Received: 29 November 2022 | Accepted: 21 November 2023

DOI: 10.1002/pan3.10591

PEOPLE AND NATURE BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Provisioning services decline for both people and Critically Endangered wildlife in a rainforest transformation landscape

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Funding information
San Diego Zoo Wildlife Alliance; American Society of Primatologists; IUCN Save Our Species, Grant/Award Number: IUCN-SOS 2018A-117; Margot Marsh Biodiversity Foundation; National Science Foundation Graduate Research Fellowship Program (NSF-GRFP), Grant/Award Number: 2016203971; Stony Brook University; Montclair State University, Grant/Award Number: SBR2020; San Diego Zoo Ocelots Fund; National Geographic Society, Grant/Award Number: NGS-55616C-20, NGS-C021-17 and NGS-C280-14; National Science Foundation SBE-IBSS Postdoctoral Research Fellowship, Grant/Award Number: 1513638

Abstract

1. The loss and degradation of forests and other ecosystems worldwide threaten both global biodiversity and the livelihoods of people who use natural resources. Understanding how natural resource use impacts landscape provisioning services for both people and wildlife is thus critical for designing comprehensive resource management strategies.
2. We used data from community focus groups, botanical plots and an inventory of plant species consumed by the Critically Endangered red-ruffed lemur (*Varecia rubra*) to assess the availability of key provisioning services for people and endemic wildlife on the Masoala Peninsula, a rainforest transformation landscape, in northeastern Madagascar (Masoala National Park and 13 surrounding communities).
3. We constructed Poisson regression mixed models to evaluate the impact of *community factors* (i.e. community population size, plot distance to community) and changes over *time* on the count and species richness of timber trees, medicinal plants and red-ruffed lemur food trees within botanical plots.

Carter W. Daniels's affiliation reflects his most recent academic affiliation; he is currently a Quantitative Scientist at Prevail Therapeutics, a wholly owned subsidiary of Eli Lilly & Company. His contribution to this work is independent of his work at Prevail Therapeutics.

Handling Editor: Patricia Carignano Torres

4. Over three-quarters of all plant species could be used for at least one purpose by local communities ($n = 238$ species). Of the 59 *V. rubra* food tree species, only 15% had no reported human use.
5. Timber and ruffed lemur food tree availability declined both with community population size and time and were predicted to be lower outside of Masoala National Park. In contrast, medicinal plant availability was not strongly predicted by any tested factors. Provisioning service availability also differed strongly across sites, suggesting that additional, untested proxies of human pressure likely also have an effect.
6. Our results highlight the importance of evaluating natural resource availability from a community-based perspective and by resource purpose to inform forest landscape restoration efforts that can support both people and wildlife.

KEYWORDS
lemur, Madagascar, Masoala Peninsula, medicinal plants, natural resource use, non-timber forest products (NTFPs), timber, *Varecia rubra*

1 | INTRODUCTION

It is estimated that one-third of the global population depends on forests and forest products for at least part of their livelihoods (FAO & UNEP, 2020). Considering energy needs alone, an estimated 880 million people collect firewood or produce charcoal (FAO, 2017) from forests and other tree-based systems worldwide (Chazdon et al., 2016). These landscapes provide additional provisioning ecosystem services by containing essential products like medicinal plants, fodder for livestock, food for human consumption and materials for housing (Razafindratsima et al., 2021). The United Nations deems guaranteed and universal access to land and natural resources an important target for poverty eradication (Goal 1.4; UN, 2015). In a global study of forest product users, however, 90% of villages surveyed reported a decrease in the availability of forest resources compared to the prior 5 years (Hermans-Neumann et al., 2016), with respondents attributing this loss largely to local resource collection and loss of the resource base itself (e.g. through forest clearing; Hermans-Neumann et al., 2016). As research demonstrates that many non-cultivated resource harvest practices are unsustainable (de Mello et al., 2020), understanding the relative extent of natural resource degradation is urgent (Sunderlin et al., 2005).

Ecosystem modifications like agricultural expansion and urbanization (Salafsky et al., 2008) threaten the availability of forest and other natural resources, as well as the livelihoods that depend upon them (Levers et al., 2021; Oldekop et al., 2020; Sunderlin et al., 2005), resulting in dynamic, 'transformation landscapes' (Drescher et al., 2016). For such landscapes in flux, it is especially important to understand where and how the availability of natural resources varies (Pritchard et al., 2019). People who use local natural resources often affect the spatial availability of those resources in several, predictable ways (Albers & Robinson, 2013). Users typically first degrade resources that are easier to access (Horn et al., 2018; López-Feldman & Wilen, 2008), including those found in areas that are closer to settlements (Ahrends et al., 2010; Brown et al., 2011; López-Feldman & Wilen, 2008) or have fewer restrictions on resource extraction (e.g. unprotected areas; Mohammed & Inoue, 2017; Sahoo & Davidar, 2013). Resources may also be less available in regions with higher human populations (Sahoo & Davidar, 2013). When targeted common-pool (i.e. open-access) resources are not sustainably managed and are extracted faster than they can be naturally replenished, they are also likely to decline in abundance over time (Gibson et al., 2000; McKean, 2000).

Importantly, natural resource use is not a 'one-size-fits-all' practice that equally affects all resources (Albers & Robinson, 2013; Pilkington et al., 2020). Instead, different species or resource qualities (Brown et al., 2011) may be preferentially selected according to their intended purpose. Extraction of forest resources can thus result in predictable, purpose-driven 'waves of degradation' over time. In an example from Tanzania, the geographic area over which charcoal and timber products were harvested was shown to increase with the economic value of each item (Ahrends et al., 2010). Knowing how such resource pools differ according to their purpose and how that leads their availability to vary across space and time is important for guiding management recommendations that support the long-term preservation of provisioning ecosystem services (perspectives on and reviews of ecosystem services management: Bennett et al., 2015; Costanza et al., 2017; Kremen, 2005).

In the Global South, regions that are subject to the most substantial changes in landscape composition—and often reductions in natural resource availability—are also those that contain a disproportionately high percentage of the world's biodiversity (Barrett et al., 2011; Newbold et al., 2015). Frequent interdependence on natural resources between human populations and endemic wildlife can result in major biodiversity conservation challenges (Ceballos et al., 2020) and the potential for human–wildlife conflict (Barrett et al., 2011; Hamann et al., 2018). Yet, while the subsistence use of timber and non-timber forest products is commonly framed as of pressing concern for biodiversity conservation (e.g. Holmes, 2007; Kremen et al., 1999), we continue to lack a quantitative understanding of whether, and in what ways, plant use within forest habitats affects provisioning services for threatened wildlife. Targeting research to provide this context is thus essential for making informed resource management recommendations that serve intertwined natural and human systems in threatened biodiversity hotspots (An & López-Carr, 2012; MacDougall et al., 2013; Ostrom, 2007; Paige et al., 2017; Pritchard et al., 2019).

Madagascar is one such global biodiversity hotspot and is subject to extensive landscape change (Ralimanana et al., 2022). The island nation lost an estimated 53% of its total forest cover over six decades (from 1953 to 2017), leaving heavily fragmented forests vulnerable to both edge effects and increased human access (Vieilledent et al., 2018a, 2018b). These landscape changes are known to limit Madagascar's ecosystem services for both wildlife (e.g. decline in habitat quality: Llopis et al., 2021; loss of forest specialist species: Martin et al., 2022) and the local human communities that rely upon them (e.g. loss of utilitarian plant traits: Brown et al., 2013; storm hazard mitigation: Dave et al., 2017; water availability and shelter: Fritz-Vietta, 2016; soil erosion: Rakotoson et al., 2007), in addition to impacting the global ecosystem services Madagascar's forests provide (e.g. decline in carbon storage: Llopis et al., 2021; Soazafy et al., 2021). Provisioning ecosystem services in Madagascar are particularly important, as many Malagasy rely on natural resources, from widespread consumption of endemic wildlife (Borgerson et al., 2022) to the use of non-cultivated plants for a variety of subsistence purposes (e.g. Borgerson, Johnson, et al., 2018; Borgerson, Randrianasolo, et al., 2019; Borgerson, Vonona, et al., 2018; Fedele et al., 2011; Moore et al., 2022; Raveloaritiana et al., 2023; Razafindraibe et al., 2013; Reuter et al., 2018).

Here we quantified the effects of the complex use of forest resources by humans on those of a threatened endemic species near Madagascar's largest national park and UNESCO World Heritage Site, the Masoala National Park. Specifically, we examined how the availability of provisioning services for both local populations and endemic wildlife is directly shaped by purpose-driven, geospatial and temporal patterns of resource extraction. We used these relationships to examine, for both conservation and public policy, whether plant-based natural resources decline in relation to (1) community factors (i.e. increasing population size and decreasing distance to settlements), (2) time, (3) spatial policies across a landscape (i.e. protected area status) and (4) the purpose of each resource. Finally, we examined how the use of each resource affects the food availability of a Critically Endangered species endemic to the region, the red-ruffed lemur (*Varecia rubra*: Borgerson et al., 2020). As lemurs are the most threatened group of mammals worldwide (IUCN, 2022), characterizing the potential for conflict between human and lemur populations over limited, shared resources is of critical conservation concern.

2 | METHODS

2.1 | Study area

Our study took place on the Masoala Peninsula (Figure 1), a region in northeastern Madagascar home to Masoala National Park. A UNESCO World Heritage site and one of the last remaining areas in Madagascar with lowland coastal rainforest (Holmes, 2007), the Masoala National Park and its surrounding region are home to 11 species of lemur, including the Critically Endangered red-ruffed lemur (*V. rubra*: Borgerson et al., 2020), as well as the second highest number of threatened endemic tree species across Madagascar's protected areas (Beech et al., 2021). A rainforest transformation landscape, the peninsula is subject to extensive land use and land cover changes driven by shifting cultivation practices, including subsistence agriculture and cash crop production (e.g. vanilla and cloves; Andriatsitohaina et al., 2020; Llopis et al., 2019). A total population of 144,650 people, the majority of whom belong to the Betsimisaraka ethnic group, live in permanent villages within 10 km of Masoala National Park (Borgerson et al., 2022).

Our study examines the impact of natural resource use on the landscapes surrounding 13 of the region's villages. Villages are located outside of Masoala National Park's boundaries, with some lying along the coast. The precise location of any of these communities is reserved to protect their anonymity. In 2015, 9810 people resided in the study communities, with a median community population of 160 people (interquartile range (IQR): 200 people). As in the rest of the region, people in the study communities are primarily subsistence agriculturalists, engaging in rice and other crop cultivation as well as cash crop production, local commerce, fishing and livestock rearing (Borgerson et al., 2016; Kremen et al., 1999).

On the Masoala Peninsula, the illegal extraction of precious hardwoods (e.g. Rosewood: *Dalbergia* spp.) for international markets is well known (Allnutt et al., 2013; Randriamalala & Liu, 2010), but local people in the region also use non-cultivated plants for a variety of purposes. These range from consumption for medicinal uses (Golden et al., 2012) and food (albeit at low documented levels; Borgerson, Razafindrapaoly, et al., 2019), use in the production of alcohol (Borgerson et al., 2016) and use in the construction and repair of housing and numerous other household products (Holmes, 2007). We focus our analyses on two illustrative examples of important regional provisioning services—that of timber and of medicinal plants—to explore resources that are extracted differently and targeted with varying specificity. Trees used for timber are commonly fully extracted, whereas medicinal plants often may be accessed by users multiple times (e.g. by taking plant parts like leaves; McKean, 2000). Medicinal plants are also targeted at a higher frequency and with greater specificity than timber trees, as only certain plant parts of

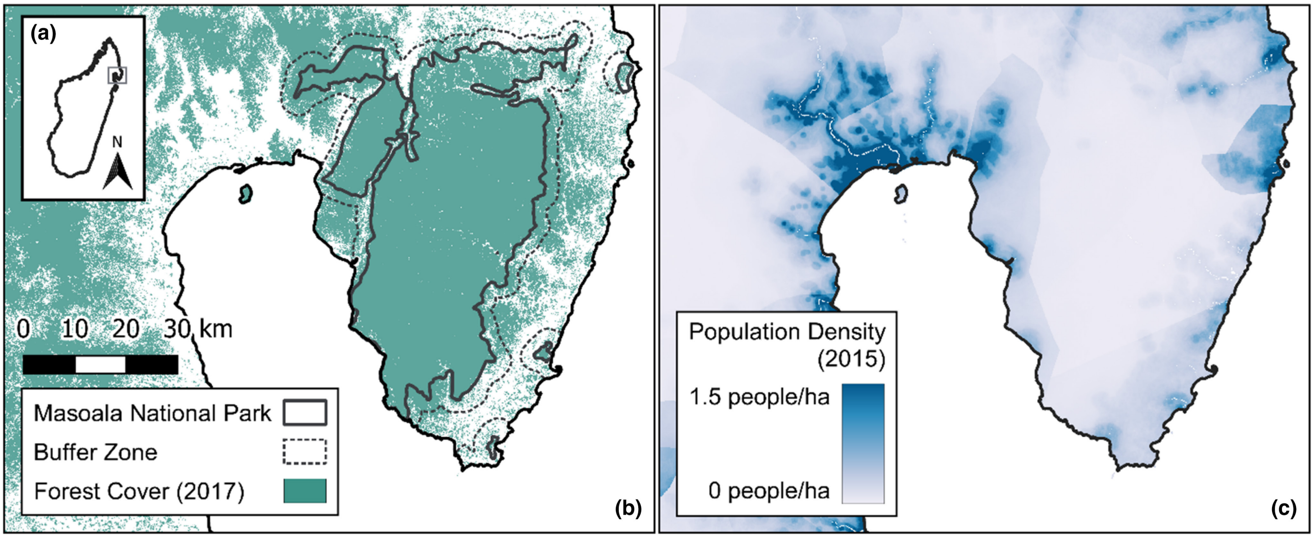

FIGURE 1 Map of the study region, the Masoala Peninsula, northeastern Madagascar. (a) Inset in panel (b): Location of study region in Madagascar as indicated by grey box; (b) Forest cover in 2017 (Vieilledent et al., 2018b) and boundaries of Masoala National Park (solid line; marine boundaries of the park not shown). Residents within the buffer zone (dashed line) are permitted the limited collection of some non-cultivated plants for subsistence purposes (excluding timber); (c) Population density in 2015 (WorldPop, 2017). The locations of communities included in the study not shown to protect their anonymity.

specific species are used for any one ethno-pharmaceutical purpose (Golden et al., 2012).

