package vegan (Okasen et al., 2022) to visualize the extent of sampling per lemur species. For each lemur species, we then calculated the ratio of our sampled species richness to the estimated species richness to assess the potential proportion of species still missing.

We examined how lemurs interact with plants based on 2 attributes: native status of the plants (endemic native, non-endemic native, or non-native introduced) and the phylogenetic relationships among the plants. We excluded from this and all following analyses 8 lemur species that had fewer than 10 interactions in the data set. We used a linear mixed-effects model performed with the R package "nlme" (Pinheiro et al., 2023) in which native status was a fixed effect and lemur species was a random effect to test whether lemurs were more likely to interact with native plant species.

We then examined the phylogenetic relationships among the plant species consumed by each lemur species. We generated 1000 rooted, ultrametric phylogenetic trees containing all the known plant species in the data set with the function "phylo.maker" in R package "v.phylomaker" (Jin & Qian, 2019). This function generates phylogenetic hypotheses of a user-provided list of species with a megatree derived from 2 published megatrees of extant vascular plants (Smith & Brown, 2018; Zanne et al., 2014). We selected scenario 2 of this function, in which the new tip is attached to a "randomly selected node at and below the genus- or family-level basal node" (Jin & Qian, 2019). With each of the 1000 trees, we measured the net relatedness index (NRI) for the plants consumed by each lemur species (Cavender-Bares et al., 2009; Webb et al., 2002) with functions in R-package "picante" (Kembel et al., 2010). This metric measures the mean phylogenetic distance (MPD) between all species pairs in a community relative to the phylogenetic distance between all species pairs in null communities: $NRI = -1 \times (MPD_{sample} - MPD_{null})/SD(MPD_{null})$, where sample is the value for our plant communities, null is the value for random communities, and SD is standard deviation. To generate null communities, we used the "phylogeny pool" model, which shuffles species identities from a pool containing all the species in the phylogenetic tree for 1000 randomizations. Positive values of NRI would indicate that the plant species consumed by lemurs are more closely related than expected by chance (clustered), whereas negative values indicate lower relatedness than expected (overdispersed). We performed this analysis with all interactions, as well as for fruit consumption only. We used t tests to determine whether the mean value of NRI differs from zero, indicating a statistically significant deviance from random expectations. Additionally, we looked at the value of each metric for each lemur species, such that a value <1.96 indicated significantly overdispersed plant relatedness in the diet of that lemur species and a value >1.96 indicated significant clustering (Vamosi et al., 2009).

Potential impacts of lemur loss

We sought to identify plant species that are most likely to be negatively affected by lemur extinctions and assessed whether these species tended to be phylogenetically clustered or overdispersed. In this analysis, we assumed that CR lemur species could go extinct and that the plant species that are only known to interact with these lemur species would experience a significant loss in seed dispersal services (Beckman & Rogers, 2013; Beckman et al., 2019; Howe & Smallwood, 1982; Rogers et al., 2019). Given the lack of knowledge on alternative, non-lemur, seed dispersal for much of Madagascar's flora (Razafindratsima, O.H, 2014; Razafindratsima et al., 2023), these assumptions allowed us to identify at-risk plants with the current data. With these criteria, we identified plant species for which the only known lemur disperser is CR and used the previously described NRI method to determine the relatedness of these plants at risk.

