Lemur diversity, habitat use, and responses to disturbance in Besariaka, Parc Naturel Makira, northeastern Madagascar

Antonin Andriamahaihavana[1,2,3], Patrick H. Ross[4], Dean Gibson[3], Megan A. Owen[3], Louis Joxe Jaofeno[5], Charles Rasolondravoavy[5], Gerlain L. Raherison[5], Guy I. Raoloniana[5], Natalie Vasey[6], Erik R. Patel[5,*] & Timothy M. Eppley[3,6,7,*]

[1] Mention Zoologie et Biodiversité Animale, Faculté des Sciences, Université d'Antananarivo, BP 906, Antananarivo 101, Madagascar
E-mail: andryantonin@yahoo.fr

[2] Duke Lemur Center, Durham, North Carolina 27705, USA

[3] Conservation Science and Wildlife Health, San Diego Zoo Wildlife Alliance, San Diego, California 92112, USA
E-mails: dgibson@sdzwa.org, mowen@sdzwa.org

[4] Department of Biology, Duke University, Biological Sciences Building 137, Durham, North Carolina 27705, USA
E-mail: patrick.ross@duke.edu

[5] Lemur Conservation Foundation, PO Box 249, Myakka City, Florida 34251, USA
E-mails: joart29@hotmail.fr, c.rasolondravoavy@gmail.com, patel.erik@gmail.com

[6] School of the Earth, Environment, and Society, Portland State University, PO Box 751, Portland, Oregon 97207, USA
E-mail: nvasey@pdx.edu

[7] Wildlife Madagascar, 2907 Shelter Island Drive, Suite 105 - PMB 1024, San Diego, California 92106, USA
E-mail: eppleyti@gmail.com

*Erik R. Patel and Timothy M. Eppley contributed equally to this work.

Abstract

Madagascar is among the world's most biodiverse nations, yet widespread habitat degradation and fragmentation threaten 98% of lemur taxa with extinction. The Parc Naturel Makira, one of the largest terrestrial protected areas in Madagascar, harbors exceptional biodiversity and supports local communities whose livelihoods depend on its resources. Despite its ecological and conservation importance, fine-scale ecological data on lemur communities within Makira remain limited. To address this gap, we used standardized line-transect surveys, semi-arboreal camera traps, and habitat assessments to investigate lemur species diversity, encounter rates, and habitat use across four forest sites in the Besariaka sector of the Parc Naturel Makira that vary in vegetation structure and anthropogenic disturbance intensity. Diurnal surveys confirmed five lemur species (*Eulemur albifrons*, *E. rubriventer*, *Hapalemur occidentalis*, *Indri indri*, and *Varecia rubra*), while camera traps detected five additional nocturnal species (*Allocebus trichotis*, *Avahi laniger*, *Cheirogaleus* sp., *Lepilemur seali*, and *Microcebus* sp.), for a total of 10 lemur species. *Eulemur albifrons* exhibited the highest encounter rates across all sites. Habitat structure differed significantly among sites. *Varecia rubra* was associated with larger and taller trees and higher canopy strata, while *H. occidentalis* was associated with lower strata and smaller diameter supports. The other species occupied the lower canopy and intermediate strata without clear habitat separation. Encounter rates did not differ significantly among sites despite variation in disturbance, suggesting broad tolerance among detected species within the range of conditions surveyed. Our findings highlight the conservation value of Makira's forests and underscore the importance of fine-scale habitat data for informing locally adapted management strategies in human-influenced tropical landscapes.

Keywords: camera traps, habitat structure, human-modified landscapes, lemur community ecology, tropical rainforest

Résumé détaillé

Madagascar figure parmi les nations les plus riches en biodiversité au monde. Ses forêts abritent une faune et une flore d'une singularité remarquable, avec un taux d'endémisme parmi les plus élevés de la planète. Les lémuriens, groupe de primates exclusivement malgache, en constituent l'un des symboles les plus emblématiques. Pourtant, la dégradation et la fragmentation généralisées des habitats menacent aujourd'hui l'extinction de 98 % des taxons de lémuriens, faisant de leur conservation l'une des priorités les plus urgentes de la biologie de la conservation tropicale.

Le Parc Naturel Makira, l'une des plus grandes aires protégées terrestres de Madagascar, représente

Andriamahaihavana, A., Ross, P. H., Gibson, D., Owen, M. A., Jaofeno, L. J., Rasolondravoavy, C., Raherison, G. L., Raoloniana, G. I., Vasey, N., Patel, E. R. & Eppley, T. M. 2026. Lemur diversity, habitat use, and responses to disturbance in Besariaka, Parc Naturel Makira, northeastern Madagascar. In The Parc Naturel Makira, the largest remaining continuous forest of Madagascar: Flora and fauna research and conservation, eds. S. M. Goodman & M. J. Raherilalao. *Malagasy Nature*, 21: 355-368.

un refuge d'importance capitale pour la biodiversité malgache. Ses forêts humides s'étendent sur plus de 374 000 ha et abritent une diversité exceptionnelle d'espèces endémiques, dont de nombreux taxons menacés. Le parc joue également un rôle socio-économique fondamental pour les communautés locales dont les moyens de subsistance dépendent étroitement de ses ressources forestières. Malgré son importance écologique et conservatoire indéniable, les données écologiques fines sur les communautés de lémuriens au sein de Makira demeurent insuffisantes, en particulier dans ses secteurs les moins accessibles.

La présente étude vise à combler ce manque de connaissances en se concentrant sur le secteur de Besariaka, situé dans la partie nord du parc, une zone largement sous-documentée. Les objectifs étaient d'évaluer la diversité spécifique des lémuriens, d'estimer leurs taux de rencontre, et de caractériser leur utilisation de l'habitat à travers quatre sites forestiers présentant des structures végétales et des niveaux de perturbation anthropique contrastés. Pour ce faire, trois méthodes ont été combinées, notamment les transects linéaires standardisés pour les espèces diurnes, les pièges photographiques semi-arboricoles pour les espèces nocturnes, ainsi que les évaluations détaillées de la structure de l'habitat.

Au total, 10 espèces de lémuriens ont été recensées sur l'ensemble des quatre sites. Les inventaires diurnes ont permis de confirmer la présence de cinq espèces : *Eulemur albifrons*, *E. rubriventer*, *Hapalemur occidentalis*, *Indri indri* et *Varecia rubra*. Les pièges photographiques ont quant à eux permis de détecter cinq espèces nocturnes supplémentaires : *Allocebus trichotis*, *Avahi laniger*, *Cheirogaleus* sp., *Lepilemur seali* et *Microcebus* sp. Parmi ces espèces, plusieurs figurent sur la Liste Rouge de l'UICN comme En danger ou En danger critique d'extinction, soulignant l'importance de la zone pour la conservation des primates malgaches. La complémentarité des deux méthodes utilisées s'est révélée particulièrement importante : les pièges photographiques arboricoles ont permis de détecter cinq espèces nocturnes supplémentaires, complétant ainsi les observations directes réalisées durant les inventaires diurnes.

Eulemur albifrons a présenté les taux de rencontre les plus élevés sur l'ensemble des sites. La structure de l'habitat différait significativement entre les quatre sites d'étude. Les analyses ont révélé une répartition claire des microhabitats entre espèces, ce qui est cohérente avec une ségrégation verticale des niches. *Varecia rubra* montrait une association marquée avec les arbres les plus grands et les plus larges, ainsi qu'avec les strates supérieures de la canopée. A l'inverse, *H. occidentalis* était systématiquement associé aux strates inférieures et aux supports de plus petit diamètre. Ces résultats indiquent que, malgré la coexistence de plusieurs espèces sur les mêmes sites, celles-ci exploitent des microhabitats distincts, ce qui réduit la compétition interspécifique et permet leur coexistence.

De manière notable, les taux de rencontre ne différaient pas significativement entre les sites malgré les variations observées dans la structure forestière et les niveaux de perturbation anthropique. Ce résultat suggère donc une tolérance relativement large des espèces détectées face aux conditions rencontrées dans cette gamme de perturbations, du moins à l'échelle spatiale et temporelle de cette étude. Il convient toutefois d'interpréter ces résultats avec prudence, dans la mesure où l'effort d'échantillonnage n'était pas uniforme entre les sites, et où la perturbation a été évaluée de manière qualitative plutôt qu'en termes d'intensité ou d'étendue spatiale.

Dans leur ensemble, les résultats mettent en lumière la valeur de conservation des forêts de Makira et confirment que le secteur de Besariaka abrite des communautés de lémuriens diversifiées, y compris des espèces hautement menacées. A notre connaissance, il s'agit du premier jeu de données écologiques systématiques reposant sur plusieurs méthodes issues de ce secteur du parc, l'un des moins documentés de l'une des plus grandes aires protégées de Madagascar. Ces données constituent une référence de base indispensable pour le suivi à long terme des populations de lémuriens dans cette région. Elles soulignent également l'importance des données d'habitat à fine échelle pour orienter des stratégies de gestion adaptées aux contextes locaux dans les paysages tropicaux influencés par l'activité humaine, une priorité croissante pour la conservation à Madagascar et au-delà.

