



Original research article



Ecological and human use traits shape lemur-tree interaction networks across human-modified landscapes

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ABSTRACT

Functional traits drive species interactions that structure ecological communities around the world. Both ecological and human-use traits may be associated with the structure of ecological networks in human-modified systems. In secondary and primary forests in northeast Madagascar, we quantified the importance of lemur species and the tree genera they consume using network measures of centrality, determined the ecological trait predictors of tree centrality, and investigated the relationships between tree centrality and human use. Our study advances understanding of ecological interactions by: combining ethnobiological data with direct observations to reduce undersampling of cryptic interactions; using a bipartite network approach to understand the connections between land use types; investigating frugivory, seed predation, and herbivory interactions; and accounting for phylogenetic signal in tree centrality. Diurnal lemurs tended to be more central to primary forests, whereas nocturnal lemurs were more central to secondary forests. Tree centrality in primary forest networks was negatively associated with tree diameter, wood density, and endemism status. Network structure was related to human use traits in the secondary forest but not in primary forest; trees central to secondary forest networks were more likely to be used by people, especially in herbivory networks. Our results highlight the importance of combining research-based observations with ethnobiological data to

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advance our understanding of the trait-based functioning of ecological networks. Conservation approaches should be attentive to the implications of ecological interactions for both ecological functioning and human well-being.

1. Introduction

Species interactions are critical for driving the structure and functioning of ecological communities (Escribano-Avila et al., 2018). Mutualisms such as seed dispersal by frugivores affect tree composition, structure, and diversity, and can promote forest restoration (Beckman and Sullivan, 2023; Chapman and Dunham, 2018; Rogers et al., 2021; Beckman et al., 2020). Antagonistic relationships like herbivory and seed predation also influence plant survival and growth, potentially limiting populations of consumed species over time (Agrawal and Maron, 2022; Chapman et al., 2013; Williams and Brodie, 2023). These species interactions are vulnerable to environmental change (Valiente-Banuet et al., 2015). Land use change, such as forest clearance, and disturbance, such as selective logging, often alter communities of species that interact both directly and indirectly in ecological networks (Raolinjanakolona et al., 2023; de Assis Bomfim et al., 2018; Tylanakis and Morris, 2017). Conserving the functioning of ecological networks is necessary for promoting biodiversity in the face of land use change and human disturbance of forests (Genes and Dirzo, 2022; Aslan et al., 2013).

Plant functional traits play a major role in structuring ecological networks. For example, in bird frugivory networks, taller trees with larger fruits were found to have higher centrality, meaning they play a more structurally important role within the network (Crestani et al., 2019). Tall trees also were more specialized and served a lesser role in connecting network subgroups compared to shorter trees in lemur-plant seed dispersal networks, while fruit size was negatively related to specialization but positively related to among-module connectivity (Raolinjanakolona et al., 2023). Plant functional traits such as seed mass affect rates of seed predation by small mammals (Chang and Zhang, 2014; Dylewski et al., 2020), and high wood density is associated with low herbivory rates (Larjavaara and Muller-Landau, 2010). Whether a plant is endemic may also relate to centrality in dietary networks. For example, garden experiments showed that endemic *Eucalyptus* species shared more traits than non-endemic congeners, and that herbivory was heavier on non-endemics (Gorman et al., 2014). Additionally, wildlife are known to feed on invasive species (DeSisto et al., 2020; Parker and Hay, 2005).

In addition to ecological traits, human use traits can influence interaction networks across human-modified landscapes. People and wildlife often overlap in the tree species they use (Buchholtz et al., 2019; Hockings et al., 2020). By determining the distribution of plants across a landscape (e.g., Bliege Bird et al. (2024)), people affect ecological networks indirectly. By harvesting forest resources, including through logging, people can directly reduce food resources available to wildlife (e.g., Rivera et al. (2022)). If species central to ecological networks are more important for human use, then the loss of those species may trigger feedback loops that degrade both ecological functioning and human resource provisioning. For example, resources for people and lemurs decline with human activity in northeast Madagascar (Kling et al., 2024). Furthermore, previous research has shown that food web and ecosystem service robustness declines most if species are lost by their order of importance to ecosystem services (Keyes et al., 2021). To understand ecological network structure, it is essential to consider the roles of both ecological and human use traits, especially across different land uses.

Ecological interactions are notoriously challenging to study, especially when the research includes low-density species or species that vary in their interactions seasonally and annually. Geographic, taxonomic, and methodological sampling biases are persistent in plant-animal interaction research (Quintero et al., 2022; Vitorino et al., 2022). Moreover, rare and cryptic interactions — which can disproportionately support ecosystem functioning — are often under-sampled using conventional scientific methods (Escribano-Avila et al., 2018; Vitorino et al., 2022; Mouillot et al., 2013). This challenge calls for novel approaches, including the use of local knowledge of species interactions. Ethnobiological data can increase network completeness by capturing more interactions, especially of cryptic species, and improving estimations of network properties (Ong et al., 2022). Ethnobiological data represent how people understand and interact with biological organisms in their particular cultural and environmental context. Ethnobiological data are derived from observations by local people and their oral histories. Combining ethnobiological data with research-focused observations can improve species detection probabilities while enhancing local engagement in biodiversity protection (Berkström et al., 2019; Braga-Pereira et al., 2022; Camino et al., 2020). Engaging with knowledge held by place-based actors can greatly advance inferences of ecological networks.

Here, we assess the relationships between ecological and human use functional traits and tree centrality in plant-animal networks. Organisms with high centrality have important contributions to the structural and functional importance of ecological networks. For example, central trees are those which are used more heavily by more lemur species, thus providing important dietary resources. We combine ethnobiological data with direct observations during research activities, hereafter “research-focused observations”. Data include three interaction types — frugivory, seed predation, and herbivory — across two land use types: primary forests and secondary forests. Across all networks, we (1) quantify the centrality of animal species and the tree genera they consume, (2) determine the ecological trait predictors of tree centrality and (3) examine the relationships between tree centrality and human use. We hypothesize that traits related to centrality differ between primary and secondary forests and across interaction types. Specifically, we expect that tree centrality in primary forest networks is positively associated with tree size, fruit size, and human use, whereas tree centrality in secondary forests is negatively associated with tree size and human use (Raolinjanakolona et al.,

2023; Brown et al., 2013). We also expect wood density to predict centrality in herbivory, but in not frugivory or predation networks, because wood density is associated with leaf toughness and structural defenses against herbivory.

