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Linking disperser traits and habitat quality to seed dispersal effectiveness[☆]

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ABSTRACT

Animal-mediated seed dispersal is a biotic interaction at risk of disruption because of the alarming decline of seed-dispersing animal populations as a result of habitat transformation. However, a cessation of seed dispersal can be masked by the continuous presence of seed dispersers in an ecosystem. Here, we assess how changes in the population and body size of a small-bodied seed disperser (brown mouse lemur, *Microcebus rufus*) and three habitat types in Madagascar's rainforest landscape affect its seed dispersal effectiveness. We calculated population size and body mass from monthly capture-release and systematic measurements of 815 individuals captured from 2021 to 2024. We collected 285 fecal samples from captured individuals to calculate the diversity, number, and size of 1641 defecated seeds. In addition, we conducted germination experiments on 1035 defecated seeds. We found a significant positive association of the diversity and germination time of dispersed seeds with *M. rufus*' population size and habitat types. We also found similar results for the number of dispersed seeds with *M. rufus*' population and body size and seasons. Our findings show that *M. rufus* provide seed dispersal services with fluctuating effectiveness depending on its population and body size, as well as habitat types and seasons. Such results highlight the importance of protecting the animal dispersers populations to promote the persistence of ecological services and support the ecosystem's resilience.

Fintina (extended abstract in Malagasy): Tsy misy zava-mananaina mahavita tena irery fa miara-miasa daholo ary miara-mahazo vokatsoa avokoa. Isan'ny mampifandray ny zava-maniry sy ny biby ny fanaparitahana vihy. Mahazo ny angovo sy otrikaina ilainy ny biby rehefa miremby sy mihinana voankazo ary entin'ireto farany amin'ny toerana vaovao kosa ireo vihy izay nohanin'izy ireo mba hitombo sy hamokatra indray. Noho ireo fahasimban'ny rohivoahary samihafa nefa dia tsy mitsahatra mihena ny isan'ny biby, izay lasa mampihena ny fanaparitahana vihy sy ny isa ary karazan-java-maniry misy eo amin'ny toerana iray. Matetika ihany koa dia tsy tsikaritra ny fitsaharan'ny fanaparitahana vihy ao amin'ny rohivoahary iray satria mbola hita miaina ao ilay biby mpanatanteraka izany; kanefa misy fetrany ny fahafahan'ireo biby manaparitaka vihy na dia mbola mitoeatra eo aza izy ireo. Eto izahay dia nijery ny fiovaovan'ny isa sy lanjan'ny antsidy mena (*Microcebus rufus*) ao amin'ny ala mando sy ny manodidina ny valan-java-boaharin-dRanomafana Ifanadiana (atsimo atsinanan'i Madagasikara) sy izay fiatraikan'izany eo amin'ny fanaparitahana vihy ataon'izy ireo. Namandrika sy nandrefy antsidy miisa 815 nanomboka ny taona 2021 katramin'ny 2024 izahay, ary nahangona vihy miisa 1 641 avy amin'ny karazan-java-maniry miisa 23. Hita tamin'izany fa mitombo miaraka amin'ny habetsaky ny antsidy ny karazan-java-maniry aparitaky izy ireo, ary miamalaky ihany koa ny fitsimohan'ny vihy, indrindra any amin'ny ala akaiky toeram-pambolena sy ala lavitry ny tsindry sy tandindona samihafa. Hita ihany koa fa mitombo ny isan'ny zava-maniry voaparitaka rehefa lehibe vatana ny antsidy mena ary miaavy ny orana. Mampiseho ireto voka-pikarohana ireto fa misy fiatraikany ratsy amin'ny fanaparitahana vihy sy fiazonana ny tamba-java-maniry ny fiovaovan'ny isa sy lanjan'ny biby mpanaparitaka vihy, izay mazana vokatry ny fahasimban'ny toera-ponanana sy rohivoahary. Noho izany, tsara arovana ireo biby mpanaparitaka vihy, no tandrovana rohivoahary mbola tsy simba ary arenina kosa ireo efa simba mba hiarovana ny biby sy ny zava-maniry tsy ho lany tamingana vetivety.

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1. Introduction

Biotic interactions, or interactions among species, are critical for the maintenance of biodiversity. They ensure the resilience and integrity of ecosystems, and the continuation of services humans rely on for their well-being (Montoya and Raffaelli, 2010; Tylianakis et al., 2008, 2010). Unfortunately, rampant habitat transformation and loss threaten the persistence of biotic interactions because species partners are lost faster than new partnerships are built (Burkle et al., 2013; Montoya and Raffaelli, 2010). Therefore, some vital biotic interactions are declining and disappearing, ultimately eroding the provision of vital ecosystem services (Aslan et al., 2013; Montoya and Raffaelli, 2010). Animal-mediated seed dispersal (zoochory) is one of the biotic interactions at risk of disruption (Aslan et al., 2013; McConkey and O'Farrill, 2016), mainly due to the rapid decline of animal seed dispersers (e.g., McConkey and Drake, 2006), their extirpation from their habitats (e.g., Babweteera and Brown, 2009; Fricke et al., 2025; Galetti and Dirzo, 2013), and habitat transformation (e.g., Markl et al., 2012). Because zoochory depends on animals and their persistence in natural habitats, changes in any of these components can affect how seeds are spread across ecosystems and landscapes (McConkey and O'Farrill, 2016; Schupp et al., 2010). Most importantly, the loss of seed dispersal itself is often less noticeable than the extirpation of an animal seed disperser (McConkey and Drake, 2006; McConkey and O'Farrill, 2015, 2016).

Cryptic seed dispersal loss, or the loss of seed dispersal before the loss of seed dispersers, can occur at different levels, affecting the structure of ecosystems (McConkey and O'Farrill, 2016). Animal seed dispersers adapt their behavior, body conditions, and demography in response to disturbances (e.g., Culliney et al., 2012; Dáttilo et al., 2014; McConkey and Drake, 2006; McConkey and O'Farrill, 2015). As a result, their contribution to seed dispersal can be altered or halted depending on the severity of the changes (e.g., McConkey and O'Farrill, 2015, 2016; Sengupta et al., 2015; Uriarte et al., 2011). For instance, recruitment of animal-dispersed seeds is lower in forest edges and in degraded forests compared to forest interiors and less-degraded forests (e.g., Cordeiro et al., 2009) as resources vary in availability and quantity (e.g., Fricke et al., 2025; Sengupta et al., 2015). Moreover, changes in population or individual sizes could affect the seed dispersal effectiveness of a seed disperser species, mainly the number of seeds dispersed as well as the deposition and germination outcomes (McConkey and O'Farrill, 2016). For example, lower population and body size have led to less diversity, downsizing, and poor germination of the dispersed seeds, affecting the regeneration and composition of the plant communities (Donoso et al., 2020; Fricke et al., 2019; Fricke et al., 2025). Understanding the direct effects of population and body size is then critical because (1) ongoing habitat transformation affects plant and animal communities' composition and survival conditions (Aslan et al., 2013; Fricke et al., 2025), (2) some seed dispersers' populations appear stable but have stopped providing seed dispersal services (McConkey and Drake, 2006; McConkey and O'Farrill, 2015, 2016), and (3) several components of seed dispersal effectiveness (e.g., size of dispersed seeds and dispersal distance) depend on the body size of seed dispersers (Razafindratsima et al., 2014; Schupp et al., 2010). Furthermore, such knowledge can inform us on the resilience of biotic interactions and help us design robust but less costly conservation and restoration strategies (Aslan et al., 2013; Ganzhorn et al., 2024; Montoya and Raffaelli, 2010; Tylianakis et al., 2010).