Mots clés : pièges photographiques, structure de l'habitat, paysages anthropisés, écologie des communautés de lémuriens, forêt tropicale humide

Introduction

Understanding how species persist within increasingly human-modified landscapes remains a central challenge in ecology and conservation biology (Gibson *et al*., 2011; Laurance *et al*., 2014). Across the tropics, deforestation, fragmentation, and

climate variability have reshaped natural ecosystems into mosaics of degraded and anthropogenic habitats. These transformations alter community composition, resource availability, and interspecific interactions, ultimately influencing population persistence and ecosystem functioning. Identifying which species tolerate, adapt to, or decline under such pressures, and the mechanisms behind these responses is essential for predicting biodiversity trajectories and informing effective conservation management. Importantly, anthropogenic landscape change is a primary driver of global declines, with land-use change and infrastructure expansion strongly associated with reduced species richness and increased extinction risk (Torres-Romero *et al*., 2023).

Madagascar is one of the world's foremost biodiversity hotspots (Myers *et al*., 2000; Mittermeier *et al*., 2023), harboring extraordinary levels of endemism shaped by millions of years of isolation. Approximately 98% of lemur taxa, the island's flagship mammal group, are currently threatened with extinction (IUCN, 2025). Deforestation, swidden agriculture, charcoal production, and illegal timber extraction remain the primary drivers of ongoing forest loss (Harper *et al*., 2007; Vieilledent *et al*., 2018; Andrianambinina *et al*., 2025), often compounded by socio-economic crises including drought, food insecurity, and political instability (Ralimanana *et al*., 2022). These overlapping threats intensify pressure on Madagascar's unique biota and complicate conservation efforts.

Lemurs occupy nearly all forest types across Madagascar and fulfill essential ecological roles as seed dispersers, pollinators, and herbivores, thereby maintaining forest structure and regeneration (Ganzhorn *et al*., 2024; Ramananjato, 2025). Their responses to environmental disturbance vary widely according to traits such as body size, dietary specialization, locomotor behavior, and activity pattern (Lehman *et al*., 2006; Herrera *et al*., 2011; Eppley *et al*., 2020, 2022). Smaller-bodied nocturnal species, particularly those in the genus *Microcebus*, often exhibit greater resilience due to their omnivorous diets (Atsalis, 1999; Sawyer *et al*., 2017; Schüßler *et al*., 2020). However, their persistence is often associated with increased ecological flexibility, including the ability to exploit secondary and/or degraded habitats, rather than strictly reduced habitat requirements (Sawyer *et al*., 2017; Knoop *et al*., 2018; Mittermeier *et al*., 2023). Importantly, this generalization risks obscuring substantial interspecific variation: several small-bodied nocturnal taxa may be more specialized and consequently more vulnerable than commonly assumed, particularly when treated as ecological equivalents of *M. murinus* (Kappeler *et al*., 2022; Giertz *et al*., in press). In contrast, larger-bodied species such as *Indri indri* and *Varecia rubra* are typically more vulnerable to disturbance due to their specialized dietary requirements and low reproductive rates (Lehman *et al*., 2006; Mittermeier *et al*., 2023).

The Parc Naturel Makira is one of the largest terrestrial protected areas on Madagascar and one of the most biologically important regions of the island (Goodman *et al*., 2018). Its moist evergreen forests contain remarkable levels of biodiversity, including numerous endemic and threatened species. Despite its biological significance, published ecological data from Makira's interior forest remain sparse, and its lemur communities are among the least documented in the region. The Besariaka sector in the northern part of the park represents a largely unstudied landscape within this vast protected area.

This study investigates how lemur diversity, encounter rates, and habitat use vary across four forest sites that differ in exposure to anthropogenic and natural disturbance. Specifically, we 1) document diurnal and nocturnal lemur species richness, 2) estimate species encounter rates using standardized line-transect surveys, 3) evaluate how habitat structure and disturbance influence species' distribution and abundance, and 4) characterize microhabitat use by the most frequently detected species. By providing updated, spatially explicit data from this under-surveyed region, we aim to advance understanding of how primate communities, and by extension, other forest-dependent taxa, respond to disturbance gradients in Madagascar's humid forests.

Methods

Study site

This study was conducted in the Besariaka sector, in the northern part of the Parc Naturel Makira(14°10'-16°00'S, 49°00'-49°55'E), which is a terrestrial area, encompassing 374,083 ha of moist evergreen forest. The park protects a continuous block of low altitude and mid-altitude moist evergreen forest across an elevational gradient from 0 m to 1500 m above sea level, supporting exceptional levels of biodiversity and endemism, including 17 lemur species (Goodman *et al*., 2018).

We surveyed four forest sites around the Besariaka area (Figure 1): Analambolo (14°54.848'S 49°35.801'E), Andranovato (14°49.435'S

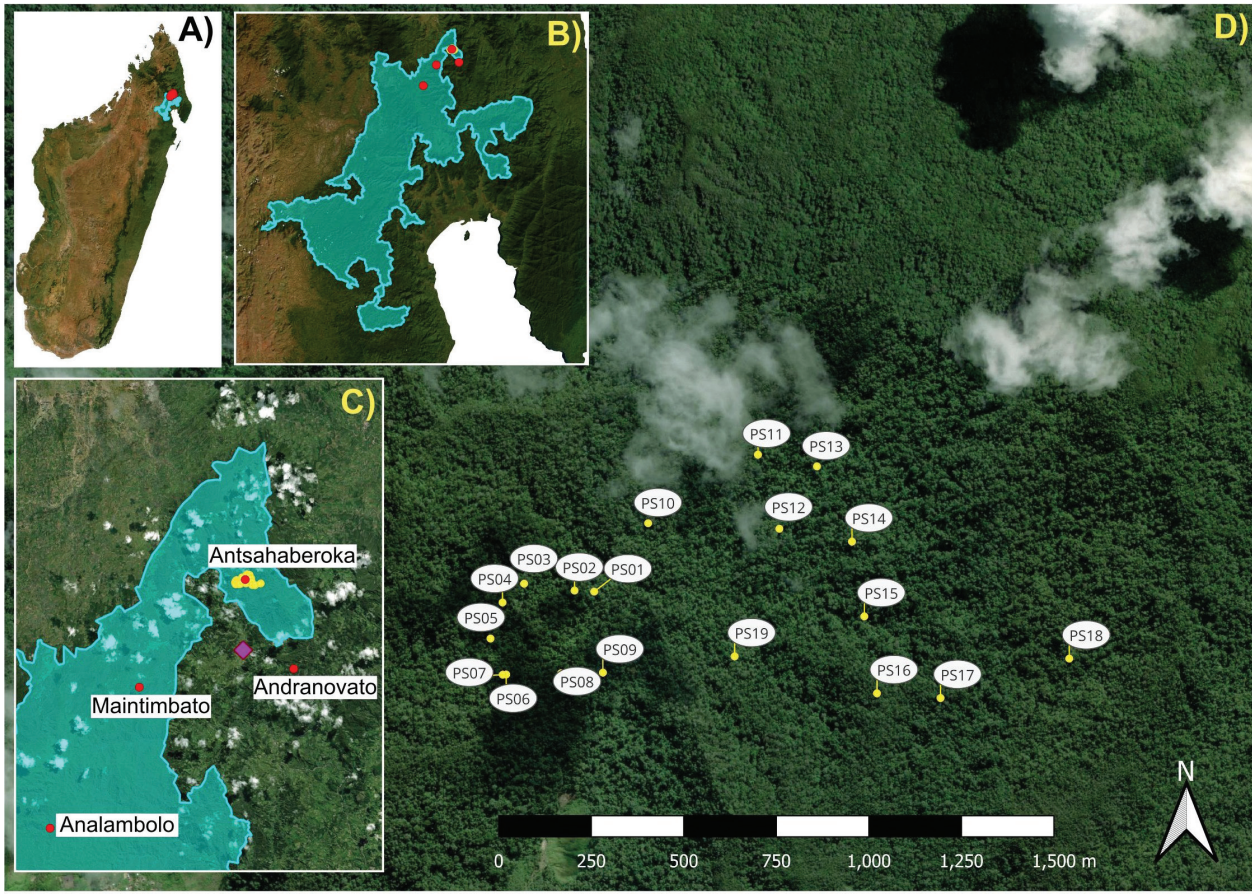

Figure 1. Map of the **A**) placement of the study area in northeastern Madagascar, **B**) The Parc Naturel Makira, **C**) locations of the four study sites (Analambolo, Andranovato, Antsahaberoka, and Maintimbato) in the northern sector of the protected area, and **D**) locations of 19 arboreal camera trap stations across survey transects at Antsahaberoka. Cameras were deployed from December 2021 to March 2022 (Esri, 2024; QGIS Association, 2024).

