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Depth of Edge Influence in a Madagascar Lowland Rainforest and Its Effects on Lemurs' Abundance

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Abstract: Edge effects result from interactions between adjacent habitats, which can modify abiotic and biotic conditions and produce various negative effects on biodiversity. Given the high degree of forest fragmentation in Madagascar, understanding lemur responses to edges is a conservation priority. We aim to determine the depth of edge influence in a continuous low-land rainforest of south-eastern Madagascar and identify the response of six lemur species. We surveyed lemur abundance along nine 1 km transects from May 2015 to July 2016 totaling 112.2 km of survey effort during the day and 88.5 km at night. We characterized the habitat structure via 33 plots centered along the line transects. We used Generalized Additive Models and Generalized Linear Models to test the effect of distance from the forest edge on vegetation parameters and animal encounter rates. Edge effect on the vegetation structure can be detected up to around 100 m in terms of tree diversity and density. We found a negative edge response for Madame Fleurette's sportive lemurs (*Lepilemur fleuretae*) and collared brown lemurs (*Eulemur collaris*), and a positive edge response for Anosy mouse lemurs (*Microcebus tanosi*), Southern bamboo lemurs (*Hapalemur meridionalis*) and Southern woolly lemurs (*Avahi meridionalis*). Since around half of the forested areas in Madagascar are within 100 m of forest edge, taking into account edge effect is vital when producing estimates of population sizes and informing conservation management.

Keywords: edge effect; distance sampling; tree diversity; vegetation; Tsitongambarika; edge response; species vulnerability; edge tolerance; habitat loss; fragmentation

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1. Introduction

An edge is defined as the boundary of two adjacent habitat types and the resulting interactions between them [1–3]. Edges consist of a dynamic zone characterized by the penetration of conditions from the surrounding environment, spatially separated resources, changes in resource mapping, and changes in species interactions [4,5]. Edge effects can thus modify biotic (e.g., tree species density) and abiotic (e.g., light, temperature) conditions and change the dynamic of a forest [6–9]. Edge zones can have several effects on biodiversity such as increased predation rates [10], reduction in available food species (in particular fruiting trees; [11]), increased tree mortality [12], increased parasite loads [8], and increased hunting from humans [13]. Therefore, a species ability to cope with edge effects is likely to influence its population distribution [14].

Understanding animals' response to habitat edges is particularly important since tropical forests are becoming increasingly fragmented due to human expansion and encroachment [15]. Human human pressures, both direct and indirect, are having significant effects on the natural environment and are the main cause of species extinctions, bringing scientists to argue that we are in the middle of the sixth great mass extinction [16]. Forest fragmentation globally has reached such proportions that 70% and 19% of remaining forest is within 1 km and 100 m of a forest edge, respectively [17,18]. Species react in different ways to forest edges depending on their ecological niches and in particular their diet and microclimate preferences [19,20]. Three responses have been identified: a negative edge response (abundance highest in the forest interior), a positive edge response (abundance highest in the forest edge) and a neutral edge response (no significant difference in abundance between the forest edge and interior) [5].

Large frugivores are expected to exhibit a negative edge response since the mortality of large trees increases in proximity of forest edges [12,14]. Hibernating animals are also expected to show negative edge effects since temperatures fluctuate more at edges [6]. Animals with an omnivorous and diverse diet, in contrast, are expected to be attracted to habitat edges, since these zones may contain a mixture of the floral and faunal communities of adjacent habitats [21]. Edges may also be preferred by insectivorous species due to a high abundance of invertebrates [4,22,23]. Folivores are expected to exhibit neutral to positive edge responses since food abundance does not usually change between edge and interior [21], but edges may include abundant pioneer trees with a low concentration of secondary compounds and a high protein content [24,25]. Locomotion style is another factor influencing animals' responses to edges, with species that require either small or large substrates differently affected by edge zones [26]. Finally, seasonality may affect animals' response [27].

The depth of edge influence (DEI) is a key factor to be considered when investigating animal responses to edge effects in a specific area. DEI is the distance at which biotic or biotic parameters change significantly from the edge to the interior of the forest [28,29]. DEI is difficult to define since it depends on regional variations and habitat type, as well as the biotic and abiotic parameters considered [28,30]. DEI is usually 50-100 m for species diversity, canopy and understorey cover, and seedling mortality but can reach up to 400 m for some variable such as tree mortality [30]. Additionally, DEI is usually lower in forests with a diverse canopy and with low degree of invasion of exotic species (e.g., mature rainforests) and it increases with higher degrees of habitat degradation [30].

Madagascar is a biodiversity hotspot in which many endemic species are threatened [31]. Ninety-four percent of lemurs, one of the island's flagship taxonomic groups, are threatened with extinction [32]. Slash-and-burn agriculture has played a major contribution to deforestation and fragmentation on the island [33]. Harper et al. [34] estimated that 80% of all remaining forest in Madagascar occurs within 1 km of non-forest edge. Vieilledent et al. [35] indicated that 46% of the remaining forest on the highland is within 100 m of non-forest edge. Since the depth of the edge effect is likely to vary between habitats, these country-wide figures are unable to provide a picture on local response and estimate the severity of fragmentation in specific areas. Still, the level of local endemism in Madagascar is such that local DEI is likely to have a large effect on species population size.

The Tsitongambarika Protected Area (TGK) is a priority conservation and research site in Madagascar as it represents one of the largest continuous blocks of lowland rainforest remaining on the island [36]. It thus represents an ideal area to study edge effects since these are not confounded with other fragment area effects [37]. The encroachment of villages on the eastern side of TGK has generated a higher proportion of edge habitat that is likely to affect the faunal and floral communities within the forest. Since all the seven species of lemurs at TGK are included in one of the categories of threat on the IUCN Red List of Threatened Species [36], it is urgent to have accurate estimates of population size.

Here, we aim to (1) determine the DEI of four vegetation parameters (tree diversity, tree richness, tree circumference, and coefficient of variation of the tree circumference) in the lowland rainforest of TGK (2) identify the response of six lemur species to edge effect inhabiting TGK in terms of abundance; (3) estimate the density of the lemur species inhabiting the area to compare to neighbouring areas with different edge impact. We predict Southern bamboo lemur *Hapalemur meridionalis* and Southern woolly lemur *Avahi meridionalis* will exhibit a neutral edge response; aye-aye *Daubentonia madagascariensis*, collared brown lemur *Eulemur collaris*, dwarf lemur *Cheirogaleus* sp., and Madame Fleurette's sportive lemur *Lepilemur fleuretae* will exhibit a negative edge response; and Anosy mouse lemur *Microcebus tanosi* will exhibit a positive edge response (Table 1).

Table 1. Traits considered to predict the edge responses of lemur species at the Ampasy valley, north of the Tsitongambarika lowland rainforest, southeast Madagascar. When information on the species was not available, we considered information on other species from the same genus. The prediction is based on the category with more frequent traits. If no category is dominant, we predicted a neutral edge response since we predict the animals to balance these traits so that they do not prefer any particular layer.