We test these globally-relevant hypotheses using lemur-tree interactions as a study system. Lemurs are Madagascar's primary seed dispersers (Razafindratsima, 2014) and 90% of the 112 known species are endangered with extinction (IUCN, 2024). Land use change threatens lemur frugivory, seed predation, and herbivory on Madagascar (Albert-Daviaud et al., 2020; DeSisto and Herrera, 2022), a global hotspot for both biodiversity and extinction (Myers et al., 2000). Deforestation is widespread and ongoing, with Madagascar experiencing a 25% decrease in tree cover over the past 20 years (Vieilledent et al., 2018; Suzzi-Simmons, 2023). Hunting and selective logging further threaten lemurs and trees (Borgerson et al., 2022; Golden et al., 2022; Brown and Gurevitch, 2004). Consequent degradation of lemur-tree interactions may limit related ecosystem services such as carbon storage and human resource provisioning (Razafindratsima et al., 2018; Raelinjanakolona et al., 2023; Račevska et al., 2022). Nevertheless, lemurs often exhibit dietary flexibility in human-modified landscapes; for example, lemurs feed on non-native species and disperse their seeds (DeSisto et al., 2020). Lemurs can therefore promote succession of native and nonnative species in regenerating forests (Steffens et al., 2022).

2. Materials and methods

2.1. Study site

We conducted fieldwork in the COMATSA (Corridor Marojejy, Anjanaharibe-Sud and Tsaratanana) protected area in the SAVA region of northeast Madagascar. Established in 2015, COMATSA is co-managed by the World Wildlife Fund and a de-centralized system of local forest management associations called *Vondron'Olona Ifotony* (VOI). COMATSA is a mountainous rainforest habitat that connects Marojejy National Park, Anjanaharibe-Sud Special Reserve, and Tsaratanana Reserve. It is characterized by medium altitude moist evergreen forest between ~800 and 2000 m a.s.l. Goodman et al. (2019). Our research focused on COMATSA-Sud, the southern region of the protected area. Three cathemeral (active during day and night; *Eulemur albifrons*, *Eulemur rubriventer*, *Haplemur occidentalis*; family Lemuridae), one diurnal (*Propithecus candidus*; family Indriidae) and six nocturnal [*Allocebus trichotis* (Cheirogaleidae), *Cheirogaleus crossleyi* (Cheirogaleidae), *Microcebus lehilahysara* (Cheirogaleidae), *Avahi laniger* (Indriidae), *Lepilemur seali* (Lepilemuridae)] lemur species occur in COMATSA-Sud. The nocturnal *Daubentonia madagascariensis* likely also occurs (Rabearivony et al., 2015). We conducted research in primary and secondary forests near the village of Ambodivoara, in the rural commune Ambodiangezoka, Andapa district. We defined secondary forests as areas that were clear-cut for agriculture 15–20 years before the research began and have since regenerated (Chokkalingam and De Jong, 2001). Primary forests were semi-intact forests that have never been clear-cut. Lemur snare traps, small artisanal mining pits, and newly-felled trees were found in both primary and secondary forests prior to and occasionally during our research.

2.2. Data collection

2.2.1. Research-focused observations

To identify lemur-plant interactions, we installed six ~1 km transects across the study site, four in primary forest and two in secondary forest matrix, primarily following pre-existing trails. During diurnal and nocturnal lemur transect surveys (June 2022–January 2024), we collected data on lemur-tree feeding interactions. For each observed feeding interaction, we recorded the lemur species consumer, tree species, and tree part consumed (fruit, seeds, leaves, bark, flowers, or buds). Trees were identified to the vernacular name, later translated to the Latin name based on herbarium specimens which were confirmed by a collaborating botanist from the Missouri Botanical Garden. We collected lemur feces after we observed a lemur defecating to identify additional frugivory interactions. We also opportunistically collected fecal samples from the forest floor, identifying dispersers to the genus level based on fecal morphology such as size, shape, and texture. We collected lemur fecal samples (n = 760) from diurnal lemur species. Within 24 h of sample collection, we identified gut-passed seeds, when possible. The majority (99%) of fecal samples were collected from *E. rubriventer* or *E. albifrons*.

To enable estimation of lemur densities, we also surveyed lemurs on the six transects using standardized methods for primate sampling (Whitesides et al., 1988; Buckland et al., 2010; Herrera, 2016). Distance sampling data were collected between June 2022 and November 2023. Transects were placed at least 500 m apart to reduce the chance of individuals moving between them and to preserve data independence. Some lemurs may still have traversed multiple transects. Each transect was surveyed for nocturnal (between 17:15 and 22:30 h; mean 21.50 repetitions per transect, sd 1.05) and diurnal (between 07:15 and 11:00 h for morning surveys, between; mean 33.00 repetitions per transect, sd 10.12) lemurs, for a total of 318.5 km surveyed (Table S1). We conducted lemur transect walks slowly (~1 km/h for diurnal surveys and ~0.5 km/h for nocturnal surveys) in teams of 2–5 surveyors. When a lemur group was detected, we recorded species identity, group size, angle from transect, estimated perpendicular distance from transect, geographic coordinates, date and time of observation, and any tree feeding interactions. We collected 676 unique lemur observations used for density modeling (described below).

To quantify tree densities (individuals/ha) in the primary and secondary forests, we established 49 20 m × 50 m botanical plots, 29 in primary forest and 20 in secondary forest. We identified (based on the vernacular name, later translated to the Latin name) and measured every living tree (and palm) ≥ 5 cm diameter at breast height (subsequently referred to as diameter) in each plot (n = 9094). Trees were identified to the species level when possible (33.5% of individuals), otherwise to the genus level (66.3% of individuals) and morphospecies (0.1% of individuals). Due to the high proportion of individuals identified to the genus level,

we conducted analyses with genus as the taxonomic unit. Our botanical plots sampled a relatively circumscribed area and may not represent the full diversity of genera in the protected area, although they comprehensively represent plant genera at the study site (Fig. S3). We sampled areas that varied in terms of human-use history and topography, and we therefore consider the sample representative of this site. Plots were surveyed between June 2022 and August 2023.

Methods were approved by Duke IACUC protocol A048-22-03 and the Ministère de l'Environnement et du Développement Durable (071/22, 348/22, and 400/23/MEDD/SG/DGGE/DAPRNE/SCBE.Re), with authorization from the WWF.

2.2.2. Ethnobiological data

We surveyed local community members knowledgeable about both forest trees and lemurs to identify lemur-plant ecological interactions, following Ong et al. (2021). Based on data from 17 botanical plots that we surveyed in 2022, we compiled a catalogue representing the 82 genera that occurred in both the primary and secondary forests (93% of genera sampled from all 49 botanical plots), including local vernacular names and photographs. We created a lemur species catalogue with vernacular names and photographs of nine observed lemur species and *D. madagascariensis*, for which we had observed their characteristic percussive foraging marks on tree bark, indicating they occur in the area.