Table 1. Habitat characteristics and disturbance measured in vegetation surveys across the four study sites in the Parc Naturel Makira.

Parameter	Analambolo	Andranovato	Antsahaberoka	Maintimbato
Altitude (m)	976	783	811	825
Number of PCQ per site	181	170	177	182
DBH (cm)*	22.04 ± 13.39^{a}	20.57 ± 12.04^{b}	21.12 ± 13.02^{b}	23.20 ± 12.41^{c}
Tree height (m)*	16.59 ± 5.29^{d}	17.14 ± 4.19^{d}	15.52 ± 5.53^{e}	16.85 ± 5.53^{d}
Bole height (m)*	11.57 ± 5.67^{f}	12.13 ± 5.21^{g}	10.65 ± 5.69^{h}	11.22 ± 6.05^{f}
Distance (m)	2.94 ± 1.88	2.61 ± 1.88	2.40 ± 1.51	2.37 ± 1.73
Density (DBH ≥10 cm/ha)	1157 ± 429	1471 ± 497	1735 ± 651	1775 ± 595
Disturbance types (total events)	(0, 0)	(5, 13)	(1, 1)	(1, 1)
Distance to nearest village (m)	14,300	3500	4100	6900

Values are means ± SD; Disturbance format: (number of disturbance types, total number of disturbance events); values for a given variable that share the same superscript letter are not significantly different, and different superscript letters indicate significant pairwise differences among sites based on Dunn's post hoc tests ($P \leq 0.05$). DBH = diameter at breast height. * Significant Kruskal-Wallis test result ($P \leq 0.05$).

49°44.072'E), Antsahaberoka (14°46.407'S 49°42.427'E), and Maintimbato (14°50.062'S 49°38.830'E). These sites were selected to represent variation in vegetation structure and degree of habitat disturbance, from the relatively intact forest of Analambolo to more accessible sites with evidence of anthropogenic activity. Euclidean distance from the nearest village ranged from 14.3 km (Analambolo) to 3.5 km (Andranovato) (Table 1).

Vegetation assessment

We conducted fieldwork during two seasons. The first expedition spanned the period from 6 August to 13

November 2021, during which we surveyed all four sites (Maintimbato, Antsahaberoka, Andranovato, and Analambolo), spending 20-25 days per site. The second expedition, conducted from 6 December 2021 to 10 March 2022, focused exclusively on Antsahaberoka.

We used Point Centered Quarter (PCQ) sampling and vertical vegetation profile surveys to quantify habitat characteristics (Gautier *et al*., 1994; Mitchell, 2010; Ganzhorn *et al*., 2011). At each site, we established six transects ranging from 1-1.7 km in length, marked with cumulative distance every 25 m with flagging tape. The total transect lengths were 9.08 km at Analambolo, 8.51 km at Andranovato, 8.89 km at Antsahaberoka, and 9.16 km at Maintimbato. PCQ samples were collected every 50 m along the complete length of each transect. For each quarter, we recorded all trees with a diameter at breast height (DBH) ≥ 10 cm. Structural data collected included tree DBH (cm), tree height (m), bole height (m) (vertical distance from the ground to the first live branch), and the horizontal distance from the point center to the base of the tree stem. Tree density (number of trees ≥ 10 cm DBH per hectare) was calculated using the formula: tree density = 10,000 / (mean distance in meters)^2. To assess vertical vegetation structure, we established 50-m vegetation profile transects perpendicular to the left side of the main transects every 1000 m, beginning at 500 m. Along each transect, sampling points were recorded at 1-m intervals. At each point, an imaginary vertical line extending from the ground to the canopy was visualized, and all vegetation contacts were recorded by height class and growth form to characterize forest stratification. Vernacular names for all botanical species were provided by experienced local field assistants and cross-referenced with standard regional floras to assign scientific names.

We recorded signs of habitat disturbance along transects, including human presence, snares, cut trees, shifting agriculture, fire, charcoal production, artisanal mining, temporary shelters, and spent gun shells. All signs were quantified as presence/absence and frequency rather than intensity or spatial extent, limiting direct inference about their ecological impact.

Lemur surveys

We conducted diurnal lemur surveys using a standardized line-transect method with multiple observers, a widely used approach for arboreal primates (Buckland *et al*., 2001, 2010). The same transects were used for lemur surveys, and we followed pre-existing paths to minimize additional disturbance. Each transect was repeated six times per site. In total, we conducted 36 diurnal surveys per site, except at Antsahaberoka (n = 180 diurnal surveys, i.e., 36 during the first expedition and 144 during the second). This yielded total survey efforts of 54.5 km at Analambolo, 51.1 km at Andranovato, 160.0 km at Antsahaberoka, and 63.7 km at Maintimbato, for a combined total of 329.2 km. Transects were walked slowly at approximately 0.5-1 km/h (Sawyer *et al*., 2017) between 06:00 and 10:00. Observers maintained approximately 10 m spacing, scanning both sides of the transect and checking behind frequently to minimize missed detections (Nekaris *et al*., 2014; Sawyer *et al*., 2017). We alternated the starting point of each survey repetition to reduce potential bias (Fashing & Cords, 2000; Ross & Reeve, 2011) and avoided surveys during heavy rainfall (i.e., when rainfall intensity was sufficient to reduce visibility and animal detectability).

For each sighting, we recorded the date, time, transect name, species, number of individuals, GPS coordinates (accuracy ≤ 5 m), estimated perpendicular distance from the transect to the individual or group center, observed behavior (e.g., feeding, resting, traveling, other), and estimated height above ground (Marshall *et al*., 2008; Meyler *et al*., 2012; Sawyer *et al*., 2017; Fenosoa *et al*., 2018). We marked the tree where the first individual was detected with flagging tape and labeled it with the date and time to facilitate subsequent habitat-use measurements. Only visual detections were included in analyses. Survey teams consisted of four observers and two local guides.

Photographic sampling (camera traps)

To complement diurnal line-transect surveys and document nocturnal species, we deployed semi-arboreal camera traps at Antsahaberoka from 6 December 2021 to 10 March 2022 (Ross *et al*., 2020; Chen *et al*., 2021). We installed 19 Browning trail cameras (model Prometheus BTC5HDPX) on trees at heights ranging from 3 to 5 m above ground, positioned across survey transects (Figure 1D). Inter-camera distances ranged from 10 to 365 m. Eighteen cameras were configured to capture high-resolution photographs; one camera (station PS-07) was set to record high-definition video.

Habitat use

To assess habitat use, we revisited all marked trees where lemurs were first observed during line-transect surveys. At each location, we measured tree DBH, visually estimated total tree height (m) and bole height (m), recorded the height at which the focal lemur was first observed (i.e., height above ground), and noted the Malagasy vernacular name of the tree species (Sawyer *et al*., 2017; Fenosoa *et al*., 2018), following the same identification procedure described above.

Statistical analysis and image tagging

We performed all statistical analyses in RStudio (v2025.5.1.513; Posit Team, 2025) using R (v4.2.3; R Core Team, 2025). Analyses were restricted to *Eulemur albifrons*, *E*. *rubriventer*, *Hapalemur occidentalis*, *Indri indri*, and *Varecia rubra* due to limited detections of other species during line-transect surveys. We used the Shapiro-Wilk test to assess data normality. Given unequal sampling effort among sites (e.g., higher sampling intensity at Antsahaberoka), encounter rate comparisons should be interpreted cautiously, as detection probability and sampling effort were not explicitly modeled (e.g., via distance sampling or occupancy frameworks). Because data were non-normally distributed, we applied Kruskal-Wallis tests to compare habitat variables among the four forest sites, with tree height, DBH, bole height, and distance as dependent variables and site as the independent variable.

We applied the same non-parametric approach to compare microhabitat use among species, including lemur height, tree height, tree DBH, and bole height as dependent variables and species as the independent variable. We calculated species-specific encounter rates as the number of individuals observed per kilometer surveyed (N/km) (Murphy *et al*., 2016), recognizing that encounter rates represent indices of relative abundance rather than absolute density estimates. We then used those results to compare encounter rates among species and among sites using Kruskal-Wallis tests. When Kruskal-Wallis results were significant, we conducted post hoc pairwise comparisons using Dunn's test (Dunn, 1964) with Bonferroni correction to adjust for multiple testing. All results are reported as mean ± SD, unless otherwise noted, and significance was set at $\alpha = 0.05$.