Here, we aim to understand the impacts of seed dispersers' population size, body mass, and habitat quality on seed dispersal effectiveness. Specifically, we hypothesized that the population size and body mass of a seed disperser would be positively associated with seed dispersal effectiveness because 1) high abundance increases the probability of seeds to be dispersed as well as their number (Nevo et al., 2023; Schupp, 1993; Schupp et al., 2010); and 2) high body mass allow longer dispersal distances and gut-passage, improving seed germination and seedling growth (McConkey and O'Farrill, 2015, 2016). Additionally, we

hypothesized that 3) less-disturbed forest habitats sustain higher population and body sizes as resources are continuously available (McConkey and O'Farrill, 2016; Sengupta et al., 2015). We used the Seed Dispersal Effectiveness (SDE) framework (Schupp, 1993; Schupp et al., 2010) – which is based on the quantitative and qualitative components of seed dispersal – to describe and assess how seed dispersal varies with population and body sizes and across different forest habitat types. We then used the diversity, number, and size of dispersed seeds as quantitative components of seed dispersal effectiveness, and seed dispersal distance, germination rate, and germination time as qualitative components (McConkey and O'Farrill, 2016; Nevo et al., 2023; Schupp et al., 2010). We also measured the overall effectiveness of the seed disperser regardless of habitat types. We tested these hypotheses using the wild populations of brown mouse lemur, *Microcebus rufus* (family: Cheirogaleidae, Order: Primates), in Madagascar's rainforests to address our goals.

2. Methods

2.1. Study species

We focused this study on the brown mouse lemur, *Microcebus rufus*, in the forest landscape of Ranomafana National Park (RNP) for several reasons. First, this species is an effective seed disperser of both native and non-native plant species in the region (Ganzhorn et al., 2024; Ramananjato, 2024; Ramananjato et al., 2020). Second, they are tolerant to forest degradation and continue to occur in the different forest habitats (Knoop et al., 2018; Ramananjato et al., 2025; Ramananjato and Razafindratsima, 2021). *M. rufus* have a body mass range of 28–98 g and feed mainly upon fruits and arthropods at various rates year-round (Atsalis, 1999a; Ramananjato et al., 2020; Ramananjato, 2024). Finally, they consume fruits from trees, shrubs, herbs, lianas, and epiphytes, which other seed dispersers do not usually consume and disperse (Ramananjato, 2024; Ramananjato et al., 2020; Razafindratsima et al., 2022).

Additionally, population size and body mass of *M. rufus* vary from one site to another in RNP, depending on the habitat quality and resources available (Ramananjato et al., 2025; Ramananjato and Razafindratsima, 2021), with higher abundance in less disturbed habitats and sites with year-round food sources availability. Its body mass also changes seasonally mainly because of a fattening period to sustain its daily torpor (i.e., a short form of hibernation) during the dry season, followed by the reproductive season (Blanco et al., 2018; Ramananjato et al., 2022).

2.2. Study site and period

We conducted fieldwork from July 2021 to November 2024 (27 months total through five non-consecutive field seasons: Jul–Sep 2021, Jan–Mar 2022 & Jul–Sep 2022, Mar–Dec 2023, and Jun–Dec 2024) within and around RNP, southeastern Madagascar (47°18'–47°37' E, 21°02'–21°25' S; Fig. S1). These periods covered dry season for each year and the first half of the rainy season in 2023 and 2024 (Dunham et al., 2011, 2018). We collected data in five sites with four different levels of degradation (Ramananjato et al., 2025; Ramananjato and Razafindratsima, 2021; Razafindratsima, 2017). Valohoaka is a primary forest with a very low disturbance from human activities and is part of the biggest forest block of RNP. Vohiparara is a secondary forest with moderate disturbance and is at the edge of the forest block. Bevoahazo, which we only sampled for 2021 and early 2022 as it was wiped out by two cyclones in early 2022 (Ramananjato et al., 2025), is a forest fragment adjacent to RNP limits. Ankazomasina and Nantehana (hereafter crop fields) are both forest edges at the RNP limits overlapping with various crop plantings (banana, lychee, coffee, and cassava) with very high and frequent disturbances from human activities. We collected data in these five sites simultaneously in 2023 and 2024 but alternated sites

for 2021 and 2022.

2.3. Capture abundance and body mass of *Microcebus rufus*

Following the protocol in Ramananjato et al. (2020), we set up 45 banana-baited live traps (35 Large Folding Aluminum (LFA) $7.63 \times 8.89 \times 22.86$ cm, and 10 LFA $10.16 \times 11.42 \times 38.10$ cm traps, Sherman traps, Inc.) every 25 m along a 1250 m non-linear transect for four consecutive nights at 0–2.5 m above the ground. We alternated capture-release in two transects per site for a total of 5760 trap nights (45 traps $\times$ 4 nights $\times$ 2 transects $\times$ 4 habitat types $\times$ 4 field seasons) across sites during our study period. Finally, we systematically measured the body mass of 824 captured individuals during the study, of which 437 were recaptured. Handling of each captured individual did not exceed 15 min to reduce stress on the animals; and each individual was kept in a unique breathable cloth sack until dusk, when they were released at their respective capture location (Ramananjato et al., 2020, 2025). We excluded capture abundance and body mass data from forest fragments as they were only represented by a single individual as well as six gestating female individuals and two juveniles, giving a total of 815 observations and three habitat types for the subsequent analyses. We used capture abundance, which is the number of individuals per 45 traps deployed, as an index for population size commonly used when animal populations are not considered closed (i.e., there are still birth/death, and immigration/emigration between populations; Andriatsitohaina et al., 2020; Ramananjato et al., 2025).

2.4. Seed dispersal effectiveness components

2.4.1. Quantity of seed dispersal

Following the protocol in Ramananjato et al. (2020), we collected the fecal samples left by captured individuals in the traps. If they had not defecated in the trap, each individual was gently transferred into a unique breathable cloth sack until it defecated (up to 15 min; Ramananjato et al., 2020). We meticulously examined each fecal sample to extract, identify, count, and measure the seeds with a diameter > 1 mm (Ramananjato et al., 2020). We identified each seed species to its vernacular name with the help of local technicians familiar with the local flora, and we later matched them with a local plant database that we have established over the years (Ramananjato et al., 2020, 2025; Ramananjato and Razafindratsima, 2021). We used the diversity, number, and size of these defecated seeds to assess the quantity of seed dispersal by *Microcebus rufus*.

