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Structure and Stability of Lemur-Tree Ecological Networks Across Primary and Secondary Forests

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ABSTRACT

Forest degradation is disrupting species interactions, altering the structure and stability of ecological communities. Understanding the organization of species interactions across human-modified landscapes is urgent in biodiverse areas experiencing major conservation threats, such as Madagascar. In both primary and secondary forests in northeast Madagascar, we investigated lemur-tree network structure and stability. We combined ethnobiological data (interviews with 81 local knowledge holders) with direct observations during field work to construct ecological networks representing frugivory, herbivory, and seed predation. In a multilayer approach, we examined interactions both within and between forest types. We found that primary forest networks supported substantially higher interaction abundances, diversity, and evenness compared to secondary forest networks. There were also differences in structure across interaction types; for example, herbivory networks had a more modular structure than frugivory or seed predation networks. Simulated species extirpation showed that primary forests were more stable to perturbations than secondary forests or multilayer systems, even after accounting for how lemurs likely adjust their diets as plants go locally extinct (i.e., interaction rewiring). While seven lemur species connected primary and secondary forests, multilayer networks were consistently less stable than single-layer networks, emphasizing the likely vulnerability of human-modified landscapes to environmental change and the ecological importance of species that connect the primary and secondary forest networks.

James P. Herrera and John R. Poulsen are co-last authors.

Résumé

La dégradation des forêts perturbe les interactions entre les espèces, modifiant la structure et la stabilité des communautés écologiques. Il est urgent de comprendre l'organisation des interactions entre espèces dans les paysages modifiés par l'homme dans les zones de biodiversité confrontées à d'importantes menaces pour la conservation, comme Madagascar. Dans les forêts primaires et secondaires du nord-est de Madagascar, nous avons étudié la structure et la stabilité des réseaux. Nous avons combiné des données ethnobiologiques (entretiens avec 81 détenteurs de savoirs locaux) avec des observations directes pendant les travaux sur terrain pour construire des réseaux écologiques représentant la frugivorie, l'herbivorie et la prédation des graines. En utilisant une approche multicouche, nous avons examiné les interactions au sein des types de forêts et entre eux. Nous avons constaté que les réseaux de forêts primaires présentaient des abondances, une diversité et une régularité des interactions nettement supérieures à celles des réseaux de forêts secondaires. Des différences de structure ont également été observées selon les types d'interaction; par exemple, les réseaux d'herbivorie présentaient une structure plus modulaire que les réseaux de frugivorie ou de prédation des graines. La simulation de la disparition des espèces a montré que les forêts primaires étaient plus stables aux perturbations que les forêts secondaires ou les systèmes multicouches, même après avoir pris en compte la manière dont les lémuriens adaptent probablement leur régime alimentaire à mesure que les plantes disparaissent localement (c'est-à-dire le recâblage des interactions). Alors que sept espèces de lémuriens reliaient les forêts primaires et secondaires, les réseaux multicouches étaient systématiquement moins stables que les réseaux monocouches, soulignant la vulnérabilité probable des paysages modifiés par l'homme aux changements environnementaux et l'importance écologique des espèces qui relient les réseaux forestiers primaires et secondaires.

1 | Introduction

Accelerating deforestation is threatening Earth's terrestrial biodiversity (Newbold et al. 2015). The world has lost 178 million ha of forest since 1990 (FAO 2020) and 68% of vertebrates since 1970 (Almond et al. 2020). The tropics, home to 45% of the world's forests, are experiencing the highest rates of forest loss globally (FAO 2020). Activities like selective logging and hunting can further exacerbate tropical biodiversity loss. Biodiversity reduction—largely driven by high-income consumer countries (Hoang and Kanemoto 2021)—diminishes ecosystem services such as carbon storage and human resource provisioning (Borma et al. 2022; Gibson et al. 2011). Forest conservation and regeneration is therefore critical for mitigating the consequences of deforestation on biodiversity and human well-being (Strassburg et al. 2020).

In particular, understanding functional differences between regenerating secondary forests and primary forests is a conservation priority. Primary forests make up only 34% of the total forested area worldwide and 38% of forested area in Africa (FAO 2020). While aboveground biomass can recover quickly in regenerating tropical forests, regrowth is nutrient-limited and recovery of plant biodiversity can be slow (Martin et al. 2013; Powers and Marʹın-Spiotta 2017). In addition to diminished plant diversity, tropical secondary forests tend to support lower levels of faunal diversity compared to primary forests (Barlow et al. 2007). The functional outcomes of succession, such as its consequences for ecological interactions, depend on animal foraging behaviors. For example, in the Brazilian Atlantic forest, primary forests were characterized by more complex forest structure which may benefit specialist animals, whereas early-successional forests supported higher total fruit availability, which may benefit generalist animals (Pinotti et al. 2012). Species interactions are a key component of successional dynamics in human-modified systems.

Anthropogenic activities such as forest degradation affect the structure of ecological interactions within communities (Tylianakis and Morris 2017). For example, modular network structure, where species in one subgroup interact more with each other than those in other subgroups, is associated with low anthropogenic impacts (Morrison et al. 2020; Sebastián-González et al. 2015). In turn, ecological network structure affects community stability—i.e., resilience to perturbations in the environment. Modularity tends to increase stability (Grilli et al. 2016). Anthropogenic activities may therefore decrease network stability (e.g., Vitali et al. 2023), although this is not always the case (e.g., Morrison et al. 2020; Vizentin-Bugoni et al. 2019). Comparing the structure and stability of interactions in different environmental contexts sheds light onto the consequences of human activities for ecosystem functioning. Adjacent forests with different land use histories are, however, rarely ecologically isolated. Accounting for interactions both within and among different environmental contexts is therefore an important research frontier.

The response of network structure and stability to forest conversion is particularly important in biodiverse areas experiencing major conservation threats, such as Madagascar (Antonelli et al. 2022; Ralimanana et al. 2022). Madagascar's endemic primate group—lemurs—promote ecosystem functioning across the island through a diversity of feeding interactions including frugivory, herbivory, and seed predation (Albert-Daviaud et al. 2018; Razafindratsima 2014; Razafindratsima et al. 2025; Steffens 2020). However, anthropogenic activities such as widespread deforestation (Vieilledent et al. 2018, 2023) threaten 94% of extant lemurs with extinction (Schwitzer et al. 2014). Lemurs exhibit response variation to disturbance; for example, species with high behavioral flexibility (e.g., *Eulemur* spp.) and small nocturnal species (family Cheirogalidae) can be tolerant to forest edge habitat (Andriatsitohaina et al. 2020; Lehman and Mercado Malabet 2022; Schüßler et al. 2018). Behavioral flexibility may enhance network stability by promoting interaction redundancy and/or increasing robustness through rewiring.