Photos from the camera traps were processed in DigiKam (digiKam Development Team, 2026); we manually tagged each image twice, identifying species, individual counts, and camera stations in the tags. This double-tagging approach ensured data accuracy by identifying missed or incorrect entries. All tags including location, date, time, and species details were saved directly to the image metadata. Camera-trap events were defined as independent photographic detections of the same species at the same camera station (n = 19) separated by at least 30 minutes. Finally, we used the CamtrapR package (Niedballa *et al*., 2016) to export these records into a Microsoft Excel file (Microsoft Corporation, 2026) capture history for analysis.

Results

Habitat structure across sites

Vegetation structure differed significantly among the four study sites (Table 1). Mean tree DBH differed significantly among sites (Kruskal-Wallis: $\chi^2 = 41.97$, df = 3, $P < 0.001$). Post hoc Dunn's tests indicated that Maintimbato had significantly larger trees (23.20 ± 12.41 cm) compared to all other sites (all $P \leq 0.001$), while Analambolo (22.04 ± 13.39 cm) had significantly larger trees than Andranovato (20.57 ± 12.04 cm; $P = 0.005$) and Antsahaberoka (21.12 ± 13.02 cm; $P = 0.016$). DBH did not differ significantly between Andranovato and Antsahaberoka ($P = 0.32$).

Mean tree height differed significantly among sites (Kruskal-Wallis: $\chi^2 = 33.57$, df = 3, $P < 0.001$). Antsahaberoka had significantly shorter trees (15.52 ± 5.53 m) than Analambolo (16.59 ± 5.29 m; $P < 0.001$), Andranovato (17.14 ± 4.19 m; $P < 0.001$), and Maintimbato (16.85 ± 5.53 m; $P < 0.001$). Tree heights at Analambolo and Andranovato did not differ significantly from each other ($P = 0.19$), nor did Analambolo and Maintimbato (16.85 ± 5.53 m; $P = 0.053$) or Andranovato and Maintimbato ($P = 0.24$).

Bole height also differed among sites (Kruskal-Wallis: $\chi^2 = 22.54$, df = 3, $P < 0.001$). Antsahaberoka exhibited the lowest bole heights (10.65 ± 5.69 m), significantly shorter than Analambolo (11.57 ± 5.67 m; $P = 0.002$), Andranovato (12.13 ± 5.21 m; $P < 0.001$), and Maintimbato (11.22 ± 6.05 m; $P = 0.04$). Andranovato also differed from Analambolo ($P = 0.037$) and Maintimbato ($P = 0.001$). There was no significant difference between Analambolo and Maintimbato ($P = 0.13$).

Tree density (DBH ≥ 10 cm/ha) varied among sites, ranging from 1157 ± 429 trees/ha in Analambolo to 1775 ± 595 trees/ha in Maintimbato. In terms of anthropogenic disturbance, Analambolo was the least disturbed site, with no recorded disturbance events. Andranovato was the most heavily affected, with

five types of disturbances and 13 recorded events (including cut trees, evidence of charcoal production, and human presence), followed by Antsahaberoka and Maintimbato (one disturbance type each, with one event each).

Lemur species composition and encounter rates across sites

A total of 10 lemur species were recorded across the four study sites (Table 2). Diurnal line-transect surveys confirmed five species: *Eulemur albifrons*, *E. rubriventer*, *Hapalemur occidentalis*, *Indri indri*, and *Varecia rubra*. Camera trap surveys at Antsahaberoka, conducted over 1805 camera-trap nights, recorded an additional five nocturnal species: *Allocebus trichotis*, *Avahi laniger*, *Cheirogaleus* sp., *Lepilemur seali*, and *Microcebus* sp. Across 488 camera trap capture events over the study period, *E. albifrons* (79 events) and *L. seali* (78 events) were the most frequently captured species. *Hapalemur occidentalis* (46 events), *Cheirogaleus* sp. (38 events), and *A. laniger* (29 events) were also well represented. The cryptic *Allocebus trichotis* was captured six times, confirming its presence at Antsahaberoka (Figure 2). No *Propithecus candidus*, *Phaner furcifer*, *V. variegata*, or *Daubentonia madagascariensis* were observed, though feeding remains by *D. madagascariensis* were recorded at each site.

Encounter rates differed significantly among the five diurnally surveyed species (Kruskal-Wallis: $\chi^2 = 34.85$, df = 4, $P < 0.001$). *Eulemur albifrons* had the highest encounter rates across all sites and differed significantly from all other species (all $P < 0.001$; Table 2). No significant differences were detected among the remaining four species (all $P > 0.09$). Encounter rates did not differ significantly

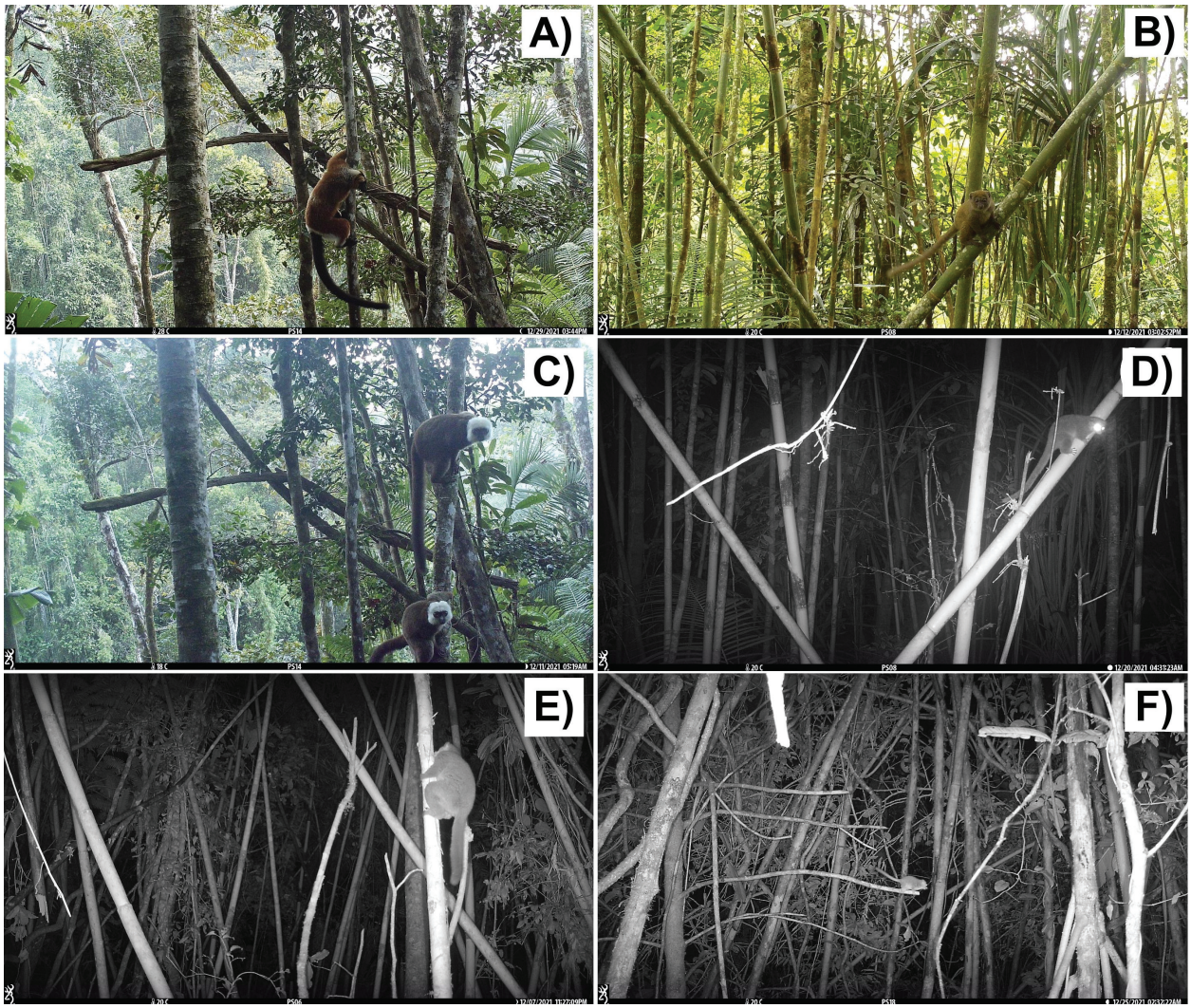

Figure 2. Examples of arboreal camera trap photographs of lemur species captured at Antsahaberoka, Parc Naturel Makira. **A**) *Varecia rubra*, **B**) *Hapalemur occidentalis*, **C**) *Eulemur albifrons*, **D**) *Cheirogaleus* sp., **E**) *Lepilemur seali*, and **F**) *Microcebus* sp.