We calculated Shannon's diversity index of the defecated seeds (Hill, 1971) to represent diversity and used the length of the seeds as proxy to seed size in the subsequent analyses of seed dispersal quantity. In this study system, seed length is highly correlated with seed width (Fig. S2; Razafindratsima et al., 2018) and had higher values than seed width – thus, it is often a limiting trait for fruit or seed consumption in many frugivores (Galetti and Dirzo, 2013; Ganzhorn et al., 2024; Razafindratsima et al., 2018).

2.4.2. Quality of seed dispersal

We used distance from the potential parent as a proxy to seed dispersal distance, germination rate, and germination time to assess the quality of seed dispersal by *M. rufus*. In this study, seed dispersal distance refers to the distance between the defecation locations and the potential parents of the defecated seeds in each site, germination rate as the percentage of germinated seeds compared to the total number of seeds set for germination, and germination time as the number of days until the seeds germinate.

2.4.2.1. Seed dispersal distance. As mouse lemur species usually forage in the forest understory (0.5–9 m above ground; Andriambeloson et al., 2021; Dammhahn, 2009; Joly and Zimmermann, 2011), we obtained

potential parent plants from the survey and mapping of all plants with >0.5 m high in 104 botanical plots of $4 \text{ m} \times 50 \text{ m}$ (13 plots $\times$ 2 transects $\times$ 4 sites). In each site, we set these plots perpendicular to the capture trail every 100 m around the trapping locations (Fig. S3; Gentry, 1993; Rakotondrany and Ganzhorn, 2011). We identified the vernacular name of each plant with the help of local technicians familiar with the local flora, which we later matched with a local plant database (Razafindratsima and Centre ValBio unpublished data), estimated its height, measured its diameter at breast height (DBH; taken at ~ 1.3 m above the ground), and recorded the reproductive phenophases, if applicable (flowers, unripe and ripe fruits; Dunham et al., 2018; Ramananjato et al., 2025). We also mapped the position of each plant inside each plot using a distance-measuring equipment (DME, Haglöf).

For each defecated seed species, we measured the distance from potential parents as the distance between its defecation locations (i.e., trapping locations) and potential parent plants of the same species. We defined a potential parent for a given plant species as an individual whose DBH exceeds the minimum size at which individuals of said species bear fruits (Fig. S3; Table S4). We used phenological data collected from plants in the same sites from 2022 to 2025 to determine such a minimum DBH for each dispersed plant species (V. Ramananjato and O.H. Razafindratsima, unpublished data). We thus filtered out any individual plants that did not fulfill this criterion and used the resulting data for seed dispersal distance calculation. We used the Euclidean distance equation to calculate the distance from potential parents:

$Distance = \sqrt{\sum_{i=1}^n (x - y)^2}$, with x representing the position of the potential parent along the trapping transects (0–1250 m) and y referring to its position along the botanical plot length (0–50 m). We considered all 13 plots in one transect as one big unit ($50 \text{ m} \times 1250 \text{ m}$) to calculate seed dispersal distance for all dispersed plant species in that transect (Fig. S3). Therefore, the seed dispersal distance in this study is an estimation of the median and maximum distances to which *M. rufus* could go to forage for fruits and later deposit seeds.

2.4.2.2. Germination rate and time. We planted the seeds extracted from the feces of *M. rufus* to assess germination rate and time in a clearing without direct sunlight to the ground in Valohoaka forest. We chose this site for the germination experiment because it has the lowest disturbance level, which we assume is an ideal habitat for *M. rufus* and where they can complete optimal seed dispersal service. Following the protocol of Ramananjato et al. (2020), we pressed each seed directly into the forest soil at a 3–4 cm distance from each other ($N = 764$). We covered the germination experiment with a metal mesh with a diameter of 0.5 cm to prevent seed predation from ground-dwelling animals. For epiphytic plant species, we set the seeds for germination onto a wet paper filter in Petri dishes with a maximum of 15 seeds per dish ($N = 271$, (DeSisto et al., 2020; Ramananjato et al., 2020). We monitored the seeds bimonthly for at least 12 weeks, during which we recorded the germination status of each seed and watered the soil or paper filter, if they felt dry to the touch (Ramananjato et al., 2020). We did not include control seeds (i.e., seeds extracted from ripe fruits) in these experiments as previous studies in RNP already demonstrated the effectiveness of *M. rufus* in enhancing germination rates and time for the same plant species (Ganzhorn et al., 2024; Ramananjato et al., 2020). Four additional species were not surveyed in these previous studies, and we compared them to the germination rates of control seeds of the same species planted in similar protocol (Razafindratsima and Dunham, 2015).

2.4.3. Seed dispersal effectiveness value of *Microcebus rufus*

We computed a value of seed dispersal effectiveness (SDE) of *M. rufus* for each plant species they disperse, which assesses how they contribute to the dispersal of these plant species (Schupp, 1993; Schupp et al., 2010). SDE is the product of the quantity and quality of animal-mediated seed dispersal (Schupp, 1993; Schupp et al., 2010). Here, we are

calculating an SDE for each plant species using only the number of dispersed seeds, seed dispersal distance, and germination rate (i.e., $SDE = \text{number of seeds} \times \text{seed dispersal distance} \times \text{germination rate}$). Diversity of dispersed seeds and seed size were not included in the calculations as they are specific to each plant species, thus, do not directly affect the effectiveness for that plant species. We then built a two-dimensional isocline map, which represents all the possible combinations of quantity and quality of seed dispersal (Fig. 1; Schupp, 1993; Schupp et al., 2010). On the isocline map, *M. rufus* is a 1) good seed disperser for the plant species if SDE falls on the upper right as they provide a high quantity and quality of seed dispersal, 2) moderate seed disperser for plants in the upper left (low quantity but high quality) and lower right (high quantity but low quality), and 3) limited seed disperser for plants in the lower left (low quantity and quality; Fig. 1; Schupp, 1993; Schupp et al., 2010).

2.5. Statistical analyses

We processed all data visualization and analyses in R 4.4.1 (R Core Team, 2024). We performed a Kruskal-Wallis test to compare the capture abundance and body mass of *M. rufus* across forest habitats with a threshold of 0.05 statistical significance. If a significant difference was detected, we performed a Dunn test using the “dunnTest” function in the R-package “FSA” to identify which forest habitat types are significantly different from the others (Ogle et al., 2023).

We fitted Linear Mixed-effects Models (LMM) with a “both” model selection of fixed and random effects using the “step” function in the R-package “lmerTest” to assess the impacts of *M. rufus*’ population and body sizes on the components of seed dispersal quantity and quality and which among those variables changes the patterns of seed dispersal (Kuznetsova et al., 2017). We set each component of seed dispersal (diversity, number, size, seed dispersal distance, germination rate, and germination time) as response variables in six separate models, capture abundance and body mass as fixed effects, and forest habitat types, transects, and seasons as random effects. We used the value per transect for response variables and fixed effects in our models and value per site for the random effects. We then run a Type-III ANOVA with the generated models to test the significance of the fixed effects after controlling for the other variables (West et al., 2022).

