Ecological fragmentation effects in mouse lemurs and small mammals in northwestern Madagascar

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Abstract
Habitat loss and fragmentation are major ecological forces threatening animal communities across the globe. These issues are especially true in Madagascar, where forest loss is ongoing. We examined the effects of forest fragmentation on the distribution and abundance of sympatric, endemic gray, and golden-brown mouse lemurs (Microcebus murinus and Microcebus ravelobensis), the endemic western tuft-tailed rat (Eliurus myoxinus), and the invasive black rat (Rattus rattus) in two regions in northwestern Madagascar. We used systematic capture procedures in 40 forest fragments and four continuous forest sites which differed in size, shape, and degree of isolation. With a trapping effort of 11,567 trap nights during two dry seasons (2017–2018), we captured 929 individuals (432 M. ravelobensis, 196 M. murinus, 116 E. myoxinus, and 185 R. rattus). We examined the influence of study region, forest type (fragment vs. continuous), forest size, forest shape, the proportion of 50-m forest edge and distance to continuous forest on the abundance and interaction of the four species. Responses to fragmentation differed strongly between species, but no interaction could be detected between the abundance of the different species. Thus competition within and between native and invasive species may not be regulating abundances in these regions. On the contrary, the abundance of M. ravelobensis and E. myoxinus differed significantly between study regions and was negatively affected by fragmentation. In contrast, there was no evidence of an impact of fragmentation on the abundance of M. murinus. Finally, the invasive R. rattus responded positively to the increasing distance to the continuous forest. In conclusion, the response of small Malagasy mammals to forest fragmentation varies largely between species, and fragmentation effects need to be examined at a species-specific level to fully understand their ecological dynamics and complexity.

KEYWORDS
abundance, edge effect, Eliurus, Forest fragmentation, Madagascar, Microcebus, Rattus
Habitat loss and fragmentation are considered a serious threat to biodiversity worldwide. Of the remaining worldwide forest cover, 70% is within 1 km of the nearest forest edge (Haddad et al., 2015). These processes lead to changes in habitat composition (Laurance et al., 2007) and to changes in vegetation structure (Malcolm, Valenta, & Lehman, 2016). Additionally, other ecological changes near habitat edges, often termed edge effects, can affect the distribution (e.g., Lehman, Rajaonson, & Day, 2006; Lenz, Jack, & Spironello, 2014; Skrinyer, 2016) and the behavior of primates and other mammals (e.g., Bentley, Catterall, & Smith, 2000; Schreier & Swedell, 2008; Schwitzer, Glatt, Nekaris, & Ganzhorn, 2011; Singh, Kumara, Kumar, & Sharma, 2001).

However, responses to fragmentation and the resulting habitat edges can be very different between species, ranging from population declines in fragments to rather neutral responses, and even to the attraction of certain species to forest edges. As examples, Offerman, Dale, Pearson, O’Neill, and Bierregaard (1995) detected positive effects of fragmentation on abundance that was triggered by the increasing availability of preferred food near the forest edge in some New World primates (Alouatta seniculus, Pithecia pithecia, and Saguinus midas). Conversely, a negative effect of increasing isolation on connectivity and recolonization potential was described in crested capuchins (Sapajus robustus; Mota, Leite, & Martins, 2018), and decreasing fragment size negatively affected the occurrence of black capuchin and black-fronted titi monkeys (Sapajus nigritus and Callithrix nigrifrons; da Silva, Ribeiro, Hasui, da Costa, & da Cunha, 2015) and the species richness and abundance of ground-dwelling small mammals (e.g., Rattus fuscipes and Antechinus stuartii; Dunstan & Fox, 1996) and some families of Afrosciridae and Soricidae; Goodman & Rakotondravony, 2000). A neutral response to fragmentation was documented in the black and gold howler monkey (A. caraya), whose density and number of groups were not affected by fragmentation in semideciduous forests in northern Argentina (Zunino, Kowalewski, Oklander, & Gonzalez, 2007).

