



Article Facilitated Forest Restoration Using Pioneer Seed Dispersers in Madagascar: The Example of *Microcebus* spp.

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Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). **Abstract:** The concept of "facilitated restoration" aims at native biodiversity reinstatement with the help of animal seed dispersers attracted by fruiting trees. Yet, large-crowned trees will have to develop in the early stages of restoration; therefore, seed dispersal provided by small generalist mammals and birds that use rapidly growing herbs, shrubs, and small trees at early stages of forest succession would accelerate biodiversity restoration. Due to the elusive lifestyle of these small animals, it is unclear what species can contribute to the early stages of this process. Using the primate genus *Microcebus* (adult body mass about 60 g) as an example, we illustrate that these small generalists are possible seed dispersers in the early stages of forest restoration, not yet used by larger frugivores. We show that *Microcebus* spp. dispersed more seeds from herbs, shrubs, and small trees than large frugivorous primate species. These plants tend to have smaller seeds than large tree species and are often pioneer species not considered in forest restoration projects. Facilitating the colonization of restoration plots by generalist small seed dispersers that use shrubby habitats may improve plant diversity by adding a more natural sequence of successional stages towards mature forests in Madagascar and elsewhere in the tropics.

Keywords: reforestation; forest succession; fallow land; seed dispersal; lemurs; frugivores

1. Introduction

Madagascar is known globally for its unique biodiversity that is threatened by the need for land and resources of the growing human population coupled with demands from the international market, poor governance, and climate change [1–4]. While these threats affect all natural ecosystems of the island, conservation efforts have focused on forests as the majority of the endemic species seem to have evolved in ecosystems that suffer from very high deforestation rates [5,6]. At the same time, the rural human population relies heavily on natural forest resources, especially during times of food shortages [7]. Thus, Madagascar's forest ecosystems are in desperate need of protection and degraded landscapes need to be restored to maintain ecosystem services for the human population, and to extend the remaining, often very small blocks of remnant forest to allow endemic forest species to maintain viable populations [8–10].

The concept of "facilitated restoration" aims at reducing the costs and logistics for the restoration of forests with native tree species with the help of animal seed dispersers [11]. This concept revolves around large fruiting trees in a modified matrix that attracts seed dispersers. According to this idea, birds and mammals disperse seeds into the matrix via their feces and thereby support forest restoration when they visit areas of remaining or newly planted trees for food, shelter, or support, or cross the matrix when moving between forest remnants. The idea addresses mainly mobile frugivorous bird and bat species and large mammals that can bridge open landscapes [11–13]. In Madagascar, the application of this concept has been proposed repeatedly [8,9,14–21]. Yet, for the initial restoration of open areas, the reliance on the attractiveness of large-crowned, fruit-bearing native trees might be problematic, because many of them are unlikely to grow in the early stages of successions associated with forest restorations [22], are no longer present in the matrix, or there is an extended period before they produce fruits and can attract seed dispersers. At an early stage, reforestation could be supplemented by introduced and native plant species used by small vertebrate seed dispersers that use scrub vegetation [23–25].

In Madagascar, members of the family Cheirogaleidae, small nocturnal lemurs, might be good candidates for seed dispersal from native forests into areas in the process of being restored [18]. Within this family are the mouse lemurs (*Microcebus* spp.), which are the smallest-bodied lemurs and are known to eat a variety of fruits and to defecate intact seeds [23,26]. They would be good candidates as seed dispersers because some members of the genus use secondary and degraded forest habitats [27–32], persist in forest fragments that are too small to maintain other lemur species, descend to the ground to cross nonforested spaces [33–36], prefer forest edges because of higher fruit and insect abundance as

compared to the forest interior [37–40], use the lower strata of the forest with very small twigs [41,42], and reside in mangroves, eucalyptus, and pine plantations and agroforestry systems [28,34,43–46]; thus, they can act as seed dispersers that contribute to tree species regeneration in a variety of conditions not used by very few other frugivores [16,23,26]. While there is ample information on the feeding behavior of *Microcebus* spp. and the plants exploited by members of this genus [16,18], which plant species are actually dispersed is an open question, because the size of the animals (about 60 g) prevents them from swallowing and endogenously disperse seeds above a certain size [18].

Here, we address the questions:

- 1. Which size of seeds are dispersed by *Microcebus* spp.?
- 2. Can observations of fruit-eating be used as a proxy for the actual dispersal of seeds of the fruits consumed?
- 3. Which proportion and size of seeds dispersed by frugivores in general are also dispersed by *Microcebus* spp.?
- 4. Do Microcebus spp. disperse seeds of plants not consumed by other frugivorous lemurs?
- 5. How does seed size relate to plant life forms?

We approached these questions on two levels: first, we provide new data from a detailed feeding study of *Microcebus griseorufus* designed to identify plant species that are actually dispersed by this lemur in the dry forest and xerophytic thicket of southwestern Madagascar. Second, we compiled information from published data on the size of seeds that were swallowed and passed through the digestive tract of *Microcebus* spp. in other forest types across Madagascar.

2. Methods

2.1. Case Study of Microcebus griseorufus in Tsimanampetsotse National Park

Microcebus griseorufus is one of about 25 species of mouse lemurs recognized today [47]. It occurs in the dry and spiny forest of southwestern Madagascar. The case study on *M. griseorufus* was conducted in the northwestern part of Tsimanampetsotse National Park in southwestern Madagascar, ca. 85 km south of Toliara (24°01′ S; 43°44′ E). The study area is part of the dry and spiny forest ecosystem [48] and characterized by two different seasons: eight dry months (April–November) and four wet months (December–March). Annual rainfall averages around 400 mm but is highly variable within and between years, accompanied by recurrent droughts without rain for several years [49–51].