2.6. Ethical statement

We obtained ethical and legal approval before the start of this study. Animal trapping and handling complied with the protocols approved by the University of California Berkeley’s Animal Care and Use Committee (AUP-2021-10-14771 & 14771-1), and the Ministère de l’Environnement et du Développement Durable of Madagascar (authorization #297/21, #428/21, #137/22, #048/23, #260/23, and #182/24). Additionally, this research adhered to the legal requirements and ethical

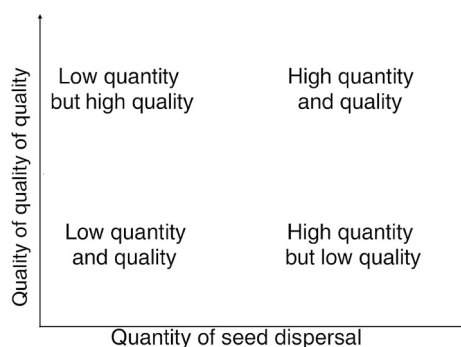


Fig. 1. Conceptual isocline map of the effectiveness of an animal seed disperser.

code of conduct for research in Madagascar (Wilmé et al., 2016) and recommendation for equitable fieldwork from Ramananjato and Blanco (2024). This research project also received approval from Madagascar National Parks, all Vondron’Olona Ifotony (VOI; community-based and led association) from each village, and the ethical committee at Mention Zoologie et Biodiversité Animale (Université d’Antananarivo).

3. Results

3.1. Capture abundance and body mass of *Microcebus rufus*

The capture abundance of *M. rufus* was highest in crop fields and lowest in primary forest, though the difference was only marginally significant (Kruskal-Wallis: $\chi^2 = 5.977$, $df = 2$, $p = 0.050$; Fig. S5). The body mass of *M. rufus* was significantly higher in crop fields than in any other forest habitat types (Kruskal-Wallis: $\chi^2 = 16.068$, $df = 2$, $p < 0.001$; Fig. S6).

3.2. Seed dispersal by *Microcebus rufus*

M. rufus dispersed seeds from 23 plant species, of which two could not be identified at the family level (Table 1). Most fecal samples contained the seeds of one plant species, although in four instances, we identified up to four plant species in a single fecal sample. We collected a total number of 1641 seeds whose size ranged from 1 to 11.03 mm (Table 1). We found that the median diversity of seeds dispersed by *M. rufus* was high in the primary forest, while the maximum diversity was recorded in the crop fields (Fig. S7). The median and maximum number of seeds dispersed were highest in the crop fields (Fig. S8). Seeds from the primary forest were 1–9 mm long, while seeds from crop fields were 1–11 mm long and seeds from secondary forest were all less than 8 mm long (Fig. S9).

We could not measure the seed dispersal distance of lianas, herbaceous, and epiphytic plant species because their vegetative organs were high up in the canopy, precluding accurate species identification. Seed dispersal distance ranged from 9 m to 1097 m with a median of 397 m for plants dispersed in the primary forest, from 0.5 m to 1203 m with a median of 223 m for plants dispersed in the secondary forest, and from 0.2 m to 1225 m with a median of 378 m for plants dispersed in crop fields (Fig. S10). The longest seed dispersal was recorded for *Dypsis linearis* in primary forest (1077 m), *Gaertnera brevipedicellata* in secondary forest (1203 m), and *Coffea* sp. and *Psidium cattleianum* in crop fields (1225 m; Fig. S8). Additionally, individuals of *Maesa lanceolata*, *Scolopia madagascariensis*, and *Solanum mauritianum* were not surveyed in the botanical plots in the secondary forest, while we collected their seeds in the fecal samples of *M. rufus*, indicating that *M. rufus* could forage and deposit their seeds further than 1203 m.

Not all seeds defecated by *M. rufus* germinated by the end of our monitoring. Only *Bakerella clavata* and *Ficus tiliifolia* germinated among the seeds from primary forest with a median germination percentage of 100% (Fig. S10), *P. cattleianum* and *S. mauritianum* among the seeds from secondary forest with a median germination percentage of 13% and 62% respectively (Fig. S11), and 7 out of 13 species germinated with median germination percentage from 2% to 100% among the seeds from crop fields (Fig. S11). Germination time varied from 44 to 54 days for seeds from primary forest, 81–160 days for seeds from secondary forest, and 23–122 days for seeds from crop fields (Fig. S12). Seeds of *B. clavata* from primary forest (44 days) and crop fields (23 days), and *S. mauritianum* from secondary forest (80 days) had the shortest germination time (Fig. S12).

3.3. Seed dispersal effectiveness value of *Microcebus rufus*

Overall, we found that *M. rufus* contributed to increasing the quantity of seed dispersal of most plants they disperse by consuming and dispersing a high number of their seeds (Fig. 2). They also enhanced the

Table 1

Plants dispersed by *Microcebus rufus* within and around Ranomafana National Park in 2021–2024, regardless of germination experiments. Seed size is represented by the seed length. Distribution status refers to the origin and biogeographical range of the plant species: “endemic” when native and only distributed in Madagascar, “native” when native to Madagascar, other tropical regions, or common to the African region, “introduced” when not native to Madagascar, and “invasive” when not native to Madagascar and have proliferated at the expenses of the local flora.

Family	Vernacular name	Scientific name	Distribution status	Growth form	Number	Size (mm)	Forest habitat types			
							Primary	Secondary	Fragment	Crop field
Aphloiaceae	Fandramanana	<i>Aphloia theiformis</i>	Endemic	Tree	1	3	–	1	–	–
Arecaceae	Fanikara	<i>Dypsis linearis</i>	Endemic	Tree	5	5.47–9.00	3	–	–	2
Hypericaceae	Harongana	<i>Harungana madagascariensis</i>	Native	Tree	4	3.27–3.51	–	–	–	4
Loranthaceae	Tongoalahy	<i>Bakerella clavata</i>	Native	Epiphyte	214	2–9.01	28	74	–	92
	Tongoalahy bory voany	<i>Bakerella</i> sp.	Native	Epiphyte	15	4.27–7.00	–	8	–	7
Melastomataceae	Mazambody/Taindelotsinoa	<i>Clidemia hirta</i>	Introduced	Herbaceous	892	1	–	–	–	892
Moraceae	Voara	<i>Ficus tiliifolia</i>	Endemic	Tree	66	1	65	–	–	1
	Voararano	<i>Ficus botryoides</i>	Endemic	Tree	21	1	–	–	–	21
Myrtaceae	Goavitsinahy	<i>Psidium cattleianum</i>	Invasive	Tree	55	2–6.45	–	38	–	11
Primulaceae	Kalafambakaka	<i>Oncostemum nervosum</i>	Endemic	Tree	6	5–7	–	–	–	6
Rubiaceae	Voarafy	<i>Maesa lanceolata</i>	Native	Tree	1	1.62	–	1	–	–
	Voananananala	<i>Chassalia ternifolia</i>	Endemic	Tree	17	2–10	–	–	–	17
	Kafe	<i>Coffea</i> sp.	Native	Tree	2	10.83–11.03	–	–	–	2
	Ranjopody	<i>Gaertnera brevipedicellata</i>	Endemic	Tree	27	1–5.23	8	15	–	4
Salicaceae	Anambahy	<i>Mussaenda arcuata</i>	Endemic	Liana	107	1	–	–	–	107
	Fohaninasy mena	<i>Psychotria parkeri</i>	Endemic	Tree	80	2–10	–	–	80	–
	Tongely	<i>Salidina</i> sp.	Native	Herbaceous	20	2.70–3.43	20	–	–	–
Solanaceae	Faritraty	<i>Scolopia madagascariensis</i>	Endemic	Tree	2	4.68–6.58	–	2	–	–
	Seva/Seva be	<i>Solanum mauritianum</i>	Introduced	Shrub	60	1	–	48	–	2
Verbenaceae	Radiaka	<i>Lantana camara</i>	Introduced	Shrub	6	4.41–5.46	–	–	–	6
Xanthorrhoeaceae	Vazavazaha	<i>Dianella ensifolia</i>	Native	Herbaceous	16	4.16–6.71	–	–	–	16
Unteretermined	Fanerambavy	–	Tree	–	18	2.90–4.88	–	18	–	–
–	–	–	–	–	3	4.31–5.04	–	–	–	3

