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RESEARCH ARTICLE

Lemur Distribution in Relation to Treefall Canopy Gaps in Masoala National Park, Northeast Madagascar

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ABSTRACT

Madagascar is a biodiversity hotspot facing increasing anthropogenic pressures, with 95% of lemur species threatened with extinction. In addition to habitat loss and hunting, cyclones create treefall gaps with unknown effects on arboreal species. We examined the effect of Cyclone Eliakim, which struck Masoala National Park in March 2018 with sustained wind speeds reaching 151 km/h. We assessed whether lemur densities and their microhabitat niches changed in relation to the cyclone, and whether their distributions were related to treefall gaps. We conducted 110.42 km of transect walks for diurnal and 86.93 km for nocturnal lemurs between 2017 and 2022 in Andranobe, Masoala National Park, a region regularly hit by cyclones. Microhabitat data were recorded for each observation, and distance to the nearest canopy gap was used as a measure of association with treefall gaps. Densities of *Varecia rubra, Eulemur albifrons*, *Avahi mooreorum*, *Lepilemur scottorum*, and *Microcebus* sp. did not decline after the cyclone. Species niche separation was strongest directly after the cyclone (suggesting intensified competition over limited resources) and relaxed progressively as the forest recovered. Gap size increased after the cyclone and decreased by 59.9% 4.5 years later, indicating progressive canopy closure. Large diurnal lemurs were positively associated with gaps > 150 m^2, likely reflecting increased food availability in sun-exposed areas. Small nocturnal lemurs were positively associated with small gaps (< 150 m^2) but avoided larger gaps, possibly due to aerial predator risk. These data aid our understanding of species interactions and ecosystem dynamics under climate-driven habitat change.

1 | Introduction

Climate change is a major threat to various biota across the globe (Nunez et al. 2019; Trew and Maclean 2021). Increasing sea surface temperature is leading to more intense tropical cyclones, often with negative impacts on terrestrial systems (Lin et al. 2020; Murakami et al. 2020). As disturbances of this kind are likely to become more severe in the future, understanding species responses to these events is important (Korstjens and Hillyer 2016).

Among the endemic fauna of Madagascar, there are currently 112 lemur taxa (i.e., species and subspecies) distributed throughout Madagascar's remaining forest habitats, 95% of which are threatened with extinction, with 31% listed as Critically Endangered (IUCN 2023; Mittermeier et al. 2023; Ralimanana et al. 2022). Lemur responses to anthropogenic threats have been studied for some time (Gardner 2009), while more recent studies have also investigated effects of gradual climate changes, weather variability, and cyclone effects on distribution patterns (Behie et al. 2024; Brown and Yoder 2015; Ratovonamana et al. 2024), population dynamics (Dunham et al. 2011; Ozgul et al. 2023), and behavior (Axel et al. 2024; Dinsmore et al. 2021; Paige et al. 2024).

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Cyclones, as part of Madagascar's hypervariable climate, are likely to have played a major role in the evolution of Madagascar's biota (Dewar and Richard 2007; Wright 1999), and are stochastic though frequent phenomena in Madagascar, with up to 10 cyclone making landfall per year (Fitchett and Grab 2014; De Gouvenain and Silander 2003). The intense and sometimes sustained winds from cyclones can strip plants of fruits and leaves and cause widespread destruction, contributing to significant canopy gaps caused by fallen branches and trees (Birkinshaw and Randrianjanahary 2007; Mogilewsky 2020; Paige et al. 2024). Large-scale effects of forest openings may impact primates in many ways, including increased predation pressure (Enstam 2007) and reduced reproduction in or after years with cyclones because of sudden drops in food availability (Dunham et al. 2011), resulting in population decline after cyclones (Korstjens and Hillyer 2016; Ratsisetraina 2013). Yet, other studies did not report any effect of cyclones on population size, suggesting lemurs are resilient to cyclone damage through behavioral flexibility, utilizing the altered environment in the weeks and months following the cyclone to some extent (Axel et al. 2024; Behie et al. 2024; Dinsmore et al. 2021). Understanding these apparently different responses might be facilitated by investigating not only the phenomenon in general, but also by quantifying cyclone effects in a standardized way and investigating the impacts of single, measurable components.

Treefall gaps might represent such a component that is relevant for species interactions and forest dynamics (Gorgens et al. 2023; Hossain and Olson 2023). Increased penetration of sun into the forest contributes to habitat heterogeneity (Schnitzer and Carson 2001). The resulting habitat mosaic is associated with varied light intensity, soil temperature, humidity, and the successful germination of seedlings (Whitmore 1998). Heliophile trees regenerate in canopy gaps, and fruit and leaf production, and also insect abundance, increase at the edges (Ganzhorn 1995a, 1995b; Gorgens et al. 2023; Hossain and Olson 2023; Houle et al. 2007; Mogilewsky 2020; Takahashi et al. 2015). Thus, food availability should be higher at the edges of canopy gaps than in the forest interior, because canopy gaps increase light availability, which can promote fruiting of plants and enhance resource availability for frugivores (Takahashi et al. 2015). From an animal's perspective, following the principles of behavioral ecology, food patches warrant visitation only once they exceed a certain size that is positively related to the size and number of consumers (Krebs and Davies 1978). If so, the rewards of canopy gaps should increase with increasing size. Diet may also influence these patterns, with larger-bodied or group-living species benefiting most from larger patches.

In contrast, if canopy gaps were used by aerial predators to hunt, lemur species that are possible prey for owls and diurnal birds of prey (Goodman and Ganzhorn 2022) should avoid canopy gaps above a certain size. Thus, the response of lemur species to forest canopy gaps is expected to be modulated by gap size and to be more complex than the already complex interactions at forest edges (Lehman et al. 2006). For nocturnal lemurs, canopy gaps allow more moonlight to penetrate the forest and potentially illuminate individuals typically reliant on solitary crypticity, thereby increasing their vulnerability to predation (Prugh and Golden 2014). Apart from the food and predation aspects, spots with increased sun penetration offer opportunities for sun bathing, a very prominent component for behavioral thermoregulation, especially for the diurnal and cathemeral species (Donati et al. 2011).

With respect to forest and resource dynamics, food resources should be scarce immediately following a cyclone and recover as branches, leaves, and fruit regenerate in the gaps. These changes in resource availability should be reflected quickly by changes in microhabitat utilization or behavioral niche separation of consumer species. During a shortage of their preferred food, lemurs could expand their feeding niche and include food types not used previously. But this might lead to increased competition and lead to increased species separation. Once resources become abundant and animals cannot build up populations quickly to exploit the resources up to their carrying capacity, competition and species separation are relaxed (Begon et al. 2006; Connell 1978). Thus, the different dimensions of the ecological niche might change in opposite directions under the impact of disturbances. For primates, differences in the vertical distribution of species in the forest and the size of trees used have often been used as one tractable proxy for niche separation that can be measured easily (e.g., Charles-Dominique 1977; Vasey 2000). The way lemurs display changes along this niche dimension after disturbances caused by cyclones might offer an opportunity to generate a better understanding of constraints and adaptations in the evolution of lemurs.

With this background, we initiated a long-term study in 2017 to assess the effects of Cyclone Eliakim on lemur species at Andranobe Forest, located in the southwestern part of Masoala National Park (NP). Seasonally, the region is prone to cyclones with an average number of 1–2 cyclones per year (Behie et al. 2024; Birkinshaw and Randrianjanahary 2007; Fitchett and Grab 2014; Mogilewsky 2020), making it an area where stochastic cyclone effects can be studied with some probability of success.

Within the first year of our study, Cyclone Eliakim made landfall in this region, moving westward across the Masoala Peninsula. The eye of the storm passed within 5 km of the Andranobe study site with sustained wind speeds of 110 km/h and wind gusts reaching 151 km/h (Paige et al. 2024). No further cyclone made landfall in this region until the end of 2022. This allowed us to examine how lemur species responded to cyclone effects.

First, to address long-term consequences, we assessed whether lemur species densities declined from the time of the cyclone to 4 years afterwards. Second, we describe the changes in gap size over time and relate these changes to microhabitat utilization and niche separation of the five lemur species considered. Third, for the effects of canopy gaps, we hypothesized that all lemur species are positively associated with canopy gaps because of improved food quality and quantity at the edges. Thus, (i) the distance between lemurs and the nearest gap should decline with increasing gap size and (ii) smaller lemur species should be associated with smaller gaps than larger and group living species. Fourth, all lemur species considered here are preyed upon by aerial predators. Thus, lemurs should maintain some distance from gaps, where aerial predators can fly in for attack. As a result, lemurs should avoid gaps above a certain (yet unspecified) threshold. This effect should be more important for the smaller nocturnal species (*Avahi mooreorum*, *Lepilemur scottorum*, and *Microcebus* sp.) than for the larger *Varecia rubra* and *Eulemur albifrons*.