Madagascar is known for its overall high proportion of endemic species, yet suffers from severe and omnipresent habitat loss and forest fragmentation. Between 1953 and 2014, forest cover on Madagascar decreased by almost 44% and around half of the remaining forest (46%) is situated less than 100 m away from the edge (Vieilledent et al., 2018). As a result of this major habitat loss and various other anthropogenic activities (e.g., hunting, bush fires, pet trade), the vast majority of Madagascar’s biodiversity is currently threatened, including an estimated 94% of the 100+ species of lemurs (Schwitzer et al., 2014).

So far, the species-specific responses of the endemic fauna to forest fragmentation are not well understood. Earlier studies indicated that large-bodied species suffered the most from habitat fragmentation because of general resource limitations in smaller fragments (Ganzhorn et al., 2000). However, other studies found that even small-bodied species react to edges and forest fragmentation (Lehtinen, Ramanamanjato, & Raveloarison, 2003). For example, mouse lemur species were shown to differ in their responses to edge effects. Burke and Lehman (2014) found that capture rates of Microcebus ravelobensis were significantly higher at the forest edge than in the interior whereas the opposite was found in M. murinus in Ankarafantsika National Park (ANP). To study the effects of habitat loss and fragmentation systematically across a range of sites with different habitat properties, it is advisable to focus on a set of smaller target taxa, such as mouse lemurs (Microcebus spp.) and rodents which can still survive in smaller fragments.

Several studies have already investigated responses of small mammals to forest fragmentation but generated different results. In western Madagascar, capture rates of M. murinus and Rattus rattus declined with increasing size of forest fragments (Ganzhorn, 2003). On the contrary, capture rates of these two species were uncorrelated with fragment size in southeastern Madagascar (Ramanamanjato & Ganzhorn, 2001).

It is also possible that species with similar lifestyles compete over limited resources (e.g., food and shelter) when living in forest fragments (Stokes, Banks, Pech, & Williams, 2009). This competition may also be due to the overall constraints on movements and space use in and between fragments. As a consequence, negative relationships can be expected between the abundance of species of similar size and ecology. However, previous studies on mouse lemurs have produced contradictory results on this matter. The abundances of M. murinus and M. ravelobensis were positively correlated in a fragmented landscape in northwestern Madagascar (Steffens & Lehman, 2016), but negatively correlated in the continuous forest in the same region (Rakotondravony & Rakotondravony, 2009). Such conflicting results call for further research that should also take into account various ecological parameters and several potentially interacting target species at the same time.

In this study, we aimed to investigate how different facets of forest fragmentation influence the distribution and abundance of two mouse lemur species (M. murinus and M. ravelobensis) and rodents (E. myoxinus and R. rattus) in two fragmented regions in northwestern Madagascar. M. murinus is a widespread species ranging from southern to western Madagascar (Mittermeier et al., 2010) and forms female sleeping groups in protected wooden shelters (tree holes; Radespiel, Cepok, Zietemann, & Zimmermann, 1998). In contrast, M. ravelobensis (Zimmermann, Cepok, Rakotoarison, Zietemann, & Radespiel, 1998) has a limited geographic range size between the large rivers Betsiboka and Mahajamba and forms mixed-sex sleeping groups in diverse substrates that are often less protected (lianas and leaves; Radespiel, Ehresmann, & Zimmermann, 2003). Both species are small-bodied (~60 g), nocturnal, arboreal, omnivorous solitary foragers, and are partially sympatric in northwestern Madagascar. M. murinus has a more diverse and seasonal diet than its sympatric congener (Thorén et al., 2011).

The endemic E. myoxinus is a widespread species in western dry deciduous forests and often occupies transitional habitats (Carleton, Goodman, & Rakotondravony, 2001). They are small (~60 g), nocturnal, and, in general, more arboreal than terrestrial. They use nests, burrows, and tree holes as sleeping sites, and are generally frugivorous (Randrianjafy, 2003; Shi et al., 2013). The invasive R. rattus is a nocturnal,
omnivorous species with a high dispersal capacity (Soarimalala, Jean, & Rakotovao, 2019), and has been described as arboreal and terrestrial (Goodman, 1995).

Here, we investigate the impact of (a) study region, (b) forest type (fragment vs. continuous), (c) forest size, (d) proportion of 50-m forest edge, (e) forest shape, and (f) distance to the nearest continuous forest on the abundance of these four small mammal species in two fragmented regions. In addition, we examine the possible impact of all four species on each other. If they show similar effects of fragmentation on their distribution and abundance, then we expect a positive relationship between them. A negative relationship between the abundance of any two species suggests the presence of interspecific competition.