Hunting can also affect lemur populations, especially for large-bodied species (Borgerson et al. 2022). Consequently, small-bodied lemurs may play an important role in ecological stability in Madagascar's human-modified forests.

Ecological networks across Madagascar are less stable to lemur loss compared to plant loss (DeSisto and Herrera 2022), and the loss of Critically Endangered lemurs could leave 164 plant species without dispersal services (Tonos et al. 2024). Frugivory networks in Madagascar's edge forests are, however, similarly stable compared to those in the forest interior (Raoelinjanakolona et al. 2023). Despite the urgency of conserving lemur-plant interactions and the rich literature on Madagascar's lemur-plant interactions (Razafindratsima et al. 2022; Steffens et al. 2022), substantial gaps in our knowledge persist, even in the most comprehensive academic compilations (Tonos et al. 2024).

Accounting for place-based knowledge provides a means to address these sampling gaps, particularly in areas where local people have a rich understanding of plants, animals, and their ecological interactions. Most ecological network studies primarily use data collected by academically trained researchers following standardized scientific methods. While highly valuable, field sampling of interactions is challenging and often geographically and taxonomically biased (Jordano 2016; Vitorino et al. 2022). Combining data from different methodologies is therefore an important tool for mitigating undersampling and improving estimates of network structure (Quintero et al. 2022). In particular, ethnobiological data—information from people who engage with and depend on their natural environments—greatly enriches our understanding of ecological networks (Berkstrom et al. 2019; Braga-Pereira et al. 2022; Camino et al. 2020; Durand-Bessart et al. 2024; Ong et al. 2022). Ethnobiological data collected by place-based actors also promotes more effective biodiversity science and conservation (Copete et al. 2023). Addressing conservation threats to lemurs and their ecological interactions requires trans-disciplinary, anti-colonial approaches, and strong community engagement (Ramananjato et al. 2025; Razafindratsima et al. 2025).

Combining standard scientific methods and ethnobiological data, we examined ecological network (a) structure and (b) stability in the COMATSA-Sud protected area of northeast Madagascar. COMATSA-Sud is characterized by primary forests with no known history of clear-cutting, along with secondary forests that have experienced historic clear-cutting due to agriculture and ongoing selective logging and hunting pressure. We constructed single layer networks representing interactions within primary and secondary forests and multi-layer networks representing interactions both within and among forest types. The three interaction types—frugivory, herbivory, and seed predation—are examined in separate networks. We hypothesized that past forest conversion drives network structure by reducing tree biodiversity and altering lemur foraging behavior. However, flows between secondary and primary forests likely also regulate network properties. Compared to primary forest networks, we predicted that secondary forests would be less taxonomically diverse and less strongly organized into subgroups (Brown et al. 2013; Felipe-Lucia et al. 2020; Takemoto and Kajihara 2016). We expected secondary forest networks to be less stable than primary forest networks (Raoelinjanakolona et al. 2023; Vitali et al. 2023), but that multilayer networks would be more stable due to increased interactions. Networks are predicted to be more stable under plant loss than lemur loss (DeSisto and Herrera 2022; Raoelinjanakolona et al. 2023). Accounting for multiple knowledge systems, interaction types, and land use histories is essential for advancing conservation in human-modified landscapes.

2 | Methods

2.1 | Study Site

We conducted research in the COMATSA-Sud protected area in the SAVA region of northeast Madagascar. COMATSA-Sud is managed by local forest management associations called *Vondron'Olona Ifotony* (VOI), with support from the World Wildlife Fund, and is underrepresented in lemur science (Ramananjato et al. 2025). Ten lemur species occur in the area: three cathemeral (active during day and night; *Eulemur albifrons, Eulemur rubriventer, Hapalemur occidentalis*; family Lemuridae), one diurnal (*Propithecus candidus*; family Indriidae), and six nocturnal [*Allocebus trichotis* (Cheirogaleidae), *Cheirogaleus crossleyi* (Cheirogaleidae), *Microcebus lehilahytsara* (Cheirogaleidae), *Avahi laniger* (Indriidae), *Lepilemur seali* (Lepilemuridae), and the highly cryptic *Daubentonia madagascariensis* (Daubentoniidae)] (Rabearivony et al. 2015). We conducted research in primary forests—areas that have never been clear-cut but where some anthropogenic disturbances such as hunting with snare traps and selective logging still occur, although rarely while researchers are present—and secondary forests—re-grown areas that were clear-cut for agriculture 15–20 years prior to research (Chokkalingam and De Jong 2001). At our study site, secondary forests were regenerating from past burning for agriculture, as well as other disturbances such as erosion from a landslide. Ongoing logging and hunting also occur in secondary forests.

2.2 | Network Construction

We constructed lemur frugivory, herbivory, and seed predation bipartite networks for primary and secondary forests by combining empirical observations of interactions from fieldwork and collected from the literature (Lyons 2013; Steffens 2020) with ethnobotanical survey data representing local knowledge of lemur-plant interactions (Figure 1). Frugivory networks represented tree fruit consumption by lemurs, herbivory networks represented lemur consumption of non-vegetative plant material (e.g., leaves, flowers, wood, bark), and seed predation networks represented the destructive consumption of seeds by lemurs. Many frugivory interactions result in seed dispersal (i.e., the movement of seed from the parent plant, resulting in a new plant recruit (Schupp et al. 2010)), but some frugivory interactions may not result in seed dispersal. Interactions were identified at the species level for lemurs and at the genus level for trees and subset to include only the 82 tree genera occurring in our study site, as identified by botanical plots. Lemur species were

