



Lessons learned from *Lepilemur* spp. for habitat restoration in Madagascar

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Abstract – Forest restoration has become a conservation priority in Madagascar, with most initiatives guided by current national or international forest restoration standards. These frameworks predominantly focus on tree species composition, often considering food trees for targeted conservation taxa, but neglect structural habitat requirements of forest-dependent fauna. Given the long-term perspective of forest restoration, we argue that the needs of animals should be explicitly considered from the initial phase of project design. Using a nation-wide comparison of tree characteristics, we demonstrate that 17-18 species of the Malagasy lemur genus *Lepilemur* from 24 sites show rather consistent associations with large trees. We interpret this association as an indication of the reliance on vertical structures to facilitate their locomotion by clinging and leaping and for tree holes as shelter for resting, thermoregulation or predation. To facilitate locomotion, some fast growth tree species might provide the supports needed for efficient locomotion. Because a substantial time lag exists between tree establishment and the development of suitable cavities, artificial shelters (e.g., nest-boxes) could be one option to make growing forests more attractive not only for colonisation by some lemur species, but also for a large variety of other taxa, ranging from fungi to many vertebrate species. Planting tree species known to produce cavities rather quickly would accelerate the development towards comprehensive ecological restoration.

Keywords – forest restoration, lemurs, locomotion, nest boxes, tree holes.

Introduction

Restoration of native forests has become an important component of conservation efforts

globally, including Madagascar (e.g., Culbertson *et al.*, 2022; Eppley *et al.*, 2024). Although comprehensive national and international guidelines exist for ecological restoration

(ALAMINO: <http://www.environnement.mg/>; The Global Biodiversity Standard: <https://www.biodiversitystandard.org/our-method/>; or the standards of the Society for Ecological Restoration; Gann *et al.*, 2019), restoration activities are often largely influenced by the constraints that seeds and seedlings are available in sufficient quantities for a variety of species and that the sown or planted saplings actually survive (Corlett, 2016; Reid *et al.*, 2025). Specific guidelines to optimise faunal restoration are not available yet, though restoration planners commonly plan to restore forest connectivity more for animals than for plants – in Madagascar mostly with a focus on lemurs (e.g., Manjaribe *et al.*, 2013). Food trees are often incorporated into restoration concepts for frugivores (Holloway, 2003; Beeby *et al.*, 2023) and in the context of facilitated forest restoration via seed dispersal (Steffens *et al.*, 2022, 2023; Ganzhorn *et al.*, 2024; Ramananjato, 2025). Food trees for specialised folivores or exudate-feeding species have received far less attention, though the latter face a higher risk of extinction in forests lacking specific resources (Eppley *et al.*, 2020). Moreover, although numerous studies have investigated structural habitat components within the home range of species, relatively few studies have addressed the question of which specific structural components are associated with the presence or abundance of species, such as structures needed for locomotion, sleeping sites, hibernation and breeding in mammals and birds (e.g., Ganzhorn, 1989; Warren and Crompton, 1998a,b; Hino *et al.*, 2002; Dausmann *et al.*, 2004; Rasoloaharijaona *et al.*, 2008; Rakotomalala *et al.*, 2017; Steffens *et al.*, 2017, 2023; Ratovonamana *et al.*, 2024; Rabemananjara *et al.*, 2026).

Certainly, any restoration project has to start with planting a subset of the botanical diversity found in the habitat to be restored, assuming that additional plants and animals will colonise the area over time. Yet, forest restoration is a long-term project, often requiring several decades before restored forests become usable

by even a subset of Madagascar's endemic animals (Andriamandimbiarisoa *et al.*, 2015). Consequently, it would be advantageous to integrate, from the outset, native plant species with the potential to develop into essential structural habitat components for animal species.

To draw attention to possible improvements of restoration planning, we compiled island-wide data on tree size and tree species, using their relationships to the presence or abundance of sportive lemurs (*Lepilemur* spp.) as an example. Sportive lemurs might be one of the easiest primate genera to illustrate faunal needs apart from food in restoration guidelines, because they have small and stable home-ranges that can be described in more detail than habitat requirements of other species with much larger home ranges. We are not arguing that the needs of these species should be prioritised over the importance of other guilds or main ecological restoration principles, but simply that their requirements illustrate an additional dimension that may need to be taken into account.

Our objective was to assess whether areas used by different species of *Lepilemur* differed in tree structural or floristic components from areas used less frequently or not at all by the same lemur species within the same site. If the results could be generalised, they may help inform guidelines for forest restoration, initially from a lemur-centered perspective, but then also for comprehensive ecological restoration.

Material and methods

We extracted information or reanalysed data from published literature and supplemented the database with several unpublished datasets on *Lepilemur* spp. yielding 24 studies on 17 or 18 different species of *Lepilemur* (fig 1; table 1). The *Lepilemur* species present at one site in the Analanjirofo region could not be identified without genetic information that was not available.

We included studies that had measured tree densities and/or tree species richness and relative densities of *Lepilemur* spp. and where different abundances of *Lepilemur* spp. could be linked to different botanical descriptions within a given site. Methods used to inventory lemurs

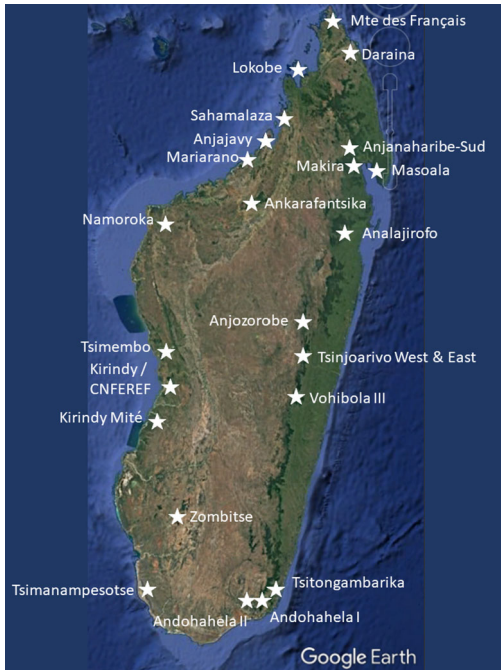


Figure 1. Locations of studies on *Lepilemur* spp. that allowed vegetation characteristics to be linked with variation in *Lepilemur* abundance or occurrence.

and to quantify tree characteristics varied substantially among studies. However, within each study area, methods for assessing *Lepilemur* abundance and associated botanical descriptions were consistent.

