Journal of Biogeography   WILEY

Functional redundancy of non-volant small mammals increases in human-modified habitats

André Luís Luza[1,2] 🄳 | Catherine Helen Graham[2] | Sandra Maria Hartz[1] |
Dirk Nikolaus Karger[2] 🄳

[1]Programa de Pós-Graduação em Ecologia, Departamento de Ecologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

[2]Swiss Federal Research Institute, Birmensdorf, Switzerland

Correspondence
André Luís Luza, Programa de Pós-Graduação em Ecologia, Departamento de Ecologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Avenida Bento Gonçalves 9500, Porto Alegre, Brazil.
Email: luza.andre@gmail.com

Abstract

Aim: Humans are rapidly altering natural habitats across much of the globe. Here we compared 264 globally distributed communities in natural and human-modified habitats to detect changes in community richness and functional diversity with human influence.

Location: Global.

Taxon: Non-volant small mammals.

Methods: We calculated differences in observed to potential species richness (ΔSR) and observed to potential functional diversity (ΔFD) to account for regional pool differences. Then we determined the prevalence of four distinct scenarios of richness and functional diversity differences between human-modified and natural habitats, and evaluated local and geographical variation in these differences. We obtained potential richness by calculating a probabilistic species pool and obtained potential functional diversity through the n-dimensional hypervolume based on pool composition. We tested for differences in average ΔSR and ΔFD between habitats, and determined the most common scenario of ΔSR and ΔFD in human-modified and natural habitats.

Results: We found lower ΔSR in human-modified than natural habitats, but no difference in ΔFD. Low ΔSR and high ΔFD predominated in human-modified habitats, and high ΔSR and ΔFD in natural habitats. Low ΔSR and high ΔFD predominated in temperate forests, whereas high ΔSR and ΔFD in tropical forests and grasslands. Scenarios of low ΔSR and high ΔFD, and high ΔSR and low ΔFD, were most common in human-modified and natural habitats of temperate grasslands.

Main conclusions: A larger richness in human-modified habitats does not result in larger functional diversity. Rather there seems to be an increase in functional redundancy because species which profit from human modification do not bring new functions into human-modified habitats. While greater richness is found in human-modified habitats from temperate biomes, this is not the case in extremely biodiverse tropical biomes. Assuming a positive relationship between richness, functional traits and ecosystem function, greater richness in modified habitats may not yield greater function.

---

1 | INTRODUCTION

Human activities are rapidly altering natural habitats across much of the globe, which makes it challenging to determine how these activities influence species and functional diversity in local communities (Blowes et al., 2019; Bogoni et al., 2018; Davidson et al., 2017; Newbold et al., 2018). Functional diversity, the range of functional traits found in ecological communities (Diaz & Cabido, 2001), has become central in biodiversity assessments as it can help reveal which ecological functions are lost with human influence (Brodie et al., 2021; Carmona et al., 2021; Cooke et al., 2019; Mouillot et al., 2013). Of particular interest for biodiversity assessments is functional redundancy, a facet of functional diversity that depicts how similar the species are regarding their functional traits (Mouillot et al., 2013). Functional redundancy can inform us on how many species and traits can be lost before communities lose functions (Carmona et al., 2021; Cooke et al., 2019), as well whether communities are gaining functionally common species through colonization (Mori et al., 2015; Newbold et al., 2018).

Biodiversity assessments are, however, hampered by globally idiosyncratic changes in local species richness and functional diversity with habitat alteration (Blowes et al., 2019; Dornelas et al., 2014). These changes can occur between habitat types such as temperate or tropical forests (Blowes et al., 2019; Murphy & Romanuk, 2014; Newbold, Hudson, Hill, et al., 2016) and subtropical forests or temperate grasslands (Corbelli et al., 2015). Idiosyncratic responses of local communities are partly expected because of compositional differences among larger biogeographical regions in which local habitats are embedded (Karger et al., 2016; Lessard et al., 2016). The composition of a local community results, to a large degree, from sorting the regionally available species pool which consists of those species that could potentially colonize and establish within a community (Cornell, & Harrison, 2014). This sorting is mediated by a combination of factors (also known as filters), such as species ability to disperse to and survive in a site given its environmental conditions (Karger et al., 2016; Lessard et al., 2016). Including the species pool into analysis of local community composition has the advantage that large regional differences, such as those between temperate and tropical forests, are already accounted for and the effects of local factors can be analysed in isolation (Karger et al., 2020).