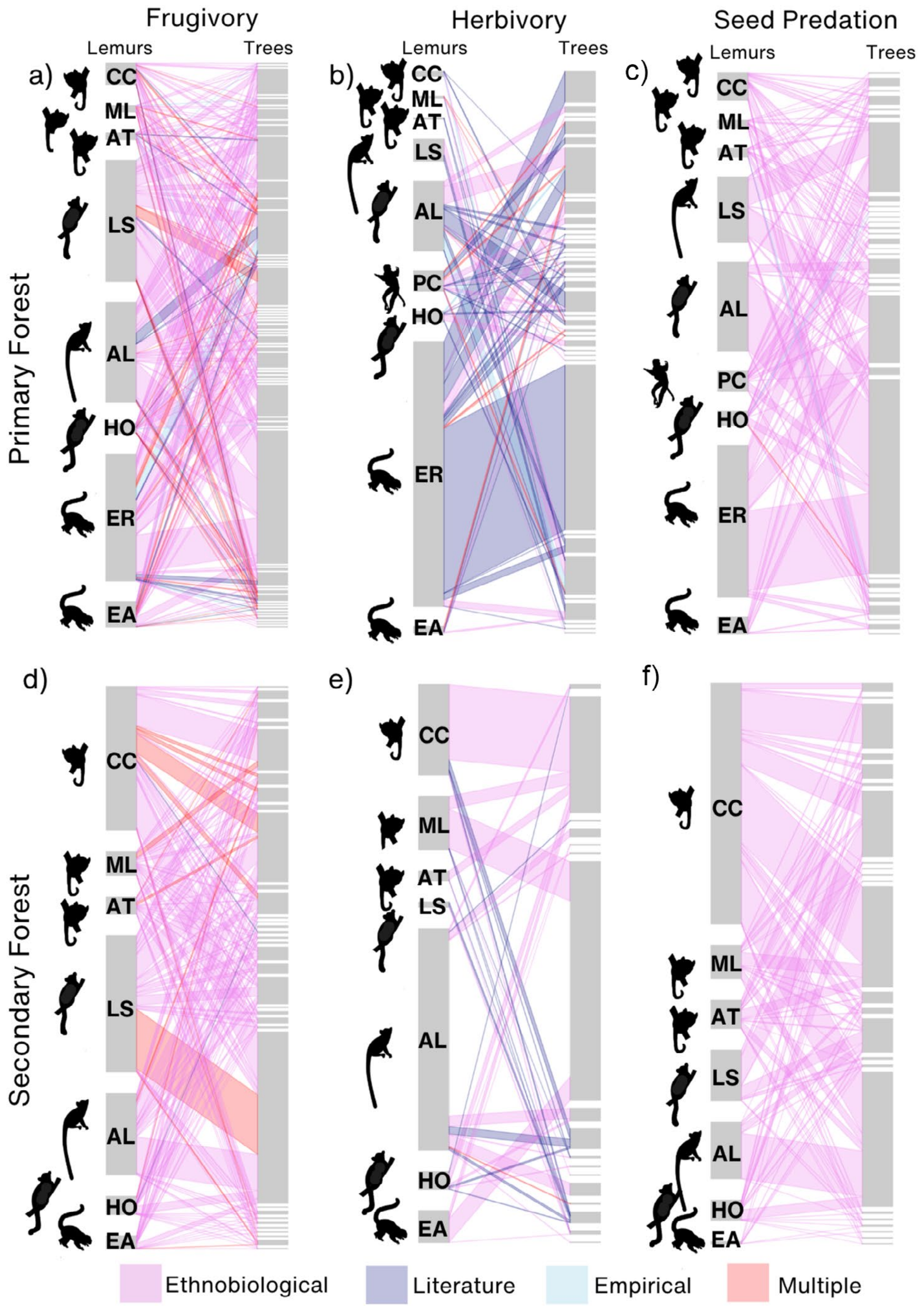

FIGURE 1 | Food web plots showing the bipartite networks for the primary forest (a–c) and secondary forest (d–f). Edge widths represent the mean product of species-level lemur biomass and genus-level tree basal area. Pink lines represent interactions identified by ethnobiological data, purple lines represent interactions identified by literature data, blue lines represent interactions identified by empirical observations, and red lines represent interactions identified by multiple data sources. Lemur species are grouped by family: Cheirogaleidae (CC = *Cheirogaleus crossleyi*, ML = *Microcebus lehylahitsara*, AT = *Allocebus trichotis*), Lepilemuridae (LS = *Lepilemur seali*), Indriidae (AL = *Avahi laniger*, PC = *Propithecus candidus*), and Lemuridae (HO = *Hapalemur occidentalis*, ER = *Eulemur rubriventer*, EA = *Eulemur albifrons*). Created using bipartite (Dormann et al. 2008), BioRender, Canva, and PhyloPic.

one mode in the bipartite network, plant genera were the second mode, and edges represented the feeding interactions connecting these two modes.

We also constructed a multilayer network for each interaction type, with primary and secondary forests as the two layers. The two layers were connected by lemurs that occurred in and provided ecological services for both forest types. We weighted interlayer edges as the proportion of lemurs occurring in the primary and secondary forests.

2.2.1 | Edge Weights

Edge weights were quantified as the product of lemur body mass and tree basal area, a proxy for interaction frequency.

To estimate lemur population densities for constructing edge weights, we surveyed lemur populations in the primary and secondary forests. We used standardized line-transect surveys and distance sampling methods that account for survey effort (Buckland et al. 2010; Herrera 2016; Whitesides et al. 1988). We established four ~1 km transects in the primary forest and two in the secondary forest (Table S1), representing approximately 40 ha of secondary forest and 100 ha of primary forest samples. Due to the fragmented, discontinuous nature of secondary forest patches in the study site, it was not feasible to establish additional secondary forest transects. To account for the uncertainty associated with the limited spatial sample size, we generated 100 density estimates for each lemur species from posterior distributions of density models (detailed below). This approach enabled us to account for sampling limitations and capture the full range of plausible density values of each lemur species given the observed data and model structure. Transects were established at least 500 m apart to minimize the likelihood of individuals moving between them and to maintain the independence of our data. However, it is possible that lemur individuals could traverse multiple transects in some cases.

Two to four trained researchers conducted surveys during the day (between 7:15 and 11:00 h for morning surveys; $\bar{X}$ 33.00 repetitions per transect, SD 10.12; ~1 km/h) and night (between 17:15 and 22:30 h; $\bar{X}$ 21.50 repetitions per transect, SD 1.05; ~0.5 km/h) for a total of 318.5 km (Table S1). Researchers rotated between nocturnal and diurnal surveys. For all observed lemur groups, 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. These data were collected from June 2022 to November 2023.

For all nine lemur species observed, we estimated population densities (individuals/ha) in the primary and secondary forests using the R package unmarked (Table S2; Kellner et al. 2023). We did not observe *Daubentonia madagascariensis*. This modeling approach allowed us to estimate lemur group density while accounting for imperfect detection by explicitly separating detection probability from true density (Fiske and Chandler 2011), thus reducing bias introduced by heterogeneity in habitat openness and animal behavior. Due to limited sample sizes for some species (particularly the rarer and threatened diurnal species; Table S3), we were unable to model detection separately for the primary and secondary forest. Sighting distances were similar between primary (mean = 9 m, SD = 7) and secondary (mean = 13 m, SD = 9) forests (Figure S1), so we modeled detection probability separately for both habitat types.

We compared half-normal, hazard, and null functional form models of detection probability based on the Akaike information criterion (AIC), removing extremely far data points (1.5% of observations) and accounting for survey effort in km surveyed. If AIC values were equivalent (within 2), we used half normal functions. Using the best model for each species, we jointly estimated lemur group densities for primary and secondary forests. We calculated population abundances per forest type by multiplying predicted group densities by mean species group size, rounding to the neared integer. To obtain lemur density values, we generated distributions of 100 density estimates based on the model posterior distributions. Based on the posterior draws from the fitted distance sampling models, we constructed 100 networks for each interaction type (frugivory, herbivory, seed predation) × land use type (primary forest, secondary forest), for a total of 600 networks. We weighted edges by interaction frequency—i.e., the product of lemur biomass (population density multiplied by mean species-level body mass) and tree basal area (abundance multiplied by mean genus basal area) from the primary and secondary forests, rounded to the nearest integer.