We displayed the lemur and plant photographic catalogues as visual tools to conduct the survey. For each plant in the catalogue, we asked respondents if they knew the species. If “yes”, we asked if lemurs consume the species and, if so, which lemur species consume which plant parts. We identified interactions involving frugivory (fruits with seeds swallowed whole, no mastication), seed predation (fruits with seeds destroyed due to mastication), and herbivory (consumption of leaves, flowers, wood, bark, and/or “other”). To collect human-use information, we asked participants if people consume or use each plant species. We recorded the plant part eaten and/or used, as well as the specific use of the plant (artisanal materials, rope, charcoal, fodder, fertilizer, construction, fiber, shade, vanilla tutor tree, dye, firewood, medicine, and/or timber). Prior to deploying the survey, we tested it with knowledgeable local experts recruited to the team as parobotanists and with community members to verify vernacular names improve comprehension of the questions.

To collect ethnobiological data on lemur-plant interactions, we conducted key informant surveys with 81 people, including 6 co-authors (WR, DR, MR, GR, JT, FZ), from three villages proximate to the study site. Participants were identified based on recommendations from VOI leadership and through “snowball” sampling, whereby participants were asked to identify other members of their communities who were especially knowledgeable about forest plants and/or lemurs. Surveys were implemented in Qualtrics and lasted approximately 4 h each, depending on the knowledge level of the interviewee. Surveys were conducted in Malagasy by residents of the local region (CD, RB). Given the survey's length and the depth of information shared by participants, we adhered to the Malagasy custom of *findramana* (borrowing), respectfully asking to borrow the participants' time and energy. We honored this local practice through the following actions: (1) a *tangalamena* (a respected elder; in our case, a member of VOI leadership) requested to borrow a participant's time and energy before beginning the survey; (2) we provided a refreshment break during the survey; (3) a full meal was offered to participants; (4) we compensated participants with phone credits (4000MGA/~1USD); and (5) we concluded with a speech expressing our gratitude.

Before the survey, participants were read an informed consent form explaining the purpose of the research — to understand plant-lemur interactions and human uses of plants — and informed that they could refuse to answer any or all questions. We explained that the results would be used for academic purposes and all responses would be kept confidential. All informants willingly agreed to participate in the study. This research was led by CMMMD, an American researcher, who worked in close collaboration for the previous two years with researchers and forest managers from the study area. Methods were approved by the Duke IRB (protocol 2020-0599).

2.3. Density estimations

We estimated lemur population densities (individuals/ha) for each species using the R package *unmarked* (Fiske and Chandler, 2011). First, we calculated perpendicular distance of the observed lemur from the transect using the angle and estimated distance from the observer. We manually truncated lemur group observations to remove extreme data points (1.5% of observations). Then, we jointly modeled for density and detection probability using the multinomial-Poisson mixture model (Royle et al., 2004; Chandler et al., 2011). For each lemur species, we built three models (half-normal, hazard, and null), comparing fit based on the Akaike information criterion (AIC) and opting for half normal functions given functionally equivalent AIC values (within 2 AIC). Effort was calculated as the total distance surveyed in km (i.e., transect lengths multiplied by number of repetitions). We used the best model to jointly estimate lemur group densities for both primary and secondary forests. We then multiplied predicted densities by mean species group size to determine population abundances per land use type, calculating confidence intervals by multiplying standard errors of density by mean lemur species group size. Density calculations were repeated for all nine lemur species observed in our study site. Lemur density estimates were rounded to the nearest integer for subsequent analyses.

We modeled detection probability jointly across both habitat types. We could not model detection separately for primary and secondary forests due to limited sample sizes for certain lemur species — particularly rare and threatened diurnal species such as *Hapalemur occidentalis*. However, distances of sightings between the transect and lemur observations were comparable between secondary (mean = 13 m, SD = 9) and primary (mean = 9 m, SD = 7) forests, justifying jointly modeling both habitat types. We had fewer than the recommended number of sightings for distance modeling (Buckland, 2001; Marshall et al., 2008) for three lemur species. Nevertheless, our models fit the data well. We assessed model fit using the Shapiro–Wilk test. We also visually inspected histograms and detection functions (Fig. S1). Model fit was adequate and the functions appropriately captured the observed lemur

distributions. Additionally, the sighting distance histograms were right-skewed, and the data followed expected patterns, with most lemur sightings occurring near the transect line.

Tree genus densities were calculated as the number of individuals of a certain genus and in a given land use type divided by the total area surveyed (2.9 km² in the primary forest and 2 km² in the secondary forest).

2.4. Ecological network construction

To compile plant–lemur interactions, we pooled empirical observations, survey results, and interaction data collected from the literature (Steffens, 2020; Lyons, 2013) by tree genera (Fig. 1). To prevent false positives while avoiding the exclusion of rare interactions, we only included an interaction from ethnobiological data in the network if it (1) was identified by more than one participant and/or, (2) was identified by a plant “expert”. We defined “expert” as self-reported knowledge of ≥ 150 plant species from the catalogue. Experts ($n = 7$) tended to be VOI members. For tree genera with conflicting information between the ethnobiological data and the author’s expertise (*Trema*, *Ocotea*, *Dombeya*, *Pandanus*), we convened a focus group with five survey participants to reach a consensus. We then subsetted all interactions to include only the 82 tree genera present in our study site, based on the botanical surveys.

We used these data to construct bipartite lemur frugivory, seed predation, and herbivory networks (Fig. 1). As observed in this study and confirmed from previous behavioral studies (Patel, 2014), all *P. candidus* fruit consumption was considered seed predation. For both primary and secondary forests, we used lemur and tree surveys to subset the networks to only include lemur species and tree genera found in the respective land use types. Edges were weighted by a proxy for interaction frequency, the product of lemur biomass (density \times species mean biomass) and tree basal area (abundance \times genus mean diameter at breast height) from the respective land use types, rounded to the nearest integer. To obtain lemur density values, we generated distributions of 100 density estimates based on the posterior distributions from the distance sampling models. These networks varied in their weights to address uncertainty in lemur density. This approach allowed us to incorporate the uncertainty associated with estimating lemur density from a limited sample size of lemur transects. Based on the posterior draws from the fitted distance sampling models, we constructed 100 networks for each interaction type (frugivory, seed predation, herbivory) by land use type (primary forest, secondary forest), for a total of 600 networks. We did not incorporate uncertainty in the tree component, as relative basal area estimates were derived from botanical surveys and thus considered more reliable. In contrast, lemur densities were modeled using distance sampling methods, which are associated with greater uncertainty. All networks were completely connected with no isolates.

2.5. Centrality

2.5.1. Trait-based mechanisms of centrality

We calculated the structural importance of lemurs and trees using network centrality metrics. Specifically, we calculated PageRank, strength, and betweenness centrality for each tree genus and lemur species in the network. In Google’s PageRank centrality, node centrality was the probability that a random walker visited a given tree genus or lemur species (Brin and Page, 1998). In other words, PageRank centrality quantified the importance of a node based on the importance of its neighbors, incorporating both the number and strength of ecological interactions. PageRank centrality reflects the movement of energy throughout an ecological network. Strength centrality is the sum of edge weights of each node in a network. A tree with high strength provides more food resources to the lemur community, and a lemur with high strength consumes a wider diversity of trees more heavily. To calculate strength, the edges were weighted to reflect different amounts of contact and then summed at each node. Betweenness centrality quantifies a node’s importance by measuring how frequently it lies on the shortest paths between all other pairs of nodes in the network. A node with high betweenness centrality is therefore important at connecting other nodes in the network.