quality of seed dispersal by promoting long-distance seed dispersal and facilitate seed germination (Fig. 2). Consequently, *M. rufus* can be a good seed disperser for *P. cattleianum* and *S. mauritianum*, and a moderate seed disperser for *G. brevipedicellata* (Fig. 2). It is worth noting that such results could be biased by the number of seeds that have germinated by the end of our monitoring.

3.4. Impact of *Microcebus rufus* population and body sizes on the components of its seed dispersal effectiveness

The diversity and germination time of dispersed seeds was significantly and positively associated with *M. rufus* capture abundance (Fig. 3a and f; Table 2). The number of dispersed seeds was also significantly and positively associated with *M. rufus* population and body sizes (Figs. 3b and 4b; Table 2). We also observed positive association of seed length, seed dispersal distance, and germination rate with capture abundance and body mass, though the differences were not significant (Figs. 3d and 4d; Table 2). Finally, we found that habitat types significantly were associated the diversity and germination time of dispersed seeds, and seasons was significantly associated the number of dispersed seeds (Table 2).

4. Discussion

Our multi-year monitoring of an animal seed disperser species and various aspects of its contribution to seed dispersal shows that the population and body size of a seed disperser mediate the effectiveness of its seed dispersal service. Specifically, we found that the 1) capture abundance of *Microcebus rufus* was positively associated with higher diversity and number as well as shorter germination time of the dispersed seeds, 2) body mass of *M. rufus* was positively associated with

higher number of dispersed seeds, and 3) habitat types and seasons played a critical role in the diversity and germination time, as well as number of dispersed seeds, respectively. Although not significant, we found that capture abundance and body mass were also positively associated with longer seed dispersal distance. Surprisingly, *M. rufus* in crop fields provided higher values of seed dispersal components than in other habitat types. Therefore, our results suggest that mouse lemurs are effective seed dispersers, supporting previous studies (Ganzhorn et al., 2024; Ramananjato, 2024; Ramananjato et al., 2020). Most importantly, our results indicate that they perform seed dispersal in all habitats of human-modified landscapes, but its effectiveness partially depends on its individual and population states and external factors that can affect such states. Our results thus stress the need to preserve diverse forest habitats to promote the persistence of interacting populations and ecological functions.

4.1. Change in the capture abundance and body mass of *Microcebus rufus*

Variations in the capture abundance and body mass of *M. rufus* can be associated with the seasonality in RNP. RNP has two distinct seasons: a dry season (May–August) corresponding to low temperatures and precipitations, and a rainy season (September–April) with high temperatures and precipitations (Dunham et al., 2011, 2018). Although fruits are available year-round in RNP, they are more diverse and abundant during the rainy season (Dunham et al., 2018), and so are the arthropods and insects (Atsalis, 1999a). We thus argue that the available food sources are more attractive to *M. rufus* than bananas in the trap, explaining the lower capture abundance during the rainy season than during the dry season (Ramananjato et al., 2020). As for body mass, it can fluctuate depending on food resources, daily torpor patterns, and their reproductive schedule in mouse lemurs (Atsalis, 1999b; Blanco,

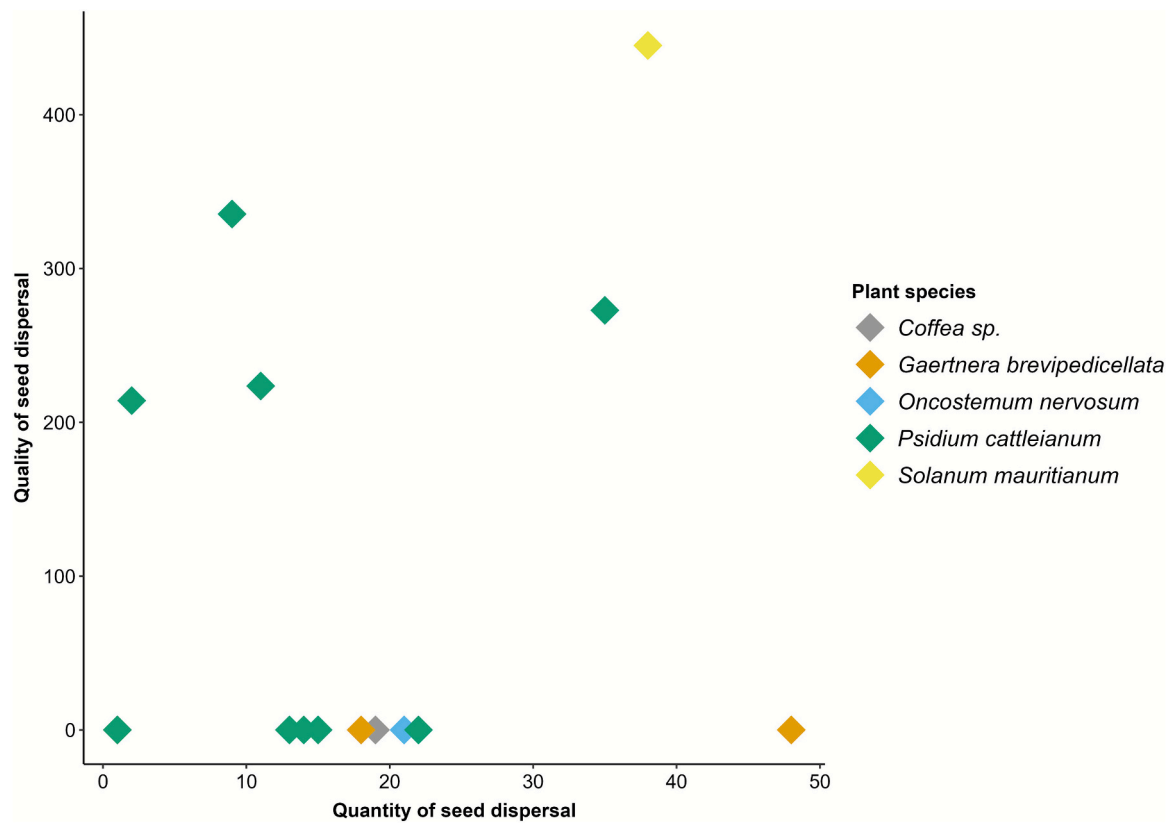


Fig. 2. Seed dispersal effectiveness of *Microcebus rufus* based on the number of seeds dispersed, distance from potential parents, and germination rate.