Forest descriptions of 15 of the 24 studies were based on vegetation plots, eight were based on point-centred quarters, and one study used tree counts along transects (Supplement S1). For forest characteristics, we considered the number of trees with diameters at breast height (DBH) of 5–9.9 cm, trees with a DBH ≥ 10 cm, and combining the two size classes (i.e., all trees with a DBH ≥ 5 cm). We also recorded the number of tree species, the number of food trees, and the number of food tree species per site and size class and for the two size classes combined. Not all of this information was available for all *Lepilemur* species. Fifteen studies recorded tree species composition in their botanical inventories, and ten studies also identified food trees and food tree species (table 1, Supplement material S2).

Study sites and the methods used for *Lepilemur* inventories are only summarised briefly here; detailed site-specific information is provided in Supplementary material S1. More general information on the protected areas is available in Goodman *et al.* (2018).

STATISTICAL ANALYSES

In 23 of the studies, transects represented the primary unit of analysis, with *Lepilemur* presence/absence or high/low abundance classified at the transect level within each study area. We associated these transects with the botanical descriptions derived from plots, PCQs, or tree counts conducted along the transects. One study at Montagne des Français was based on radio-tracking *L. septentrionalis*. Here, we distinguished between botanical plots that had been visited frequently or rarely by the animals. Due to different survey methods, “abundant” and “rare” are site-specific and represent relative classifications.

At each site we compared plots or transects associated with high abundances or the presence of *Lepilemur* spp. with plots or transects in which individuals were rare or absent. For each site, we performed Mann-Whitney *U*-tests (Sokal and Rohlf, 1981) on the various botanical measures. Significance levels for these intra-site comparisons were not considered meaningful, because the comparisons within sites were based on very different and, in most cases, very low sample sizes. We calculated effect sizes (*r*) for the various Mann-Whitney *U*-tests as $r = z/\sqrt{N}$, with *N* = sample size (Fritz *et al.*, 2012). This allows a multi-site comparative analysis using standardised effect sizes as the primary response variable.

LEPILEMUR TAXONOMY

The taxonomy of the genus *Lepilemur* has been highly dynamic in recent years, with several new species descriptions published and others potentially pending. Since many species were described primarily on the basis of genetic data and external morphological measurements, and because morphological differences among species can be subtle, comparable genetic or

Table 1. Characteristics of habitats associated with the presence of *Lepilemur* spp.

Botanical descriptions	Number of trees		Number of tree species			Number of food trees			Number of food tree species			
	5-9.9	≥ 10	All ≥ 5	5-9.9	≥ 10	All ≥ 5	5-9.9	≥ 10	All ≥ 5	5-9.9	≥ 10	All ≥ 5
<i>Lepilemur cf ahmansonii</i> : Namoroka												
Abundant (N = 4) PCQ	79.5	79.5	159	25	30.5	39.5						
	77-80	72-80	149-160	20-26.8	28-32.5	36-41						
Rare (N = 1)	68	67	135	35	31	47						
Z	1.45	1.45	1.45	-1.41	-0.36	-1.45						
<i>Lepilemur betsileo</i> : Vohibola III												
Abundant (N = 4) 1000 m ² plots	43	251	326	23	42	52						
	33-78	78-483	133-584	17-36	26-56	37-57						
Rare (N = 4)	18	508	623	13	63	64						
	10-40	292-787	448-913	8-22	57-69	58-73						
Z	1.44	-1.16	-1.44	-1.16	-2.02	-2.02						
<i>Lepilemur edwardsi</i> : Ankarafantsika												
Present (N = 2) Plots	0.9 / 1.1	1.0 / 1.1	0.9 / 1.0									
Absent (N = 2) (Relative units)	0.9 / 1.1	0.9 / 1.0	1.0 / 1.1									
Z	0.78	0.78	-0.78									
<i>Lepilemur edwardsi</i> : Mariarano												
Abundant (N = 3) 40 m ² plots	87	9	96									
	58-130	9-27	67-157									
Rare (N = 3)	68	19	87									
	43-118	11-57	54-175									
Z	0.66	-1.11	0.23									
<i>Lepilemur fleuretae</i> : Andohahela Parcel I												
Abundant (N = 2) PCQ	184	295.5	479.5	42.5	47.5	57.5	1.5	7	8.5	1.0	1.5	1.5
	181-187	292.8-298.3	479.3-479.8	40.8-44.3	44.3-50.8	55.3-59.8	0.8-2.3	4.5-9.5	5.3-11.85	0.5-1.5	1.3-1.8	1.3-1.85
Rare (N = 10)	118.5	136.0	248	39.5	46.5	60.5	3.5	4	8.0	1.5	2.0	2.0
	102.5-221.8	129.5-247.3	240-480	37.5-55.3	42.8-49.5	54-72.8	2.0-6.8	1.5-8.8	4.0-15.0	1.0-2.0	1.0-2.0	2.0-2.0
Z	0.43	2.15	0.86	0.00	0.21	-0.32	-1.18	0.64	0.54	-0.64	-0.11	-1.07

Table 1. (Continued.)