RESULTS

Structure of the plant–lemur interactions across Madagascar

Of the 71 study sites in our data set, most were poorly studied, with much of the island showing no published data on plant–lemur frugivory interactions (Figure 1). The number of research studies at each location ranged from 1 to 44, with over 50% of the locations having only one research study, whereas only about 1% of locations had 10 or more studies. Generally, and as might be expected, the sites where most research studies were done are also the sites with the most recorded plant–lemur interactions. Over 45% of the sites had fewer than 20 interactions recorded, whereas <20% had over 200 interactions recorded. The site that exhibited both the most numerous research studies and the most recorded lemur interactions was Ranomafana National Park, in Madagascar's eastern rainforest, with 44 research studies and 1498 interactions. In contrast, understudied sites (representing a single interaction) were located primarily along the southwestern coast of Madagascar (e.g., Menabe Reserve, Tsimembo Forest, and Tsinjoriake New Protected Area). Of the 59 lemur species recorded in the data set, the most studied were the ring-tailed lemurs (*Lemur catta*) and the black-and-white ruffed lemurs (*Varecia variegate* spp.); together, they represented 16% of all recorded lemur–plant interactions (Figure 2). For *Varecia variegata*, this translated into the highest number of known plant species frugivory interactions, followed by *Eulemur rubriventer* and *Eulemur rufifrons*. All 3 of these species are present within Ranomafana National Park and have been relatively well studied. The number of studies had a large and significant impact on the
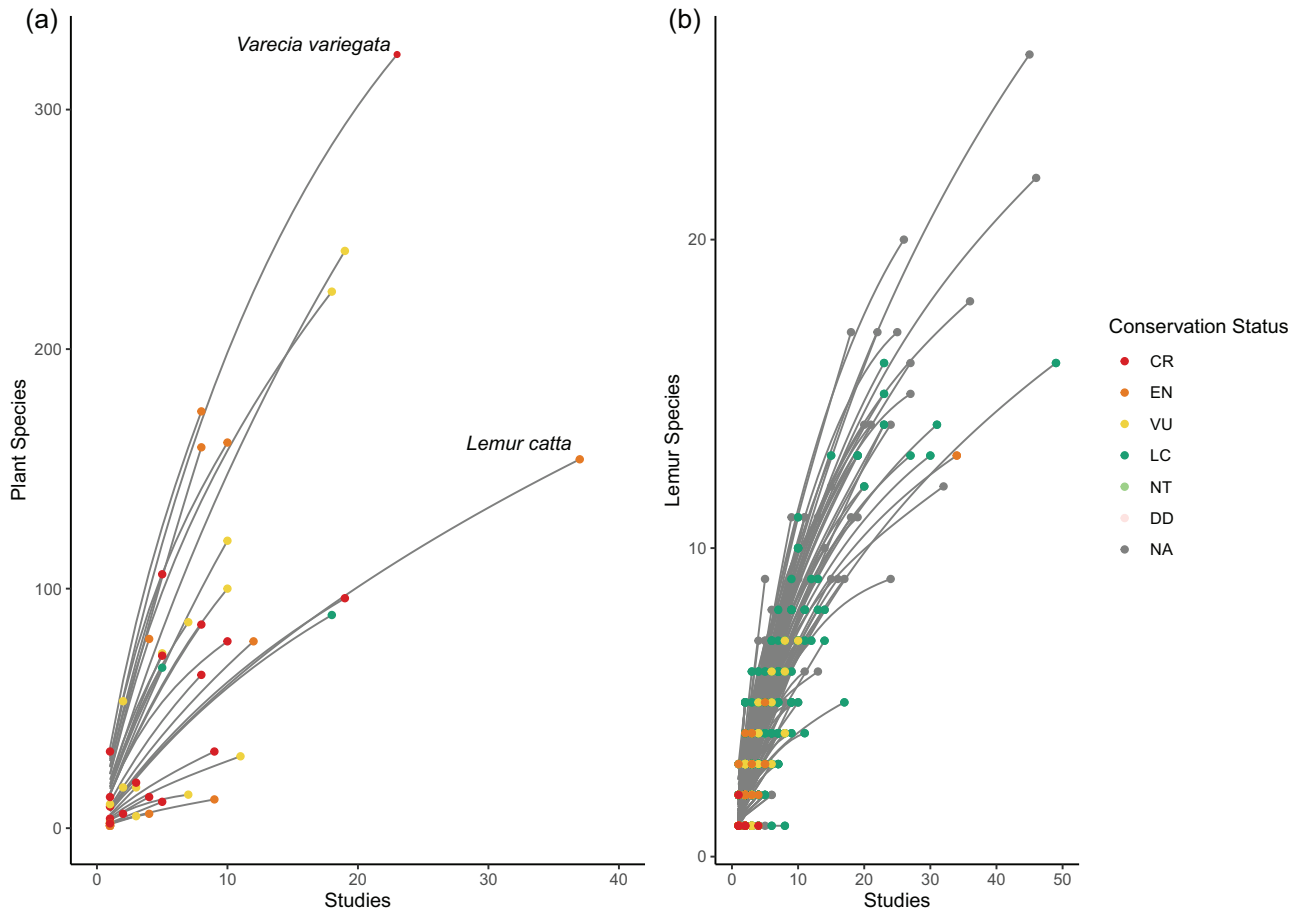
FIGURE 2 Number (points) of (a) plant frugivory interactions for each lemur species and (b) lemur frugivory interactions for each plant species by the number of studies completed for each (gray lines, species accumulation curves used to examine sampling completeness for each lemur and plant species; colors, lemur and plant conservation status; CR, critically endangered; EN, endangered; VU, vulnerable; LC, least concern; NT, not threatened; DD, data deficient; NA, no classification data).

number of interactions recorded per lemur species ($p < 0.001$). Our species accumulation curves (SAC) and richness estimates showed that most species, across lemur and plants, were undersampled. Sampling completeness across lemur species ranged from 0.16 to 0.81 (mean and median = 0.40), so for most lemur species, more than half of fruiting plant partners were unknown (Table 1). The lemur species with the highest sampling completeness (0.81) was the golden-brown mouse lemur (*Microcebus ravelobensis*). It had 7 studies in one habitat and study site. These small-bodied lemurs had a small range in a single habitat type such that these 7 studies captured 14 of the predicted 17 plant species they consume fruit from. Among the most-studied lemurs (>10 studies), *V. variegata* has the second highest sampling completeness (0.73). This species consumed the fruits of 323 plant species, recorded across 23 studies from 7 locations within 1 habitat type. In comparison, the ring-tailed lemur (*Lemur catta*), with 37 studies across 6 habitats and 9 study sites, had a sampling completeness of 0.45 because almost 200 of its predicted 341 partner plant species remain unresolved. Because sampling effort was unequal and hard to

quantify across studies, we cautiously interpreted curves and extrapolated richness values that suggest an approach to sufficient sampling for lemur species with low study numbers. Body size was not significantly associated with the number of studies per species, though most of the best studied lemur were large-to-medium-sized (>1500 g) species from the genus *Lemur*, *Eulemur*, *Varecia*, and *Propithecus*. Activity pattern had a significant effect on the number of studies per species ($p = 0.03$), with nocturnal species having the lowest mean and crepuscular species being significantly ($p < 0.02$) better studied than nocturnal species (Figure 3). No significant difference was found between diurnal species and either nocturnal or crepuscular species.

A large proportion of the plant species interacting with lemurs were endemic, significantly more than the proportions of native ($t = -17.07$, $p < 0.0001$) and introduced plant species consumed ($t = -28.05$, $p < 0.0001$) (Appendices S3.1 & S3.2).

Overall, lemurs consumed plant species that were more closely related than expected by chance. The same pattern was

TABLE 1 Plant-partner richness for fruit-eating lemur species obtained from literature and from extrapolated species richness.