2.2 | Red-ruffed lemur (*V. rubra*)

The red-ruffed lemur (*V. rubra*) is an excellent model with which to examine human–wildlife resource conflict in Madagascar. This relatively large-bodied lemur species is highly sensitive to both habitat disturbance (Borgerson, 2015a; Morelli et al., 2020) and habitat loss (Eppley et al., 2020) and has a predominantly frugivorous, and thus resource-restricted diet (Vasey, 2000; but see Martinez & Razafindratsima, 2014). *V. rubra* is also largely restricted to the Masoala Peninsula; in Masoala National Park alone, it is projected habitat suitability for the species may decline by as much as 75% in the next 30 years (with deforestation and impacts of climate change; SI: Morelli et al., 2020). Populations are further threatened in the region by extensive hunting for local consumption (Borgerson, 2015a, 2015b). However, understanding threats to *V. rubra* is important, not only for conserving the species itself. Lemurs are critical seed dispersers (Albert-Daviaud et al., 2018), and ruffed lemurs are in particular important propagators of large-seeded plants (*Varecia variegata*: Manjaribe et al., 2013; *V. rubra*: Razafindratsima & Martinez, 2012). The loss of *V. rubra* would thus yield significant changes in the regional pool of available plant resources for human and wildlife populations alike. Determining what plant species consumed by *V. rubra* are also extracted by local human populations—and for what resource purposes—will help to better target natural resource management and policy recommendations to support both humans and lemurs.

2.3 | Data collection

We used data from 155 botanical plots (Table 1), two community focus groups and 34 months of behavioural observation of *V. rubra* to assess the availability of wild plant provisioning services across study communities and in Masoala National Park. As our research focuses on how plant resources are used by local communities, we collected all data on plant identity using vernacular names. For readability, however, we refer to all plant ethnonyms hereafter as 'species'. For a full list of plant ethnonyms and any known associated scientific names, refer to Appendix S1.

2.3.1 | Botanical plots

To evaluate the availability and diversity of plant species across the study region, we used data obtained from 155 botanical plots ($n = 130$ community plots with 10 plots per site sampled; $n = 25$ protected area plots; Table 1). We collected data in each plot using the methods established by IFRI (2008), whereby data are collected for small (DBH < 2.5 cm), medium (2.5 ≤ DBH < 10 cm) and large (DBH ≥ 10 cm) plants in three concentric circles centred on each plot point. We sampled all small plants within a 1-m radius of the plot's centre, all medium plants within a 3-m radius and all large plants within a 10-m radius. Two perpendicular transects and 10 botanical plots were established in each study village in 2015 (hereafter 'community plots'; $n = 130$ community plots). Plots were also repeatedly sampled in five of these villages for a total of 5 years (2015, 2017, 2019, 2020 and 2021). In this longitudinal dataset, 50 plots were sampled, for a total of 250 plot surveys. These five villages had a mean population of

TABLE 1 Characteristics of botanical plots sampled 2015–2021 on the Masoala Peninsula, Madagascar.

Plot type	Location	*n* plots	Additional characteristics	
Plots sampled in 2015–2016			Distance to nearest community	Population size
Outside protected area ('community plots')	13 villages on Masoala Peninsula	130 ($n=10$ per village)	Plots along transects from each focal community placed 0.5, 1.0, 1.5, 2.0 and 2.5 km from settlement edge ($n=26$ per distance category)	40–4000 people (median: 160)
Protected area	Masoala National Park	25	1.5–18 km (median: 11 km)	0 people
Plots sampled to evaluate change over time				
Multi-year	5 villages[a]	$N=50$ plots ($n=10$ per village) sampled 5× each	Time: Plots sampled in 2015, 2017, 2019, 2020 and 2021	

Note: A total of 155 plots were sampled between 2015 and 2016 across study communities and in Masoala National Park. We sampled a subset of plots outside of the protected area annually for 5 years (2015, 2017, 2019, 2020 and 2021).

[a] A subset of the plots, in five communities of the 13 villages sampled in 2015, were sampled to evaluate change over time.

156.00 ± SD 83.57 people in 2015 and grew in population through 2021, with a mean growth rate of 23.86 ± 19.36% across this time period. We additionally sampled 25 botanical plots along two parallel, cross-peninsular transects in the Masoala National Park in 2016. These transects each spanned from the park's western boundaries to the eastern coast.

Community plots were spaced 500 m apart and were located 0.5, 1.0, 1.5, 2.0 and 2.5 km from each village's edge. As such, botanical plots occurred across a variety of land cover types, including grassy plains, herbaceous fallow and woody fallow. Botanical plots did not occur in fields growing crops at the time data were collected, so that none of the plants sampled, including medicinal plants, were cultivated by local people. As protected area plots bisected the park, they were located both at park boundaries and within its core; as such, plots were predominantly located in old-growth forest, but herbaceous and woody fallow also occurred. While protected area plots were each spaced 5 km apart, we calculated the straight-line distance from protected area plots to the nearest village using QGIS 3.30.1, even if the nearest settlement was not one of the 13 sampled (communities visually identified from satellite imagery of the Masoala Peninsula in 2014: Google Earth Pro 7.3.6, 2023). Protected area plots were located a mean 10.4 ± SD 5.7 km from a village (Table 1).

2.3.2 | Focus groups

To obtain information about how local communities in the study region use wild plants, we conducted two focus groups of adult community members in October and December 2021 (see Appendix S2 for the focus group questionnaire). Focus groups, led by local team members in the Betsimisaraka dialect, were held in two villages, one located on the coast and the other further inland, to capture a wider breadth of potential plants used ($N=24$ participants; $n=12$ per community, equal split between men and women in both groups; $N=64$ total hours of discussion; $n=43$ h for the coastal community and $n=21$ h for the inland community). For every plant that had been identified across the botanical surveys and for additional plants named by the focus groups, we asked participants whether the species was used for any of the following purposes: (1) Construction (for housing and/or other purposes); (2) medicine; (3) food; (4) alcohol production; (5) cordage; (6) weaving; (7) fodder for livestock; and/or (8) 'other' purposes. While we asked what species might be used for firewood, fuelwood is collected as deadwood in the study communities (as it is elsewhere in Madagascar: Računevska et al., 2022) and is thus not considered in our analyses.

We asked subsequent questions about medicinal plants and those used in construction. For construction species, we asked whether the wood, bark, leaves and/or other plant parts were used and whether the species was used for building or repairing housing, fences, furniture, boats and/or other purposes. For medicinal plants, we asked what each species was used for, what plant parts were consumed and/or used, whether the species treated and/or prevented conditions and how frequently the species was used (i.e. 'often' or 'rarely'). We combined all the data from both focus groups to create a comprehensive dataset of wild plant uses. If information for a plant species varied between focus groups (e.g. a species was used for medicine in one community but not the other), we combined all listed uses for our analyses. Within both focus groups, we confirmed that our final list of plant species contained no repeat species; we consolidated information for any species that were referred to by multiple names.

2.3.3 | Red-ruffed lemur food inventory

Finally, to evaluate whether human use of wild plant resources further conflicted with *V. rubra* resource needs, we identified what plant species in our dataset were known to be consumed by red-ruffed lemur in Masoala National Park. Using 34 months (March

2018–November 2020) of observational data collected as part of a long-term behavioural ecology study, we classified a species as food (hereafter referred to as 'Ruffed Lemur Food Tree' species) if we had observed *V. rubra* eat its fruit, leaves, flowers and/or other plant parts at least once during the study period (examples of plant species identification and data collection protocol, respectively, in Martinez & Razafindratsima, 2014; Vasey, 2004).

2.4 | Data analysis

We performed all analyses using the R statistical environment (R Core Team, 2023). To characterize the provisioning services of the plant community studied, we calculated the number and proportion of species reported in our focus groups to be used by local human communities, as well as those consumed by *V. rubra*. We then focused our analyses on the quantity and species richness of plant species used for two key human purposes—construction and medicine—as well as for ruffed lemur food tree species. We restricted analyses of plants used for construction only to large trees (DBH ≥ 10 cm) used by local communities for wood (hereafter 'Timber' species), as smaller individuals would not be targeted by resource users. Medicinal plant analyses included all plants, regardless of size. Ruffed lemur food tree analyses also focused only on the large plant class, as *V. rubra* are forest-obligate, arboreal species that occur predominantly in large trees (Borgerson, 2015a; Vasey, 2000). We calculated the count and species richness of plants per plot for timber species, medicinal plants and ruffed lemur food trees using the 'BiodiversityR' package (Kindt & Coe, 2005; count: *n* individual plants per plot; richness: *n* species per plot).

We used the following variables as measures of human pressure on sampled botanical plots in order to test the following related assumptions about the availability of timber, medicinal plants and ruffed lemur food trees across landscapes in the study region: *Community population size*, with plots sampled near larger human populations assumed to be associated with greater use of natural resources; *distance from community*, with resources closer to population centres assumed to be more likely to be extracted; and *time*. For *time*, as the resources being measured were not actively being cultivated (i.e. replenished) by local people, we assumed plant availability would decline year-to-year. Finally, we evaluated *protected area status* as a distinct grouping in our analysis of population, whereby land within the protected area of Masoala National Park (i.e. with a population of 0 people) is assumed to be less subject to human pressure.

We constructed a series of Poisson regressions with mixed effects ('glmmTMB' package; Brooks et al., 2017), wherein timber, medicinal plant and lemur food tree count and species richness were set as the response variables of interest. As botanical plots were only resampled over time in a subset of communities—and not in Masoala National Park—we assessed the effects of population, distance and protected area status using the plots sampled in 2015 and 2016 only (community plots: $N = 13$ sites; $n = 10$ plots per site; protected area plots: $N = 2$ sites; $n = 12$ and 13 plots per site) and evaluated the longitudinal dataset separately ($N = 5$ sites; $n = 10$ plots per site, each sampled over 5 years between 2015 and 2021). We used a model selection process to determine the best-performing model (i.e. candidate model with the lowest corrected Akaike information criterion, AICc; Burnham & Anderson, 2004) for each response variable from models that included a combination of population size, distance to community and an interaction between population and distance as fixed effects (i.e. all nested within the global model: Plot Metric ~ Population + Distance + Population × Distance + (1| Site: Plot ID)). We did not employ a model selection process to evaluate change over time. Rather, we modelled time (years 0, 2, 4, 5 and 6 for plots sampled in 2015, 2017, 2019, 2020 and 2021, respectively) alongside the same fixed effects as that of the best-performing general model for each response variable. We included a random intercept of plot ID nested within site ID for the 2015–2016 dataset analyses and a random intercept and slope for time that nested plot ID within site ID for the longitudinal dataset (the analysis of medicinal plant count over time could not include time as a random effect, as this model was unable to converge). We log-transformed both population and distance to community for all models to reduce the differences between these predictor values, due to both their skew and being sampled on different scales. We include model specifications for each analysis in Table S1. Finally, we did not consider a negative binomial model structure, as visualization of the data did not suggest overinflation.

We visually assessed each model's fit against our data to describe the differences between protected area and community plots, but we emphasize caution in how these results may be interpreted. In our data, protected area status and population were perfectly correlated (i.e. all population sizes within the national park are inherently '0 people'), and most protected area plots were farther from villages than community plots, both presenting statistical challenges. However, we chose not to subset our data to avoid Simpson's paradox (Kievit et al., 2013; Simpson, 1951), a statistical phenomenon whereby making inferences over data subsets can lead to inaccurate interpretations. As such, we discuss the differences in protected area and non-protected area plots only over the ranges for which data have been collected for each category (i.e. for protected area plots, we evaluate the effects of distance 1.5–18 km from the nearest community; for non-protected area plots, we evaluate the distance effects between 0.5 and 2.5 km). For analyses using the 2015–2016 plot dataset, we report the marginal effects of distance on plot metrics at the following representative population values: 0 (all protected area plots) in comparison to 50, 250 and 2000 people, again only over appropriate distance measures. We also report the marginal effects of population at 1.5 km, where distance values for protected area- and non-protected area plots overlap. All our models were at least $e^{3.71}$ times more likely than the null model (i.e. $7.42 \leq \Delta\text{AICc} \leq 315.62$; see Table S1 for model likelihood values and weights). We additionally report marginal and conditional R^2_{GLMM} values for each model via the 'MuMIn' package (Barton, 2022), which uses methods proposed by Johnson (2014) that can accommodate both random intercepts and slopes in mixed models. Variable significance was established at $p < 0.05$. To visualize model-predicted values of count and species richness for the community factors and time analyses, we used the 'ggeffects' package (Lüdecke, 2018). We used the 'venneuler' package (Wilkinson, 2022) to construct an Euler diagram that best shows the interrelationships between provisioning services in the study's plant assemblage.