Botanical descriptions	Number of trees			Number of tree species			Number of food trees			Number of food tree species		
	5-9.9	≥ 10	All ≥ 5	5-9.9	≥ 10	All ≥ 5	5-9.9	≥ 10	All ≥ 5	5-9.9	≥ 10	All ≥ 5
<i>Lepilemur fleuretae</i> : Tsitongambarika												
Abundant (N = 9) 1000 m ² plots	68.0	103.0	172.0	33.0	37.0	49.0	21.0	39.0	59.0	7.0	10.0	11.0
	58.0-96.0	72.5-134.5	130.5-224.0	27.0-38.0	33.5-43.5	45.0-55.5	11.5-25.0	27.5-57.5	43.5-81.5	5.0-8.0	9.5-11.0	10.0-11.0
Rare (N = 4)	44.0	40.5	81.5	29.5	21.0	41.5	10.5	15.0	25.0	7.0	6.5	8.5
	39.0-56.5	35.5-74.8	78.5-130.3	26.5-33.3	19.3-30.3	34.3-42.0	6.3-21.5	7.3-31.0	14.0-52.5	5.5-10.0	4.3-9.5	6.3-12.3
Z	1.85	1.93	1.85	0.85	2.47	2.32	1.09	2.01	1.71	-0.16	2.16	1.20
<i>Lepilemur grevillorum</i> : Anjajavy												
Abundant (N = 3) 1000 m ² plots	134	128	262	33	35	43	79	76	155	18	17	22
	133-146.5	121.5-129	254.5-275.5	31.5-37	33-38.5	38.5-47.5	75.0-93.0	68.5-91.5	143.5-184.5	18-18.5	16.0-17.5	21-23
Rare (N = 3)	156	104	245	31	31	40	104	67	171	18	18	23
	148.5-170	92.5-108.5	241-271	30.5-33.5	31-34	39-44.5	95.5-123.5	64.5-69.5	160-193	18-18.5	16.5-19.5	22-24
Z	-1.09	1.96	0.65	0.44	0.65	0.21	-0.65	1.09	-0.65	0.65	0.00	-0.65
<i>Lepilemur hubbardorum</i> : Zombitse												
Abundant (N = 5) 1000 m ² plots	78	62	139	27	22	39						
	71-88	38-64	115-146	24-32	16-26	31-42						
Rare (N = 5)	91	48	136	33	20	38						
	80-102	32-61	125-151	29-34	18-23	37-40						
Z	-1.68	-0.74	0.10	-1.79	0.52	0.21						
<i>Lepilemur leucopus</i> : Andohahela Parcel II												
Present (N = 3) PCQ	2297	2033	4277									
	1381-2596	1681-2146	3417-4443									
Absent (N = 4)	2432	1154	3523									
	1913-3282	1089-1535	3099-4785									
Z	-0.53	1.94	0.53									
<i>Lepilemur milanoii</i> : Daraina												
Abundant (N = 8) PCQ	0.95	1.1	1.0	1.0	1.1	1.1						
	0.9-1.9	1-1.15	0.94-1.05	0.93-1.11	0.99-1.19	1.01-1.08						
Rare (N = 8)	1.1	1.0	1.0	1.0	0.9	1.0						
	0.97-1.12	0.85-1.01	0.95-1.06	0.89-1.07	0.81-1.01	0.93-0.99						
Z	-1.16	1.58	0.00	0.00	2.10	3.16						

Table 1. (Continued.)

Botanical descriptions	Number of trees			Number of tree species			Number of food trees			Number of food tree species		
	5-9.9	≥ 10	All ≥ 5	5-9.9	≥ 10	All ≥ 5	5-9.9	≥ 10	All ≥ 5	5-9.9	≥ 10	All ≥ 5
<i>Lepilemur mustelinus</i> : Anjozorobe												
Abundant (N = 64) 20 m ² plots	3.0	4.0	7.0									
	1.85-4.0	3.5-4.8	5.3-8.8									
Rare (N = 4)	4.0	2.0	6.0									
	2.0-5.0	2.0-3.0	4.3-8.0									
Z	-0.87	1.80	0.46									
<i>Lepilemur mustelinus</i> : Tsinjoarivo West (Ankadiavory)												
Present (N = 6) 1000 m ² plots	58	87	152									
	40-85	78-105	118-179									
Absent (N = 4)	68	83	149									
	58-75	78-85	138-160									
Z	-0.43	0.85	0.21									
<i>Lepilemur mustelinus</i> : Tsinjoarivo East (Ambalaomby)												
Present (N = 24) PCQ	123	110	228									
	91-222	47-193	143-392									
Absent (N = 5)	207	122	279									
	98-847	54-819	177-1666									
Z	-1.21	-0.52	-0.92									
<i>Lepilemur petterii</i> : Tsimanampesotse												
Present (N = 9) 900 m ² plots	93	90	184	18	19	24	17	25	58	5	5	7
	34-114	75-102	105-219	8-25	13-22	16-32	4-37	9-57	18-101	2-8	4-7	5-9
Absent (N = 8)	78	70	148	19	14	22	20	20	38	5	4	6
	69-127	54-79	121-191	16-20	12-16	19-25	14-31	11-33	23-61	3-6	3-4	4-6
Z	0.53	2.02	0.58	-0.05	1.55	0.48	-0.43	0.58	0.39	0.34	2.40	1.52
<i>Lepilemur cf. randrianasoloi</i> : Tsimenbo												
Abundant (N = 6) 1000 m ² plots	98.5	63	161	25	22	34	48.5	25.5	76	9	5	9
	92.3-152	51-83	144-243	22-29	17.8-26.3	29-38.3	36.8-73.5	16-31.3	50.8-102.3	8-10	3.8-6.5	8.8-10.8
Rare (N = 4)	114.5	77	191.5	28	25	39	49	23	76.5	8	6.5	10.5
	98.5-132.8	73-85.5	183.5-206.3	27.3-30.3	21.8-28.3	35.3-40.5	38.3-62	16.8-30.8	57.8-85.5	7.3-10.3	3.5-9.5	7.5-13.5
Z	-0.21	-0.96	-0.86	-1.29	-0.96	-1.73	-0.21	0	-0.11	0.89	-0.65	-0.33

Table 1. (Continued.)