2 | Methods

2.1 | Study Site and Species

We conducted fieldwork in Andranobe (15°40′27″S, 49°57′08″E), a strictly enforced research zone covering approximately 150 ha in Masoala NP (Figure 1). Created in 1997, the park consists of 230,000 ha and is one of the largest protected areas in Madagascar (Goodman et al. 2018). It contains a variety of terrestrial habitats, including littoral forest, swamp, lowland to medium-altitude humid evergreen forest, and mangroves (Goodman et al. 2018). The Andranobe forest ranges from sea level to 260 m and has a closed canopy (Mogilewsky 2020; Sawyer et al. 2017; Vasey 2000). Within Masoala, the average annual precipitation ranges from 2200 to 7000 mm, and the average annual temperature ranges from 21°C to 24°C (Martinez 2010). Rainfall and phenology varied between-years, but the general pattern remained similar (Paige et al. 2024). At least 10 lemur species inhabit Masoala NP, including the Andranobe study area (Mittermeier et al. 2023; Table 1). The local species of *Microcebus* has not yet been identified (Fenosoa et al. 2018; Sawyer et al. 2017).

2.2 | Lemur Surveys

We conducted lemur surveys in the warm Austral summer from November 3, 2017 to January 9, 2018 (Period 1, prior to Cyclone Eliakim on March 16, 2018) and the cool Austral winter season from May 17 to July 12, 2018 (Period 2, after Cyclone Eliakim). For studying the effect of the cyclone on lemur population size, we pooled these two survey periods. We acknowledge that cyclones can cause mortality or induce short-term shifts in ranging behavior in primates (Korstjens and Hillyer 2016; Mittermeier et al. 2023; Ratsisetraina 2013). Because we did not follow individuals over time, it is impossible to quantify these effects in our study. Cyclones may also have negative effects on long-term survival and reproduction. However, except for *Eulemur* sp., and based on studies of congeneric species, the other lemur species are known to maintain relatively stable home ranges for years (Behie et al. 2024; Mittermeier et al. 2023), suggesting that population densities are unlikely to change drastically within a few weeks of the cyclone. Separating the survey periods would result in prohibitively small sample sizes for the calculation of densities. However, population changes should still be visible at the population level, with some lag time. The lemur surveys meant to assess long-term effects on the population level were conducted from April 26 to May 26, 2021 for the cool Austral winter (Period 3) and from December 1 to 22, 2022 for the warm Austral summer (Period 4). Again,

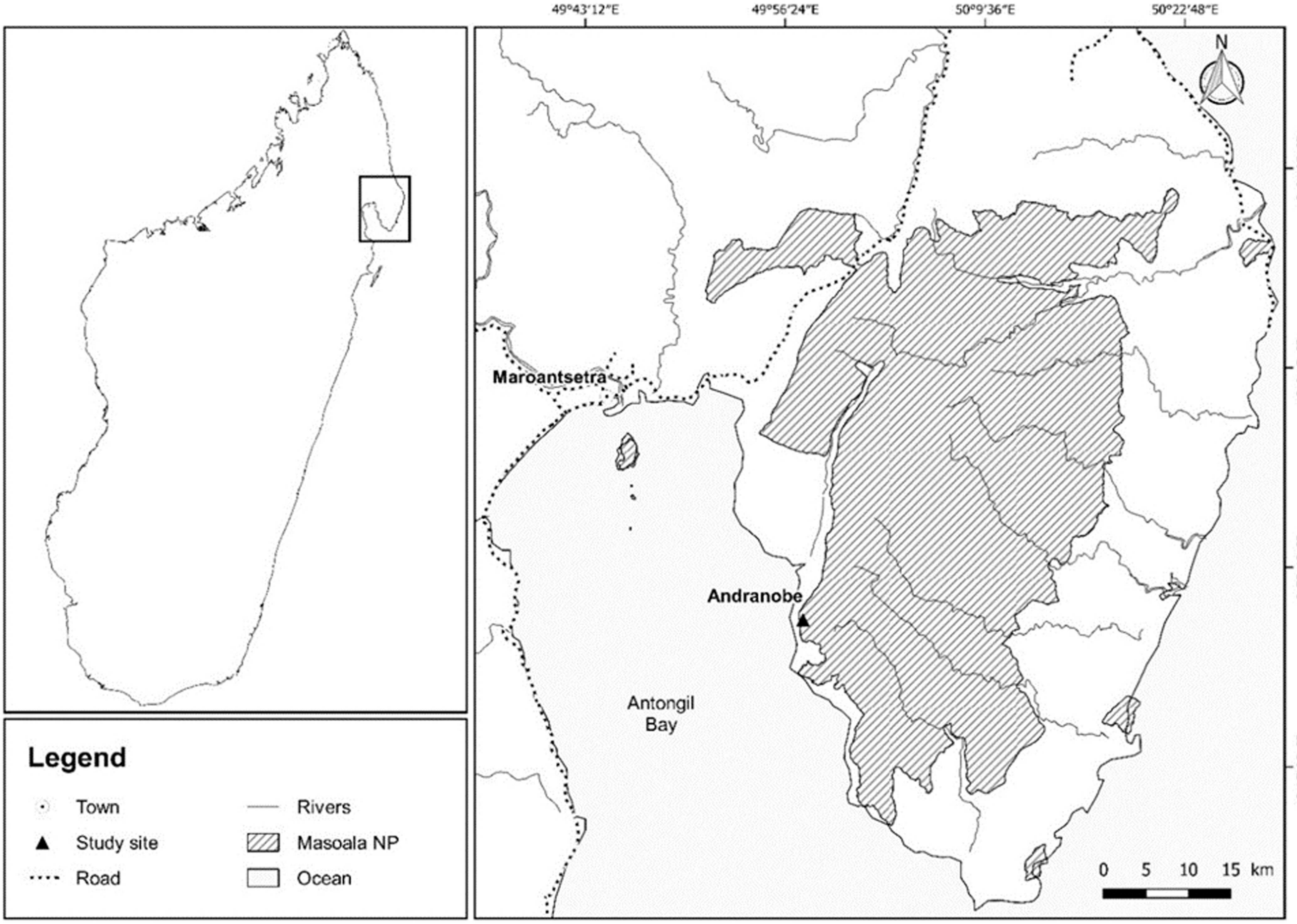

FIGURE 1 | Location of Andranobe, with respect to Madagascar, on the Masoala Peninsula and in the southwestern portion of the Masoala National Park.

TABLE 1 | Lemur species present within Andranobe in western Masoala National Park, northeastern Madagascar.

Species	Activity pattern	Diet	Body mass (g)	IUCN RL	Observed	2017–2018/2021–2022		
						n	**Encounter rate (ind./km)**	**Density (ind./km²)**
Eulemur albifrons	Cathemeral	Frugivore	1900	VU	Yes	335/196	6.49/3.33	206.81/300.98
Hapalemur occidentalis	Cathemeral	Folivore	1000	VU	Yes	3/3	0.06/0.05	—
Varecia rubra	Diurnal	Frugivore	3400	CR	Yes	107/173	2.07/2.94	31.80/40.33
Allocebus trichotis	Nocturnal	Frugivore Insectivore	75	EN	No	0/0	—	—
Avahi mooreorum	Nocturnal	Folivore	920	EN	Yes	39/61	1.63/0.97	86.98/81.54
Cheirogaleus major	Nocturnal	Frugivore Insectivore	400	VU	Yes	4/1	0.17/0.02	—
Daubentonia madagascariensis	Nocturnal	Frugivore Insectivore	2500	EN	Yes	0/1	0.00/0.02	—
Lepilemur scottorum	Nocturnal	Folivore	880	EN	Yes	48/166	2.01/2.63	76.92/148.02
Microcebus sp.	Nocturnal	Frugivore Insectivore	50	Unknown	Yes	23/26	0.96/0.41	—
Phaner furcifer	Nocturnal	Gummivore	—	EN	No	0/0	—	—

IUCN Red List (2023): CR = critically endangered, EN = endangered, and VU = vulnerable; *n* Total number of individuals observed; Density estimates were calculated in Distance 7.5 with $n \geq 30$ individuals observed; There are no published weights for *Phaner furcifer*.

these two periods were pooled for the lemur population analyses to match the first two surveys (each including surveys during the cold and the hot seasons). There were no additional cyclones after Eliakim.

We conducted surveys using the line-transect method of distance sampling with multiple observers (Buckland et al. 2010). We selected six preexisting transects (between 620 and 1210 m in length) for the survey to minimize disturbance. We marked the transect trails every 25 m with flagging tape. Survey teams comprised at least three observers, including at least one of us (AA, DCR, MSM, TME), and two local guides. We walked each transect with a 10-m distance between team members and a travel speed of approximately 0.5–1 km/h between 5:30 and 10:00 for the diurnal surveys, and 17:30 and 22:00 for nocturnal surveys. We carefully scanned both sides of the transect. Double counting the same individual during a single transect survey was unlikely, but we probably encountered the same individuals on the same transect during subsequent transect walks. This is an unresolved issue for density estimations, but should not affect our analyses of lemur microhabitat utilization. For the time being, the association between lemurs and gaps remains hypothetical and should be seen as a starting point for further studies, including individual follows.

We started transects at seasonally changing times, with diurnal surveys commencing after sunrise and nocturnal surveys commencing after sunset. Diurnal surveys were consistently conducted between 6:00 and 10:00 and nocturnal surveys between 18:00 and 22:00 throughout each season. Each transect was repeated two to seven times per season for each study period, resulting in total observation efforts of 110.42 and 86.93 km of diurnal and nocturnal surveys, respectively (Supporting Information S1: Table S1). We alternated the starting point on each transect repetition to reduce timing biases (Ross and Reeve 2011). We limited our surveys to periods without heavy rain.