Species	Observed richness	Estimated richness	Sample completeness	Number of studies
Avahi laniger	5.00	11.67	0.43	3.00
Cheirogaleus crossleyi	17.00	85.00	0.20	2.00
Cheirogaleus major	86.00	164.52	0.52	7.00
Cheirogaleus medius	100.00	193.15	0.52	10.00
Daubentonia madagascariensis	12.00	48.00	0.25	9.00
Eulemur albifrons	17.00	107.67	0.16	3.00
Eulemur cinereiceps	106.00	344.28	0.31	5.00
Eulemur collaris	174.00	407.33	0.43	8.00
Eulemur coronatus	159.00	694.94	0.23	8.00
Eulemur fulvus	120.00	336.09	0.36	10.00
Eulemur macaco	161.00	320.05	0.50	10.00
Eulemur mongoz	64.00	148.00	0.43	8.00
Eulemur rubriventer	224.00	434.01	0.52	18.00
Eulemur rufifrons	241.00	552.77	0.44	19.00
Eulemur rufus	73.00	243.84	0.30	5.00
Eulemur sanfordi	79.00	236.64	0.33	4.00
Hapalemur aureus	13.00	67.00	0.19	4.00
Hapalemur griseus	30.00	140.00	0.21	11.00
Indri indri	32.00	96.00	0.33	9.00
Lemur catta	154.00	341.46	0.45	37.00
Lepilemur leucopus	6.00	9.00	0.67	4.00
Lepilemur ruficaudatus	19.00	67.17	0.28	3.00
Microcebus griseorufus	67.00	173.04	0.39	5.00
Microcebus murinus	89.00	171.19	0.52	18.00
Microcebus ravelobensis	14.00	17.09	0.82	7.00
Microcebus rufus	53.00	261.33	0.20	2.00
Prolemur simus	11.00	55.00	0.20	5.00
Propithecus coquereli	6.00	12.25	0.49	2.00
Propithecus coronatus	78.00	122.50	0.64	10.00
Propithecus diadema	85.00	200.53	0.42	8.00
Propithecus edwardsi	78.00	228.00	0.34	12.00
Propithecus verreauxi	96.00	181.46	0.53	19.00
Varecia rubra	72.00	201.60	0.36	5.00
Varecia variegata	323.00	442.69	0.73	23.00

observed when limiting our analyses to angiosperms (Appendix S3). The NRI values indicated significant divergence from random toward clustered when considering all plant species consumed ($t_{50} = 6.32$, $p < 0.0001$) or species for which lemurs consumed fruits ($t_{43} = 4.63$, $p < 0.0001$) or leaves ($t_{42} = 3.69$, $p < 0.0001$). The observed clustering was significant (i.e., value > 1.96) for 9 lemur species when we considered all plant species, 10 for fruits, and 4 for leaves (Appendix S1.2). *Hapalemur alaotrensis* and *Propithecus diadema*, which are both highly folivorous, consumed plant species that were significantly less closely related than expected by chance (NRI values < 1.96) (Appendix S1.3).

Potential impacts in the absence of CR lemur species

A total of 164 plant species were solely associated with CR lemur species (Appendix S3.4). These plant species were not significantly clustered or overdispersed phylogenetically ($t_8 = 1.28$; $p = 0.24$) (Figure 4). Thus, overall, the loss of CR lemur species did not disproportionately affect a specific clade. However, there were certain exceptions. Specifically, the loss of *Indri indri*, *Propithecus verreauxi*, and *Varecia rubra* could affect plant species more closely related than expected by chance (values of NRI > 1.96) (Figure 4; Appendix S1)
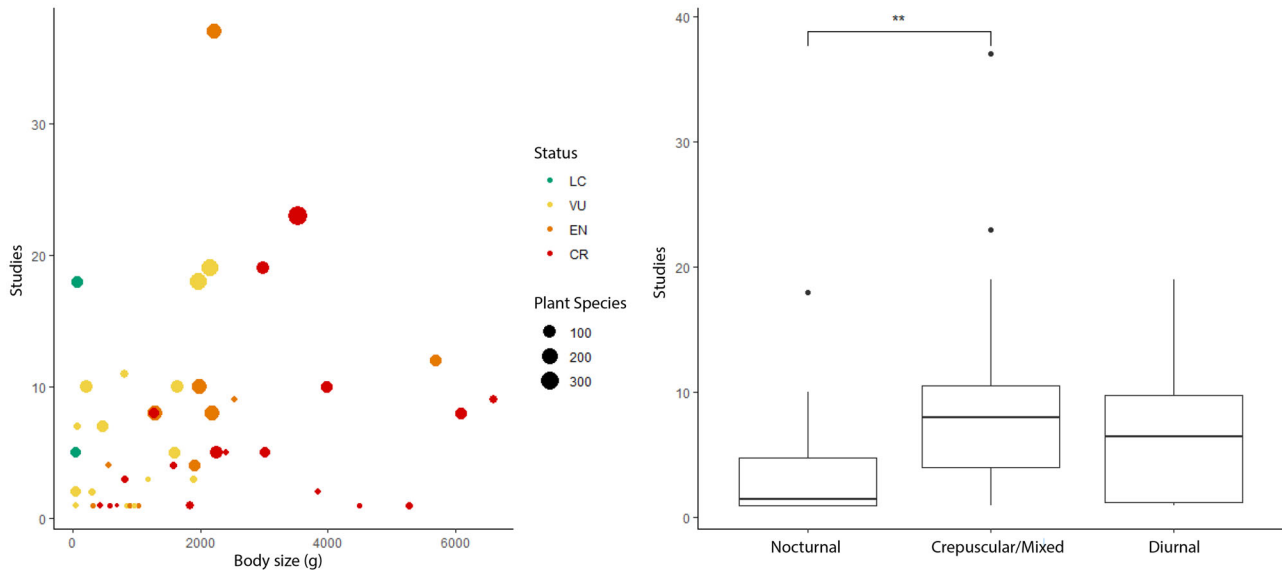
FIGURE 3 Number of (a) studies and plant species interactions recorded for lemurs of differing body sizes and conservation statuses and (b) studies describing plant–lemur interactions by lemur activity pattern (**$p < 0.01$; horizontal lines and whiskers, pairs with significant differences in number of studies).
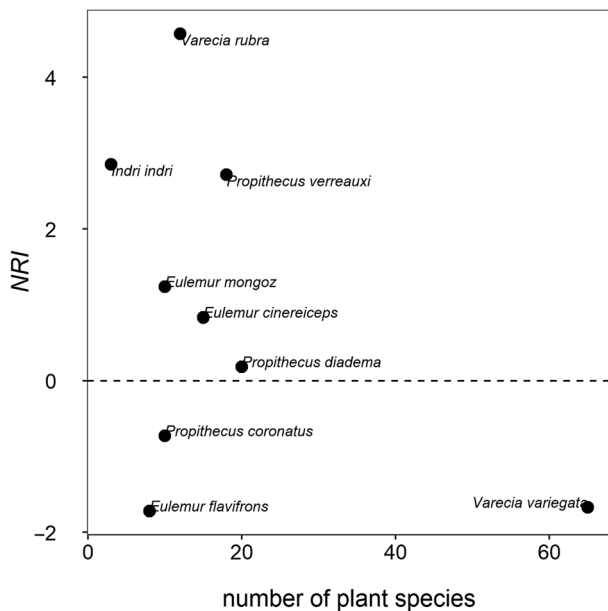