Botanical descriptions	Number of trees		Number of tree species		Number of food trees		Number of food tree species	
	5-9.9	≥ 10	All ≥ 5	5-9.9	≥ 10	All ≥ 5	5-9.9	≥ 10
<i>Lepilemur ruficaudatus</i> : Kirindy / CNFEREF Present (N = 121)	40	19	61	13	6	16	13	3
Random sample (N = 76)	34-53	14-22	50-73	11-15	5-8	14-19	9-22	2-4
	42	16	55	13	6	16	14	3
	29-54	11-22	44-71	11-16	4-9	14-19	8-22	1-5
Z	-0.40	2.28	1.34	-0.25	-0.53	-0.05	-0.14	-1.00
<i>Lepilemur ruficaudatus</i> : Kirindy Mité								
Abundant (N = 4)	10.4	5.1	14.9	6.2	4.0	9.2	6.1	1.8
Rare (N = 1)	8.3-11.8	45-6.4	14.6-16.9	6.0-6.5	3.4-4.9	8.4-9.8	3.6-7.5	1.4-2.13
	4.1	4.3	8.4	3.0	3.1	5.1	0.5	0.4
Z	1.41	1.41	1.41	1.41	1.41	1.41	1.41	1.41
<i>Lepilemur sahamalaza</i> : SahamalaZa								
Abundant (N = 22)	10.5	6	16.5	6	4	9	5.5	3.5
Rare (N = 14)	5-12.5	4-10	12-21.3	3-8.3	3-5.5	6.8-12	2-10	2-7
	4	3.5	8.5	3.5	3	6	2	2.5
	2-11.5	2-6.3	5.8-16.5	2-6	1.8-4	5-8.3	2-5.5	1-3.3
Z	1.68	2.33	2.13	1.80	2.39	2.16	1.41	1.74
<i>Lepilemur scottorum</i> : Masoala								
Abundant (N = 4)	95.0	127	229	42	52	70	72	97.5
Rare (N = 2)	81.8-104.0	121-133	213-233	41-44	51-54	67-74	60-75	81.5-108.0
	76.5	108.5	185	40	53	70.5	57.5	84.5
	68.3-84.8	107.8-109.3	176-194	36.5-43.5	52.50-53.5	69.3-71.8	52.3-62.8	83.35-85.8
Z	0.69	1.85	1.38	0.00	-0.69	-0.23	0.92	0.93
<i>Lepilemur seali</i> : Anjanaharibe-Sud								
Abundant (N = 3)		814			67			
Rare (N = 2)		705-1208			67-73			
		1038 / 1401			47 / 55			
Z		-1.16			1.78			

Table 1. (Continued.)

Botanical descriptions	Number of trees			Number of tree species			Number of food trees			Number of food tree species		
	5-9.9	≥ 10	All ≥ 5	5-9.9	≥ 10	All ≥ 5	5-9.9	≥ 10	All ≥ 5	5-9.9	≥ 10	All ≥ 5
<i>Lepilemur seali</i> : Makira region												
Present (N = 9)	0.6	0.8	1.7									
PCQ	0.2-0.8	0.3-1.3	0.5-2.0									
Absent (N = 5)	0.8	1.3	1.9									
Z	0.6-1.2	0.98-1.7	1.5-2.8									
	-1.47	-1.53	-1.20									
<i>Lepilemur septentrionalis</i> : Montagne des Français												
Abundant (N = 18)	1.03	1.00	1.01	0.98	0.97	1.03	1.01	0.91	1.05	1.00	1.01	
200 m ² plots	0.79-1.20	0.81-1.11	0.92-1.23	0.59-1.21	0.85-1.24	0.74-1.20	0.79-1.24	0.84-1.27	0.90-1.21	0.77-1.25	0.79-1.22	
Rare (N = 18)	0.92	0.98	0.99	1.04	0.92	1.06	0.90	0.96	0.96	1.03	1.00	
Z	0.75-1.14	0.81-1.21	0.85-1.09	0.80-1.22	0.74-1.24	0.81-1.22	0.56-1.13	0.75-1.15	0.71-1.15	0.75-1.20	0.78-1.27	
	0.78	0.14	0.68	-0.60	0.57	-0.35	1.20	-0.44	1.47	-0.13	0.35	
<i>Lepilemur tymerlachsoni</i> : Lokobe												
Abundant (N = 7)	4	7	10									
Tree counts	3-5	5-8	8-12									
along	3	2	6									
transects	1-4	0.8-2.3	1.8-6.3									
Z	1.41	2.90	2.84									
<i>Lepilemur</i> spp. Analanjirofo region												
Present (N = 9)	1.3	0.9	2.4									
PCQ	0.8-1.6	0.5-1.4	1.5-2.8									
Absent (N = 5)	0.92	0.92	1.85									
Z	0.7-1.0	0.8-1.1	1.5-2.0									
	1.00	0.07	0.87									

Forest composition was measured in different sized plots, the Point Centered Quarter method (PCQ), or by measures of trees used by *Lepilemur* along transects. Values are medians and quartiles. For plots, they refer to the number of individuals or species per plot. For $N < 3$, we list the original numbers. For $N = 3$, we list the median and the range. For PCQ, values are relative densities. Z-values for each site are based on Mann-Whitney U -tests. Methods for botanical descriptions and lemur surveys are provided in Supplementary material S1

morphological data are not available for all study sites. Accordingly, we use the classification and geographic ranges for *Lepilemur* species as defined by Mittermeier *et al.* (2023). Species identification remains unclear for *L. cf randrianasoloi* at Tsimembo, and the *Lepilemur* sp. from the Analanjirofo region (Supplementary material S1).