2.4.1 | Ethical note

Institutional Animal Care and Use (Protocol No. 18-012: San Diego Zoo Wildlife Alliance) and Human Subjects Institutional Review boards (Protocols No. 2010-0595: University of Massachusetts Amherst; No. 15-2230: Harvard T. H. Chan School of Public Health; No. 18-19-1349: Montclair State University) approved all research. We obtained all necessary in-country permissions for this research through the Republic of Madagascar and Madagascar National Parks, specifically from the *Madagascar Direction Générale de l'Environnement et des Forêts* and *Madagascar Direction de la Gestion des Ressources Naturelles Renouvelables et des Ecosystèmes* (Permits No. 325/14, 105/17, 85/18, 202/18, 117/19, 17/20, 36/21). We also received verbal informed consent from all participants and each local administrator. Consent was verbal to further protect participant identities.

3 | RESULTS

3.1 | Regional non-cultivated plant assemblage and provisioning services

Focus groups and the red-ruffed lemur (*V. rubra*) food inventory provided information on the provisioning services of 408 locally occurring plants, 270 of which (66.2%) are reported to be used by local communities for at least one purpose. Information on the full assemblage of plant species and their provisioning services may be found in Appendix S1.

3.1.1 | Provisioning services for local communities

The assemblage of plants in the 2015–2016 botanical plots contained a total of 308 plant species. Of these, three-quarters (77.3%; $n=238$ plant species) provided at least one provisioning service for people in local communities (Figure 2). One-third of all plant species (32.5%) could be used by local communities for timber ($n=100$ species; Figure S1). Seventy-two species, nearly one quarter of all plant species (23.4%), were reportedly used as medicinal plants, while 57 species could be eaten as food (18.5% of assemblage; Figure S1). Relatively few species

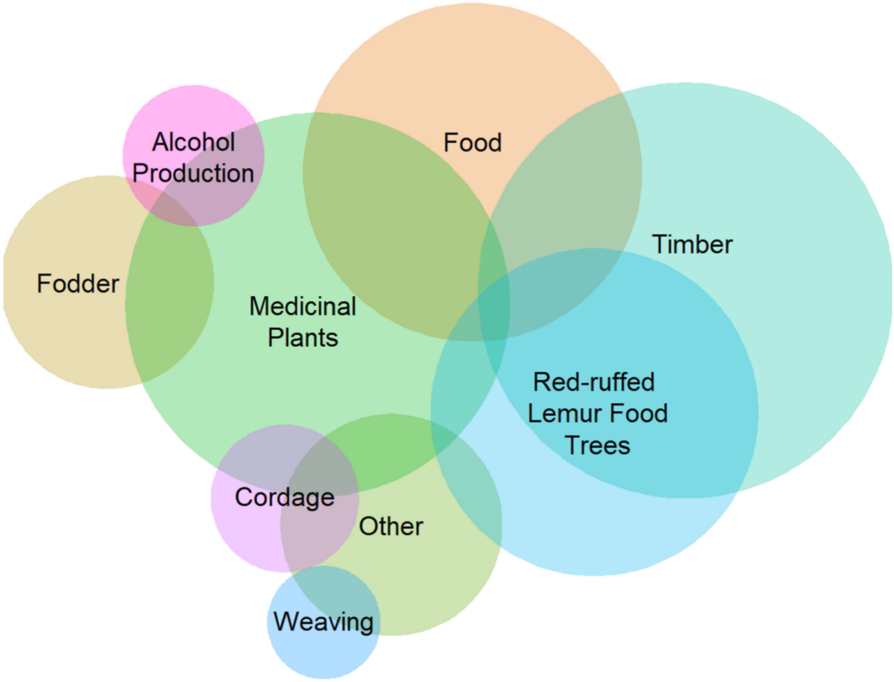

FIGURE 2 Assemblage of non-cultivated plant species occurring in botanical plots by provisioning service on the Masoala Peninsula of Madagascar (2015–2016). Circle diameter is proportional to the number of species per category (e.g. 100 species used for timber). The overlap between categories is proportional to the number of shared species (e.g. 46 species used for both timber and as red-ruffed lemur foods). Provisioning services per plant species as reported by focus groups in two local communities ($N=2$ focus groups). Ruffed lemur food trees observed to have been consumed (i.e. species' flowers, fruit and/or leaves eaten) by red-ruffed lemurs (*Varecia rubra*) during 34 months of behavioural observation from March 2018 to November 2020 in Masoala National Park (MNP), northeastern Madagascar. Botanical surveys conducted within Masoala National Park and in 13 surrounding communities in northeastern Madagascar from 2015 to 2016 ($N=155$ plots). $N=238$ species total in assemblage with one or more provisioning services. For a full list of plants and their services, see Appendix S1.

could be used as fodder for livestock, as cordage, in alcohol production or for weaving ($n=21$, 12, 11 and 6 species, respectively; Figure S1). Beyond the categories listed, 26 species were also used for 'other' purposes (10.9% of all utilitarian species; Figure S1), which included using plant products for agricultural trellises, waterproof sealants, pest management and hunting and cultural ceremonies among other uses (see Appendix S1 for all uses). While many human-use species were single-purpose (44.1%), substantial overlap did occur between species (Figure 2) used for both food and medicine ($n=21$ species), food and timber ($n=14$ species) and fodder and medicine ($n=8$ species). Within medicinal plants and species used in construction or repair specifically, the number of species and types of plant parts used varied widely depending on their intended purpose (Table 2). Two-thirds of reported medicinal plants could be used to treat conditions ($n=47$ medicinal plant species), with the remaining used to prevent unwanted health issues. Finally, most medicinal plant species (56.3%) were reported as being taken 'often' and another one-third (33.8%) 'rarely'. We did not have data for the remaining species. These results highlight the heterogeneity of our study's plant assemblage.

Provisioning services were not exclusively found either inside or outside of the national park (Figure S1). The majority of timber species ($n=78$ species; 78.0%) could be found in both Masoala National Park and near local communities (Figure S1). Most medicinal plant and food species were not exclusively documented in the protected area; rather, over two-fifths of both medicinal plant and food species were only found outside of the national park (44.4% and 42.1%, respectively; Figure S1). The plurality of plant species used as fodder and cordage and those used in alcohol production were also only found outside of the protected area ($n=13$, 5 and 7 species, respectively; Figure S1).

3.1.2 | Resources shared by red-ruffed lemurs and local communities

Fifty-nine tree species in the assemblage were known red-ruffed lemur food tree species (Figure S1). As shown in Figure 2, the majority of species consumed by *V. rubra* (84.7%) could be used by local communities, but nine ruffed lemur food tree species had no reported human use (15.3% of all ruffed lemur food tree species; see Appendix S1 for all ruffed lemur food tree species). Forty-six ruffed lemur food tree species, the majority of lemur resources in the 2015–2016 plant survey assemblage (78.0%), could be used for timber specifically (Figure 2). Additionally, ruffed lemur food tree species could be used for medicine ($n=5$ species), as well as consumed as food by local people ($n=10$ species; three species in common with medicinal plants; Figure 2). Ruffed lemur food trees were not predominantly restricted to either the Masoala National Park or near local communities but could be found in both plot types (89.8% of species; Figure S1). Thus, as with human provisioning services, lemur food resources were found both within and outside of the national park.

3.2 | Factors affecting timber and medicinal plant availability

All measures of timber and medicinal plant availability declined with community population size and were predicted to be higher in Masoala National Park than outside of the park boundaries. All but medicinal plant abundance (i.e. count) also declined with time. Contrary to expectations, medicinal plant count increased with

TABLE 2 Characteristics of species used in construction and repair and as medicinal plants, as reported by focus groups on the Masoala Peninsula, Madagascar.

Plant provisioning service	*N* species	Plant parts used[a] (*n* species)	Plant purpose (*n* species)
Construction and repair	156	Wood (133) Bark (11) Leaves (9) Other (2)	Housing (134) Wall Materials (115) Roofing Materials (21) Flooring Materials (106) Other (94) Boats (66) Fencing (60) Furniture (52) Other (44)
Medicinal plants	72	Leaves (29) Pith (23) Bark (6) Stem (4) Roots (3) Sap (3) Fruit (2) Heart (2)	Medicine usage As a treatment (47) As a prophylactic (24) Frequency of use[b] Often (40) Rarely (24)

Note: Included species were those documented in botanical plot surveys of the Masoala Peninsula conducted in 2015–2016. For a full list of plants and services, see Appendix S1.

[a] The following plant parts were not reportedly used as medicine: Flowers/Nectar, Seeds.

[b] No data were provided on frequency of use for eight species.

closer proximity to communities. However, all models for medicinal plants had low goodness-of-fit, suggesting the availability of these plants cannot be explained well by the factors tested. The full set of plots (2015–2016, $N=155$ plots) had a median 5 trees eligible for timber per plot, with an interquartile range (IQR) of 10 trees (total range: 0–26 trees per plot). Plots had a median 4 (IQR: 8) timber species (total range: 0–20 species/plot). Nearly a third (30.3%) of plots had no trees that could be used as timber, though 89.4% of these plots had no large trees at all. Medicinal plants occurred in higher abundance (median (IQR): 7 (11) plants per plot; range: 0–80 plants per plot), yet plots contained only nine species maximum (median (IQR): 3 (2) medicinal plant species per plot). A lower proportion of plots also contained no medicinal plants (11.0%), but only two-fifths of these (41.2%) contained no plants. Both timber and medicinal plant abundance were skewed towards a few species (Figure S2; for abundance of all species: Appendix S1). Eleven timber species comprised half of all timber trees in the plots, with Mandravokina (*Anthostema madagascariensis*), Tavolo (*Cryptocarya* spp.) and Rara (*Brochoneura chapelieri*) as the top three most common taxa (12.0%, 5.9% and 5.6% of individuals, respectively; Figure S2). Only four medicinal plant species comprised 50% of medicinal plants found in the plots (Figure S2): Lingoza (*Aframomum angustifolium*; 18.4% of medicinal plants), Trotrobato (*Clidemia hirta*; 12.0%), Asina (*Dracaena elliptica* and *D. reflexa*; 7.5%) and Tegny (*Imperata cylindrica*; 7.2%).

Comparing total plot count at the community level at the start and end of our study (2015 and 2021; see Figures S3 and S4 for plot-level changes over time), timber count declined by a median 13.0% per site (range: 0.0%–77.6% loss of timber trees per site); likewise, timber and medicinal plant species richness declined by a median 38.5% and 15.8% per site, respectively (range of timber species richness loss: 4.2%–54.3% loss of timber species per site; range medicinal plant species richness loss: 10.0%–29.4% loss of medicinal plant species per year). In contrast, medicinal plant count increased by a median 23.3% per site over the study period (range: −33.3%–101.7% change in medicinal plant count per site).

Timber provisioning services (i.e. count and species richness of timber trees per plot) significantly varied according to the population size of the nearest community (Figure 3a,b) and exhibited changes over time (Figure 4a,b; between 2015 and 2021), meeting our expectations of landscapes subject to human pressure. Significant interactions between the population of a plot's nearest community and its distance to human settlements additionally revealed an interplay between the effects of distance and protected area status for both timber measures (Table 3; count: $z=2.22$, $p=0.03$; species richness: $z=2.23$, $p=0.03$; $N=13$ sites with $n=10$ plots per site near communities and $n=25$ plots in Masoala National Park). Timber count and species richness were predicted to increase with increasing distance from plots outside of the protected area (Table S2 for marginal effects of distance at representative population values), but this relationship did not hold for plots within Masoala National Park (Figure 3a,b; see Table S3 for median (IQR) timber metrics per plot by protected area status). Indeed, population did not have a significant marginal effect at 1.5 km from the nearest community for either timber count or species richness, where both protected area and non-protected area plots were located (Table S4), though population had a significant negative effect on both metrics overall (Table 3; count: $z=-2.63$, $p=0.009$; species richness: $z=-2.66$, $p=0.008$). Taken together, these results suggest that, once plots are far enough away from a community, protected area status itself may not have an additive effect on plant abundance; future research is needed to evaluate this further, as our data could not explore this effect in-depth. Finally, while timber provisioning services significantly declined near communities over time (Table 4; count: $z=-4.17$, $p<0.001$; species richness: $z=-4.27$, $p<0.001$; model estimates for population and distance in Table S5), this relationship was primarily driven by declines in just two of the five communities sampled (villages 'A' and 'B'; see Figures S3a and S4a; Table S6 for marginal effects of time per site). These communities are both located on the Masoala Peninsula's coast, while all others are inland (i.e. sites 'C', 'D' and 'E'), indicating that more than population size could have been used to explain between-site differences (e.g. geographic or infrastructural differences between coastal and inland communities). Marginal R^2_{GLMM} values for all timber models ranged between 0.28 and 0.38, suggesting the effects of population and distance explain a moderate proportion of variation found across plot timber metrics (Table S1). Conditional R^2_{GLMM} values demonstrated a high goodness-of-fit across all timber models (range: 0.91–0.97; Table S1), underscoring again the importance of site-specific effects on measures of plant availability.