Table 2. Lemur species recorded across the four study sites in Parc Naturel Makira during diurnal line-transect surveys and camera-trap sampling, including total number of individuals observed per site, encounter rates (ind./km), and independent camera-trap events.

Lemur species	Activity pattern	IUCN (2025)	Analambolo N (ER)	Andranovato N (ER)	Antsahaberoka N (ER)	Maintimbato N (ER)	Camera-trap events (n)
Eulemur albifrons	Cathemeral	VU	96 (1.76 ± 1.11)	13 (0.25 ± 0.28)	187 (1.17 ± 0.72)	26 (0.41 ± 0.40)	79
Eulemur rubriventer	Cathemeral	VU	2 (0.04 ± 0.09)	0 (0.00 ± 0.00)	30 (0.19 ± 0.24)	23 (0.36 ± 0.51)	3
Hapalemur occidentalis	Cathemeral	VU	2 (0.04 ± 0.06)	1 (0.02 ± 0.05)	24 (0.15 ± 0.12)	0 (0.00 ± 0.00)	46
Indri indri	Diurnal	CR	15 (0.28 ± 0.33)	6 (0.12 ± 0.12)	0 (0.00 ± 0.00)	1 (0.02 ± 0.05)	-
Varecia rubra	Diurnal	CR	0 (0.00 ± 0.00)	8 (0.16 ± 0.22)	29 (0.18 ± 0.11)	22 (0.35 ± 0.42)	2
Allocebus trichotis	Nocturnal	EN	-	-	-	-	6
Avahi laniger	Nocturnal	VU	-	-	-	-	29
Cheirogaleus sp.	Nocturnal	-	-	-	-	-	38
Lepilemur seali	Nocturnal	VU	-	-	-	-	78
Microcebus sp.	Nocturnal	-	-	-	-	-	11

N: total number of individuals observed in line-transect surveys; ER: encounter rate (ind./km); Values of ER are means ± SD; IUCN Red List categories: VU = Vulnerable, EN = Endangered, CR = Critically Endangered (IUCN, 2025); Camera-trap events (n): number of independent photographic detection events of the same species at Antsahaberoka, defined using a 30-minute temporal independence threshold; Activity patterns from Mittermeier *et al*. (2023).

among sites (Kruskal-Wallis: $\chi^2 = 5.88$, df = 3, $P = 0.12$), although *E. albifrons* was most frequently observed at Analambolo (1.76 ± 1.11 ind./km) and least frequently at Andranovato (0.25 ± 0.28 ind./km). *Eulemur rubriventer* and *V. rubra* showed their highest encounter rates at Maintimbato (0.36 ± 0.51 and 0.35 ± 0.42 ind./km, respectively). *Indri indri* was absent from Antsahaberoka and had low encounter rates elsewhere (0.02 ± 0.05-0.28 ± 0.33 ind./km). These results should be interpreted with caution given potential differences in detection probability among habitats and methodological constraints associated with field surveys.

Habitat use by lemurs

Microhabitat use differed significantly among the five species surveyed (Figure 3). Overall, patterns were largely driven by strong vertical and structural separation between *Varecia rubra* and *Hapalemur occidentalis*, whereas the remaining species occupied intermediate and overlapping strata. Lemur height above ground differed significantly among species (Kruskal-Wallis: $\chi^2 = 28.32$, df = 4, $P < 0.001$; Figure 3A). *Varecia rubra* was observed at significantly greater heights (mean ± SD: 18.50 ± 3.45 m) than all other species (all $P \leq 0.001$), consistent with its preference for upper canopy strata. In contrast, *H. occidentalis* was found at significantly lower heights (8.70 ± 4.34 m) than both *Eulemur albifrons* (12.07 ± 4.38 m; $P = 0.004$) and *E. rubriventer* (12.18 ± 3.97 m; $P = 0.020$). No significant differences were detected among *E. albifrons*, *E. rubriventer*, and *Indri indri* in lemur height (all $P > 0.21$).

Tree height at observation points also differed significantly among species (Kruskal-Wallis: $\chi^2 = 26.24$, df = 4, $P < 0.001$; Figure 3B). *Varecia rubra* used significantly taller trees (22.66 ± 3.61 m) than all other species (all $P \leq 0.004$), while *H. occidentalis* used significantly shorter trees (15.25 ± 3.75 m) than both *E. albifrons* ($P = 0.009$) and *E. rubriventer* ($P = 0.010$). No significant differences in tree height were detected among *E. albifrons*, *E. rubriventer*, and *I. indri* (all $P > 0.07$).

Tree DBH at observation points differed significantly among species (Kruskal-Wallis: $\chi^2 = 35.49$, df = 4, $P < 0.001$; Figure 3C). *Varecia rubra* consistently used the largest trees (58.75 ± 29.36 cm), significantly larger than all other species (all $P \leq 0.002$). *Hapalemur occidentalis* used significantly smaller trees (13.30 ± 14.26 cm) than both *E. albifrons* ($P < 0.001$) and *E. rubriventer* ($P < 0.001$). No significant differences were found among *E. albifrons*, *E. rubriventer*, and *I. indri* (all $P > 0.10$).

Bole height differed significantly among species (Kruskal-Wallis: $\chi^2 = 17.84$, df = 4, $P = 0.001$; Figure 3D). *Varecia rubra* used trees with significantly higher boles (15.16 ± 4.15 m) compared to all other species (all $P \leq 0.021$). No significant differences in bole height were detected among *E. albifrons*, *E. rubriventer*, *H. occidentalis*, and *I. indri* (all $P > 0.25$).

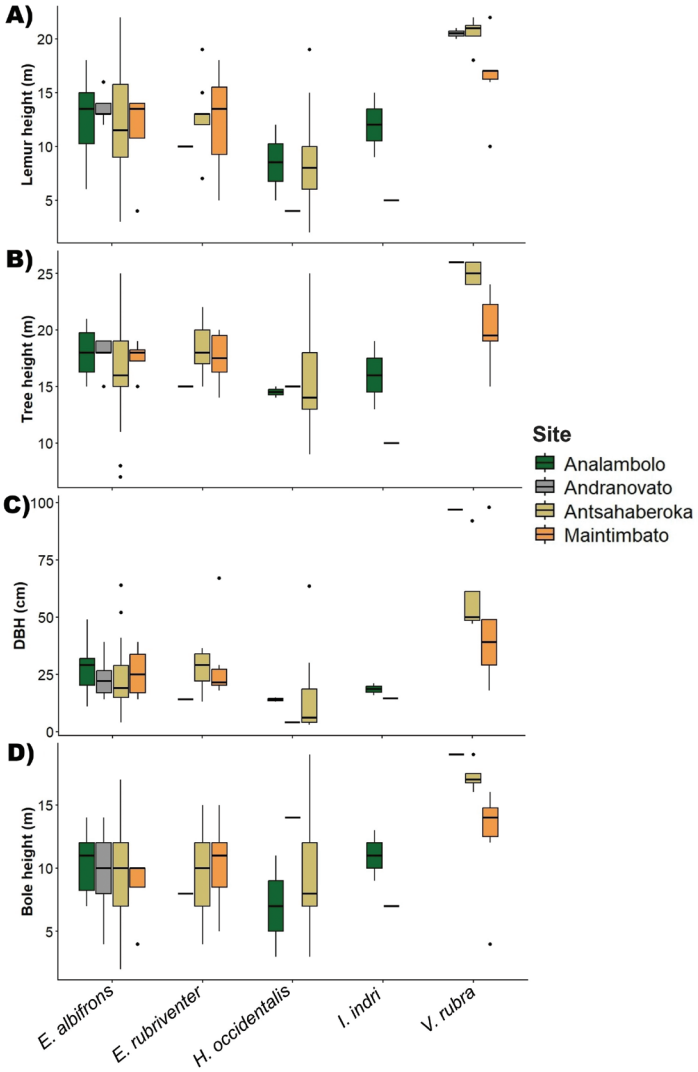

Figure 3. Comparison of lemur species microhabitat preferences across study sites in Parc Naturel Makira: **A**) vertical distribution (lemur height above ground), **B**) tree height, **C**) tree DBH, and **D**) bole height. Boxes represent interquartile ranges; horizontal lines indicate medians; whiskers extend to 1.5 × IQR.

Discussion

This study provides new ecological data on lemur communities in the Besariaka sector of the Parc Naturel Makira, one of the largest and most biologically important protected areas in northeastern Madagascar. Our surveys confirmed 10 species, five detected by line-transect surveys and five nocturnal species recorded exclusively by arboreal camera traps, contributing to a growing body of evidence documenting the rich lemur fauna of this understudied region.