FIGURE 4 Phylogenetic relationships among plant species consumed by Critically Endangered lemur species based on the net relatedness index (NRI) (positive values, plant species consumed more closely related than expected by chance [clustered]; negative values, consumed plant species more evenly spread on the phylogenetic tree [overdispersed]).

DISCUSSION

We found significant gaps in knowledge on plant–lemur interactions, which limited our ability to fully assess the risks posed by lemur extinctions. Currently available data on plant–lemur interactions showed how lemurs primarily feed on endemic plants and that the plants included in the diet of a lemur species were more closely related than one would expect by chance. This demonstrated how the loss of lemur

species may have particular costs for endemic plants and cause nonrandom impacts across plant clades. We identified 164 plants species most likely to be negatively affected by lemur extinctions and found that the loss of 3 lemur species (*I. indri*, *P. verreauxi*, and *V. rubra*) would affect a subset of closely related plants. Although plant species may persist beyond the loss of their only known frugivorous partners (Albert-Daviaud et al., 2020; Fricke et al., 2017), identifying lemur species with a particular impact on plant communities can help set conservation goals. This process is currently hampered by a significant skew in knowledge on plant–lemur interactions across habitats and lemur species and by a significant lack of information on the dispersal services provided by Madagascar's non-lemur frugivores.

Critical trends and gaps in research on plant–lemur interactions

We found a substantial skew in our knowledge of plant–lemur interactions toward a few, well-studied lemur species and sites. With most sites having a single study, often representing a single lemur species, much work is needed to complete knowledge of interactions across the island. In fact, most lemur and plant species included in our study were undersampled in terms of their frugivory interactions. With the limited data available, researchers can start highlighting certain important lemur species and examining the risks of losing these species, but it is not possible to assess the importance of many understudied and highly threatened species. Most studies are focused on a few, well-funded, and internationally recognized locations, many of which are established explicitly for the study of large-bodied or charismatic lemur species (Newsome & Hassell, 2014; Rothman et al., 2022; Wright & Andriamihaja, 2002). Ranomafana National Park, established for the protection of the golden

bamboo lemur, is a perfect example of a heavily studied ecosystem, largely thanks to the Centre ValBio research station (Figure 1). In this ecosystem, multiple long-term studies of *V. variegata* across a few sites contributed substantially to the relative high coverage of partner plant species for this frugivore. Similarly, many of the lemurs in Ankarafantsika National Park, one of the biggest remaining fragments of Madagascar western dry forest, were among the best studied. *Microcebus ravelobensis* had the best coverage of all lemur species at about 80% (Albignac et al., 1992). For the species with the best resolution of plant partners, *V. variegata* and *M. ravelobensis*, limited geographic distributions, use of a single habitat type, and sensitivity to disturbance likely facilitated the full assessment of plant partner biodiversity (Andriatsitohaina et al., 2020; White et al., 1995). In comparison, the ring-tailed lemur, one of the best studied species, had a relatively low sampling completeness (45%) despite many studies taking place across multiple habitats and sites. This makes sense for a generalist species, particularly with high levels of plant microendemism in Malagasy forests, for which many new plant-species partners may be uncovered by each new study in a new location (Cameron, 2007; Vences et al., 2009). Further work may be necessary to fully resolve the role of this species across ecosystems. However, hard-to-access, nascent, or indigenously stewarded lands remain largely unexamined by Western science, and nocturnal lemur species are understudied (Gardner, 2011; Gardner et al., 2018; Ramananjato et al., 2020; Razafindratsima et al., 2023).

Plant–lemur interaction structure

Although lemurs appeared to prefer endemic native species, lemur diets can reflect the composition of the available plants in terms of the proportions of species in each of these categories in Madagascar (Callmander et al., 2011). This pattern suggests that with the increasing spread of introduced species, their presence in lemur diets may also increase. For example, strawberry guava (*Psidium cattleyanum*) is an aggressive invasive plant species in Madagascar capable of dominating forests and altering the structure of plant communities (DeSisto et al., 2020). Despite these negative effects, it has become an important source of forage for frugivore lemur communities in many degraded and invaded forests (Carrière et al., 2008; DeSisto et al., 2020). Lemurs may favor foraging on the fruits of such an invasive species because of their nutritional content. They may seek alternative sources of otherwise limited nutrients because Malagasy fruits contain relatively low nitrogen and protein compared to those in other tropical forests (Donati et al., 2017; LaFleur & Gould, 2009). We also found that lemur species tended to consume a subset of closely related plants species, likely representing plants with shared functional traits relevant to lemur diets. This may also indicate the importance of evolutionary history in structuring these plant–lemur interactions, although evidence of coevolution in plant–lemur interaction networks has been weak (Fuzessy et al., 2023). Results of a recent study showed a similar phylogenetic structure in lemur diets and that closely related lemur species do not necessarily interact with

the same plant species (DeSisto & Herrera, 2022). This is likely due to low co-occurrence among closely related lemurs, leading closely related species to interact with geographically distinct plant communities. This pattern may lead to further trouble for plant communities that lose their lemur dispersers. When a lemur species is lost, it may leave a taxonomic subset of plant at risk, with reduced probability of rescue by a closely related lemur species with fruit handling and dispersal traits like those lost.

