Received: 11 September 2023 | Revised: 14 February 2024 | Accepted: 24 February 2024

DOI: 10.1002/ajp.23615

RESEARCH ARTICLE

AMERICAN JOURNAL OF PRIMATOLOGY WILEY

Losing lemurs: Declining populations and land cover changes over space and time

Pamela R. Narváez-Torres[1] | Nicola K. Guthrie[1] | Typhenn A. Brichieri-Colombi[2] | Cressant P. Razafindravelo[3] | Zachary S. Jacobson[1] | Fredo Tera[3] | Daniel V. Rafidimanana[4] | Zé-Elinah Rahasivelo[5] | Melody A. Petersen[6] | Hasinala Ramangason[1] | Lea Randall[2] | Jana M. McPherson[2] | Cynthia L. Frasier[7] | Axel Moehrenschlager[8] | Sheila M. Holmes[9] | Edward E. Louis Jr.[3,7] | Steig E. Johnson[1]

[1]Department of Anthropology and Archaeology, University of Calgary, Calgary, Alberta, Canada

[2]Wilder Institute/Calgary Zoo, Calgary, Alberta, Canada

[3]Madagascar Biodiversity Partnership, Antananarivo, Madagascar

[4]Faculty of Sciences, University of Antananarivo, Antananarivo, Madagascar

[5]Faculty of Sciences, Technologies, and Environment, University of Mahajanga, Mahajanga, Madagascar

[6]Nature Conservancy of Canada, Calgary, Alberta, Canada

[7]Conservation Genetics Department, Omaha's Henry Doorly Zoo and Aquarium, Omaha, Nebraska, USA

[8]Panthera, New York, New York, USA

[9]Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden

Correspondence

Steig E. Johnson, Department of Anthropology and Archaeology, University of Calgary, 2500 University Dr NW, Calgary, AB, T2N 1N4, Canada.
Email: steig.johnson@ucalgary.ca

Abstract

Forest loss and degradation due to land cover changes imperil biodiversity worldwide. Subtropical and tropical ecosystems experience high deforestation rates, negatively affecting species like primates. Madagascar's endemic lemurs face exceptionally high risks of population declines and extirpation. We examined how short-term land cover changes within a fragmented landscape in southeastern Madagascar impacted the density of lemur species. Using line transects, we assessed density changes in nine lemur species across five forest fragments. Diurnal surveys were conducted monthly from 2015 to 2019 on 35 transects (total effort = 1268 km). Additionally, 21 transects were surveyed nocturnally in 2015 and 2016 (total effort = 107.5 km). To quantify forest cover changes, we generated land use/land cover (LULC) maps from Sentinel-2 imagery using supervised classification for each year. For the LULC maps, we overlayed species-specific buffers around all transects and calculated the proportion of land cover classes within them. We observed declines in the annual densities of four diurnal and cathemeral lemur species between 2015 and 2019, with species-specific declines of up to 80% (*Varecia variegata*). While the density of two nocturnal species decreased, one increased fivefold (*Cheirogaleus major*) between 2015 and 2016. By 2019, Grassland was the dominant land type (50%), while Paddy Fields had the smallest coverage (1.03%). Mature Agricultural Land increased the most (63.37%), while New Agricultural Land

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Abbreviations: AOI, area of interest; COFAV, Corridor Forestier d'Ambositra-Vondrozo; GLMM, generalized linear mixed models; HMM, hurdle mixed models; KAFS, Kianjavato Ahmanson Field Station; LULC, Land Use Land Cover; MBP, Madagascar Biodiversity Partnership; RNP, Ranomafana National Park; VOI, Vondron'Olona Ifotony.

Pamela R. Narváez-Torres and Nicola K. Guthrie contributed equally to this study.

Funding information
Consejo Nacional de Ciencia y Tecnología; Government of Alberta; Natural Sciences and Engineering Research Council of Canada; Mitacs; Omaha's Henry Doorly Zoo and Aquarium; Calgary Zoological Society; Conservation International; International Primatological Society; Primate Conservation Inc; Ahmanson Family Foundation

decreased the most (−66.36%). Unexpectedly, we did not find evidence that higher forest cover supported a higher lemur population density within sampled areas, but we found support for the negative impact of degraded land cover types on three lemur species. Our study underscores the urgent need to address land-use changes and their repercussions for primate populations in tropical ecosystems. The diverse responses of lemur species to modified habitats highlight the complexity of these impacts and emphasize the importance of targeted conservation efforts.

KEYWORDS
conservation, deforestation, density, habitat loss, Madagascar

1 | INTRODUCTION

Human activities have been modifying the natural surface of our planet for thousands of years (Goudie, 2018; Pyne, 1997). However, the current extent and speed of land cover changes far exceed historical levels (IPCC, 2023). These changes have a significant impact on ecosystems and environmental processes at local, regional, and global scales (Hasan et al., 2020; IPCC, 2023; Roy et al., 2022). Moreover, they represent one of the most critical threats to terrestrial biodiversity, notably due to the loss, degradation, and fragmentation of forests, largely attributed to their conversion into other land types, such as agricultural areas (Almeida-Rocha et al., 2017; Estrada et al., 2017; 2018; Maxwell et al., 2016). The impact of these threats is particularly pronounced in tropical regions, where subtropical and tropical ecosystems experience alarmingly high rates of forest loss, accounting for more than 90% of global deforestation between 2000 and 2018 (FAO, 2022). Primates, being mainly arboreal and forest-dwelling species inhabiting tropical regions, are highly susceptible to land cover changes (Almeida-Rocha et al., 2017; Fernández et al., 2022). This vulnerability has led to around 67% of primate species worldwide being threatened with extinction, with human-induced deforestation being one of the leading causes International Union for Conservation of Nature (IUCN, 2020; Torres-Romero et al., 2023).

In fragmented landscapes, forest patches—large or small—do not exist in isolation from the matrix that surrounds them. The matrix, sometimes referred to as “nonhabitat” for forest-reliant species, is the mosaic of different land cover types that surround forests and may include anything from urban developments to agricultural lands to anthropogenic grasslands (Fahrig, 2017). These land cover types can influence the ability of forest-dwelling organisms to travel between habitat patches and/or find resources or breeding sites and, thus, can impact the local abundance and the persistence of these organisms in fragmented landscapes (Fahrig, 2007; Prevedello & Vieira, 2010; Sanches et al., 2022; Tiang et al., 2021). However, the persistence of primates in disturbed or fragmented landscapes is closely tied to their ecological traits, for example, degree of dietary specialization, activity pattern, body size, and home range extent (Boyle & Smith, 2010; Eppley et al., 2020; Machado et al., 2023). Species with highly specific habitat and dietary requirements are likely to be more affected than generalist species, as the latter can access and make use of a wider variety of resources (Boyle & Smith, 2010; Calle-Rendón et al., 2019; Eppley et al., 2020; Machado et al., 2023). Large-bodied species with highly frugivorous diets are more vulnerable to habitat loss and fragmentation because they require larger home ranges, which can limit their ability to respond to habitat alteration (Boyle & Smith, 2010; Lehman et al., 2006a; Lenz et al., 2014; Machado et al., 2023). Folivorous species, on the other hand, have been observed to do well with certain levels of disturbance and even increase in abundance in disturbed areas due to increased leaf quality and productivity (Ganzhorn, 1995; Johns & Skorupa, 1987; Lenz et al., 2014). For instance, omnivorous primate species like *Sapajus flavius* (Lins & Ferreira, 2019) and *Rungwecebus kipunji* (Bracebridge et al., 2013) or highly folivorous species like *Colobus angolensis palliatus* (Anderson et al., 2007; Dunham, 2017) and *Chlorocebus djamdjamensis* (Mekonnen et al., 2017, 2018) have been documented to use agricultural lands.

Despite some species' ability to use the matrix, it may be challenging for some arboreal animals to navigate the matrix if its structure is too different or isolated from the forest. Matrix-use depends on factors such as canopy height, food availability, and the distance from the forest (Galán-Acedo et al., 2019; Pozo-Montuy et al., 2011). In general, navigating the matrix can also lead to increased risks of predation or being hunted by humans or dogs due to lack of vegetation cover, as well as transmission of parasites and diseases between humans and primates (Candelero & Pozo-Montuy, 2010; Chapman et al., 2005; Chaves et al., 2022; Estrada et al., 2012; Galán-Acedo et al., 2019; Sanches et al., 2022).

Madagascar is a biodiversity hotspot where forest loss and fragmentation have occurred on a large scale since the 1950s (Harper et al., 2007; Ralimanana et al., 2022). Over the past 70 years, this country has lost 44% of its natural forest cover, and approximately 46% of the remaining forests are located within 100 m of an edge (Vieilledent et al., 2018a). In eastern Madagascar, forests are converted to agricultural land for small-scale shifting agriculture, locally known as *tavy*. However, after a few crop cycles, soil quality often decreases, and the land is abandoned, forming grasslands or eroded, bare soils (Styger et al., 2007). The remaining forests are crucial habitats for most of the island's endemic species, including over 100 species of lemurs, which are some of the world's most imperiled mammals (Schwitzer et al., 2014). Due to diverse factors such as forest loss, fragmentation, and hunting, 96.3% of these species are now at risk of extinction (Borgerson et al., 2022; Fernández et al., 2022; IUCN, 2020), with declining population trends recorded for most species (IUCN, 2020). As many lemur species are nearly exclusively arboreal (Mittermeier et al., 2023), they are highly susceptible to the effects of forest conversion to other land cover types. However, some lemur species, especially nocturnal or cathemeral species, are capable of navigating matrix environments, either as areas of regular use (e.g., *Cheirogaleus shethi*, Hending et al., 2017; *Microcebus* spp., Guthrie et al., 2022; Steffens et al., 2021), for intermittent foraging (e.g., *Lemur catta*, LaFleur & Gould, 2009), or for transitory use while moving among forest patches (e.g., *Eulemur flavifrons*, Prodger et al., 2018). Additionally, Webber et al. (2019) reported that five species of nocturnal and mostly solitary lemurs (*Mirza zaza*, *Phaner parienti*, *Microcebus* sp., *Cheirogaleus* sp., and *Lepilemur dorsalis*) are regularly found in shade plantations in Northern Madagascar. Despite these observations of nonforest use (see Eppley & Goodman, 2022 for a review), little is currently known about how variation in matrix composition may impact lemur populations.

We investigated lemur population trends in the forest fragments of Kianjavato Commune and surrounding areas, a priority site for lemur conservation in southeastern Madagascar (Schwitzer et al., 2013). Our objectives were to assess lemur density trends and evaluate how land cover composition outside of forests impacts lemur density. We hypothesized that the impact of land cover in the matrix on the density of lemurs in remaining forest fragments would depend on (a) how qualitatively similar to forest the vegetation structure of land cover types in the matrix is; and (b) the ecological traits, specifically diet and home range size, of each lemur species. In particular, we anticipated that a matrix dominated by open land cover types with limited vertical structure (e.g., rice fields or grassland) would have a greater negative impact on lemur density in remaining forest fragments than a matrix containing forest-like vegetation structures (e.g., tree fallows or fruit tree plantations). Forest-like vegetation structure might, after all, facilitate lemur mobility and provide foraging opportunities, and thus improve connectivity among remaining forests (Anderson et al., 2007; Prevedello & Vieira, 2010; Steffens et al., 2021). We also anticipated that highly frugivorous lemur species that require relatively larger home ranges, such as *Varecia variegata* and *Eulemur rufifrons* will be most negatively affected by land cover changes, while lemur species with folivorous or omnivorous diets and smaller home ranges, such as *Avahi peyrierasi*, *Hapalemur griseus*, and *Microcebus jollyae*, would be the least affected by land cover changes. We expected *Cheirogaleus major* and *Eulemur rubriventer* with mainly frugivorous diets and small home ranges, *Daubentonia madagascariensis*, with an omnivorous diet and large home range, and *Prolemur simus*, with a folivorous diet and large home range, to show an intermediate response to land cover changes. These expectations reflect the greater likelihood for folivorous and omnivorous species than frugivores to find appropriate food resources in nonforest land-use types and the relatively lower importance of large tracts of contiguous forest for species with smaller home ranges (Boyle & Smith, 2010; Galán-Acedo et al., 2023; Johns & Skorupa, 1987).

2 | METHODS

2.1 | Ethics statement

The research reported was covered by ACC Certificates AC15-0041 and AC19-0026, issued by the University of Calgary Animal Care Committee. The study followed all legal requirements for conducting research in Madagascar (permits 074/14/MEF/SG/DGF/DCB. SAP/SCB, 036/15/MEEF/SG/DGF/DCB. SAP/SCB, 161/16/MEEF/SG/DGF/DSAP/SCB, 97/17/MEEF/SG/DGF/DSAP/SCB. Re, 164/18/MEEF/SG/DGF/DSAP/SCB. Re, 050/19/MEEF/SG/DGF/DSAP/SCB. Re) and adhered to the ethical principles for the treatment of nonhuman primates set forth by the American Society of Primatologists (ASP).