Medicinal plant provisioning services, in contrast to timber, did not wholly meet our expectations of how plant assemblages respond to human pressures. As expected and as shown in Figure 3c,d, both medicinal plant metrics (i.e. count and species richness) significantly declined with the population size of the nearest community (Table 3; count: $z=-3.28$, $p=0.001$; species richness: $z=-5.92$, $p<0.001$) and were always predicted to be higher in Masoala National Park than in non-protected areas (see Table S3 for summary statistics of medicinal plant metrics in and outside of the national park; Table S2 for marginal effects of distance by population on medicinal plant count). Medicinal plant species richness also significantly declined over time (between 2015 and 2021; Figure 4d; Table 4; $z=-3.38$, $p<0.001$). Contrary to expectations, medicinal plant count increased with proximity to human settlements (i.e. declined with distance; Figure 3c; $z=-3.11$, $p=0.002$), the only plant metric examined that was significantly directly affected by distance in any direction (the best-performing model for medicinal plant species richness did not include distance as a fixed effect; Table 3). Furthermore, medicinal plant count did not significantly decline over time (Figure 4c; $z=0.72$, $p=0.47$) in any of the communities sampled (Table S6; Figure S3b). In contrast to model goodness-of-fit for timber availability, marginal R^2_{GLMM} for medicinal plant models suggest our tested factors—distance, population and time—explained very little of the variation in medicinal plant availability in our data (i.e. marginal R^2_{GLMM} range from 0.03 to 0.18; Table S1). Interestingly, site-specific differences

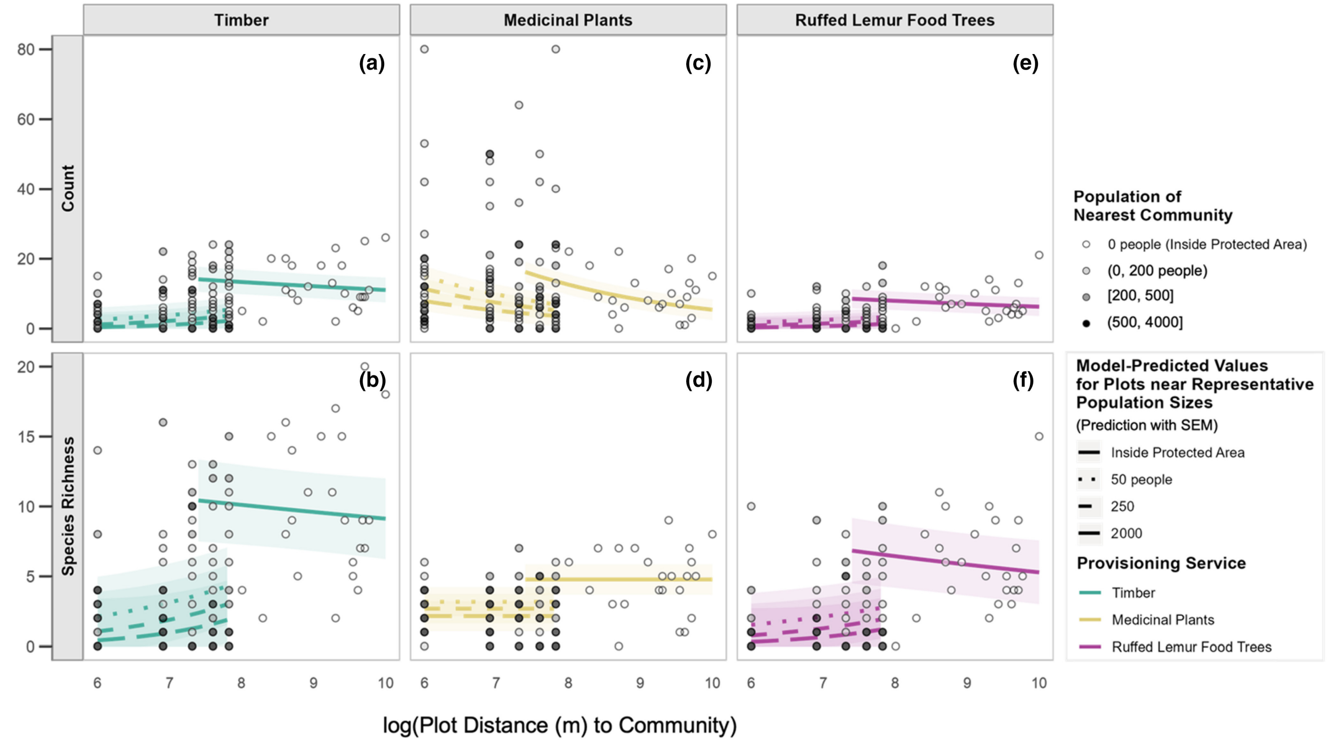

FIGURE 3 Plant count and species richness of timber, medicinal plants and ruffed lemur food trees per plot by distance to and population size of the nearest community on the Masoala Peninsula, Madagascar. Lines and line type represent model-predicted values of plot metrics at representative population sizes and in the protected area of Masoala National Park (i.e. communities of 50, 250 and 2000 people, and protected areas with '0 people', respectively) from best-performing Poisson regressions for each response metric. Bands represent the standard error of the mean (SEM) for predicted values. Predictions for protected area and non-protected area plots only made for the range of distance values over which data were collected within each category (protected area plots: 1.5–18 km from the nearest community; non-protected area: 0.5–2.5 km). Data points indicate individual plot values, where colour represents the population of the plot's nearest community (while population was modelled as a continuous variable, values here have been binned for readability). Plant count determined for all trees with a DBH ≥10 cm for timber and ruffed lemur food trees and for all plants, regardless of size, for medicinal plants. Botanical surveys conducted in 2015 in 13 communities surrounding Masoala National Park, northeastern Madagascar ($n = 10$ plots per community) and in 2016 in Masoala National Park ($n = 25$ plots). Refer to Table 3 for statistical results. Table S2 provides the marginal effects of distance at depicted representative population values, and Table S4 provides the marginal effects of population at 1.5 km, the distance at which both protected and non-protected area plots occurred. Plots (a-f) show actual and model-predicted values of the following metrics, by log-transformed distance to the nearest community: (a) Timber Count, (b) Timber Species Richness, (c) Medicinal Plant Count, (d) Medicinal Plant Species Richness, (e) Ruffed Lemur Food Tree Count, and (f) Ruffed Lemur Food Tree Species Richness.

had a stronger effect on medicinal plant count than on species richness (conditional R^2_{GLMM} for count: 0.91 and 0.94 for models of population and distance and change over time, respectively; species richness: 0.18 and 0.36; Table S1). Future research is needed to identify factors impacting medicinal plant availability, though our results also demonstrate how proxies of human pressure on plant assemblages may vary by provisioning service.

3.3 | Factors affecting availability of red-ruffed lemur food trees

Community population and time also affected the availability of red-ruffed lemur food trees, with both abundance and species richness likewise predicted to be higher in the protected area. A median 3 (IQR: 5) ruffed lemur food trees occurred per plot (range: 0–21 trees per plot), with plots having between 0 and 15 ruffed lemur food tree species each (median (IQR): 2 (4) species per plot). Like timber trees, ruffed lemur food trees were absent in roughly a third (33.6%) of plots, 80.8% of which were empty of all large trees. Ruffed lemur food tree abundance was also skewed towards a small number of species, with eight species (Tavolo: *Cryptocarya* spp.; Rotro: *Eugenia emirnensis*, *Morella spathulata*, *Psidium cattlenium*, *Syzigium danguyanum*; Ravinala: *Ravenala madagascariensis*; Asimbe: *Dracaena xiphophylla*; Haramibe: *Canarium madagascariensis*; Asina: *Draecana elliptica*, *D. reflexa*; Sodipaso: *Streblus* sp.; and Vongo: *Garcinia punctata*, *G. verrucose*, *Mammea bongo*, *M. perrieri*) comprising half of all ruffed lemur food trees within the plots (Figure S2; Appendix S1 for abundance of all species). Of the three most common species (Figure S2), Tavolo (*Cryptocarya* spp.) was the most abundant (10.9% of individuals), followed by Rotro (*Eugenia emirnensis*, *Morella spathulata*, *Psidium cattlenium*, *Syzigium danguyanum*; 9.5%) and Ravinala (*Ravenala madagascariensis*; 9.3%). Food provisioning services for ruffed lemurs also declined over the study period, with a median

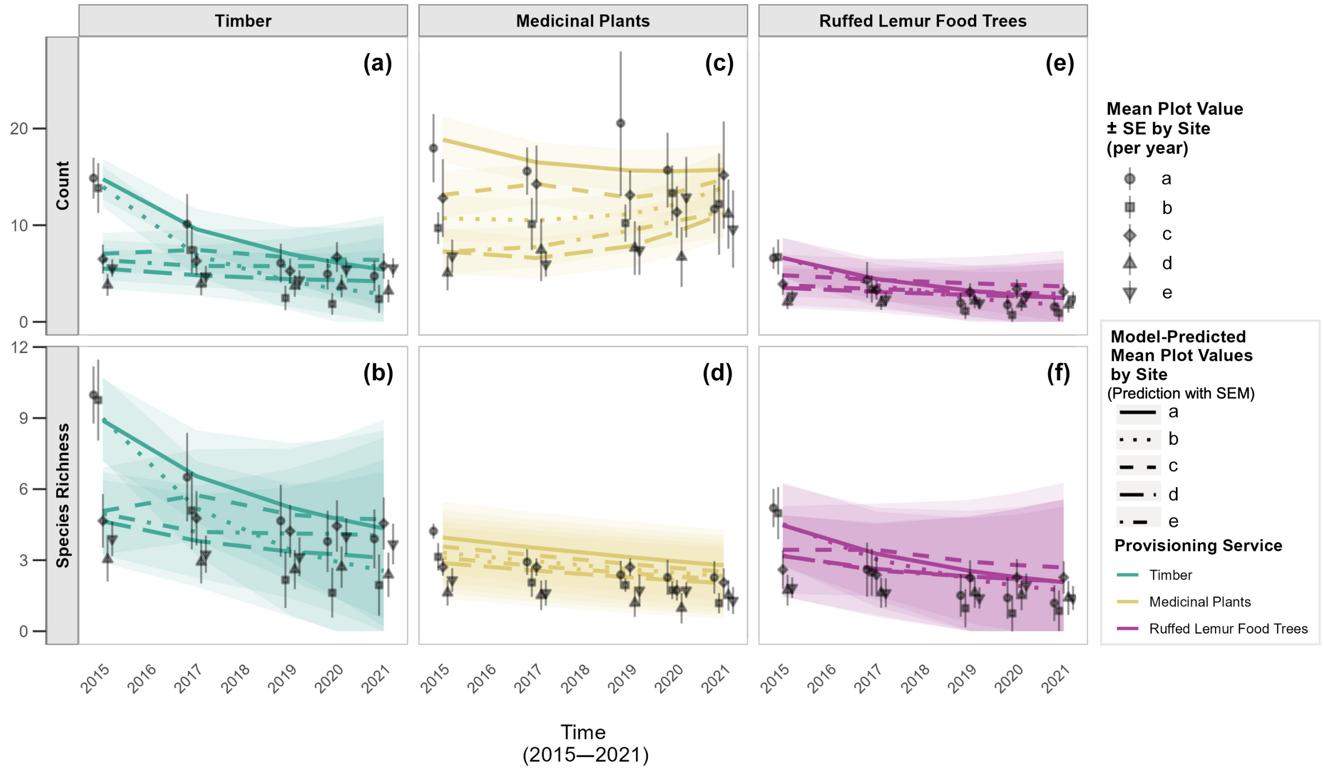

FIGURE 4 Plant count and species richness of timber, medicinal plant and ruffed lemur food trees per plot over time and by sampled site on the Masoala Peninsula, Madagascar (2015–2021). Lines and line types represent model-predicted values for plant count or species richness per year by site sampled (communities 'a' through 'e'), with bands indicating the standard error of the mean (SEM). Data points indicate the mean plot count or species richness (± SE) per year for each plant type, grouped by site. Plant count and species richness determined for all trees with a DBH ≥10 cm for timber and ruffed lemur food trees and for all plants, regardless of size, for medicinal plants. Botanical surveys conducted in 2015, 2017, 2019, 2020 and 2021 in five communities surrounding Masoala National Park, northeastern Madagascar ($N=250$ botanical plot surveys; 50 botanical plots; 10 plots per community, each sampled once per year indicated). Community identifiers are not provided to preserve their anonymity. Refer to Table 4 and Table S5 for statistical results. See Figures S3 and S4 for data points and model-predicted values for each sampled botanical plot and Table S6 for marginal effects of time by sampled site. Plots (a-f) show actual (SE) and model-predicted mean plot value per sampled site of the following metrics, by year: (a) Timber Count, (b) Timber Species Richness, (c) Medicinal Plant Count, (d) Medicinal Plant Species Richness, (e) Ruffed Lemur Food Tree Count, and (f) Ruffed Lemur Food Tree Species Richness.