While we had fewer than the recommended number of sightings for distance modeling for three lemur species (Table S3; Buckland 2001; Marshall et al. 2008), we restricted our model set to simpler models and inspected the models for goodness-of-fit using the Shapiro-Wilks test. The tests and visual inspection of the histograms and detection functions (Figure S2) showed that, even for species with small sample sizes, which, the models were adequate, and the functions realistically fit the distributions. Further, the histograms were right-skewed, and the data followed predicted patterns (e.g., most sightings were closer to the transect).

We quantified tree densities (individuals/ha) in the primary and secondary forests by establishing botanical plots (20 m × 50 m), 29 in primary forest and 20 in secondary forest. We identified trees to the vernacular name, later translated into Latin names based on herbarium specimens identified by a technician from the Missouri Botanical Garden office in Anjangoveritra, Sambava district. In each plot, we measured every tree and palm ≥ 5 cm diameter at breast height (DBH), for a total of 9094. Over 99% of individual trees were identified to at least the genus, across 86 genera. We chose to include every tree ≥ 5 cm DBH instead of the more commonly used ≥ 10 cm DBH to ensure that we account for smaller adult trees that still contribute to the ecological networks, especially because we were considering secondary forests which tend to be characterized by smaller-sized trees. We used basal area for edge weight calculations; consequently, compared to primary forest trees, the smaller basal area characteristic of individual secondary forest trees reflected their smaller functional contributions, despite higher stem densities. Plots were established between June 2022 and August 2023.

2.2.2 | Ecological Interactions

We collected direct observations of lemur-tree interactions during the distance sampling transects. To identify other lemur-tree interactions, we conducted additional transect walks from February 2023 to January 2024, maximizing survey effort for interaction observations rather than distance sampling. For any observed lemurs, we identified the species, recorded any feeding interactions, collected fecal samples, and followed the lemur group for as long as possible to record observations and collect samples. We also opportunistically collected fecal samples on the forest floor, which we identified to the genus level based on fecal morphology (size, shape, and texture). We conducted approximately 1000 h of interaction walks. The number of hours spent in direct observation was not recorded. When possible, we identified lemur passed seeds from fecal samples, noting if gut-passed seeds were intact or destroyed.

In collaboration with knowledgeable local experts, we conducted 81 key informant interviews to identify additional lemur-tree interactions. We designed an ethnobiological survey of lemur species in COMATSA-Sud ($n=10$) and their interactions with plant species ($n=179$ species representing 82 genera, based on the 17 botanical plots we surveyed in 2022). These data encompassed 93% of the genera surveyed across the total 49 botanical plots (Figure S3). We also developed lemur and plant catalogues displaying their vernacular names, Latin names, and photographs. Residents of the region (C.D., R.B.) conducted ethnobiological surveys in the local dialect. The team presented an image for each plant from photographic catalogues and asked participants if they knew the plant. If they answered "yes", we asked if lemurs consume the species and, if so, which lemur species consume which plant parts. From these data, we classified interactions into three categories: 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"). We only included ecological interactions from these surveys if the interaction (1) was identified by more than one participant and/or, (2) was identified by a plant "expert". We defined "expert" ($n=7$, all men, mean age = 50) as self-reported knowledge of at least 150 plant species from the catalogue. The survey was implemented in Qualtrics, and lasted ~4 h each. One of the unique values of ethnobiological data is that data collection "effort" includes decades of individuals' time spent in the forest making detailed observations, which cannot be quantified using standardized measures of survey effort.

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. Participants included 11 women and 70 men; mean age was 55 years (SD = 13). All participants were red an informed consent form prior to beginning the survey. Additionally, we respected the Malagasy custom of *findramana* (borrowing): (1) a *tangalamena* (wise, respected elder; in our case, a member of VOI leadership) asked to borrow a participant's time and energy before the survey, (2) we offered a refreshment break and full meal during the survey, (3) we compensated participants with phone credit (4000 MGA/~1USD) after the survey, and (4) we conducted a speech of gratitude after the survey. All informants willingly agreed to participate in the study. This research was led by C.M.M.D., an US researcher, who worked in close collaboration with researchers and forest managers from the study area.

Ethnobiological data were responsible for identifying the majority of unique pairwise interactions: 78% of the primary forest frugivory network, 92% for the secondary forest frugivory network, 41% for the primary forest herbivory network, 67% for the secondary forest herbivory network, 92% for the primary forest predation network, and 100% for the secondary forest predation network. For a complete quantitative summary of the data types used to generate each network, see Table S4.

2.3 | Statistical Analysis

2.3.1 | Structure

We calculated structural metrics for each of the primary and secondary forest frugivory, herbivory, and seed predation networks ($n=600$). We estimated interaction richness (a.k.a. total network degree) as the number of unique interactions, abundance (a.k. total network strength) as the sum of edge weights, diversity as Shannon's diversity index (H), calculated in the package vegan (Oksanen et al. 2019), and evenness (E) as diversity divided by the natural log of richness. All analyses were conducted using R Version 4.3.1 (R Core Team 2023).

To further assess the structural differences between primary and secondary forest ecological networks, we calculated the number of modules—how strongly the networks were organized into subgroups—for the single-layer and multilayer networks. We used Infomap to identify modules (Farage et al. 2021; Rosvall and Bergstrom 2008), using the packages infomapecology and emln (Edler et al. 2023; Frydman et al. 2023; Pilosof 2022).

We compared network structural values using two-sided *t*-tests.

2.3.2 | Stability

We compared network stability—tolerance to species loss—using a stochastic extirpation model to estimate area under the curve (AUC) of the robustness function using the package bipartite (Dormann et al. 2017, 2008). The robustness function was defined as the number of lemur species randomly removed compared to the number of tree genera with remaining interactions. We conducted other models where robustness was defined as the number of plant genera removed compared to the number of lemur species with remaining interactions. In the case of the multilayer networks, the primary and secondary forest networks were aggregated. We ran 100 simulations of both lemur and tree removal for each network, for a total of 1800 extirpation simulations. In these simulations, lemurs and trees could not form different interactions from those present in the network.