Eulemur albifrons was the most frequently encountered species across all sites, consistent with its characterization as a relatively flexible species capable of persisting across a range of habitat conditions in northeastern Madagascar (Sawyer *et al*., 2017; Eppley *et al*., 2024). Its dominance at Analambolo, the most remote and least disturbed site, may reflect a preference for intact forest structure and/or lower hunting pressure, although its broad distribution across all four sites indicates considerable ecological flexibility. In contrast, *Varecia rubra* (all individuals identified in this study; no evidence of hybrid morphology with *V. variegata*) is a Critically Endangered species with strict nutritional requirements and a specialized frugivorous diet (Vasey, 2000), and it showed higher encounter rates at Maintimbato and Antsahaberoka, where tree density was greatest. This pattern may reflect an association with structurally complex forest conditions to support its energetically demanding, large-bodied lifestyle; however, without direct measures of resource availability (e.g., fruiting phenology), causal inference remains limited (Rafidimanana *et al*., 2017; Mittermeier *et al*., 2023).

Camera trap results revealed a diverse nocturnal community at Antsahaberoka that would have been missed by diurnal line-transect surveys alone. The capture of *Allocebus trichotis*, an Endangered and cryptic nocturnal species, is particularly noteworthy, as this species has a restricted known range and is infrequently recorded (Mittermeier *et al*., 2023). The high capture rates of *Lepilemur seali* (78 events) and *E*. *albifrons* (79 events) confirm the utility of arboreal camera traps for both nocturnal and cathemeral species in this habitat (Chen *et al*., 2021; Wampole *et al*., 2022). These findings further support the complementary value of arboreal camera trapping for detecting cryptic and nocturnal taxa that are underrepresented in traditional survey methods.

Habitat structure differed significantly among sites, with vegetation at Antsahaberoka characterized by shorter trees and lower bole heights than the other sites. Despite these structural differences, encounter rates did not differ significantly among sites, suggesting broad tolerance to habitat variation among the detected species. However, the distinct microhabitat preferences we document, particularly the strong vertical niche separation between *V*. *rubra* in the upper canopy and *H*. *occidentalis* in lower strata, indicate that species rely on specific structural features within their habitat range. The consistent use of large, tall trees by *V*. *rubra* parallels patterns observed for this genus in Masoala and other humid forests (Rafidimanana *et al*., 2017; Ratsisetraina, 2013; Ratsisetraina *et al*., 2023; Andriamahaihavana *et al*., 2026) and underscores the importance of maintaining old-growth forest attributes, including large-diameter trees, as essential resources for this Critically Endangered species.

Vertical niche partitioning among the diurnal and cathemeral species followed patterns documented in other Malagasy humid forests (Fenosoa *et al*., 2018; Tinsman *et al*., 2022), with larger-bodied species occupying higher strata and using larger-diameter trees (Andriamahaihavana *et al*., 2026). The separation between *V*. *rubra* and the remaining species was particularly pronounced across all microhabitat variables, reflecting its specialization for upper-canopy use (Vasey, 2000; Andriamahaihavana *et al*., 2026). These patterns of resource partitioning likely reduce interspecific competition and promote coexistence in structurally diverse forests. The absence of significant interspecific differences in microhabitat use among *E*. *albifrons*, *E*. *rubriventer*, and *I*. *indri* suggests that these species may rely on resource partitioning through other axes, such as dietary specialization, temporal activity patterns, or spatial ranging, rather than vertical segregation.

Andranovato was the most disturbed site, with five types of anthropogenic disturbance totaling 13 recorded events, including cut trees, charcoal production, and direct human presence, despite its relatively remote location (~3.5 km from the nearest village). This high level of disturbance may contribute to lower encounter rates, particularly for *E*. *albifrons*, which is also one of the most heavily hunted species in northeastern Madagascar (Borgerson *et al*., 2022; Jenkins *et al*., 2011). Analambolo, the most remote site (>14 km from the nearest village), showed no disturbance evidence and harbored the highest encounter rates for *E*. *albifrons*, reinforcing the importance of remoteness and low human access as a buffer against anthropogenic pressure in Makira (Eppley *et al*., 2024). However, given the lack of significant differences among the sites and absence of formal modeling of disturbance effects, this relationship should be interpreted as tentative.

Several lemur species known from the Parc Naturel Makira were not detected during this study, including *Propithecus candidus*, *V*. *variegata*, and *Phaner furcifer* (Brook *et al*., 2019; Mittermeier *et al*., 2023). Their apparent absence in the Besariaka sector may reflect naturally low population densities or patchy distributions within Makira. Although *Daubentonia madagascariensis* was not directly observed, feeding traces attributable to this species were recorded at all sites, suggesting its presence within the study area.

Of particular interest was the observation at Maintimbato that may represent the Critically Endangered *Prolemur simus*. During prior survey efforts in this region, a group of three individuals was reportedly observed by an experienced field team, including personnel familiar with the species, suggesting the possibility of occurrence in northern Makira. However, subsequent systematic surveys, including extensive line-transect effort and semi-arboreal camera trapping conducted across Maintimbato and adjacent sites, did not yield any direct detections of *P*. *simus*, despite targeted search efforts. Indirect evidence, including putative feeding remains, latrine sites, and local ecological knowledge indicating the recognition of the species, was recorded at several sites, particularly Antsahaberoka and Maintimbato. However, these indicators remain inconclusive in the absence of genetic or photographic confirmation, particularly given the potential for confusion with other bamboo lemur taxa such as

Hapalemur occidentalis. If confirmed, the presence of *P. simus* in the Besariaka region would represent a substantial northern range extension (Dolch *et al*., 2010) and a potentially important population within Madagascar's largest remaining contiguous moist evergreen forest block. Nevertheless, given the lack of direct evidence from repeated surveys, we treat the occurrence of *P. simus* in this study as provisional.

Our results collectively underscore the conservation importance of Makira's forests for a diverse and threatened lemur assemblage. These findings align with broader evidence that northeastern Madagascar represents both a biodiversity stronghold and a region where conservation success depends on integrating ecological monitoring with local management and livelihood strategies (Eppley *et al*., 2024). The detection of 10 lemur species, including several Critically Endangered and Endangered taxa from a relatively limited survey effort, highlights the need for continued and expanded ecological monitoring across this vast protected area. The combination of line-transect surveys and arboreal camera trapping proved highly complementary, revealing species and behaviors that would have been overlooked by either method alone. Ongoing and repeated surveys using both methods will be essential to track population trends, particularly for rare or cryptic species such as *Allocebus trichotis* and *I. indri*. Future research should also address fine-scale dietary ecology and movement patterns of *V. rubra* and *E. albifrons*, as well as the occurrence of *P. simus* and other range-restricted taxa within the park.

Conclusion

This study provides baseline, site-level ecological data on lemur communities in the Besariaka sector of the Parc Naturel Makira. We confirmed the presence of 10 lemur species, including two Critically Endangered (*I. indri* and *V. rubra*), and documented significant differences in forest structure and clear patterns of microhabitat use among species, consistent with vertical niche partitioning. Despite variation in disturbance and habitat structure, encounter rates did not vary significantly among sites, suggesting that the species detected may exhibit a degree of tolerance to the range of conditions surveyed, or alternatively that differences were not detectable given the sampling design. The combined use of standardized line-transect surveys and arboreal camera trapping proved effective for documenting both diurnal and nocturnal lemur communities, highlighting the importance of multi-method approaches for comprehensive biodiversity assessments. From a conservation perspective, our results emphasize the importance of maintaining large, contiguous areas of structurally complex forests, including large trees and intact canopy strata, which support species with specialized habitat requirements. Furthermore, strengthening community-based protection measures, particularly in areas with increasing anthropogenic access is crucial for preserving forest health. These findings provide a valuable foundation for long-term monitoring and adaptive management strategies within one of Madagascar's most important protected landscapes.

Acknowledgements

We thank the Republic of Madagascar, Madagascar National Parks, Wildlife Conservation Society Madagascar, the Vondron'olona Ifotony (VOI; local community-based forest management association) Besariaka, and all of our local field assistants for their valuable support. We are also grateful to Patrick Rafalimanana, Jörg U. Ganzhorn, and Steven M. Goodman for their helpful comments on earlier versions of this manuscript. We also thank Re:wild, the Margot Marsh Biodiversity Fund, the San Diego Zoo Wildlife Alliance, and Lemur Conservation Foundation for their generous financial support, and to Mention Anthropobiologie et Développement Durable (MADD), Université d'Antananarivo, for administrative and logistical help. We obtained all necessary in-country permissions for this research through the Ministère de l'Environnement et du Développement Durable (Permit No. 52/21/MEDD/SG/DGGE/DAPRNE/SCBE.Re on 21 April 2021 and 324/22/MEDD/SG/DGGE/DAPRNE/SCBE.Re on 28 October 2022).