As a result of the topography and edaphic differences, the study site contains dry forest on white sand in the coastal area or in depressions of the plateau, filled with ferruginous red sand. Xerophytic thicket grows on calcareous soil, covering the slope from the soda lake to the limestone plateau and extending on the plateau towards the east. The dry forests on white and ferruginous sand are floristically similar and data from these two habitats were combined. The xerophytic thicket is structurally and floristically distinct [50] (Figure 1).

The study was carried out between 2007 and 2009. Although this work was conducted some time ago, the ecological setting has not changed and therefore the results reported here are still valid.

Microcebus griseorufus were captured between October 2007 and March 2009 in three 6 ha grids (150 m \times 400 m), with traps spaced at 25 m intervals and grids 500 m apart (Figure 1). Using 119 Sherman live traps per grid, baited with ripe bananas and set 1–2 m high before sunset, traps were checked and closed before sunrise or at midnight during the lactation and weaning season (February) to avoid separating females from their young for too long. Traps were set for four nights per session. To follow the phenology of mouse lemurs' life history but to keep our impact on the population low, we refrained from trapping each month. We conducted two trapping sessions in the late dry season (October 2007, October 2008), four during the wet seasons (December 2007, 2008, and February 2008, 2009), one in the late wet season 2008 (April), and one in the dry season (July 2008).



Figure 1. Study area and arrangement of trapping grids for the study of *Microcebus griseorufus in Tsimanampetsotse National Park* in dry forest on sand (DFS), xerophytic thicket (XBC), and dry forest on ferruginous soil (DFF) (photo credits: Y. R. Ratovonamana and P. Giertz).

Captured mouse lemurs were sedated with 0.01 mL i.m. Ketaminhydrochlorid (Ketamin[®] 100 mg/mL, Parke-Davis, Berlin, Germany; [52]) and marked individually either by coded ear clipping or a subcutaneous transponder (Trovan[®] Passive Transponder System, EURO ID, Identifikationssysteme GmbH and CoKG, Weilerswist, Germany). Betadine was used to disinfect the mouse lemur skin in areas associated with marking interventions and none of the recaptured individuals showed signs of infection. After examination, animals were kept in their Sherman traps in a shaded area to recover from

sedation, provided with bananas and water, and released at their capture sites at dusk or pre-dawn on the trapping day [53,54].

Feces were removed from the traps and stored in 70% ethanol. During further analyses, individual fecal samples were examined for seeds and seed fragments under a binocular scope. Seeds were cleaned, measured, and photographed on scale paper. The photos were then viewed by the field staff and identified using comparative local samples. Seeds from Tsimanampetsotse were collected by P. Giertz and Y. R. Ratovonamana, fecal samples were analyzed by L. Behrendt and F. Holst, and seeds were identified by members of the Association Analasoa (C. Kasola, F. Atrefony, F. Louis, G. N. Odilon, R. G. Ralahinirina, T. Menjanahary and Y. R. Ratovonamana).

Each fecal sample was assigned to known individual animals. Some individuals were captured repeatedly during the same month and in different periods. Recaptures within one month were excluded from the data set; however, recaptures in different months were considered independent samples because they represent different phenophases.

2.2. Ethics Approval for the Case Study

All animal work followed Malagasy and German guidelines. Our research was conducted under the Accord de Collaboration between the Universities of Antananarivo and Hamburg, and in collaboration with the Mention Zoologie et Biodiversité Animale (formerly the Département de Biologie Animale), the Mention Anthropologique et Développement Durable, as well as the Mention Biologie et Ecologie Végétales (formerly Département Biologie et Ecologie Végétale) of the Université d'Antananarivo. Authorizations to enter Tsimanampetsotse National Park, as well as to capture and handle small mammals, were delivered by the Ministère de l'Environement, des Eaux et Forêts et du Tourisme de Madagascar in accordance with Madagascar National Parks (MNP, former ANGAP; permit n° 057/07 issued on 12 March 2007, permit n° 009/08 issued on 15 January 2008, and permit n° 261/08 issued on 9 October 2008). The research was approved by the Ethics Commission of the Institute of Zoology of the Universität Hamburg.

2.3. Review of Microcebus Fruit Eating and Comparison with Other Lemur Genera

To put the role of *Microcebus* spp. into the perspective of the Malagasy frugivore community (and thus possible seed dispersers), we used published data and unpublished data provided by MBB to compare the defecated seed size and the life (growth) form of food plants consumed by other frugivores.

2.4. Seed Size

We searched the Web of Science, regional journals not covered by the Web of Science, and unpublished theses for information on fruit-eating by *Microcebus* spp. We also contacted researchers working on species of this genus for unpublished data. The comprehensive data set on *M. tanosi* [55] seemed to have suffered from transcription errors as seed size for *Brexia* sp. reported to be 15.1 mm is out of the range of published data for this genus (maximum length reported: 7 mm; [56]. Therefore, this measure was excluded from the analyses. We compared the seed size of fruits dispersed by *Microcebus* spp. with the size of seeds measured for fruits consumed by frugivores at a site in the eastern humid forest of Ranomafana [57] and in the eastern littoral forest of Sainte Luce [55,58].