An example of such local factors is the alteration of habitats due to human influence. Natural forests and grasslands (hereafter: natural habitats) are, for example, expected to have low rates of extinction and colonization with slow changes in species composition (Gibson et al., 2011; Newbold et al., 2018; Pfeifer et al., 2017) so that the potential SR and FD from the regional species pool are locally well represented (Figure 1). Natural habitats contain a set of often functionally unique species which are adapted to the specific local environment (Lessard et al., 2016; Newbold et al., 2018). When humans change the quality, size and connectivity of natural habitats, they also alter the local environment and trigger a re-assembly of communities from the available species pool (Dornelas et al., 2014; Newbold, Hudson, Hill, et al., 2016). This re-assembly can either decrease or increase SR depending on the rates of extinction and colonization (Jackson & Sax, 2010; Sax et al., 2005), as well either decrease or increase FD depending on whether species have the functional traits that allow to profit from modifications on habitats created by humans (Brodie et al., 2021; Carmona et al., 2021; Cooke et al., 2019; Mori et al., 2015; Newbold et al., 2018).

We aimed to assess how human influence alters local biodiversity by measuring the difference in observed species richness (ΔSR) and functional diversity (ΔFD) relative to their potential in the species pool. We estimated the potential SR and FD using the probabilistic species pool approach (Karger et al., 2016) where the probability of occurrence of each species present in the pool is a function of its dispersal ability and the site environmental suitability. We treated ΔFD as its standard deviation from a null ΔFD produced by a null model (i.e. ΔFD_{SES}), as needed to deal with the richness effect on FD (Oliveira et al., 2016), and with species with probabilities close to zero in the probabilistic species pool. Both ΔSR and ΔFD_{SES} reach positive values when many species and traits present in the pool are absent in local communities, indicating a loss relative to community potential. We quantified variation in ΔSR and ΔFD_{SES} under two perspectives: (1) comparing states of habitat modification (either human-modified or natural) and (2) comparing types of habitats (natural: natural forests, natural grasslands; modified: crop fields, clearcuts, tree plantations, grassland edges, forest edges). We expected higher ΔSR and ΔFD_{SES} in modified than in natural habitats in both perspectives, as the loss of species adapted to natural conditions (the 'losers') and the colonization of species that profit under human influence (the 'winners') can increase the difference in observed and potential richness and functional diversity found in a site (Lewis et al., 2017). We then assessed the type of human influence on local communities and its geographical variation. To do so, we adapted the framework of Sax et al. (2005, see also Jackson & Sax, 2010) to incorporate the combinations of ΔSR and ΔFD_{SES}—compared to the average ΔSR across all sites (global average) and ΔFD_{SES} equal to zero (a null ΔFD), respectively—to distinguish four scenarios in which local communities could fit into (Figure 1):

- S1: ΔSR and ΔFD_{SES}, for a given habitat, are lower than average ΔSR and zero, respectively, across habitats (Figure 1). This indicates no local change in SR and FD so that potential SR and FD from the species pool are locally well represented. This result suggests that there has been limited local extinction and replacement as a result of human influence (Jackson & Sax, 2010; Sax et al., 2005).