Results

Differences between transects or plots with high or low abundances (or presence versus absence) of *Lepilemur* spp. were most often related to the presence of large trees (table 1). Considering all studies available, effect sizes differed significantly from zero only for the number of trees ≥ 10 cm DBH, the number of food tree species ≥ 10 cm DBH, and for both size classes of food trees combined (all trees ≥ 5 cm DBH; fig. 2). Effect sizes of three predictor variables showed positive deviations from zero, indicating a positive association of *Lepilemur* spp. with large trees and food trees, the latter seems to be driven by large rather than small trees (trees between 5 and 9.9 cm DBH). No other vegetation variable showed significant deviations from zero.

The number of large trees is not correlated with $p < 0.05$, neither with large food trees nor with all food trees (Spearman rank correlation: $r_s = 0.62$, $P = 0.08$ and $r_s = 0.58$, $P = 0.10$, $N = 9$, respectively). Given the small sample size, the effect of these variables on the presence of *Lepilemur* spp. cannot be separated.

Discussion

In response to the widespread destruction of Madagascar's forest ecosystems (Harper *et al.*, 2007; Vieilledent *et al.*, 2018; Rafanoharana *et al.*, 2024; Andrianambinina *et al.*, 2025) conservation stakeholders have proposed and implemented various forms of forest restoration approaches. These include enrichment planting with native tree species (Deleporte *et al.*, 1996), agroforestry that combines utilitarian plants for both people and wildlife (Martin *et al.*, 2009; Gérard *et al.*, 2015; Lavalie *et al.*, 2015; Rafidison *et al.*, 2020; Konersmann *et al.*, 2022;

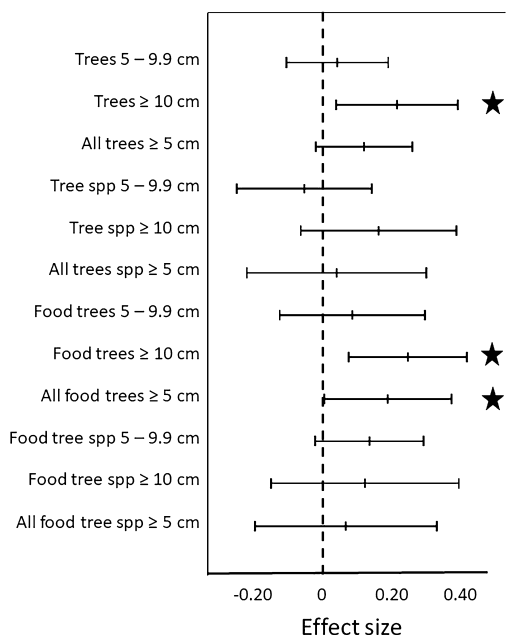


Figure 2. Effect size (means and 95% confidence intervals) for predictor variables on the abundance of *Lepilemur* spp. Positive effects indicate positive associations with *Lepilemur* and the variable in question. Asterisks indicate significant deviations from zero ($P < 0.05$). Predictor variables are: the number of small trees (DBH: 5-9.9 cm), large trees (DBH ≥ 10 cm) and small and large trees combined (= all trees with DBH ≥ 5 cm), as well as for the number of tree species, food trees and food tree species within the corresponding size classes.

Beeby *et al.*, 2023), efforts to attract animals as seed dispersers into restoration areas (Holloway, 2003; Ganzhorn *et al.*, 2024; Ramananjato, 2025), planting native tree species (Birkinshaw *et al.*, 2009, 2013; Vahatra, 2023, 2024) or combinations thereof (Manjaribe *et al.*, 2013; Donati *et al.*, 2021). All of these approaches prioritise tree establishment, ideally using regionally appropriate native tree species and following established restoration guidelines, such as the national guidelines ALAMINO or the international Global Biodiversity Standard. Given the considerable challenges associated with tree survival and growth, any successfully restored forest composed of native tree species in Madagascar must be considered a conservation success. This is further illustrated by the monospecific Nosiarivo Forest at Ankaratra, planted at

the end of the 18th century with only a single tree species but surrounded by native forest. Today, this plantation supports similar species richness of bird and small mammals comparable to that of nearby national parks (Goodman *et al.*, 1996).

In contrast to trees, the needs of the faunal components have received far less attention in Madagascar's restoration projects. At the landscape level, animal habitat requirements have largely been inferred from remote sensing data (Smith *et al.*, 1997; Irwin *et al.*, 2005; Kremen *et al.*, 2008; Lahoz-Monfort *et al.*, 2010; Brown & Yoder, 2015). At finer spatial scales, remote sensing information has been combined with ground-based vegetation measurements (Steffens *et al.*, 2023; Ratovonamana *et al.*, 2024). At an even more detailed level, several studies have identified tree species important for lemur food and recommended their inclusion in restoration efforts (Rafidison *et al.*, 2020; Steffens, 2020; Eppley *et al.*, 2022; Konersmann *et al.*, 2022). Yet, for practical reasons, lemur foods cannot be included as intended, because restoration projects struggle with the availability of seeds or seedlings for plantation, and achieving tree survival rates that might turn a site into a forest. If food trees are included in restoration planning, the question of food trees revolves around fruit trees with the underlying assumption that, by the time fruit trees will actually provide fruit, these trees and the developing forest will provide food also for other species. This might be true for many species, but specialised frugivores and folivores are more affected by habitat degradation than mixed folivore-frugivores (Eppley *et al.*, 2020). Strict insectivory might be an issue for non-lemur taxa. Malagasy lemurs (many *Microcebus* spp.) that include substantial proportions of invertebrates are mostly omnivorous and seem to be rather flexible (Knoop *et al.*, 2018). For them, but also for other lemurs and birds in Madagascar and many taxa globally, trees that are likely to produce exudates are important for specialists, such as *Phaner* spp.; Charles-Dominique and Petter, 1980; Hladik *et al.*, 1980) and might be important as fallback food sources for other species during times of