17.0% loss of lemur food trees per site from 2015 to 2021 (range: 8.6%–75.7% loss per site) and a median 51.5% loss of lemur food tree species per site (range: 5.6%–55.9% loss per site).

Factors affecting the availability of ruffed lemur food resources mirrored those impacting timber provisioning services. Both ruffed lemur food tree count and species richness declined with the population size of the nearest community (Table 3; count: $z=-2.61$, $p=0.009$; species richness: $z=-2.66$, $p=0.008$) and decreased over time (Table 4; count: $z=-4.26$, $p<0.001$; species richness: $z=-4.23$, $p<0.001$). Likewise, a significant interaction between population and distance for both metrics (Table 3) led to predicted ruffed lemur provisioning services being higher in Masoala National Park than near communities (Figure 3e,f; see Table S3 for median (IQR) ruffed lemur tree plot metrics according to protected area status). As with timber availability, however, the marginal effects of population on plots 1.5 km from the nearest village were not significant for either ruffed lemur food tree count or species richness (Table S4), suggesting again that protected area status alone may not have a significant effect on tree availability. Models showed that sites 'A' and 'B' had sharper declines in lemur food tree counts and species richness over time than did other communities sampled (Figures S3c and S4c), but these differences were not as great as those between 'A' and 'B' and other communities for timber availability (Table S6). The proxies of human pressure that we evaluated explained a moderate amount of the variance across lemur food tree availability in our data (marginal R^2_{GLMM} range across lemur food tree models: 0.30–0.36; Table S1), while site-specific differences provided strong model goodness-of-fit (conditional R^2_{GLMM} range: 0.79–0.94; Table S1).

4 | DISCUSSION

People in local communities on the Masoala Peninsula in Madagascar access a wide variety of non-cultivated plant species, using over three-quarters of all non-cultivated plants identified in our study. Local people use the widest variety of these plant species

TABLE 3 Best-performing model results for counts and species richness of timber, medicinal plants and lemur food trees in botanical plots as predicted by the (1) population and (2) distance to the nearest community on the Masoala Peninsula, Madagascar.

		Population of nearest community			Distance to nearest community			Pop × Dist		
Category	**Model**	**Estimate ± SE**	***z***	***p*-value**	**Estimate ± SE**	***z***	***p*-value**	**Estimate ± SE**	***z***	***p*-value**
Timber										
Count	Pop × Dist + (1| Site: Plot ID)	**−1.23 ± 0.47**	**−2.63**	**0.009****	−0.09 ± 0.25	−0.37	0.71	**0.13 ± 0.06**	**2.22**	**0.03***
Species richness	Pop × Dist + (1| Site: Plot ID)	**−1.11 ± 0.42**	**−2.66**	**0.008****	−0.05 ± 0.22	−0.23	0.82	**0.11 ± 0.05**	**2.23**	**0.03***
Medicinal plants										
Count	Pop + Dist + (1| Site: Plot ID)	**−0.17 ± 0.05**	**−3.28**	**0.001****	**−0.42 ± 0.13**	**−3.11**	**0.002****	—	—	—
Species richness	Pop + (1| Site: Plot ID)	**−0.10 ± 0.02**	**−5.92**	**<0.001*****	—	—	—	—	—	—
Lemur food trees										
Count	Pop × Dist + (1| Site: Plot ID)	**−1.10 ± 0.42**	**−2.61**	**0.009****	−0.12 ± 0.22	−0.54	0.59	**0.11 ± 0.05**	**2.15**	**0.03***
Species richness	Pop × Dist + (1| Site: Plot ID)	**−1.06 ± 0.40**	**−2.66**	**0.008****	−0.10 ± 0.20	−0.49	0.62	**0.11 ± 0.05**	**2.2**	**0.03***

Note: The model structure (all Poisson regressions with mixed effects) for each analysis is provided. Population and distance to the community were each log-transformed. Estimates ± SE, Wald test statistics (i.e. *z*) and *p*-values for each model's fixed effects are included. Predictors that had a significant effect on each response variable are indicated in bold. The size of plants sampled for timber/lemur food trees and medicinal plant metrics differed. All trees with a DBH ≥10 cm were sampled for timber and lemur food trees, whereas medicinal plant metrics were determined for all plants. $N = 13$ community sites; $n = 10$ plots per site; $n = 25$ protected area plots, in Masoala National Park. All plots sampled in 2015–2016.

$^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

TABLE 4 Model results for counts and species richness of timber, medicinal plants and lemur food trees in botanical plots as predicted by time (i.e. years since 2015) on the Masoala Peninsula, Madagascar (2015–2021).

		Time		
Category	**Model**	**Estimate ± SE**	***z***	***p*-value**
Timber				
Count	Time + Pop × Dist + (1 + Time|Site: Plot ID)	**−0.19 ± 0.05**	**−4.17**	**<0.001*****
Species richness	Pop × Dist + Time + (1 + Time|Site: Plot ID)	**−0.18 ± 0.04**	**−4.27**	**<0.001*****
Medicinal plants				
Count	Time + Pop + Dist + (1 + Time|Site: Plot ID)	0.02 ± 0.03	0.72	0.47
Species richness[a]	Time + Pop + (1|Site: Plot ID)	**−0.06 ± 0.02**	**−3.38**	**<0.001*****
Lemur food trees				
Count	Time + Pop × Dist + (1 + Time|Site: Plot ID)	**−0.17 ± 0.04**	**−4.26**	**<0.001*****
Species richness	Time + Pop × Dist + (1 + Time|Site: Plot ID)	**−0.17 ± 0.04**	**−4.23**	**<0.001*****

Note: The model structure (all Poisson regressions with mixed effects) for each analysis is provided. Each model includes the fixed effects from the best-performing model structure of analyses of population and distance alone (i.e. population, distance and/or an interaction between population and distance) for each plot metric. Estimates ± SE, Wald test statistics (i.e. *z*) and *p*-values for time for each model are included. Analyses where time had a significant effect on each response variable are indicated in bold. The size of plants sampled for timber and medicinal plant metrics differed. All trees with a DBH ≥10 cm were sampled for timber, whereas medicinal plant metrics were determined for all plants. *N* = 5 sites; *n* = 10 plots per site sampled once each in 2015, 2017, 2019, 2020 and 2021. See Table S5 for full model results of analyses using this longitudinal dataset.

[a] The medicinal plant species richness analysis was the only one for which a random slope for time was not included.

***$p < 0.001$.

for construction, as well as for food and medicinal purposes. Wild plant resources are also used as fodder for livestock, cordage, alcohol production and weaving among other uses. Our study found that a minority of human-used plant species, across all categories of provisioning services surveyed, were found exclusively in Masoala National Park, where Critically Endangered endemic wildlife like the red-ruffed lemur (*V. rubra*; Borgerson et al., 2020) are most abundant. The availabilities of food resources for *V. rubra* and timber for local human populations largely follow patterns expected for plant communities subject to human pressure. We found weak to no support, however, for medicinal plant availability being impacted by our tested measures.

Most food tree species used by *V. rubra* are also used by local people. The majority of *V. rubra* tree species may also be extracted as timber, as is true in southeastern Madagascar for the collared brown lemur (*Eulemur collaris*; Račevska et al., 2022). Both cases constitute a human–wildlife conflict, as timber trees are fully removed when used. The availability (i.e. abundance and species richness) of both timber and ruffed lemur food trees in our study was lower near larger communities and decreased in all communities over time. Both were also more abundant and diverse in the Masoala National Park, where national policies restrict the use of natural resources. The wide diversity of timber species used by people, however, suggests two directions for management: (1) That communities may be able to adapt if specific timber species were to be locally extirpated; and (2) that the extraction of non-lemur-food trees could be encouraged over those containing resources eaten by *V. rubra*. Preserving Tavolo (*Cryptocarya* spp.), for example, the most commonly occurring ruffed lemur food resource in our sample, would support an important food base. *Cryptocarya* fruit was also identified as a preferred food for *V. variegata*, a closely related ruffed lemur species in eastern Madagascar (Balko, 1998; SI: Beeby & Baden, 2021), suggesting the broad potential for such recommendations. Such policy recommendations, however, lack important, actionable context without knowing how the relative importance of timber species is driven by consumer choices (as in Lavialle et al., 2015)—and how these choices might vary across different construction and repair purposes (e.g. by accessibility, affordability, durability and aesthetic values). Only subsets of timber species, after all, are used for any one construction purpose (e.g. for roofing vs. flooring materials in house construction). As timber extraction for construction represents the highest threat to Madagascar's endemic trees (Beech et al., 2021), identifying alternative timber sources and/or non-timber construction materials is critical.

Both medicinal plant abundance (i.e. count) and species richness declined with community population size and were predicted to be higher in Masoala National Park. The medicinal plant count did not significantly decrease over time and even increased for plots closer to human settlements, contrary to expectations. However, these results received very weak support in our models, strongly suggesting that factors beyond distance, population, time or protected area status affect the availability of this provisioning service. In the region, medicinal plant resources are typically not collected by removing (i.e. killing) the entire plant, so that plant abundance and richness may not be impacted by human use as much as timber is; indeed, our results suggest that local people may even be managing or promoting the availability of useful medicinal plants, so that their prevalence would increase with human proxies. While our botanical plots were not 'pristine' at the start of this study, higher availability over time and closer to human settlements may also be indicative of an increase in successional and/or introduced plants associated with human disturbance, as has been documented in human landscapes elsewhere in Madagascar (Raveloaritiana et al., 2021). We know little about whether different types of plant species on the Masoala Peninsula—endemic, native, introduced and 'invasive'—provide meaningfully different services to local communities (see Lavialle et al., 2015; Raveloaritiana et al., 2023). In a study in southeastern Madagascar, as an example, however, introduced *Eucalyptus* species were perceived to be of lower quality for construction purposes than native plants (Račevska et al., 2022). Ultimately, the decline of timber provisioning services overall and the high number of medicinal plants accessed by local communities point to the considerable need for non-cultivated plants for these purposes. Each is not easily or affordably substituted with other products. Timber, especially, runs the risk of being unsustainably harvested.

To address pressures on natural resources in a way that supports the needs of resource users, the priorities of proposed reforestation efforts must be clearly defined and both social and ecological outcomes considered (Mansourian et al., 2017). In our study region, as elsewhere, different plant species would be recommended for different objectives (see Appendix S1 for information on plant species and provisioning services) and even at different stages of succession (Konersmann et al., 2021). Projects aimed at promoting multi-use landscapes would (1) ensure that resources are available for any resource use cases prioritized by stakeholders that target only a few species (e.g. focus groups reported few species used for weaving and cordage in our study) and (2) not overlook the roles played by plant species that support multiple provisioning services (e.g. in our sample, *Ravenala madagascariensis* and *Brochoneura chapelieri*). In contrast, reforestation efforts primarily intended to improve connectivity for wildlife—and thus to restrict extraction of resources in particular zones—would need to ensure that local communities have access to key resources elsewhere (Manjaribe et al., 2013).

As the provisioning services of natural resources can vastly differ across land cover types (Cocks et al., 2008)—and can even *increase* with human disturbance (Pritchard et al., 2019)—we must continue to develop methods of understanding the degradation of landscape provisioning services in a way that is meaningful to the needs of local residents (Pritchard et al., 2019). Thus, it is essential that ethnobotanical studies examine provisioning services and resource extraction practices from the perspectives of a diversity of local stakeholders (e.g. in Madagascar, that of children: Porcher et al., 2022; women: Razafindraibe et al., 2013). Efforts aimed at the sustainable management of such resources for both human and biodiversity concerns will not be successful without local voices—and land rights (Rakotonarivo et al., 2023)—at the fore (Löfqvist et al., 2022).

4.1 | Study limitations and future directions

A number of study limitations warrant caution in the interpretation of our results and also point to avenues for future research. First, focus groups were only conducted in two of our study communities, with a relatively small number of participants each. We were additionally not able to evaluate the importance of individual lemur food tree species to *V. rubra* diets, as we gave equal weight to all species consumed. Though we documented the decline of provisioning services over time, we were also unable to assess whether the harvest of non-cultivated plants is sustainable in the study region. As people across Madagascar may travel far distances to access particular resources (e.g. >1 h walk to access firewood, timber and honey in Ankarafantsika: Borgerson, Randrianasolo, et al., 2019), our study would have further benefitted from examining non-protected area plots located farther than 2.5 km from population centres. This limitation also prevented us from being able to explore the effects of protected area status in-depth, though we recommend further research to test the implications of our study's findings (that, as plots outside of protected areas are located near increasingly small human populations or at increasingly far distances from human settlements, plant availability metrics are expected to converge at values seen within protected areas). Further considering population size, however, we especially caution the attribution of population size alone as driving the decline in natural resources, as this metric can be frequently confounded with other, context-specific factors (Hughes et al., 2023). For our study, village age and its distance to forest frontiers may be confounding factors, in addition to historic relocations and relationships associated with the creation of the park (Ormsby & Kaplin, 2005). Species abundance and richness can also vary broadly across land cover types, particularly within transformation landscapes (Drescher et al., 2016; Osen et al., 2021), something our analyses did not account for. Indeed, our results showed coastal plant assemblages declining more sharply over time than those near communities further inland, warranting further explanation. The proportion of variation explained by our models' random effects (i.e. by 'site;' as evidenced by the difference between models' marginal and conditional R^2_{GLMM} values) underscores the importance of considering site-specific drivers of plant use and/or distribution, whether they be human and/or landscape factors. Future work that evaluates natural resource use within a landscape's context, assesses resource availability alongside the sustainability of current extraction rates and incorporates wider participation of local users (e.g. in focus groups explicitly accounting for diversity in age, sex, livelihood strategies and socioeconomic status of participants) is vital for better understanding the complex drivers and consequences of the use of non-cultivated plants.