2.5. Plant Life Forms and Plant Species

We compared the life forms of plant species dispersed by *Microcebus* spp. (=seeds found unharmed in fecal samples and thus proven dispersal) with those fruits observed to be consumed by *Microcebus* spp. (=unknown whether seeds are being dispersed or not), and those whose fruits have been reported to be eaten by other lemur species (most also based only on observations, and thus, it is unknown whether seeds are being dispersed or not). For records on fruit-eating by *Microcebus* spp. and other lemur species, we used the database provided by Steffens [16], which reports all records of published studies on

lemur feeding. Since, for several lemur species, multiple studies have shown that the same plant species are consumed, we considered each plant species only once per group (*Microcebus* feees, *Microcebus* feeding records, feeding records of all other lemur species). Plant life forms were simplified and pooled into herbs + shrubs, small trees, trees, vines, and epiphytes. We then compared the life forms of food plants associated with consumed fruits based on *Microcebus* feeal samples with the behavioral observations of fruit-eating by *Microcebus* and with all other non-*Microcebus* lemur genera.

2.6. Plant Life Form and Seed Size

For the comparison of seed size in relation to the different life forms of plants, we used all plant species for which we had measures of seed length. This included the *Microcebus* fecal samples (Table A1) plus the data compiled by Bollen for the littoral forest [55] and by Razafindratsima and Dunham for the eastern humid forest of Ranomafana [57]. Each plant species was considered only once. The sampling of plants for the littoral forest and for the eastern humid forest had not been designed to be representative of the forests as a whole. Therefore, the data do not reflect the seed properties of the whole plant community and results should be considered preliminary.

Statistical analyses were performed with SPSS. We used chi-square tests for nominal data, parametric tests for data for which residuals did not deviate from normality (*t*-tests, linear regression), and non-parametric tests (Mann–Whitney-U test, Kruskal–Wallis test, Kolmogorov–Smirnov test) for data that deviated from normality. Linear regression between seed length and seed width was not used to indicate a causal relationship between these variables, but to provide a quantitative estimate about the relation between them.

3. Results

3.1. Case Study: Fecal Seed Content of Microcebus griseorufus in Tsimanampetsotse National Park

We analyzed a total of 421 fecal samples derived from 300 unique individuals of *Microcebus griseorufus* from Tsimanampetsotse National Park. We did not find seed fragments or seeds with gnaw marks that would indicate seed predation. Seeds corresponded to 25 different plant species. Of the 25 species, 18 were found in samples from the dry forest and 15 species in samples from the xerophytic thicket. Seeds of one species from the dry forest could not be identified Figure A1).

Overall, 185 of the fecal samples (43.9%) contained seeds (Table 1). More fecal samples of females (51.8%) contained seeds than of males (34.9%; chi-square test: $\chi^2 = 12.13$, df = 1, p < 0.001, N = 421). There were no marked seasonal differences in the representation of seeds in fecal samples of females and males: 50.3% and 55.5% of the female fecal samples contained seeds during the wet and the dry season respectively, and 34.6% and 44.4% of male fecal samples contained seeds during the two seasons. A higher percentage of fecal samples from the dry forest contained seeds than from the xerophytic thicket (47.2% versus 36.1%, respectively; chi-square test: $\chi^2 = 4.33$, df = 1, p = 0.038, N = 421; Table 1).

Table 1. Number of fecal samples from *Microcebus griseorufus* without (–) or with seeds (+) in different vegetation types of Tsimanampetsotse National Park during the wet and dry seasons; samples collected between 2007 and 2009 and those from Dry Forest include dry forests on the sand and dry forest on ferruginous soil.

Vegetation	Dry Forest				Xerophytic Thicket			
Season	W	Wet Dry		ry	Wet		Dry	
Presence of Seeds	_	+	_	+	_	+	_	+
Females	54	70	20	23	27	12	8	12
Males	56	33	28	15	31	13	12	7

Seed length of the 24 species identified at least to the genus level varied between 1.0 and 9.1 mm with a median of 4.8 mm. Seed width varied between 1.0 and 5.4 mm with a median of 3.8 mm (Tables 2 and A1). The unidentified seed was not measured.

3.2. Review of Microcebus Fruit Eating and Comparison with Other Lemur Genera

We found seven studies that reported the size of seeds from fruits that had been swallowed by mouse lemurs and recovered from fecal samples (Tables 2 and A1) and an additional eight studies that reported fruit consumption by several different species of *Microcebus* but did not report plant species identity, seed size or seeds in fecal samples [26,40,59–64]. The latter set of data was not considered herein for the analyses of seed size but was included for the comparisons of food plant growth forms between *Microcebus* and other lemur species.

Table 2. *Microcebus* spp. Fruit consumption with or without information on endogenous seed dispersal; values are presented as minimum–median–maximum.

Microcebus spp. (Body Mass)	Study Site and Vegetation Type	Length of Seeds from Fruits Consumed but Seeds not Found in Feces [mm]	Width of Seeds from Fruits Consumed but Seeds not Found in Feces [mm]	Length of Seeds in Feces [mm]	Width of Seeds in Feces [mm]	Reference
M. griseorufus 60 g	Tsimanampetsotse: Dry forest and xerophytic thicket			1.0–4.8–9.1 N = 24	1.0–3.9–5.4 N = 24	This study
M. lehilahytsara 42 g	Ankafobe: Humid central forest			1.8–4.4–5.6 N = 6	1.8–3.3–4.3 N = 6	[34]
M. jollyae 64 g	Kianjavato: Humid eastern forest			0.3–1.3–8.5 N = 9	0.2–1.0–5.0 N = 9	[23]
M. rufus 44 g	Ranomafana: Humid eastern forest			1.0–4.0–10.7 N = 13	1.0–2.9–6.9 N = 13	[23]
M. rufus 44 g	Ranomafana: Humid eastern forest			1.3–5.0–9.5 N = 16	0.3–2.3–5.6 N = 16	[65–67]
M. murinus 63 g	Mandena: Littoral forest	3.2–10.3–19.5 N = 24	0.5–7.0–13.6 N = 18	1.0–4.5–6.3 N = 14	1.0–2.9–5.3 N = 13	[68]
M. tanosi 55 g	Ste Luce: Littoral forest	1.0–7.2–20.1 N = 34		1.4–6.5–10.4 N = 4		[55]

For all species of *Microcebus*, seeds found in fecal samples varied between 0.3 and 10.7 mm in length and 0.2–6.9 mm in width (medians: 4.5 mm and 3.2 mm; N = 86 and 83, respectively). Seed length and seed width were closely correlated (linear regression: seed width = $0.58 \times$ seed length + 0.47, R² = 0.71, *p* < 0.001; Figure 2; Table 2). Thus, seeds are on average twice as long as wide.