We used high-lumen headlamps to sight nocturnal lemurs and strong handheld torches to confirm sightings and identify species. Each time a lemur was visually detected, we recorded the observation date, time (hour, minute), transect name, species, group size, GPS coordinates to an accuracy of < 5 m, estimated perpendicular distance from line transect to individual/group center, animal activity (e.g., feeding, resting, traveling). Animals heard but not seen were not included in the present analyses.

2.3 | Habitat Use and Gap Descriptions

To assess habitat use by lemurs, we measured tree DBH (diameter at breast height; cm), visually estimated tree height (m), and recorded the Malagasy vernacular name of the tree where the first individual was observed. We confirmed tree species identification in the field with a trained local botanist. The survey team was trained to estimate distances and heights using practice sessions before data collection. We recorded lemur heights using seven height categories. Height categories were: 0: on the ground; 1: > 0–5 m high; 2: > 5–10 m; 3: > 10–15 m; 4: > 15–20 m; 5: > 20–25 m; 6: > 25–30 m; 7: > 30 m. During nocturnal surveys, we marked the trees with flags where we observed the animals. The following day, we returned to the locations of lemur sightings, searched the vicinity for canopy gaps, and measured the distance to the nearest canopy gap. We recorded the distance between the closest canopy gap from the individual/group center with a measuring tape. We measured the length (=largest diameter of the gap) and width (perpendicular to the length) of gaps. For these measurements, we stood immediately under the leaves at the edge of the canopy gap. We used a Laser Technology, Inc. TruPulse 200 rangefinder to measure the opposite side of the gap. The TruPulse 200 automatically calculates true horizontal distance (distance parallel to ground), eliminating the need to do calculations based on the true distance between the instrument and the target. We calculated gap area using the formula for the area of an ellipse and the measured gap width and length: gap area $(\mathrm{m}^2) = (\pi^*\text{gap length}^*\text{gap width})/4$. Canopy gaps were defined as a hole in the canopy caused by the death of one or more trees, or branch(es), either through uprooting or snapping (Brokaw 1982). Most treefall canopy gaps occur during or immediately following a tropical storm or cyclone and are immediately evident (Birkinshaw and Randrianjanahary 2007). We did not know the age of most gaps; therefore, we did not classify gaps any further but simply used their size for all analyses.

2.4 | Encounter Rate and Population Density Estimate

We calculated mean encounter rates for each species by dividing the number of individuals observed by the total transect distance surveyed (n/km). We then calculated mean encounter rates for each species in the warm Austral summer and the cool Austral winter season and during the two study periods in 2017–2018 and 2021–2022. We also calculated encounter rates per lemur species for each survey period (Supporting Information S1; Table S3). To calculate population density for each lemur species, we use the conventional distance sampling (CDS) engine in Distance 7.5 software (Buckland et al. 2010).

2.5 | Statistical Analysis

We used each distinct encounter of a lemur or a group of lemurs as the unit for statistical analyses of habitat utilization. We restricted statistical analyses to *E. albifrons*, *Varecia rubra*, *A. mooreorum*, *L. scottorum*, and *Microcebus* sp. because sample sizes were too small for the other species. We used the Shapiro–Wilk test to assess normality of data. We computed Mann–Whitney U tests to compare any differences in encounter rates and densities between 2017/2018 and 2021/2022, treating each transect walk as an independent observation. To illustrate niche separation, we compared the height of the animals, tree DBH, distance of the lemur to the nearest canopy gap, and gap size among species using Kruskal–Wallis tests, with Dunn's post hoc tests performed to identify which species contributed to the significant result. We calculated effect sizes for Kruskal–Wallis test as $\text{eta}^2[H] = (H - k + 1)/(n - k)$; where H is the value obtained in the Kruskal–Wallis test, k is the number of groups, and n is the total number of observations (Tomczak and Tomczak 2014).

For the analyses of lemur associations with canopy gaps, we assigned lemur species to two distinct categories based on their predominant activity patterns: diurnal (*E. albifrons* and *V. rubra*) and nocturnal (*A. mooreorum*, *L. scottorum*, and *Microcebus* sp.). This way, we accounted for the limited sample size, which was further reduced when we restricted the analyses to specific size categories of the canopy gaps. Gap size was therefore analyzed sequentially using all gaps, gaps $> 50\,\mathrm{m}^2$, gaps $> 100\,\mathrm{m}^2$, and gaps $> 150\,\mathrm{m}^2$ (Supporting Information S1: Table S2). For interpretative purposes, gaps $> 150\,\mathrm{m}^2$ were considered large. We used linear, inverse, and polynomial (quadratic and cubic) regression models to describe the relationships between the distance of lemurs to the nearest canopy gap (dependent variable) and canopy gap size (independent variable). We chose the model based on effect size represented by R^2 (i.e., the model that explained the greatest amount of variation in the dependent variable).

We performed statistical analyses in RStudio (Version 2023.3.1.446; RStudio 2023), R (version 4.2.2; R Core Team 2022), and SPSS. We are aware of the discussion around binary thinking about significance and the need to report effect sizes. Yet, effect sizes (or “impacts”) are difficult to compare between tests, in particular between parametric and non-parametric tests. Therefore, we report the term “significant,” using a threshold of $\alpha = 0.05$, without implying that non-significant results indicate no effect.

3 | Results

During the first lemur surveys in 2017 and 2018, we recorded seven lemur species from four families with a total of 559 lemur sightings (445 sightings on diurnal surveys, 114 sightings on nocturnal surveys; Table 1). No hairy-eared dwarf lemurs (*Allocebus trichotis*), Masoala fork-marked lemurs (*Phaner furcifer*), or aye-ayes (*Daubentonia madagascariensis*) were observed, though feeding remains by *D. madagascariensis* were recorded. In 2021 and 2022, we observed eight lemur species from five families. In total, we observed 627 lemur sightings, including 372 sightings on diurnal surveys and 255 sightings on nocturnal surveys (Table 1). This time, we also observed *D. madagascariensis.*

3.1 | Population Density and Encounter Rate

For both study periods, we observed *E. albifrons* most frequently, with this species maintaining the highest density of all lemur taxa (Table 1), followed by *A. mooreorum* and *L. scottorum*. We recorded *Cheirogaleus major*, *D. madagascariensis*, *Hapalemur occidentalis*, and *Microcebus* sp. only a few times, indicating low densities. We found no evidence that encounter rates or densities differed between seasons or study periods (Table 1; Mann–Whitney U test: $p > 0.05$ for all comparisons).

3.2 | Habitat Use and Canopy Gaps

The mean height of lemurs observed on trees differed significantly among species (Kruskal–Wallis: $X^2 = 84.99$, $df = 4$, $p < 0.001$; Table 2; Supporting Information S1: Table S2). *V. rubra* was higher in the forest canopy than any other lemur species (Dunn's post hoc tests: $p \leq 0.001$ for the difference between *V. rubra* and all species). There was no evidence of height differences among the remaining species.

TABLE 2 | Height of lemurs in trees, DBH of trees used by lemurs, and distance to nearest forest canopy gap of the lemur species in Andranobe, western Masoala National Park.

	Diurnal/Large-bodied		**Nocturnal/Small-bodied**		
Lemur species	***E. albifrons***	***V. rubra***	***A. mooreorum***	***L. scottorum***	***Microcebus* sp.**
Number of encounters	87	70	63	174	49
Height (m)	5.0^{b}	10.5^{a}	5.0^{b}	3.0^{c}	4.0^{c}
	2.0 –27.0	2.0–28.0	2.0–20.0	1.0–25.0	1.0–16.0
DBH (cm)	30.0^{b}	65.0^{a}	16.0^{c}	20.0^{c}	11.0^{d}
	7.0–123.0	19.0–200.0	5.0–99.0	5.0–125.0	2.0–45.0
Distance (m) to nearest canopy gap	5.5	5.5	6.0	5.0	5.0
	0.0–14.0	0.0–29.0	0.0–40.0	0.0–25.0	0.0–16.0
Gap size (m^2)	21.2	25.1	28.3	23.6	21.2
	0.8–294.4	1.6–235.5	1.6–714.4	0.8–314.0	2.4–565.2

Note: Values are medians and ranges based on the number of encounters. Different superscripts indicate differences between species with $p < 0.05$ according to Dunn's post hoc tests.

The mean DBH of trees used by the lemurs was significantly different among species (Kruskal–Wallis: $X^2 = 140.06$, $df = 4$, $p < 0.001$; Table 2; Supporting Information S1: Table S2). *V. rubra* used trees with larger DBHs than any other species (*A. mooreorum*, $Z = -8.42$, $p < 0.001$; *E. albifrons*, $Z = -5.17$, $p < 0.001$; *L. scottorum*, $Z = -9.21$, $p < 0.001$; *Microcebus* sp., $Z = -10.35$, $p < 0.001$), and trees used by *Microcebus* sp. were smaller than those used by *E. albifrons* ($Z = 6.15$, $p < 0.001$), *L. scottorum* ($Z = 3.87$, $p < 0.001$), and *V. rubra* ($Z = -10.35$, $p < 0.001$).