FIGURE 1 Analytical framework used to analyse differences in natural vs. human-modified habitats with respect to loser (grey) and winner species (black). Each of the 264 observed communities has a potential species richness (SR) and functional diversity (FD) given by its local probabilistic species pool, which consists of all species that can disperse into a site (defined as a 2° grid cell) and persists there given the environmental conditions (from the niche models, species distribution modeling [SDMs]). Observed communities were assigned to either natural or human-modified habitats based on the state of human modification in which the field observation took place (see Section 2). Differences in observed to potential SR (ΔSR), and differences in observed to potential FD (ΔFD) between these habitat types were tested using an ANOVA with a subsequent Post-hoc Tukey honestly significant difference (HSD) test. Small mammal communities could show different scenarios (S1–S4) of ΔSR and ΔFD. These scenarios can be distinguished by comparing ΔSR and ΔFD to $\overline{\Delta SR}$ and $\Delta FD_{SES} = 0$ and subsequently testing scenario prevalence using a Pearson's chi-squared test. The $\Delta FD_{SES} = 0$ depicts a ΔFD that is equal to the null ΔFD
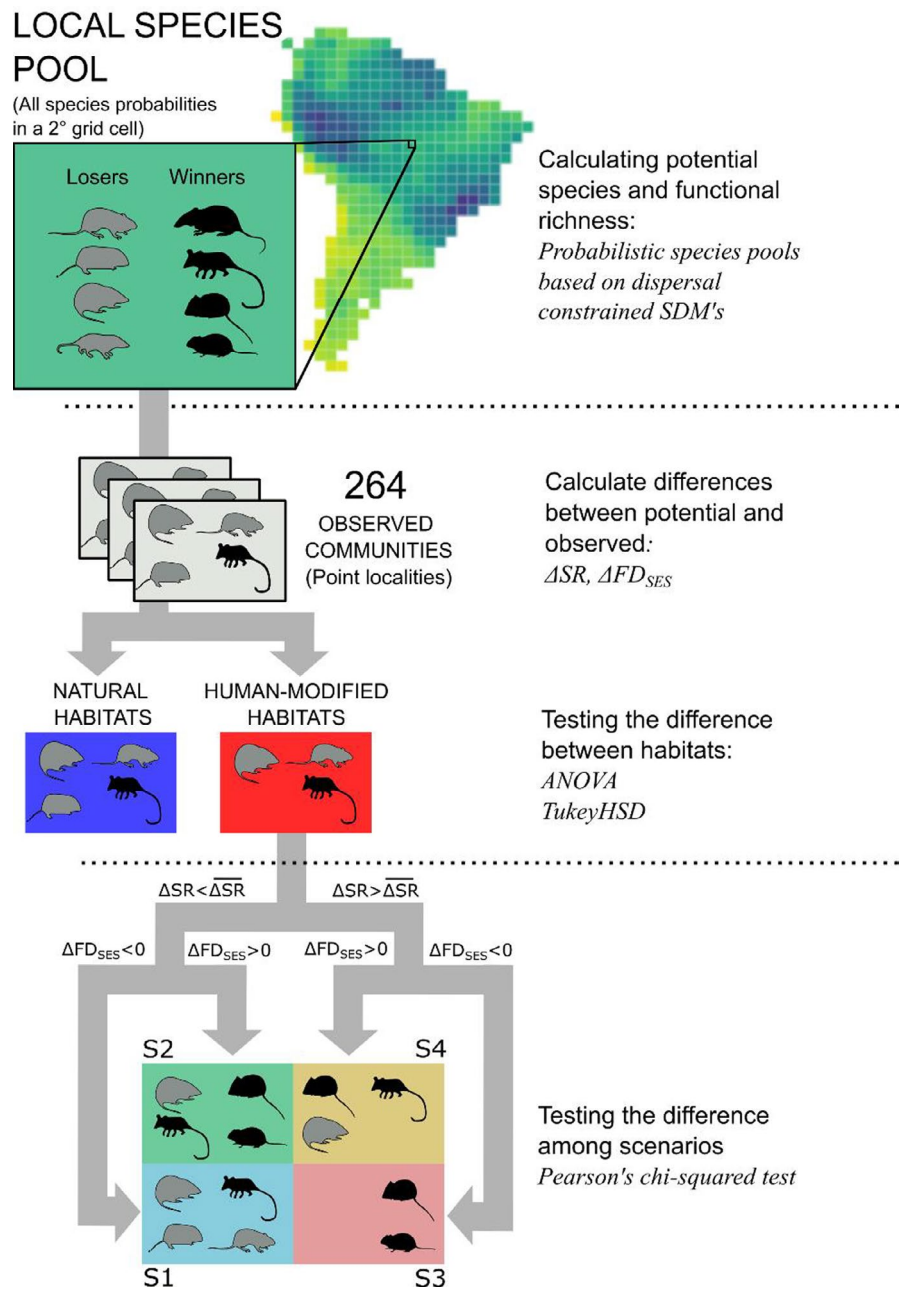
- S2: ΔSR is lower than average and ΔFD_{SES} is higher than zero (Figure 1). This indicates that local extinctions are counterbalanced by the immigrations so that ΔSR remains low (Dornelas et al., 2014). However, locally extinct species (the 'losers') are not replaced from a functional perspective. Instead, they are replaced by winner species with functions similar to those species that persist in a given habitat, leading to a reduction in functional diversity and increase in functional redundancy (Mori et al., 2015; Mouillot et al., 2013; Sobral et al., 2016).
- S3: ΔSR is higher than average and ΔFD_{SES} is lower than zero (Figure 1). This indicates a relative loss of species, but a gain in FD. In this case, immigrants add functions to the local communities (e.g. granivores immigrating into crop fields in previously forested landscapes; Corbelli et al., 2015).
- S4: ΔSR and ΔFD_{SES} are higher than average ΔSR and zero,

respectively, across habitats (Figure 1). This indicates deficits in both SR and FD. This is the worst-case scenario as local extinctions are not counterbalanced by immigration, resulting in large differences in observed relative to potential species richness and functional diversity (Bogoni et al., 2018; Carmona et al., 2021; Pfeifer et al., 2017).