Given a lack of consensus in previous studies, we made the following basic predictions:

- **Because M. murinus and M. ravelobensis have previously been found in forest fragments and in continuous forest sites, both species will be present in both forest types, but their distribution may vary across sites and differ between species due to different microhabitat preferences.**

- **Decreasing forest size and an increasing distance to the continuous forest will negatively affect the abundance of all native target species due to increasing difficulties to connect to larger source populations and to maintain subpopulations in smaller forest fragments.**

- **Edge effects will negatively impact ecological responses in the edge-sensitive M. murinus and the forest-dependent E. myoxinus more than the edge-tolerant M. ravelobensis and the invasive R. rattus.**

- **The abundance of R. rattus will not be constrained by ecological factors and may be highest in forest fragments.**

## METHODS

### 2.1 Study sites and their characterization

We performed this study in 40 forest fragments ranging from 0.8 to 114.6 ha and in four adjacent continuous forest sites ranging from 3,683 to 130,390 ha in ANP and in Mariarano forest (Mar; Figure 1). Both study regions mostly contain dry deciduous forest and undergo a dry season from May to October and a hot, rainy season from November to April. They are about 90-km apart from each other and represent fragmented ecological networks at different spatial scales (closest and farthest edge-to-edge distance between all study sites: 30–18,182 m in Mariarano and 20–6,342 m in ANP). In Mariarano, forest habitats are more humid, closer to surface water, and are situated at lower altitudes (10–100 m.a.s.l.) than the ANP sites (90–208 m.a.s.l.). In ANP, the forest fragments were surrounded by a homogeneous matrix of grassland savannah (Steffens & Lehman, 2016). In contrast, forest fragments in Mariarano were surrounded...
either by rice fields or by savannah containing some palm trees at variable density.

We defined fragment and continuous forest sites following methods described in Steffens (2017). We measured the size of each fragment by walking around the perimeter with a global positioning system and transferred the data into QGIS, Version 3.6.1 to determine its size. Continuous forest size was measured by tracing the perimeter of the forest from satellite imagery (taken in December 2018) in Google Earth Pro Inc. and then importing the polygon into QGIS. We defined the distance to the continuous forest as the nearest distance between the fragment and the continuous forest. The proportion of forest surface within 50-m distance to the edge (% edge) in relation to the total forest size was calculated for all forest fragments, as some abiotic parameters change markedly at this distance from the edge to the interior (McGoogan, 2011). Following Laurance and Yensen (1991), we combined forest size (S in hectare) with a perimeter length (P in meters) to determine a shape index (SI) for each site as $SI = P/(200^nS)^{0.5}$. The SI quantifies the deviation of a fragment from circularity and varies from 1.0 for a perfect circle to increasingly more complex shapes with SI values > 1 (see Table S1).

### 2.2 Data collection on abundance

We established 62 transects ranging from 40 to 1,000 m length that ran perpendicular to the forest edge in the 44 sites. Some sites (n = 9) contained more than one transect due to their larger area. Results from different transects were combined per site before further analyses. Mouse lemurs and rodents were captured using Sherman live traps along all transects. Traps were baited with banana and set up every 10 m on either side of a transect at 0.5–2.0 m height above ground. We set up traps at least three times over a 2-week period along each transect. After the identification of species by means of morphometric characterization (following Zimmermann et al., 1998) and the collection of tissue samples for future genetic analyses, all individuals were released at the exact location where they were caught. We accumulated a trapping effort of 11,567 trap nights during two dry seasons (between May and October) in 2017 and 2018 in both regions together. We determined abundances of species by calculating the number of individuals captured per 100 installed traps across all trapping sessions for each of the 44 sites.

In addition, and to validate abundances established based on capture data at least for mouse lemurs (see below), line transect surveys were conducted along each transect by two observers between 6 p.m. and 9 p.m. by walking at a very low speed (0.5 km/hr) as described in Rakotondravony and Radespiel (2009). Trapping nights and survey nights were always conducted in tandem with a 1-day interval between the two. Each transect was surveyed three times and starting points for all surveys were rotated between the edge and interior points to ensure that data were not biased. All mouse lemur encounters were noted for each survey, and species were identified whenever possible (in 9.6% of encounters) using the diagnostic parameters tail length and coloration (Zimmermann et al., 1998). If the mouse lemur species could not be determined during the survey, we only noted Microcebus spp. We then determined the abundance of Microcebus spp based on the number of individuals seen per 100 m across the three surveys.