The effect size of the vertical separation of the different lemur species increased after Cyclone Eliakim, indicating stronger microhabitat niche partitioning right after the cyclone. The effect decreased over time and became minimal 4 to 5 years after the cyclone (Table 3). The changes in effect sizes were similar for DBH but not as pronounced as with the vertical separation.

We measured 440 canopy gaps, ranging from 0.8 to 714.5 m^2, with a median of 23.5 m^2. The size distribution was skewed towards small gaps, resulting from broken branches rather than trees (Figure 2). Median gap size was 26.5 m^2 in the months (November 2017–January 2018) before Cyclone Eliakim, then increased to 31.4 m^2 in July 2018 after the cyclone, and became 59.9% smaller towards the end of the study in December 2022, about 4.5 years after the last cyclone. The size of gaps between the four study periods was not statistically significant (Kruskal–Wallis: $X^2 = 6.67$, $df = 3$, $p = 0.083$; Table 3).

Except for the solitary *Microcebus* sp., the group size of all lemur species declined immediately after Cyclone Eliakim and increased again over the next 4 years after the cyclone. This variation was evident to us when we calculated mean group sizes, but they are not reflected well by the median group size for the pair-living *L. scottorum* and *A. mooreorum*. They are significant for *A. mooreorum* (Kruskal–Wallis: $X^2 = 19.08$, $df = 3$, $p < 0.001$) and *E. albifrons* ($X^2 = 12.08$, $df = 3$, $p = 0.007$) (Table 3).

3.3 | Lemur Response to Forest Canopy Gap

We found no between-species differences in the distance to the nearest forest canopy gap or in the size of the nearest gap among the five species considered (Kruskal–Wallis; distance: $X^2 = 1.86$, $df = 4$, $p = 0.76$; gap size: $X^2 = 0.67$, $df = 4$, $p = 0.95$; Table 2). These variables were also not significantly different when we compared the two largest diurnal species with the three smaller, nocturnal species (Mann–Whitney *U* test: $z = 0.765$ and 0.480 for the distance between lemurs and gaps and gap size, respectively; $p > 0.05$ for both variables).

3.4 | Modeling the Relationship Between Gap Size and Lemur Proximity

For the diurnal species (*V. rubra* and *E. albifrons*), the distance to the nearest canopy gap was best described by a quadratic regression as distance between diurnal lemurs and gap size = 4.956 + 0.0428*gap size – 0.00024*gap size^2 ($R^2 = 0.042$, $F = 3.388$, $p = 0.036$; Figure 3a). Since we aimed to identify the size at which gaps become important for the lemurs, we sequentially eliminated smaller gaps from the model. According to the effect sizes, the relationship between gap size and lemur distance to the nearest gap became consistently stronger as gap size increased, indicating that large lemurs were found more often closer to large gaps than to smaller gaps (Supporting Information S1: Table S2).

The situation was more complex for the three nocturnal species. For the combined data of *A. mooreorum*, *L. scottorum*, and *Microcebus* sp., the relationship was best and significantly described by a cubic equation as distance between nocturnal lemurs and gap size = 5.98 + 0.024*gap size – 0.00015837*gap size^2 + 2.227E-07*gap size^3 ($R^2 = 0.032$, $F = 3.130$, $p = 0.026$; Figure 3b). At smaller gap sizes, diurnal and nocturnal species showed similar relations to gaps, but at larger sized gaps, the diurnal species were found closer to them or even right at the edge, while nocturnal species were never found close to the edge of larger gaps and kept their distance to larger gaps.

4 | Discussion

Habitat quality and resource availability are important for primate populations and communities (Miller et al. 2018; Sawyer et al. 2017). Under stable conditions, the spatial and temporal distribution of resources should allow species to fill a habitat to

TABLE 3 | Changes in canopy gap size, lemur group size, and lemur microhabitat separation in relation to Cyclone Eliakim.

Survey period	1	2	3	4	Kruskal–Wallis
Relation to cyclone Eliakim	2–4 mo. before	2–4 mo. after	37–38 mo. after	57 mo. after	
Gap size	26.5 2.4–294.4 (136)	31.4 1.6–714.4 (48)	25.5 0.8–565.2 (120)	18.8 0.8–253.6 (136)	$X^2 = 6.67$ $p = 0.083$
Lemur group size					
Microcebus sp.	1 (1.0) 1–1 (12)	1 (1.0) 1–1 (11)	1 (1.0) 1–1 (13)	1 (1.0) 1–1 (13)	$X^2 = 0.00$ $p = 1.000$
L. scottorum	1 (1.2) 1–3 (25)	1 (1.1) 1–2 (17)	1 (1.2) 1–2 (56)	1 (1.3) 1–4 (76)	$X^2 = 2.74$ $p = 0.434$
A. mooreorum	1 (1.4) 1–3 (18)	1 (1.1) 1–2 (12)	1 (1.4) 1–2 (17)	2 (2.2) 1–4 (17)	$X^2 = 19.08$ $p < 0.001$
E. albifrons	7 (7.3) 2–17 (44)	3 (3.0) 1–5 (4)	5.5 (5.7) 2–13 (24)	5.5 (5.6) 1–11 (16)	$X^2 = 12.08$ $p = 0.007$
V. rubra	2 (2.6) 1–6 (37)	1 (1.4) 1–2 (7)	2 (2.4) 1–3 (12)	2 (2.5) 1–9 (17)	$X^2 = 5.87$ $p = 0.118$
Lemur spp separation					
Effect size: Height	0.239 (0.233)	0.333 (0.415)	0.246 (0.257)	0.191 (0.191)	
Effect: DBH	0.382 (0.324)	0.352 (0.382)	0.337 (0.324)	0.193 (0.204)	

Note: Survey periods: 1 = November 2017–January 2018, 2 = May–July 2018, 3 = April–May 2021, 4 = December 2022. Values are medians and ranges, sample size in brackets; $df = 3$ for the Kruskal–Wallis test. Since medians do not capture the changes in pair-living species, we list mean group sizes in brackets. Effect sizes for species separation with respect to height and DBH based on Kruskal–Wallis tests provided in brackets.

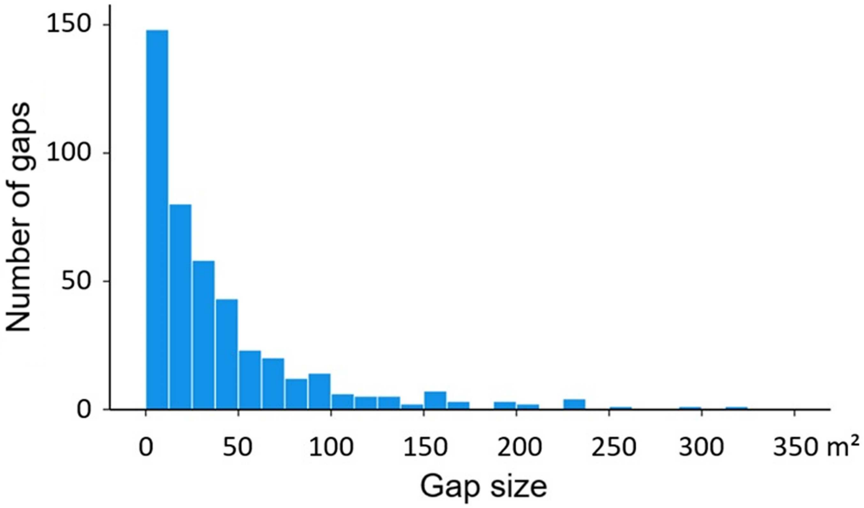

FIGURE 2 | Size distribution of canopy gaps. The largest gaps of 565 and 714 m^2 were excluded from the figure for a more easily interpretable distribution illustration.

carrying capacity and avoid competition by exploiting distinct ecological niches. While these deterministic processes could be implied in various studies (e.g., Tinsman et al. 2022; Vasey 2000), stochastic disturbances can upset deterministic community structures, reduce populations below habitat carrying capacity, and lead to changes in the niche separation of species (Connell 1978). Cyclones, with their unpredictable occurrence and disturbances, could be such stochastic events. Yet, cyclones have been an integral component in the evolution of primates, including lemurs and Malagasy ecosystems. The few lemur species for which cyclone effects have been studied showed substantial resilience and were able to compensate for population losses (Dinsmore et al. 2021; Dunham et al. 2011).