Here, we assessed the influence of human habitat modification on 264 local communities of non-volant small mammals. These communities are within the most common types of natural and modified habitats found in land (Newbold, Hudson, Arnell, et al., 2016; Newbold, Hudson, Hill, et al., 2016; Newbold et al., 2018), and small mammals among the most functionally specialized and perhaps resilient organisms to human influence (Bovendorp et al., 2019; Flynn et al., 2009; Pfeifer et al., 2017;

Umetsu et al., 2008). As our communities are globally distributed, we could assess local variation in observed species richness and functional diversity while accounting for regional differences in the species pool.

2 | MATERIALS AND METHODS

2.1 | Study group and data

Non-volant small mammals are relatively well sampled across the globe, and have been used as a model group to test the effect of land-use changes on biodiversity (e.g. Fleming et al., 2014; Luza et al., 2019; Pfeifer et al., 2017; Umetsu et al., 2008). We used species composition data for non-volant small mammals weighing ≤5 kg belonging to Afrosoricida, Dasyuromorphia, Didelphimorphia, Diprotodontia, Eulipotyphla, Lagomorpha, Peramelemorphia and Rodentia, from Luza et al. (2019) and the PREDICTS database (Hudson et al., 2017). A total of 1112 non-volant small mammal species were analysed, being Rodentia, Eulipotyphla, Didelphimorphia and Lagomorpha the most representative orders in the dataset (73%, 12%, 5% and 4% of the analysed species).

The database of Luza et al. (2019) contributed with 90% of the data and PREDICTS with the remaining 10%. These databases were created to foster spatial assessments of biodiversity variation between natural and human-modified habitats (e.g. Newbold, Hudson, Arnell, et al., 2016; Newbold, Hudson, Hill, et al., 2016; Newbold et al., 2018). In both databases, small mammal data were collected in paired patches of human-modified and natural habitats, mostly from Neotropics and Nearctic. Generally, the community data in spatially close habitats were collected in the same study. Data were accompanied by information of sampling effort (trap-nights) and sampling techniques (mostly live traps such as tomahawk, Sherman and pitfall traps), which allowed to standardize effort across databases. PREDICTS data were gathered directly with data owners, whereas Luza et al. (2019) data were gathered from literature reviews. Although these databases have some differences in habitat classification scheme, both provide enough information to create a common classification. Classification of tree plantations, crop fields and clear-cuts is consistent across databases. The differences were as follows: (1) while PREDICTS did not differentiate grasslands from forests (grouped in 'Primary vegetation'), Luza et al. did so due to differences in species and functional composition between these natural habitats (e.g. Luza et al., 2015, 2016; Wilson et al., 2010). Luza et al. (2019) used the major biome of PREDICTS's sites to differentiate if data were collected in forests or grasslands. We used a similar scheme to the one presented below in *Geographical variation in scenarios*. (2) Edges were only included in the database of Luza et al., which was further separated into grassland edges and forest edges to capture the variation in edge effects with the modification of these natural habitats.

2.2 | Habitat classification into natural and human-modified habitats

We analysed variation in ΔSR and ΔFD based on state of human modification (either natural or modified) and habitat type (two types of natural habitats, and five types of human-modified habitats). Types of natural habitats in our study comprised forests and grasslands, the most common natural habitats found in land. Natural forests were defined as forests with minimum disturbance, advanced secondary regeneration and remnants in landscapes with an alternative land use. Natural grasslands were native grasslands and savannas, generally grazed by domesticated ungulates, and remnants in landscapes with an alternative land use (Veldman et al., 2015). These habitats are assumed to reflect the structure of natural habitats and having a similar species composition as natural habitats (Gibson et al., 2011; Newbold et al., 2015). Types of human-modified habitats included tree plantations (monocultures of trees), clear-cuts (cleared land at an early stage of regeneration), crop fields (fields covered by soybean, hay, maize tillage, sugarcane, among others), artificial forest edges (edge between a natural forest and a human-modified habitat) and artificial grassland edges (edge between a natural grassland and a human-modified habitat).

2.3 | Species traits for functional diversity

We used body mass, litter size, gestation length, weaning age, sexual maturity age (days) and population density from Penone et al. (2016) to estimate functional diversity. These traits distinguish fast- from slow-life histories and specialized from generalized life styles among small mammal species (Davidson et al., 2017; Flynn et al., 2009; Penone et al., 2016). All traits had pairwise correlation <0.5 and were standardized to zero mean and unit variance before analysis.

2.4 | Delineating the local probabilistic species pool

The local probabilistic species pool (LPSP; sensu: Karger et al., 2016) provides a baseline to assess whether SR and FD are different from their potential. A LPSP considers the probability of occurrence of a global set of species into a site based on (1) species dispersal abilities (the dispersal pool) and (2) the match between a species environmental preference and environmental conditions at a given site (the environmental pool).