We calculated centrality values of each lemur species and tree genus for each network using the package *igraph* (Csardi and Nepusz, 2006) for each of the 600 networks. We then calculated mean centrality values by each interaction and \times land use type. PageRank, strength, and betweenness centralities were strongly and positively correlated (Fig. S5). This manuscript focuses on PageRank centrality; see Figs. S6–S9 for analyses of strength and betweenness centrality.

2.5.2. Phylogenetic general linear models

We tested the relationships between mean tree genera centrality and both ecological and human use traits by constructing phylogenetic generalized least squares (PGLS) models for each network. PGLS accounts for phylogenetic non-independence when estimating the effects of functional traits on centrality. In these models, log-transformed centrality was treated as the dependent variable and functional traits were treated as independent variables. We estimated Pagel’s λ , a measure of phylogenetic signal, using maximum likelihood to account for phylogenetic signal in the residuals of the statistical models. We used the package *caper* (Orme et al., 2023) to build the PGLS models.

We fit PGLS models to determine the ecological traits that predict tree centrality. Genus-level tree phylogenies were constructed using the package *V. PhyloMaker* (Jin and Qian, 2019) and the GBOTB angiosperm megatree (Smith and Brown, 2018). Ecological traits included genus-level mean fruit length, mean diameter, mean wood density, endemism status, and mean seed mass. Fruit lengths and seed mass were collected from the literature, diameter values from the empirical botanical plots, mean genus wood density values from the R package *BIOMASS*, and endemism status from the *Tropicos* database (Albert-Daviaud et al., 2018; Rosin and Poulsen, 2017; Society for Ecological Restoration and Kew, 2023; Rejou-Mechain et al., 2017; Missouri Botanical Garden, 2021). Functional traits were scaled to the z-score distribution. Diameter, wood density, and endemism status were included as

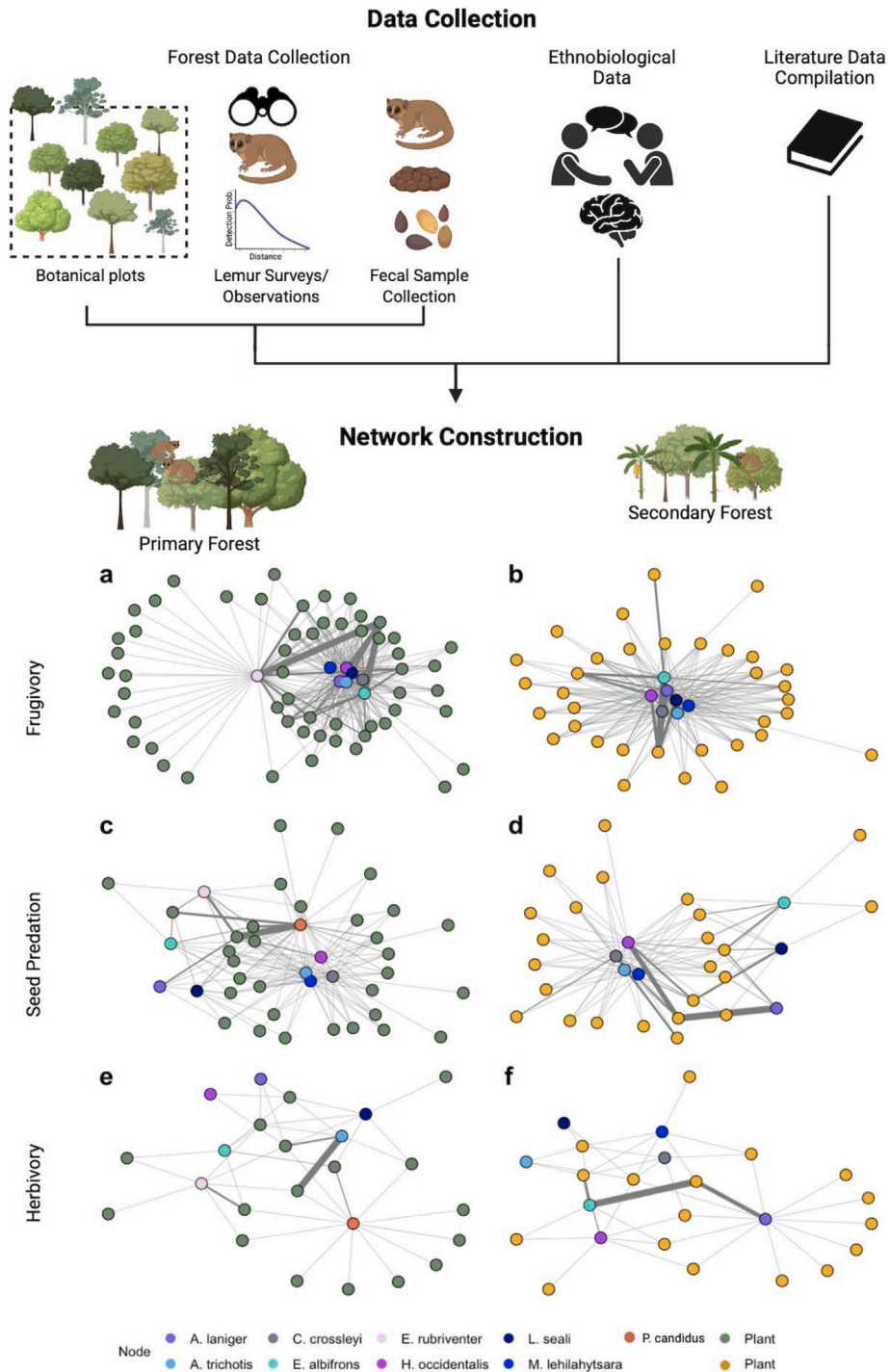


Fig. 1. Schematic diagram highlighting data collection and network compilation methods. Network visualization represents the weighted single-layer networks for the primary forest and secondary forest for frugivory, seed predation, and herbivory, where each network was best represented by one highly-connected module. Green nodes represent primary forest tree genera, yellow nodes represent secondary forest tree genera, and other colors represent lemur species. All networks are completely connected. Edge width represents edge weights, but weak edges are visualized as the same width to enable visualization of each edge. Created using BioRender.com and ggnet (Briatte, 2023).

predictors for all interactions. Fruit length was included for frugivory whereas seed mass was included for seed predation networks. Because we expect that fruit length and seed mass are not relevant predictors for herbivory interactions, we excluded fruit length in the herbivory PGLS models.