2.1.1 | Study site and study species

This study was based at the Kianjavato Ahmanson Field Station (KAFS), located in the Kianjavato Commune in southeastern Madagascar (Figure 1) and managed by the Madagascar Biodiversity Partnership, a Malagasy nongovernmental organization. The study site ranges in elevation from 52 to 571 m above sea level and is characterized by an annual rainfall of 1800 mm, falling mostly between December and March (Manjaribe et al., 2013). The vegetation consists of remnants of lowland primary and secondary humid forest and dense bamboo (Manjaribe et al., 2013). Seven forest fragments in the area serve as habitat for nine lemur species (Table 1; Holmes et al., 2015). We collected data for this study from five forest fragments: Karakandatra, Sangasanga, Tsiazombazaha, Tsitola, and Vatovavy. These fragments vary in size (from 45 to 518 ha, Tsitola being the largest) and isolation distances (from 67 to 6900 m, Vatovavy being the most isolated).

Aerial photography in the 1950s indicates that forest cover was high in and around the Kianjavato area, with estimates suggesting 62.50% of our area of interest (see Figure 1 for AOI) was covered in forest at the time. However, more recent satellite imagery revealed a significant decrease in forest cover since; by 1973, only 9.89% (38.59 km^2) remained, and this further decreased to 4.65% (18.12 km^2) by 2010 (data for calculation obtained from Vieilledent et al., 2018b). Deforestation in the Kianjavato commune is mainly caused by *tavy*. This practice is similar to that described in Styger et al. (2007) and involves cycling through different crops with fallow periods to restore soil nutrients. The cycle consists of cutting down and burning the forest before growing crops, eventually leading to soil nutrient depletion and land abandonment. The land is left to

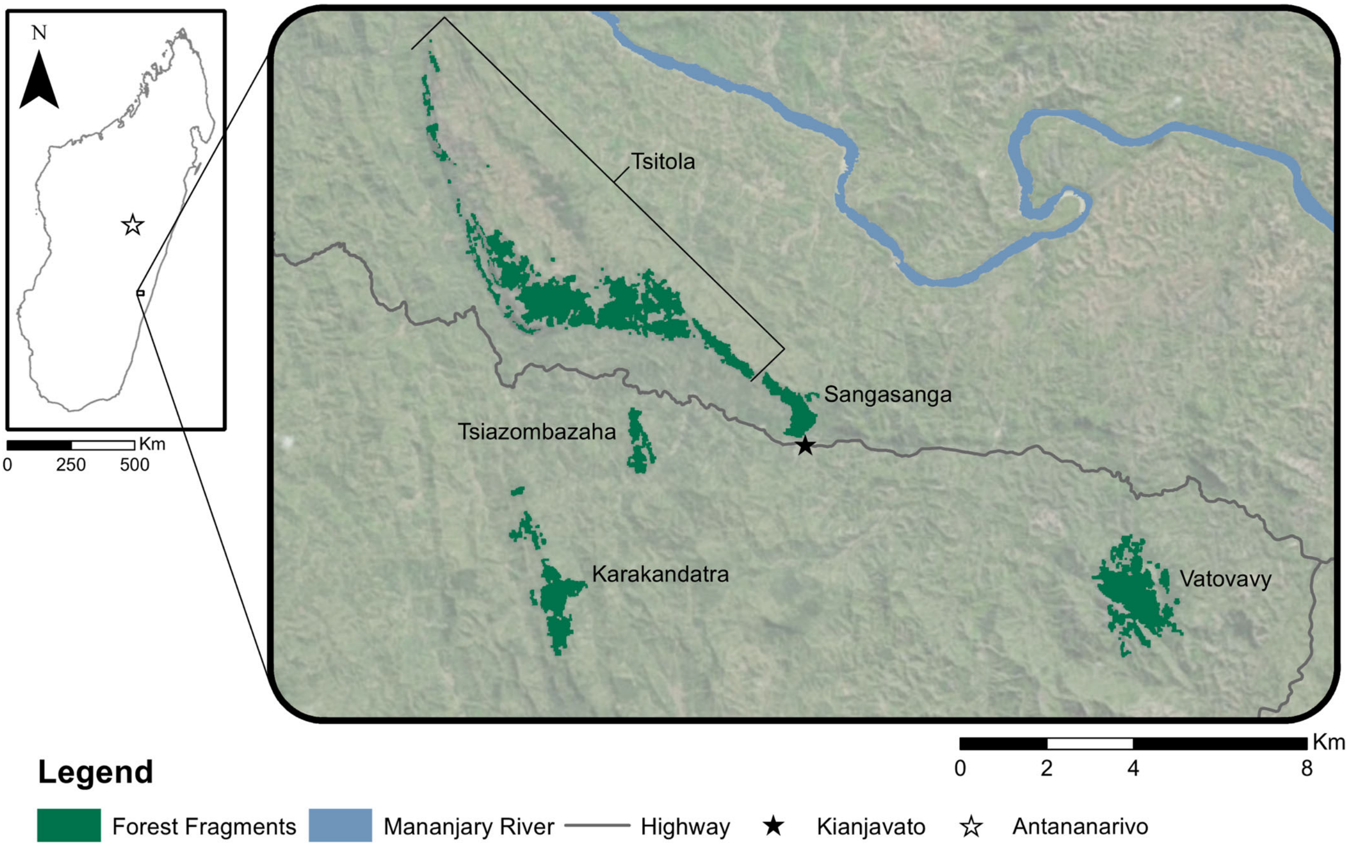

FIGURE 1 Map of the area of interest (AOI) for 2019, including five forest fragments in the Kianjavato region. Satellite imagery obtained from ESRI (2021).

regrow vegetation, but only grasses and ferns tend to grow back after several crop cycles (Styger et al., 2007). In some cases, fires used to clear the land can become uncontrolled and spread to neighboring crops, forests, and reforestation areas (Styger et al., 2007).

2.1.2 | Lemur survey methods

To assess the abundance of lemurs in the Kianjavato forest fragments, we conducted diurnal and nocturnal surveys using a line-transect distance sampling methodology (Buckland et al., 2010). We conducted diurnal surveys monthly (thus all seasons were included) from 2015 to 2019, with a total of 35 transects across five forest fragments. We surveyed 10 transects in Karakandatra, three in Sangasanga, three in Tsiazombazaha, 11 in Tsitola, and eight in Vatovavy (Figure 2). Each diurnal transect was walked 6–29 times per year, with a mean of 14 walks per year. All transects were 0.5 km long, making the total effort for diurnal surveys 1268 km (annual average = 211 km; annual range 194–300.5 km). We conducted nocturnal surveys in 2015 and 2016 using a subset of 21 transects in Sangasanga, Tsiazombazaha, Tsitola, and Vatovavy. As some nocturnal species go into torpor or hibernation during the Austral winter months (e.g., *C. major*; Blanco et al. 2018), we conducted all nocturnal surveys between September and May. The nocturnal transects were walked three to seven times per year with an average of five walks per year, resulting in a total effort of 107.5 km (annual average = 53.75 km; annual range 51–56.5 km). We conducted all surveys at a speed of approximately 1 km/h, from 6:30 to 14:00 h for diurnal surveys and 18:30 to 23:00 h for nocturnal surveys. We collected the following data during surveys: lemur species sighted, the number of individuals detected, and the height of the animals in the canopy. Additionally, the distance and bearing from the observer were recorded to calculate the perpendicular distance from the transect to the detected individuals. We considered all species that were detected more than 20 times for our density estimation and further analysis.

2.1.3 | Lemur annual density estimations

Annual density estimates were produced for seven lemur species using the Distance package (Miller et al., 2019) in R (R Core Team, 2022). We could not estimate annual densities for *H. griseus* and *D. madagascariensis* as they were only sighted two times. To model detection functions for the remaining species, that is, the probability of an animal being detected based on its distance from a given line (Buckland et al., 2010), we pooled each species' sightings across years (2015–2019 for diurnal and cathemeral species, 2015–2016 for nocturnal species) given the low number ($N < 30$) of annual sightings (Buckland et al., 2015; Rodríguez-Caro et al., 2017). By combining the data for all years, we assumed that

TABLE 1 Lemur species that inhabit the Kianjavato region, their diet, activity pattern, mean body mass, home range size (species mean ± SD), and IUCN status.

Scientific name	Common name	Diet	Activity pattern	Body mass (kg)	Home range size (ha)	IUCN Red list status[b]
Avahi peyrierasi	Peyrieras' woolly lemur	Folivorous[c]	Nocturnal[c]	1.04[d]	1.4[e]	VU
Cheirogaleus major	Greater dwarf lemur	Frugivorous[f]	Nocturnal[c]	0.34[g]	4.4[h]	VU
Daubentonia madagascariensis[a]	Aye-aye	Omnivorous[h]	Nocturnal[i]	2.40[i]	973.12[j]	EN
Eulemur rubriventer	Red-bellied lemur	Frugivorous[i]	Cathemeral[i]	2.00[i]	15.27 ± 4.5[k]	VU
Eulemur rufifrons	Red-fronted brown lemur	Frugivorous[i]	Cathemeral[i]	2.25[i]	45.9 ± 24.2[k]	VU
Hapalemur griseus[a]	Eastern lesser bamboo lemur	Folivorous[l]	Diurnal[m]	0.80[c]	15[l]	VU
Microcebus jollyae	Jolly's mouse lemur	Omnivorous[i]	Nocturnal[i]	0.064[o]	0.26 ± 0.14[o]	EN
Prolemur simus	Greater bamboo lemur	Folivorous[p]	Cathemeral[c]	2.61[q]	50.2[r]	CR
Varecia variegata	Black-and-white ruffed lemur	Frugivorous[i]	Diurnal[c]	3.81[e]	37.41 ± 6.4[k]	CR

Abbreviations: CR, critically endangered; EN, endangered; IUCN, international union for conservation of nature; VU, vulnerable.

[a] Species not included in the analyses due to a small number of detections during transect surveys (see below).

[b] IUCN (2020).

[c] Rowe and Myers (2017.)

[d] Lei et al. (2008).

[e] Harcourt (1991).

[f] Lahann (2007).

[g] Lei et al. (2014).

[h] Burrows and Nash (2010).

[i] Mittermeier et al. (2023).

[j] Randimbiharinirina et al.(2018).

[k] Holmes et al. (2019).

[l] Tan (1999).

[m] Kappeler (2012).

[n] N. Guthrie, unpublished data.

[o] Mihaminekena et al. (2024).

[p] Frasier et al. (2015).

[q] McGuire et al. (2009).

[r] Baden et al. (2008).

the detection probability of a species was the same throughout the study period. We modeled detection functions and evaluated the fit of the half-normal, hazard rate, and uniform key functions with and without cosine series adjustments (Buckland et al., 2015; Rodríguez-Caro et al., 2017). The best models were selected based on Akaike's Information Criterion corrected for small sample sizes akaike information criterion (ΔAICc < 2; Hurvich & Tsai, 1989), the goodness of fit, and the shape of the detection function (Buckland et al., 2001). We calculated species-specific annual densities by including year as a stratification factor (Buckland et al., 2015).

2.1.4 | Land-Use Land Cover (LULC) changes

We derived LULC maps of our field site for each year (2015–2019) from Sentinel 2 A—Level 1 C imagery with 10 m spatial resolution. Five satellite images were downloaded from the USGS EarthExplorer website (https://earthexplorer.usgs.gov/); these images were taken on 29/09/2015, 04/08/2016, 20/07/2017, 14/08/2018, and 29/08/2019. We chose images with <10% cloud cover over our study area and within the same season across years to reduce the effects of seasonal variation in vegetation and agricultural practices (The European Space Agency, 2023).