2.4.1 | Dispersal pool

The dispersal pool consists of all species from the global pool of 1112 non-volant small mammal species which are able to potentially reach a specific site. We calculated the dispersal pool based on the annual dispersal rate *k*. The parameter *k* was based on published data on natal

dispersal distances—the period in which an individual is more likely to disperse (Whitmee, & Orme, 2013) and its generation length—the age at which an individual achieves half of its total reproductive output (Pacifici et al., 2013). As natal dispersal distances were available only for 49 species and six orders (Dasyuromorphia, Didelphimorphia, Diprotodontia, Eulipotyphla, Lagomorpha and Rodentia), we used data imputation based on a random forest (RF) algorithm (Stekhoven & Buehlmann, 2012). The RF algorithm provides a solution to estimate natal dispersal distances in face of uncertainty and lack of large amounts of data, as is the case of dispersal here (availability of data for 49 out of 3079 species with generation length data). This solution resulted in a linear relationship between body size and dispersal distance (Figure S1.1), a similar relationship as found by Santini et al. (2013) using allometric equations to imputing missing data (see Appendix S1, Figure S1.1 for details on the imputation procedure). After imputing, we calculated k using natal dispersal distances and generation length for the 1112 species included in our analyses.

We used k to estimate the probability of dispersal of each species to the cell n (D_n) as:

$$D_n = 1 - \prod_{n=1}^{N} \left(1 - e^{-k \cdot t_n}\right),$$

(Bischoff, 2005) where the exponent of species dispersal rate k during the time t defines the ability a species has to disperse from n to N cells (Karger et al., 2016). Dispersal was calculated starting from each grid cell of a species current range based on IUCN range maps (IUCN, 2017) for $t = 40$ years. However, because we imputed many estimates, we conducted a sensitivity analysis and recalculated the dispersal pool with three measures of k: (1) $k = 0.04$, which is the overall mean dispersal of all species, (2) $k = 0.5$ and (3) $k = 1$, which were among the most extreme dispersal values we found in our data (Appendix S1). We reported only analyses using pools based on species-specific dispersal k as sensitivity analysis returned qualitatively similar results. Species-specific dispersal kernels at 2° horizontal resolution were calculated using the *disppool* function, in the 'probpool' package in R (Koenig et al., 2018).

2.4.2 | Environmental species pool

We estimated species occurrence probability given climate conditions using species distribution modelling (Guisan, & Thuiller, 2005). As predictors, we used mean annual temperature, standard deviation of annual temperature, mean annual precipitation and standard deviation of annual precipitation at a 0.5-degree grid cell from CHELSA v1.2 (Karger et al., 2017). For presence–absence data, we used the IUCN range maps (IUCN, 2017). Absences were weighted so that the sum of the absences equals the sum of the presences. We used an ensemble of generalized linear models (Nelder, & Wedderburn, 1972), generalized additive models (Hastie, & Tibshirani, 1986), and RFs to estimate a species probability of occurrence E_n in a given cell (n) (Thuiller et al., 2019). We used a 10-fold cross-validation of the models and calculated the area under curve (AUC) statistics, kappa

statistics and true skills statistics (TSS) to evaluate model goodness-of-fit (Appendix S2, Table S2.1). Overall, 997 of 1112 species were included in the environment-based pool. The missing 115 species had no IUCN range maps, or had distributions too small to fit species distribution models. These 115 species without environmental probability scores were added into to the LPSP by assigning a value of 1, highly suitable, to locations where they have been observed.

2.5 | Observed relative to potential species richness (ΔSR) and functional diversity (ΔFD)

To estimate potential species richness (PSR) of the LPSP, we calculated the probabilistic species pool size index $^i\psi_{DE}$ for each site, using:

$$^i\psi_{DE} = \sum_{s=1}^{S} \prod_{x=1}^{X} P_{xs}.$$

The index is based on the sum of probabilities P of occurrence of all species $s = 1$ to S, considering the product of the probabilities for all species generated by $x = 1$ to X factors (dispersal (D_n) and environment (E_n) in the cell n) used to delineate the pool. The ΔSR of each site was calculated as ΔSR = PSR − LSR, being LSR the local species richness calculated as the sum of all species incidences in a site n. Positive values of ΔSR indicate loss of species so that potential SR is not locally well represented.