To test relationships between tree structural importance to the network and functional importance to people, we built additional models that examined two human use traits: use proportion and use richness. Human use proportion was defined as the proportion of survey participants who reported any human uses of that plant. Human use richness was defined as the number of all reported uses of the plant (eating, artisanal materials, rope, charcoal, fodder, fertilizer, construction, fiber, shade, vanilla tutor tree, dye, firewood, medicine, and timber) divided by the number of study participants.

All analyses were conducted using R Version 4.3.1 (R Core Team, 2023).

3. Results

3.1. Network description

Seven out of nine lemur species present in the primary forest also existed in the secondary forest (Table S2). *Propithecus candidus* and *Eulemur rubriventer* were not observed in the secondary forest. Estimated lemur population densities tended to be lower in the secondary forest compared to the primary forest (Table S2).

The majority of ecological interactions were identified from ethnobiological surveys (Fig. S2). Research-focused observations and literature compilation yielded 58 frugivory, 11 seed predation, and 52 herbivory tree-lemur interactions between the 82 tree genera inventoried in our botanical plots and nine lemur species detected along the transects. Ethnobiological data identified 258 frugivory, 144 seed predation, and 43 herbivory interactions between taxa at our study site. Literature data were especially useful for identifying herbivory interactions; however, for all three interaction types, literature and research-based observations were less effective than ethnobiological data in detecting interactions in secondary forests (Fig. S2).

3.2. Centrality

Eulemur rubriventer and *Propithecus candidus* were most central in the primary forest (Fig. 2, Table S4). Nocturnal lemurs were more central to secondary forest networks, with *Cheirogaleus crossleyi* most central to the frugivory and seed predation networks and *Avahi laniger* most central to the herbivory network. For centrality results for tree genera, see Table S5 and Table S6.

PageRank centrality values for tree genera were associated with both ecological and human traits, but relationships differed between land use and interaction types. Tree centrality for the primary forest frugivory network was negatively related to endemism (estimate = -0.707 , $p = 0.031$) and wood density (estimate = -0.263 , $p = 0.053$, marginally significant; Fig. 3a). Wood density was also negatively associated with tree centrality in the primary forest herbivory network (estimate = 0.321 , $p = 0.078$, marginally significant; Fig. 3c). Traits were not significantly associated with centrality in the primary forest seed predation network. While diameter, endemism, and wood density were consistently negatively associated with tree centrality in the secondary forest networks, results were not statistically significant (Fig. 3). We did not detect evidence of phylogenetic signal in the relationship between functional traits and centrality, except for some evidence for very weak phylogenetic signal. See Table S7 for full model results and Table S8 for λ values.

Tree centrality in the primary forest networks was not significantly related to the proportion of participants reporting human use (Fig. 4a, Table S9). Genera central to secondary forests, however, were more likely to be used by people in the frugivory (estimate = 0.787 , $p = 0.069$, marginally significant) and herbivory (estimate = 1.578 , $p = 0.015$) networks than non-central genera. Likewise, there were no significant relationships between tree centrality and human use richness, a measure of use versatility, for the primary forest networks (Fig. 4b, Table S9). Centrality was positively associated with human use richness in the secondary forest herbivory network (estimate = 34.58 , $p = 0.040$), but not for the frugivory (estimate = 11.607 , $p = 0.233$) or predation (estimate = 12.204 , $p = 0.634$) networks. In other words, tree genera more central to the secondary forest herbivory network also provided more multipurpose uses for people compared to non-central genera. We detected evidence that closely related tree genera had similar centrality measures in the predation primary forest network. See Table S9 for full model results and Table S10 for λ values.

4. Discussion

Ecological and human use traits were associated with lemur-tree interactions across a human-modified landscape. Despite substantial differences in network species composition between primary and secondary forests, seven lemur species connected primary and secondary forests, feeding on trees in both land use types and driving the flow of ecological resources across the landscape. Nocturnal lemurs played a key role in the secondary forest networks, highlighting the potential importance of nocturnal, small-bodied animals for promoting ecological functioning (Ramananjato, 2024). Tree centrality was related to both ecological and human use traits, but results varied by land use and interaction types. Notably, human use was positively associated with tree centrality in the secondary forest, but not in the primary forest.