The length of seeds found in fecal samples did not differ between the different species of *Microcebus* (Kruskal–Wallis test: H = 6.45, p = 0.265, df = 5), although there was a significant difference in the width of seeds (H = 11.24, p = 0.024, df = 4). The seeds found in fecal samples of *M. griseorufus* from Tsimanampetsotse were significantly larger than the seeds found in fecal samples of *M. jollyae* from Kianjavato (Table 2; p = 0.018; Mann–Whitney-U test after Bonferroni correction for multiple pairwise comparisons).

Only the study by Lahann [68] on *M. murinus* in the littoral forest of Mandena provided a robust analysis of seed dispersal on the level of the plant community. She distinguished between the size of seeds that actually identified from feces, the size of seeds in fruits that seemed to have been swallowed according to intensive behavioral observations, and the size of seeds in fruits where *Microcebus* had only been feeding on pulp but the seeds either remained on the plant or were dropped to the ground. Not considering seeds that were probably swallowed but had not been found in fecal samples, the length and width of seeds found in the feces of *M. murinus* were significantly smaller than the length and width of



seeds from fruits where the animals were only feeding on pulp but did not swallow the seeds (Mann–Whitney U test; length: z = 4.84, p < 0.001; width: z = 3.57, p < 0.001; Table 2).

Figure 2. Length and width of seeds found in feces of different *Microcebus* spp. *Microcebus tanosi* was not considered due to the lack of measurements of seed width.

The study by Bollen [55] did not focus on the analysis of *Microcebus* fecal samples and therefore the data on seed dispersal by *M. tanosi* have to be considered in a preliminary manner. In her study, the length of seeds swallowed by *M. tanosi* was also smaller than the length of seed from fruits where the animals had only been seen feeding on pulp but their seeds had not been found in fecal samples, though this difference was not significant (Mann–Whitney U test; length: z = 0.48, p = 0.63; Table 2).

3.3. Size of Seeds Dispersed by Microcebus spp. Versus Other Frugivores

For the humid eastern forest at Ranomafana seed size has been measured for fruits dispersed by the community of frugivorous lemurs and birds [57]. We assume that this database can also be used for comparisons with the humid eastern forest of Kianjavato, some 50 km east of Ranomafana. For the humid littoral forest of Ste Luce in southeastern Madagascar fruits consumed by bats and small mammals were also studied [21,55,58]. We compared the size of seeds in fecal samples of the *Microcebus* spp. Occurring in these vegetation types with the size of seeds recorded for all frugivores at these sites. For the eastern humid forest, these were *M. jollyae*, mostly at Kianjavato, and *M. rufus* at Ranomafana [23,65–67]. For the littoral forests of southeastern Madagascar, these were *M. murinus* and *M. tanosi* [55,58,68] (Table 2). Since seed length and width were closely correlated, we restricted the following analyses to length.

The distribution and median of seed length of fruits consumed by different frugivores did not differ between the humid eastern forest of Ranomafana (seed length [minimum-median-maximum]: 1.0–9.8–35.8 mm, N = 99; [57]) and the littoral forest of Ste Luce (seed length: 1.0–8.4–36.4 mm, N = 124 [55]; Kolmogorov–Smirnov test: z = 0.77, p = 0.59).

The maximum length of seeds present in *Microcebus* feces was 10.7 mm in the humid eastern forest of Ranomafana and Kianjavato, and 10.4 mm in the littoral forest of Mandena and Ste. Luce (Table 2). Thus, based on seed length, *Microcebus* spp. would have the poten-

tial to disperse seeds of more than half of all fruit species occurring in the humid and littoral forests, most seeds swallowed by *Microcebus* are well below the maxima (Figure 3). The differences in seed length between those passed through the digestive tract of *Microcebus* and the length of all seeds measured were significant for Ranomafana and Kianjavato, as well as for Mandena and Ste. Luce (Mann–Whitney-U tests: z > 3.8, p < 0.001 in both cases). It should be noted that both databases do not consider dry fruits and hard-shelled fruits that are not typically consumed by frugivores and cannot be opened by *Microcebus* spp.



Figure 3. The number of different-sized fruit seeds consumed by frugivores in the humid eastern forest of Ranomafana and Kianjavato (**a**), and the littoral forests of southeastern Madagascar (**b**), compared with seeds appearing in fecal samples of *M. jollyae* and *M. rufus* in the eastern humid forests of Kianjavato and Ranomafana, and with *M. murinus* and *M. tanosi* in the littoral forests of Mandena and Ste. Luce; seed length in 2 mm intervals: ≤ 2.0 mm, 2.1–4.0 mm, etc.