All fieldwork protocols were reviewed and approved by the Institute of Zoology, University of Veterinary Medicine Hannover, Germany and the University of Toronto, Canada. All research reported in this manuscript adhered to the legal requirements of Madagascar and were approved by the Ministère de l’Environnement, de l’Écologie et des forêts and Madagascar National Parks (permit number 81/17/MEEF/SG/DGF/DSAP/SCB.Re and 82/18/MEEF/SG/DGF/DSAP/SCB.Re This study also adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

### 2.3 Statistical analyses

The standardized number of individuals caught per 100 installed traps for each species and site was used as a proxy for abundance (dependent variable) in all analyses. All sites were categorized by a set of two categorical (forest type, region) and four continuous predictor variables (forest size, distance to continuous forest, SI, the proportion of 50-m forest edge: see above for definitions). Normality of all continuous variables was assessed using the Shapiro-Wilk’s test (Shapiro & Wilk, 1965). If a variable was not normally distributed, it was log-transformed (forest size, distance to continuous forest, number of individuals captured per 100 traps for four species) and Q–Q plots were visually inspected before and after transformation to ensure improvement.

We next tested for correlations between all continuous predictor variables to ensure the independence of parameters used together in a given model. We included only independent (uncorrelated, p > .05) predictor variables together in a model (see Table S2 for correlation results) and, as a consequence, forest size was not modeled together with the SI or with the proportion of 50-m forest edge.

To identify fragmentation-related determinants of the abundance of each target species, two generalized additive models (GAMs) were constructed for each species (link function = identity, family = Gaussian) using maximum likelihood estimation. One model was calculated for the complete data set (n = 44 sites) and one for the forest fragments only (n = 40 sites). This division was necessary because some variables could only be determined for forest fragments but not for the continuous forest sites (proportion of 50-m forest edge, distance to continuous forest, forest shape). The first model (all sites) contained the predictor variables region (ANP and Mariarano), forest size, and forest type (continuous and fragment). The second model (fragments only) contained the predictor variables region, the proportion of 50-m forest edge (in %), distance to the continuous forest (in meters), and forest shape (SI).

We used a model-averaging algorithm applying the dredge command from the “MuMIn” package in R (version 3.6.0) to determine the best model. This process uses all possible combinations of factors in different models and ranks them according to their Akaike’s Information Criterion value corrected for small sample sizes.
3 | RESULTS

3.1 | Distribution of mouse lemurs and rodents across space

We captured a total of 929 individuals (M. ravelobensis: 432, M. murinus: 196, E. myoxinus: 116, and R. rattus: 185). Although the four species were trapped in continuous sites as well as in fragments, they were not evenly represented across these two forest types. Whereas M. ravelobensis was mostly trapped in the continuous forest (79.4%, n = 343 individuals) and infrequently in fragments (19.9%, n = 89 individuals), M. murinus, E. myoxinus, and R. rattus were captured more often in fragments (M. murinus: 80.1%, n = 157 individuals; E. myoxinus: 69.8%, n = 81 individuals; R. rattus: 82.2%, n = 152 individuals) than in continuous forest sites (19.9%, n = 39; 30.2%, n = 35%; and 17.8%, n = 33, respectively; Figure 2).