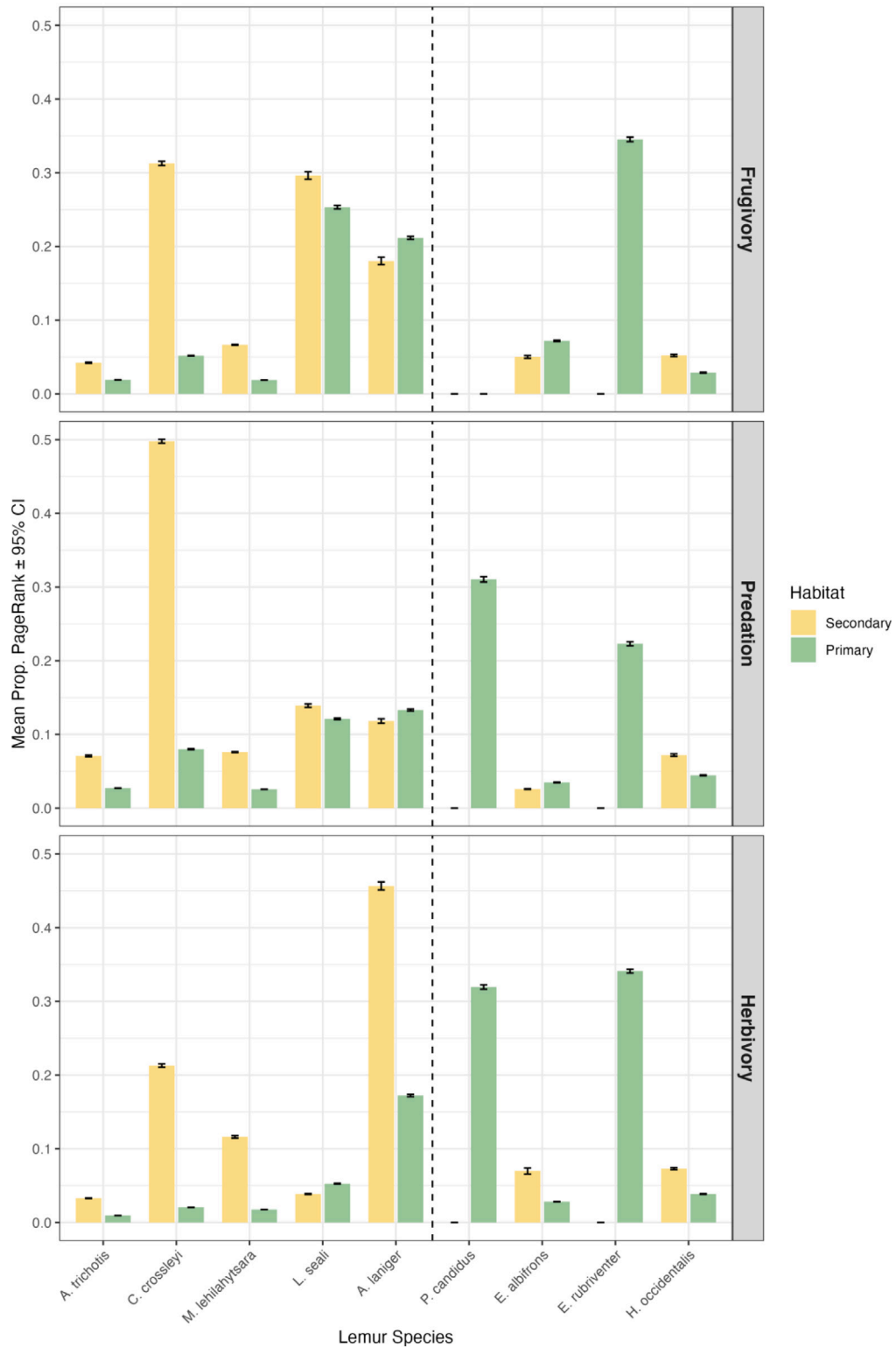


Fig. 2. PageRank centrality values and 95% confidence intervals for lemur species. Colors represent land use type. Values are presented as the proportion of total PageRank for each habitat/ interaction combination. The dashed line separates nocturnal (left) from diurnal/ cathemeral (right) lemur species. For tree genera centrality, see Figure S4.

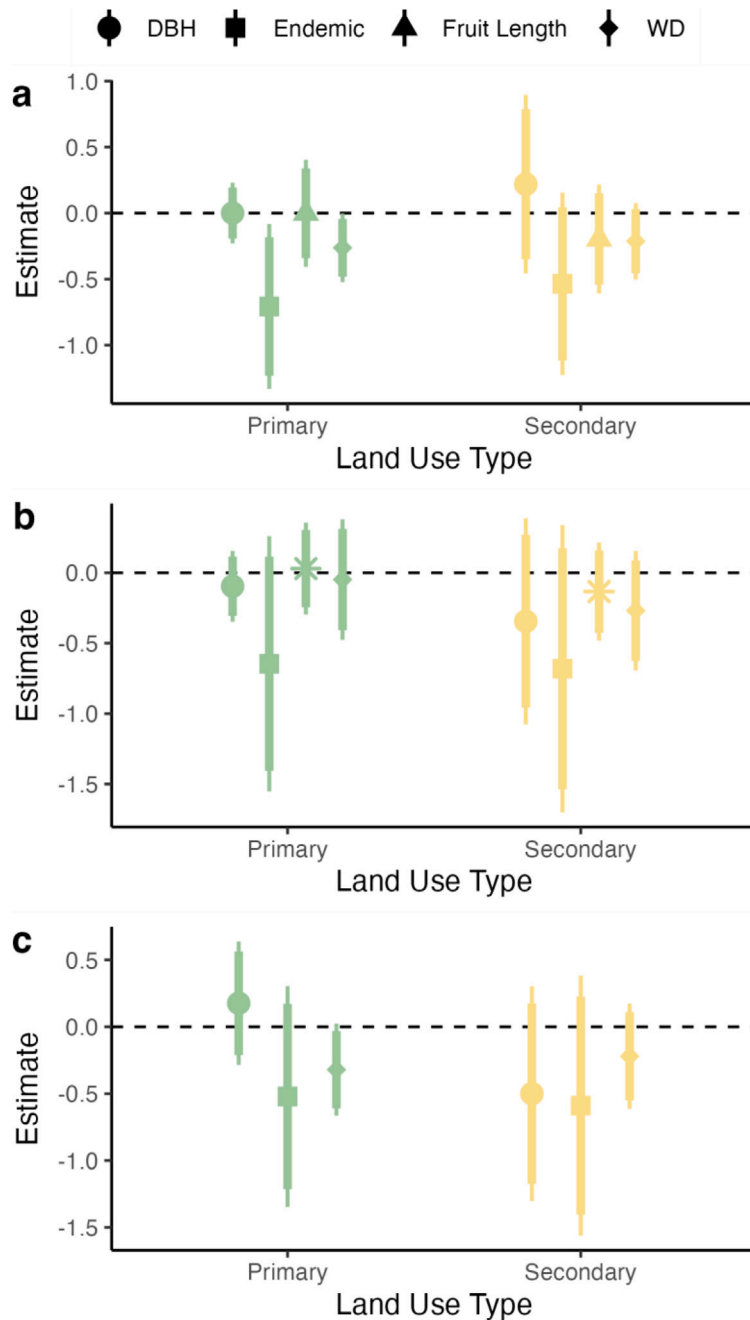


Fig. 3. PGLS results of the relationships between tree genera structural importance (log PageRank centrality) and ecological traits for (a) frugivory, (b) predation, and (c) herbivory networks. DBH is diameter at breast height and WD is wood density. Points represent mean estimates, thick vertical bars represent 95% confidence intervals, and thin vertical bars represent 90% confidence intervals. Colors indicate land use type, where green is primary forest and yellow is secondary forest. λ values are in Table S8.

4.1. Mechanisms of centrality

While large-bodied lemurs tended to be central to primary forest networks, nocturnal lemurs — including small-bodied species — tended to play the largest role in secondary forest network structure, emphasizing their importance for ecological functioning across human-modified landscapes (Fig. 2). Nocturnal lemurs did not necessarily interact with more trees than diurnal lemurs; rather, they were more abundant than diurnal lemurs in both primary and secondary forests (Table S2). Nocturnal lemurs are often more abundant than diurnal lemurs in secondary habitats (Herrera et al., 2011). Small nocturnal lemurs (family