3.4. Life Forms of Plants Dispersed by Microcebus Versus Other Lemur Genera

Microcebus spp. feed significantly more often on the fruits of herbs, shrubs, vines, and epiphytes than other lemur genera that rely more on fruits from larger trees ($\chi^2 = 22.89$, df = 4, p < 0.001; Figure 4; Table A1; data for other lemur genera are from the Supplementary Table in [16]; the combined tables can be obtained from JUG upon request). This difference was reinforced when comparing the feeding observations of all other lemur genera with plants whose seeds had been found in the feces of *Microcebus* spp. ($\chi^2 = 60.94$, df = 4, p < 0.001). The life forms of plants recorded as food sources for *Microcebus* spp. were skewed towards trees and small trees, while herbs, shrubs, vines, and epiphytes were underrepresented in observations compared to fecal samples ($\chi^2 = 7.66$, df = 4, not significant after Bonferroni correction). Despite the predominance of seeds from herbs, vines, and



shrubs in the feces of *Microcebus* spp., about 20% of seeds dispersed by *Microcebus* spp. with certainty are from trees (Figure 4).

Figure 4. Life forms of plant species (in %) used by all lemur genera for fruit-eating (without *Microcebus* spp.; N = 953 plant species), *Microcebus* spp. (N = 123 plant species; fruits of plant species consumed but seeds may or may not be dispersed), or seeds found in fecal samples of *Microcebus* spp. (N = 79 plant species dispersed).

3.5. Plant Life Form and Seed Size

Seed lengths differed between plant species with different life forms (Kruskal–Wallis test: H = 24.41, p < 0.001, df = 4). The difference is due to the higher proportion of large-sized seeds in trees than in other life forms, though about half of the tree species considered have seeds that could be swallowed by *Microcebus* spp. (Table 3).

Table 3. Seed length of different plant life forms. Values are presented as minimum–median– maximum; different letters indicate significant differences in the median seed length (p < 0.01) between life forms according to the Mann–Whitney-U test after Bonferroni correction. Sample size in brackets.

	Herbs, Shrubs	Small Trees	Trees	Vines	Epiphytes
Seed length [mm]	0.8–5.1 ^a –11.0	1.0–7.3 ^{ab} –27.3	1.0–10.6 ^b –35.8	3.1–5.9 ^{ab} –36.4	1.3–4.6 ^{ab} –5.7
	(39)	(62)	(113)	(14)	(6)

4. Discussion

Using mouse lemurs from Madagascar as an example, we explored to what extent small generalist frugivores as native seed dispersers can contribute to biodiversity restoration. The considerations outlined for Madagascar could also be applied to other regions of the world. From a restoration perspective, these small frugivores have the advantage over large frugivores in that they can use shrub habitats and thus the early stages of natural succession. Due to the small size of *Microcebus* spp. (60 g), they disperse mainly small seeds characteristic of herbs, shrubs, and epiphytes. Especially herbs and shrubs represent the early stages of succession and thus provide a more natural sequence than is applied in most reforestation projects. These pioneer and undergrowth plant species, together with vines and epiphytes, tend to be underrepresented in observational studies compared to fecal analyses. This might be due to the difficulties of observing these small nocturnal

species in dense understory vegetation at night. However, the dispersal of these pioneer species could be an important initial step for successional reforestation. Apart from many pioneer plants, Microcebus spp. also disperse the seeds of large trees and thus can cover a wide array of plant types and species. Yet, their most important role could be that they use shrub vegetation that cannot be used by large-bodied frugivores and disperse forest seeds into this type of pioneer vegetation. Frugivorous birds are also good candidates for dispersing small seeds in shrub vegetation; however, their diversity in Madagascar is limited compared to continent avifauna, and they are subject to hunting as they are diurnal and therefore easier targets for people than the small nocturnal lemurs [49,58,69,70]. Similar to most other lemur species, except for *Propithecus edwardsi* [71], mouse lemurs also have the advantage that they do not act as seed predators but pass seeds intact. Though we did not test the viability of seeds found in the feces of *M. griseorufus* in our case study, we assume that the seeds were still fertile, as had been demonstrated for M. griseorufus at another site [26] and for other Microcebus species [23]. Also similar to other lemur species, passage through the digestive tract does not impede but rather improves germination rates [23,26,71–73].

While the role of lemurs including mouse lemurs as important seed dispersers in wet and dry forests of Madagascar has been acknowledged for some time [18,23,71,72,74–79], lemur fecal samples or the information provided by the various studies on seed dispersal have rarely been used for forest restoration in practice [8]. Conceptually, the approach of "facilitated restoration" revolves around large fruiting trees that attract frugivores (and other animals) due to their structural properties (shelter, support for arboreal species) and fruit crops [15,19,20]. If large remnant trees still occur in the area to be restored or fast-growing fruit trees can be planted, this approach remains valuable. However, when these trees are isolated in open habitats, other than for birds and fruit bats [21,58,80], they probably are less important for lemurs that are unable to cross large expanses of non-forested habitat. "Isolation" is certainly a question of scale that has not yet been explored in sufficient detail in Madagascar [15,17,33,81]. In any case, forest restoration might be more efficient by not starting only with planting large canopy trees, but by adding pioneer understory plant species that grow fast, create abiotic and biotic conditions for climax species, and attract *Microcebus* at an early stage of succession. They, in turn, can then supplement the first successional stages by dispersing seeds from the nearby forest. This seems to be relevant, particularly in dry areas where seasonality is pronounced with extended dry periods and, as a consequence, large tree species are more difficult to grow than at more humid sites [82].

In a conservationist's ideal world, reforestation should be carried with as many native forest species as possible [83]. Yet, due to economic constraints, the lack of seed supplies for many native species, and lacking knowledge of efficient tree propagation, most large-scale reforestation programs are based on only a handful of species [84]. Clearly, reforestation is first and in most cases planting trees for local human needs and not a sort of ecological restoration for the conservation of plants and animals (e.g., [85]), that is to say, an attempt to regrow the forest to something close to its natural state. But especially in cases where wood production does not have the potential to result in conflicts of interest between humans and animals (e.g., in fruit-producing agroforestry projects [86]), introducing more biodiversity in the understory would contribute to biodiversity conservation, such as illustrated by the home gardens of Kilimanjaro [87,88]. In Madagascar, some local projects aim to maximize the tree species diversity in reforestation [8,9,22,89–98]. However, costs and efforts are high, and even the most successful projects cannot mimic natural succession and biodiversity. Thus, any additional help at no cost would be most welcome. In addition, even the initial restoration with pioneer species may require a substantial amount of effort and experience before successful results can be obtained, such as illustrated in Figure 5 [22]. Selecting pioneer shrub species that are known to be dispersed by mouse lemurs may facilitate these initial phases.