We used the CATALYST Professional program version 2222.0.1 (PCI Geomatics, 2024) to crop each image to the study extent and run atmospheric corrections, which decreased the spatial resolution to 20 m. Based on familiarity with the region and Environmental Systems Research Institute (ESRI) World Imagery Wayback (ESRI, 2021), local guides and authors identified 18 land cover types. We ran a supervised maximum likelihood classification using 800 polygons generated in ArcGIS 10.8.1 (ESRI, 2020) of the 18 different

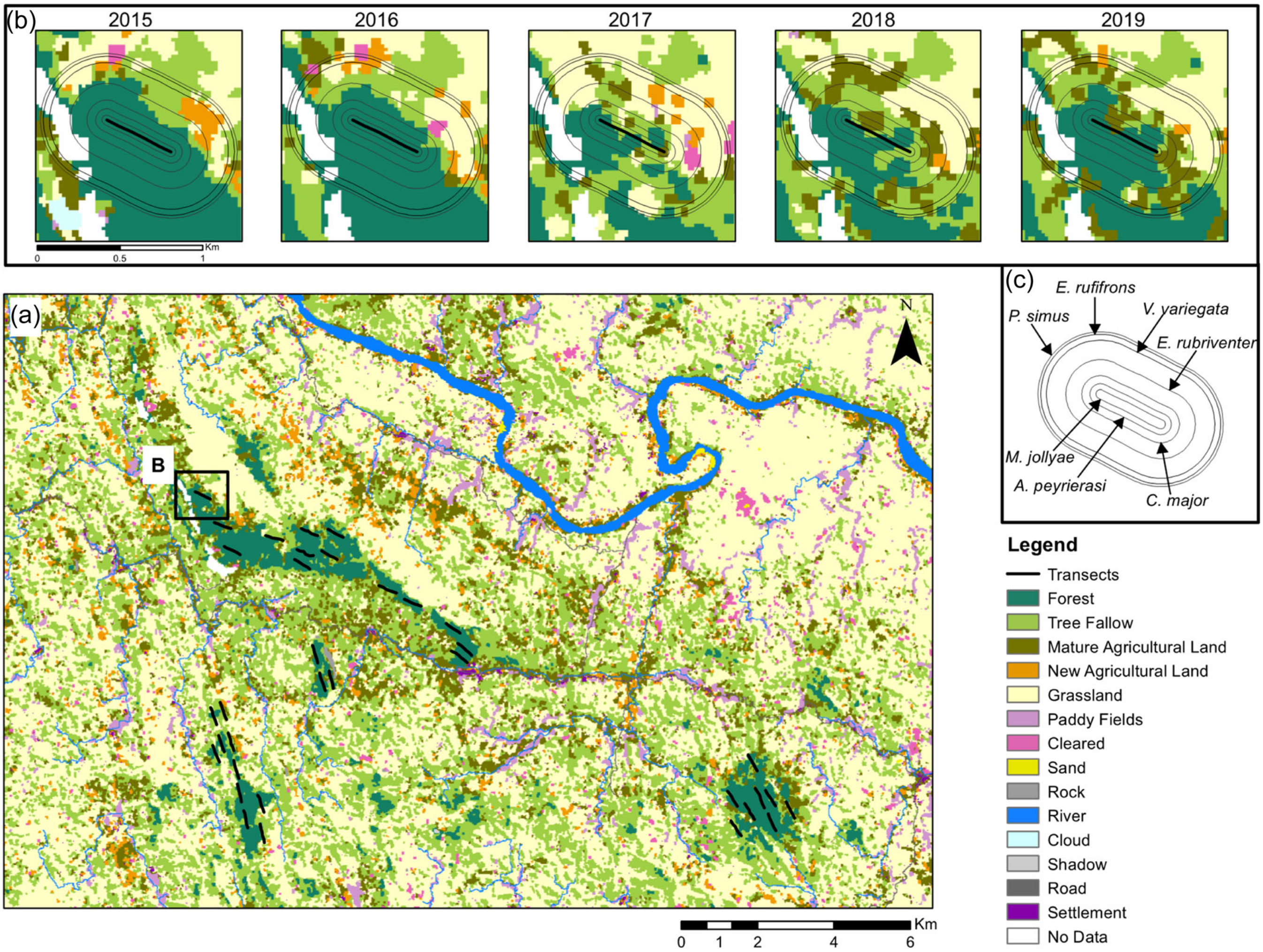

FIGURE 2 (a) Map of the area of interest in Kianjavato, Madagascar, with the classification of the land use and land cover types for 2019. The map also shows the 35 transects used in this study. (b) The upper panel shows an example of the species-specific buffers overlayed around each transect from 2015 to 2019. (c) The radii of the buffers (range: 29–400 m) were selected using the reported home ranges of each study species. Satellite imagery obtained from ESRI (2021).

land cover types. We retained 30% of polygons for each land cover type to test the map classification accuracy with confusion matrices and Cohen's Kappa statistic (Cohen, 1960). We combined some land cover types to achieve an overall classification accuracy >80% for each year. The final land cover types derived from image classification included Forest, Tree Fallow, Grassland, Mature Agricultural Land, New Agricultural Land, Cleared Land, Paddy Fields, Sand, Water, and Rock, as well as Shadow and Cloud (Table 2). Average and overall classification accuracy for each year were: 2015 kappa = 0.849 (sd = 0.003), overall accuracy = 86.93%; 2016 kappa = 0.765 (sd = 0.004), overall accuracy 80.16%; 2017 kappa = 0.844 (sd = 0.003), overall accuracy 85.37%; 2018 kappa = 0.810 (sd = 0.004), overall accuracy 83.44%; 2019 kappa = 0.827 (sd = 0.004), overall accuracy 85.45%. We identified seven of the 12 land cover types as relevant to our research question (i.e., Forest, Tree Fallow, Grassland, Mature Agricultural Land, New Agricultural Land, Cleared Land, and Paddy Fields) and used them as predictor variables in the models (Table 2). We excluded Sand, Water, Rock, Shadow, and Cloud from our analyses as we were focused on the impacts of changing land cover types. Sand, Water, and Rock remained unchanged during the study period. We also made an effort to obtain satellite images that did not include Shadow and Cloud.

We refined LULC maps in ArcGIS; we removed clouds and shadows from known forested areas and combined shadows in unknown areas to ensure consistency for any changes detected between years. Shadow and cloud coverage could cause some negligible impact on summary metrics. We digitized the roads (both the paved highway and secondary unpaved roads), large and small rivers, and villages using high-resolution imagery (0.5 m) ESRI World Imagery Wayback from 2019 (23/09/2019; ESRI, 2020). Because high-resolution Wayback Imagery was unavailable for all years, we assumed that roads, rivers, villages, and lone houses did not vary between years, and the digitized features for 2019 were integrated into the LULC classification maps for each year (2015–2018; See supporting Information S1: Figure S1).

TABLE 2 Description of the land cover types in the Kianjavato landscape used in the analysis and qualitative assessment of canopy cover.

Land cover type	Description	Canopy coverage
Forest	Primary and secondary rainforests, as well as a mature agroforest planted within a forest fragment that retained the canopy structure of the rainforest.	Higher coverage
Tree Fallow	Treed fallow land that included the following tree species: *Ravenala* sp., *Valiha diffusa*, *Albizia* spp, and *Macaranga obovata*	Higher coverage
Mature Agricultural Land	Plantations of fruit trees with crown connections that were maintained for several years. These plantations were usually a mix of large trees (e.g., *Artocarpus heterophyllus*, and *Litchi chinensis*) with dense canopy cover, as well as banana and coffee trees.	Higher coverage
New Agricultural Land	Areas where crops were planted without crown connections. These may eventually become mature agricultural land as the plants grow larger or could be crops on a cycle where they are entirely removed during harvesting.	Lower coverage
Grassland	Land consisting of grasses with the occasional tree or shrub. Also known as *roranga* and usually 0.4-1.5 m in height (see Manjaribe et al., 2013 for more details).	Lower coverage
Paddy Fields	Lowland, usually irrigated, rice fields.	Lower coverage
Cleared	Land was recently cleared of vegetation.	Lower coverage

Source: S. Andriamampianina, unpublished data; N. Guthrie, unpublished data.

From the refined LULC maps, we measured land cover change across years within species-specific buffer distances around the 35 transects (Figure 2) created in QGIS 3.28.2 (QGIS.org, 2022). Buffer radii (range: 29–400 m) were selected using the reported home range sizes of the seven species for which we calculated annual density estimates (Table 1). We then overlayed the species-specific buffers on the LULC maps for each year and calculated the proportion of land cover types within the buffer extents using the *LecoS* plugin in QGIS (Jung, 2016).

2.1.5 | LULC and lemur abundance

Using multivariate models, we investigated the relationship between the proportion of different land cover types and lemur density. To avoid overfitting the models, we merged Paddy Fields, Cleared Land, and Grassland into a single predictor "Open Land" as we considered the biological relevance of these three variables to be similar. Forest was significantly correlated with multiple variables and thus was not included in models with other predictor variables; we ran separate models with Forest only to evaluate the effect of this land cover type on lemur density.

We followed a two-step approach in our models (Buckland et al., 2015; Rodríguez-Caro et al., 2017). First, we modeled the detection functions and included animal height in the canopy (meters), forest fragment ID, and year as detection covariates (i.e., covariates that could influence the probability of detection). We evaluated the fit of the key functions, and the best-fitting models were selected based on AICc (Hurvich & Tsai,1989), the goodness of fit, and the shape of the detection function (Buckland et al., 2001). The best-fitting model was then utilized to estimate the effective area, which we included as an offset in models in the second step (Buckland et al., 2015). Second, we used mixed models to model lemur density, with the number of individuals sighted per transect per year as the response variable. We used hurdle mixed models (HMM) due to the zero inflation and overdispersion present in the data of some species (*E. rubriventer*, *E. rufifrons*, *P. simus*, and *V. variegata*) and generalized linear mixed models (GLMM) for the other species (*Avahi peyrierasi*, *C. major*, and *M. jollyae*). Both types of models assumed negative binomial distributions. We ran the models using the glmmTMB package (Brooks et al., 2017), and ΔAICc values were compared using the AICcmodavg package (Mazerolle, 2020). The predictor variables were the proportions of the different types of land cover types within the buffer of each species (i.e., Mature Agricultural Land, New Agricultural Land, Tree Fallow, and Open Land); we also included the log-transformed effective area as an offset term and transect and fragment ID as random effects. We selected candidate models with variables that best explained the variation in lemur density based on ΔAICc scores and weights (Burnham & Anderson, 2002).

3 | RESULTS

3.1 | Changes in lemur density

We recorded all nine species of lemurs living in the Kianjavato forests during line-transect surveys. However, two species, *H. griseus* and *D. madagascariensis*, were only observed during the first year of our study. *E. rufifrons* was the only day-active species observed in all five forest fragments surveyed, while nocturnal *M. jollyae* and *A. peyrierasi* were the only nocturnal species observed in all the fragments surveyed at night.

There was an apparent decrease in the annual density of the diurnal and cathemeral lemur species over 5 years (Table 3). Note that due to our low number of sightings, standard errors (SE) were

TABLE 3 Estimated annual densities (individuals/km^2 ± SE) of the lemur species present in the Kianjavato forest fragments.

Year	*Avahi peyrierasi*	*Cheirogaleus major*	*Eulemur rubriventer*	*Eulemur rufifrons*	*Microcebus jollyae*	*Prolemur simus*	*Varecia variegata*
2015	17.24 (± 5.66)	3.45 (± 1.99)	1.59 (± 0.88)	6.16 (± 1.78)	72.32 (± 16.43)	1.29 (± 1.01)	7.40 (± 2.40)
2016	11.67 (± 4.42)	17.21 (± 10.15)	2.65 (± 1.18)	4.81 (± 1.31)	42.34 (± 12.29)	1.92 (± 1.34)	4.08 (± 1.44)
2017	-	-	0.80 (± 0.78)	4.32 (± 1.72)	-	1.06 (± 0.77)	4.45 (± 2.44)
2018	-	-	0.73 (± 0.55)	2.55 (± 0.87)	-	0.72 (± 0.56)	2.66 (± 1.14)
2019	-	-	0.47 (± 0.22)	2.33 (± 0.98)	-	0[a]	1.61 (± 0.81)

Note: Nocturnal surveys were only conducted in 2015–2016.

[a] The estimated density of *Prolemur simus* in 2019 does not indicate the absence of the species in our study site; other studies and long-term monitoring have confirmed its presence in the study area.