Impact of lemur extinctions

The loss of CR lemur species may leave 164 plant species without the services of their only known lemur frugivore. In a worse-case scenario, where CR lemur extinctions occur and no other frugivore can take their place, these plants may lose a service with substantial impacts on population dynamics. Though these losses may be mitigated by the existence of frugivore–plant interactions not captured in our data, the loss or significant reduction in these lemur populations may still have an impact. The loss of the specific function played by an extinct mutualist partner may impact the genetic structure of a plant population (da Silva Carvalho et al., 2016), alter the frequency of traits across a plant community (Albert et al., 2020), and reduce dispersal toward specific microhabitats or at long distances (da Silva Carvalho et al., 2021; Pérez-Méndez et al., 2016). Except for 3 lemur species, the loss of CR lemurs did not appear to affect closely related plant species. These lemur species are 3 examples of relatively large-bodied lemurs in their respective ecosystems, which may interact with a specific subset of closely related large-seeded plants species (*I. indri*, *P. verreauxi*, and *V. rubra*) (Gerhold et al., 2015; Peterson, 2011). As is the case across many ecosystems, the loss of the relatively large-bodied frugivores in a system may leave a hard-to-fill gap in the dispersal of slow-growing large-seeded species. Most of the plant species imperiled by CR lemur extinction were also endemic to Madagascar and are found in Madagascar's humid forests. This is not surprising because Madagascar hosts tremendous levels of endemism, and the humid forests contain a high diversity of plants relying on a limited number of lemur dispersers (Albert-Daviaud et al., 2018; Goodman & Benstead, 2005). Madagascar's humid forests are also under considerable threat from deforestation and climate change, worsening the conservation scenarios for these plant species when combined with the loss of their seed dispersers (Brown et al., 2015).

Current knowledge of Madagascar's plant–lemur interactions reveals how lemur species primarily interact with closely related subsets of Madagascar's endemic plants. This phylogenetic structure in lemur diets may leave specific plant clades at risk when lemur populations are lost or reduced. Without the assistance of their frugivorous seed dispersers, these plants may fail to regenerate, fail to colonize restored and regenerating habitats, and fail to escape harmful environmental conditions through range shifts. Even when these plant species persist, it is likely that the loss of dispersal function will affect plant population and community dynamics. The loss of one species in

an already limited number of mutualist dispersers may leave a functional gap that cannot be filled by the remaining frugivore community, although the risk is hard to assess because there are significant gaps in understanding of plant–lemur interactions and in the involvement of Madagascar's nonlemur seed dispersers (i.e., birds and fruit bats). To effectively plan for the protection, or restoration, of Malagasy forests in the face of continuing habitat disruption, climate change, and species loss, a more complete understating of plant–frugivore interactions across the island must be pursued.

ACKNOWLEDGMENTS

ORCID

Jadelys Tonos https://orcid.org/0000-0001-8792-9717
Bastien Papinot https://orcid.org/0000-0002-5830-5080
Daniel S. Park https://orcid.org/0000-0003-2783-530X
Onja H. Razafindratsima https://orcid.org/0000-0003-1655-6647

REFERENCES

Albert, S., Flores, O., Baider, C., Florens, F. B. V., & Strasberg, D. (2021). Differing severity of frugivore loss contrasts the fate of native forests on the land of the Dodo (*Mascarene archipelago*). *Biological Conservation*, 257, 109131.

Albert, S., Flores, O., & Strasberg, D. (2020). Collapse of dispersal trait diversity across a long-term chronosequence reveals a strong negative impact of frugivore extinctions on forest resilience. *Journal of Ecology*, 108(4), 1386–1397.

Albert-Daviaud, A., Buerki, S., Onjalalaina, G. E., Perillo, S., Rabarijaona, R., Razafindratsima, O. H., Sato, H., Valenta, K., Wright, P. C., & Stuppy, W. (2020). The ghost fruits of Madagascar: Identifying dysfunctional seed dispersal in Madagascar's endemic flora. *Biological Conservation*, 242, 108438.

Albert-Daviaud, A., Perillo, S., & Stuppy, W. (2018). Seed dispersal syndromes in the Madagascan flora: The unusual importance of primates. *Oryx*, 52(3), 418–426.

Albignac, R., Ramangason, G. S., Rakotonirina, V. S., Andriatsarafara, S., & Rabetaliana, H. (1992). *Ecodéveloppement des Communautés Rurales pour la Conservation de la Biodiversité*. Plaquette. UNESCO/PNUD. Tsipika Editeur Antananarivo.

Andriatsitohaina, B., Romero-Mujalli, D., Ramsay, M. S., Kiene, F., Rasoloharijaona, S., Rakotondravony, R., Lehman, S. M., & Radespiel, U. (2020). Effects of habitat edges on vegetation structure and the vulnerable golden-brown mouse lemur (*Microcebus ravelobensis*) in northwestern Madagascar. *BMC Ecology*, 20(1), 69.

Aslan, C. E., Zavaleta, E. S., Tershy, B., & Croll, D. (2013). Mutualism disruption threatens global plant biodiversity: A systematic review. *PLoS ONE*, 8(6), e66993.

Beckman, N. G., Aslan, C. E., Rogers, H. S., Kogan, O., Bronstein, J. L., Bullock, J. M., Hartig, F., HilleRisLambers, J., Zhou, Y., Zurell, D., Brodie, J. F., Bruna, E. M., Cantrell, R. S., Decker, R. R., Efiom, E., Fricke, E. C., Gurski, K., Hastings, A., Johnson, J. S., … Zambrano, J. (2019). Advancing an interdisciplinary framework to study seed dispersal ecology. *AoB Plants*, 12(2), plz048.

Beckman, N. G., & Rogers, H. S. (2013). Consequences of seed dispersal for plant recruitment in tropical forests: Interactions within the seedscape. *Biotropica*, 45(6), 666–681.

Beckman, N. G., & Sullivan, L. L. (2023). The causes and consequences of seed dispersal. *Annual Review of Ecology, Evolution, and Systematics*, 54(1), 403–427.