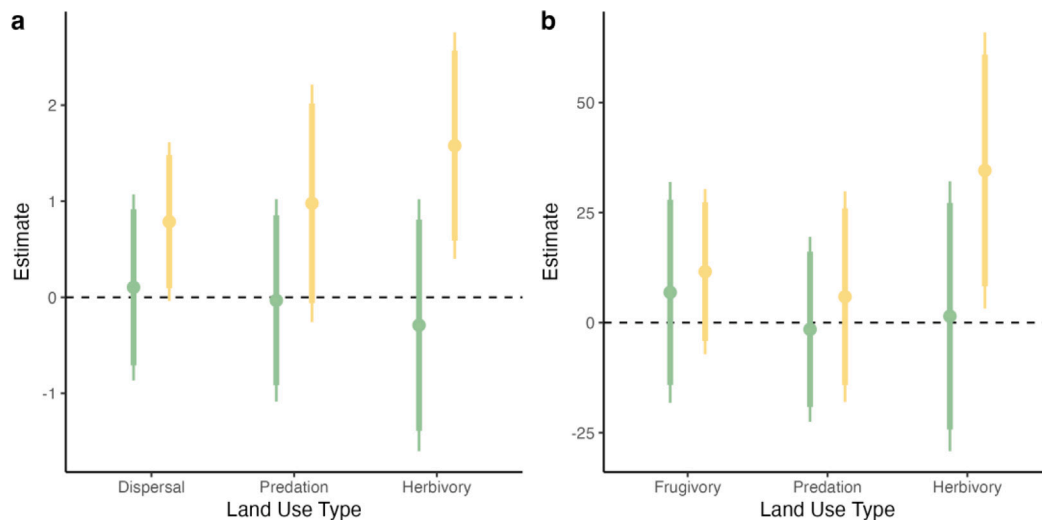


Fig. 4. PGLS results of the relationships between tree genera structural importance (log PageRank values) and human use traits: (a) human use proportion and (b) human use richness. Points represent mean estimates, thick vertical bars represent 95% confidence intervals, and thin vertical bars represent 90% confidence intervals. Colors indicate land use type, where green is primary forest and yellow is secondary forest. λ values are in Table S10.

Cheirogaleidae) have a generalized diet and are known to exhibit dietary flexibility in degraded habitats, for example by feeding on invasive species (Hending, 2021; Ramananjato et al., 2020; Ramananjato, 2024). Disturbance can also increase forest light gaps, prompting understory growth and new leaf flushes that provide habitat and food that may be preferred by some small nocturnal species (Hending et al., 2024). Furthermore, nocturnal lemurs are less vulnerable to hunting compared to diurnal lemurs (Borgerson et al., 2022). Nocturnal lemurs are also important for network stability in forest edges (Raolinjanakolona et al., 2023). Given the growing evidence that small nocturnal mammals can be important seed dispersers and facilitate seedling recruitment in regenerating forests, greater attention should be paid to their role in forest regeneration (Godó et al., 2022; Ramananjato, 2024).

Ecological tree traits predicted network centrality, an indicator of importance of tree genera to network structure. Wood density tended to be negatively associated with tree genera centrality (Fig. 3). In particular, the negative relationship between wood density and tree centrality to the herbivory network is likely related to the leaf economic spectrum, whereby plant traits depend on resource acquisition strategy (Wright et al., 2007; Chave et al., 2009). Low wood density plants tend to have palatable, high-nutrient leaves. Trees with low wood density tend to be fast-growing (King et al., 2006) and seasonally flush with young leaves that are preferable to folivorous lemurs. Trees with low wood density typically grow more quickly and have higher fruit production, though the fruits they produce are often lower in nutritional content. Low wood density trees may also be less dependent on particular environmental conditions for fruit production (Lima and Rodal, 2010). In contrast, high wood density plants tend to have more conservative resource acquisition strategies, growing slowly leading to thicker, less palatable leaves and fewer, nutritionally-dense fruits. Furthermore, wood density is closely related to phenology in tropical trees (Lima and Rodal, 2010), which drives patterns in lemur food availability. The negative relationships between wood density and centrality suggests that land use change may alter forest carbon storage through its effects on species interactions (Razafindratsima et al., 2018). However, wood density had no relationship with tree centrality in the primary forest seed predation network, which may reflect opportunistic seed predation on a high diversity of plants.

Surprisingly, tree centrality was not associated with fruit length in frugivory networks or seed mass in predation networks. While fruit size is often positively related to ecological network centrality (e.g., Crestani et al. (2019)), research has shown that more lemur species disperse small-fruited than large-fruited trees (Albert-Daviaud et al., 2020). In line with previous research (DeSisto et al., 2020), the negative relationships we observed between tree centrality and endemism status highlight that non-endemic trees can be important food sources for frugivorous lemurs in human-modified landscapes. Endemic trees may be consumed by fewer lemurs in these networks due to their relatively low abundances compared to non-endemic trees. Other than endemism status, the focus of our study was primarily on morphological ecological traits; future research should consider how other fruit traits predict network centrality. For example, lemurs are sensory foragers, with fruit color and odor predicting fruit selection (Valenta et al., 2013, 2015).

Tree centrality was also related to human use traits. Contrary to our predictions and other research (Brown et al., 2013), tree genera central to secondary forest networks were more frequently reported to be used by people than those in the primary forest (Fig. 3a). There is likely a proximity effect whereby people use secondary forest trees for certain everyday uses such as firewood because it is more convenient. People must weigh trade-offs between the labor required to harvest forest resources and the quality or purpose of the trees. Additionally, people could be propagating the tree species they use by protecting the useful trees, selectively removing less useful trees, and/or dispersing seeds or seedlings (Levis et al., 2018). Central trees had greater human use richness, i.e., they were used for more distinct purposes, but only in the secondary forest herbivory network (Fig. 4b). Many tree genera commonly found in the secondary forest are multipurpose; *Harungana*, for example, was the most central genus to the secondary

forest network and had the fourth highest use richness score of any genus in our data. Given the reliance of local communities on plant resources for their livelihoods (Vezina et al., 2020), ecological interactions in secondary forests are important for human resource provisioning.

Tree centrality to ecological networks was generally not shaped by evolutionary history (Tables S8, S10). However, we found some weak evidence for phylogenetic signal in the primary forest seed predation network. Our results suggest that lemurs did not tend to feed on trees based on shared ancestry, especially in frugivory and herbivory networks. Instead, centrality of trees to ecological networks may be driven at least in part by functional trait convergence of ecologically unrelated genera (Donatti et al., 2011). Ecological trait convergence in frugivory networks can be explained by the Dispersal Syndrome hypothesis, whereby fruit traits result from selection by seed dispersing frugivores. For example, fruit color (not measured in this study) is independent of phylogeny but can be an important signal for frugivores (Lomáscolo and Schaefer, 2010). Anthropogenic trait filtering may also explain the lack of phylogenetic signal in our data; people alter plant community composition by selective foraging, cultivation, and disturbance (Suding et al., 2008).

4.2. Limitations

Our approach to weighting the network edges influenced our results. Our estimates of population densities, and consequently edge weights, are subject to potential biases. The rarity of lemur species resulted in relatively few observations for some species. In the rarest species (*H. occidentalis*), for example, we documented only 19 observations. Most of the species in the dataset were observed at higher frequencies (mean=109; sd=52), providing more robust estimates of density. Furthermore, we used the product of species-level lemur biomass and genus-level tree basal area as a proxy for interaction frequency, and therefore did not consider species-specific variation in interaction quality, such as foraging rates and frugivory outcomes. In reality, interaction frequencies are also shaped by their environment, individual foraging behaviors, and the spatial distribution of plants (Schupp et al., 2010; Wells and O'Hara, 2013; Eppley et al., 2016). By assuming that feeding interactions are proportional to lemur biomass and tree basal area, our approach therefore obscures ecological nuances. In particular, this approach may overestimate the importance of abundant generalists. While interaction frequency proxies are valuable and often necessary given resource constraints and cryptic interactions, investment in long-term, field-validated feeding observations will improve ecological network analysis.