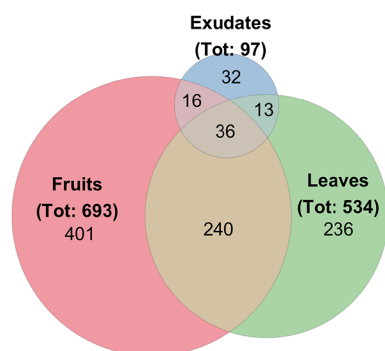


Figure 3. Number of plant species used by lemurs for feeding on fruits, leaves or exudates or any combination of the three categories; data from Steffens (2020).

fruit scarcity (Bollen and Donati, 2005; Burrows and Nash, 2010; Razafimandimby *et al.*, 2026). Considering also other food tree species apart from fruit trees is important because many tree species used for feeding on exudates or leaves are not used for fruit eating by lemurs. Steffens (2020) lists 984 plant species identified at the species level as food plants for lemurs. Almost 700 plant species have been documented to be used by frugivores, 534 for leaf eating, and 97 for exudates. Different portions are used for more than one food resource, but leaves or exudates were eaten from only 39.8% and 7.5% of the species used for fruits (fig. 3). Thirty-six tree or shrub species were used for all three categories (fruits, leaves and exudates). Four of them are not indigenous and are considered invasives (Supplementary material S3). Considering more food categories might even be more relevant, as it is certainly easier to grow trees to the stage that provides leaves than fruit. Therefore, restoration towards the reference forest could be accelerated by adding a variety of trees with different functions. These will be relevant not just for lemurs but for many other taxa as well, as illustrated below for tree holes.

Beyond food plants, plantation schemes for biodiversity conservation may be improved by also considering structural components (e.g., Lindenmayer *et al.*, 2009; Ellis *et al.*, 2022). In temperate deciduous forests multiple taxonomic groups, ranging from lichens and fungi to invertebrates and vertebrate species, benefit from the

presence of large trees, deadwood and tree cavities (Wagenaar *et al.*, 2025). In line with these results, several studies in Madagascar have also demonstrated an association of different lemurs including *Lepilemur* species with large trees (e.g., Salmona *et al.*, 2015; Steffens *et al.*, 2017, 2023; Tinsman *et al.*, 2022; Rabemananjara *et al.*, 2026). Since *Lepilemur* spp. do not consume a lot of fruit, mainly provided by mature and therefore large trees (Steffens, 2020), the preference for large trees could be interpreted as their structural components being key for this (and other) lemur species. These structures might be relevant for locomotion and as nesting and denning habitats for cavity-dependent lemurs. Though the actual costs of locomotion are low for *Lepilemur* under the forest conditions where they occur, this could change if they had to use forests that lack suitable substrates (Warren and Crompton, 1998a,b; Drack *et al.*, 1999; Stalenberg, 2019). Studies with accelerometers, such as by Campera *et al.* (2019) would allow to calculate proxies for energy expenditures in different portions of the forest with different predominating tree structures.

Though the preference of *Lepilemur* spp. for large trees as illustrated in our review is a recurrent theme even in studies using very different methods for botanical descriptions, the response of the animals towards large trees is not linear throughout the forests. Once large trees prevail, such as in Mariarano or Vohibola III (Lehman, 2006; Andriatsitohaina *et al.*, 2020a,b) the response of *Lepilemur* spp. towards large trees becomes negligible or even negative. This is consistent with previous observations in Ranomafana National Park, where *L. microdon* was less abundant in old-growth with larger tree cavities than in disturbed forest (Porter, 1998). It might be, that under these conditions, the stems of large trees become too large for the vertical clinging and leaping for these animals with a body mass of about 1 kg (Nash, 1998). Certainly, the notion of “large” depends on the context. A large tree for *Lepilemur* can be a tree too small to sit on for *Varecia*.

The importance of tree holes for many animal groups has been shown in forests around



Figure 4. *Microcebus griseorufus* feeding on a hissing cockroach in Tsimanapesotse National Park (photo by P. Giertz).

the world (Wagenaar *et al.*, 2025). Since hollow formation in trees has a long lag time, various interventions have been suggested to promote the formation of cavities in restoration projects. These include inoculating trees with wood-decaying fungi, reducing tree densities to accelerate growth and therefore the likelihood to produce crevices, damaging trees so that they would provide cavities, creating access to trees that rot inside but where the internal cavities do not have any access from the outside, or attaching nest boxes or log hollows, though the latter requires continuous follow-up to remain effective (Lindenmayer *et al.*, 2009; reviewed by Ellis *et al.*, 2022). The same importance of tree hollows on an ecosystem level is to be expected in Madagascar’s forests. Water-filled tree holes are used by many frogs as phytotelms for breeding (J. Glos, C. Raxworthy, M. Vences, pers. comm.). Apart from using phytotelms in the humid as well as in the dry forest (Cumberlidge *et al.*, 2005; M. Dinsmore, unpubl.), land-crabs seem to use hollow trees also as resonating chamber for communication (N. Vasey, unpubl.). Dry tree crevices are used by many insects, such as cockroaches that are important food for insectivorous lemurs (fig. 4), and shelters for reptiles (many geckos, iguanids, snakes; C. Raxworthy, M. Vences, pers. comm.). Birds, such as Madagascar’s parrots, some owls, rollers, the Madagascar kestrel or the forest rock thrush breed in tree holes (Hino, 2002; L.-A. René de Roland, unpubl.).