These studies and indirect evidence suggest that different lemur species have different strategies and capacities to cope with

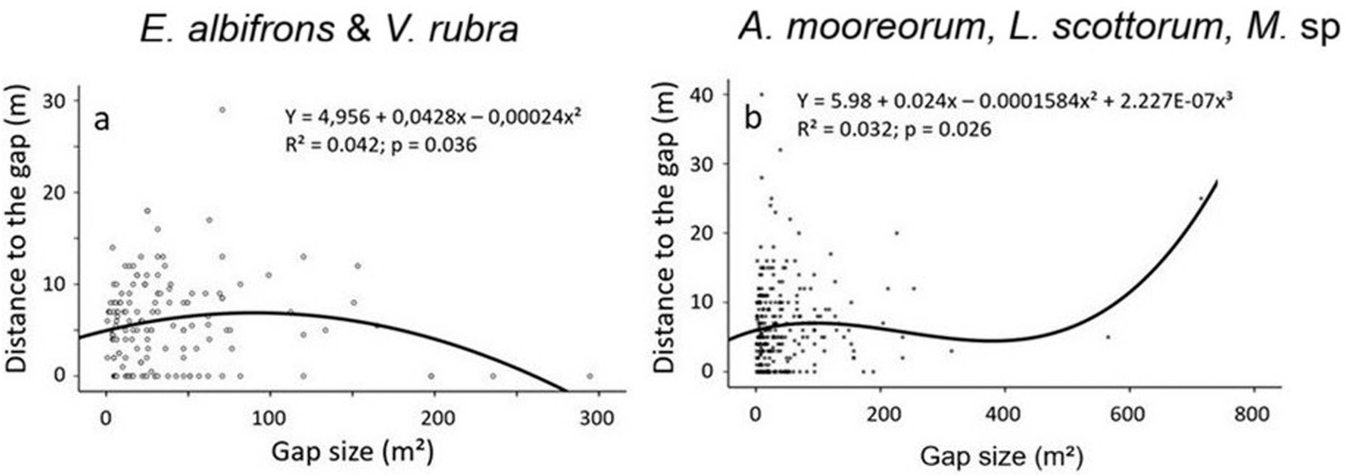

FIGURE 3 | Models for the relationships between the location of lemurs and their distance to the nearest canopy gaps: (a) large diurnal species and gaps of all sizes; (b) small nocturnal species and gaps of all sizes. The solid lines represent the models; the points represent the actual measurements.

cyclone effects (Behie et al. 2024). By conducting extensive systematic surveys, we first documented encounter rates and densities for the Andranobe Forest for future studies on environmental and anthropogenic impacts on the various lemur populations (Eppley et al. 2023; Paige et al. 2024). Second, we derived information on possible cyclone effects on lemurs by analyzing the responses and spatial association of the different species with canopy gaps.

4.1 | Lemur Encounter Rate and Population Density

During our surveys, we encountered 8 of the 10 lemur species recorded for Andranobe. *A. trichotis* and *P. furcifer* were not observed, though they were reported from other forest sites of Masoala NP (Sawyer et al. 2017), where they are also very rare (Biebouw 2009). Similarly, we saw *D. madagascariensis* and *C. major* only once. While this was not surprising for *D. madagascariensis*, as this species has vast home ranges which can exceed 600 ha (Randimbiharinirina et al. 2018) and occurs in very low densities throughout most of mainland Madagascar (Mittermeier et al. 2023), the near absence of *C. major* was unexpected. It had been recorded in similar numbers as *Microcebus* sp. at the site of Iketra (Sterling and Rakotoarison 1998), but had also not been seen at Ambodiforaha during surveys at the beginning of the Austral summer (Sawyer et al. 2017). The latter could be explained by the hibernation of *Cheirogaleus* spp. during the cool Austral winter (Blanco et al. 2018), but the species should have been present during the warm humid season. Reasons for the low encounter rates remain unknown but seem unrelated to the predominant threats in Madagascar (e.g., hunting, forest degradation; Schwitzer et al. 2014).

For the remaining nocturnal species, the density of *A. mooreorum* in Andranobe was similar to that observed by Sawyer et al. (2017) and Sterling and Rakotoarison (1998). On the other hand, the density of *L. scottorum* was much higher in Andranobe than at other sites. A possible explanation could be that the other studies included primary and secondary forests. Lemurs in secondary forest are more threatened by hunting. Though hunters target primarily the large species such as *Eulemur* spp., *Varecia* spp., and *Propithecus* spp. (Borgerson et al. 2021), hunting also affects larger nocturnal species such as *A. mooreorum* and *L. scottorum*, especially in disturbed areas where large trees are less available (Seiler et al. 2014), making these species more visible and accessible to hunters during the day. The low hunting pressure in the Andranobe might be one reason for the different population densities of these species between sites. For *Microcebus* sp., the situation might be reversed. *Microcebus* sp. has been recorded in similar densities in Andranobe as at Iketra (Sterling and Rakotoarison 1998), but reached much higher densities at sites with secondary vegetation at Ambodiforaha (Sawyer et al. 2017). This difference may be related to food availability across sites and their dietary flexibility.

Among the cathemeral and diurnal species, *H. occidentalis* was rarely observed during this study, which may be associated with the limited availability of bamboo in Andranobe, one of its principal food sources (Eppley et al. 2022). Our results match the low encounter rates of *H. occidentalis* by Sterling and Rakotoarison (1998). *E. albifrons* live in cohesive multi-male-multi-female groups of 7–11 individuals (Vasey 2000). The home range of this species is known to reach 13.1 ha, which corresponds to an estimated density of approximately 113 ind./km^2 in Andranobe (Rakotonirina 2013). Our more recent estimates are notably higher at 206.81 ind./km^2 in 2017–2018 and 300.98 ind./km^2 in 2021–2022. These differences are within the margins of error inherent in density estimates, but could also be related to the high mobility of *Eulemur* spp. that travel long distances to exploit ephemeral food patches, resulting in high variation in encounter rates in permanent plots (Overdorff 1996). The density of *V. rubra* was similar to that reported from the same and other sites previously (31.2–53.4 ind./km^2: Vasey 2000; Sterling and Rakotoarison 1998).

These lemur densities at Andranobe are similar to other parts of Masoala National Park (Sawyer et al. 2017; Sterling and Rakotoarison 1998). Populations did not decline after Cyclone Eliakim hit the study site. Though the cyclone created substantial damage (Paige et al. 2024), all species considered were resilient to the disturbances, showing behavioral flexibility by utilizing the altered environment in the weeks and months following the cyclone. After the cyclone, we found one dead female *E. albifrons*, but the cause of death was unknown, and it was unclear whether it was related to the cyclone. In general, the survey method requires considerable effort to demonstrate even very large differences in population densities or encounter rates. Therefore, even population changes of 10% or more would go unnoticed.

4.2 | Niche Separation

Ecological separation of lemur species could be achieved by horizontal separation of home ranges (Holmes et al. 2019; Schwab and Ganzhorn 2004), dietary differences, different activity patterns, or different microhabitat utilization (Ganzhorn 1989; Overdorff 1996; Schreier et al. 2009). It should also be noted that this study examined only vertical stratification and tree DBH as proxies for niche separation; other dimensions such as dietary shifts, home range adjustments, or fission-fusion dynamics may have been operating simultaneously and were not considered here. Habitat utilization and niche separation of the five lemur species considered at Andranobe follow the pattern described for most lemur communities: larger species stay higher in the forest and use larger supports (Fenosoa et al. 2018; Ganzhorn 1988; Overdorff 1996; Tinsman et al. 2022). In contrast to other lemur communities, *V. rubra* is separated clearly from all other species by using the largest trees and being found mostly high in the canopy (Vasey 2000). Competition is often invoked when interpreting different habitat utilization patterns, though it is impossible to prove without experimental manipulations (e.g., Begon et al. 2006; Connell 1978). Primates also show a wide range of behavioral responses to food shortage that can be interpreted in various ways (Hemingway and Bynum 2005). While we are aware of these caveats, the observed changes in the vertical distribution of lemur species in relation to the disturbances imposed by Cyclone Eliakim could be explained by changes in interspecific competitive interactions.

In a parallel study, Paige et al. (2024) recorded 375 new gaps per km^2 at Andranobe after the passage of the cyclone. In our study, we did not distinguish between newly created and pre-existing gaps, and gaps were not measured prior to 2017, so a direct comparison with newly created gaps could not be made. Average gap size increased from 26.5 m^2 before the cyclone to 31.4 m^2 following the cyclone, and then gradually became smaller over the years. Gap size, as a proxy for disturbance, was inversely related to the strength of microhabitat (height and DBH) separation as measured by effect sizes (Table 3). While we do not have information on changes in the food composition of the other lemur species, *V. rubra* broadened its feeding niche after the cyclone and went back to its frugivorous diet over the following years (Paige et al. 2024). Broadening its feeding niche could be interpreted as a response to food shortage (Hemingway and Bynum 2005; Paige et al. 2024). Considering these dietary changes and associated changes in species distribution patterns, we can postulate that cyclones cause food shortages, and as a response, consumer species broaden their feeding niche (Birkinshaw and Randrianjanahary 2007; Mogilewsky 2020; Paige et al. 2024). To avoid increased competition, they achieve more pronounced microhabitat separation by a clearer vertical separation. While speculative, the idea that lemurs face increased interspecific competition after a cyclone is consistent with the observed decline in group size, a pattern that may suggest increased intraspecific competition, though other unmeasured axes of niche partitioning may also play a role. The decline of group sizes and their return to larger groups over time matches previous observations, especially of group-living lemurs that feed in smaller groups when food resources are small and scarce compared to when food is abundant (Ganzhorn 1988; Hemingway and Bynum 2005; Donati et al. 2011).