Bonfim, F. C. G., Dodonov, P., Guimarães, P. R., & Cazetta, E. (2023). Habitat loss shapes the structure and species roles in tropical plant–frugivore networks. *Oikos*, 2023(4), e09399.

Brown, K. A., Parks, K. E., Bethell, C. A., Johnson, S. E., & Mulligan, M. (2015). Predicting plant diversity patterns in Madagascar: Understanding the effects of climate and land cover change in a biodiversity hotspot. *PLoS ONE*, 10(4), e0122721.

Callmander, M. W., Phillipson, P. B., Schatz, G. E., Andriambololonera, S., Rabarimanarivo, M., Rakotonirina, N., Raharimampionona, J., Chatelain, C., Gautier, L., & Lowry II, P. P. (2011). The endemic and non-endemic vascular flora of Madagascar updated. *Plant Ecology and Evolution*, 144(2), 121–125.

Cameron, A. (2007). *Behavioural surveys and edge-sensitivity estimates of two populations of free-ranging ringtailed lemurs (Lemur catta) in rocky outcrop/savannah mosaic habitat at Anja Special Reserve and the Tsaranoro Valley, Southcentral Madagascar*. University of Victoria.

Carrière, S. M., Randrianasolo, E., & Hennenfent, J. (2008). Protected areas and control of bioinvasions: Conflicting objectives? The case of *Psidium cattleianum* Sabine (Myrtaceae) around Ranomafana National Park, Madagascar. *VertigO*, 8(1), 1–14.

Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters*, 12(7), 693–715.

da Silva Carvalho, C., García, C., Lucas, M. S., Jordano, P., & Côrtes, M. C. (2021). Extant fruit-eating birds promote genetically diverse seed rain, but disperse to fewer sites in defaunated tropical forests. *Journal of Ecology*, 109(2), 1055–1067.

da Silva Carvalho, C., Galetti, M., Colevatti, R. G., & Jordano, P. (2016). Defaunation leads to microevolutionary changes in a tropical palm. *Scientific Reports*, 6(1), 31957.

DeSisto, C. M. M., & Herrera, J. P. (2022). Drivers and consequences of structure in plant–lemur ecological networks. *Journal of Animal Ecology*, 91(10), 2010–2022.

DeSisto, C. M. M., Park, D. S., Davis, C. C., Ramananjato, V., Tonos, J. L., & Razafindratsima, O. H. (2020). An invasive species spread by threatened diurnal lemurs impacts rainforest structure in Madagascar. *Biological Invasions*, 22(9), 2845–2858.

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, 345(6195), 401–406.

Donati, G., Santini, L., Eppley, T. M., Arrigo-Nelson, S. J., Balestri, M., Boinski, S., Bollen, A., Bridgeman, L. L., Campera, M., Carrai, V., Chalise, M. K., Derby Lewis, A., Hohmann, G., Kinnaird, M. F., Koenig, A., Kowalewski, M., Lahann, P., McLennan, M. R., Nekaris, A. K. I., … Ganzhorn, J. U. (2017). Low levels of fruit nitrogen as drivers for the evolution of Madagascar's primate communities. *Scientific Reports*, 7(1), 14406.

Dunham, A. E. (2008). Battle of the sexes: Cost asymmetry explains female dominance in lemurs. *Animal Behaviour*, 76(4), 1435–1439.

Farwig, N., & Berens, D. G. (2012). Imagine a world without seed dispersers: A review of threats, consequences and future directions. *Basic and Applied Ecology*, 13(2), 109–115.

Federman, S., Dornburg, A., Daly, D. C., Downie, A., Perry, G. H., Yoder, A. D., Sargis, E. J., Richard, A. F., Donoghue, M. J., & Baden, A. L. (2016). Implications of lemuriform extinctions for the Malagasy flora. *Proceedings of the National Academy of Sciences of the United States of America*, 113(18), 5041–5046.

Fricke, E. C., Tewksbury, J. J., & Rogers, H. S. (2018). Defaunation leads to interaction deficits, not interaction compensation, in an island seed dispersal network. *Global Change Biology*, 24(1), e190–e200.

Fricke, E. C., Tewksbury, J. J., Wandrag, E. M., & Rogers, H. S. (2017). Mutualistic strategies minimize coextinction in plant–disperser networks. *Proceedings of the Royal Society B: Biological Sciences*, 284(1854), 20162302.

Fuzessy, L., Balbuena, J. A., Nevo, O., Tonos, J., Papinot, B., Park, D., Sol, D., Valenta, K., Razafindratsima, O. H., & Verdu, M. (2023). Friends or foes? Plant-animal coevolutionary history is driven by both mutualistic and antagonistic interactions. *Authorea*, 00, 00–00. https://doi.org/10.22541/au.168190585.53405707/v1

Galetti, M., Guevara, R., Côrtes, M. C., Fadini, R., Von Matter, S., Leite, A. B., Labecca, F., Ribeiro, T., Carvalho, C. S., Collevatti, R. G., Pires, M. M., Guimarães, P. R., Brancalion, P. H., Ribeiro, M. C., & Jordano, P. (2013). Functional extinction of birds drives rapid evolutionary changes in seed size. *Science*, *340*(6136), 1086–1090.

Gardner, C. J. (2011). IUCN management categories fail to represent new, multiple-use protected areas in Madagascar. *Oryx*, *45*(3), 336–346.

Gardner, C. J., Nicoll, M. E., Birkinshaw, C., Harris, A., Lewis, R. E., Rakotomalala, D., & Ratsifandrihamanana, A. N. (2018). The rapid expansion of Madagascar's protected area system. *Biological Conservation*, *220*, 29–36.

Gerhold, P., Cahill, J. F., Winter, M., Bartish, I. V., & Prinzing, A. (2015). Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology*, *29*(5), 600–614.

Goodman, S. M., & Benstead, J. P. (2005). Updated estimates of biotic diversity and endemism for Madagascar. *Oryx*, *39*(1), 73–77.