Species	**Traits Supporting Edge Responses**			**Prediction**
	Positive Edge Response	**Neutral Edge Response**	**Negative Edge Response**	
Anosy mouse lemur (*Microcebus tanosi*)	1. Diet potentially high in insect intake [38] 2. Small-sized (~50 g), prefers small supports for locomotion [38]	1. Omnivorous diet [38]	1. Potential torpor during dry periods [39]	Positive
Aye-aye (*Daubentonia madagascariensis*)			1. Highly frugivorous diet, mainly *Canarium* trees [40] 2. Dependent on availability of dead wood [40]	Negative
Collared brown lemur (*Eulemur collaris*)		1. Complement its diet with young leaves and invertebrates [41]	1. Highly hunted [36] 2. Highly frugivorous diet [41].	Negative
Dwarf lemur (*Cheirogaleus* sp.)			1. Hibernation during dry periods [42] 2. Potentially frugivorous diet [43]	Negative
Madame Fleurette's sportive lemur (*Lepilemur fleuretae*)		1. Mainly folivorous but ~25% of the diet consists of fruits and flowers [25]	1. Sleep in holes of large trees [25] 2. Hunted during the day when spotted sleeping in tree holes [36]. 3. Vertical leaper and clinger, need availability of large vertical supports [44]	Negative
Southern bamboo lemur (*Hapalemur meridionalis*)	1. Diet rich in grasses Poaceae [45,46] 2. Highly folivorous diet [45,46]		1. Highly hunted [36] 2. Select large trees as sleeping sites [47]	Neutral
Southern woolly lemur (*Avahi meridionalis*)	1. Highly folivorous diet [25]		1. Vertical leaper, need availability of large vertical supports [44]	Neutral

2. Materials and Methods

2.1. Study Site

The study was conducted at the research site of Ampasy (24°34′58″ S, 47°09′01″ E) [36]. The Ampasy valley is around 900 ha, and it is located in the northernmost portion of the TGK forest. The annual rainfall from July 2015 to July 2016 was 2382 mm, and the only months with less than 100 mm rainfall were July, September, and October. The TGK forest consists of an area of around 605 km^2 of continuous rainforest at a maximum altitude of 1358 m a.s.l. and encompasses large areas of lowland rainforests (0–600 m a.s.l.) [36].

2.2. Survey Design

We established nine independent transects of around one km each along pre-existing trails throughout the forest (Figure 1). Transects started from the edge and continued into the forest so that we could have a representation of both the edge and the forest interior. We did not cut new transects to avoid potential negative effects on wildlife by increasing access to hunters [48]. We put a flag every 25 m along the transects that encompassed both interior and edge of the forest. We flagged a total of 309 locations at a mean distance from the forest edge of 174.0 ± SD 143.9 m (range: 0.0–560.0 m). Transects were divided into 11 edge and 10 interior sub-transects based on vegetation characteristics (see below for details on vegetation surveys, data analysis, and results). The average length of the edge sub-transects was 252.3 ± SD 150.6 m (range: 100.0–525.0 m) and the average length of the interior sub-transects was 562.5 ± SD 314.3 m (range: 100.0–925.0 m).

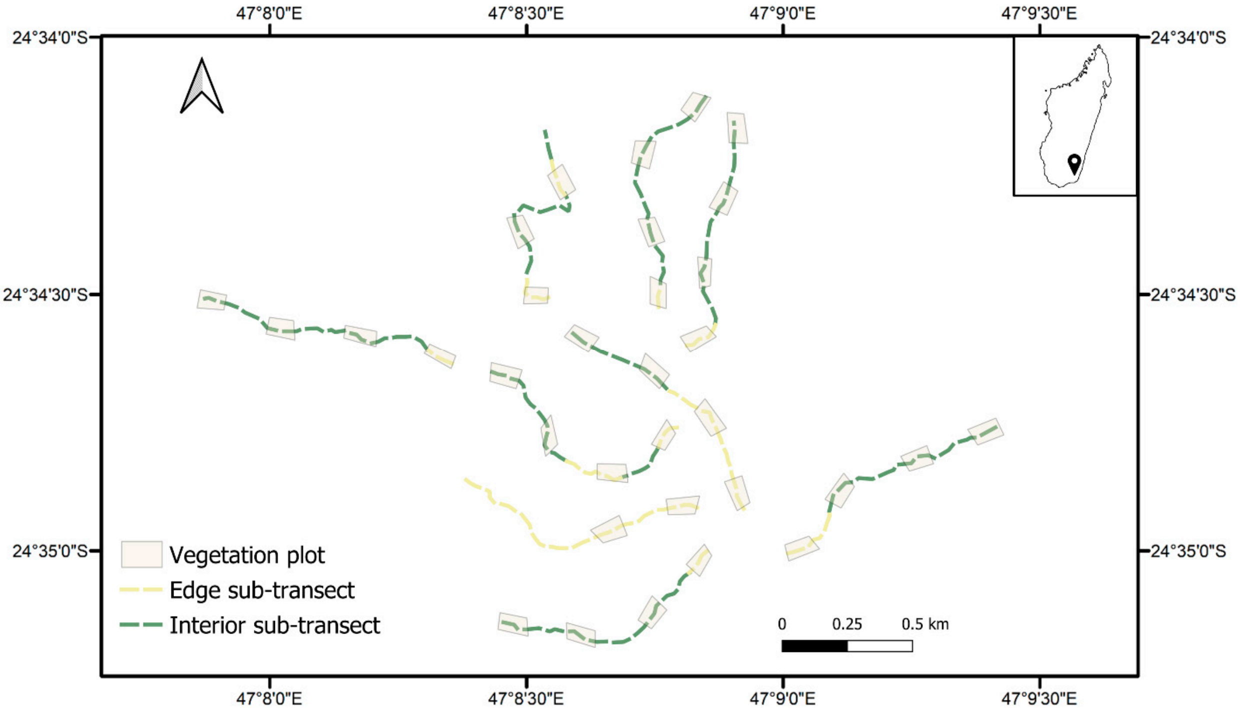

Figure 1. Location of the Ampasy valley in relation to Madagascar. The map indicates the location of the nine transects. used for the lemur surveys and the 33 plots used for the collection of vegetation data.

2.3. Vegetation Surveys

We established rectangular vegetation plots of 10 m × 100 m along the line transects and spaced them at a regular distance of 200 m for a total of 33 plots (Figure 1). Numbered flagging tape marked 10 m increments along the plots, with 5 m flagged either side of the transect line to ensure data collected remained inside the plots. We calculated the distance from the forest edge to the centre of the plot (mean distance: 177.0 ± SD 160.0 m; range: 0.0–560.0 m) via ArcGIS software v 10.7.1. We collected data on diameter at breast height (DBH) and vernacular name of all trees within each plot. Tree identification was made in the field using vernacular names obtained from field assistants and associated with the plant list compiled by botanists from Asity Madagascar and from the Parc Botanique et Zoologique de Tsimbazaza [26]. We collected herbarium specimens whenever possible to double-check correspondence between vernacular and scientific names. In total, 63 species identified via vernacular names were not present in the list. Scientific names of these specimens were identified by botanists from the Faculty of Sciences of the University of Antananarivo. It was not possible to identify five of these species for which we used vernacular names [26].