References

Andriamahaihavana, A., Rakotomalala, Z., Rasamisoa, D. C., Ganzhorn, J. U., Gibson, D., Mogilewsky, M. S., Owen, M. A., Vasey, N. & Eppley, T. M. 2026. Lemur distribution in relation to treefall canopy gaps in Masoala National Park, northeast Madagascar. *American Journal of Primatology,* 88(6), e70180.

Andrianambinina, F. O. D., Ganzhorn, J. U., Waeber, P. O. & Wilmé, L. 2025. Complex deforestation patterns in and around the protected areas of Madagascar from 2015 to 2023. *Land*, 14: 698.

Atsalis, S. 1999. Diet of the brown mouse lemur (*Microcebus rufus*) in Ranomafana National Park, Madagascar. *International Journal of Primatology*, 20: 193-229.

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 Jr, E. E. & Golden, C. D. 2022. A national-level assessment of lemur hunting pressure in Madagascar. *International Journal of Primatology*, 43: 92-113.

Brook, C. E., Herrera, J. P., Borgerson, C., Fuller, E. C., Andriamahazoarivosoa, P., Rasolofoniaina, B. J. R., Randrianasolo, J. L. R. R., Rakotondrafarasata, Z. R. E., Randriamady, H. J., Dobson, A. P. & Golden, C. D. 2019. Population viability and harvest sustainability for Madagascar lemurs. *Conservation Biology*, 33 (1): 99-111.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. & Thomas, L. 2001. *Introduction to distance sampling.* Oxford University Press, Oxford.

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: 833-847.

Chen, D. M., Narváez-Torres, P. R., Tiafinjaka, O., Farris, Z. J., Rasoloharijaona, S., Louis Jr, 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: e23312.

digiKam Development Team. 2026. *digiKam* (Version 8.3.0) [Computer software]. https://www.digikam.org

Dolch, R., Patel, E. R., Ratsimbazafy, J. H., Golden, C. D., Ratolojanahary, T., Rafalimandimby, J. & Fiely, J. L. 2010. Distribution of *Prolemur simus* north of the Mangoro-Nosivolo River – how far north do we really have to look? *Lemur News*, 15: 32-34.

Dunn, O. J. 1964. Multiple comparisons using rank sums. *Technometrics*, 6: 241-252.

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.

Eppley, T. M., Hoeks, S., Chapman, C. A., Ganzhorn, J. U., Hall, K., Owen, M. A., Adams, D. B., Allgas, N., Amato, K. R., Andriamahaihavana, A., Aristizabal, J. F., Baden, A. L., Balestri, M., Barnett, A. A., Bicca-Marques, J. C., Bowler, M., Boyle, S. A., Brown, M., Caillaud, D., Calegaro-Marques, C., Campbell, C. J., Campera, M., Campos, F. A., Cardoso, T. S., Carretero-Pinzón, X., Champion, J., Chaves, Ó. M., Chen-Kraus, C., Colquhoun, I. C., Dean, B., Dubrueil, C., Ellis, K. M., Erhart, E. M., Evans, K. J. E., Fedigan, L. M., Felton, A. M., Ferreira, R. G., Fichtel, C., Fonseca, M. L., Fontes, I. P., Fortes, V. B., Fumian, I., Gibson, D., Guzzo, G. B., Hartwell, K. S., Heymann, E. W., Hilário, R. R., Holmes, S. M., Irwin, M. T., Johnson, S. E., Kappeler, P. M., Kelley, E. A., King, T., Knogge, C., Koch, F., Kowalewski, M. M., Lange, L. R., Lauterbur, M. E., Louis Jr, E. E., Lutz, M. C., Martínez, J., Melin, A. D., de Melo, F. R., Mihaminekena, T. H., Mogilewsky, M. S., Moreira, L. S., Moura, L. A., Muhle, C. B., Nagy-Reis, M. B., Norconk, M. A., Notman, H., O'Mara, M. T., Ostner, J., Patel, E. R., Pavelka, M. S. M., Pinacho-Guendulain, B., Porter, L. M., Pozo-Montuy, G., Raboy, B. E., Rahalinarivo, V., Raharinoro, N. A., Rakotomalala, Z., Ramos-Fernández, G., Rasamisoa, D. C., Ratsimbazafy, J., Ravaloharimanitra, M., Razafindramanana, J., Razanaparany, T. P., Righini, N., Robson, N. M., da Rosa Gonçalves, J., Sanamo, J., Santacruz, N., Sato, H., Sauther, M. L., Scarry, C. J., Serio-Silva, J. C., Shanee, S., de Souza Lins, P. G. A., Smith, A. C., Smith Aguilar, S. E., Souza-Alves, J. P., Stavis, V. K., Steffens, K. J. E., Stone, A. I., Strier, K. B., Suarez, S. A., Talebi, M., Tecot, S. R., Tujague, M. P., Valenta, K., Van Belle, S., Vasey, N., Wallace, R. B., Welch, G., Wright, P. C., Donati, G. & Santini, L. 2022. Factors influencing terrestriality in primates of the Americas and Madagascar. *Proceedings of the National Academy of Sciences*, 119: e2121105119.

Eppley, T. M., Borgerson, C., Patel, E. R., Herrera, J. P., Kirkby, A. E., Golden, C. D., Andriamahaihavana, A., Andrianandrasana, L., Bóveda, A., Gibson, D., Jaofeno, L. J., Rakotondrasoa, F., Ramahaleo, T. A., Rasamisoa, D. C., Ratelolahy, F., Razafindramanana, J., Spira, C., Welch, C. & Vasey, N. 2024. A habitat stronghold on the precipice: A call-to-action for supporting lemur conservation in northeast Madagascar. *American Journal of Primatology*, 86: e23483.

Esri. 2024. *World Imagery* [Basemap]. https://www.arcgis.com/home/item.html?id=10df2279f9684e4a9f6a7f08febac2a9

Fashing, P. J. & Cords, M. 2000. Diurnal primate densities and biomass in the Kakamega Forest. *American Journal of Primatology*, 50: 139-152.

Fenosoa, Z. S. E., Sawyer, R. M., Andrianarimisa, A., Razafindraibe, H., Rakotomanana, H. & Donati, G. 2018. Height and support use of three sympatric nocturnal lemurs in different habitats varying in disturbance on the Masoala Peninsula. *Lemur News*, 21: 39-43.

Ganzhorn, J. U., Rakotondranary, J. & Ratovonamana, Y. R. 2011. Habitat description and phenology. In *Field and laboratory methods in primatology*, eds. J. M. Setchell & D. J. Curtis, pp. 51-68. Cambridge University Press, Cambridge.

Ganzhorn, J. U., Andriambeloson, J. B., Atsalis, S., Behrendt, L. M., Blanco, M. B., Bollen, A., Carrière, S. M., Chikhi, L., Dammhahn, M., Donati, G., Eppley, T. M., Ernest, R., Giertz, P., Goodman, S. M., Hending, D., Holst, F., Hyde Roberts, S., Irwin, M. T., Lahann, P., Louis Jr, E. E., Radespiel, U., Rakotondranary, S. J., Ramanamanjato, J. B., Ramananjato, V., Randriatafika, F., Ratovonamana, Y. R., Razafindratsima, O. H., Salmona, J., Schwab, D. & Tsagnangara, C. 2024. Facilitated forest restoration using pioneer seed dispersers in Madagascar: The example of *Microcebus* spp. *Land*, 13: 1971.

Gautier, L. C., Chatelain, C. & Spichiger, R. 1994. Presentation of a relevé method for vegetation

studies based on high-resolution satellite imagery. In *Proceedings of the XIIIth plenary meeting of AETFAT*, eds. J. H. Seyani & A. C. Chikuni, pp. 1339-1350. National Herbarium and Botanic Gardens of Malawi, Zomba, Malawi.

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J., Laurance, W. F., Lovejoy, T. E. & Sodhi, N. S. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 478: 378-381.

Giertz, P., Rakotondranary, S. J., Ratovonamana, Y. R., Andriaharimalala, T., Blanco, M. B., Bohr, Y. E. M., Fadeeva, A., Godfrey, L. R., Jöhrens, A. K., Kuhn, L., Rasoazanabary, E. & Ganzhorn, J. U. In press. Variable and seemingly invariant traits of *Microcebus griseorufus* in Madagascar's variable environments. *Folia Primatologica.*

Goodman, S. M., Raherilalao, M. J. & Wohlhauser, S. (eds.). 2018. *The terrestrial protected areas of Madagascar: Their history, description, and biota*. Volume II. Association Vahatra, Antananarivo.

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.

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 (5): 1091-1108.

IUCN. 2025. *The IUCN Red List of Threatened Species*. https://www.iucnredlist.org/. Accessed March 2026.