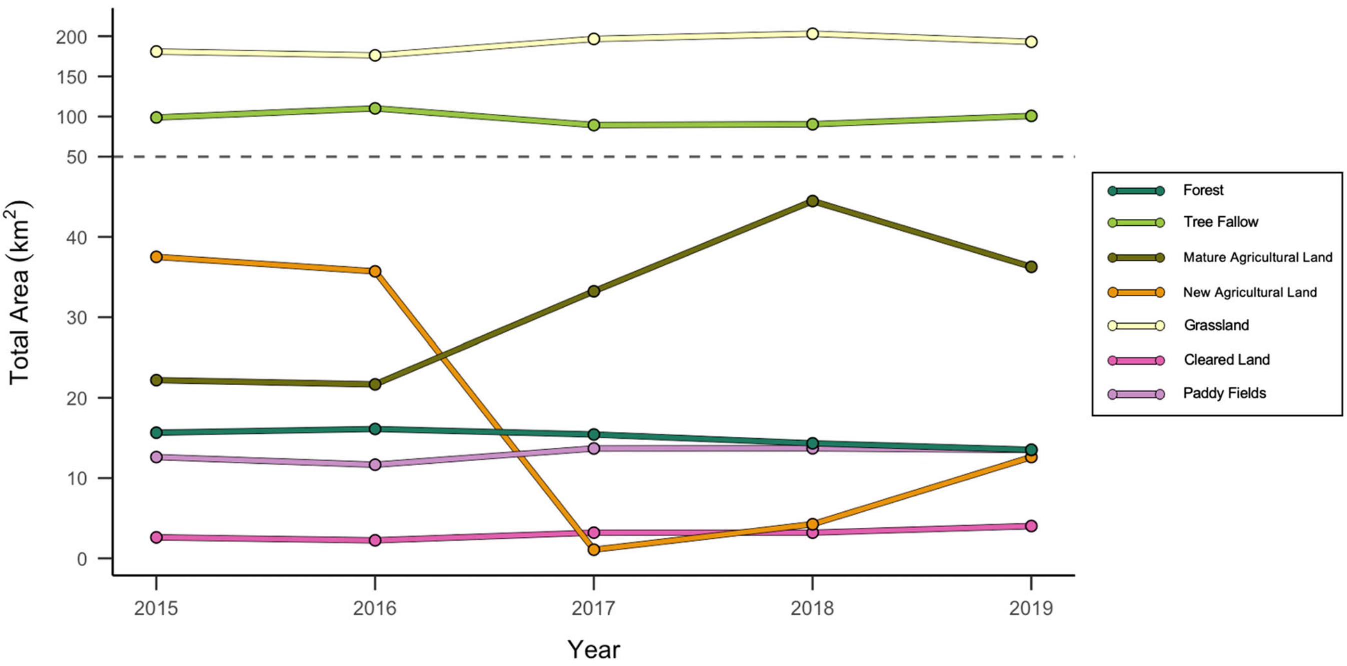

FIGURE 3 Changes in total area for seven land use and land cover types over five years in Kianjavato, Madagascar.

high for some species and years (see Table 3; Buckland et al., 2015). For the day-active species, *V. variegata*, with the highest density in 2015, decreased by approximately 80% by 2019. Further, *P. simus* was not sighted in the last year of surveys. *E. rubriventer* densities decreased by roughly 70% during the study period, and *E. rufifrons* by almost 40%. Among nocturnal species (with only 2015–2016 data), we observed a substantial decrease (> 30%) in the densities of *A. peyrierasi* and *M. jollyae* during the second year of the study, while *C. major* increased five-fold.

3.2 | Changes in LULC

In 2019, across our area of interest (total area = 390 km^2), Grassland was the most prevalent land cover type, covering ~49.49% of the total area (Figure 3), followed by Tree Fallow (25.83%) and Mature Agricultural Land (9.30%). Forest, New Agricultural Land, Cleared Land, and Paddy Fields each covered less than 5% of the total area (Figure 3). Forest, decreased by 2.13 km^2 between 2015 and 2019 (Figure 4), with a mean annual loss of 0.53 km^2 (3.51%; see Supporting Information S1: Table S1). However, it is worth noting that even though we saw a decrease in forest area overall, between 2015 and 2016, we saw an increase in forest of 0.46 km^2 or 2.97%. During the 5-year period, Mature Agricultural Land had the largest increase in land cover (63.37%), while New Agricultural Land saw the largest decline (66.39%).

The general trends across the land cover types in the Kianjavato landscape between 2015 and 2019 (Figure 3) were also found within the species-specific buffers (Table 4). Forest and New Agricultural Land decreased, while Tree Fallow, Grassland, and Mature Agricultural Land increased. Cleared Land and Paddy Fields increased by less

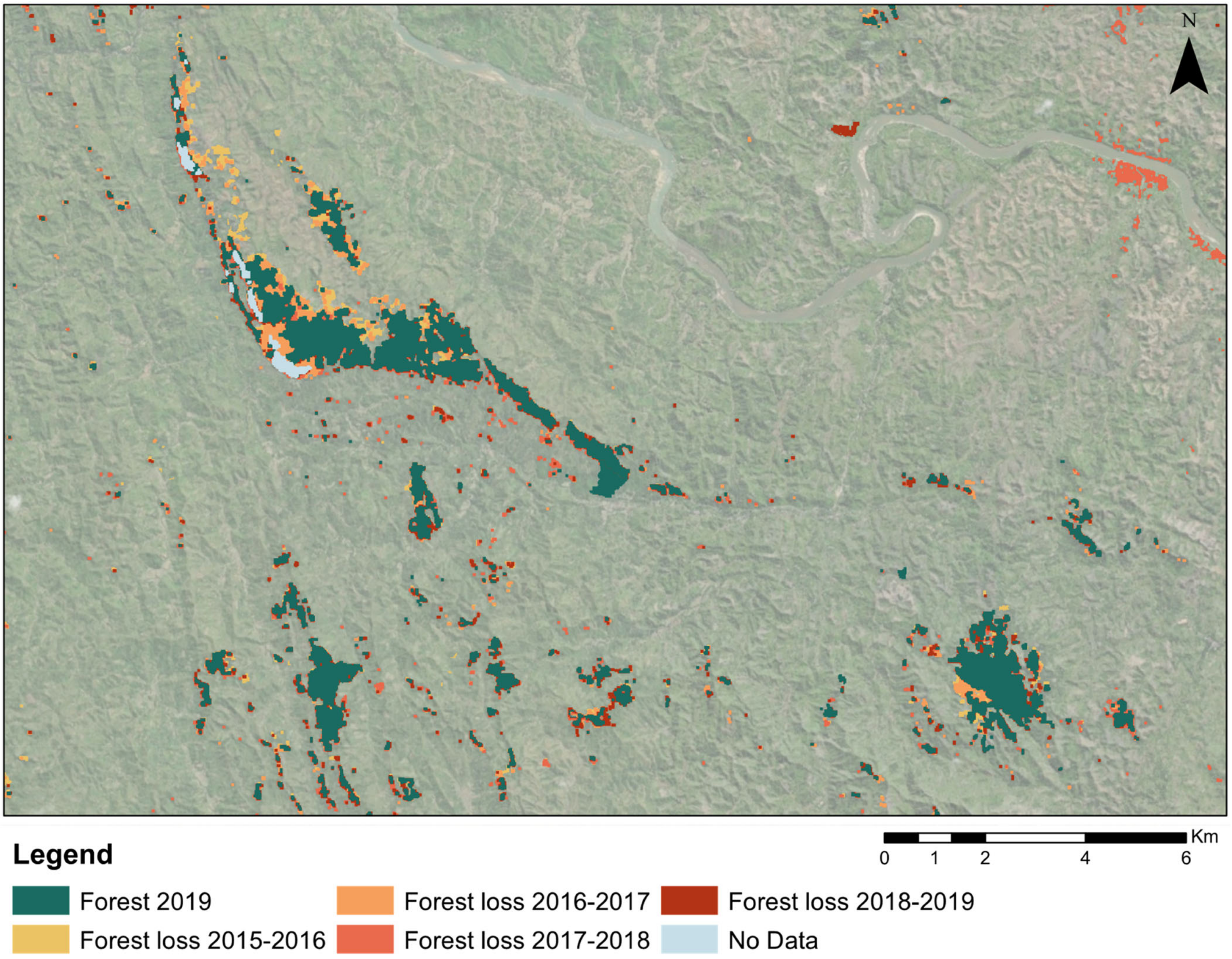

FIGURE 4 Forest loss between 2015 and 2019 in Kianjavato, Madagascar. Satellite imagery obtained from ESRI (2021).

TABLE 4 Percentage change in mean area of the land cover types within species-specific buffers from 2015 to 2019 in Kianjavato, Madagascar.

Land cover type	*Avahi peyrierasi*	*Cheirogaleus major*	*Eulemur rubriventer*	*Eulemur rufifrons*	*Microcebus jollyae*	*Prolemur simus*	*Varecia variegata*
Forest	−6.9%	−6.5%	−6.4%	−5.3%	−6.1%	−5.2%	−5.5%
Tree fallow	9.0%	8.1%	7.0%	6.2%	9.8%	6.0%	6.5%
Mature Agricultural Land	2.3%	3.4%	3.5%	3.4%	0.9%	3.5%	3.4%
New Agricultural Land	−2.4%	−2.6%	−3.0%	−4.4%	−2.0%	−4.5%	−4.2%
Grassland	1.2%	1.0%	2.4%	4.2%	0.0%	4.3%	3.9%
Paddy Fields	−0.1%	−0.1%	0.0%	0.0%	−0.1%	−0.1%	0.0%
Cleared	−0.1%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%

than 2% at the landscape level but remained stable at the lemur species-specific level (see Supporting Information for areas per land cover type within the species-specific buffers; Supporting Information S1: Tables S2-S8).

3.3 | LULC changes and lemur density

For the first step of our modeling (lemur detection functions), the key functions and covariates included in the best detection models varied per species (Supporting Information S1: Table S9). The null detection model was the best-fitting model for *A. peyrierasi* (hazard rate key function), *E. rubriventer* (half-normal key function), *E. rufifrons* (hazard rate key function), and *V. variegata* (hazard rate key function). The detection model with year as a covariate and half-normal key function provided the best fit for *C. major*. For *M. jollyae* and *P. simus*, the best-fitting model included animal height in the canopy as a covariate and hazard rate and half-normal key functions, respectively.

In the second step of our analysis (land cover predictors of lemur density), our results showed that Open Land was the only land cover type included in the top models of most species. This land cover type had a negative effect on the density of *C. major*, *E. rufifrons*, and *V. variegata* but had a positive effect on *E. rubriventer* (Table 5). Tree Fallow positively affected three species: *C. major*, *E. rubriventer*, and *M. jollyae*. Additionally, New Agricultural Land positively affected the density of *E. rufifrons* and *V. variegata*, while Mature Agricultural Land had a positive effect on *E. rufifrons* and a negative effect on *C. major*. None of the land cover types predicted the densities of *A. peyrierasi* or *P. simus*. Due to the high correlation of Forest with other land types, we ran separate models with this predictor only and found that it was included in the top model only for *C. major* (with a positive effect on density).

4 | DISCUSSION

We observed a trend of declining lemur densities across six of the seven species for which we were able to gather sufficient data within the Kianjavato forest fragments. We also observed an increase in the density of the 7th species. The dominant land cover type within the Kianjavato landscape was Open Land, primarily comprised of Grassland, and roughly 50% of the area throughout the study period. During our study period, Mature Agricultural Land experienced the greatest increase, while New Agricultural Land experienced the most substantial decrease. Open Land impacted the densities of four lemur species (mostly negatively), followed by Tree Fallow with a positive effect on the densities of three species. Forest cover in our area of interest decreased by 13.60% from 2015 to 2019, with a mean annual deforestation rate of 3.51%. However, Forest was included as a (positive) predictor in the best-fitting model for only a single species, *C. major*. Overall, our findings show partial support for the hypothesis that a more treed matrix, including Tree Fallow and Mature Agricultural Land, supports a higher lemur densities; whereas a greater proportion of structurally simpler land cover types in the matrix impacts lemur densities negatively in adjacent forest patches. Although these effects appear to be modulated by species traits to

TABLE 5 Models predicting the variation in the density of seven lemur species in the Kianjavato forest fragments.

Species	Top models	*K*	ΔAICc	AICc w	LogLik
Avahi peyrierasi	Null model	3	0	1	−46.91
Cheirogaleus major	Open Land (−35.71)	4	0	0.23	−33.94
	Null model	2	1.17	0.13	−36.91
	Mature Agricultural Land (−9.55)	4	1.58	0.11	−34.73
	Forest (3.10)	4	1.82	0.09	−34.85
	Open Land (-48.88) + Tree Fallow (7.10)	5	1.86	0.09	−33.58
	Mature Agricultural Land (-4.69) + Open Land (−34.68)	5	1.98	0.09	−33.64
Eulemur rubriventer	Open Land (5.48)	3	0	0.43	−106.02
	Open Land (1.95) + Tree Fallow (3.88)	9	0.66	0.31	−104.15
Eulemur rufifrons	Mature Agricultural Land (2.56) + New Agricultural Land (2.16)	11	0	0.31	−250.41
	Mature Agricultural Land (2.46)	9	1.08	0.18	−253.22
	Mature Agricultural Land (2.46) + Open Land (-0.04)	11	1.35	0.16	−251.09
Microcebus jollyae	Null model	2	0	0.28	−90.20
	Tree Fallow (4.08)	4	1.75	0.12	−88.69
Prolemur simus	Null model	3	0	0.97	−49.23
Varecia variegata	New Agricultural Land (11.09) + Open Land (-0.92)	11	0	0.32	−190.77
	New Agricultural Land (10.51)	9	0.99	0.20	−193.53

Note: Each model includes: the variables in the model with effect sizes in parenthesis, the number of model parameters (K), the difference in AICc between the given model and the best model (ΔAICc), the AICc weight (AICc w), and the log-likelihood (LogLik). “Open Land” included the land use types: Grassland (including upland rice), Paddy Fields, and Cleared Land. We only included models ΔAICc <2 units from the top model.

some degree, the trait categorizations considered in our study are likely too coarse to provide an adequate picture of the interactions between species-specific needs and behaviors on the one hand and habitat loss and fragmentation on the other.