3.2 | Factors influencing the abundance of mouse lemurs and rodents

Across all study sites (n = 44 sites), the abundance of M. ravelobensis was significantly influenced by forest size (Table S3) and its abundance increased with increasing forest size (E = 0.225, SE = 0.045, p < .001, Figure 3a). In forest fragments, there was a negative relationship between M. ravelobensis abundance and the proportion of 50-m forest edge (n = 40, E = −0.015, SE = 0.005, p = .010; Table S4, Figure 4b), and abundance was significantly higher in Mariarano versus ANP (n = 40, E = 0.576, SE = 0.218, p = .012). None of the other

FIGURE 2  Distribution of mouse lemurs and rodents in two fragmented regions (Mar: Mariarano, ANP: Ankarafantsika National Park) in northwestern Madagascar. The size of the pie charts depicts four categories for the absolute number of trapped individuals per site (see legend below). Different colors indicate the different species.
predictor variables revealed significant effects. The abundance of *M. murinus* was not significantly influenced by any of the predictor variables, neither with the overall nor the fragment data set (Tables S3 and S4). The abundance of *E. myoxinus* was significantly affected by region across all sites and by the proportion of 50-m forest edge in fragments. More specifically, its abundance was higher in ANP compared to Mariarano (\( n = 44, E = -0.432, SE = 0.185, p = .024; \) Figure 3b) and decreased as the proportion of 50-m forest edge increased in fragments (\( n = 40, E = -0.016, SE = 0.005, p = .002; \) Figure 4c). None of the other predictor variables contributed significantly to the models. The abundance of the invasive *R. rattus* in fragments was significantly and positively affected by the distance to the continuous forest (\( n = 40, E = 0.165, SE = 0.047, p = .001, \) Table S4, Figure 4d). Other factors did not significantly influence the abundance of this species, neither in the overall data set nor in the fragments.

### 3.3 | Interspecific interactions

There were no signals of species interactions between any of the four species in the overall and fragment datasets (Table S5). In all models, however, the previously significant factors were again significant.

### 4 | DISCUSSION

This study evaluated the impact of habitat loss and habitat fragmentation on mouse lemur and rodent distribution and abundance in northwestern Madagascar. We found that the four species showed different responses to the predictor variables and these factors shall, therefore, be subsequently discussed.

#### 4.1 | Impact of region on species abundance

Regional differences in species abundance were found for *M. ravelobensis* in the forest fragments and for *E. myoxinus* across all study sites, although the direction of the regional difference differed between these species. Specifically, the abundance of *M. ravelobensis* was higher in the Mariarano forest fragments than in ANP. Both regions vary in terms of humidity and altitude (Long et al., 2013; Salmona et al., 2014); forest habitats in Mariarano are more humid, closer to surface water, and are situated at lower altitudes than the ANP sites. Higher abundances in the more humid forest fragments of Mariarano are congruent with a previous study within the continuous forest of the ANP (Rakotondravony & Radespiel, 2009).

Abundances of *E. myoxinus* were higher in ANP than in Mariarano. These results could be related to a preference for dry conditions in ANP, a response to differences in vegetation structure or to differences in the human disturbance. Stephenson (1993) found that human disturbance correlated negatively with endemic rodent species richness in eastern Madagascar. In addition, a previous study in southeastern Madagascar showed that the abundance of *Eliurus* spp. was positively affected by altitude and distance from human habitation (Lehtonen, Mustonen, Ramiarinjahary, Niemelä, & Rita, 2001).

We suggest that abiotic factors are driving species-specific fragmentation responses of at least some native species on Madagascar. Habitat preferences along the humidity/aridity axis or for certain temperature regimes have also been described in various other small mammals in other regions of the world and are an important universal component of ecological habitat selection (Lima, Stenseth, & Jaksic, 2002; Porter, Budaraju, Stewart, & Ramankutty, 2000; Schmid-Holmes & Drickamer, 2001).

A lack of regional differences in *M. murinus* and *R. rattus* likely results from their ecological plasticity which is further reflected in their biogeographic patterns: *M. murinus* is a widespread species...
(Blair, Heckman, Russell, & Yoder, 2014) and has previously been reported to have a high habitat plasticity (reviewed in Radespiel, 2016 and see below). *R. rattus* is an invasive, ubiquitous species which also has highly plastic feeding niches (Bentley et al., 2000; Clark, 1982; Dammhahn, Randriamoria, & Goodman, 2017; Harper, Dickinson, & Seddon, 2005).