Rewiring is a process whereby some edges in a network are broken or changed, resulting in new connections. Lemurs and trees may "rewire" to form novel interactions following species loss. Following Vizentin-Bugoni et al. (2020), we calculated network stability under scenarios of rewiring, where lemurs and trees were able to form novel interactions. For the frugivory and predation networks, rewiring probability was the product of the relative abundances of the surviving species in the other trophic guild and morphological trait resemblance. For example, when lemurs were removed, rewiring probability was based on the relative abundance of plant genera. Trait resemblance was calculated based on within-guild trait similarity of lemur body sizes and tree fruit lengths, where we assigned every taxon in each trophic guild a similarity value ranging from zero to one. We calculated similarity values based on Euclidean distances between two species in the same trophic guild using the package vegan (Oksanen et al. 2019). A lemur had a higher rewiring probability to tree genera that interacted with lemur species of similar body sizes, and a tree genus had a higher rewiring probability to lemur species that interacted with tree genera with similar fruit lengths. For the herbivory networks, rewiring probability was based on relative abundances of tree genera and their inverse wood density (scaled between 0 and 1), assuming that herbivores fed more often on genera with lower wood density. Lemurs and trees were only able to form novel interactions with species already present in the interaction networks. Body size, fruit length, and wood density data were collected from the literature (Albert-Daviaud et al. 2018; Razafindratsima et al. 2018; Rejou-Mechain et al. 2017).

To estimate additional aspects of ecological stability, we calculated network nestedness, interaction redundancy, and interaction turnover. We computed nestedness and interaction turnover for each of the 600 single layer networks. Nestedness is a network structural term referring to the extent to which interaction partners of low degree nodes are a subset of the partners of high degree nodes. In other words, higher nestedness values indicate a more nested organization, where specialists tend to interact with a subset of the partners of generalists. We quantified nestedess of each interaction matrix, accounting for edge weights, using the R package bipartite (Dormann et al. 2017). Interaction redundancy is the extent to which nodes share the same interaction partners (i.e., functional overlap). We quantified interaction redundancy pairwise similarity between all nodes, using the Bray–Curtis dissimilarity index and the R package vegan (Oksanen et al. 2019). Higher similarity indicates that a lemur's role is functionally redundant, whereas a lower similarity indicates a distinctive interaction profile. To quantify changes in network structure between primary and secondary forest, we calculated interaction turnover—i.e., the extent to which edges differ between environmental contexts. We used the Bray–Curtis dissimilarity index for the each of the 100 weighted frugivory, herbivory, and seed predation network pairs. Interaction turnover reflects changes in lemur-tree interactions across primary and secondary forest.

3 | Results

3.1 | Structure

Interaction abundance, diversity, and evenness were lower in the secondary forest compared to the primary forest for all interaction types, except for interaction evenness in the seed predation network (Figure 2, Table S6). The primary forest frugivory network had the highest interaction abundance (mean 738,728 [95% CI = 733,956–743,501] total pairwise interactions), and diversity (4.1 [4.0–4.1] H). Primary forest networks were more even than secondary forests for frugivory and herbivory, but not seed predation, and the frugivory networks were more even than the herbivory or seed predation networks. The secondary forest herbivory network had the lowest interaction abundance (10,005 [9817–10,193] total pairwise interactions), diversity (2.2 [2.2–2.2] H), and evenness (0.59 [0.59–0.59] E). See Table S6 for full results.

The dispersal and predation single-layer networks tended to be best explained by one highly-connected module (Figure 2d). However, in 7% of the simulations, the secondary forest seed predation network was represented by two distinct modules, one including *E. albifrons* and *L. seali* and the other including the remaining five lemur species which were observed in the secondary forest. The primary forest herbivory network was characterized by five modules and the secondary forest tended to be characterized by three modules. In the primary forest folivory network, *E. albifrons* and *A. laniger* shared a module and the Cheirogaleidae species (*M. lehilahytsara*, *A. trichotis*, and *C. crossleyi*) as well as *L. seali* shared another module. In the secondary forest folivory network, *E. albifrons* and *A. laniger* shared a module with *M. lehilahytsara*, whereas *A. trichotis* and *C. crossleyi* shared another module with *H. occidentalis*. The remaining modules each included one lemur species. The number of multilayer modules was highest for the herbivory network (frugivory = mean 8.5, seed predation = mean 6, herbivory = mean 4.8; Figure 2d). For multilayer module assignment of lemur species, see Data S1.

3.2 | Stability

Network robustness varied by interaction type, forest type, and whether lemurs or trees were removed (Figure 3, Table S7). With simulated lemur extirpation, herbivory networks (primary forest robustness $\bar{X} = 0.728$, $SD = 0.150$; secondary forest robustness $\bar{X} = 0.649$, $SD = 0.092$, multilayer robustness $\bar{X} = 0.397$, $SD = 0.079$) tended to be less robust than frugivory networks (primary forest robustness $\bar{X} = 0.723$, $SD = 0.035$; secondary forest robustness $\bar{X} = 0.758$, $SD = 0.013$, multilayer robustness $\bar{X} = 0.574$, $SD = 0.012$) or seed predation networks (primary forest robustness $\bar{X} = 0.750$, $SD = 0.046$; secondary forest robustness $\bar{X} = 0.721$, $SD = 0.032$, multilayer robustness $\bar{X} = 0.667$, $SD = 0.037$). All networks were significantly more robust under tree loss than lemur loss. In the context of tree loss, robustness was comparable and high across interaction types for primary and secondary forest networks (~0.95, Table S7), but varied substantially across the multilayer networks (dispersal robustness $\bar{X} = 0.896$, $SD = 0.016$; herbivory robustness $\bar{X} = 0.752$, $SD = 0.009$; predation robustness $\bar{X} = 0.568$, $SD = 0.006$). Multilayer networks were consistently and significantly less robust than primary and secondary forest networks (Figure 3a). Primary forest networks tended to be most robust, except for lemur loss in the frugivory networks. These patterns were consistent with or without rewiring, which significantly but weakly mitigated network robustness to tree and lemur loss (Figure S4). For results without accounting for rewiring, see Figure S4 and Table S7.

Considering nestedness and interaction redundancy, primary forest networks tended to be more stable than secondary forest networks (Figure 4). Seed predation functional redundancy was, however, higher in the secondary forest (mean = 0.169 [95% CI = 0.168–0.169]) compared to the primary forest (mean = 0.131 [95% CI = 0.131–0.132]). Notably, nestedness and redundancy were lower, while interaction turnover was