2.4. Lemur Surveys

We walked each transect once a month in pairs of one researcher and one local assistant during the day and at night from May 2015 until July 2016. We did not walk some of the transects during the season of heavy rains (i.e., January/February) as some areas of the forest were unreachable and dangerous especially at night. We walked the transects at an average speed of about 1 km/h, in the early morning (between 6:30 and 8:30) or late afternoon (between 15:00 and 17:00) for diurnal transects, and early night (between 19:00 and 21:00) for nocturnal transects. We did not walk transects during heavy rain to avoid biases due to poor visibility [49]. During nocturnal transects we used zoom headlamps. Survey time per transect averaged 1 h 13 min (range: 54 min–1 h 57 min). On observing a primate group, we recorded: time, species, number of individuals seen, perpendicular distance from the transect, and nearest flag. In case of clusters, we estimated the distance from the observer to the centre of the group [49,50]. We performed extensive team training in estimating perpendicular distances and heights before starting the data collection to ensure quick and consistent estimates. In total, we walked 112.2 km during the day and 88.5 km at night. In the analysis, we considered only diurnal transect for cathemeral lemurs (collared brown lemur and Southern bamboo lemur) and nocturnal transects for nocturnal lemurs (all the other lemurs present in the area). To calculate the encounter rates of dwarf lemur we excluded the months of hibernation (April–September [51]), so the total effort for this species was 35.0 km.

2.5. Data Analysis

We first used Generalised Additive Models to test the effect of distance from the forest edge on four vegetation parameters: Shannon Index, tree richness, tree DBH, and coefficient of variation of the DBH. Based on these models, we defined a distance at which we considered the edge effect to be significant, and divided between forest edge and forest interior. We estimated a total of 180 ha of forest edge and 720 ha of forest interior at the Ampasy valley via ArcGIS software v 10.7.1. We then divided the transects into sub-transects based on this distance into edge or interior sub-transects. This resulted in 11 edge sub-transects and 10 interior sub-transects. The total sampling effort for nocturnal lemurs was 28.6 km at forest edge and 59.9 km at forest interior. We estimated animal encounter rates for each species as the number of individuals divided by the distance (km) surveyed and considering the variability among transects. We tested whether there was a difference in encounter rates of individuals and groups (response variables) between forest edge and interior (factor) via Generalised Linear Models. To take into account the different size of the sub-transects, we used encounter rates and not count of individuals, plus we added the distance walked in each transect as weight (i.e., known values that varies from observation to observation and are used to control for different observation efforts) in the analysis. We used the “glmmTMB” function in the “glmmTMB” package as this function allows different fit families. We tested different fit functions available in the “glmmTMB” package and included or excluded a zero-inflation term based on the QQ plot residuals and residual vs. predicted plot from the package “DHARMa”. The Tweedie family was selected for all the species. For the Tweedie family, we used an automatic selection of the variance function ($1< p < 2$) that is a mixture of Poisson and Gamma distributions for continuous distributions with a spike at zero [52]. For all tests, we considered $p = 0.05$ as level of significance. We ran all the analyses with R v 4.1.0.

We calculated the densities of lemurs present at the Ampasy valley. We analysed the data via the Multiple Covariate Distance Sampling method in Distance software [50,53] considering edge (11 sub-transects) vs. interior (10 sub-transects) as covariate in the analysis, thus using a total of 21 sub-transects. We firstly explored the untruncated and unbinned data fitted with key functions (half-normal, hazard rate, and uniform) and series adjustments (cosine and simple polynomial) [54]. Based on histograms, we determined whether and where to right-truncate data and how to bin observations into discrete distance classes to improve key function fit [54]. After the potential truncation, we compared models with the three key functions and their respective series expansions using Akaike's Information Criteria corrected for small sample sizes (AICc) and selected species-specific models based on the lowest AICc score (Table A1). All the models we report passed the goodness-of-fit test [50,53].

3. Results

3.1. Vegetation Surveys

We recorded 203 species from vegetation surveys, with *Pandanus longistylus*, *Brochoneura acumita*, *Uapaca thouarsii*, *Homalium planiflorum*, *Syzygium* sp. as most abundant species (Table A2). Edge effect on the vegetation structure can be detected until around 100 m in terms of tree diversity and abundance. The mean DBH and the coefficient of variation of the DBH did not have a significant variation depending on the distance from the forest edge (Figure 2; Table 2).

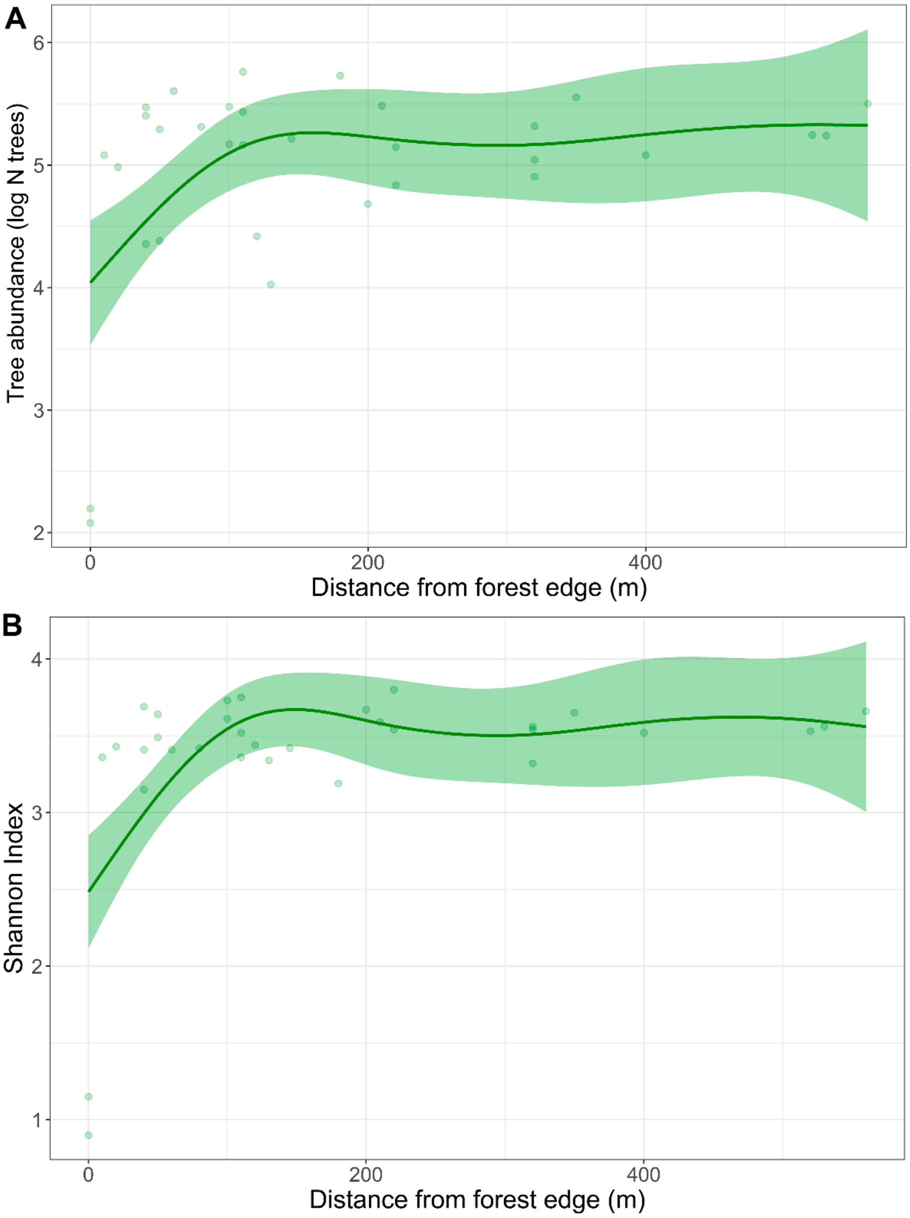

Figure 2. Significant results of the Generalised Additive Models to test the effect of distance from the forest edge on four vegetation parameters. The vegetation parameters are based on 33 vegetation plots at the Ampasy research station, north of the Tsitongambarika lowland rainforest, southeast Madagascar.