Among mammals, other than lemurs, at least 10 species of bats, some rodents (*Brachytaromys* spp.) and tenrecs (e.g., *Echinops telfairi*) use tree holes as day roosts (Goodman and Raherilalao, 2013). Most of the endemic carnivorans use holes in standing or fallen trees as dens or shelters (contributors to Goodman, 2022).

For several lemur species (genera *Varecia*, *Propithecus*, *Eulemur*), tree cavities are important sources for water (Vasey, 2000; Scholz and Kappeler, 2004), shelters for sleeping, torpor and hibernation, such as in the genera *Microcebus* and *Cheirogaleus* (e.g., Schmid, 1998; Radespiel et al., 2003; Blanco et al., 2018; Blanco, 2022; Kappeler et al., 2022), or predation (Goodman and Ganzhorn, 2022). *Lepilemur* spp. use hollows for sleeping (e.g., Rasoloharijaona et al., 2003, 2008; Salmons et al., 2015) and for thermoregulation (Stalenberg, 2019; Radespiel et al., 2022). Though it is difficult to quantify the availability of tree cavities available in a forest, suitable cavities might be in short supply in some forests. This assumption is derived from the observations that more than 40 *Microcebus* came out of the same tree hole in Ranomafana (P.C. Wright, unpubl.), that *Cheirogaleus medius* were fighting with the iguanid *Oplurus cuvieri* over a tree hole (the reptile won), or that *Cheirogaleus medius* and *Lepilemur ruficaudatus* were using the same hole as day shelter (K. Dausmann, pers. comm.). In contrast, the availability of tree hollows seemed to be a subordinate driver for the abundance of *L. microdon* in old-growth forest (Porter, 1998).

For *Lepilemur* spp., cavities used can range from tree holes of all kinds to shelf-like supports (fig. 5). In the dry spiny forest *L. petteri* often sleeps in bundles of *Alluaudia* stems that provide some shade but possibly more important, perfect protection against aerial or other predators (Nevermann et al., 2023). Remarkable cases of hole utilisations have been reported for *L. milanoii* at Daraina where animals have been found in a tree hole below ground and crevices in stones (Semel et al., 2021), and a *L. cf. seali* found in a ground hole at Marojejy (fig. 5). As illustrated by nest boxes supplied for birds,

bats and several groups of small mammals (Lindenmayer et al., 2009; Vinuela-Hidalgo et al., 2024; Ridley et al., 2025), resting or nest boxes could also be installed that might be of value for many taxa in Madagascar, including lemurs (Andrews et al., 1998). Yet, while *Lepilemur ruficaudatus* also used nest boxes in captivity (Pages and Petter-Rousseaux, 1980), they did not use them in the dry forest of Ankoatsifaka in Kirindy Mité National Park (Romanello, in press).

If animal needs were to be taken into account in a wider concept, restoration projects should not only consider food tree species but also the many different functions of trees already at early stages of restoration (Lindenmayer et al., 2009; Ellis et al., 2022). In Madagascar, where local people rely heavily on forest resources, ecological restoration aiming to develop into the original native forest, could be supplemented at well defined sites with non-native trees for timber and fruit production and for providing firewood for the local communities (e.g., Manjaribe et al., 2013). Some exotic tree species are known for the respective properties, though they are always seen with scepticism. Yet, similar to some forms of anthropogenic habitats (Eppley and Goodman, 2022), some exotic tree species might actually be able to provide services that cannot be replaced quickly by native tree species given our present knowledge. In Tsinjoarivo-Ambatolampy, *Nuxia* spp. might be a possible candidate (M. Irwin, unpubl.). In the littoral forest of southeastern Madagascar, no sleeping hole of *Cheirogaleus major* was found in trees below 47 cm DBH (Lahann, 2007), a diameter achieved by native trees only after decades of growth but much earlier by some introduced tree species. In the littoral forest, *Microcebus murinus* has been observed to use the native forest during their activity time, but resort to cavities in exotic tree plantations for sleeping (P. Lahann, pers. comm.). The importance of large and tall trees is not restricted to species that rely on cavities. Where available, various species of *Eulemur* sleep high up in Eucalyptus plantations, possibly as shelter against predation. The possible importance