4.1 | Trends in lemur densities

We observed a decline in the density of six lemur species in the Kianjavato forest fragments. Our estimates for the densities of all day-active species in 2019, the final year of our study, were lower than those reported for these species in the literature. In particular, the densities of *E. rubriventer* (0.47 individuals/km^2), *E. rufifrons* (2.33 individuals/km^2), and *V. variegata* (1.61 individuals/km^2) were substantially lower than those found in nearby continuous, relatively pristine forest in Ranomafana National Park (RNP; *E. rubriventer:* 8.17–13.96 individuals/km^2; *E. rufifrons:* 8.05–26 individuals/km^2; Herrera et al., 2011; *V. variegata*: 24.3 individuals/km^2; Baden, 2011). In the case of *P. simus*, the Kianjavato population was estimated to be around 100 individuals in 2008 (McGuire et al., 2009). Although our estimate for 2019 suggests that the *P. simus* population may have been extirpated from the study site, other studies (Chen et al., 2021; Narváez-Torres et al., 2022; Rakotonanahary et al., 2021) and a monitoring program by the Madagascar Biodiversity Partnership (MBP; Madagascar Biodiversity Partnership, 2023) have confirmed its continued presence in the area. Density estimates for this group-living species were low throughout the study. It is possible that we saw so few *P. simus* or none at all during our surveys because our transects were located inside the forest fragments, whereas this species uses food sources that are often located outside the forest fragments (see below).

Our estimates for 2016 (the latest survey year) yielded mixed results for the nocturnal species. The density of *M. jollyae* (42.32 individuals/km^2) was notably higher when compared with those of other *Microcebus* species, such as *Microcebus rufus* (15.81 individuals/km^2) at RNP (Herrera et al., 2011), while the density of *A. peyrierasi* (11.67 individuals/km^2) was lower than the reported range for RNP (19.31–40.31 individuals/km^2; Herrera et al., 2011). Conversely, our density estimates for *C. major* (17.21 individuals/km^2) fell within the range reported for this species in Vohibola III (10.4–62.5 individuals/km^2; Lehman et al., 2006b), another continuous eastern rainforest site north of RNP. *C. major* was also the only species that increased density within the 2015–2016 period. These findings suggest that the cheirogaleids *M. jollyae* and *C. major*, with relatively high or increasing densities, may display greater resilience to land cover types characterized by intense human activities, particularly areas previously forested but converted to different land uses. Species in both genera are known to regularly use nonforest habitats (Hending, 2021; Steffens et al., 2021), and their population densities can vary positively with lower tree cover and a higher degree of human impact (Hending, 2021).

Even though we only observed *H. griseus* and *D. madagascariensis* at the beginning of our study, we know that these species are still present in the area (Chen et al., 2021; Madagascar Biodiversity Partnership, 2023; Rakotondrazandry et al., 2021). The lack of observations of these species is likely attributed to their elusive behavior. *D. madagascariensis* is particularly challenging to study due to its unique traits such as its nocturnal pattern, solitary nature, and a very large home range (Table 1; Sterling & McCreless, 2007).

4.2 | LULC changes and effects on lemur densities

Although Kianjavato was designated as a priority site for lemur conservation (Schwitzer et al., 2013), the area has gone through substantial forest loss. In 2010, the forest in Kianjavato covered 18.12 km^2, representing 4.65% of the total area (Vieilledent et al., 2018b). However, by 2019, further deforestation had reduced the forested area to 13.53 km^2, accounting for only 3.49% of the land cover. During the 5-year span of our study (2015–2019), the forest cover experienced a substantial decline of 2.14 km^2 or 13.60%. This resulted in a mean annual deforestation rate of 3.51%, far exceeding the national rate reported by Vieilledent et al. (2018a) for the 2010–2014 period, which was 1.1% per year. Additionally, when compared with other similarly affected eastern sites like the Mananara Nord District (Schüßler et al., 2018), the deforestation rate at Kianjavato remained notably higher. However, a devastating forest fire in 2017 destroyed a large area within the Tsitola fragment, which is still recovering, and this may account for some of the forest loss during our study.

Our results aligned with our prediction that land cover changes would most strongly affect highly frugivorous species with relatively larger home ranges (i.e., *V. variegata* and *E. rufifrons*). Open Land had a negative effect on the density of *V. variegata*, whose density declined by 80% over the study period, and *E. rufifrons*, whose density declined by roughly 40%. The negative effects of Open Land on these species may reflect these lemurs avoiding structurally simpler land cover types that lack physical supports, such as branches or trunks big enough to accommodate the locomotion needs of arboreal primates (Cudney-Valenzuela et al., 2022; Pozo-Montuy et al., 2011). Moreover, *V. variegata* is known to be sensitive to disturbance and to prefer forested habitats with abundant resources (Balko & Brian Underwood, 2005). However, recent research by Petersen et al. (2023) suggests that the diet of *V. variegata* in Kianjavato can be flexible, showing higher dietary diversity compared with populations in continuous forests. For example, the diet of *V. variegata* at this site includes a high percentage of *Ravenala* flowers (Petersen, 2022); *Ravenala* is mostly found in Tree Fallow (see Table 2). Nonetheless, and in line with the density decline observed in our study, Kianjavato's small forest fragments represent low-quality habitat for *V. variegata* (Petersen et al., 2023).

Species we had expected to be least affected by land cover changes due to their folivorous or omnivorous diets and smaller home range sizes (i.e., *H. griseus*, *A. peyrierasi*, and *M. jollyae*) were not immune to land cover change. We were unable to test land cover effects on *H. griseus* due to the low sample size of observations and the consequent lack of density estimates for this species. For *A. peyrierasi*, however, we observed a (1-year) 32% decrease in density in our study. Yet none of the selected predictor variables could explain this decrease. Given observations elsewhere of higher densities at lightly disturbed sites compared with highly disturbed ones (Herrera et al., 2011), it seems that *A. peyrierasi* prefers higher quality habitats. *M. jollyae* also declined in density by 42% over the 1 year for which we had data. Our models suggested that its density responded positively to Tree Fallow. It is possible that *M. jollyae* prefers Tree Fallow over intact forest. Other *Microcebus* species prefer more degraded habitats, such as edge or matrix vegetation over forest interiors, likely due to the presence of insects, insect secretions, and other food sources that increase in the forest edge or in areas with moderate disturbance (Ganzhorn, 1995; Guthrie et al., 2022; Lehman et al., 2006b). More highly disturbed habitats, like the grasslands dominating in Kianjavato, may lack such food sources and explain the species' overall decline.

We expected an intermediate response to land cover changes from *D. madagascariensis* (a relatively large, nocturnal and omnivorous species), *C. major* (small, nocturnal, and frugivorous species), *E. rubriventer*, and *P. simus* (relatively large, cathemeral and folivorous species). We were unable to test land cover effects on *D. madagascariensis* due to the low sample size of observations. We found that the predictor variables we selected could not explain density changes for *P. simus*, perhaps because our transects did not cover core areas of the species' habitat. However, throughout this species' known range, *P. simus* populations were typically observed in matrix vegetation (e.g., Tree Fallow) or edge habitats (e.g., King et al., 2013, Mihaminekena et al. 2024, Olson et al., 2013). Mihaminekena et al. (2024) reported that *P. simus* are not obligate bamboo feeders and can expand their realized dietary niche to include a greater variety of food items than previously documented. This lemur species seems to specialize in plants that thrive in low to moderately disturbed areas such as woody bamboos, *Clidemia hirta*, *Setaria* sp., and *Ravenala* spp., along with numerous agricultural crops often grown near human settlements (Dransfield, 1998; King et al., 2013; Mihaminekena et al. 2024; Tan, 2007). *C. major* was the only species to increase in density, at least in the 1-year interval we had data for. In alignment with the species' preference for using the upper parts of trees and reliance on tree holes for sleeping and hibernating (Lahann, 2008), our models suggested that its density responded positively to forest area and Tree Fallow, but negatively to Mature Agricultural Landscapes and Open Land. This suggests that degraded but structurally forest-like habitats such as Tree Fallow provide at least some of the physical structures the species requires, but that these are absent in plantations and structurally simple, open habitats.

E. rubriventer, another frugivore with a small home range, showed large declines in density, suggesting it remains vulnerable to environmental changes at Kianjavato. Surprisingly, however, our models suggested that Open Land influenced its density positively. The higher density in presumably more marginal habitat might result from reduced competition with closely related *E. rufifrons* (which, as noted, had lower densities in proximity to Open Land). While evidence for active avoidance is mixed, these species can maintain nonoverlapping home ranges in the Kianjavato landscape (Holmes et al., 2019). Another possibility is that density increases in response to Open Land reflect (temporary) crowding as individuals concentrate in the shrinking area of suitable habitat (Bolt et al., 2022; Grez et al., 2004). Given that *E. rubriventer* is highly territorial (Overdorff, 1993), it is also possible that its density responds positively to more Open Land if that equates to greater habitat fragmentation. Territorial species have been observed to benefit from habitat fragmentation when patch boundaries help define territories and reduce conflict with conspecifics (Grez et al. 2004).

Our findings revealed that no individual land cover type impacted all lemur species. Even variables included in most top models, such as Open Land, could have opposing (species-specific) effects on lemur densities. Notably, forest cover did not emerge as a robust predictor of lemur densities, despite all of these species being arboreal and dependent on forest habitats to varying degrees. Heavily treed areas in proximity to natural forest (Tree Fallow) did have the predicted positive impact on the densities of several species that we expected to be more resilient (e.g., *C. major* and *M. jollyae*); however, this effect was not universal and other relatively intensive land cover categories (e.g., both New and Mature Agricultural Land) also had positive effects on the densities of some species. The limitations of these variables in predicting lemur densities may be due to other important but unmeasured drivers of lemur abundance. Importantly, hunting may be a major threat to lemur populations across Madagascar (Borgerson et al., 2022; Schwitzer et al., 2013). However, recent analysis suggests that consumption of lemurs is very low for all species in the Kianjavato region, except for the highly abundant (but potentially declining) *M. jollyae* (Borgerson et al., 2018). Aspects of fragmentation that were not specifically considered here, for example, patch size and isolation (i.e., fragmentation per se), as well as different aspects of vegetation structure (e.g., tree height, tree diameter at 1.3 m height, canopy openness), may have impacted species densities (Arroyo-Rodríguez et al., 2013; Hilário et al., 2022). Moreover, the temporal scope of our study, spanning 5 years, may encompass population changes within the bounds of normal fluctuations. Lemur populations may not be responding to immediate or recent changes in landscape structure. Rather, the declines may follow previous land cover changes, the impacts of which are only now registering in lemur densities. In the extreme, this may represent an extinction debt, where populations have been set on a path of steep decline from such earlier environmental disturbances (Kuussaari et al., 2009).

5 | CONSERVATION IMPLICATIONS

Lemurs are involved in a complex set of interactions with their habitat. Through activities like seed dispersal and pollination, lemurs play a critical ecological role in maintaining healthy and diverse forests that, in turn, provide essential support for the well-being of local human communities (Ganzhorn et al., 1999; Razafindratsima et al., 2018; Valenta & Lehman, 2016). Thus, the decline in lemur populations could have severe ecological and social consequences.

Our study did not reveal a clear link between the decrease in forest cover and the densities of all lemur species. However, the reduction in forest cover in the Kianjavato area, combined with the consistent declines and low densities of five lemur species, highlights the urgent need to continue conservation efforts in the region. The observed negative relationship between several lemur species and structurally simpler land cover types also emphasizes the importance of preserving forest habitats. Since 2008, MBP and the local community have worked together on an extensive reforestation initiative (Madagascar Biodiversity Partnership, 2023). As of February 2024, they have successfully planted 6,697,664 trees in the area, aiming to establish lemur habitats and create corridors connecting forest fragments (Madagascar Biodiversity Partnership, 2023)—actions which, owing to slow maturation of forest trees, will likely take many years to positively impact lemur populations.