Table 2. Results of the Generalised Additive Models to explain the effect of distance from the forest edge on four vegetation parameters. The vegetation parameters are based on 33 vegetation plots at the Ampasy valley, north of the Tsitongambarika lowland rainforest, southeast Madagascar.

Response Variable	R-Squared	Intercept	Smooth Term		
		Estimate (St. Error)	Edf	F	p
Shannon Index	0.375	3.36 (0.09) **	3.67	5.68 **	0.003
Number of trees	0.280	4.96 (0.13) **	3.60	4.00 *	0.020
DBH	0.001	13.95 (0.32) **	1.00	0.08	0.785
DBH CV	0.028	4.01 (0.18) **	1.37	1.34	0.363

* $p < 0.05$ ** $p < 0.01$.

3.2. Lemur Surveys

The aye-aye was recorded twice in the forest interior and was not considered for further analyses. Collared brown lemurs and Madame Fleurette's sportive lemurs had significantly higher encounter rates in the forest interior than in the forest edge, while Southern bamboo lemurs, Southern woolly lemurs, and Anosy mouse lemurs had significantly higher encounter rates at forest edge (Tables 3 and A3). We estimated 0.96 groups/ha (95% CI: 0.78–1.19 groups/ha) of Anosy mouse lemur, 0.65 groups/ha (95% CI: 0.54–0.78 groups/ha) of Madame Fleurette's sportive lemur, 0.25 groups/ha of Southern woolly lemur (95% CI: 0.18–0.34 groups/ha) and dwarf lemur (95% CI: 0.10–0.60 groups/ha), 0.19 groups/ha (95% CI: 0.12–0.30 groups/ha) of collared brown lemur, and 0.13 groups/ha (95% CI: 0.08–0.23 groups/ha) of Southern bamboo lemur (Table 4).

Table 3. Encounter rates of individuals and groups, and total times individuals were encountered in 11 transects of forest edge and 10 transects of forest interior. The total distance walked at edge transects was 37.4 km for cathemeral lemurs, 28.6 km for nocturnal lemurs, 10.0 km for dwarf lemur. The total distance walked at interior transects was 74.8 for cathemeral lemurs, 59.9 km for nocturnal lemurs, 25.0 km for dwarf lemur. We compared the values between edge and interior transects via Generalised Linear Models (Tweedie distribution). Values are estimated model means and S.E.

Species	Forest Edge (≤100 m)			Forest Interior (>100 m)		
	Ind./km	Groups/km	N Encounters	Ind./km	Groups/km	N Encounters
Anosy mouse lemur (*Microcebus tanosi*)	1.99 ± 0.26 *	1.92 ± 0.25 *	57	1.28 ± 0.23	1.27 ± 0.12	77
Collared brown lemur (*Eulemur collaris*)	0.80 ± 0.16	0.19 ± 0.04	30	1.61 ± 0.16 *	0.35 ± 0.04 *	120
Dwarf lemur (*Cheirogaleus* sp.)	0.40 ± 0.13	0.40 ± 0.12	4	0.28 ± 0.07	0.24 ± 0.06	7
Madame Fleurette's sportive lemur (*Lepilemur fleuretae*)	1.57 ± 0.17	1.43 ± 0.16	45	2.57 ± 0.15*	2.31 ± 0.14 *	154
Southern bamboo lemur (*Hapalemur meridionalis*)	0.75 ± 0.17 *	0.27 ± 0.05	25	0.33 ± 0.07	0.20 ± 0.03	25
Southern woolly lemur (*Avahi meridionalis*)	1.54 ± 0.15 *	1.12 ± 0.09 *	32	0.69 ± 0.07	0.50 ± 0.04	41

* significantly higher ($p < 0.05$) based on Generalised Linear Models.

Table 4. Density estimates (groups and individuals per hectare) and total estimated number of individuals for six lemur species at the Ampasy valley (900 ha), north of the Tsitongambarika lowland rainforest, southeast Madagascar. Estimates are means and 95% CI obtained via Multiple Covariate Distance Sampling method. ESW: effective strip width.

Species	ESW	Probability of Detection	Mean Group Size	Density of Groups	Density of Individuals	N Total
Anosy mouse lemur (*Microcebus tanosi*)	7.38 (6.56–8.31)	0.57 (0.51–0.64)	1.02 (1.00–1.04)	0.96 (0.78–1.19)	0.97 (0.78–1.19)	869 (703–1075)
Collared brown lemur (*Eulemur collaris*)	7.64 (5.87–9.93)	0.51 (0.39–0.66)	4.55 (3.77–5.48)	0.19 (0.12–0.30)	0.57 (0.36–0.91)	513 (320–820)
Dwarf lemur (*Cheirogaleus* sp.)	5.36 (2.51–11.46)	0.45 (0.21–0.95)	1.10 (1.00–1.35)	0.25 (0.10–0.60)	0.27 (0.11–0.64)	233 (92–541)
Madame Fleurette's sportive lemur (*Lepilemur fleuretae*)	14.84 (13.46–16.35)	0.59 (0.54–0.65)	1.12 (1.08–1.15)	0.65 (0.54–0.78)	0.73 (0.61–0.87)	654 (545–784)
Southern bamboo lemur (*Hapalemur meridionalis*)	7.95 (5.87–10.79)	0.57 (0.42–0.77)	2.12 (1.57–2.87)	0.13 (0.08–0.23)	0.27 (0.15–0.45)	231 (132–403)
Southern woolly lemur (*Avahi meridionalis*)	11.83 (10.13–13.81)	0.74 (0.63–0.86)	1.38 (1.23–1.56)	0.25 (0.18–0.34)	0.32 (0.23–0.44)	286 (206–398)

4. Discussion

4.1. Depth of Edge Influence

We found that the depth of edge in the continuous lowland rainforest of Tsitongambarika, South-East Madagascar, is around 100 m for tree diversity and abundance. Understanding the distance at which biotic and abiotic parameters change significantly from the edge to the interior of the forest is of paramount importance for conservation in the tropics considering the proportions of remaining forest affected by forest edges globally [17,18] andin Madagascar in particular [34,35]. Several studies attempted to estimate a DEI in tropical forests (e.g., [28,30]), but there is a variability depending on the parameters used, the degree of habitat degradation, and the type of habitat.

The maximum DEI in primary tropical forests is expected to be lower (~25 m) than in degraded tropical forests (~350 m), and when the forest is primary but exposed to selective logging a DEI of 100 m, like in the study area, is often suitable [30]. In the dry deciduous forest of Mariarano in Madagascar, for example, the DEI for tree abundance was 200 m [28]. This may suggest that dry tropical forests might have a higher DEI than tropical rainforests. Andiratsitohaina et al. [28] also found a DEI up to 460 m for the height of large trees, although most of the other vegetation parameters had a DEI between 50 m and 240 m. However, previous research rarely assessed the DEI before distinguishing between edge and interior areas when estimating population densities of lemurs. For example, Lehman et al. [7] in Vohibola III rainforest defined as interior the transects that started after 750 m from forest edge and edge the transects until 500 m from forest edge, but vegetation parameters are not presented to support the choice of such large thresholds. In Lehman and Mercado-Malabet [27] it is suggested that that threshold was based on a mean depth of edge influence on vegetation of 526 m. For other taxonomic groups (herpetofauna and invertebrates), however, the DEI in rainforests is considered up to 25 m (e.g., [55,56]). Ries et al. [5] suggested to always estimate the DEI on site. As a general rule for studies that do not statistically estimate the DEI, they suggest abiotic and plant responses to extend up to 50 m, invertebrate responses up to 100 m, and bird responses 50–200 m. It is evident that there is a need for consistency when assessing edge effects, and that edge effect varies depending on the taxa studied.