Jenkins, R. K. B., Keane, A., Rakotoarivelo, A. R., Rakotomboavonjy, V., Randrianandrianina, F. H., Razafimanahaka, H. J., Ralaiarimalala, S. R. & Jones, J. P. G. 2011. Analysis of patterns of bushmeat consumption reveals extensive exploitation of protected species in eastern Madagascar. *PLos One*, 6 (12): e27570.

Kappeler, P. M., Markolf, M., Rasoloarison, R. M., Fichtel, C. & Durbin, J. 2022. Complex social and political factors threaten the world's smallest primate with extinction. *Conservation Science and Practice*, 4: e12776.

Knoop, S., Chikhi, L. & Salmona, J. 2018. Mouse lemurs' use of degraded habitat: A review of the literature. *Lemur News*, 21: 20-31.

Laurance, W. F., Sayer, J. & Cassman, K. G. 2014. Agricultural expansion and its impacts on tropical nature. *Trends in Ecology & Evolution*, 29 (2): 107-116.

Lehman, S. M., Rajaonson, A. & Day, S. 2006. Edge effects and their influence on lemur density and distribution in southeast Madagascar. *American Journal of Physical Anthropology*, 129 (2): 232-241.

Marshall, A. R., Lovett, J. C. & White, P. C. 2008. Selection of line-transect methods for estimating the density of group-living animals. *American Journal of Primatology*, 70 (5): 452-462.

Meyler, S. V., Salmona, J., Ibouroi, M. T., Besolo, A., Rasolondraibe, E., Radespiel, U., Rabarivola, C. & Chikhi, L. 2012. Density estimates of two endangered nocturnal lemur species from northern Madagascar. *American Journal of Primatology*, 74 (5): 414-422.

Microsoft Corporation. 2026. *Microsoft Excel* [Computer software]. https://www.microsoft.com/en-us/microsoft-365/excel

Mitchell, K. 2010. Quantitative analysis by the point-centered quarter method. ArXiv:1010.3303.

Mittermeier, R. A., Reuter, K. E., Rylands, A. B., Louis Jr, E. E., Ratsimbazafy, J. H., Rene de Roland, L.-A., Langrand, O., 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. 2023. *Lemurs of Madagascar*, 5th ed. Re:wild / Lynx Edicions, Barcelona.

Murphy, A. J., Farris, Z. J., Karpanty, S., Ratelolahy, F. & Kelly, M. J. 2016. Estimating encounter rates and densities of three lemur species in northeastern Madagascar. *International Journal of Primatology*, 37 (3): 371-389.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature*, 403: 853-858.

Nekaris, K. A. I., Pambudi, J. A. A., Susanto, D., Ahmad, R. D. & Nijman, V. 2014. Densities, distribution and detectability of a small nocturnal primate (Javan slow loris) in a montane rainforest. *Endangered Species Research*, 24: 95-103.

Niedballa, J., Sollmann, R., Courtiol, A. & Wilting, A. 2016. camtrapR: An R package for efficient camera trap data management. *Methods in Ecology and Evolution*, 7 (12): 1457-1462.

Posit Team. 2025. *RStudio: Integrated development environment for R.* Posit Software, PBC, Boston. https://posit.co/

QGIS Association. 2024. *QGIS Geographic Information System* (Version 3.34) [Computer software]. https://www.qgis.org

R Core Team. 2025. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. https://www.r-project.org/

Rafidimanana, D. V., Holmes, S. M., Johnson, S. E., Louis Jr, E. E. & Rakouth, B. 2017. Relationship between vegetation characteristics and the presence of lemurs: *Varecia variegata, Eulemur rubriventer,* and *Eulemur rufifrons* in Kianjavato forest fragments. *Lemur News*, 20: 15-19.

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., Birkinshaw, C., Cable, S., Canales, N. A., Carrillo, J. D., Clegg, R., Clubbe, C., Crottini, A.,

Damasco, G., Dhanda, S., Edler, D., Farooq, H., de Lima Ferreira, P., Fisher, B. L., Forest, F., Gardiner, L. M., Goodman, S. M., Grace, O. M., Guedes, T. B., Hackel, J., Henniges, M. C., Hill, R., Lehmann, C. E. R., Lowry, P. P. Jr., Marline, L., Matos-Maraví, P., Moat, J., Neves, B., Nogueira, M. G. C., Onstein, R. E., Papadopulos, A. S. T., Perez-Escobar, O. A., Phillipson, P. B., Pironon, S., Przelomska, N. A. S., Rabarimanarivo, M., Rabehevitra, D., Raharimampionona, J., Rajaonary, F., Rajaovelona, L. R., Rakotoarinivo, M., Rakotoarisoa, A. A., Rakotoarisoa, S. E., Rakotomalala, H. N., Rakotonasolo, F., Ralaiveloarisoa, B. A., Ramirez-Herranz, M., Randriamamonjy, J. E. N., Randrianasolo, V., Rasolohery, A., Ratsifandrihamanana, A. N., Ravololomanana, N., Razafiniary, V., Razanajatovo, H., Razanatsoa, E., Rivers, M., Silvestro, D., Testo, W., Torres Jiménez, M. F., Walker, K., Walker, B. E., Wilkin, P., Williams, J., Ziegler, T., Zizka, A. & Antonelli, A. 2022. Madagascar's extraordinary biodiversity: Threats and opportunities. *Science*, 378: eadf1466.

Ramananjato, V. 2025. Contribution of small nocturnal lemurs to seed dispersal in Madagascar: A review. *Biotropica*, 57 (1): e13379.

Ratsisetraina, R. I. 2013. Population recovery of two diurnal lemur species, *Varecia rubra* and *Eulemur albifrons*, following cyclonic disturbance in Masoala National Park, Madagascar. *Lemur News*, 17: 27-32.

Ratsisetraina, R. I., Gray, C., Ratsirarson, J., Ratsimbazafy, J. H., Birkinshaw, C. & Andrianarimisa, A. 2023. Responses of *Varecia rubra* to a frequently disturbed habitat by cyclones in Masoala National Park, Madagascar. *Lemur News,* 23: 69-74.

Ross, C. & Reeve, N. 2011. Survey and census methods: Population distribution and density. In *Field and laboratory methods in primatology,* eds. J. M. Setchell & D. J. Curtis, pp. 111-131. Cambridge University Press, Cambridge.

Ross, P. H., Patel, E. R., Ferguson, B., Ravelijaona, N. R., Raoloniana, G. I., Wampole, E. M., Gerber, B. D. & Farris, Z. J. 2020. Assessment of the threatened carnivore community in the recently expanded rainforest protected area Anjanaharibe-Sud Special Reserve, Madagascar. *Endangered Species Research*, 43: 89-98.

Sawyer, R. M., Fenosoa, Z. S. E., Andrianarimisa, A. & Donati, G. 2017. The effect of habitat disturbance on the abundance of nocturnal lemur species on the Masoala Peninsula, northeastern Madagascar. *Primates*, 58 (2): 187-197.

Schüßler, D., Blanco, M. B., Salmona, J., Poelstra, J., Andriambeloson, J. B., Miller, A., Randrianambinina, B., Rasolofoson, D. W., Mantilla-Contreras, J., Chikhi, L., Louis Jr, E. E., Yoder, A. D. & Radespiel, U. 2020. Ecology and morphology of mouse lemurs (*Microcebus* spp.) in a hotspot of microendemism in northeastern Madagascar, with the description of a new species. *American Journal of Primatology*, 82 (9): e23180.

Tinsman, J., Volampeno, S., Ganas-Swaray, J., Gann, D., Andrianirina, N., Chamizo, M., Ralazampirenena, C., Ranaivoarisoa, J. F., Ravaoarisoa, H., Rivero, J., Zamora, A. & Gomes, C. M. 2022. Habitat use by the island lemurs of Nosy Be, Madagascar. *American Journal of Primatology*, 84: e23362.

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

Vasey, N. 2000. Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*: Interspecific patterns. *American Journal of Physical Anthropology*, 112: 411-431.

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

Wampole, E. M., Gerber, B. D., Farris, Z. J., Razafimahaimodison, J. C., Andrianarisoa, M. H., Ralazampirenena, C. J., Wright, P. C., Rasamisoa, D. C., Gibson, D., Tobler, M. W., Eppley, T. M., Vasey, N., Johnson, S. E., Filla, C., Valenta, K., Ross, P., Murphy, A., Karpanty, S. M., Kelly, M. J., Anderson, C., Cardinal, C., Donati, G., Razafy, P., Rafaliarison, R., Rasambainarivo, F., Razafindramanana, J., Merson, S. D. & Larney, E. 2022. Madagascar terrestrial camera survey database 2021: A collation of protected forest camera surveys from 2007-2021. *Ecology*, 103 (6): e3687.