Goodman, S. M., & Ganzhorn, J. U. (1997). Rarity of figs (Ficus) on Madagascar and its relationship to a depauperate frugivore community. *Revue D'Ecologie*, *52*(4), 321–329.

Heinen, J. H., Florens, F. B. V., Baider, C., Hume, J. P., Kissling, W. D., Whittaker, R. J., Rahbek, C., & Borregaard, M. K. (2023). Novel plant–frugivore network on Mauritius is unlikely to compensate for the extinction of seed dispersers. *Nature Communications*, *14*(1), 1019.

Heinen, J. H., Rahbek, C., & Borregaard, M. K. (2020). Conservation of species interactions to achieve self-sustaining ecosystems. *Ecography*, *43*(11), 1603–1611.

Howe, H. F., & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, *13*, 201–228.

International Union for Conservation of Nature (IUCN). (2020). *The IUCN Red List of Threatened Species. Version 2018-1*. http://www.iucnredlist.org

Janzen, D. H. (2001). Latent extinction—The living dead. In S. A. Leven (Ed.), *Encyclopedia of biodiversity* (pp. 590–598). Elsevier.

Jin, Y., & Qian, H. (2019). V.PhyloMaker: An R package that can generate very large phylogenies for vascular plants. *Ecography*, *42*(8), 1353–1359.

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, *26*(11), 1463–1464.

LaFleur, M., & Gould, L. (2009). Feeding outside the forest: The importance of crop raiding and an invasive weed in the diet of gallery forest ring-tailed lemurs (*Lemur catta*) following a cyclone at the Beza Mahafaly special reserve, Madagascar. *Folia Primatologica*, *80*(3), 233–246.

Lamperty, T., & Brosi, B. J. (2022). Loss of endangered frugivores from seed dispersal networks generates severe mutualism disruption. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1984), 20220887.

McConkey, K. R., & Drake, D. R. (2015). Low redundancy in seed dispersal within an island frugivore community. *AoB Plants*, *7*, plv088.

Meehan, H. J., McConkey, K. R., & Drake, D. R. (2002). Potential disruptions to seed dispersal mutualisms in Tonga, Western Polynesia. *Journal of Biogeography*, *29*(5–6), 695–712.

Mertl-Millhollen, A. S., Blumenfeld-Jones, K., Raharison, S. M., Tsaramanana, D. R., & Rasamimanana, H. (2011). Tamarind tree seed dispersal by ring-tailed lemurs. *Primates; Journal of Primatology*, *52*(4), 391–396.

Morelli, T. L., Smith, A. B., Mancini, A. N., Balko, E. A., Borgerson, C., Dolch, R., Farris, Z., Federman, S., Golden, C. D., Holmes, S. M., Irwin, M., Jacobs, R. L., Johnson, S., King, T., Lehman, S. M., Louis, E. E., Murphy, A., Randriahaingo, H. N. T., Randrianarimanana, H. L. L., & Baden, A. L. (2020). The fate of Madagascar's rainforest habitat. *Nature Climate Change*, *10*(1), 89–96.

Mubamba, S., Nduna, N., Siachoono, S., Chibesa, M., Phiri, D., & Chama, L. (2022). Plant–frugivore networks are robust to species loss even in highly built-up urban ecosystems. *Oecologia*, *199*(3), 637–648.

Newsome, D., & Hassell, S. (2014). Tourism and conservation in Madagascar: The importance of Andasibe National Park. *Koedoe*, *56*(2), a1144.

Okasen, J., Simpson, G., Blanchet, F., Kindt, R., LegendrE, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., … Weedon, J. (2022). *vegan: Community ecology package*. R package version 2.6-4. https://CRAN.R-project.org/package=vegan

Pérez-Méndez, N., Jordano, P., García, C., & Valido, A. (2016). The signatures of Anthropocene defaunation: Cascading effects of the seed dispersal collapse. *Scientific Reports*, *6*, 24820.

Pérez-Méndez, N., Jordano, P., & Valido, A. (2018). Persisting in defaunated landscapes: Reduced plant population connectivity after seed dispersal collapse. *Journal of Ecology*, *106*(3), 936–947.

Peterson, A. T. (2011). Ecological niche conservatism: A time-structured review of evidence: Ecological niche conservatism. *Journal of Biogeography*, *38*(5), 817–827.

Pinheiro, J., Bates, D., & R Core Team. (2023). *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-164. https://CRAN.R-project.org/package=nlme

Ramananjato, V., Rakotomalala, Z., Park, D. S., DeSisto, C. M. M., Raoelinjanakolona, N. N., Guthrie, N. K., Fenosoa, Z. E. S., Jonhson, S. E., & Razafindratsima, O. H. (2020). The role of nocturnal omnivorous lemurs as seed dispersers in Malagasy rain forests. *Biotropica*, *52*(4), 758–765.

Razafindratsima, O. H. (2014). Seed dispersal by vertebrates in Madagascar's forests: Review and future directions. *Madagascar Conservation and Development*, *9*(2), 90–97.

Razafindratsima, O. H., & Dunham, A. E. (2015). Assessing the impacts of non-random seed dispersal by multiple frugivore partners on plant recruitment. *Ecology*, *96*(1), 24–30.

Razafindratsima, O. H., & Dunham, A. E. (2016). Frugivores bias seed-adult tree associations through nonrandom dispersal: A phylogenetic approach. *Ecology*, *97*(8), 2094–2102.

Razafindratsima, O. H., & Martinez, B. T. (2012). Seed dispersal by red ruffed lemurs, seed size, viability, and beneficial effect on seedling growth. *Ecotropica*, *18*(1), 15–26.

Razafindratsima, O. H., Sato, H., Tsuji, Y., & Culot, L. (2018). Advances and frontiers in primate seed dispersal. *International Journal of Primatology*, *39*(3), 315–320.