4.2. Lemur Edge Responses

The lemur community at Ampasy responds to edge effects to different degrees, with Anosy mouse lemur, Southern bamboo lemur and Southern woolly lemur showing a positive edge response, and collared brown lemur and Madame Fleurette's sportive lemur showing edge repulsion. Southern bamboo lemur did not show a difference in group encounter rates. A possible explanation for this is that within the 100 m boundary of the edge groups become larger compared to the more interior forest as they are more exposed to predators during feeding. This species, in fact, has been shown to spend a large amount of time feeding on graminoids on the ground [45], and this may be the main reason why it prefers forest edges for foraging. In addition, leaves in general have higher protein concentrations at the forest edge due to increased sun exposure [24,45]. Therefore, the increased quality of leaves at the forest edge may attract folivorous primates. We cannot exclude, however, that the visibility in the forest interior is lower and that we underestimated the individual encounter rate in the interior, meaning that Southern bamboo lemur might show a neutral response. The neutral edge response is supported by the fact that the species is expected to prefer the forest interior for resting since it gives more options to find large sleeping trees and provides more protection from hunting [36,57].

The folivorous Southern woolly lemur also showed a positive edge response. The pattern observed in Southern woolly lemur is different than the other nocturnal folivore present in this habitat, Madame Fleurette's sportive lemur, that showed a negative edge response, and this can be part of the strategies of habitat selection used to reduce competition between the two species. Madame Fleurette's sportive lemur and Southern woolly lemur at Ampasy, in fact, have been shown to rely on mechanisms of niche separation [25,58]. Southern woolly lemur is also more flexible and is adapted to live in forests with smaller trees (e.g., the littoral forest [59]). Madame Fleurette's sportive lemur at Ampasy has a diet higher in fruits and flowers than sportive lemurs in other regions of Madagascar [25]. The diet, combined with the need to sleep in large trees with holes [60], and the need to use large vertical supports for locomotion [44] were the main reasoning why we expected a negative edge response by Madame Fleurette's sportive lemur. Dwarf lemur was also expected to show a negative edge response due to the need to find tree holes where to hibernate for months [6], but we found a neutral edge response. This might be due to the limited sightings for this species, which was only detected 11 times; thus our findings on dwarf lemur should be taken with caution.

The response of collared brown lemur is in line with recent, country-scaled analysis showing that habitat fragmentation and edge density negatively affects the distribution of *Eulemur* species in general and of collared brown lemur in particular [47]. Similar to collared brown lemur, red-fronted brown lemurs (*E. rufus*) also displayed a negative edge response at Vohilbola III [21]. The lower density of red-fronted brown lemurs within the forest edge was tentatively linked to a lower abundance of fruiting trees in this forest section. Balko and Underwood [61] found that tree DBH and fruit abundance usually covary in Madagascar, which may explain the observed negative response. The density of specific tree species (e.g., *Uapaca thouarsii*), priority food items for collared brown lemur [62] may also have determined the preference towards the interior part of the forest. The density of large trees is, in fact, often a determinant of the abundance for frugivorous species [14]. An alternative explanation for collared brown lemur to avoid forest edges might be related to the higher visibility and thus vulnerability to hunting pressure in the area [36], presumably higher at forest edges. The response to habitat edge of this genus, however, is not a unitary one. Red-bellied lemurs (*E. rubriventer*) in Vohibola III, for example, were classified as having a neutral to positive edge response [21]. Lehman et al. [21] attributed this response to seasonal effects of the study as it was conducted during the dry season when fruit availability is low and *Eulemur* can supplement their diet with leaves and stems [41,63,64]. Lehman and Mercado-Malabet [27], however, further investigated this aspect and found that red-bellied lemurs did not show a seasonal edge response.

4.3. Lemur Abundance

Understanding animals' edge responses is key to producing accurate population size estimates and assessing the correct conservation status of threatened species. For example, significant overestimates are potentially generated by assuming that edge density estimates may be used to calculate population size over the entire area of occupancy of an edge positive species [2,65]. Considering that the abundance of 85% of vertebrate species is affected, either positively or negatively, by forest edges [2], it is clear that this correction factor should be included while estimating population sizes. Almost half of the Malagasy rainforest is within 100 m distance from the edge [35], meaning that most of the lemur species are affected by edge effect to some extent.

When comparing density estimates at Ampasy to the density of the same species in other rainforests (Table 5), we can see that moderate to high edge impacts can determine much lower density estimates even for the species that showed an edge preference. Estimates of population abundance based on single sites may thus be very divergent. Furthermore, additional factors apart from edge could have concurred in explaining densities. For example, the Ampasy forest hosts high abundances of folivorous lemurs considering that the density of Madame Fleurette's sportive lemur and Southern woolly lemur there is higher than in the adjacent rainforest of Andohahela (Table 5) and in other rainforests (e.g., Andringitra [66], Marojejy [67]). One possible explanation for this might be the lack of competition of other highly folivorous species such as the diurnal Indriidae. Other sites that host diurnal Indriidae, however, still host species of *Avahi* and *Lepilemur* at high densities (e.g., Marotandrano [68], Analamay-Mantadia forest corridor and Ankerana [69]. Altitude might also have an influence on these two species in terms of tree size and leaf productivity [70].

Table 5. Density estimates of lemurs present in the study area and in neighbouring areas in South-East Madagascar. We considered edge effect as low when the total area within 100 m from forest edge in proximity of the coordinates of the study area (~1km radius) is ≤20%, moderate for values 20 < x ≤ 50%, high for values >50%. None means that edge is >1km from the coordinates of the study area. Sources: Ampasy (this study); Andohahela [71]; Andringitra [66]; Beakora [68]; Kalambatritra [72,73]; Midongy-Sud [74].