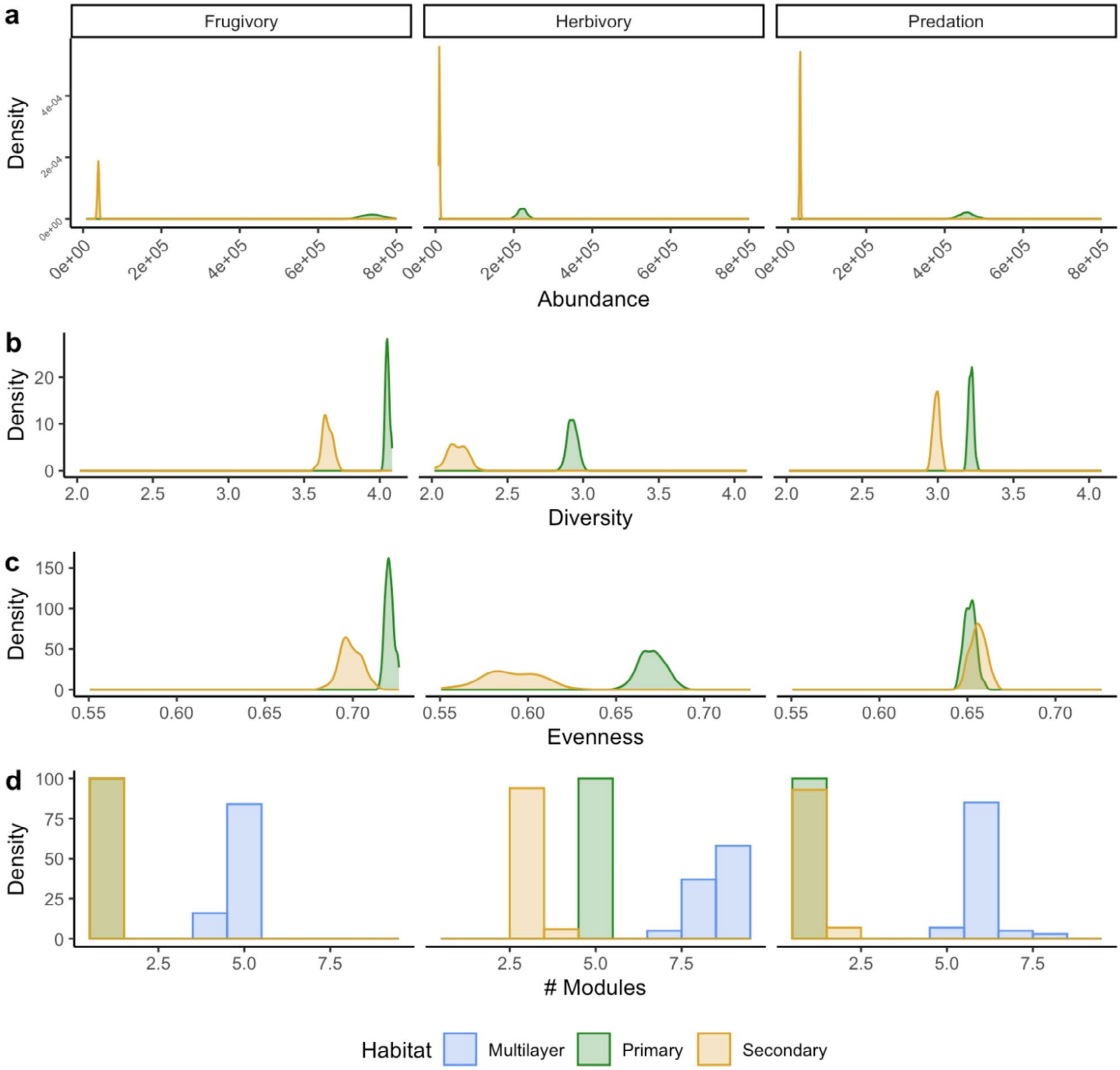

FIGURE 2 | Interaction (a) abundance, (b) diversity, (c) evenness, and (d) number of modules for the frugivory, herbivory, and seed predation networks in the secondary and primary forests. Panel (d) also includes the number of multilayer modules. Green represents primary forest, orange secondary forest, and blue multilayer. Density plots and histograms represent null distributions and dashed lines represent observed values.

higher, for herbivory compared to frugivory and seed predation, indicating lower stability of herbivory compared to other interaction types in this ecosystem. For full results, see Table S8.

4 | Discussion

We combined research-focused observations and ethnobiological data to shed light on the structure and stability of ecological networks across human-modified landscapes. Network structure in primary and secondary forest varied by interaction type. We observed high abundances of nocturnal seed dispersers in secondary forests, highlighting their role in maintaining frugivory in human-modified habitats. Notably, multilayer networks were less stable to perturbations than single-layer networks; thus, neglecting the ecological processes that occur between primary and secondary forests may result in underestimating forest vulnerability to species extirpation.

4.1 | Structure

The general lack of modular organization of the single-layer networks was surprising and is often associated with reduced ecological stability (Grilli et al. 2016). However, there were no singleton modules, which would indicate a propensity for specialized interactions. Generalized interactions tend to be less vulnerable to environmental disturbances than specialized interactions because they are not dependent on a specific subset of species (Aizen et al. 2012). In the multilayer networks, lemurs tended to form modules across secondary and primary forests,