4.3 | Lemur-Canopy Gap Interactions

Canopy gaps are an integral component of forest structure and their development plays a major role in forest dynamics. After their formation, gaps can be in the state of expansion, persistence, and recovery, resulting finally in their closure (Gorgens et al. 2023; Hossain and Olson 2023). Because we do not have phenological or any other vegetation data related to specific gaps, we base our interpretations on the assumption that gaps were recovering, that is, their fringes were sun-exposed and on their way towards gap closure (Gorgens et al. 2023). This assumption is supported by the reduced size of gaps several years after the cyclone. Based on published studies, we assume that the average food availability is reduced right after a cyclone because of the creation of gaps in the canopy and the stripping of fruits and leaves (Birkinshaw and Randrianjanahary 2007; Mogilewsky 2020; Paige et al. 2024). However, once these areas start regenerating, the fringes of gaps present high-quality food patches within this depauperate environment, likely driven by increased light availability (Takahashi et al. 2015).

Yet, different lemur species in Andranobe showed different patterns in relation to forest gaps. The larger (*V. rubra* and *E. albifrons*) seemed to have been associated with gaps larger than 150 m^2 and were encountered right at the edge of these large gaps. The smaller lemur species (body mass below 1 kg) also seemed to be associated with gaps up to 100 m^2 but then were found further away from larger gaps. Following our arguments, the reduced distance of small lemurs to gaps could be related to improved food conditions that might satisfy the needs of a small-bodied solitary lemur but would be irrelevant for groups of lemurs. However, more data are necessary to support this explanation. Also, the larger species are mostly frugivorous, while *A. mooreorum* and *L. scottorum* are mostly folivorous. Though actual data are lacking, fruits might need minimum-sized gaps to develop in numbers that make them attractive for large and group-living consumers. At larger gaps, these patterns of lemur responses to gaps might reverse the situation, in that larger gaps could also provide enough food for the larger species, but there, the smaller lemur species may fall prey to aerial predators like the Madagascar long-eared owl (*Asio madagascariensis*). This combination of factors might be why small lemur species avoid larger gaps. In addition, the largest gaps might also represent barriers that cannot be crossed without descending to the ground and might therefore be avoided for the small species.

These interpretations are in contrast to the findings that *Avahi* spp. and *Microcebus* spp. are edge tolerant and are more often encountered close to the forest edge than in the forest interior, while *Lepilemur* spp. and *Eulemur collaris* were seen more often in the forest interior or did not show any marked response to edges (Campera et al. 2023; Lehman et al. 2006; Mandl et al. 2023). Comparisons between gaps and forest edges may not be legitimate as forest edges represent ecotones that remain stable over longer periods than gaps. Also, our arguments on tree responses at gaps and animal responses to these changes assume changes at spatial scales of a few meters (Ganzhorn 1995a; Houle et al. 2007), while edge effects were measured at scales of tens or hundreds of meters (Campera et al. 2023; Lehman et al. 2006; Mandl et al. 2023) or in the context of whole landscapes (Eppley et al. 2020). Similarly, natural canopy gaps should not be considered to represent just another form of forest degradation. The relationships among animal groups with food distribution link with the resource-risk distribution, which depends on a species' diet and habitat (Crook and Gartlan 1966). Windfall and gaps caused by stochastic weather events were part of the evolution of Madagascar's biota and its species are likely to have evolved adaptations to cope with these events (Dewar and Richard 2007; Krebs and Davies 1978; Wright 1999), while anthropogenic forest degradation is a new phenomenon for Madagascar in evolutionary terms.

The diverging results could be related to behavioral thermoregulation. Most lemur species use behavioral thermoregulation during their active period as well in their selection of sleeping sites (Thompson and Hermann 2024). Here, the benefits of thermoregulation and costs of predation strongly intersect (e.g., Mills et al. 2021). Larger gaps with increased sunlight might have attracted the larger diurnal species not only for food but also for sunbathing to heat up after cold nights. Sunbathing is not relevant for the nocturnal species at night. As our study was restricted to the active period of the different species, and the effects of thermoregulation on the ranging behavior of nocturnal species have not been studied yet, we cannot further test these hypotheses.

Similar to the previous considerations, the effects of canopy gaps of the size considered here on predation have not yet been investigated. The assumption that *Asio madagascariensis* needs open space to maneuver and attack seems logical; dense structural environments are known to reduce raptor hunting effectiveness by providing prey with refuge from predation (Johnson et al. 2024), though detailed observations on this species remain lacking. Several of the diurnal birds of prey, such as *Accipiter henstii* and *Polyboroides radiatus* enter dense parts of forests and take nocturnal lemurs from their day shelters, sometimes by reaching into holes and pulling out the animal (reviewed by Goodman and Ganzhorn 2022). Additionally, canopy gaps may reduce the crypticity of nocturnal species and increase their exposure to potential predators on nights of greater lunar luminosity (Prugh and Golden 2014). Thus, evidence for predation in canopy gaps remains elusive and the interpretations speculative. Consistent with this predation hypothesis, our results showed that nocturnal lemurs were not observed near the edges of larger canopy gaps ($>150\ \text{m}^2$), suggesting active avoidance that may reflect heightened predation risk in such open areas.

5 | Conclusion

Our study provided density estimates, information on habitat utilization, and the effects of the forest canopy gaps on the lemur species in the Andranobe Forest in relation to the passage of Cyclone Eliakim. Though cyclones may not be increasing in frequency in the southern Indian Ocean (Fitchett and Grab 2014), their effects will become more important as they might increase in intensity and the remaining forest blocks become smaller (Rafanoharana et al. 2024). Measuring canopy gaps after cyclones might be a standardizable approach to assess ecological impacts on forest processes. Understanding these relationships is important for conservation strategies in landscapes that consist of a mosaic of forest blocks declining in size, secondary vegetation, and agricultural matrices, rather than large tracts of forest that still dominate our thinking about forest conservation in Madagascar.

Author Contributions

A.A., Z.R., M.S.M., and T.M.E. designed the study; A.A., M.S.M., D.C.R., and T.M.E. collected data; A.A., J.U.G., D.C.R., and T.M.E. analyzed the data; A.A. drafted the original manuscript; all authors revised and approved the final manuscript.

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Ethics Statement

All research was approved by the Institutional Animal Care and Use Committee at San Diego Zoo Wildlife Alliance (Protocol No. 18-012) and Portland State University (Protocol No. 84). We obtained all necessary in-country permissions for this research through the Republic of Madagascar and Madagascar National Parks, specifically from the *Direction Générale de l'Environnement et des Forêts* and *Direction de la Gestion des Ressources Naturelles Renouvelables et des Ecosystèmes* (Permits No. 189/17, 85/18, 36/21, 52/21, and 324/22).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

Axel, A. C., B. M. Harshbarger, R. J. Lewis, and S. R. Tecot. 2024. “Consistency in Verreaux's Sifaka Home Range and Core Area Size Despite Seasonal Variation in Resource Availability as Assessed by Enhanced Vegetation Index (EVI).” *American Journal of Primatology* 86, no. 6: e23617. https://doi.org/10.1002/ajp.23617.

Begon, M., J. L. Harper, and C. R. Townsend. 2006. *Ecology*. Blackwell.

Behie, A. M., T. S. Steffens, K. Yaxley, et al. 2024. “Can Cyclone Exposure Explain Behavioural and Demographic Variation Among Lemur Species?” *PLoS One* 19, no. 3: e0300972. https://doi.org/10.1371/journal.pone.0300972.

Biebouw, K. 2009. “Home Range Size and Use in *Allocebus trichotis* in Analamazaotra Special Reserve, Central Eastern Madagascar.” *International Journal of Primatology* 30, no. 2: 367–386. https://doi.org/10.1007/s10764-009-9349-y.

Birkinshaw, C., and M. Randrianjanahary. 2007. “The Effects of Cyclone Hudah on the Forest of Masoala Peninsula, Madagascar.” *Madagascar Conservation and Development* 2, no. 1: 17–20. https://doi.org/10.4314/mcd.v2i1.44125.

Blanco, M. B., K. H. Dausmann, S. L. Faherty, and A. D. Yoder. 2018. “Tropical Heterothermy Is “Cool”: The Expression of Daily Torpor and Hibernation in Primates.” *Evolutionary Anthropology: Issues, News, and Reviews* 27, no. 4: 147–161. https://doi.org/10.1002/evan.21588.

Borgerson. 2021. A National-Level Assessment of Lemur Hunting Pressure in Madagascar.” *International Journal of Primatology* 43, no. 1: 92–113. https://doi.org/10.1007/s10764-021-00215-5.

Brokaw, N. V. L. 1982. “The Definition of Treefall Gap and Its Effect on Measures of Forest Dynamics.” *Biotropica* 14, no. 2: 158–160. https://doi.org/10.2307/2387750.

Brown, J. L., and A. D. Yoder. 2015. “Shifting Ranges and Conservation Challenges for Lemurs in the Face of Climate Change.” *Ecology and Evolution* 5, no. 6: 1131–1142. https://doi.org/10.1002/ece3.1418.

Buckland, S. T., A. J. Plumptre, L. Thomas, and E. A. Rexstad. 2010. “Design and Analysis of Line Transect Surveys for Primates.” *International Journal of Primatology* 31, no. 5: 833–847. https://doi.org/10.1007/s10764-010-9431-5.

Campera, M., M. Balestri, M. Phelps, et al. 2023. “Depth of Edge Influence in a Madagascar Lowland Rainforest and Its Effects on Lemurs' Abundance.” *Land* 12, no. 1: 81. https://doi.org/10.3390/land12010081.