5 | CONCLUSION

Our findings demonstrate that the decline of provisioning services for human populations, like timber and medicinal plants, can also signal a loss of resources for endemic wildlife. Indeed, the availability and diversity of red-ruffed lemur food trees decreased over the years of this study. While lemurs are sensitive to a range of anthropogenic activities (de Almeida-Rocha et al., 2017; Eppley et al., 2020; Torres-Romero et al., 2023), the potential for resource competition with human populations *can* be minimized. As critical seed dispersers on Madagascar (Albert-Daviaud et al., 2018), lemurs have an important role to play in 'becom[ing] part of their own conservation' (Konersmann et al., 2021, p. 1525). Indeed, with research on lemur food resources documenting nearly 600 plant genera consumed by lemurs to date (Eppley et al., 2022; Steffens, 2020), lemurs likely stand to benefit from restoration efforts designed to support ecosystem services for human populations (Konersmann et al., 2021). For forest landscape restoration efforts (Mansourian et al., 2017) and other such projects focused on plant provisioning services, particularly in rainforest transformation landscapes, we recommend the following general considerations: (1) To determine what resources are targeted for multiple provisioning services; (2) to identify which provisioning services are most constrained by available plants; and (3) to shift consumption of vulnerable resources to alternatives, where possible. This understanding of available provisioning services, as we have shown, allows stakeholders to take informed actions that safeguard or even improve both local human and wildlife resource bases.

AUTHOR CONTRIBUTIONS

Katherine J. Kling, A. Catherine Markham, Patricia C. Wright and Cortni Borgerson conceived the ideas and designed methodology; Cortni Borgerson, Timothy M. Eppley, Be Noel Razafindrapaoly, Rajaona Delox, Be Jean Rodolph Rasolofoniaina, Jeanne Mathilde Randriamanetsy, Pascal Elison, McAntonin Andriamahaihavana, Dean Gibson, Delaïd Claudin Rasamisoa, Josia Razafindramanana and Natalie Vasey collected and contributed the data; Katherine J. Kling and Carter W. Daniels analysed the data; Katherine J. Kling led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank the Masoala communities, families and individuals that generously collaborated with us; your knowledge is extensive, and without you, our work would be impossible. A Graduate Council Fellowship (Graduate School of Stony Brook University) and an NSF Graduate Research Fellowship (2016203971) supported Katherine J. Kling during analysis and writing. Community and botanical data collection was funded by the International Union for the Conservation of Nature Save our Species (IUCN-SOS 2018A-117), Montclair State University (SBR2020), a National Science Foundation SBE-IBSS Postdoctoral Research Fellowship (1513638) and the National Geographic Society (NGS-C280-14, NGS-C021-17, NGS-55616C-20). Red-ruffed lemur data collection received financial support from the American Society of Primatologists, the Margot Marsh Biodiversity Foundation, the San Diego Zoo Ocelots Fund and the San Diego Zoo Wildlife Alliance. We thank H. Resit Akçakaya, Liliana M. Dávalos and Richard Bankoff for their constructive comments. Finally, we are grateful for the thoughtful and immensely constructive feedback provided by our reviewers, Dominic A. Martin and Karen M. Bailey, as well as by the editors at *People & Nature*.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code used in analyses are available from the Zenodo Repository https://doi.org/10.5281/zenodo.7943053 (Kling et al., 2023).

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REFERENCES

Ahrends, A., Burgess, N. D., Milledge, S. A. H., Bulling, M. T., Fisher, B., Smart, J. C. R., Clarke, G. P., Mhoro, B. E., & Lewis, S. L. (2010). Predictable waves of sequential forest degradation and biodiversity loss spreading from an African city. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(33), 14556–14561. https://doi.org/10.1073/pnas.0914471107

Albers, H. J., & Robinson, E. J. Z. (2013). A review of the spatial economics of non-timber forest product extraction: Implications for policy. *Ecological Economics*, *92*, 87–95. https://doi.org/10.1016/j.ecolecon.2012.01.021

Albert-Daviaud, A., Perillo, S., & Stuppy, W. (2018). Seed dispersal syndromes in the Madagascan flora: The unusual importance of primates. *Oryx*, *52*(3), 418–426. https://doi.org/10.1017/S0030605317001600

Allnutt, T. F., Asner, G. P., Golden, C. D., & Powell, G. V. N. (2013). Mapping recent deforestation and forest disturbance in northeastern Madagascar. *Tropical Conservation Science*, *6*(1), 1–15. https://doi.org/10.1177/194008291300600101

An, L., & López-Carr, D. (2012). Understanding human decisions in coupled natural and human systems. *Ecological Modelling*, *229*, 1–4. https://doi.org/10.1016/j.ecolmodel.2011.10.023

Andriatsitohaina, R. N. N., Celio, E., Llopis, J. C., Rabemananjara, Z. H., Ramamonjisoa, B. S., & Grêt-Regamey, A. (2020). Participatory Bayesian network modeling to understand driving factors of land-use change decisions: Insights from two case studies in northeast Madagascar. *Journal of Land Use Science*, *15*(1), 69–90. https://doi.org/10.1080/1747423X.2020.1742810

Balko, E. A. (1998). *A behaviorally plastic response to forest composition and logging disturbance by Varecia variegata variegata in Ranomafana National Park, Madagascar* (Publication Number 9841254) [Ph.D., State University of New York College of Environmental Science and Forestry]. ProQuest Dissertations & Theses Global.

Barrett, C. B., Travis, A. J., & Dasgupta, P. (2011). On biodiversity conservation and poverty traps. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(34), 13907–13912. https://doi.org/10.1073/pnas.1011521108

Barton, K. (2022). *MuMIn: Multi-model inference*. R package version 1.46.0 https://CRAN.R-project.org/package=MuMIn

Beeby, N., & Baden, A. L. (2021). Seasonal variability in the diet and feeding ecology of black-and-white ruffed lemurs (*Varecia variegata*) in Ranomafana National Park, southeastern Madagascar. *American Journal of Physical Anthropology*, *174*(4), 763–775. https://doi.org/10.1002/ajpa.24230

Beech, E., Rivers, M. C., Rabarimanarivo, M., Ravololomanana, N., Manjato, N., Lantoarisoa, F., Andriambololonera, S., Ramandimbisoa, B., Ralimanana, H., Rakotoarisoa, S. E., Razanajatovo, H., Razafiniary, V., Andriamanohera, A., Randrianasolo, V., Rakotonasolo, F., Rakotoarisoa, A., Randriamamonjy, N., Rajaovelona, L. R., Rakotomalala, N. H., … Vololoniaina, J. (2021). *The Red List of trees of Madagascar*. Botanic Gardens Conservation International (BGCI).

Bennett, E. M., Cramer, W., Begossi, A., Cundill, G., Díaz, S., Egoh, B. N., Geijzendorffer, I. R., Krug, C. B., Lavorel, S., Lazos, E., Lebel, L., Martín-López, B., Meyfroidt, P., Mooney, H. A., Nel, J. L., Pascual, U., Payet, K., Harguindeguy, N. P., Peterson, G. D., … Woodward, G. (2015). Linking biodiversity, ecosystem services, and human well-being: Three challenges for designing research for sustainability. *Current Opinion in Environmental Sustainability*, *14*, 76–85. https://doi.org/10.1016/j.cosust.2015.03.007

Borgerson, C. (2015a). The effects of illegal hunting and habitat on two sympatric endangered primates. *International Journal of Primatology*, *36*(1), 74–93. https://doi.org/10.1007/s10764-015-9812-x

Borgerson, C. (2015b). *Illegal hunting on the Masoala Peninsula of Madagascar: Its extent, causes, and impact on lemurs and humans*. Doctoral Dissertations, 347. https://doi.org/10.7275/6899987.0

Borgerson, C., Eppley, T. M., Patel, E., Johnson, S., Louis, E. E., & Razafindramanana, J. (2020). *Varecia rubra*. The IUCN Red List of threatened species 2020, e.T22920A115574598. https://doi.org/10.2305/IUCN.UK.2020-2.RLTS.T22920A115574598.en

Borgerson, C., Johnson, S. E., Hall, E., Brown, K. A., Narváez-Torres, P. R., Rasolofoniaina, B. J. R., Razafindrapaoly, B. N., Merson, S. D., Thompson, K. E. T., Holmes, S. M., Louis, E. E., & Golden, C. D. (2022). A national-level assessment of lemur hunting pressure in Madagascar. *International Journal of Primatology*, *43*(1), 92–113. https://doi.org/10.1007/s10764-021-00215-5

Borgerson, C., Johnson, S. E., Louis, E. E., Jr., Holmes, S. M., Anjaranirina, E. J., Randriamady, H. J., & Golden, C. D. (2018). The use of natural resources to improve household income, health, and nutrition within the forests of Kianjavato, Madagascar. *Madagascar Conservation & Development*, *13*(1), 45–52. https://doi.org/10.4314/mcd.v13i1.6

Borgerson, C., McKean, M. A., Sutherland, M. R., & Godfrey, L. R. (2016). Who hunts lemurs and why they hunt them. *Biological Conservation*, *197*, 124–130. https://doi.org/10.1016/j.biocon.2016.02.012

Borgerson, C., Randrianasolo, J. F., Andraina, T. R., Anjaranirina, E. J., Randriamady, H. J., Merson, S., Dollar, L., & Golden, C. D. (2019). Wildlife hunting in complex human-environmental systems: How understanding natural resource use and human welfare can improve conservation in the Ankarafantsika National Park, Madagascar. *Madagascar Conservation & Development*, *14*(1), 37–45. https://doi.org/10.4314/mcd.v14i1.7

Borgerson, C., Razafindrapaoly, B., Rajaona, D., Rasolofoniaina, B. J. R., & Golden, C. D. (2019). Food insecurity and the unsustainable hunting of wildlife in a UNESCO world heritage site. *Frontiers in Sustainable Food Systems*, *3*, 99. https://doi.org/10.3389/fsufs.2019.00099

Borgerson, C., Vonona, M. A., Vonona, T., Anjaranirina, E. J., Lewis, R., Ralainasolo, F., & Golden, C. D. (2018). An evaluation of the interactions among household economies, human health, and wildlife hunting in the Lac Alaotra wetland complex of Madagascar. *Madagascar Conservation & Development*, *13*(1), 25–33. https://doi.org/10.4314/mcd.v13i1.5

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378–400. https://doi.org/10.3929/ethz-b-000240890

Brown, K. A., Flynn, D. F. B., Abram, N. K., Ingram, J. C., Johnson, S. E., & Wright, P. (2011). Assessing natural resource use by forest-reliant communities in Madagascar using functional diversity and functional redundancy metrics. *PLoS ONE*, *6*(9), e24107. https://doi.org/10.1371/journal.pone.0024107

Brown, K. A., Johnson, S. E., Parks, K. E., Holmes, S. M., Ivoandry, T., Abram, N. K., Delmore, K. E., Ludovic, R., Andriamaharoa, H. E., Wyman, T. M., & Wright, P. C. (2013). Use of provisioning ecosystem services drives loss of functional traits across land use intensification gradients in tropical forests in Madagascar. *Biological Conservation*, *161*, 118–127. https://doi.org/10.1016/j.biocon.2013.03.014

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods & Research*, *33*(2), 261–304. https://doi.org/10.1177/0049124104268644

Ceballos, G., Ehrlich, P. R., & Raven, P. H. (2020). Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(24), 13596–13602. https://doi.org/10.1073/pnas.1922686117

Chazdon, R. L., Brancalion, P. H. S., Laestadius, L., Bennett-Curry, A., Buckingham, K., Kumar, C., Moll-Rocek, J., Vieira, I. C. G., & Wilson, S. J. (2016). When is a forest a forest? Forest concepts and definitions in the era of forest and landscape restoration. *Ambio*, *45*(5), 538–550. https://doi.org/10.1007/s13280-016-0772-y

Cocks, M. L., Bangay, L., Shackleton, C. M., & Wiersum, F. K. (2008). 'Rich man poor man'—Inter-household and community factors influencing the use of wild plant resources amongst rural households in South Africa. *International Journal of Sustainable Development and World Ecology*, *15*(3), 198–210. https://doi.org/10.3843/SusDev.15.3:3

Costanza, R., de Groot, R., Braat, L., Kubiszewski, I., Fioramonti, L., Sutton, P., Farber, S., & Grasso, M. (2017). Twenty years of ecosystem services: How far have we come and how far do we still need to go? *Ecosystem Services*, *28*, 1–16. https://doi.org/10.1016/j.ecoser.2017.09.008

Dave, R., Tompkins, E. L., & Schreckenberg, K. (2017). Forest ecosystem services derived by smallholder farmers in northwestern Madagascar: Storm hazard mitigation and participation in forest management. *Forest Policy and Economics*, *84*, 72–82. https://doi.org/10.1016/j.forpol.2016.09.002

de Almeida-Rocha, J. M., Peres, C. A., & Oliveira, L. C. (2017). Primate responses to anthropogenic habitat disturbance: A pantropical meta-analysis. *Biological Conservation*, *215*, 30–38. https://doi.org/10.1016/j.biocon.2017.08.018

de Mello, N. G. R., Gulinck, H., Van den Broeck, P., & Parra, C. (2020). Social-ecological sustainability of non-timber forest products: A review and theoretical considerations for future research. *Forest Policy and Economics*, *112*, 102109. https://doi.org/10.1016/j.forpol.2020.102109

Drescher, J., Rembold, K., Allen, K., Beckschäfer, P., Buchori, D., Clough, Y., Faust, H., Fauzi, A. M., Gunawan, D., Hertel, D., Irawan, B., Jaya, I. N. S., Klarner, B., Kleinn, C., Knohl, A., Kotowska, M. M., Krashevska, V., Krishna, V., Leuschner, C., … Scheu, S. (2016). Ecological and socio-economic functions across tropical land use systems after rainforest conversion. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1694), 20150275. https://doi.org/10.1098/rstb.2015.0275

Eppley, T. M., Santini, L., Tinsman, J. C., & Donati, G. (2020). Do functional traits offset the effects of fragmentation? The case of large-bodied diurnal lemur species. *American Journal of Primatology*, *82*(4), e23104. https://doi.org/10.1002/ajp.23104

Eppley, T. M., Steffens, K. J. E., Colquhoun, I. C., & Birkinshaw, C. R. (2022). Lemur food plants. In S. M. Goodman (Ed.), *The new natural history of Madagascar* (Vol. 2, pp. 1839–1859). Princeton University Press.