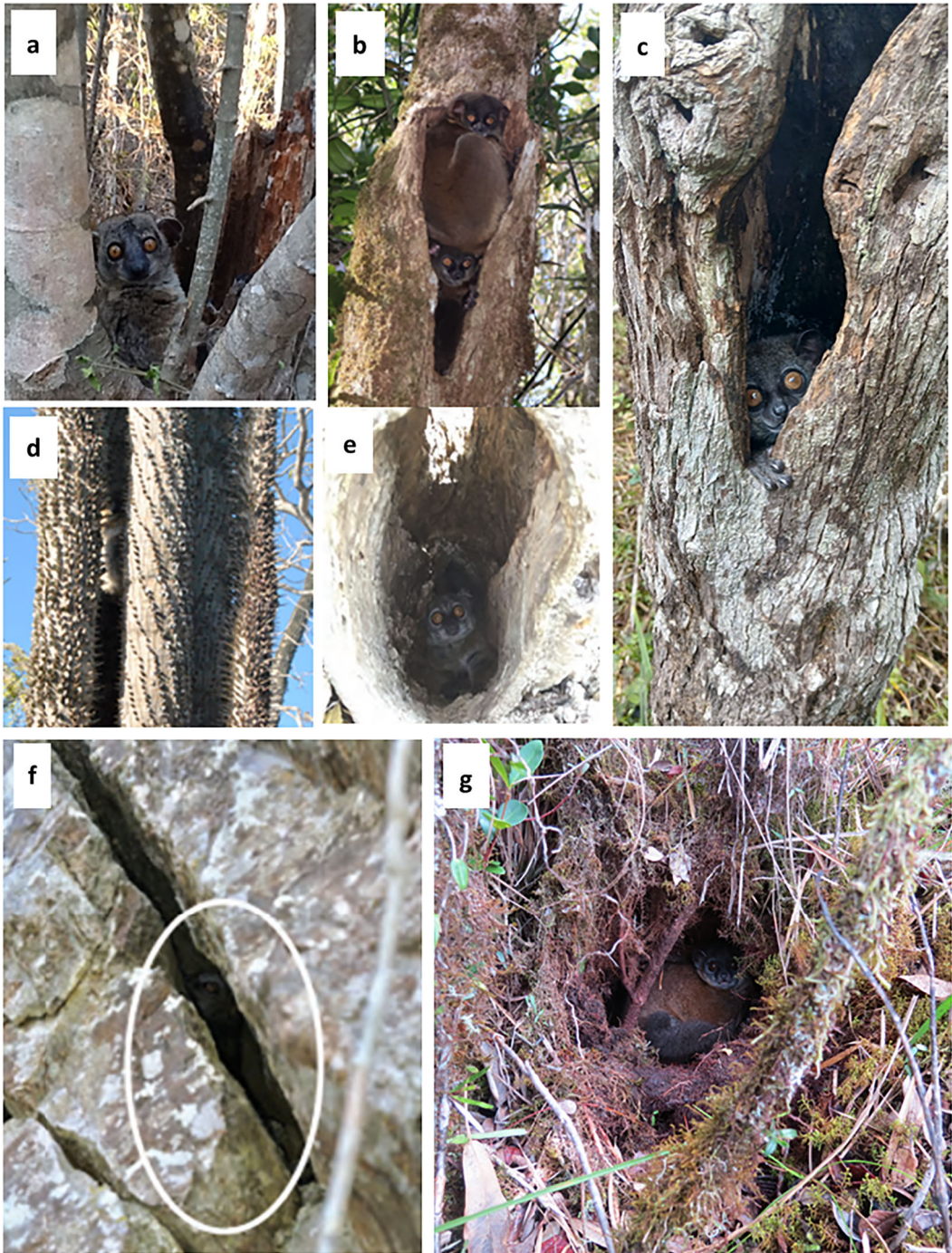


Figure 5. Shelters for *Lepilemur* spp. (a, b) *L. ruficaudatus* and *L. microdon* in standard tree crevices at Kirindy Mité and Ranomafana (photo by E. Rakotomalala and D. Andrianoely); (c) *L. microdon* in a tree hole where the animal survived a forest fire in Ranomafana in 2025 (photo by D. Andrianoely); (d) *L. petteri* in bundles of spiny *Alluaudia* stems in the spiny forest of Tsimanampesotse, where tree holes are absent (photo by Y.R. Ratovonamana); (e, f) *L. milanoii* in a tree hole below ground and in a rock crevice (photo by B. Semel, from Semel *et al.*, 2021); (g) *L. cf seali* in a ground hole at Marojejy (photo by E. Patel).

and utility of non-native habitats for Madagascar's lemurs and other native fauna have been summarised by Gérard *et al.* (2015). One hundred of the 1379 plant species introduced into Madagascar are used by about 100 endemic vertebrate species for food and habitat. Yet, the endemic fauna has been found mostly in non-native habitats that occurred in close vicinity to native forests. Therefore, it is unlikely that non-native habitats would provide substitutes for native forests that allow viable populations of native animals to persist. Rather, these non-native habitats might provide options to act as buffer zones, corridors and as an auxiliary component to bridge the temporal gap until native forests become functional for the conservation of the native fauna (Eppley and Goodman, 2022).

Certainly, none of these auxiliary initiatives can substitute the ecological functions of native forests. For comprehensive ecological restoration, the need to get a clearer idea about the needs of faunal components in restoration projects in Madagascar is urgent. Botanists have defined their path ahead very clearly and with great competence (such as by ALAMINO, The Society for Ecological Restoration, or The Global Biodiversity Standard). During an interim period, satisfying the needs of animals requires compromises to account for the diverging needs of different animal groups (e.g., Szarvas *et al.*, 2026). Otherwise, we risk to have restored native forests but only very few native animals left.

Conclusion

Though the goal of restoration projects is to approach the characteristics of the reference model, including all kinds of parameters (e.g., as expressed in the ecological recovery wheel illustrated in the manual of the The Global Biodiversity Standard; <https://www.biodiversitystandard.org/our-method/>), in reality, project success is often measured by the numbers and survival rates of the planted trees. While this goal is certainly important and possibly the only one that can be measured during

the first years (= funding periods) of restoration, we should not forget that forest restorations are long-term projects and deficits in the initial phase are likely to become visible only many years later. Certainly, any kind of native forest will be colonised by native animals eventually, but it might take much longer if we do not consider that not all species are frugivores, that even the frugivorous species need suitable leaves or exudates during times when fruits are not available, and many species also need structural components, such as tree holes to allow species to persist in a given forest.

Supplementary materials

Data are available on <https://doi.org/10.1163/14219980-bja10093> under Supplementary Materials.

Supplement material S1. Descriptions of sites, botanical inventories and lemur surveys for the different studies used for the comparison.

Supplement material S2. Food species of different *Lepilemur* spp. not yet included in the compilation by Steffens (2020).

Supplement material S3. Food species used for feeding on fruits, leaves and exudates; extracted from Steffens (2020).

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Author contribution

JUG and DZ conceived the study. All authors collected data, provided raw or processed data and further information on their study system.

Conflict of Interest

The authors declare no conflict of interest.

Ethics statement

Our study is based primarily on re-analyses of published studies, cited in the Supplement S1. Some authors provided data from yet unpublished work or work in progress. Their Statements of Ethics are added in the Supplement S1. We confirm that the research adhered to the legal requirements of Madagascar and that this research adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates, where applicable.

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