Figure 5. Example of four-year-old forest restoration plots with exotic *Acacia* trees to the left of the path and with native shrubs and tree species in Mandena littoral forest to the right of the path, used at this stage by *Microcebus murinus* but not by other lemur species (QIT Madagascar Minerals restoration project; photo by J. U. Ganzhorn).

This idea has to be put into the real-world conservation context, such as filling in corridors between forested zones that are separated by a few hundred meters. Initially, shrubs are present at the forest edge and not in the expanse of the planted zone. Until the trees grow and fill in some cover, dispersing mouse lemurs would be subjected to high predation rates from owls; for example [99], it is hard to imagine that *Microcebus* would move into the reforested zone as long as there are no remaining forest fragments or at least some stands of trees, including introduced species [34,81]. Hence, their role in the context of dispersing seeds might be limited, except at the forest edge. For forest restoration projects that are in place from the forest edge across an expanse of open areas, a possible solution to propose is that bands of shrubs be planted across areas being planted for forest restoration, which would provide a corridor for *Microcebus* and other frugivores to occupy and diffuse seeds in ([29]; Figure 5).

The phenomenon that native mammals can use various forms of agroforestry may be of limited value for forest restoration, as early successional plant species and most regenerating trees (apart from some shade trees) are likely to be removed from the area targeted to grow crops. But areas no longer useable for agriculture due to soil degradation could be targeted for ecological restoration [100,101]. Different forms or stages of fallow land that temporarily or permanently are no longer used for agriculture have different names in the local terminology and can develop differently. The local knowledge of characteristics of fallow land is rarely considered in development projects but could be combined with revised restoration strategies based on natural succession [8,9,101–106]. Here, the restored forests should also provide benefits for the rural human population. This could be achieved by adding native and also exotic utilitarian trees whose growth requirements are better known than the requirements of most native tree species [8,25]. The regeneration of native shrubs and trees in exotic tree plantations, such as *Eucalyptus* spp. or

Pinus spp., might provide starting points to replace conventional forestry practices with modern, biodiversity-oriented reforestation (Figure 5; [8,25,107–111]).

5. Conclusions

We analyzed the possible relevance of small generalist lemurs of the genus *Microcebus* as seed dispersers for forest restoration. Building in part from previous studies, we base our conclusions not on the fruits consumed, but on seeds that were actually passed through the digestive tract. Due to the diminutive size of these animals, they disperse mostly small seeds. Many of these small-seeded plants are pioneer herbs and shrubs, but Microcebus also disperses seeds of some large trees. Since these small seed dispersers can use degraded or restored habitats at a much earlier successional stage than large frugivorous seed dispersers, they play an important role in transporting seeds from natural forests into reforestation areas than larger seed dispersers and thus increase the diversity of plant species in the restoration plots [83]. Certainly, reforestations have a wide array of purposes ranging from rehabilitation and industrial forests to agroforestry and ecological restoration. The information compiled in this study is not relevant for all initiatives but may help to design the composition of pioneer plants for restoration not only from the plant perspective but also from the perspective of improving soil fertility and attracting seed dispersers that are most likely to use these early stages of restoration. Their consideration could accelerate the trajectory towards a species-rich plant community that otherwise might remain species-poor for long [82].

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Conflicts of Interest: Author Sylvia Atsalis was employed by Professional Development for Good, Author Edward E. Louis Jr. was employed by Madagascar Biodiversity Partnership, Omaha Zoo, Authors Jean-Baptiste Ramanamanjato, Cedric Tsagnangara, and Refaly Ernest were employed by Tropical Biodiversity & Social Enterprise, Author Faly Randriatafika was employed by QIT Madagascar Minerals. The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Appendix A

Seeds from *Microcebus griseorufus*, Tsimanampetsotse; one square = 1 x 1 mm²





Aspargus schumanianus

Azima tetracantha



Alluaudia comosa



Cadabra virgate





Commiphora sinuata



Diospyros manampetsae

Bakerella sp.

Commiphora sp.



Ficus menabensis

Figure A1. Cont.

Cordia caffra



Grewia sp.



Cyphostema laza



Gymnosporia linearis



Karomia microphylla



Scrophullaria sp. or Socratea vertina



Maerua filiformis



Tallinela microphylla



Maerua nuda



Terminalia ulexoïdes



Salvadora angustifolia

Viscum sp.

Seeds from *Microcebus lehilahytsara*, Ankafobe; one square = 5 x 5 mm²



Adenia sp.



Viscum sp.



Bakerella sp.



Not identified "B"



Chassalia sp.



Not identified "C"

Figure A1. Illustrations of seeds collected from feces of *Microcebus* spp. Seeds from Tsimanampetsotse were collected by P. Giertz, Y. R. Ratovonamana, L. Behrendt, and F. Holst and identified by members of the Association Analasoa: C. Kasola, F. Atrefony, F. Louis, G. N. Odilon, R. G. Ralahinirina, T. Menjanahary, and Y. R. Ratovonamana. Seeds from Ankafobe were collected by [34] and identified by D. Tahirinirainy (Missouri Botanical Garden).