Our data collection methods are subject to bias. Notably, empirical observations are subject to diurnal bias and under-represent nocturnal lemur species. We therefore combined ethnobiological data with research-focused observations and literature sources to improve network completeness (Braga-Pereira et al., 2022; Camino et al., 2020; Ong et al., 2022). Ethnobiological data substantially increased the number of interactions we documented in COMATSA-Sud — especially cryptic interactions such as those by nocturnal lemurs. We would have therefore failed to identify the importance of nocturnal lemurs to ecological networks without the inclusion of ethnobiological data. However, additional cryptic species and rare interactions are likely missing from our networks. We combined data from ethnobiological interviews, field observations, and literature sources rather than using different data types for cross-validation. Through this approach, we were able to take advantage of the unique strengths of each data type. However, this approach may leave the networks vulnerable to recall bias, which can influence the completeness and reliability of ethnobiological data (e.g., Medeiros et al. (2014a,b)). In Madagascar's rainforests, recall and identification accuracy are likely biased against nocturnal lemur species but in favor of plant species that people commonly use. Ethnobiological data are often network subsets and can induce other biases, such as overestimating connectance and underestimating modularity (Zhu et al., 2023). Future research would benefit from explicitly evaluating bias in ethnobiological data of species interactions.

Genus-level analysis of trees may mask nuances of species-specific interactions. Genus-level analyses of plant data are prevalent in research across Madagascar, where the flora is highly diverse and endemic (Goodman et al., 2019) and where many plant species are not yet described in the scientific literature (Antonelli et al., 2022). Species-level trait data are also challenging, and often unfeasible, to collect. To mitigate this limitation and avoid introducing systematic bias that could favor specific hypotheses, we applied the genus-level approach consistently across all land-use and interaction types. Nevertheless, genus-level pooling may obscure ecological patterns, especially of rare species and specialist interactions (Table S11). In particular, we identified at least four genera which represented multiple species across our botanical plots: *Albizia*, *Dombeya*, *Ficus*, and *Solanum*. Future research considering species-specific variation in interaction quantity and quality would provide valuable insights into the ecological roles of different plant and lemur species (González-Castro et al., 2022).

4.3. Conservation implications and conclusions

Our results show that both ecological and human use traits were related to the structure of frugivory, seed predation, and herbivory networks. Trait-based relationships, however, differed according to land use type; forest conversion likely affects both ecological functioning and human resource provisioning by altering plant-animal interactions. Globally, unsustainable anthropogenic resource extraction jeopardizes the structural integrity of ecological processes (Aslan et al., 2013; Valiente-Banuet et al., 2015). In Madagascar, deforestation is threatening diverse species with extinction (Vieilledent et al., 2018; Suzzi-Simmons, 2023), and our results show that functional traits may mediate the cascading impacts on ecosystems and people by influencing lemur-plant interactions. Unsustainable natural resource use therefore threatens both biodiversity and human well-being in a habitat stronghold for endangered species (Eppley et al., 2024). Nevertheless, human-modified forests still support high levels of interaction richness, biodiversity (Wurz et al., 2022), and resources to local communities, including water, food, and medicinal plants. Combining

research-focused observations with ethnobiological data provides critical insights into the role of functional traits in ecological functioning within and among different land use types across heterogeneous landscapes.

Network centrality can be a valuable conservation tool. Conserving lemur species that are central to seed dispersal networks may promote forest restoration by contributing to regeneration (Chapman and Dunham, 2018). Central tree genera (Fig. S4) should be considered for planting in reforestation efforts (Windsor et al., 2021) because they may promote a positive feedback loop for the benefit of both lemurs and trees. Furthermore, attention to human use traits of tree species can help conservation practitioners design planting regimes that promote ecological functioning while conserving cultural resources. Conserving lemur-plant interactions may also be important for other ecosystems such as grassland matrices. For example, certain lemur species feed on grasses (Eppley et al., 2011), and Steffens et al. (2020) found that *Microcebus* encounter rates were similar in grassland matrices compared to nearby forest fragments. Our trait-based network framework may therefore be extended to advance conservation across additional ecosystems in Madagascar (dry forests, grassland matrices, etc.) and beyond. Conservationists should also consider different interaction types in multifunctional systems. For example, it is possible that networks of antagonistic interactions, such as those involving seed predation, are more specialized than mutualistic interactions, such as seed dispersal, although we did not necessarily find evidence for that in our data (Fig. S2).

Overall, our study contributes to the literature on ecological interactions in human-modified systems in several key respects. First, we combined research-focused observations with ethnobiological data to improve understanding of ecological networks, building on recent research frameworks (e.g., Ong et al. (2021), Durand-Bessart et al. (2024)). We also employed trait-based network analysis of multiple trophic interaction types — frugivory, seed predation, and herbivory — rather than focusing on a single interaction, to capture important ecological nuances. Additionally, we compared networks in primary and secondary forests to advance understanding of ecological functioning under contrasting land use regimes. Together, these approaches represent a nuanced framework for assessing ecological functioning in human-modified landscapes.

CRedit authorship contribution statement

Camille M.M. DeSisto: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Roméo Bezaralahy:** Writing – review & editing, Methodology, Investigation. **Candidier Dimbiarijaonina:** Writing – review & editing, Methodology, Investigation. **Razara Emerancine:** Writing – review & editing, Investigation. **Telesy Feno:** Writing – review & editing, Investigation. **Edouard Mahazandry:** Writing – review & editing, Investigation, Conceptualization. **Jeantauné Njakandrina:** Writing – review & editing, Investigation. **Charles L. Nunn:** Writing – review & editing, Supervision. **Edgar Rabevaeo:** Writing – review & editing, Investigation. **Mamy Omega Raharizafinirina:** Writing – review & editing, Investigation. **Sidonie Olivia Rakotoarisoa:** Writing – review & editing, Investigation. **William Ramalanjaona:** Writing – review & editing, Investigation. **Dominique Randrianasolo:** Writing – review & editing, Investigation. **Jean Randrianasy:** Writing – review & editing, Investigation. **Manadina Rasolofo:** Writing – review & editing, Investigation. **George Raveloson:** Writing – review & editing, Investigation. **Marie Rolande Soazafy:** Writing – review & editing, Investigation. **Jean Tiamanana:** Writing – review & editing, Investigation. **Eric Tsilanizara:** Writing – review & editing, Investigation. **Zico Zandry:** Writing – review & editing, Investigation. **Franclin Zerimanana:** Writing – review & editing, Investigation. **John R. Poulsen:** Writing – review & editing, Supervision, Methodology. **James P. Herrera:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.gecco.2025.e03729>.

Data availability

Research Link Provided

[LemurTraitNetwork \(Original data\)](#) (GitHub)

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