Meanwhile, during our study, in 2015, the Corridor Forestier d'Ambositra-Vondrozo (COFAV) was formalized as a vast protected area safeguarding forests between the major National Parks of southeastern Madagascar. This new protected area includes a portion of the study area (Tsitola and Sangasanga). By the end of 2017, there was also greater awareness in the local community of the severe legal penalties for engaging in *tavy* in protected areas. Finally, toward the end of our study, local bodies called *Vondron'Olona Ifotony* (VOI) were established to monitor and enforce land-use laws. The VOIs, including Tsitola (finalized in July 2018), Vatovavy (finalized in April 2019), and Sangasanga (finalized in December 2020), were created to address forest loss and land cover changes. While their impact may not be fully reflected in our study period, the VOIs represent a crucial response to the environmental challenges the Kianjavato community faces. These efforts, coupled with MBP's reforestation project and the establishment of stringent laws and community awareness, offer hope for mitigating deforestation and fostering a positive trajectory for lemur habitats in the region.

AUTHOR CONTRIBUTIONS

Pamela R. Narváez-Torres: Conceptualization (equal); data curation (lead); formal analysis (lead); funding acquisition (supporting); investigation (equal); methodology (equal); project administration (equal); resources (supporting); validation (lead); writing—original draft (lead); writing—review & editing (equal). **Nicola K. Guthrie**: Conceptualization (equal); data curation (lead); formal analysis (lead); investigation (equal); methodology (equal); project administration (equal); resources (supporting); validation (lead); visualization (lead); writing—original draft (equal); writing—review & editing (equal). **Typhenn A. Brichieri-Colombi**: Conceptualization (supporting); data curation (equal); formal analysis (equal); investigation (supporting); methodology (supporting); validation (equal); writing—original draft (supporting); writing—review & editing (equal). **Cressant P. Razafindravelo**: Data curation (equal); investigation (equal); methodology (supporting); project administration (equal); writing—review & editing (equal). **Zachary S. Jacobson**: Conceptualization (equal); data curation (supporting); formal analysis (supporting); investigation (equal); methodology (supporting); visualization (supporting); writing—original draft (supporting); writing—review & editing (equal). **Fredo Tera**: Investigation (supporting); methodology (supporting); project administration (equal); writing—review & editing (equal). **Daniel Rafidimanana**: Investigation (equal); methodology (equal); writing—review & editing (equal). **Zé-Elinah Rahasivelo**: Investigation (equal); writing—review & editing (equal). **Melody A. Petersen**: Conceptualization (equal); writing—original draft (supporting); writing—review & editing (equal). **Hasinala Ramangason**: Conceptualization (equal); formal analysis (supporting); writing—original draft (supporting); writing—review & editing (equal). **Lea Randall**: Conceptualization (equal); writing—review & editing (equal). **Jana M. McPherson**: Conceptualization (equal); formal analysis (supporting); writing—review & editing (equal). **Cynthia L. Frasier**: Data curation (supporting); funding acquisition (supporting); resources (supporting); writing—review & editing (supporting). **Axel Moehrenschlager**: Conceptualization (equal); funding acquisition (equal); supervision (equal); writing—review & editing (equal). **Sheila M. Holmes**: Data curation (equal); funding acquisition (supporting); investigation (equal); methodology (equal); project administration (equal); resources (equal); supervision (supporting); writing—review & editing (equal). **Edward E. Louis**: Funding acquisition (equal); project administration (equal); resources (equal); supervision (equal); writing—review & editing (equal). **Steig E. Johnson**: Conceptualization (equal); formal analysis (supporting); funding acquisition (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); validation (equal); writing—original draft (equal); writing—review & editing (equal).

ACKNOWLEDGMENTS

The authors would like to thank the editor, Karen Bales; the organizers of this special issue, Amanda Melin and Julie Teichroeb; the anonymous reviewers; and Madagascar National Parks for their permission to conduct research. The authors would also like to acknowledge the invaluable contribution of Randrianasolo Rantomampianina, Razafindrenabo Gilbert, Rabesoa Delphin, Tiana Berthin, Ramarolahy Jean Fulbert, Rakotoson Emilys Edgarçon, Mbana Ferdinah, Zafimahazo Pierre and Rakotoarisoa Patrick, the local guides who assisted with data collection in the field. The authors would also like to thank Danica J. Stark for the assistance with data analysis. Furthermore, the authors are thankful for the generous funding provided by the Natural Sciences and Engineering Research Council of Canada, the Government of Alberta, Mexico's National Council for Science and Technology, Mitacs, Conservation International, Primate Conservation Inc., the International Primatological Society, the Calgary Zoological Society, Omaha's Henry Doorly Zoo and Aquarium, and the Ahmanson Family Foundation.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data supporting this study's findings are available from the corresponding author upon reasonable request.

ORCID

Pamela R. Narváez-Torres http://orcid.org/0000-0003-2777-0470
Nicola K. Guthrie https://orcid.org/0009-0003-7702-3518
Typhenn A. Brichieri-Colombi https://orcid.org/0000-0001-7539-3521
Daniel V. Rafidimanana https://orcid.org/0000-0003-1186-6742
Hasinala Ramangason http://orcid.org/0000-0003-4222-7476
Lea Randall https://orcid.org/0000-0002-6144-855X
Jana M. McPherson https://orcid.org/0000-0001-6354-6404
Cynthia L. Frasier https://orcid.org/0000-0002-5416-2000
Axel Moehrenschlager https://orcid.org/0000-0003-2789-0376
Sheila M. Holmes https://orcid.org/0000-0002-6420-5510
Edward E. Louis https://orcid.org/0000-0002-3634-4943
Steig E. Johnson http://orcid.org/0000-0003-2257-8949

REFERENCES

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

Anderson, J., Rowcliffe, J. M., & Cowlishaw, G. (2007). Does the matrix matter? A forest primate in a complex agricultural landscape. *Biological Conservation*, *135*(2), 212–222. https://doi.org/10.1016/j.biocon.2006.10.022

Arroyo-Rodríguez, V., Moral, E. C., Mandujano, S., Chapman, C. A., Reyna-Hurtado, R., & Fahrig, L. (2013). Assessing habitat fragmentation effects on primates: The importance of evaluating questions at the correct scale. In L. Marsh & C. A. Chapman, (Eds.), *Primates in fragments. Developments in primatology: progress and prospects*. Springer.

Baden, A. (2011). *Communal infant care in black-and-white ruffed lemurs (Varecia variegata)*. [PhD Thesis]. State University of New York.

Baden, A. L., Brenneman, R. A., & Louis, Jr., E. E. (2008). Morphometrics of wild black-and-white ruffed lemurs [*Varecia variegata*; Kerr, 1792]. *American Journal of Primatology*, *70*(10), 913–926. https://doi.org/10.1002/ajp.20583

Balko, E. A., & Brian Underwood, H. (2005). Effects of forest structure and composition on food availability for *Varecia variegata* at Ranomafana National Park, Madagascar. *American Journal of Primatology*, *66*, 45–70. https://doi.org/10.1002/ajp.20127

Blanco, M. B., Dausmann, K. H., Faherty, S. L., & Yoder, A. D. (2018). Tropical heterothermy is "cool": The expression of daily torpor and hibernation in primates. *Evolutionary Anthropology: Issues, News, and Reviews*, *27*(4), 147–161. https://doi.org/10.1002/evan.21588

Bolt, L. M., Hadley, C. M., & Schreier, A. L. (2022). Crowded in a fragment : High population density of mantled howler monkeys (Alouatta palliata) in an anthropogenically-disturbed Costa Rican Rainforest. *Primate Conservation*, *36*, 1–9.

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., Holmes, S. M., Anjaranirina, E. J. G., 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*(01), A. https://doi.org/10.4314/mcd

Boyle, S. A., & Smith, A. T. (2010). Can landscape and species characteristics predict primate presence in forest fragments in the Brazilian Amazon? *Biological Conservation*, *143*, 1134–1143. https://doi.org/10.1016/j.biocon.2010.02.008

Bracebridge, C. E., Davenport, T. R. B., Mbofu, V. F., & Marsden, S. J. (2013). Is there a role for human-dominated landscapes in the Long-Term conservation management of the critically endangered kipunji (*Rungwecebus kipunji*)? *International Journal of Primatology*, *34*(6), 1122–1136. https://doi.org/10.1007/s10764-013-9719-3

Brooks, E., Kristensen, K., Benthem, J., Magnusson, A., Berg, W., Nielsen, A., Skaug, J., Mächler, M., & Bolker, M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(22), 378–400. https://doi.org/10.32614/RJ-2017-066

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L., & Thomas, L. (2001). *Introduction to distance sampling: Estimating abundance of biological populations*. Oxford University Press.

Buckland, S. T., Plumptre, A. J., Thomas, L., & Rexstad, E. A. (2010). Design and analysis of line transect surveys for primates. *International Journal of Primatology*, *31*(5), 833–847. https://doi.org/10.1007/s10764-010-9431-5

Buckland, S. T., Rexstad, E. A., Marques, T. A., & Oedekoven, C. S. (2015). *Distance sampling: Methods and applications*. Springer International Publishing, 431. https://doi.org/10.1007/978-3-319-19219-2

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (Second edition). Springer.

Burrows, A. & Nash, L., (Eds.). (2010). *The evolution of exudativory in* primates. Springer.

Calle-Rendón, B. R., Hilário, R. R., & de Toledo, J. J. (2019). Effect of site attributes and matrix composition on neotropical primate species richness and functional traits: A comparison among regions. *Diversity*, *11*(5), 83. https://doi.org/10.3390/d11050083

Candelero, R. A. R., & Pozo-Montuy, G. (2010). Mortalidad de monos aulladores negros *Alouatta pigra* en paisajes altamente fragmentados de Balancán, Tabasco. In L. Gama Campillo, G. Pozo-Montuy, W. M. Contreras Sánchez & S. L. Arriaga Weiss, (Eds.), *Perspectivas en primatología mexicana*. Universidad Juárez Autónoma de Tabasco.

Chapman, C. A., Gillespie, T. R., & Goldberg, T. L. (2005). Primates and the ecology of their infectious diseases: How will anthropogenic change affect host-parasite interactions. *Evolutionary Anthropology: Issues, News, and Reviews*, *14*(Issue 4), 134–144. https://doi.org/10.1002/evan.20068

Chaves, M., Júnior, J. C. S., Buss, G., Hirano, Z. M. B., Jardim, M. M. A., Amaral, E. L. S., Godoy, J. C., Peruchi, A. R., Michel, T., & Bicca-Marques, J. C. (2022). Wildlife is imperiled in peri-urban landscapes: Threats to arboreal mammals. *Science of the Total Environment*, *821*, 152883. https://doi.org/10.1016/j.scitotenv.2021.152883

Chen, D. M., Narváez-Torres, P. R., Tiafinjaka, O., Farris, Z. J., Rasoloharijaona, S., Louis, E. E., & Johnson, S. E. (2021). Lemur paparazzi: Arboreal camera trapping and occupancy modeling as conservation tools for monitoring threatened lemur species. *American Journal of Primatology*, *83*, 23270. https://doi.org/10.1002/ajp.23270

Cohen, J. (1960). A coefficient of agreement for nominal scales. *Educational and Psychological Measurement*, *20*, 37–46.

Cudney-Valenzuela, S. J., Arroyo-Rodríguez, V., Morante-Filho, J. C., Toledo-Aceves, T., & Andresen, E. (2022). Tropical forest loss impoverishes arboreal mammal assemblages by increasing tree canopy openness. *Ecological Applications*, *33*(1), https://doi.org/10.1002/eap.2744

Dransfield, S. (1998). Valiha and Cathariostachys, two new bamboo genera (Gramineae-Bambusoideae) from Madagascar. *Kew Bulletin*, *53*(2), 375–397.

Dunham, N. T. (2017). Feeding ecology and dietary flexibility of colobus angolensis palliatus in relation to habitat disturbance. *International Journal of Primatology*, *38*(3), 553–571. https://doi.org/10.1007/s10764-017-9965-x

Eppley, T. M., & Goodman, S. M. (2022). Non-native habitat use by endemic terrestrial malagasy mammals. In S. M. Goodman, (Ed.), *The natural history of madagascar* (2, pp. 1818–1821). Princeton University Press.

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*(e23104), 23104. https://doi.org/10.1002/ajp.23104

ESRI. (2020). *ArcGIS desktop: Release* 10. Environmental Systems Research Institute.