Table A1. Characteristics of plants with confirmed dispersal by *Microcebus* spp. na = not available; Study site and Reference: Tsimanampetsotse (dry forest and xerophytic thicket [], this study; Ranomafana, Kianjavato (eastern humid forest) [23]; Ankafobe (humid forest on central highland [34]; Tsinjoarivo (eastern humid forest) [112]; Mandena (littoral forest) [68]; Ranomafana, Talatakely (eastern humid forest) [65–67]; Ste Luce (littoral forest) [55]; na = not applicable. For Madagascar, there is no rigorous database or experimental evidence for assigning plant species to different successional stages (such as pioneer, early or late secondary stage, climax). The dry forest and spiny thicket of Tsimanampetsotse is rather open and species distribution seems to be determined rather by abiotic conditions than by succession [50]. For the humid eastern forests, some species have been assigned to different stages [8,22]. However, the data available are too scant to provide a comprehensive picture of the situation.

Plant Family	Plant Species	Growth Form	Microcebus sp.	Seed Length [mm]	Seed Width [mm]	Study Site and Reference
Fabaceae	Acacia rovumae	Tree	M. griseorufus	4.5	3.8	[]
Passifloraceae	Adenia sp.	Vine	M. griseorufus	5.0	4.3	[]
Didieraceae	Alluaudia comosa	Tree	M. griseorufus	6.0	4.6	[]
Asperagaceae	Asparagus schumanianus	Herb	M. griseorufus	4.2	3.8	[]
Salvadoraceae	Azima tetracantha	Shrub	M. griseorufus	4.3	3.5	[]
Loranthaceae	Bakerella sp.	Epiphyte	M. griseorufus	4.4	3.6	[]
Capparaceae	Cadaba virgata	Shrub	M. griseorufus	2.2	2.2	[]
Burseraceae	Commiphora orbicularis	Shrub	M. griseorufus	5.5	5.0	[]
Burseraceae	Commiphora sinuata	Shrub	M. griseorufus	6.9	5.4	[]
Burseraceae	Commiphora sp.	Small tree	M. griseorufus	6.0	4.0	[]
Boraginaceae	Cordia caffra	Tree	M. griseorufus	6.0	4.0	[]
Passifloraceae	Cyphostema laza	Vine	M. griseorufus	9.1	5.4	[]
Ebenaceae	Diospyros manampetsae	Shrub	M. griseorufus	4.5	2.8	[]
Moraceae	Ficus menabensis	Tree	M. griseorufus	1.0	1.0	[]
Malvaceae	<i>Grewia</i> sp.	Shrub	M. griseorufus	3.2	2.2	[]
Celastraceae	Gymnosporia linearis	Shrub	M. griseorufus	5.3	4.8	[]
Lamiaceae	Karomia microphylla	Shrub	M. griseorufus	4.4	4.1	[]
Capparaceae	Maerua filiformis	Tree	M. griseorufus	4.8	4.2	[]
Capparaceae	Maerua nuda	Shrub	M. griseorufus	4.9	4.5	[]
Salvadoraceae	Salvadora angustifolia	Tree	M. griseorufus	4.4	3.8	[]
Scrophulariaceae	Scrophularia sp.	Shrub	M. griseorufus	7.3	4.1	[]
Arecaceae	Socratea vertina	Tree	M. griseorufus	4.7	3.8	[]
Portulariaceae	Tallinela microphylla	Shrub	M. griseorufus	2.2	2.2	[]
Combretaceae	Terminalia ulexoïdes	Shrub	M. griseorufus	5.4	3.2	[]
Melastomataceae	Clidemia hirta	Herb	M. jollyae	0.8	0.5	[23]
Rubiaceae	Coffea millotii	Tree	M. jollyae	8.5	5.0	[23]
Arecaceae	Dypsis linearis	Tree	M. jollyae	6.7	3.8	[23]
Moraceae	Ficus baronii	Tree	M. jollyae	1.3	1.0	[23]
Moraceae	Ficus trichoclada	Tree	M. jollyae	1.2	0.9	[23]
Cyperaceae	Scleria madagascariensis	Herb	M. jollyae	3.5	3.2	[23]
unknown	Unknown 1		M. jollyae	0.3	0.2	[23]
unknown	Unknown 2		M. jollyae	1.1	0.9	[23]

Table A1. Cont.