FAO. (2017). *Sustainable woodfuel for food security. A smart choice: Green, renewable and affordable*. Food and Agriculture Organization of the United Nations. http://www.fao.org/3/a-i7917e.pdf

FAO & UNEP. (2020). *The state of the world's forests 2020*. Forests, Biodiversity and People. https://doi.org/10.4060/ca8642en

Fedele, G., Urech, Z. L., Rehnus, M., & Sorg, J.-P. (2011). Impact of women's harvest practices on *Pandanus guillaumetii* in Madagascar's lowland rainforests. *Economic Botany*, *65*(2), 158–168. https://doi.org/10.1007/s12231-011-9157-0

Fritz-Vietta, N. V. (2016). What can forest values tell us about human well-being? Insights from two biosphere reserves in Madagascar. *Landscape and Urban Planning*, *147*, 28–37. https://doi.org/10.1016/j.landurbplan.2015.11.006

Gibson, C. C., McKean, M. A., & Ostrom, E. (2000). 1 Explaining deforestation: The role of local institutions. In C. C. Gibson, M. A. McKean, & E. Ostrom (Eds.), *People and forests: Communities, institutions, and governance* (pp. 1–26). MIT Press.

Golden, C. D., Rasolofoniaina, B. J. R., Anjaranirina, E. J. G., Nicolas, L., Ravaoliny, L., & Kremen, C. (2012). Rainforest pharmacopeia in Madagascar provides high value for current local and prospective global uses. *PLoS ONE*, *7*(7), e41221. https://doi.org/10.1371/journal.pone.0041221

Google Earth Pro 7.3.6. (2023). *Masoala Peninsula*, 4 January 2014. http://www.earth.google.com

Hamann, M., Berry, K., Chaigneau, T., Curry, T., Heilmayr, R., Henriksson, P. J. G., Hentati-Sundberg, J., Jina, A., Lindkvist, E., Lopez-Maldonado, Y., Nieminen, E., Piaggio, M., Qiu, J., Rocha, J. C., Schill, C., Shepon, A., Tilman, A. R., van den Bijgaart, I., & Wu, T. (2018). Inequality and the biosphere. *Annual Review of Environment and Resources*, *43*(1), 61–83. https://doi.org/10.1146/annurev-environ-102017-025949

Hermans-Neumann, K., Gerstner, K., Geijzendorffer, I. R., Herold, M., Seppelt, R., & Wunder, S. (2016). Why do forest products become less available?A pan-tropical comparison of drivers of forest-resource degradation. *Environmental Research Letters*, *11*(12), 125010. https://doi.org/10.1088/1748-9326/11/12/125010

Holmes, C. (2007). Linking livelihoods, land stewardship, and resource conservation in the Antongil Bay landscape, Madagascar. In K. H. Redford & E. Fearn (Eds.), *WCS working paper no. 32—Protected areas and human livelihoods* (pp. 6–16). Wildlife Conservation Society.

Horn, C. M., Vargas Paredes, V. H., Gilmore, M. P., & Endress, B. A. (2018). Spatio-temporal patterns of *Mauritia flexuosa* fruit extraction in the Peruvian Amazon: Implications for conservation and sustainability. *Applied Geography*, *97*, 98–108. https://doi.org/10.1016/j.apgeog.2018.05.004

Hughes, A. C., Tougeron, K., Martin, D. A., Menga, F., Rosado, B. H. P., Villasante, S., Madgulkar, S., Gonçalves, F., Geneletti, D., Diele-Viegas, L. M., Berger, S., Colla, S. R., de Andrade Kamimura, V., Caggiano, H., Melo, F., de Oliveira Dias, M. G., Kellner, E., & do Couto, E. V. (2023). Smaller human populations are neither a necessary nor sufficient condition for biodiversity conservation. *Biological Conservation*, *277*, 109841. https://doi.org/10.1016/j.biocon.2022.109841

IFRI. (2008). *International Forestry Resources and Institutions (IFRI) field manual*. Indiana University, Workshop in Political Theory and Policy Analysis.

IUCN. (2022). *The IUCN red list of threatened species*. Version 2022-1. https://www.iucnredlist.org

Johnson, P. C. D. (2014). Extension of Nakagawa & Schielzeth's R2GLMM to random slopes models. *Methods in Ecology and Evolution*, *5*(9), 944–946. https://doi.org/10.1111/2041-210X.12225

Kievit, R., Frankenhuis, W., Waldorp, L., & Borsboom, D. (2013). Simpson's paradox in psychological science: A practical guide [hypothesis and theory]. *Frontiers in Psychology*, *4*, 513. https://doi.org/10.3389/fpsyg.2013.00513

Kindt, R., & Coe, R. (2005). *Tree diversity analyses: A manual and software for common statistical methods for ecological and biodiversity studies*. World Agroforestry Centre (ICRAF). http://www.worldagroforestry.org/output/tree-diversity-analysis

Kling, K. J., Eppley, T. M., Markham, A. C., Wright, P. C., Razafindrapaoly, B. N., Delox, R., Rasolofoniaina, B. J. R., Randriamanetsy, J. M., Elison, P., Andriamahaihavana, M., Gibson, D., Rasamisoa, D. C. R., Josia Vasey, N., Daniels, C. W., & Borgerson, C. (2023). *kj-kling/Kling-etal-People-Nature: Code, results outputs, & datasets*. https://doi.org/10.5281/zenodo.7943053

Konersmann, C., Noromiarilanto, F., Ratovonamana, Y. R., Brinkmann, K., Jensen, K., Kobbe, S., Köhl, M., Kuebler, D., Lahann, P., Steffens, K. J. E., & Ganzhorn, J. U. (2021). Using utilitarian plants for lemur conservation. *International Journal of Primatology*, *43*, 1026–1045. https://doi.org/10.1007/s10764-021-00200-y

Kremen, C. (2005). Managing ecosystem services: What do we need to know about their ecology? *Ecology Letters*, *8*(5), 468–479. https://doi.org/10.1111/j.1461-0248.2005.00751.x

Kremen, C., Razafimahatratra, V., Guillery, R. P., Rakotomalala, J., Weiss, A., & Ratsisompatrarivo, J.-S. (1999). Designing the Masoala National Park in Madagascar based on biological and socioeconomic data. *Conservation Biology*, *13*(5), 1055–1068. https://doi.org/10.1046/j.1523-1739.1999.98374.x

Lavialle, J., Carrière, S. M., Miandrimanana, C., Tilahimena, A., Birkinshaw, C. R., & Aronson, J. (2015). Complementarity of native and introduced tree species: Exploring timber supply on the east coast of Madagascar. *Madagascar Conservation & Development*, *10*(3), 137–143. https://doi.org/10.4314/mcd.v10i3.6

Levers, C., Romero-Muñoz, A., Baumann, M., Marzo, T. D., Fernández, P. D., Gasparri, N. I., Gavier-Pizarro, G. I., Waroux, Y. l. P. D., Piquer-Rodríguez, M., Semper-Pascual, A., & Kuemmerle, T. (2021). Agricultural expansion and the ecological marginalization of forest-dependent people. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(44), e2100436118. https://doi.org/10.1073/pnas.2100436118

Llopis, J. C., Chastonay, J. F., Birrer, F. C., Bär, R., Andriatsitohaina, R. N. N., Messerli, P., Heinimann, A., & Zaehringer, J. G. (2021). Year-to-year ecosystem services supply in conservation contexts in north-eastern Madagascar: Trade-offs between global demands and local needs. *Ecosystem Services*, *48*, 101249. https://doi.org/10.1016/j.ecoser.2021.101249

Llopis, J. C., Harimalala, P. C., Bär, R., Heinimann, A., Rabemananjara, Z. H., & Zaehringer, J. G. (2019). Effects of protected area establishment and cash crop price dynamics on land use transitions 1990–2017 in north-eastern Madagascar. *Journal of Land Use Science*, *14*(1), 52–80. https://doi.org/10.1080/1747423X.2019.1625979

Löfqvist, S., Kleinschroth, F., Bey, A., de Bremond, A., DeFries, R., Dong, J., Fleischman, F., Lele, S., Martin, D. A., Messerli, P., Meyfroidt, P., Pfeifer, M., Rakotonarivo, S. O., Ramankutty, N., Ramprasad, V., Rana, P., Rhemtulla, J. M., Ryan, C. M., Vieira, I. C. G., … Garrett, R. D. (2022). How social considerations improve the equity and effectiveness of ecosystem restoration. *BioScience*, *73*(2), 134–148. https://doi.org/10.1093/biosci/biac099

López-Feldman, A., & Wilen, J. E. (2008). Poverty and spatial dimensions of non-timber forest extraction. *Environment and Development Economics*, *13*(5), 621–642. https://doi.org/10.1017/S1355770X08004518

Lüdecke, D. (2018). ggeffects: Tidy data frames of marginal effects from regression models. *Journal of Open Source Software*, *3*(26), 772. https://doi.org/10.21105/joss.00772

MacDougall, A. S., McCann, K. S., Gellner, G., & Turkington, R. (2013). Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature*, *494*(7435), 86–89. https://doi.org/10.1038/nature11869

Manjaribe, C., Frasier, C. L., Rakouth, B., & Louis, E. E. (2013). Ecological restoration and reforestation of fragmented forests in Kianjavato, Madagascar. *International Journal of Ecology*, *2013*, 726275. https://doi.org/10.1155/2013/726275

Mansourian, S., Stanturf, J. A., Derkyi, M. A. A., & Engel, V. L. (2017). Forest landscape restoration: Increasing the positive impacts of forest restoration or simply the area under tree cover? *Restoration Ecology*, *25*(2), 178–183. https://doi.org/10.1111/rec.12489

Martin, D. A., Andrianisaina, F., Fulgence, T. R., Osen, K., Rakotomalala, A. A. N. A., Raveloaritiana, E., Soazafy, M. R., Wurz, A., Andriafanomezantsoa, R., Andriamaniraka, H., Andrianarimisa, A., Barkmann, J., Dröge, S., Grass, I., Guerrero-Ramirez, N., Hänke, H., Hölscher, D., Rakouth, B., Ranarijaona, H. L. T., … Kreft, H. (2022). Land-use trajectories for sustainable land system transformations: Identifying leverage points in a global biodiversity hotspot. *Proceedings of the National Academy of Sciences of the United States of America*, *119*(7), e2107747119. https://doi.org/10.1073/pnas.2107747119

Martinez, B. T., & Razafindratsima, O. H. (2014). Frugivory and seed dispersal patterns of the red-ruffed lemur, *Varecia rubra*, at a forest restoration site in Masoala National Park, Madagascar. *Folia Primatologica*, *85*(4), 228–243. https://doi.org/10.1159/000363408

McKean, M. A. (2000). 2 Common property: What is it, what is it good for, and what makes it work? In C. C. Gibson, M. A. McKean, & E. Ostrom (Eds.), *People and forests: Communities, institutions, and governance* (pp. 27–56). The MIT Press.