### 4.2 Impact of forest size and forest type on species abundance

Our findings showed strong effects of forest size on *M. ravelobensis* abundance which increased as forest size increased. Conversely, there was no evidence that this factor influenced *M. murinus* abundance. Instead, more *M. murinus* were trapped in fragments than in the continuous forest sites, although this difference was not significant. Such differences between the two mouse lemur species may relate to differences in ecological niches, interspecific competition in small areas, or in vagility (reviewed in Radespiel, 2016). It has been suggested that *M. murinus* evolved in the dryer and hotter habitats in southwestern Madagascar and only expanded to the North rather recently in the late Pleistocene (Blair et al., 2014; Schneider, Chikhi, Currat, & Radespiel, 2010). The hotter and dryer environmental conditions in the fragments may thus provide some preferred niche dimensions for this species (Rakotondravony & Radespiel, 2009).

The sensitivity of *M. ravelobensis* to decreasing forest size might also be the result of interspecific competition with *M. murinus* in small areas. Thorén, Linnenbrink, and Radespiel (2011) showed that during dyadic encounter experiments, *M. murinus* had, in general, a higher competitive potential than *M. ravelobensis*. However, there is no evidence from previous work that *M. ravelobensis* shows any preference for dryer and presumably less productive habitats, at least not in the continuous forests.

**FIGURE 4** Relationship between significant predictor variables and log-transformed abundance of species (small circles and dots) in forest fragments (*n* = 40 sites). (a) Regional differences in *Microcebus ravelobensis* abundance (*p* < .05; black circles). Median values (line in box) are shown together with quartiles (box), minimum and maximum values (whiskers) without outliers. (b) Relationship between proportion of forest edge (%) and *M. ravelobensis* abundance (*p* < .05; red circles and blue dots) in two regions. (c) Relationship between proportion of forest edge (%) and *E. myoxinus* abundance (*p* < .01; black circles). (d) Relationship between distance to the continuous forest (log-transformed) and log-transformed *R. rattus* abundance (*p* < .01; black circles). Lines represent 50% Loess lines fitted to species-abundance values represented by different symbols and colors in (b–d)
in ANP (Chanu et al., 2012; Rendigs, Radespiel, Wrogemann, & Zimmermann, 2003; Sehen et al., 2010).

We expect that species with a large geographic range size, such as M. murinus, would have a higher vagility than regional congeners with smaller range sizes (M. ravelobensis; reviewed in Radespiel, 2016). A high vagility could be expressed in higher dispersal rates or longer dispersal distances coupled with higher ability or willingness to cross open areas such as roads or the matrix between fragments. Such behavior may facilitate connectivity between subpopulations of M. murinus in fragmented regions. Steffens and Lehman (2018) used previously published home-range data to estimate the median dispersal distance of M. murinus as 1.177 m compared to 538 m for M. ravelobensis in ANP. Furthermore, previous research showed that young males of M. murinus typically disperse before their first mating season over distances of up to 1,000 m (Radespiel, Lutermann, Schmelting, Bruford & Zimmermann, 2003) with similar findings (dispersal distances: 180–960 m) being reported from the Kirindy forest in western Madagascar (Schliehe-Diecks, Eberle, & Kappeler, 2012). Preliminary population genetics studies suggested lesser connectivity between fragmented subpopulations of M. ravelobensis than of M. murinus (reviewed in Radespiel, 2016).

We did not find significant effects of forest size and forest type on abundance of E. myoxinus and R. rattus. Ganzhorn (2003) reported that capture rates of Eliurus spp. were positively correlated with forest size and conversely for R. rattus in western Madagascar. Shi et al. (2013) reported that E. myoxinus is widely distributed in western forests, whereas Eliurus spp. is found more frequently in the interior of primary forests in northeastern forests. On the contrary, R. rattus was often found near habitat edges of secondary forest (Stephenson, 1995). Given these variable results across regions, the size and type of forest might not matter strongly for rodents in northwestern Madagascar.

### 4.3 Impact of fragment characteristics on species abundance

Although the SI was supposed to express fragmentation-related perimeter, and therefore, shape irregularities in fragments, this parameter correlated positively with forest size (Table S2). However, this parameter was not significant in predicting species abundances and will, therefore, not be interpreted further.