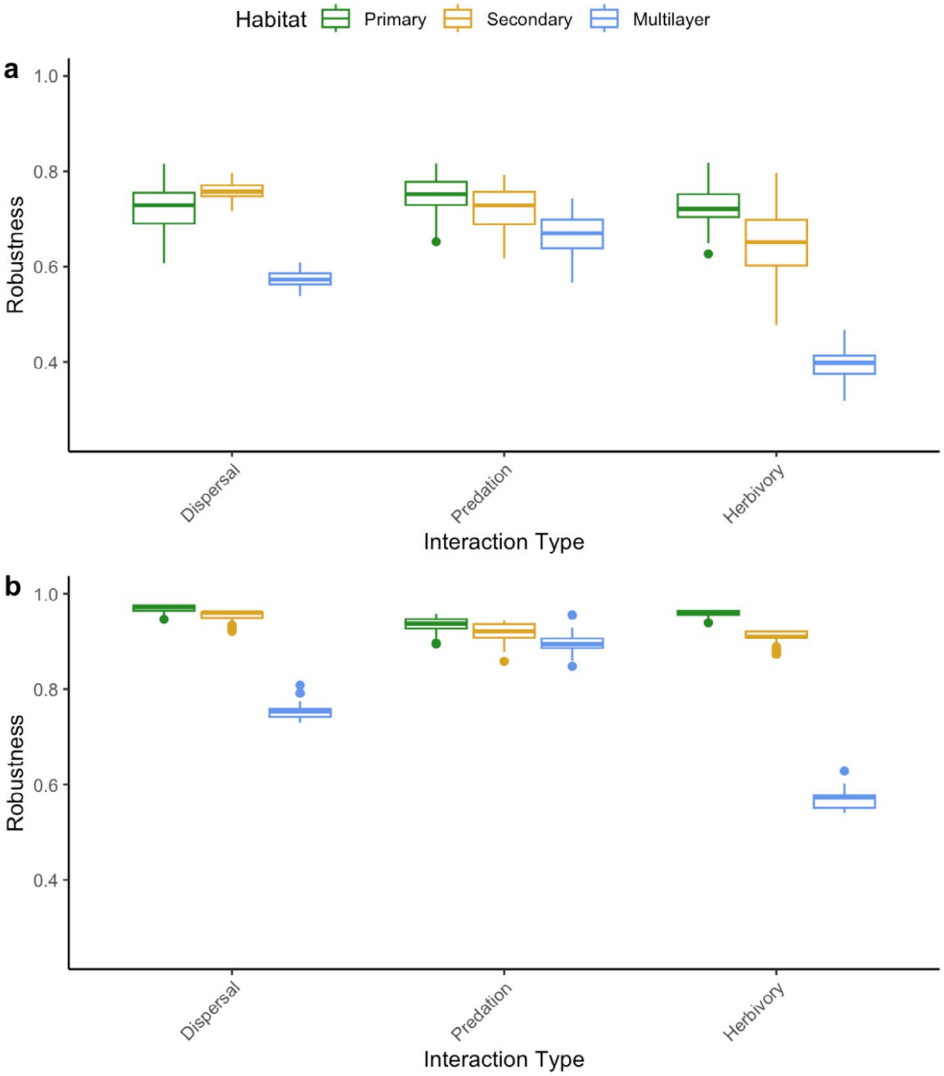

FIGURE 3 | Network stability as represented by robustness, or AUC of stochastic extirpation simulations of (a) lemur species and (b) tree genera. Figures present all three interaction (dispersal, predation, herbivory) and forest types (secondary forest, primary forest, multilayer). Each boxplot represents values from 100 simulations. Simulations account for rewiring. For estimated robustness without accounting for rewiring, see Figure S4 and Table S7.

highlighting that ecological processes extend beyond human-imposed boundaries. The occurrence of many lemur species in distinct modules suggests that they may perform distinct ecological functions. Therefore, despite few single-layer modules, many multilayer modules may facilitate network resilience to perturbation.

We identified network structure using transect surveys combined with ethnobiological interviews and literature data to capture a broad range of species and interaction types. Transect-based observations alone may under-represent less conspicuous species, particularly those not habituated to human presence, potentially biasing interaction data. The majority of interactions across all lemur-tree networks were identified using ethnobiological data (Figure 1). Other recent plant–animal interaction studies which combined field observations and ethnobiological data have also identified high (97% [Ong et al. 2021], and 39% [Durand-Bessart et al. 2024]) proportions of total interactions using surveys with community members. Using ethnobiological data can therefore be critical for identifying cryptic interactions and improving network analyses. However, ethnobiological data can present their own limitations. For example, Ong et al. (2021) identified communication and cultural differences as potential caveats in using interview data to construct ecological networks. It is also possible that people's knowledge of lemurs and plants is itself biased. For example, people may be more likely to report interactions of trees that have economic and/or cultural value or lemurs that are easier to observe (e.g., diurnal species). Overall, however, combining ethnobiological knowledge with systematic field observations has the potential to improve ecological data collection while also advancing local engagement in biodiversity research (Berkstrom et al. 2019; Braga-Pereira et al. 2022; Camino et al. 2020).

4.2 | Stability

Anthropogenic activities such as land-use intensification and hunting can jeopardize ecological processes (Aslan et al. 2013; Felipe-Lucia et al. 2020). As predicted, networks were less stable

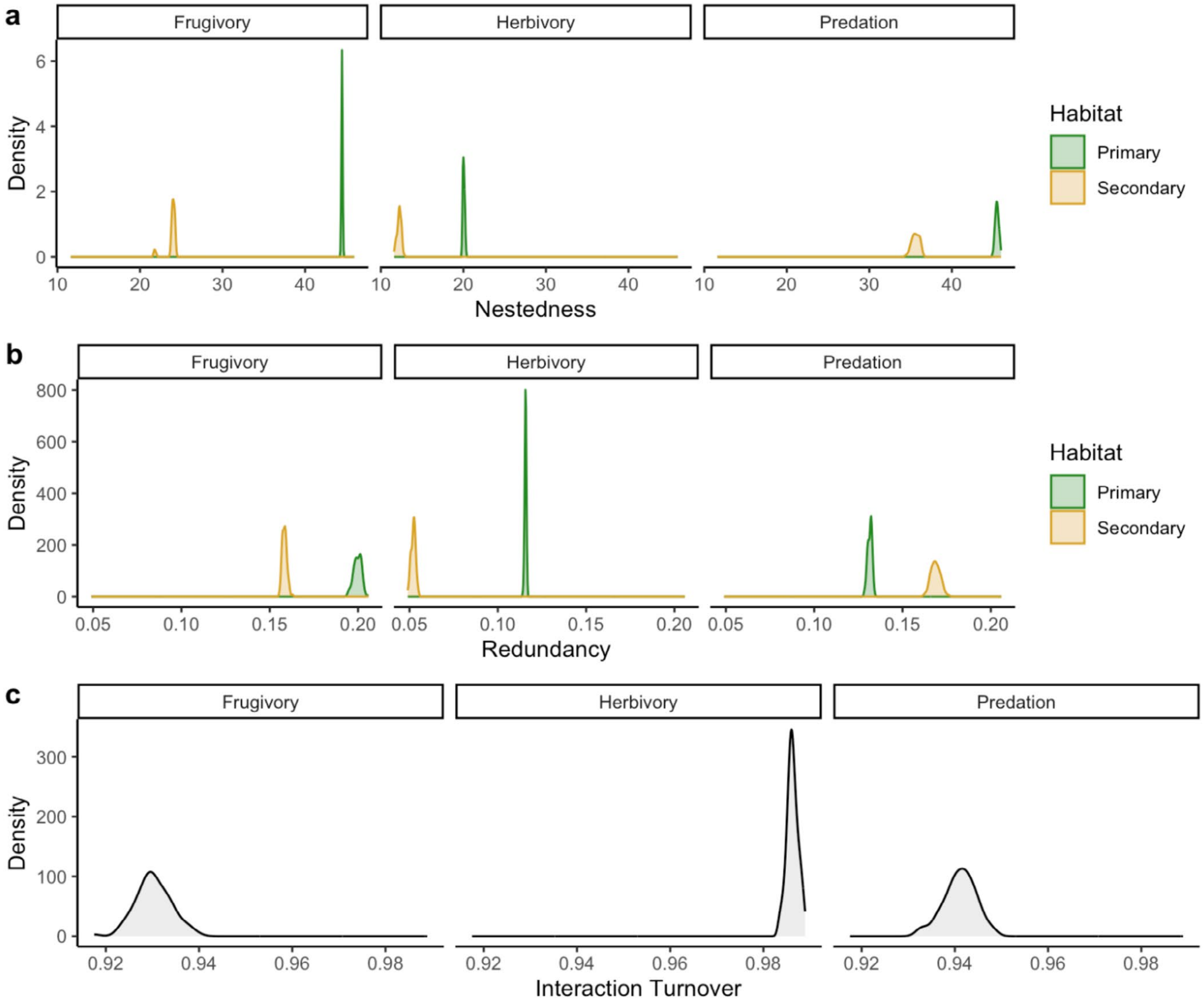

FIGURE 4 | Network stability as represented by (a) nestedness (i.e., extent to which specialist interactions are a subset of generalist interactions), (b) interaction redundancy (i.e., functional overlap), and (c) interaction turnover (i.e., differences in network edges) between land use type. Figures represent frugivory, herbivory, and seed predation networks.