Charles-Dominique, P. 1977. *Ecology and Behaviour of Nocturnal Prosimians*. Duckworth.

Connell, J. H. 1978. “Diversity in Tropical Rain Forests and Coral Reefs: High Diversity of Trees and Corals Is Maintained Only in a Nonequilibrium State.” *Science* 199, no. 4335: 1302–1310. https://doi.org/10.1126/science.199.4335.1302.

Crook, J. H., and J. S. Gartlan. 1966. “Evolution of Primate Societies.” *Nature* 210: 1200–1203. https://doi.org/10.1038/2101200a0.

De Gouvenain, R. C., and J. A. Silander. 2003. “Do Tropical Storm Regimes Influence the Structure of Tropical Lowland Rain Forests?” *Biotropica* 35: 166–180. https://doi.org/10.1111/j.1744-7429.2003.tb00276.x.

Dewar, R. E., and A. F. Richard. 2007. “Evolution in the Hypervariable Environment of Madagascar.” *Proceedings of the National Academy of Sciences* 104, no. 34: 13723–13727. https://doi.org/10.1073/pnas.0704346104.

Dinsmore, M. P., K. B. Strier, and E. E. Louis, Jr. 2021. “The Influence of Seasonality, Anthropogenic Disturbances, and Cyclonic Activity on the Behavior of Northern Sportive Lemurs (*Lepilemur septentrionalis*) at Montagne des Français, Madagascar.” *American Journal of Primatology* 83, no. 12: e23333. https://doi.org/10.1002/ajp.23333.

Donati, G., E. Ricci, N. Baldi, V. Morelli, and S. M. Borgognini-Tarli. 2011. “Behavioral Thermoregulation in a Gregarious Lemur, *Eulemur collaris*: Effects of Climatic and Dietary-Related Factors.” *American Journal of Physical Anthropology* 144, no. 3: 355–364. https://doi.org/10.1002/ajpa.21415.

Dunham, A. E., E. M. Erhart, and P. C. Wright. 2011. “Global Climate Cycles and Cyclones: Consequences for Rainfall Patterns and Lemur Reproduction in Southeastern Madagascar.” *Global Change Biology* 17, no. 1: 219–227. https://doi.org/10.1111/j.1365-2486.2010.02205.x.

Enstam, K. 2007. “Effects of Habitat Structure on Perceived Risk of Predation and Anti-Predator BehavIor of Vervet (*Cercopithecus aethiops*) and Patas (*Erythocebus patas*) Monkeys.” In *Primate Anti-Predator Strategies*, edited by In. S. L. Gursky and K. A. I. Nekaris, 308–338. Springer.

Eppley, T. M., C. Borgerson, E. R. Patel, et al. 2023. “A Habitat Stronghold on the Precipice: A Call-to-Action for Supporting Lemur Conservation in NE Madagascar.” *American Journal of Primatology* 86, no. 3: e23483. https://doi.org/10.1002/ajp.23483.

Eppley, T. M., L. Santini, J. C. Tinsman, and G. Donati. 2020. “Do Functional Traits Offset the Effects of Fragmentation? The Case of Large-Bodied Diurnal Lemur Species.” *American Journal of Primatology* 82, no. 4: e23104. https://doi.org/10.1002/ajp.23104.

Eppley, T. M., K. J. E. Steffens, I. C. Colquhoun, and C. R. Birkinshaw. 2022. “Lemur Food Plants.” In *The New Natural History of Madagascar*, edited by S. M. Goodman, 1839–1859. Princeton University Press.

Fenosoa, Z. S. E., R. M. Sawyer, A. Andrianarimisa, H. Razafindraibe, H. Rakotomanana, and G. Donati. 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.

Fitchett, J. M., and S. W. Grab. 2014. “A 66-year Tropical Cyclone Record for South-East Africa: Temporal Trends in a Global Context.” *International Journal of Climatology* 34: 3604–3615. https://doi.org/10.1002/joc.3932.

Ganzhorn, J. U. 1988. “Food Partitioning Among Malagasy Primates.” *Oecologia* 75, no. 3: 436–450. https://doi.org/10.1007/BF00376949.

Ganzhorn, J. U. 1995a. “Cyclones Over Madagascar: Fate or Fortune?” *Ambio* 24, no. 2: 124–125.

Ganzhorn, J. U. 1989. “Niche Separation of Seven Lemur Species in the Eastern Rainforest of Madagascar.” *Oecologia* 79: 279–286. https://doi.org/10.1007/BF00388489.

Ganzhorn, J. U. 1995b. “Low-Level Forest Disturbance Effects on Primary Production, Leaf Chemistry, and Lemur Populations.” *Ecology* 76, no. 7: 2084–2096. https://doi.org/10.2307/1941683.

Gardner, C. J. 2009. “A Review of the Impacts of Anthropogenic Habitat Change on Terrestrial Biodiversity in Madagascar: Implications for the Design and Management of New Protected Areas.” *Malagasy Nature* 2: 2–29.

Goodman, S. M., and J. U. Ganzhorn. 2022. “Predation on Lemurs.” In *The New Natural History of Madagascar*, edited by S. M. Goodman, 1829–1838. Princeton University Press.

Goodman, S. M., M. J. Raherilalao, and S. Wohlhauser. 2018. *The Terrestrial Protected Areas of Madagascar: Their History, Description, and Biota*. Antananarivo, Association Vahatra.

Gorgens, E. B., M. Keller, T. Jackson, et al. 2023. “Out of Steady State: Tracking Canopy Gap Dynamics Across Brazilian Amazon.” *Biotropica* 55, no. 4: 755–766. https://doi.org/10.1111/btp.13226.

Hemingway, C. A., and N. Bynum. 2005. “The Influence of Seasonality on Primate Diet and Ranging.” In *Seasonality in Primates: Studies of Living and Extinct Human and Non-human Primates*, edited by D. K. Brockman and C. P. van Schaik, 57–104. Cambridge University Press.

Holmes, S. M., E. E. Louis, Jr., and S. E. Johnson. 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.

Hossain, S. M., and M. G. Olson. 2023. “The Lateral Growth of Branches into Small Canopy Gaps: Implications for Competition Between Canopy Trees.” *Forests* 14, no. 7: 1350. https://doi.org/10.3390/f14071350.

Houle, A., C. A. Chapman, and W. L. Vickery. 2007. “Intratree Variation in Fruit Production and Implications for Primate Foraging.” *International Journal of Primatology* 28: 1197–1217. https://doi.org/10.1007/s10764-007-9214-9.

IUCN. 2023. “The IUCN Red List of Threatened Species.” www.iucnredlist.org.

Johnson, E. E., D. A. Espinosa-Lucas, R. D. Pérez-García, I. Solano-Zavaleta, J. J. Zúñiga-Vega, and G. A. Ramírez-Cruz. 2024. “Keystone Species in an

Urban Environment: Do Raptors Control the Mexican Gray Squirrel in Mexico City?" *Acta Oecologica* 125: 104034. https://doi.org/10.1016/j.actao.2024.104034.

Korstjens, A. H., and A. P. Hillyer. 2016. "Primates and Climate Change: A Review of Current Knowledge." In *An Introduction to Primate Conservation*, edited by S. A. Wich and A. J. Marshall, 175–192. Oxford Academic.

Krebs, J. R., and N. B. Davies. 1978. *Behavioural Ecology: An Evolutionary Approach*. Blackwell Scientific Publications.

Lehman, S. M., A. Rajaonson, and S. Day. 2006. "Edge Effects and Their Influence on Lemur Density and Distribution in Southeast Madagascar." *American Journal of Physical Anthropology* 129: 232–241. https://doi.org/10.1002/ajpa.20241.

Lin, T. C., J. A. Hogan, and C. T. Chang. 2020. "Tropical Cyclone Ecology: A Scale-Link Perspective." *Trends in Ecology & Evolution* 35, no. 7: 594–604. https://doi.org/10.1016/j.tree.2020.02.012.

Mandl, I., N. Rabemananjara, M. Holderied, and C. Schwitzer. 2023. "Measuring the Impact of Forest Edges on the Highly Arboreal Sahamalaza Sportive Lemur, *Lepilemur sahamalaza*, in North-Western Madagascar." *International Journal of Primatology* 44, no. 3: 458–481. https://doi.org/10.1007/s10764-022-00333-8.

Martinez, B. 2010. "Forest Restoration in Masoala National Park, Madagascar: The Contribution of the Red Ruffed Lemur (*Varecia rubra*) and the Livelihoods of Subsistence Farmers at Ambatoledama." PhD Dissertation, University of Minnesota.

Miller, A., H. Mills, T. Ralantoharijaona, et al. 2018. "Forest Type Influences Population Densities of Nocturnal Lemurs in Manompana, Northeastern Madagascar." *International Journal of Primatology* 39, no. 4: 646–669. https://doi.org/10.1007/s10764-018-0055-5.

Mills, C. J., K. A. I. Nekaris, M. Campera, and E. Patel. 2021. "Silky Sifakas Use Sleep Sites for Thermoregulation, Food Access and Predator Avoidance." *Folia Primatologica* 92, no. 5–6: 315–326. https://doi.org/10.1159/000520710.