2008; Rakotomalala et al., 2023). *M. rufus* usually enter daily torpor during the dry season after a fattening period at the end of the rainy season (Atsalis, 1999b; V. Ramananjato, unpublished data). However, our findings contradict this as body mass was higher in August and November. We, thus, suggest that increasing body mass is associated with preparation for the reproduction period, which usually occurs from September to November (Blanco, 2008) or the peak of the fruiting season for forest plant species and crop species (DeSisto et al., 2020; Dunham et al., 2018; V. Ramananjato, unpublished data).

4.2. Impact of *Microcebus rufus*' population and body sizes on the components of their seed dispersal effectiveness

The abundance of seed dispersers plays a major role in structuring the effectiveness of seed dispersal because it increases the frequency of interactions (Ganzhorn et al., 2024; Ramananjato, 2024; Schupp et al., 2010). The more individuals are present in an area, the higher the diversity of fruits is removed and consequently dispersed, which is consistent with the positive association of capture abundance and diversity of dispersed seeds here. However, we observed a negative association between body mass and diversity of dispersed seeds. This was particularly obvious for *M. rufus* in the crop fields, which had a high body mass but fecal samples full of many small seeds from one plant species, mostly from *Bakerella clavata*, *Clidemia hirta*, and *Mussaenda arcuata*. Such observations could indicate that individuals rely heavily on the most abundant fruit sources, which are often the result of a depleting number of plant food sources in an area (DeSisto et al., 2020; Jordano et al., 2010), and could result in directed seed dispersal services towards epiphytes, herbaceous, and liana species (Green et al., 2009; Ramananjato, 2024).

The number of seeds dispersed by *M. rufus* was significantly and positively associated with its body mass, probably because large-bodied individuals may need higher energy to sustain their activity than small-

bodied individuals (Schupp et al., 2010; Sivault et al., 2023). Therefore, they consume more fruits and disperse more seeds. Additionally, seasons seem to play a significant role in the change in the number of dispersed seeds, and we propose two potential reasons for this. First, different plant species are available during different seasons (Dunham et al., 2018), mediating the number of plant species and fruits/seeds available for *M. rufus*. Second, seasons also modulate the activity patterns of *M. rufus* (as seen in Figs. S5 and S6), potentially affecting the number of fruits consumed and seeds dispersed. However, it is unclear which of these mechanisms apply here or whether it is a combination of both. Therefore, future studies should consider controlled observations and experiments to disentangle the impacts of seasons and the dynamics of the seed dispersers on the number of dispersed seeds.

Germination time was also significantly and positively associated with capture abundance but negatively associated with body mass of *M. rufus*. Such results indicate that seeds take longer to germinate when there are many individuals of *M. rufus* in one area but pass quicker when individuals have large body mass. We argue that larger individuals probably have longer digestive tracts (Buerki and Miguez, 2018; Traveset and Verdú, 2002), thus providing more deinhibition effects on the seeds. The deinhibition effect is the removal of pulp and other tegument of the seeds to facilitate germination through digestion (Fergani et al., 2020). Additionally, seasonal changes in the digestion activity associated with the fattening period that precedes the daily torpor during the dry season could affect the digestive function (Giroud et al., 2021), changing the retention of seeds in their guts. However, longer germination time associated with capture abundance might be a result of our germination settings, which could have mirrored seed clumping (Muller-Landau and Hardesty, 2005; Nevo et al., 2023; Schupp et al., 2010). Indeed, seeds were not deposited in the same area but were planted in the same area despite a regular distance (3–4 cm) between each seed and each plant species. Nevertheless, we can conclude that small-bodied animals could improve the probability of dispersed seeds germinating