to simulated lemur loss than tree loss, with or without rewiring, highlighting the importance of lemur conservation for ecosystem functioning (DeSisto and Herrera 2022; Raoelinjanakolona et al. 2023). Our networks were likely more stable to tree loss because there were more tree genera than lemur species, and the lemur species tended to be generalists. Plant pollinator and frugivory research has also shown that anthropogenic effects such as invasive species reduce network stability (Vitali et al. 2023). Similarly, primary forests tended to be more resilient to lemur and tree loss than secondary forests or multilayer networks, likely in part because they had higher species and interaction richness and diversity (Figure 3, Table S5). The low robustness of multilayer compared to single-layer networks suggests that ignoring interactions between primary and secondary forests could underestimate the effects of species loss on ecological functioning. It also suggests that species that connect the two forest types (*Eulemur albifrons*, *Hapalemur occidentalis*, *Allocebus trichotis*, *Cheirogaleus crossleyi*, *Microcebus lehilahytsara*, *Avahi laniger*, and *Lepilamur seali*) may be especially important for ecological functioning in human-modified landscapes. Although primary and secondary networks were connected via lemur and tree species found in both habitats, those connections may be tenuous and vulnerable to the loss of species that connect them. Herbivory networks were consistently less stable than frugivory or seed predation networks. Stability—as measured by robustness to perturbation, nestedness, interaction strength, and interaction turnover—tended to be lowest for herbivory networks (Figures 3 and 4). Stark differences between the primary and secondary forest herbivory networks were also evident in the network web plot (Figure 1). These results reflect the lack of diverse vegetative food resources available to lemurs in the secondary forest. The majority of herbivory interactions in the secondary forest were with a single plant species, *Harungana madagascariensis*, which is a fast-growing pioneer plant. *H. madagascariensis* is known to be an important food plant for lemurs in other areas of Madagascar, especially in the dry season (Dagosto 1995; Tonos et al. 2025). Both its leaves and fruits are consumed by lemurs. Conservation efforts such as reforestation programs may consider planting a diversity of multifunctional trees (i.e., those which provide lemurs with both fruits and leaves) to promote ecological stability.

4.3 | Limitations

Our results depend on our model assumptions. For example, while our extirpation simulations were conducted at random, robustness values will differ if lemur species loss occurs nonrandomly (DeSisto and Herrera 2022). For example, hunters may target lemurs based on body sizes or activity patterns (Borgerson et al. 2022) and loggers may preferentially extract hardwood trees such as *Dalbergia* spp. (Barrett et al. 2010; Patel 2007; Schuurman and Ii 2009). While simulated interaction rewiring slightly mitigated the functional consequences of species loss (Figure 3), robustness to lemur loss remained low. Our simulated rewiring approach was based on relative abundances and ecological trait matching. Rewiring probabilities were a function of our model assumptions and based on a subset of traits, but other unmeasured traits may also be important. For example, fruit color, odor, and nutrients affect lemur foraging behavior (Greene et al. 2024; Valenta et al. 2013). Use of existing databases such as the TRY Plant Trait Database and herbarium collections may serve as useful sources for future analyses. Phenology may also affect rewiring and network stability. We addressed temporal bias in data collection through ethnobiological data collection and year-round sampling. The unpredictable fruiting phenology of tropical trees, however, prevented our ability to account for temporal dynamics in these interaction networks. Future research could investigate the extent to which lemur-tree interaction rewiring occurs in nature, as well as the diverse drivers of heterogeneity in rewiring. In particular, long-term data collection may enable temporal network analysis.

We acknowledge that analyzing interactions at the genus level for trees and species level for lemurs may obscure species-specific interactions and ecological nuances. However, we applied the genus level approach uniformly across land use and interaction types, such that it should not induce systematic bias in favor of particular hypotheses. Taxonomic resolution is a challenge for ecological research on Madagascar. Malagasy flora is highly diverse and up to 87% endemic (Goodman et al. 2019). Further, an estimated 2550 plant species remain to be scientifically described (Antonelli et al. 2022). Genus-level analysis of plants is therefore common in ecological research across Madagascar (e.g., Omollo et al. (2024)). Future taxonomic research at the species level would benefit the Madagascar research community.

Our estimations of edge weights represented a proxy for interaction frequency: the product of species-level lemur biomass and genus-level tree basal area. This approach assumes that all individuals have equal probabilities of interacting—a simplification that, while predominant in network studies (Jordano 2016) does not reflect the spatial and behavioral complexities of real-world ecosystems. In nature, interaction frequency likely also depends on factors such as microhabitat structure, individual foraging behavior, and plant spatial distributions, which can all influence the likelihood of interactions (Schupp et al. 2010; Wells and O'Hara 2013). Foraging rates may also depend on environmental variables such as weather (Eppley et al. 2016). Furthermore, functional outcomes of lemur-plant interactions are driven in part by individual functional traits of both lemurs and the plants they disperse (DeSisto et al. 2025). Future research on lemur-plant networks at the individual level would further our understanding of ecological functioning in Madagascar's rainforests.

5 | Conclusion

Our results highlight the role of land use on the structure and stability of frugivory, herbivory, and seed predation networks. Environmental gradients are known to modulate the structure of ecological networks (Tylianakis and Morris 2017; Vizentin-Bugoni et al. 2020), and we observed substantial differences in network structure between the primary and secondary forest networks (Figure 2). Nevertheless, the presence of lemurs—especially small nocturnal lemurs—in both primary and secondary forests emphasizes the persistence of ecological functioning in regenerating forests. These interactions, occurring both within and between forest types across the landscape, likely facilitate restoration (Chapman and Dunham 2018; Ganzhorn et al. 2024). Our extirpation simulations demonstrate that maintaining species interactions across human-modified landscapes is critical for ecosystem stability (Figure 3), and that ignoring interactions between primary and secondary forests could underestimate the effects of species loss on ecological functioning. Further, our results highlight the ecological importance of conserving lemur species that connect secondary and primary forest.

Author Contributions

C.M.M.D. conceived the ideas and designed methodology with guidance from J.P.H. and J.R.P. and critical input from all authors; C.M.M.D., C.D., R.E., T.F., E.M., J.N., E.R., M.O.R., S.O.R., W.R., D.R., J.R., M.R., G.R., J.T., E.T., Z.Z., and Z.Z. collected the data; C.M.M.D. analyzed the data with guidance from J.R.P., C.N., and J.P.H.; C.M.M.D. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in GitHub at https://gitfront.io/r/cdesisto/bFKs7CKL5CVs/LemurNetworkStructureStability.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** btp70109-sup-0001-DataS1.pdf.