Mittermeier, R. A., K. E. Reuter, and A. B. Rylands, et al. 2023. *Lemurs of Madagascar*, 5th ed. Re:wild.

Mogilewsky, M. S. 2020. "Before and After the Storm: Interactions Between Treefall Canopy Gaps, Plant Phenology, and Frugivorous Lemurs in Masoala National Park, Madagascar." PhD dissertation. Portland State University. https://doi.org/10.15760/etd.7291.

Murakami, H., T. L. Delworth, W. F. Cooke, M. Zhao, B. Xiang, and P. C. Hsu. 2020. "Detected Climatic Change in Global Distribution of Tropical Cyclones." *Proceedings of the National Academy of Sciences* 117, no. 20: 10706–10714. https://doi.org/10.1073/pnas.1922500117.

Nunez, S., E. Arets, R. Alkemade, C. Verwer, and R. Leemans. 2019. "Assessing the Impacts of Climate Change on Biodiversity: Is below 2°C Enough?" *Climatic Change* 154: 351–365. https://doi.org/10.1007/s10584-019-02420-x.

Overdorff, D. J. 1996. "Ecological Correlates to Activity and Habitat Use of Two Prosimian Primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar." *American Journal of Primatology* 40, no. 4: 327–342. https://doi.org/10.1002/(SICI)1098-2345(1996)40:4<327::AID-AJP3>3.0.CO;2-%23.

Ozgul, A., C. Fichtel, M. Paniw, and P. M. Kappeler. 2023. "Destabilizing Effect of Climate Change on the Persistence of a Short-Lived Primate." *Proceedings of the National Academy of Sciences* 120, no. 14: e2214244120. https://doi.org/10.1073/pnas.2214244120.

Paige, L. A., L. Santini, D. C. Rasamisoa, et al. 2024. "Weathering the Storm: Long-Term Implications on the Feeding Ecology and Habitat Use of a Frugivorous Lemur Following a Tropical Cyclone." *Biotropica* 56, no. 6: e13385. https://doi.org/10.1111/btp.13385.

Prugh, L. R., and C. D. Golden. 2014. "Does Moonlight Increase Predation Risk? Meta-Analysis Reveals Divergent Responses of Nocturnal Mammals to Lunar Cycles." *Journal of Animal Ecology* 83, no. 2: 504–514. https://doi.org/10.1111/1365-2656.12148.

R Core Team. 2022. "R: A Language and Environment for Statistical Computing." R Foundation for Statistical Computing. http://www.R-project.org.

RStudio. 2023. "RStudio: Integrated Development Environment for R." R. Studio. http://www.rstudio.org/.

Rafanoharana, S. C., F. O. D. Andrianambinina, H. A. Rasamuel, P. O. Waeber, L. Wilmé, and J. U. Ganzhorn. 2024. "Projecting Forest Cover in Madagascar's Protected Areas to 2050 and Its Implications for Lemur Conservation." *Oryx* 58, no. 2: 155–163. https://doi.org/10.1017/S0030605323001175.

Rakotonirina, H. N. 2013. "Les effets des facteurs anthropiques sur les espèces Varecia rubra et Eulemur albifrons dans la presqu'île Masoala." In *Mémoire de Capens*. Université d'Antananarivo.

Ralimanana, H., A. L. Perrigo, R. J. Smith, et al. 2022. "Madagascar's Extraordinary Biodiversity: Threats and Opportunities." *Science* 378, no. 6623: eadf1466. https://doi.org/10.1126/science.adf1466.

Randimbiharinirina, D. R., B. M. Raharivololona, M. T. R. Hawkins, et al. 2018. "Behaviour and Ecology of Male Aye-Ayes (*Daubentonia madagascariensis*) in the Kianjavato Classified Forest, South-Eastern Madagascar." *Folia Primatologica* 89, no. 2: 123–137. https://doi.org/10.1159/000486673.

Ratovonamana, Y. R., C. Apel, D. H. Hajanantenaina, et al. 2024. "Linking Vegetation Characteristics of Madagascar's Spiny Forest to Habitat Occupancy of *Lepilemur petteri*." *International Journal of Primatology* 45: 1128–1157. https://doi.org/10.1007/s10764-024-00441-7.

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.

Ross, C., and N. Reeve. 2011. "Survey and Census Methods: Population Distribution and Density." In *Field and Laboratory Methods in Primatology: A Practical Guide*, edited by J. M. Setchell and D. J. Curtis, 111–131. Cambridge University Press.

Sawyer, R. M., Z. S. E. Fenosoa, A. Andrianarimisa, and G. Donati. 2017. "The Effect of Habitat Disturbance on the Abundance of Nocturnal Lemur Species on the Masoala Peninsula, Northeastern Madagascar." *Primates* 58: 187–197. https://doi.org/10.1007/s10329-016-0552-0.

Schnitzer, S. A., and W. P. Carson. 2001. "Treefall Gaps and the Maintenance of Species Diversity in a Tropical Forest." *Ecology* 82: 913–919. https://doi.org/10.1890/0012-9658(2001)082[0913:TGATMO]2.0.CO;2.

Schreier, B. M., A. H. Harcourt, S. A. Coppeto, and M. F. Somi. 2009. "Interspecific Competition and Niche Separation in Primates: A Global Analysis." *Biotropica* 41, no. 3: 283–291. https://doi.org/10.1111/j.1744-7429.2008.00486.x.

Schwab, D., and J. U. Ganzhorn. 2004. "Distribution, Population Structure and Habitat Use of *Microcebus berthae* Compared to Those of Other Sympatric Cheirogalids." *International Journal of Primatology* 25: 307–330. https://doi.org/10.1023/B:IJOP.0000019154.17401.90.

Schwitzer, C., R. A. Mittermeier, S. E. Johnson, et al. 2014. "Averting Lemur Extinctions Amid Madagascar's Political Crisis." *Science* 343: 842–843. https://doi.org/10.1126/science.1245783.

Seiler, M., M. Holderied, and C. Schwitzer. 2014. "Habitat Selection and Use in the Critically Endangered Sahamalaza Sportive Lemur, *Lepilemur sahamalazensis*, in Altered Habitat." *Endangered Species Research* 24: 273–286. https://doi.org/10.3354/esr00596.

Sterling, E. J., and N. Rakotoarison†. 1998. "Rapid Assessment of Richness and Density of Primate Species on the Masoala Peninsula, Eastern Madagascar." *Folia Primatologica* 69: 109–116. https://doi.org/10.1159/000052703.

Takahashi, K., K. Takahashi, and I. Washitani. 2015. "Do Small Canopy Gaps Created by Japanese Black Bears Facilitate Fruiting of Fleshy-

Fruited Plants?" *PLoS One* 10, no. 7: e0130956. https://doi.org/10.1371/journal.pone.0130956.

Thompson, C. L., and E. A. Hermann. 2024. "Behavioral Thermoregulation in Primates: A Review of Literature and Future Avenues." *American Journal of Primatology* 86, no. 6: e23614. https://doi.org/10.1002/ajp.23614.

Tinsman, J., S. Volampeno, J. Ganas-Swaray, et al. 2022. "Habitat Use by the Island Lemurs of Nosy Be, Madagascar." *American Journal of Primatology* 84: e23362. https://doi.org/10.1002/ajp.23362.

Tomczak, M., and E. Tomczak. 2014. "The Need to Report Effect Size Estimates Revisited. An Overview of Some Recommended Measures of Effect Size." *Trends in Sport Science* 21, no. 1: 19–25.

Trew, B. T., and I. M. D. Maclean. 2021. "Vulnerability of Global Biodiversity Hotspots to Climate Change." *Global Ecology and Biogeography* 30, no. 4: 768–783. https://doi.org/10.1111/geb.13272.

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

Whitmore, T. C. 1998. "Potential Impact of Climatic Change on Tropical Rain Forest Seedlings and Forest Regeneration." *Climatic Change* 39: 429–438. https://doi.org/10.1023/A:1005356906898.

Wright, P. C. 1999. "Lemur Traits and Madagascar Ecology: Coping With an Island Environment." *American Journal of Physical Anthropology* 110: 31–72. https://doi.org/10.1002/(sici)1096-8644(1999)110:29+<31::aid-ajpa3>3.0.co;2-0.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.
Table S1: Number of transect visits and observation efforts during the two lemur survey periods. T: Transect; D: Diurnal observation; N: Nocturnal observation.
Table S2: Linear, invers and polynomial regression models of relationship between distance to nearest canopy gap and gap size, with statistically significant models in bold; n = number of gaps; b = beta coefficients.
Table S3: Number of sightings (N) and encounter rates (ER, sightings/km) per lemur species for each survey period at Andranobe Forest, Masoala National Park. Period 1 = Summer 2017–2018 (pre-Cyclone Eliakim; November-January); Period 2 = Winter 2018 (post-Cyclone Eliakim; May-July); Period 3 = Winter 2021 (April-May); Period 4 = Summer 2022 (December). Combined P1+P2 and P3+P4 values match those in Table 1 of the main text. Mann–Whitney *U* tests revealed a significant difference in overall encounter rates between Period 1 and Period 2 (W = 2175.5; P = 0.031), driven by Eulemur albifrons (W = 31; P = 0.037) and Varecia rubra (W = 31.5; P = 0.034).