The potential functional diversity (PFD) of the community in site n (PFD$_n$) was estimated using the probability of occurrence and trait data of species $s = 1$ to S included in the respective LPSP. We estimated PFD using the n-dimensional hypervolume approach (Blonder et al., 2014; further details in Appendix S3, Table S3.1). Estimation of the local functional diversity (LFD) followed the same method used to estimate PFD, but now considering only the species found in the local communities. The ΔFD of each site was calculated as ΔFD = PFD − LFD. Positive values of ΔFD indicate loss of function so that potential FD is not locally well represented.

One important characteristic of the LPSP is that all 1112 non-volant small mammal species we analysed are included in each LPSP. Thus, if we assume that all 1112 species in the pool have some probability to occur in a community, the values of PFD would be equal across sites. However, many species will occur with probabilities close to zero as they are very unlikely to disperse and establish in sites distant from their current occurrence. To arrive at a binary classification needed to estimate an average pool hypervolume we ran, for each site, a probability-weighted sampling of the 1112 species, with sample size equal to $^i\psi_{DE}$ species. We used 100 sampling runs per site to obtain a null average $\overline{PFD_{NULL}}$ and standard deviation ($\sigma^{PFD_{NULL}}$) of the potential functional diversity (PFD) to calculate the ΔFD (hereafter 'ΔFD$_{SES}$') for each site as follows:

$$\Delta FD_{SES} = \frac{\Delta FD_{OBS} - \overline{\Delta FD_{NULL}}}{\sigma^{\Delta FD_{NULL}}},$$

where ΔFD_{OBS} is the observed difference between LFD and the $\overline{PFD_{NULL}}$, while $\overline{\Delta FD_{NULL}}$ is the average null difference between the null LFD—now produced by a probability-weighted sampling of size equal to local species richness (LSR)—and the $\overline{PFD_{NULL}}$; $\sigma^{\Delta FD_{NULL}}$ is the standard deviation of ΔFD_{NULL} across the 100 sampling runs. An observed ΔFD higher than the $\overline{\Delta FD_{NULL}}$ will produce positive values of ΔFD_{SES} as a result of functional loss relative to community potential, whereas an observed ΔFD lower than the $\overline{\Delta FD_{NULL}}$ will produce negative values of ΔFD_{SES} as a result of no functional loss relative to community potential.

Sampling effort might be an important source of uncertainty when assessing human influence on local richness and functional diversity. We explored whether ΔSR and ΔFD_{SES} were sensitive to different sampling effort by running analyses with three datasets based on sites sampled with >100, >500 and >1000 trap-nights. The number of sites for each dataset was 357, 320 and 264, and the number of species was 443, 422 and 391. Results only varied qualitatively across datasets (Appendix S4). We report here the results using the dataset of >1000 trap-night; results for other thresholds of trap-nights are available in Appendix S4 (Figures S4.1–S4.5; Tables S4.1–S4.4).

2.6 | Statistical analyses

2.6.1 | Testing differences between states of habitat modification and habitat types

To test whether ΔSR and ΔFD_{SES} are different between natural and human-modified habitats, the two states of habitat modification, we used an analysis of variance (ANOVA). To test whether ΔSR and ΔFD_{SES} are different between all pairwise combinations of habitat types (forests, grasslands, tree plantations, clear-cuts, crop fields, forest edges, grassland edges), we used an ANOVA with a Post-hoc Tukey honest significant differences test (TukeyHSD).

2.6.2 | Distinguishing scenarios and testing their prevalence

To distinguish between the hypothetical scenarios S1–S4 (Figure 1), we defined a threshold to group sites into each of the four scenarios of human influence. To distinguish between S1 and S3, we used the global average ΔSR ($\overline{\Delta SR}$), as it represents the average difference in observed relative to potential SR across all studied communities. To distinguish between S2 and S4, we used $\Delta FD_{SES} = 0$, which depicts that the observed ΔFD is equal to the $\overline{\Delta FD_{NULL}}$. As the grouping based on $\overline{\Delta SR}$ and $\Delta FD_{SES} = 0$ is somewhat arbitrary, we conducted a sensitivity analysis where we defined thresholds along regular intervals of observed values of ΔSR and ΔFD_{SES} (Appendix S5, Figures S5.1 and S5.2). After distinguishing scenarios, we tested differences in their frequency between natural and human-modified habitats using a Pearson's chi-squared analysis under a null assumption of equal number of sites across the

combinations of scenarios and habitats. We ran this analysis using the *chisq.test* function in 'stats' package of R (R Core Team, 2020).