Mohammed, A. J., & Inoue, M. (2017). Identifying salient forest SES attributes for sustainability: A multi-country study. *Land Use Policy*, *60*, 197–205. https://doi.org/10.1016/j.landusepol.2016.10.039

Moore, M., Alpaugh, M., Razafindrina, K., Trubek, A. B., & Niles, M. T. (2022). Finding food in the hunger season: A mixed methods approach to understanding wild plant foods in relation to food security and dietary diversity in southeastern Madagascar. *Frontiers in Sustainable Food Systems*, *6*. https://doi.org/10.3389/fsufs.2022.929308

Morelli, T. L., Smith, A. B., Mancini, A. N., Balko, E. A., Borgerson, C., Dolch, R., Farris, Z., Federman, S., Golden, C. D., Holmes, S. M., Irwin, M., Jacobs, R. L., Johnson, S., King, T., Lehman, S. M., Louis, E. E., Murphy, A., Randriahaingo, H. N. T., Randrianarimanana, H. L. L., … Baden, A. L. (2020). The fate of Madagascar's rainforest habitat. *Nature Climate Change*, *10*(1), 89–96. https://doi.org/10.1038/s41558-019-0647-x

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., … Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*(7545), 45–50. https://doi.org/10.1038/nature14324

Oldekop, J. A., Rasmussen, L. V., Agrawal, A., Bebbington, A. J., Meyfroidt, P., Bengston, D. N., Blackman, A., Brooks, S., Davidson-Hunt, I., Davies, P., Dinsi, S. C., Fontana, L. B., Gumucio, T., Kumar, C., Kumar, K., Moran, D., Mwampamba, T. H., Nasi, R., Nilsson, M., … Wilson, S. J. (2020). Forest-linked livelihoods in a globalized world. *Nature Plants*, *6*(12), 1400–1407. https://doi.org/10.1038/s41477-020-00814-9

Ormsby, A., & Kaplin, B. A. (2005). A framework for understanding community resident perceptions of Masoala National Park, Madagascar. *Environmental Conservation*, *32*(2), 156–164. https://doi.org/10.1017/S0376892905002146

Osen, K., Soazafy, M. R., Martin, D. A., Wurz, A., März, A., Ranarijaona, H. L. T., & Hölscher, D. (2021). Land-use history determines stand structure and tree diversity in vanilla agroforests of northeastern Madagascar. *Applied Vegetation Science*, *24*(1), e12563. https://doi.org/10.1111/avsc.12563

Ostrom, E. (2007). A diagnostic approach for going beyond panaceas. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(39), 15181–15187. https://doi.org/10.1073/pnas.0702288104

Paige, S. B., Bleecker, J., Mayer, J., & Goldberg, T. (2017). Spatial overlap between people and non-human primates in a fragmented landscape. *EcoHealth*, *14*(1), 88–99. https://doi.org/10.1007/s10393-016-1194-9

Pilkington, F., Singh, M., Wilkins, V., & Clubbe, C. (2020). The first rapid forest inventory and resource use assessment of Dashtijum Nature Reserve, Tajikistan: A mixed methods approach. *Oryx*, *54*(4), 443–450. https://doi.org/10.1017/S0030605319001170

Porcher, V., Carrière, S. M., Gallois, S., Randriambanona, H., Rafidison, V. M., & Reyes-García, V. (2022). Growing up in the Betsileo landscape: Children's wild edible plants knowledge in Madagascar. *PLoS ONE*, *17*(2), e0264147. https://doi.org/10.1371/journal.pone.0264147

Pritchard, R., Grundy, I. M., van der Horst, D., & Ryan, C. M. (2019). Environmental incomes sustained as provisioning ecosystem service availability declines along a woodland resource gradient in Zimbabwe. *World Development*, *122*, 325–338. https://doi.org/10.1016/j.worlddev.2019.05.008

R Core Team. (2023). *R: A language and environment for statistical computing*. http://www.R-project.org/

Račevska, E., Hill, C. M., Longosoa, H. T., & Donati, G. (2022). People, lemurs and utilitarian plants of the littoral forests in southeast Madagascar. *International Journal of Primatology*, *43*, 1000–1025. https://doi.org/10.1007/s10764-022-00319-6

Rakotonarivo, O. S., Rakotoarisoa, M., Rajaonarivelo, H. M., Raharijaona, S., Jones, J. P. G., & Hockley, N. (2023). Resolving land tenure security is essential to deliver forest restoration. *Communications Earth & Environment*, *4*(1), 179. https://doi.org/10.1038/s43247-023-00847-w

Rakotoson, D. J., Rakotonirina, A., & Serpantié, G. (2007). La contrainte érosion chez les Tanala: Savoirs et gestion. In G. Serpantié, B. M. Rasolofoharinoro, & S. M. Carrière (Eds.), *Transitions agraires, dynamiques écologiques et conservation: Le "corridor" Ranomafana-Andringitra (Madagascar): Actes du séminaire GEREM* (pp. 155–165). MDG.

Ralimanana, H., Perrigo, A. L., Smith, R. J., Borrell, J. S., Faurby, S., Rajaonah, M. T., Randriamboavonjy, T., Vorontsova, M. S., Cooke, R. S. C., Phelps, L. N., Sayol, F., Andela, N., Andermann, T., Andriamanohera, A. M., Andriambololonera, S., Bachman, S. P., Bacon, C. D., Baker, W. J., Belluardo, F., … Antonelli, A. (2022). Madagascar's extraordinary biodiversity: Threats and opportunities. *Science*, *378*(6623), eadf1466. https://doi.org/10.1126/science.adf1466

Randriamalala, H., & Liu, Z. (2010). Rosewood of Madagascar: Between democracy and conservation. *Madagascar Conservation & Development*, *5*(1), 11–22. https://doi.org/10.4314/mcd.v5i1.57336

Raveloaritiana, E., Wurz, A., Grass, I., Osen, K., Soazafy, M. R., Martin, D. A., Faliniaina, L., Rakotomalala, N. H., Vorontsova, M. S., Tscharntke, T., & Rakouth, B. (2021). Land-use intensification increases richness of native and exotic herbaceous plants, but not endemics, in Malagasy vanilla landscapes. *Diversity and Distributions*, *27*(5), 784–798. https://doi.org/10.1111/ddi.13226

Raveloaritiana, E., Wurz, A., Osen, K., Soazafy, M. R., Grass, I., Martin, D. A., Bemamy, C., Ranarijaona, H. L. T., Borgerson, C., Kreft, H., Hölscher, D., Rakouth, B., & Tscharntke, T. (2023). Complementary ecosystem services from multiple land uses highlight the importance of tropical mosaic landscapes. *Ambio*, *52*, 1558–1574. https://doi.org/10.1007/s13280-023-01888-3

Razafindraibe, M., Kuhlman, A. R., Rabarison, H., Rakotoarimanana, V., Rajeriarison, C., Rakotoarivelo, N., Randrianarivony, T., Rakotoarivony, F., Ludovic, R., Randrianasolo, A., & Bussmann, R. W. (2013). Medicinal plants used by women from Agnalazaha littoral forest (southeastern Madagascar). *Journal of Ethnobiology and Ethnomedicine*, *9*(1), 73. https://doi.org/10.1186/1746-4269-9-73

Razafindratsima, O. H., Kamoto, J. F. M., Sills, E. O., Mutta, D. N., Song, C., Kabwe, G., Castle, S. E., Kristjanson, P. M., Ryan, C. M., Brockhaus, M., & Sunderland, T. (2021). Reviewing the evidence on the roles of forests and tree-based systems in poverty dynamics. *Forest Policy and Economics*, *131*, 102576. https://doi.org/10.1016/j.forpol.2021.102576

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

Reuter, K. E., Sewall, B. J., & Di Minin, E. (2018). Drivers of present and lifetime natural resource use in a tropical biodiversity hotspot. *Animal Conservation*, *21*(2), 127–136. https://doi.org/10.1111/acv.12355

Sahoo, S., & Davidar, P. (2013). Effect of harvesting pressure on plant diversity and vegetation structure of Sal forests of Similipal Tiger Reserve, Odisha. *Tropical Ecology*, *54*(1), 97–107.

Salafsky, N., Salzer, D., Stattersfield, A. J., Hilton-Taylor, C., Neugarten, R., Butchart, S. H. M., Collen, B. E. N., Cox, N., Master, L. L., O'Connor, S., & Wilkie, D. (2008). A standard lexicon for biodiversity conservation: Unified classifications of threats and actions. *Conservation Biology*, *22*(4), 897–911. https://doi.org/10.1111/j.1523-1739.2008.00937.x

Simpson, E. H. (1951). The interpretation of interaction in contingency tables. *Journal of the Royal Statistical Society: Series B (Methodological)*, *13*(2), 238–241. https://doi.org/10.1111/j.2517-6161.1951.tb00088.x

Soazafy, M. R., Osen, K., Wurz, A., Raveloaritiana, E., Martin, D. A., Ranarijaona, H. L. T., & Hölscher, D. (2021). Aboveground carbon stocks in Madagascar's vanilla production landscape—Exploring rehabilitation through agroforestry in the light of land-use history. *Global Ecology and Conservation*, *31*, e01853. https://doi.org/10.1016/j.gecco.2021.e01853

Steffens, K. J. E. (2020). Lemur food plants as options for forest restoration in Madagascar. *Restoration Ecology*, *28*(6), 1517–1527. https://doi.org/10.1111/rec.13234

Sunderlin, W. D., Angelsen, A., Belcher, B., Burgers, P., Nasi, R., Santoso, L., & Wunder, S. (2005). Livelihoods, forests, and conservation in developing countries: An overview. *World Development*, *33*(9), 1383–1402. https://doi.org/10.1016/j.worlddev.2004.10.004

Torres-Romero, E. J., Nijman, V., Fernández, D., & Eppley, T. M. (2023). Human-modified landscapes driving the global primate extinction crisis. *Global Change Biology*, *29*(20), 5775–5787. https://doi.org/10.1111/gcb.16902

UN. (2015). *Transforming our world: The 2030 agenda for sustainable development*. United Nations.

Vasey, N. (2000). Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*: I. Interspecific patterns. *American Journal of Physical Anthropology*, *112*(3), 411–431. https://doi.org/10.1002/1096-8644(200007)112:3<411::AID-AJPA10>3.0.CO;2-R

Vasey, N. (2004). Circadian rhythms in diet and habitat use in red ruffed lemurs (*Varecia rubra*) and white-fronted brown lemurs (*Eulemur fulvus albifrons*). *American Journal of Physical Anthropology*, *124*(4), 353–363. https://doi.org/10.1002/ajpa.10357

Vieilledent, G., Grinand, C., Rakotomalala, F. A., Ranaivosoa, R., Rakotoarijaona, J.-R., Allnutt, T. F., & Achard, F. (2018a). Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. *Biological Conservation*, *222*, 189–197. https://doi.org/10.1016/j.biocon.2018.04.008

Vieilledent, G., Grinand, C., Rakotomalala, F. A., Ranaivosoa, R., Rakotoarijaona, J.-R., Allnutt, T. F., & Achard, F. (2018b). *Output data from: Combining global tree cover loss data with historical national forest-cover maps to look at six decades of deforestation and forest fragmentation in Madagascar*. Version V2. CIRAD Dataverse. https://doi.org/10.18167/DVN1/AUBRRC

Wilkinson, L. (2022). *venneuler: Venn and Euler diagrams*. R package version 1.1-3. https://CRAN.R-project.org/package=venneuler

WorldPop. (2017). *Madagascar 100m Population, Version 2.0*. (www.worldpop.org—School of Geography and Environmental Science, University of Southampton). https://doi.org/10.5258/soton/wp00535

SUPPORTING INFORMATION

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

Data S1: R Markdown code and output of models examining the effects of population and distance and time on plant metrics.

Appendix S1: Plant inventory by provisioning service, with vernacular and known scientific names.

Appendix S2: Focus group questionnaire.

Figure S1: Number and location of plant species by provisioning service on the Masoala Peninsula, Madagascar (2015–2016).

Figure S2: Rank abundance curves for the assemblage of timber, medicinal plant and ruffed lemur food tree species across all surveyed plots on the Masoala Peninsula, Madagascar (2015–2016).

Figure S3: Plant count of timber, medicinal plant and ruffed lemur food trees per plot per study community over time.

Figure S4: Plant species richness of timber, medicinal plant and ruffed lemur food trees per plot per study community over time.

Table S1: Model likelihood, weight and marginal and conditional R^2_{GLMM} values of all models included in analyses of plot count and species richness by provisioning service and model type.

Table S2: Marginal effects of botanical plot distance to the nearest community at representative community population values on counts and species richness by provisioning service and for both community and protected area plots on the Masoala Peninsula, Madagascar.

Table S3: Summary statistics for botanical plot count and species richness of timber, medicinal plants and ruffed lemur food trees by protected area status on the Masoala Peninsula, Madagascar.

Table S4: Marginal effects of population of community on counts and species richness of plots 1.5 km away, by provisioning service on the Masoala Peninsula, Madagascar.

Table S5: Full model results for counts and species richness of timber, medicinal plants and lemur food trees in botanical plots as predicted by (1) time (2015–2021), (2) population and (3) distance to the nearest community on the Masoala Peninsula, Madagascar.

Table S6: Marginal effects of time (i.e. years since 2015) in each sampled community on counts and species richness by provisioning service on the Masoala Peninsula, Madagascar (2015–2021).

How to cite this article: Kling, K. J., Eppley, T. M., Markham, A. C., Wright, P. C., Razafindrapaoly, B. N., Delox, R., Rasolofoniaina, B. J. R., Randriamanetsy, J. M., Elison, P., Andriamahaihavana, M., Gibson, D., Rasamisoa, D. C., Razafindramanana, J., Vasey, N., Daniels, C. W., & Borgerson, C. (2024). Provisioning services decline for both people and Critically Endangered wildlife in a rainforest transformation landscape. *People and Nature*, *00*, 1–19. https://doi.org/10.1002/pan3.10591