Species	Site	Edge Effect	Density (ind/ha)
Anosy mouse lemur (*Microcebus tanosi*)	Andohahela	None	1.02
	Ampasy	Low	0.97
	Kalambatritra	Moderate	0.11
	Beakora	High	0.06
Collared brown lemur (*Eulemur collaris*)	Andohahela	None	0.11
	Ampasy	Low	0.57
	Midongy-Sud	Low	0.11
	Kalambatritra	Moderate	0.15
	Beakora	High	0.12
Dwarf lemur (*Cheirogaleus* sp.)	Andohahela	None	0.97
	Andringitra	None	1.10
	Ampasy	Low	0.27
	Kalambatritra	Moderate	0.08
	Beakora	High	0.08
Madame Fleurette's sportive lemur (*Lepilemur fleuretae*)	Andohahela	None	0.07
	Ampasy	Low	0.73
Southern bamboo lemur (*Hapalemur meridionalis*)	Andohahela	None	0.15
	Andringitra	None	0.21
	Ampasy	Low	0.27
	Kalambatritra	Moderate	0.07
	Beakora	High	0.11
Southern woolly lemur (*Avahi meridionalis*)	Andohahela	None	0.17
	Ampasy	Low	0.32
	Kalambatritra	Moderate	0.03
	Beakora	High	0.02

In contrast to *Lepilemur*, we found low densities of dwarf lemur at Ampasy. Although we do not have direct evidence of a negative correlation between encounter rates of the two species, a low encounter rates of *L. fleuretae* at Andohahela [71] and *L. mustelinus* at Anjaharibe Sud [75] corresponded to high encounter rates of greater dwarf lemur *Cheirogaleus major*. A possible explanation of this relationship is an interspecific resource competition between *Lepilemur* and *Cheirogaleus*. In fact, *Cheirogaleus* use tree holes for their hibernation period [51] and the high density of Madame Fleurette's sportive lemur at Ampasy might be a limiting factor for finding suitable tree holes. Other areas, however, host a high density of both *Cheirogaleus* and *Lepilemur* species (e.g., Ankerana [69]), and this might be favoured by a high density of suitable sleeping sites. Dwarf lemur at Ampasy may also be at low density given the seasonal availability of fruits in this forest [25] that may represent a limitation also considering the relatively high density of collared brown lemur. Other factors such as human disturbance, altitude, and plant productivity may also concur in shaping animal abundances and edge responses [27,70,76].

5. Conclusions

Our results suggest that the lemur community at Ampasy cope to different degrees with edge effects, with Anosy mouse lemur, Southern bamboo lemur and Southern woolly lemur showing a positive edge response, and collared brown lemur and Madame Fleurette's sportive lemur showing an edge repulsion. Ampasy is a well-preserved forest area with low anthropogenic disturbance but with high levels of hunting especially in the past, and these responses may change with increasing human encroachment that is indicated by the ratio of edge to interior forest [77]. Campera et al. [70] highlighted that the remnant lowland rainforests of Madagascar host some of the highest abundance of lemurs and need to be preserved with high priority. It is important to reduce the human pressure on the forest to avoid the increase in edge areas that may determine the future decrease in lemur population especially for collared brown lemur that is the largest frugivore in the area and one of the most sensitive species to edge expansions [78]. Conservation-related activities such as forest management by local stakeholders, researchers' presence, and conservation education may reduce forest exploitation and limit the edge effect [36,79,80]. The effect of edge on the abundance of primates is often understudied despite its recognised effect in 85% of vertebrate species [3]. We highlight the importance of considering edge effect and the relative ecological and anthropogenic consequences when producing estimates of population sizes and informing conservation management.

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Appendix A

Table A1. List of model tested via the Multiple Covariate Distance Sampling method in Distance software and their AIC scores. In bold we highlight the selected model for each species.

Species	Key Function	Expansion	AIC
Anosy mouse lemur	Half-normal	Simple polynomial	603.6
		Cosine	605.3
	Hazard-rate	Simple polynomial	606.4
		Cosine	**601.9**
	Uniform	Simple polynomial	604.5
		Cosine	606.8
Collared brown lemur	Half-normal	Simple polynomial	**167.7**
		Cosine	168.0
	Hazard-rate	Simple polynomial	168.4
		Cosine	168.9
	Uniform	Simple polynomial	168.5
		Cosine	169.1
Dwarf lemur	Half-normal	Simple polynomial	50.7
		Cosine	52.2
	Hazard-rate	Simple polynomial	**49.4**
		Cosine	49.8
	Uniform	Simple polynomial	49.7
		Cosine	50.0
Madame Fleurette’s sportive lemur	Half-normal	Simple polynomial	1058.0
		Cosine	1059.4
	Hazard-rate	Simple polynomial	**1056.1**
		Cosine	1057.2
	Uniform	Simple polynomial	1059.1
		Cosine	1060.2
Southern bamboo lemur	Half-normal	Simple polynomial	**123.8**
		Cosine	125.9
	Hazard-rate	Simple polynomial	125.3
		Cosine	126.9
	Uniform	Simple polynomial	125.1
		Cosine	126.7
Southern woolly lemur	Half-normal	Simple polynomial	**287.2**
		Cosine	289.6
	Hazard-rate	Simple polynomial	288.8
		Cosine	290.3
	Uniform	Simple polynomial	289.1
		Cosine	289.8

Table A2. Species present at the Ampasy forest with relative abundance in edge and interior based on 33 vegetation plots.

Clade	Order	Family	Species	Common Name	Edge (trees/ha)	Interior (trees/ha)
Magnoliids	Laurales	Lauraceae	*Aspidostemon lacrimans*	Viary	2.5	0.3
			Cryptocarya sp. 1	Remilaza	0.6	0.0
			Cryptocarya sp. 2	Tavolohazo	20.2	15.9
			Ocotea racemosa	Varongy	24.4	18.0
			Ocotea grayi	Valotry	7.6	4.3
			Potameia incisa	Tsalela	0.0	0.1
		Monimiaceae	*Tambourissa religiosa*	Ambora	16.8	35.5
			Tambourissa thouvenotii	Bety	9.8	7.3
	Magnoliales	Annonaceae	*Fenerivia chapelieri*	Hazaomby	0.0	0.1
			Monanthotaxis madagascariensis	Rangomafotry	3.6	13.3
			Xylopia buxifolia	Fotsivavy	17.8	16.1
		Myristicaceae	*Brochoneura acumita*	Mafotra	91.8	104.2
Monocots	Alismatales	Araceae	*Pothos scandens*	Mandrio	0.0	1.0
	Arecales	Araliaceae	*Cuphocarpus aculeatus*	Tsitongampossa	4.5	0.0
			Neocussonia vantsilana	Voantsila	23.2	19.7
			Polyscias pentamera	Batsiala	1.3	0.7
		Arecaceae	*Dypsis arenarum*	Hirihiry	0.0	2.3
			Dypsis lilacina	Telopoloambilany	6.2	15.2
			Dypsis mananjarensis	Lafa	0.9	3.2
			Dypsis nodifera	Tavilokoko	0.0	0.3
			Dypsis prestoniana	Mangidy	2.7	3.2
			Dypsis pustulata	Vonotry	25.8	16.1
			Louvelia lakatra	Lakatry	0.0	1.4
			Orania longisquama	Tsindro	1.8	0.9
			Ravenala madagascariensis	Ravinala	0.7	0.0
			Ravenea nana	Hanivo	3.6	5.1
	Asparagales	Asparagaceae	*Dracaena reflexa*	Falinandro	11.6	16.1
		Iridaceae	*Aristea angustifolia*	Midinigiavy	0.0	1.0
	Pandanales	Pandanaceae	*Pandanus longistylus*	Fandra	123.9	105.1
Eudicots	Aquifoliales	Aquifoloaceae	*Ilex mitis*	Hazondrano	30.3	34.0
	Asterales	Asteraceae	*Brachylaena merana*	Hazotona	0.0	0.5
			Centauropsis antanossi	Fotsivaliky	0.0	1.7
	Boraginales	Boraginaceae	*Ehretia seyrigii*	Vatoa	0.0	0.5
	Brassicales	Capparaceae	*Crateva obovata*	Faritraty	0.9	3.2
	Buxales	Buxaceae	*Buxus rabenantoandroi*	Retsiriky	0.0	0.7
			Didymeles perrieri	Fanala	0.0	0.3
	Caryophyllales	Asteropeiaceae	*Asteropeia micraster*	Fanolantolo	0.0	0.3
			Asteropeia multiflora	Fanolabemavao	0.0	0.9
			Asteropeia rhopaloides	Fanola	0.9	0.0
		Physenaceae	*Physena madagascariensis*	Retsonzo	0.9	1.7
	Celastrales	Celastraceae	*Brexia madagascariensis*	Voakarepoky	0.7	0.0
			Brexiella sp.	Resilaitry	0.0	0.5
			Cassine micrantha	Harambohazo	0.0	0.5
			Polycardia libera	Tsimahasoky	3.3	0.0
	Crossosomatales	Aphloiaceae	*Aphloia theiformis*	Fandramana	15.2	12.9
	Cucirbitales	Anisophylleaceae	*Anisophyllea phallax*	Hazomamy	12.5	16.1
	Dilleniales	Dilleniaceae	*Dillenia triqueta*	Varikanda	13.4	9.6
	Ericales	Ebenaceae	*Diospyros* sp. 1	Hazomety	45.5	62.0
			Diospyros sp. 2	Hazomasy	9.8	5.1
		Lecythidaceae	*Barringtonia racemosa*	Kamboky	2.0	0.0
		Primulaceae	*Oncostemum* sp. 1	Hazotoho	0.0	1.4
			Oncostemum sp. 2	Mamotanylona	4.6	8.3
		Sapotaceae	*Capurodendron pervillei*	Beladitra	0.0	1.7