ESRI. (2021). *World imagery wayback*. https://livingatlas.arcgis.com/wayback/

Estrada, A., Garber, P. A., Mittermeier, R. A., Wich, S., Gouveia, S., Dobrovolski, R., Nekaris, K. A. I., Nijman, V., Rylands, A. B., Maisels, F., Williamson, E. A., Bicca-Marques, J., Fuentes, A., Jerusalinsky, L., Johnson, S., Rodrigues de Melo, F., Oliveira, L., Schwitzer, C., Roos, C., … Setiawan, A. (2018). Primates in peril: the significance of Brazil, Madagascar, Indonesia and the Democratic Republic of the Congo for global primate conservation. *PeerJ*, *6*, e4869. https://doi.org/10.7717/peerj.4869

Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Di Fiore, A., Nekaris, K. A.-I., Nijman, V., Heymann, E. W., Lambert, J. E., Rovero, F., Barelli, C., Setchell, J. M., Gillespie, T. R., Mittermeier, R. A., Arregoitia, L. V., de Guinea, M., Gouveia, S., Dobrovolski, R., & Li, B. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances*, *3*(1), https://doi.org/10.1126/sciadv.1600946

Estrada, A., Raboy, B. E., & Oliveira, L. C. (2012). Agroecosystems and primate conservation in the tropics: A review. *American Journal of Primatology*, *74*(Issue 8), 696–711. https://doi.org/10.1002/ajp.22033

Fahrig, L. (2007). Non-optimal animal movement in human-altered landscapes. *Functional Ecology*, *21*(6), 1003–1015. https://doi.org/10.1111/j.1365-2435.2007.01326.x

Fahrig, L. (2017). Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics*, *48*, 1–23. https://doi.org/10.1146/annurev-ecolsys-110316

FAO. (2022). *FRA 2020 remote sensing survey*. FAO. https://doi.org/10.4060/cb9970en

Fernández, D., Kerhoas, D., Dempsey, A., Billany, J., McCabe, G., & Argirova, E. (2022). The current status of the world's primates: mapping threats to understand priorities for primate conservation. *International Journal of Primatology*, *43*(1), 15–39. https://doi.org/10.1007/s10764-021-00242-2

Frasier, C. L., Rakotonirina, J.-N., Razanajatovo, L. G., Nasolonjanahary, T. S., Rasolonileniraka, S. B., Mamiaritiana, S. B., Ramarolahy, J. F., & Louis, E. E. (2015). Expanding knowledge on life history traits and infant development in the greater bamboo lemur (*Prolemur simus*): Contributions from Kianjavato, Madagascar. *Primate Conservation*, *29*(1), 75–86. https://doi.org/10.1896/052.029.0110

Galán-Acedo, C., Arasa-Gisbert, R., Arroyo-Rodríguez, V., Martínez-Ruiz, M., Rosete-Vergés, F. A., & Villalobos, F. (2023). Effects of habitat loss on Brazilian primates: assessing extinction thresholds in the Amazon and Atlantic forest. *Perspectives in Ecology and Conservation*, *21*(2), 189–195. https://doi.org/10.1016/j.pecon.2023.05.001

Galán-Acedo, C., Arroyo-Rodríguez, V., Cudney-Valenzuela, S. J., & Fahrig, L. (2019). A global assessment of primate responses to landscape structure. *Biological Reviews*, *94*(5), 1605–1618. https://doi.org/10.1111/brv.12517

Ganzhorn, J. U. (1995). Low-Level forest disturbance effects on primary production, leaf chemistry, and lemur populations. *Ecology*, *76*(7), 2084–2096.

Ganzhorn, J. U., Fietz, J., Rakotovao, E., Schwab, D., & Zinner, D. (1999). Lemurs and the regeneration of dry deciduous forest in Madagascar. *Conservation Biology*, *13*(4), 794–804. https://doi.org/10.1046/j.1523-1739.1999.98245.x

Goudie, A. S. (2018). *Human impact on the natural environment. Past, Present and* Future (7th ed.). John Wiley & Sons.

Grez, A., Zaviezo, T., Tischendorf, L., & Fahrig, L. (2004). A transient, positive effect of habitat fragmentation on insect population densities. *Oecologia*, *141*(3), 444–451. https://doi.org/10.1007/s00442-004-1670-8

Guthrie, N. K., Ramananjato, V., Raoelinjanakolona, N. N., Brichieri-Colombi, T. A., Jacobson, Z. S., Randall, L., Louis, E. E., & Johnson, S. E. (2022, August 14). The influence of vegetation type on the distribution of jolly's mouse lemur, *Microcebus jollyae*, in Kianjavato, South-Eastern Madagascar. *Joint Meeting of the Ecological Society of America and the Canadian Society for Ecology and Evolution*, Montreal, Canada.

Harcourt, C. (1991). Diet and behaviour of a nocturnal lemur, *Avahi laniger*, in the wild. *Journal of Zoology*, *223*(4), 667–674. https://doi.org/10.1111/j.1469-7998.1991.tb04395.x

Harper, G. J., Steininger, M. K., Tucker, C. J., Juhn, D., & Hawkins, F. (2007). Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation*, *34*(4), 325–333. https://doi.org/10.1017/S0376892907004262

Hasan, S. S., Zhen, L., Miah, M. G., Ahamed, T., & Samie, A. (2020). Impact of land use change on ecosystem services: A review. *Environmental Development*, *34*, 100527. https://doi.org/10.1016/j.envdev.2020.100527

Hending, D. (2021). Environmental drivers of Cheirogaleidae population density: Remarkable resilience of Madagascar's smallest lemurs to habitat degradation. *Ecology and Evolution*, *11*(Issue 11), 5874–5891. https://doi.org/10.1002/ece3.7449

Hending, D., Andrianiaina, A., Rakotomalala, Z., & Cotton, S. (2017). Range extension and behavioural observations of the recently described sheth's dwarf lemur (Cheirogaleus shethi. *Folia Primatologica*, *88*(5), 401–408. https://doi.org/10.1159/000481531

Herrera, J. P., Wright, P. C., Lauterbur, E., Ratovonjanahary, L., & Taylor, L. L. (2011). The effects of habitat disturbance on lemurs at Ranomafana National Park, Madagascar. *International Journal of Primatology*, *32*, 1091–1108. https://doi.org/10.1007/s10764-011-9525-8

Hilário, R. R., Moraes, B., Souza-Alves, J. P., & Ferrari, S. F. (2022). The density of *Callicebus coimbrai* is better predicted by vegetation structure variables than by surrounding landscape. *International Journal of Primatology*, *45*(1), 54–71. https://doi.org/10.1007/s10764-022-00278-y

Holmes, S. M., Louis, E. E., & Johnson, S. E. (2019). Range overlap and spatiotemporal relationships of frugivorous lemurs at Kianjavato, Madagascar. *Animal Behaviour*, *155*, 53–65. https://doi.org/10.1016/j.anbehav.2019.06.025

Holmes, S. M., Yaney-Keller, A. M., Rafidimanana, D. V., Andrianantenaina, H. M., Louis, Jr., E. E., & Johnson, S. E. (2015). Lemur population surveys in the Kianjavato region. *Lemur News*, *19*, 9–11.

Hurvich, C. M., & Tsai, C.-L. (1989). Regression and time series model selection in small samples. *Biometrika*, *76*(2), 297–307. https://doi.org/10.1093/biomet/76.2.297

IPCC. (2023). Summary for Policymakers. In Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S. L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M. I., Huang, M., Leitsell, K., Lonnoy, E., Matthews, J. B. R., Maycock, T. K., Waterfield, T., Yelekçi, O., Yu, R. & Zhou, B., (Eds.), *Climate Change 2021: The Physical Science Basis.*

Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (pp. 3–32). Cambridge University Press. https://doi.org/10.1017/9781009157896.001

IUCN. (2020). *The IUCN Red List of Threatened Species*. Version 2023-1 http://www.iucnredlist.org

Johns, A. D., & Skorupa, J. P. (1987). Responses of rain-forest primates to habitat disturbance: A review. *International Journal of Primatology*, *8*(2), 157–191. https://doi.org/10.1007/BF02735162

Jung, M. (2016). LecoS—A python plugin for automated landscape ecology analysis. *Ecological Informatics*, *31*, 18–21. https://doi.org/10.1016/j.ecoinf.2015.11.006

Kappeler, P. M. (2012). The behavioral ecology of Strepsirrhines and Tarsiers. In J. Mitani, J. Call, P. Kappeler, R. Palombit & J. Silk, (Eds.), *The evolution of primate societies* (pp. 17–42). The University of Chicago Press.

King, T., Randrianarimanana, H. L. L., Rakotonirina, L. H. F., Mihaminekena, T. H., Andrianandrasana, Z. A., Ratolojanahary, M., Randriahaingo, H. N. T., Ratolojanahary, T., Rafalimandimby, J., Bonaventure, A., Rajaonson, A., Ravaloharimanitra, M., Rasolofoharivelo, M. T., Dolch, R., & Ratsimbazafy, J. H. (2013). Large-Culmed bamboos in Madagascar: distribution and field identification of the primary food sources of the critically endangered greater bamboo lemur *Prolemur simus*. *Primate Conservation*, *27*(1), 33–53. https://doi.org/10.1896/052.027.0105

Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M., & Steffan-Dewenter, I. (2009). Extinction debt: A challenge for biodiversity conservation. *Trends in Ecology & Evolution*, *24*(10), 564–571. https://doi.org/10.1016/j.tree.2009.04.011

LaFleur, M., & Gould, L. (2009). Feeding outside the forest: The importance of crop raiding and an invasive weed in the diet of gallery forest ring-tailed lemurs (*Lemur catta*) following a cyclone at the Beza Mahafaly Special Reserve, Madagascar. *Folia Primatologica*, *80*(3), 233–246. https://doi.org/10.1159/000240968

Lahann, P. (2007). Biology of *Cheirogaleus major* in a littoral rain forest in southeast Madagascar. *International Journal of Primatology*, *28*, 895–905. https://doi.org/10.1007/s10764-007-9163-3

Lahann, P. (2008). Habitat utilization of three sympatric cheirogaleid lemur species in a littoral rain forest of southeastern Madagascar. *International Journal of Primatology*, *29*, 117–134. https://doi.org/10.1007/s10764-007-9138-4

Lehman, S. M., Rajaonson, A., & Day, S. (2006a). Edge effects on the density of *Cheirogaleus major*. *International Journal of Primatology*, *27*(6), 1569–1588. https://doi.org/10.1007/s10764-006-9099-z

Lehman, S. M., Rajaonson, A., & Day, S. (2006b). Lemur responses to edge effects in the vohibola III classified forest, Madagascar. *American Journal of Primatology*, *68*, 293–299. https://doi.org/10.1002/ajp.20224

Lei, R., Engberg, S. E., Andriantompohavana, R., McGuire, S. M., Mittermeier, R. A., & Zaonarivelo, J. R. (2008). Nocturnal lemur diversity at Masoala National Park. *Special Publications of the Museum of Texas Tech University*, *53*, 1–41.

Lei, R., Frasier, C. L., McLain, A. T., Taylor, J. M., Bailey, C. A., Engberg, S. E., Ginter, A. L., Randriamampionona, R., Groves, C. P., Mittermeier, R. A., & Louis Jr., E. E. (2014). Revision of Madagascar's dwarf lemurs (Cheirogaleidae: Cheirogaleus): Designation of species, candidate species status and geographic boundaries based on molecular and morphological data. *Primate Conservation*, *28*, 9–35. https://doi.org/10.1896/052.028.0110

Lenz, B. B., Jack, K. M., & Spironello, W. R. (2014). Edge effects in the primate community of the biological dynamics of forest fragments project, Amazonas, Brazil. *American Journal of Physical Anthropology*, *155*, 436–446. https://doi.org/10.1002/ajpa.22590

Lins, P. G. A. S., & Ferreira, R. G. (2019). Competition during sugarcane crop raiding by blond capuchin monkeys (*Sapajus flavius*). *Primates*, *60*(1), 81–91. https://doi.org/10.1007/s10329-018-0698-z

Machado, F. F., Jardim, L., Dinnage, R., Brito, D., & Cardillo, M. (2023). Diet disparity and diversity predict extinction risk in primates. *Animal Conservation*, *26*(3), 331–339. https://doi.org/10.1111/acv.12823

Madagascar Biodiversity Partnership. (2023). Kianjavato Ahmanson Field Station (KAFS). *Projects & Programs*. https://madagascarpartnership.org/field-sites/kianjavato/

Manjaribe, C., Frasier, C. L., Rakouth, B., & Louis, Jr., E. E. (2013). Ecological restoration and reforestation of fragmented forests in Kianjavato, Madagascar. *International Journal of Ecology*, *2013*, 1–12. https://doi.org/10.1155/2013/726275

Maxwell, S. L., Fuller, R. A., Brooks, T. M., & Watson, J. E. M. (2016). Biodiversity: The ravages of guns, nets and bulldozers. *Nature*, *536*(7516), 143–145.

Mazerolle, M. J. (2020). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). *R vignette*.

McGuire, S. M., Bailey, C. A., Rakotonirina, J.-N., Razanajatovo, L. G., Ranaivoarisoa, J. F., Kimmel, L. M., & Louis, E. E. (2009). Population survey of the greater bamboo lemur (*Prolemur simus*) at Kianjavato Classified Forest. *Lemur News*, *14*, 41–43.