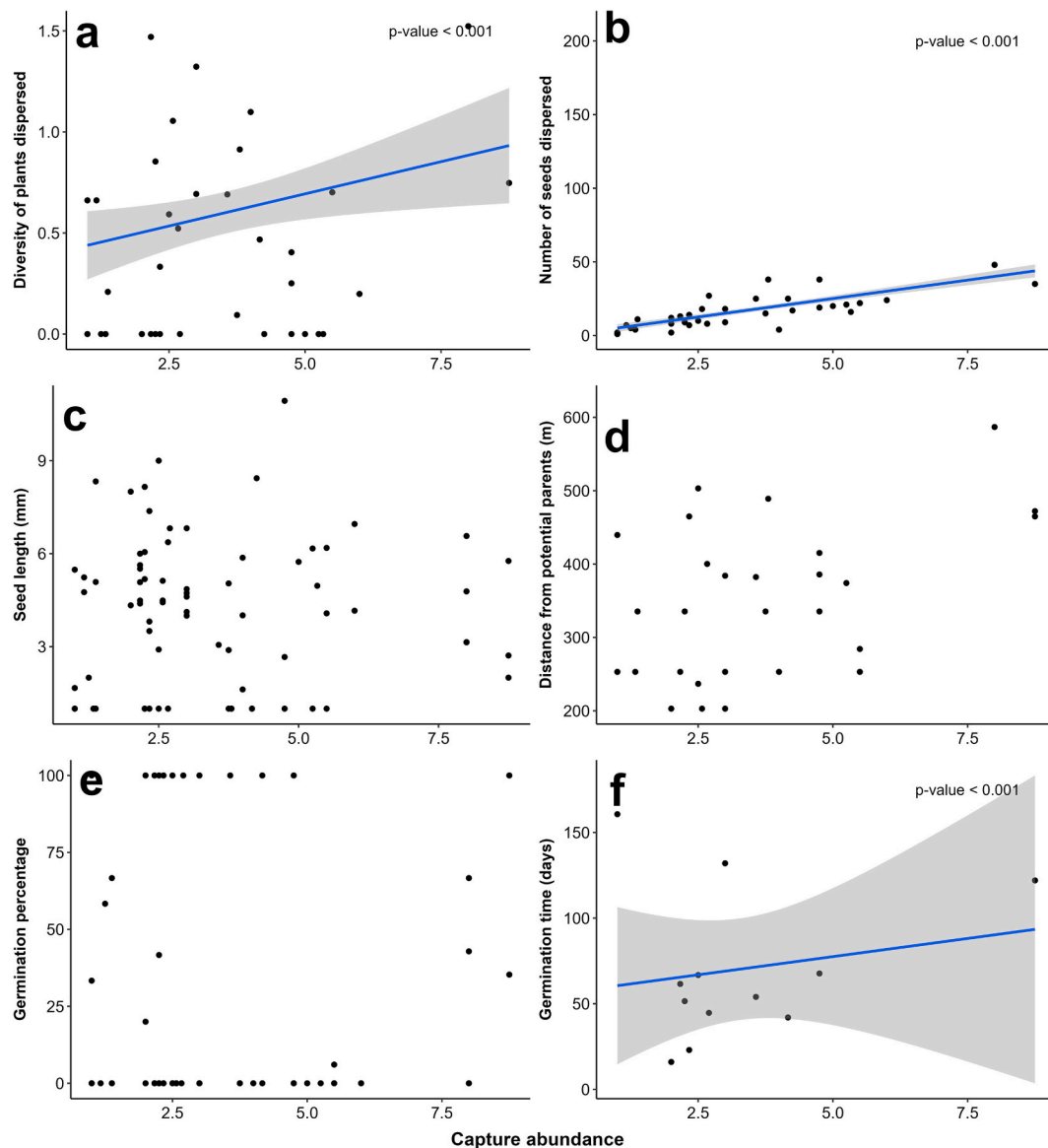


Fig. 3. Impacts of the capture abundance of *Microcebus rufus* on the plants they disperse. Model lines are from the conditional models, and the smoothing are from the data used in the model. *p*-values are from LMM model selection of fixed effects.

and becoming adults, but further investigation into the characteristics of the seed deposition locations and interactions between seeds after deposition are needed.

We found a non-significant positive association of seed dispersal distance with capture abundance and body mass. This suggests that individuals may forage far to avoid competition with their conspecifics (Ismail et al., 2017; Jordano, 2017) as most mouse lemurs are solitary foragers (Dammhahn, 2009; Joly and Zimmermann, 2011). Alternatively, this might also indicate that fruit sources may be scattered or available fruits are not suitable to their needs, motivating them to move far (Dáttilo et al., 2014; Nevo et al., 2023). Most importantly, we found that *M. rufus* could be able to disperse seeds further than 1225 m, which is longer than that of other seed dispersing lemurs in RNP with a body mass that is ten times larger than mouse lemurs' (Razafindratsima et al., 2014). To the best of our knowledge, this is the most approximate value for seed dispersal distance by mouse lemurs in the wild, supporting the previous hypothesis on the long seed dispersal distance that small-bodied primates could complete (Heymann et al., 2022; Ramananjato, 2024). Additionally, in an attempt to measure the distance travelled by this species, we found that *M. rufus* could complete up to 502 m in 1 h (V.

Ramananjato, in review). Therefore, if they can retain the seeds in their digestive tract for more than 1 h, they would perform an effective long-distance seed dispersal (Jordano, 2017; Ramananjato, 2024; Razafindratsima et al., 2014), warranting the investigation of their gut retention time.

4.3. Implications for conservation

Habitat types influenced the diversity and germination time of dispersed seeds. Higher diversity of plant species from the *M. rufus* in crop fields might come from the ecotone that the overlap of forest edges and crop stands has created. Indeed, agroecosystems adjacent to forests often sustain more plant species for animals to consume and for which they can provide seed dispersal services (Ganzhorn et al., 2024; Hending et al., 2018; Heymann et al., 2019, 2022; Ramananjato, 2024; Webber et al., 2020). Shorter germination time of seeds from *M. rufus* in primary forest might indicate a local adaptation of the seeds to the microhabitat in primary forest, to which seeds from other habitat types might not be adapted to (Kendon et al., 2020; Mariano and Christianini, 2021). Moreover, although we found fluctuating quantity and quality of seed

Table 2

Statistical summary of selected models on the impacts of capture abundance and body mass of *Microcebus rufus* on their seed dispersal effectiveness components. Values in bold indicates a significant impact on the seed dispersal effectiveness component. Type-III ANOVA statistics: χ^2 = sum of squares, F = ratio of between-group and within-group variances, and p = probability of deviation. R^2_m = marginal R^2 , which is the proportion of variances explained by the fixed factors alone; and R^2_c = conditional R^2 , which is the proportion of variances explained by both the fixed and random factors, from the stepwise Linear Mixed-effect Models selection.

Response variables	Fixed effects		Random effects		
	Capture abundance	Body mass	Habitat types	Transect	Season
Diversity	$\chi^2 = 2.328$ F = 11.629 p < 0.001	$\chi^2 = 0.129$ F = 0.645 p = 0.424	$\chi^2 = -67.883$ F = 10.087 p < 0.001	$\chi^2 = -62.839$ F = 0.676 p = 0.410	$\chi^2 = -62.501$ F = 0.000 p = 0.999
	$R^2_m = 0.103$ and $R^2_c = 0.290$				
Number of seeds	$\chi^2 = 7164$ F = 162 p < 0.001	$\chi^2 = 803$ F = 18.254 p < 0.001	$\chi^2 = -288.58$ F = 2.491 p = 0.114	$\chi^2 = -287.34$ F = 0.000 p = 0.999	$\chi^2 = -291.92$ F = 6.668 p < 0.01
	$R^2_m = 0.595$ and $R^2_c = 0.727$				
Size of seeds	$\chi^2 = 0.010$ F = 0.002 p = 0.967	$\chi^2 = 0.070$ F = 0.012 p = 0.913	$\chi^2 = -175.270$ F = 0.758 p = 0.384	$\chi^2 = -174.700$ F = 0.000 p = 1.000	$\chi^2 = -174.700$ F = 0.000 p = 1.000
	$R^2_m = 0$ and $R^2_c = 0$				
Seed dispersal distance	$\chi^2 = 37,934$ F = 2.651 p = 0.119	$\chi^2 = 29,890$ F = 2.216 p = 0.153	$\chi^2 = -124.250$ F = 2.014 p = 0.156	$\chi^2 = -123.240$ F = 0.000 p = 1.000	$\chi^2 = -123.240$ F = 0.000 p = 1.000
	$R^2_m = 0$ and $R^2_c = 0$				
Germination rate	$\chi^2 = 117.400$ F = 0.072 p = 0.789	$\chi^2 = 4931.900$ F = 2.801 p = 0.09	$\chi^2 = -300.45$ F = 0.061 p = 0.434	$\chi^2 = -300.15$ F = 0.393 p = 0.530	$\chi^2 = -299.95$ F = 0.000 p = 1.000
	$R^2_m = 0$ and $R^2_c = 0$				
Germination time	$\chi^2 = 4304.700$ F = 9.706 p < 0.05	$\chi^2 = 44.700$ F = 0.089 p = 0.773	$\chi^2 = -53.910$ F = 8.102 p < 0.01	$\chi^2 = -49.859$ F = 0.957 p = 0.327	$\chi^2 = -49.380$ F = 0.000 p = 1.000
	$R^2_m = 0.100$ and $R^2_c = 0.899$				

dispersal services, we did not find any evidence of cryptic seed dispersal loss. Nevertheless, this study showed the impact of habitat degradation on seed dispersal mechanisms. It directly affects plants and seed dispersers by restricting their occurrence, and thus the presence and frequency of interactions, mainly in secondary forest and fragment. Additionally, it indirectly alters seed dispersal components at different levels and magnitudes, and thus restructure seed dispersal effectiveness in the long run. Therefore, we should promote the persistence and resilience of seed dispersal by protecting less disturbed habitats from further degradation and loss (Ganzhorn et al., 2024; Razafindratsima et al., 2018; Steffens, 2020), and restoring disturbed habitats, especially in a slow-recovery system such as Madagascar (Banks-Leite et al., 2020; Culbertson et al., 2022).