2.6.3 | Geographical variation in scenarios

To evaluate whether the prevalence of scenarios varied by biome, we assigned each site to one of the WWF biomes (Olson et al., 2001). We grouped biomes to show differences between temperate and tropical biomes, and forest- and grassland-like vegetation as (1) tropical forests: tropical and subtropical moist broadleaf forests, tropical and subtropical dry broadleaf forests; (2) temperate forests: boreal forests/taiga, Mediterranean forests, woodlands and scrub, temperate broadleaf and mixed forests, temperate conifer forests; (3) tropical grasslands: montane grasslands and shrublands, tropical and subtropical grasslands, savannas and shrublands; (4) temperate grasslands: temperate grasslands, savannas and shrublands. We used a Pearson's chi-squared analysis to identify significant differences among biomes and habitats in the number of sites assigned to each scenario.

3 | RESULTS

3.1 | Testing differences between states of habitat modification and habitat types

Average ΔSR across natural habitat communities was 14.63 ± 8.28 species, and it was 10.98 ± 6.31 species across human-modified habitats; the global average of ΔSR was 13.12 ± 7.72 species. Average ΔFD_{SES} across natural habitat communities was 0.58 ± 0.39 SDs, and it was 0.65 ± 0.41 SDs from the $\overline{\Delta FD_{NULL}}$ across human-modified habitats; the global average of ΔFD_{SES} was 0.61 ± 0.40 SDs from the $\overline{\Delta FD_{NULL}}$.

Analysis of variance showed a difference in observed relative to potential species richness (ΔSR) between states of habitat modification. The ΔSR was 3.66 species higher in natural habitats when compared with human-modified habitats ($F_{1,262} = 15.08$, $p < 0.001$, Figure 2; Figure S4.1). We found no difference in ΔFD_{SES} between natural and human-modified habitats ($F_{1,262} = 1.62$, $p = 0.2$).

Analysis of variance with post-hoc TukeyHSD test showed that habitat type influenced ΔSR ($F_{7,256} = 116.2$, $p < 0.001$). Forests and grassland had higher ΔSR than clear-cuts (Figure 3). We also found that habitat type influenced ΔFD_{SES} ($F_{7,256} = 100.1$, $p < 0.001$). TukeyHSD tests showed that clear-cuts and forest edges had higher ΔFD_{SES} than crop fields (Figure 3). The ANOVA identified an influence of habitat type on both ΔSR and ΔFD_{SES} for the datasets based on 100 ($F_{7,349} = 144.8$, $p < 0.001$ for ΔSR, $F_{7,349} = 130.6$, $p < 0.001$ for ΔFD_{SES}) and 500 trap-nights ($F_{7,312} = 137.2$, $p < 0.001$ for ΔSR, $F_{7,312} = 128.9$, $p < 0.001$ for ΔFD_{SES}). TukeyHSD showed that clear-cuts and forest edges had higher ΔFD_{SES} than natural grasslands
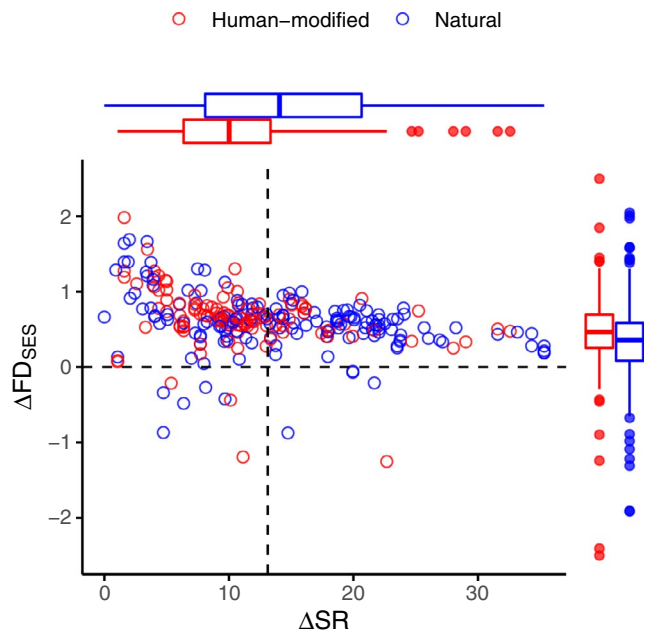
—WILEY—

FIGURE 2 Bivariate plot showing the relationship between ΔSR and ΔFD$_{SES}$. Each point represents the relationship for one small mammal community from either natural (blue points) or human-modified habitat (red points). The vertical dashed line is the average ΔSR ($\overline{\Delta SR}$) and the horizontal dashed line is ΔFD$_{SES}$ = 0. In the margin, we present boxplots of the habitat average and first and third quartiles of the distribution of ΔSR (top) and ΔFD$_{SES}$ (right). The unit of ΔSR is number of species while the unit of ΔFD$_{SES}$ is standard deviations from the null ΔFD average. The null ΔFD average was estimated using estimates from 100 runs of a null model using a probability-weighted sampling of species from the probabilistic pool. These results are based on >1000 trap-nights effort dataset. FD, functional diversity; SR, species richness

for both datasets (Figures S4.2 and S4.3), and that forest edges had higher ΔFD$_{SES}$ than crop fields for the dataset of 500 trap-nights (Figure S4.3). No difference in ΔSR was found between pairs of habitat types considering these datasets (Figures S4.2 and S4.3).