Table A2. *Cont.*

Clade	Order	Family	Species	Common Name	Edge (trees/ha)	Interior (trees/ha)
			Capurodendron sp.	Nanto	57.0	53.7
			Chrysophyllum boivinianum	Rehiaky	8.0	14.2
			Donella delphinensis	Hazomiteraky	4.6	3.7
			Faucherea tampoloensis	Natoroboky	0.7	0.3
			Mimusops coriacea	Tendrokazo	2.7	3.2
			Sideroxylon tambolokoko	Tambolokoko	1.3	0.3
	Fabales	Fabaceae	*Albizia graveana*	Fandrianakanga	1.3	2.3
			Albizia gummifera	Mendoravy	1.8	27.5
			Calliandra thouarsiana	Menbolazo	0.0	1.7
			Cynometra commersoniana	Voariotry	2.7	1.8
			Cynometra madagascariensis	Mampay	60.6	21.1
			Dalbergia baronii	Manary	1.8	0.9
			Dalbergia delphinensis	Tombobisy	5.3	1.8
			Dalbergia madagascariensis	Andromena	0.0	0.5
			Indigofera perrieri	Hengitry	2.0	0.0
			Intsia bijuga	Harandrato/Intsy	2.5	2.6
			Mimosa latispinosa	Romino	0.0	1.4
			Phylloxylon sp.	Mahasalama	0.0	1.7
			Sylvichadsia grandiflora	Fanamo	17.8	15.2
			Viguieranthus brevipennatus	Kingiza	0.0	0.5
			Viguieranthus glandulosus	Hazomallany	9.8	6.4
	Gentianales	Apocynaceae	*Carissa spinarum*	Hazolahy	0.7	0.0
			Mascarenhasia speciosa	Tsilondrano	0.0	0.9
			Petchia madagascariensis	Kabokala	9.8	18.4
			Plectaneia thouarsii	Hazomanahaky	0.0	0.7
			Sarcostemma viminale	Bemavao	0.0	0.9
		Loganiaceae	*Anthocleista madagascariensis*	Lendemilahy	1.8	2.8
		Rubiaceae	*Bremeria trichophlebia*	Tangalavo	0.0	0.5
			Bremeria scabridior	Fantora	1.8	7.8
			Breonia fragifera	Hafovalotry	0.0	1.4
			Canephora madagascariensis	Hazongalala	14.3	15.2
			Coffea sp.	Manibary	10.7	9.2
			Enterospermum sp.	Mangavoa	0.0	0.9
			Gaertnera macrostipula	Hazondengo	10.7	11.0
			Gaertnera raphaelii	Tanatananala	0.0	0.5
			Hyperacanthus poivrei	Taolana	41.0	39.5
			Hyperacanthus rajeriarisonae	Taolanampossy	0.9	1.8
			Ixora sp.	Masosoraky	0.0	1.4
			Janotia macrostipula	Valopangady	1.8	0.5
			Peponidium pallens	Robelo	2.0	0.7
			Psychotria aegialodes	Hazombato	1.3	0.0
			Psychotria glaucifolia	Fotsivoho	2.0	0.0
			Pyrostria media	Fantsikaitry	42.8	46.4
			Rothmannia sp. 1	Taolanamainty	3.3	0.0
			Rothmannia sp. 2	Taolanambariky	1.8	0.7
			Rothmannia thouarsii	Valopossy	1.3	0.0
			Saldinia proboscidea	Lengohazo	1.3	1.0

Table A2. *Cont.*

Clade	Order	Family	Species	Common Name	Edge (trees/ha)	Interior (trees/ha)
			Saldinia sp.	Hazondranoka	0.0	0.9
	Lamiales	Bignoniaceae	*Phyllarthron articulatum*	Zaha	0.0	0.5
			Phyllarthron ilicifolium	Zahambe	0.0	0.3
			Rhodocolea racemosa	Sikondrokondro	0.0	0.3
		Verbenaceae	*Coelocarpum humbertii*	Rombavola	0.0	1.0
		Lamiaceae	*Vitex beraviensis*	Hazomahavelo	0.0	0.7
	Laurales	Monimiaceae	*Decarydendron* sp.	Madinigavy	0.9	0.0
	Malpighiales	Chrysobalanaceae	*Magnistipula tamenaka*	Tamenandrano	0.0	1.0
		Clusiaceae	*Calophyllum inophyllum*	Vitao	34.8	31.7
			Garcinia aphanophlebia	Ditsaky	27.6	24.8
			Garcinia madagascariensis	Betsivo	0.0	0.3
			Garcinia pauciflora	Akily	1.3	0.7
			Garcinia verrucosa	Zambo	8.9	12.9
			Symphonia tanalensis	Haziny	33.9	44.1
		Erythroxylaceae	*Erythroxylum capitatum*	Menahihy	67.7	56.0
		Euphorbiaceae	*Acalypha* sp.	Maintsoravy	1.3	1.0
			Anthostema madagascariensis	Bamby	2.7	17.0
			Croton cassinoides	Tolaky	0.7	0.0
			Croton louvelii	Singena	3.6	2.8
			Drypetes madagascariensis	Remboky	2.0	0.0
			Macaranga cuspidata	Talaka	0.0	0.3
			Macaranga obovata	Mokarana	12.5	7.8
			Suregada adenophora	Kalavelo	10.7	6.0
		Hypericaceae	*Harungana madagascariensis*	Haronga	6.2	1.8
			Psorospermum brachypodum	Harongampanihy	3.6	4.6
		Ochnaceae	*Ouratea anceps*	Hazondraotry	26.7	24.8
			Ouratea sp.	Marandravy	4.6	1.4
		Phyllanthaceae	*Cleistanthus boivinianus*	Tainbarika	9.8	12.9
			Flueggea sp.	Tsimarefy	0.9	0.9
			Thecacoris madagascariensis	Hazondranoha	0.0	2.3
			Uapaca thouarsii	Voapaky	85.6	83.1
			Wielandia leandriana	Votakala	18.7	19.3
			Wielandia mimosoides	Korofoky	16.9	16.5
		Salicaceae	*Calantica* sp.	Marotana	0.0	0.5
			Homalium axillare	Lapivahatry	2.7	18.8
			Homalium brevipedunculatum	Roandrano	2.0	0.7
			Homalium lucidum	Tsilavimbinanto	1.8	1.8
			Homalium planiflorum	Hazofotsy	98.0	63.4
			Ludia antanosarum	Fantsikoho	1.3	1.0
			Ludia ludiifolia	Hazofotsindroka	1.3	0.0
			Scolopia erythrocarpa	Zora	21.4	31.7
			Scolopia orientalis	Tsimalanilamba	2.7	0.9
		Violaceae	*Rinorea angustifolia*	Voafontsy	1.3	0.3
			Rinorea arborea	Hazondomohy	0.0	0.3
	Malvales	Malvaceae	*Dombeya oblongifolia*	Hafomena	10.7	12.9
			Dombeya antsianakensis	Valimafy	16.9	10.6
			Dombeya australis	Berehoky	3.6	1.4
			Grewia apetala	Akolahikafitra	0.0	0.5
			Grewia cuneifolia	Hafopossy	2.7	4.6
			Grewia sp.	Vaoreoky	1.3	0.3