M. ravelobensis and E. myoxinus both responded negatively to an increasing proportion of forest edge. However, their fragmentation responses were not identical as the two species differed in distribution. Whereas most M. ravelobensis were trapped in continuous forest sites and if in fragments, only in the larger ones, most E. myoxinus were trapped in fragments and sometimes even in smaller ones (Figure 2). This pattern suggests that E. myoxinus can persist better in fragments or can maintain population connectivity between fragments better than M. ravelobensis. Nevertheless, E. myoxinus may be sensitive to the impact of habitat edges and may avoid edge habitats if possible. Previous studies also showed that capture rates of Eliurus spp. declined significantly with declining fragment size in western and southeastern Madagascar (Ganzhorn, 2003; Ramanamanjato & Ganzhorn, 2001). Burke and Lehman (2014) found that M. ravelobensis was trapped in even higher numbers near habitat edges (5–50 m distance from edge) compared to the interior of another continuous forest in ANP. Thus, M. ravelobensis does not seem to avoid habitat edges per se, and consequently, our findings for this species should rather be interpreted as an indirect forest size effect.

Our study showed a positive effect of distance to the continuous forest on R. rattus abundance. Dunstan and Fox (1996) also showed that R. rattus was more abundant in fragments further away from the forest and higher abundance was found in the more disturbed area in Australia. The latter finding was confirmed by Lehtonen et al. (2001) in Ranomafana NP, southeast Madagascar.

### 4.4 Interaction between the abundances of mouse lemurs and rodents

There was no signal of species interactions based on the abundance data between any of the four target species neither across all sites nor in fragments alone. Such a finding may either indicate that there is no such relationship or that the capture-mark-recapture method does not reflect well the real abundance of the species within sites. However, the capture-recapture abundance correlated with the abundance established by the line transect surveys for the two mouse lemur species (see Section 2) and should, therefore, be a rather reliable proxy of abundance.

According to our findings, there was no correlation between the abundances of the two mouse lemur species. In contrast, Rakotondravony and Radespiel (2009) stated that there was a negative relationship between the abundance of M. murinus and M. ravelobensis based on both capture-recapture and the line transect survey method in the continuous forest of ANP. Another study, conducted only in the fragmented landscape in ANP by means of line transect surveys alone, stated the opposite (Steffens & Lehman, 2016). As the methods, as well as the spatial setting differed between those two studies, these differences remain difficult to interpret. If results from these studies are correct, then they may indicate support for highly localized ecological responses in mouse lemurs.

The lack of negative interaction between the invasive R. rattus and the native rat we studied is surprising, as similar interaction studies have previously been conducted in other countries with contrasting results. For example, R. rattus has been shown to displace native small mammals such as R. fuscipes and Antechinus stuartii from forest habitats in southeastern Australia (Stokes et al., 2009). In conclusion, the results from this study suggest that abundance regulation of both mouse lemur species and the two rodent species with the studied regions were most likely driven by different factors and did not depend on the presence or absence of any of the other species.

### 4.5 Conservation implications

The four study species responded in very different ways to fragmentation in northwestern Madagascar. On the basis of their low numbers in fragments and the strong effects of forest size on their abundance, M. ravelobensis seems to be the most sensitive of all
four species to forest loss and fragmentation. It is likely that this species needs a certain minimum forest size to be able maintain viable subpopulations and to avoid local extinction in fragmented landscapes. Strong emphasis should be given in the future to the protection of large tracts of the remaining forest in the region between the large rivers Betsiboka and Mahajamba (Lehman, Radespiel, & Zimmermann, 2016). Forest corridors may support their persistence and survival in fragmented landscapes.

Although *E. myoxinus* may not be sensitive to forest loss per se, it did not occur in high numbers across both forest regions, had the lowest overall capture numbers of all species and was sensitive to an increasing proportion of the edge zone in fragments. These results may indicate a narrower ecological niche with a preference for dryer habitats coupled with some negative edge effects that may be related to disturbance.

The endemic *M. murinus* and the invasive *R. rattus* showed no negative fragmentation responses. Both species had their highest abundance in fragments, although the underlying reasons may be quite different. However, this does not mean that there should be no conservation concern for *M. murinus* in times of continuing deforestation, habitat degradation, and fragmentation (Vieilledent et al., 2018). The maintenance of connectivity between small subpopulations in a given metapopulation is of utmost importance and requires a certain proximity between neighboring stepping-stone populations to allow dispersal and recolonization to happen (Steffens & Lehman, 2018).

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**DATA AVAILABILITY STATEMENT**

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

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