Mekonnen, A., Fashing, P. J., Bekele, A., Hernandez-Aguilar, R. A., Rueness, E. K., Nguyen, N., & Stenseth, N. C. (2017). Impacts of habitat loss and fragmentation on the activity budget, ranging ecology and habitat use of Bale monkeys (*Chlorocebus djamdjamensis*) in the Southern Ethiopian highlands. *American Journal of Primatology*, *79*(7). https://doi.org/10.1002/ajp.22644

Mekonnen, A., Fashing, P. J., Bekele, A., Hernandez-Aguilar, R. A., Rueness, E. K., & Stenseth, N. C. (2018). Dietary flexibility of bale monkeys (*Chlorocebus djamdjamensis*) in Southern Ethiopia: Effects of habitat degradation and life in fragments. *BMC Ecology*, *18*(4), 4. https://doi.org/10.1186/s12898-018-0161-4

Mihaminekena, T. H., Rakotonanahary, A. N., Frasier, C. L., Randriahaingo, H. N. T., Sefczek, T. M., Tinsman, J., Randrianarimanana, H. L., Ravaloharimanitra, M., Rakotoarinivo, T. H., Ratsimbazafy, J., King, T., & Louis, E. E. (2024). Dietary flexibility of the greater bamboo lemur (*Prolemur simus*), a specialized feeder, in eastern Madagascar. *American Journal of Primatology*. https://doi.org/10.1002/ajp.23609

Miller, D. L., Rexstad, E., Thomas, L., Marshall, L., & Laake, J. L. (2019). Distance sampling in R. *Journal of Statistical Software*, *89*(1), 1–28. https://doi.org/10.18637/jss.v089.i01

Mittermeier, R. A., Reuter, K. E., Rylands, A. B., Louis, Jr., E. E., Ratsimbazafy, J., Rene de Roland, L.-A., Langrand, O. M., Schwitzer, C., Johnson, S. E., Godfrey, L. R., Blanco, M. B., Borgerson, C., Eppley, T. M., Andriamanana, T., Volampeno, S., Andriantsaralaza, S., Wright, P. C., Rajaobelina, S., & Sechrest, W. (2023). *Lemurs of Madagascar* (5th Ed.). Re: Wild.

Narváez-Torres, P. R., Rahariniaina, M. J. E., Razafindravelo, C. P., Louis, E. E., & Johnson, S. E. (2022, August 16).No calm after the storm: immediate effects of cyclones Batsirai and Emnati on lemur presence and vegetation structure. *Joint Meeting of the Ecological Society of America and the Canadian Society for Ecology and Evolution, Montreal, Canada*.

Olson, E. R., Marsh, R. A., Bovard, B. N., Randrianarimanana, H. L. L., Ravaloharimanitra, M., Ratsimbazafy, J. H., & King, T. (2013). Habitat preferences of the critically endangered greater bamboo lemur (*Prolemur simus*) and densities of one of its primary food sources, Madagascar giant bamboo (Cathariostachys madagascariensis), in sites with different degrees of anthropogenic and natural disturbance. *International Journal of Primatology*, *34*(3), 486–499. https://doi.org/10.1007/s10764-013-9674-z

Overdorff, D. (1993). Ecological and reproductive correlates to range use in red-bellied lemurs (*Eulemur rubriventer*) and rufous lemurs (*Eulemur* *fulvus* rufus). In P. M. Kappeler & J. U. Ganzhorn, (Eds.), *Lemur social systems and their ecological basis* (pp. 167–178). Springer.

PCI Geomatics. (2024). *CATALYST Professional* (2222.0.1) [Computer software].

Petersen, M. A., Holmes, S. M., Chen, L. D., Ravoniarinalisoa, P. V., Moehrenschlager, A., Louis, E. E., & Johnson, S. E. (2023). Flextime: Black-and-White ruffed lemurs (*Varecia variegata*) use opposing strategies to counter resource scarcity in fragmented habitats. *International Journal of Primatology*, *44*, 1200–1225. https://doi.org/10.1007/s10764-023-00397-0

Petersen, M. A. (2022). *Behavioural Responses to Habitat Fragmentation in the Frugivorous Blackand-White Ruffed Lemur (Varecia variegata): Implications for the Conservation of a Critically Endangered Species*. (MA Thesis). University of Calgary.

Pozo-Montuy, G., Serio-Silva, J. C., & Bonilla-Sánchez, Y. M. (2011). Influence of the landscape matrix on the abundance of arboreal primates in fragmented landscapes. *Primates*, *52*(2), 139–147. https://doi.org/10.1007/s10329-010-0231-5

Prevedello, J. A., & Vieira, M. V. (2010). Does the type of matrix matter? A quantitative review of the evidence. *Biodiversity and Conservation*, *19*(5), 1205–1223. https://doi.org/10.1007/s10531-009-9750-z

Prodger, I., Schwitzer, C., & Rands, S. (2018). Non-forest matrix crossing in the blue-eyed black lemur *Eulemur flavifrons*. *Lemur News*, *21*, 11–12.

Pyne, S. (1997). *World fire: The culture of fire on earth*. University of Washington Press.

QGIS.org. (2022). *QGIS Geographic information system. QGIS association*.

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rakotonanahary, A. N., Andriaholinirina, N. V., Rasoloharijaona, S., Rajaonarison, J. F., Hagenson, R. A., Sefczek, T. M., Frasier, C. L., & Louis, E. E. (2021). Habituation of greater bamboo lemurs (*Prolemur simus*) in the Vatovavy forest, Madagascar. *Primate Conservation*, *2021*(35), 117–124.

Rakotondrazandry, J. N., Ravelomandrato, F., Sefczek, T. M., Andriamalala, Y. R., Frasier, C. L., Villanova, V. L., Rasoloharijaona, S., Raveloson, H., & Louis, E. E. (2021). Developmental timeline of wild aye-aye (Daubentonia madagascariensis) infants in Kianjavato and Torotorofotsy, Madagascar. *International Journal of Primatology*, *42*(3), 344–348. https://doi.org/10.1007/s10764-021-00216-4

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

Randimbiharinirina, D. R., Raharivololona, B. M., Hawkins, M. T. R., Frasier, C. L., Culligan, R. R., Sefczek, T. M., Randriamampionona, R., & Louis, E. E. (2018). Behaviour and ecology of Male aye-ayes (*Daubentonia madagascariensis*) in the Kianjavato classified forest, South-Eastern Madagascar. *Folia Primatologica*, *89*(2), 123–137. https://doi.org/10.1159/000486673

Razafindratsima, O. H., Gentles, A., Drager, A. P., Razafimahaimodison, J.-C. A., Ralazampirenena, C. J., & Dunham, A. E. (2018). Consequences of lemur loss for above-ground carbon stocks in a malagasy rainforest. *International Journal of Primatology*, *39*(3), 415–426. https://doi.org/10.1007/s10764-018-0042-x

Rodríguez-Caro, R. C., Oedekoven, C. S., Graciá, E., Anadón, J. D., Buckland, S. T., Esteve-Selma, M. A., Martinez, J., & Giménez, A. (2017). Low tortoise abundances in pine forest plantations in forest-shrubland transition areas. *PLoS One*, *12*(3), e0173485. https://doi.org/10.1371/journal.pone.0173485

Rowe, N., & Myers, M. (2017). *All the World's Primates*. Retrieved February 15, 2020, from https://www.alltheworldsprimates.org

Roy, P. S., Ramachandran, R. M., Paul, O., Thakur, P. K., Ravan, S., Behera, M. D., Sarangi, C., & Kanawade, V. P. (2022). Anthropogenic land use and land cover Changes—A review on its environmental consequences and climate change. *Journal of the Indian Society of Remote Sensing*, *50*(Issue 8), 1615–1640. https://doi.org/10.1007/s12524-022-01569-w

Sanches, V. Q. A., Menezes, J. F. S., Prevedello, J. A., Almeida-Gomes, M., & Oliveira-Santos, L. G. R. (2022). Can matrix structure affect animal navigation between fragments? A dispersal experiment using release platforms. *Biotropica*, *54*(2), 370–380. https://doi.org/10.1111/btp.13058

Schüßler, D., Radespiel, U., Ratsimbazafy, J. H., & Mantilla-Contreras, J. (2018). Lemurs in a dying forest: Factors influencing lemur diversity and distribution in forest remnants of north-eastern Madagascar. *Biological Conservation*, *228*, 17–26. https://doi.org/10.1016/j.biocon.2018.10.008

Schwitzer, C., Mittermeier, R. A., Davies, N., Johnson, S. E., Ratsimbazafy, J., Razafindramanana, J., Louis, Jr., E. e, & Rajaobelina, S. (2013). *Lemurs of Madagascar: A strategy for their Conservation 2013-2016*. IUCN SSC primate Specialist Group, Bristol Conservation and Science Foundation, and Conservation International

Schwitzer, C., Mittermeier, R. A., Johnson, S. E., Donati, G., Irwin, M. T., Peacock, H., Ratsimbazafy, J. H., Razafindramanana, J., Louis, Jr., E. E., Chikhi, L., Colquhoun, I. C., Tinsman, J., Dolch, R., LaFleur, M., Nash, S., Patel, E., Randrianambinina, B., Rasolofoharivelo, T., & Wright, P. C. (2014). Averting lemur extinctions amid Madagascar's political crisis, *Science 343*, 842–843. https://doi.org/10.1126/science.1245783

Steffens, T. S., Ramsay, M. S., Andriatsitohaina, B., Radespiel, U., & Lehman, S. M. (2020). Enter the matrix: Use of secondary matrix by mouse lemurs. *Folia Primatologica*, *92*(1), 1–11. https://doi.org/10.1159/000510964

Sterling, E. J., & McCreless, E. E. (2007). Adaptations in the aye-aye: A review. In L. L. Gould & M. L. Sauther, (Eds.), *Lemurs: Ecology and adaptation* (pp. 159–184). Springer.

Styger, E., Rakotondramasy, H. M., Pfeffer, M. J., Fernandes, E. C. M., & Bates, D. M. (2007). Influence of slash-and-burn farming practices on fallow succession and land degradation in the rainforest region of Madagascar. *Agriculture, Ecosystems & Environment*, *119*, 257–269. https://doi.org/10.1016/j.agee.2006.07.012

Tan, C. L. (1999). Group composition, home range size, and diet of three sympatric bamboo lemur species (Genus Hapalemur) in Ranomafana National Park, Madagascar. *International Journal of Primatology*, *20*(4), 547–566.

Tan, C. L. (2007). Behavior and ecology of gentle lemurs (Genus Hapalemur). In L. Gould & M. L. Sauther, (Eds.), *Lemurs: Ecology and adaptation* (pp. 369–381). Springer.

The European Space Agency. (2023, September 14). *Cloud-free collections key for land monitoring*. News. https://earth.esa.int/eogateway/news/cloud-free-collections-key-for-land-monitoring

Tiang, D. C. F., Morris, A., Bell, M., Gibbins, C. N., Azhar, B., & Lechner, A. M. (2021). Ecological connectivity in fragmented agricultural landscapes and the importance of scattered trees and small patches. *Ecological Processes*, *10*(1), 20. https://doi.org/10.1186/s13717-021-00284-7

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*, 5775–5787. https://doi.org/10.1111/gcb.16902

Valenta, K., & Lehman, S. M. (2016). Seed dispersal by mouse lemurs: Do Microcebus represent a unique frugivorous guild. In S. M. Lehman, U. Radespiel & E. Zimmermann, (Eds.), *The dwarf and mouse lemurs of Madagascar: Biology, behavior and conservation biogeography of the cheirogaleidae (Issue November)*. Cambridge University press.

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*(January), 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. *CIRAD Dataverse*, *V2*. https://doi.org/10.18167/DVN1/AUBRRC

Webber, A. D., Solofondranohatra, J. S., Razafindramoana, S., Fernández, D., Parker, C. A., Steer, M., Abrahams, M., & Allainguillaume, J. (2019). Lemurs in cacao: Presence and abundance within the shade plantations of Northern Madagascar. *Folia Primatologica*, *91*(2), 96–107. https://doi.org/10.1159/000501987

SUPPORTING INFORMATION

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

How to cite this article: Narváez-Torres, P. R., Guthrie, N. K., Brichieri-Colombi, T. A., Razafindravelo, C. P., Jacobson, Z. S., Tera, F., Rafidimanana, D., Rahasivelo, Z.-E., Petersen, M. A., Ramangason, H., Randall, L., McPherson, J. M., Frasier, C. L., Moehrenschlager, A., Holmes, S. M., Louis, E. E., & Johnson, S. E. (2025). Losing lemurs: Declining populations and land cover changes over space and time. *American Journal of Primatology*, *87*, e23615. https://doi.org/10.1002/ajp.23615