This study and previous work have demonstrated that *M. rufus* and other mouse lemurs effectively dispersed native, introduced (*Clidemia hirta* and *Solanum mauritanium*), and invasive plant species (*Psidium cattleianum*; DeSisto et al., 2020; Ganzhorn et al., 2024; Ramananjato et al., 2020). Introduced and invasive species are dispersed at a lower rate, but the gut passage enhances their germination and their seedling survival. Small-bodied and abundant animals, and thus by extension, biotic interactions, could act as a vector of biological invasion. However, invasive plant species were currently only present in secondary forest and crop fields in Madagascar; thus, should be controlled to prevent further invasion into the forest from animal-mediated seed dispersal.

5. Conclusion

The population and body size of seed dispersers significantly differed across forests habitats because of degradation level and season. Population size and habitat types but not necessarily body mass of a seed disperser substantially altered the effectiveness of their seed dispersal services. Mouse lemurs are still providing effective seed dispersal services in degraded and human-modified landscapes, but with different plant community composition and with fluctuating effectiveness. Additionally, small-bodied animals may disperse a high quantity of small- and medium-seeded plants, which are often pioneer and early-successional plants that could be important in the maintenance and dynamics of forest successions and the regeneration of recently disturbed areas (e.g., Ganzhorn et al., 2024; Heymann et al., 2019, 2022; Ramananjato, 2024). Therefore, protecting and restoring habitats should be a priority to preserve seed dispersal interactions and prevent eventual cryptic seed dispersal loss. Additionally, studying the whole assemblage of seed dispersers in a system might be necessary to further understand the seed dispersal ecology at the community level as well as the overall resilience of the interactions in a changing world. Finally, conservation efforts should focus on preserving the seed dispersers' populations as well as maintaining their food sources to perpetuate biotic interactions and the resulting ecological services as they could contribute to minimizing the costs of ecosystem restoration.

CRedit authorship contribution statement

Veronarindra Ramananjato: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Tanjonaiaina H.N.P. Rabarijaonina:** Writing – review & editing, Methodology, Investigation, Data curation. **Ginot Kava:** Writing – review & editing, Methodology, Investigation, Data curation. **Sidonie O. Rakotoarisoa:** Writing – review & editing, Methodology, Investigation, Data curation. **Gaëtan M. Rakotondrasoa:** Writing – review & editing, Methodology, Investigation, Data curation. **Tsinjo S.A. Andriatiavina:** Writing – review & editing, Methodology, Investigation, Data curation. **Finaritra Randimbiarison:** Writing – review & editing, Visualization, Project administration, Methodology, Investigation. **Onja H. Razafindratsima:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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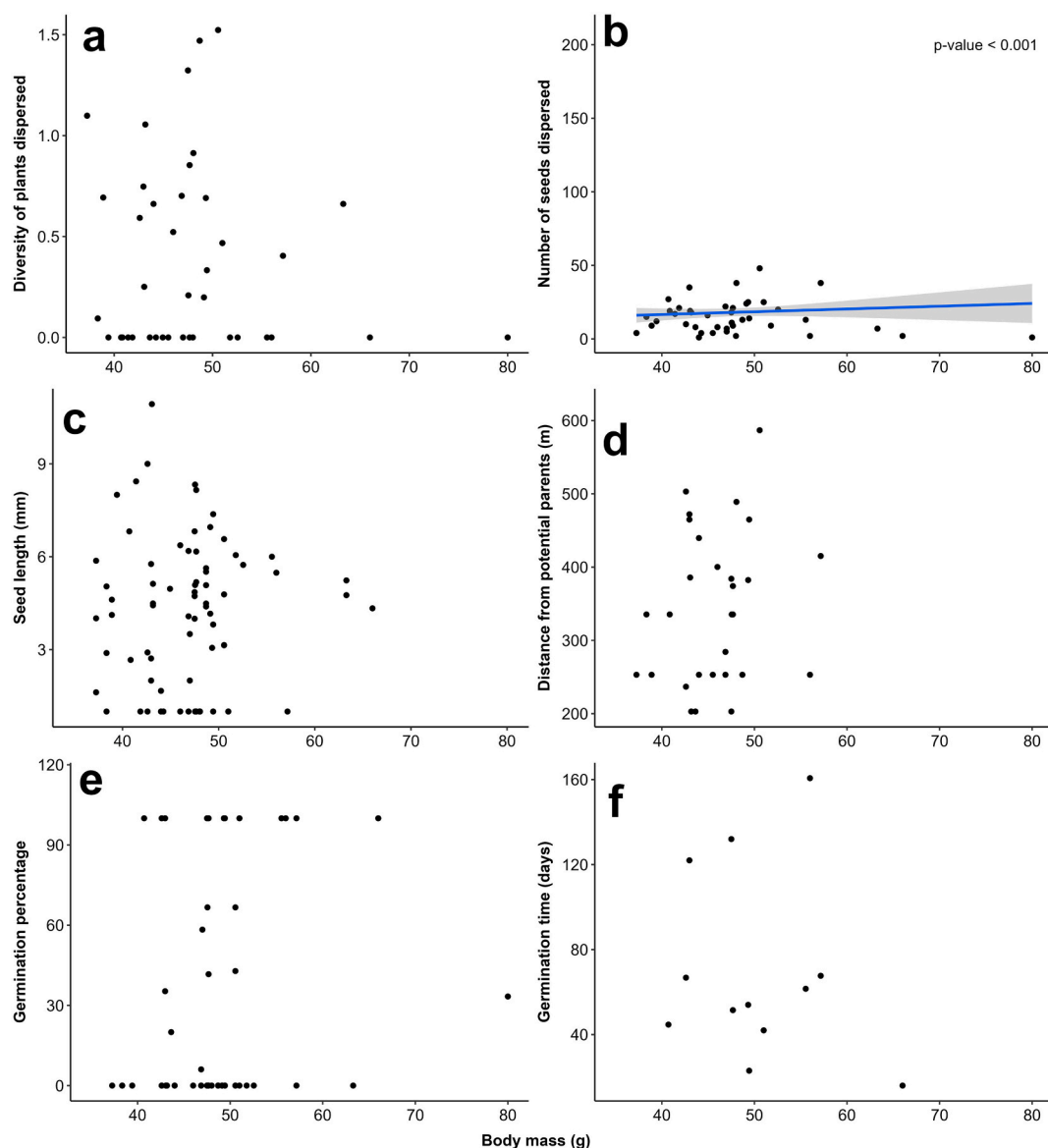


Fig. 4. Impacts of the body mass of *Microcebus rufus* on the plants they disperse. Model lines are from the conditional models, and the smoothing are from the data used in the model. p-values are from LMM model selection of fixed effects.

Declaration of competing interest

The authors do not have competing or conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2026.111745>.

Data availability

Data generated and analyzed in this study will be available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.59zw3r2ph>.

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