Table A2. *Cont.*

Clade	Order	Family	Species	Common Name	Edge (trees/ha)	Interior (trees/ha)
		Sarcolaenaceae	*Leptolaena pauciflora*	Fonto	1.8	3.2
			Schizolaena exinvolucrata	Sokazo	1.3	0.0
		Sphaerosepalaceae	*Rhopalocarpus coriaceus*	Hazondandy	9.8	2.8
		Combretaceae	*Combretum grandidieri*	Tamenaroanga	0.0	1.0
			Combretum subumbellatum	Tamenakanga	1.3	1.0
			Combretum villosum	Voatotkala	0.0	1.4
			Terminalia fatraea	Fatra	0.0	1.0
			Terminalia cephalota	Beranoampo	0.0	1.4
		Melastomataceae	*Memecylon longipetalum*	Tomizo	6.2	10.6
		Myrtaceae	*Eugenia cloiselii*	Roapasy	10.7	17.0
			Eugenia sp. 1	Mahalaza	0.0	0.3
			Eugenia sp. 2	Robavy	16.0	17.4
			Syzygium sp.	Rotry	77.5	93.2
	Oxalidales	Cunoniaceae	*Weinmannia baehniana*	Ringitry	0.9	1.8
			Weinmannia stenostachya	Lalo	16.0	11.0
		Elaeocarpaceae	*Sloanea rhodantha*	Voandoza	1.3	1.0
	Proteales	Proteaceae	*Dilobeia tenuinervis*	Hivao	0.9	3.2
			Dilobeia thouarsii	Tamenaky	51.7	34.9
			Faurea forficuliflora	Tolabao	0.7	0.0
	Rosales	Cunoniaceae	*Pterophylla rutenbergii*	Hazomena	0.7	0.0
		Moraceae	*Maillardia montana*	Homamata	0.7	0.3
			Streblus dimepate	Dipaty	9.8	8.7
			Treculia africana	Tsarepaly	0.0	1.4
			Trilepisium madagascariensis	Vetitindaza	0.0	1.4
	Sapindales	Anacardiaceae	*Baronia taratana*	Fonofononanahary	0.7	0.0
			Micronychia bemangidiensis	Taranta	8.0	5.1
			Poupartia chapelieri	Sisikandrongo	1.3	1.0
			Soreindeia madagascariensis	Voatsiringy	2.0	0.0
		Burseraceae	*Canarium boivinii*	Haramy	15.2	7.3
		Meliaceae	*Astrotrichilia rakodomena*	Rakodimena	2.0	0.0
			Malleastrum sp.	Mirangasoa	0.0	0.5
			Neobeguea leandreana	Hazolava	0.0	0.5
			Neobeguea mahafaliensis	Bemahova	0.0	0.5
			Turraea sp.	Tandria	0.0	0.9
		Rutaceae	*Vepris ampody*	Ampodinala	3.3	0.0
			Vepris elliotii	Ampoly	1.3	1.0
			Vepris fitoravina	Fitoravina	1.7	6.4
			Vepris macrophylla	Beravy	1.3	0.0
			Zanthoxylum madagascariense	Monongo	0.9	0.0
		Sapindaceae	*Allophyllus decaryi*	Malamaravy	0.0	0.7
			Cardiophyllariopsis perrieri	Kafatra	0.7	0.0
			Plagioscyphus sp.	Takombohazo	2.0	0.0
			Tina fulvinervis	Vilo	0.0	1.4
			Tina striata	Hazomoro	0.0	0.3
			Tina thouarsiana	Sanirambaza	6.2	8.7
			Tinopsis conjugata	Sanira	33.0	48.7

Table A2. *Cont.*

Clade	Order	Family	Species	Common Name	Edge (trees/ha)	Interior (trees/ha)
		Simaroubaceae	*Quassia indica*	Mangaroky	46.3	60.1
	Solanales	Convolvulaceae	*Humbertia madagascariensis*	Hendranendra	8.0	4.1
NA	NA	NA	?	Bemisiry	0.7	0.0
			?	Latakasosoa	0.7	0.0
			?	Marovola	0.0	3.2
			?	Masoranonandroa	0.7	1.4
			?	Palimisy	6.2	0.0

Table A3. Results of the Generalised Linear Models with the abundance of individuals or groups of different lemur species as response variable and edge vs. interior as predictor.

Response Variable	Response Variable	Predictor	Estimate	Std. Error	Z Value	*p* Value
Anosy mouse lemur	Groups	Intercept	0.65	0.13	5.08 **	<0.001
		Interior	−0.42	0.16	−2.60 **	0.009
	Individuals	Intercept	0.69	0.13	5.38 **	<0.001
		Interior	−0.44	0.16	−2.74 **	0.006
Collared brown lemur	Groups	Intercept	−1.68	0.22	−7.72 **	<0.001
		Interior	0.62	0.25	2.54 *	0.011
	Individuals	Intercept	−0.22	0.20	−1.09	0.274
		Interior	0.69	0.22	3.08 **	0.002
Dwarf lemur	Groups	Intercept	−0.92	0.31	−2.97 **	0.003
		Interior	−0.51	0.40	−1.30	0.194
	Individuals	Intercept	−0.92	0.32	−2.91 **	0.004
		Interior	−0.36	0.39	−0.92	0.359
Madame Fleurette's sportive lemur	Groups	Intercept	0.36	0.11	3.20 **	0.001
		Interior	0.48	0.13	3.70 **	<0.001
	Individuals	Intercept	0.45	0.11	4.11 **	<0.001
		Interior	0.49	0.13	3.91 **	<0.001
Southern bamboo lemur	Groups	Intercept	−1.32	0.20	−6.46 **	<0.001
		Interior	−0.29	0.26	−1.11	0.267
	Individuals	Intercept	−0.29	0.22	−1.31	0.192
		Interior	−0.81	0.29	−2.74 **	0.006
Southern woolly lemur	Groups	Intercept	0.11	0.08	1.35	0.176
		Interior	−0.80	0.12	−6.80 **	<0.001
	Individuals	Intercept	0.43	0.10	4.43 **	<0.001
		Interior	−0.81	0.14	−5.95 **	<0.001

* $p < 0.05$; ** $p < 0.01$.

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