Razafindratsima, O. H., Tonos, J. M., Ramananjato, V., Dunham, A. E., & Andriamasovoloarisoa, M. (2023). Frugivory and seed dispersal. In S. M. Goodman (Ed.), *The new natural history of Madagascar* (pp. 142–152). Princeton University Press.

Razafindratsima, O. H., Yacoby, Y., & Park, D. S. (2018). MADA: Malagasy animal trait data archive. *Ecology*, *99*(4), 990–990.

Razafindratsima, O. H., Yacoby, Y., & Park, D. S. (2019). *Data from: MADA: Malagasy Animal trait Data Archive* (Version 1). Dryad. https://doi.org/10.5061/DRYAD.44TT0

Rezende, E. L., Lavabre, J. E., Guimarães, P. R., Jordano, P., & Bascompte, J. (2007). Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature*, *448*(7156), 925–928.

Rogers, H. S., Beckman, N. G., Hartig, F., Johnson, J. S., Pufal, G., Shea, K., Zurell, D., Bullock, J. M., Cantrell, R. S., Loiselle, B., Pejchar, L., Razafindratsima, O. H., Sandor, M. E., Schupp, E. W., Strickland, W. C., & Zambrano, J. (2019). The total dispersal kernel: A review and future directions. *AoB Plants*, *11*(5), plz042.

Rothman, R., Kling, K., Andrianandrianina, L., Andrianoely, D., Rabeson, P., Rakotonirina, P., de Dieu Ramanantsoa, J., Randrianarista, D., Solo, J., Docherty, M., Razafimahaimodison, J. C., & Wright, P. (2022). Centre Val-Bio research station: International centre for the valorization of biodiversity. *Ecotropica*, *24*, 202203.

Sales, L. P., Kissling, W. D., Galetti, M., Naimi, B., & Pires, M. (2021). Climate change reshapes the eco-evolutionary dynamics of a Neotropical seed dispersal system. *Global Ecology and Biogeography*, *30*(5), 1129–1138.

Schleuning, M., Böhning-Gaese, K., Dehling, D. M., & Burns, K. C. (2014). At a loss for birds: Insularity increases asymmetry in seed-dispersal networks. *Global Ecology and Biogeography*, *23*(4), 385–394.

Schupp, E. W., & Fuentes, M. (1995). Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience*, *2*, 267–275.

Schwitzer, C., Mittermeier, R. A., Johnson, S. E., Donati, G., Irwin, M., Peacock, H., Ratsimbazafy, J., Razafindramanana, J., Louis, E. E., Chikhi, L., Colquhoun, I. C., Tinsman, J., Dolch, R., LaFleur, M., Nash, S., Patel, E., Randrianambinina, B., Rasolofoharivelo, T., & Wright, P. C. (2014). Averting lemur extinctions amid Madagascar's political crisis. *Science*, *343*(6173), 842–843.

Smith, S. A., & Brown, J. W. (2018). Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*, *105*(3), 302–314.

Steffens, K. J. E. (2020). Lemur food plants as options for forest restoration in Madagascar. *Restoration Ecology*, *28*(6), 1517–1527.

Timóteo, S., Ramos, J. A., Vaughan, I. P., & Memmott, J. (2016). High resilience of seed dispersal webs highlighted by the experimental removal of the dominant disperser. *Current Biology*, *26*(7), 910–915.

Toby Kiers, E., Palmer, T. M., Ives, A. R., Bruno, J. F., & Bronstein, J. L. (2010). Mutualisms in a changing world: An evolutionary perspective: Mutualism breakdown. *Ecology Letters*, *13*(12), 1459–1474.

Traveset, A., González-Varo, J. P., & Valido, A. (2012). Long-term demographic consequences of a seed dispersal disruption. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1741), 3298–3303.

Traveset, A., Heleno, R., & Nogales, M. (2014). The ecology of seed dispersal. In R. S. Gallagher (Ed.), *Seeds: The ecology of regeneration in plant communities* (pp. 62–93). CAB International.

Travis, J. M. J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., Boulangeat, I., Hodgson, J. A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V. M., & Bullock, J. M. (2013). Dispersal and species' responses to climate change. *Oikos*, *122*, 1532–1540.

Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, *11*, 1351–1363.

Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M., García, M. B., García, D., Gómez, J. M., Jordano, P., Medel, R., Navarro, L., Obeso, J. R., Oviedo, R., Ramírez, N., Rey, P. J., Traveset, A., Verdú, M., & Zamora, R. (2015). Beyond species loss: The extinction of ecological interactions in a changing world. *Functional Ecology*, *29*(3), 299–307.

Vamosi, S. M., Heard, S. B., Vamosi, J. C., & Webb, C. O. (2009). Emerging patterns in the comparative analysis of phylogenetic community structure. *Molecular Ecology*, *18*(4), 572–592.

Vences, M., Wollenberg, K. C., Vieites, D. R., & Lees, D. C. (2009). Madagascar as a model region of species diversification. *Trends in Ecology & Evolution*, *24*(8), 456–465.

Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, *33*(1), 475–505.

White, F. J., Overdorff, D. J., Balko, E. A., & Wright, P. C. (1995). Distribution of ruffed lemurs (*Varecia variegata*) in Ranomafana National Park, Madagascar. *Folia Primatologica*, *64*, 124–131.

Wright, P. C., & Andriamihaja, B. (2002). Making a rain forest national park work in Madagascar. In J. Terborgh, C. van Schaik, L. Davenport, & M. Rao (Eds.), *Making parks work* (pp. 112–136). Island Press.

Zanne, A. E., Tank, D. C., Cornwell, W. K., Eastman, J. M., Smith, S. A., FitzJohn, R. G., McGlinn, D. J., O'Meara, B. C., Moles, A. T., Reich, P. B., Royer, D. L., Soltis, D. E., Stevens, P. F., Westoby, M., Wright, I. J., Aarssen, L., Bertin, R. I., Calaminus, A., Govaerts, R., … Beaulieu, J. M. (2014). Three keys to the radiation of angiosperms into freezing environments. *Nature*, *506*(7486), 89–92.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.