Plant Family	Plant Species	Growth Form	Microcebus sp.	Seed Length [mm]	Seed Width [mm]	Study Site and Reference
unknown	Unknown 3		M. jollyae	2.2	1.6	[23]
Passifloraceae	Adenia sp.	Vine	M. lehilahytsara	4.3	3.5	[33]
Loranthaceae	Bakerella sp.	Epiphyte	M. lehilahytsara	5.6	3.1	[34]
Rubiaceae	<i>Chassalia</i> sp.	Shrub	M. lehilahytsara	5.1	4.3	[34]
unknown	Unknown B		M. lehilahytsara	4.1	2.5	[34]
unknown	Unknown C		M. lehilahytsara	1.8	1.8	[34]
Viscaceae	Viscum sp.	Epiphyte	M. lehilahytsara	4.6	3.6	[34]
Loganiaceae	Anthocleista sp.	Tree	M. lehilahytsara	na		[112]
Loranthaceae	Bakerella sp.	Epiphyte	M. lehilahytsara	na		[112]
Myrsinaceae	Embella sp.	Vine	M. lehilahytsara	na		[112]
Melastomataceae	<i>Medinilla</i> sp.	Vine	M. lehilahytsara	na		[112]
Rubiaceae	Pauridiantha sp.	Small tree	M. lehilahytsara	na		[112]
Ericaceae	Vaccinium sp.	Small tree	M. lehilahytsara	na		[112]
Viscaceae	Viscum sp.	Epiphyte	M. lehilahytsara	na		[112]
Loranthaceae	Bakerella sp.	Epiphyte	M. murinus	4.1	2.3	[68]
Rubiaceae	<i>Canthium</i> sp.	Small tree	M. murinus	6.3	4.1	[68]
Rubiaceae	Coffea commersoniana	Small tree	M. murinus	3.5	2.2	[68]
Convallariaceae	Dracaena sp.	Small tree	M. murinus	6.0	3.2	[68]
Erythroxylaceae	Erythroxylon sp.	Small tree	M. murinus	6.0	6.0	[68]
Moraceae	Ficus pyrifolia	Small tree	M. murinus	1.0	1.0	[68]
Rubiaceae	<i>Gaertnera</i> sp.	Small tree	M. murinus	5.8	4.7	[68]
Clusiaceae	Psorospermum sp.	Small tree	M. murinus	2.1	2.0	[68]
Salicaceae	Scolopia sp.	Small tree	M. murinus	3.6	3.2	[68]
Myrtaceae	Syzigium eminense	Tree	M. murinus	5.1	4.7	[68]
Rubiaceae	<i>Tarrena</i> sp.	Small tree	M. murinus	2.5	2.3	[68]
Rubiaceae	<i>Tricalysia</i> sp.	Small tree	M. murinus	4.9	2.3	[68]
Ericaceae	Vaccinium eminense	Small tree	M. murinus	1.3	1.3	[68]
Rutaceae	Vepris eliottii	Small tree	M. murinus	5.1	4.8	[68]
Loranthaceae	Bakerella clavata	Epiphyte	M. rufus	5.7	3.5	[23]
Rubiaceae	Bremeria erectiloba	Tree	M. rufus	2.0	2.0	[23]
Menispermaceae	Burasaia madagascariensis	Tree	M. rufus	4.0	3.9	[23]
Rubiaceae	Chassalia ternifolia	Shrub	M. rufus	3.6	2.0	[23]
Rubiaceae	Danais rhamnifolia	Vine	M. rufus	5.6	4.0	[23]
Dichapetalaceae	Dichapetalum chlorinum	Vine	M. rufus	4.5	2.8	[23]
Arecaceae	Dypsis nodifera	Tree	M. rufus	5.1	3.4	[23]
Primulaceae	Embelia concinna	Vine	M. rufus	3.1	2.9	[23]
Moraceae	Ficus reflexa	Tree	M. rufus	1.0	1.0	[23]
Myrthaceae	Psidium cattleianum	Tree	M. rufus	4.4	3.0	[23]
Rubiaceae	Psychotria reducta	Shrub	M. rufus	3.3	2.9	[23]

Plant Family	Plant Species	Growth Form	Microcebus sp.	Seed Length [mm]	Seed Width [mm]	Study Site and Reference
Solanaceae	Solanum mauritanium	Shrub	M. rufus	1.3	1.2	[23]
Monimiaceae	Tambourissa thouvenotii	Tree	M. rufus	10.7	6.9	[23]
Menispermaceae	"Hazotana"	Vine	M. rufus			[65-67]
Rubiaceae	"Voananamboa"	Shrub	M. rufus			[65-67]
Rubiaceae	Alberta humblotii	Shrub	M. rufus	8.3	4.5	[65-67]
Loganiaceae	Anthocleista amplexicaulis	Tree	M. rufus	2.5	1.8	[65-67]
Flacourtiaceae	Aphloia theaeformis	Tree	M. rufus	2.5	2.0	[65-67]
Loranthaceae	Bakerella grisea	Epiphyte	M. rufus	5.6	2.0	[65-67]
Loranthaceae	Bakerella sp.	Epiphyte	M. rufus	7.8	2.5	[65-67]
Vitaceae	Cissus	Vine	M. rufus	7.1	4.4	[65-67]
Moraceae	Ficus sp.	Shrub	M. rufus	2.0	2.0	[65-67]
Rubiaceae	<i>Gaertnera</i> sp.	Tree	M. rufus	5.9	4.5	[65-67]
Clusiaceae	Harungana madagascariensis	Small tree	M. rufus			[65-67]
Aquifoliaceae	Ilex mitis	Tree	M. rufus	3.2	1.7	[65-67]
Myrsinaceae	Maesa lanceolata	Small tree	M. rufus			[65-67]
Melastomataceae	<i>Medinilla</i> sp.	Epiphyte	M. rufus	1.5	0.5	[65-67]
Loganiaceae	Nuxia sp.	Tree	M. rufus	6.0	4.3	[65-67]
Myrtaceae	Psidium cattleianum	Shrub	M. rufus	4.5	0.3	[65-67]
Rubiaceae	Psychotria sp.	Shrub	M. rufus	7.2	5.6	[65-67]
Rubiaceae	Psychotria sp.	Shrub	M. rufus	5.5	4.7	[65-67]
Rubiaceae	Psychotria sp.	Shrub	M. rufus	4.5	3.6	[65-67]
Cactaceae	Rhipsalis baccifera	Epiphyte	M. rufus	1.3	0.5	[65-67]
Viscaceae	Viscum sp.	Epiphyte	M. rufus			[65-67]
Gentianaceae	Anthocleista longifolia	Tree	M. tanosi	3.4		[55]
Loranthaceae	Bakerella sp.	Epiphyte	M. tanosi	10.4		[55]
Celastraceae	<i>Brexia</i> sp.	Small tree	M. tanosi	?		[55]
Phyllanthaceae	Uapaca thouarsii	Tree	M. tanosi	9.6		[55]
Ericaceae	Vaccinium eminense	Tree	M. tanosi	1.4		[55]

Table A1. Cont.

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