3.2 | Testing the four scenarios of human influence

We found that scenarios 2 and 4 were the most common in our data. Pearson's chi-squared test showed differences in the number of sites across combinations of habitats and scenarios (χ^2 = 21.27, df = 3, p-value ≤ 0.001). The observed number of human-modified habitats fitting to the scenario 2 (i.e. ΔSR lower than average, ΔFD$_{SES}$ higher than zero) exceeded the expected number for that habitat and scenario (Table 1; Tables S4.1 and S4.2). In addition, the observed number of natural habitats in scenario 4 (i.e. ΔSR higher than global ΔSR average, ΔFD$_{SES}$ higher than zero) exceeded the expected number for that habitat and scenario (Table 1). Scenarios 1 and 3 were rare in our dataset (Figure 4; Table 1; Figures S4.4 and S4.5).
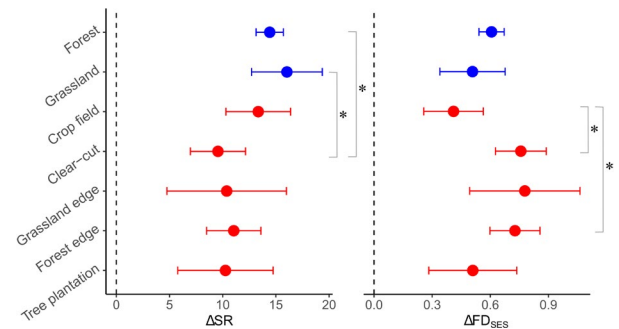

FIGURE 3 Coefficient plot showing the estimate of ΔSR and ΔFD$_{SES}$ per habitat type: natural habitats in blue and human-modified habitats in red. Bars around each estimate indicate the 95% confidence intervals. Significant differences (p ≤ 0.05) between pairs of habitat types are indicated by brackets and asterisks. Results based on >1000 trap-nights effort dataset. FD, functional diversity; SR, species richness

3.3 | Geographical variation in scenarios

Pearson's chi-squared analysis showed a significant difference in scenarios among biomes (χ^2 = 93.09, df = 21, p-value ≤ 0.001). *Scenarios* 2 was prevalent in both human-modified and natural habitats of temperate forests, whereas scenario 4 was prevalent in both human-modified and natural habitats of tropical forests (Table 2). While scenario 4 was common in natural temperate grasslands, scenario 2 was common in human-modified habitats of temperate grasslands (Table 2). Scenario 4 was prevalent in natural tropical grasslands. These results were robust to alternative sampling efforts (χ^2 = 136.1 for 100 and χ^2 = 118.14, df = 21, p-value ≤ 0.001 for 100 and 500 trap-nights; Tables S4.3 and S4.4) and alternative thresholds of ΔSR and ΔFD$_{SES}$ used for creating scenarios (Appendix S5, Figures S5.1 and S5.2).

3.4 | Sensitivity analysis

Our results were robust across sensitivity analyses considering unknown dispersal ability, differences in sampling effort or thresholds for grouping communities into scenarios. We estimated species-specific dispersal along a timeframe of 40 years, which marked the beginning of the green revolution period (Laurance et al., 2014). Using this timeframe and dispersal data from literature (Whitmee, & Orme, 2013), we found very few non-volant small mammals able to disperse more than one degree over 40 years; overall, species have low dispersal rates (average of 184.66 ± 329.93 m/year; Appendix S1). Accordingly, studies of non-volant small mammals using other methods suggest that most of dispersion events occur at 100–500 m of a site (Bowman et al., 2002; Umetsu et al., 2008). Therefore, human influence along these 40 years likely promoted immigration only to the adjacent sites (Bovendorp et al., 2019; Umetsu et al., 2008).

Habitat	S1	S2	S3	S4	Total
Natural	5 (4.70)	67 (85.13)	4 (2.93)	79 (62.23)	155
Human-modified	3 (3.30)	78 (59.87)	1 (2.06)	27 (43.77)	109
Total	8	145	5	106	264

TABLE 1 Contingency table showing the observed and expected (in parentheses) number of sites in different habitats and scenarios, considering the dataset of >1000 trap-nights effort
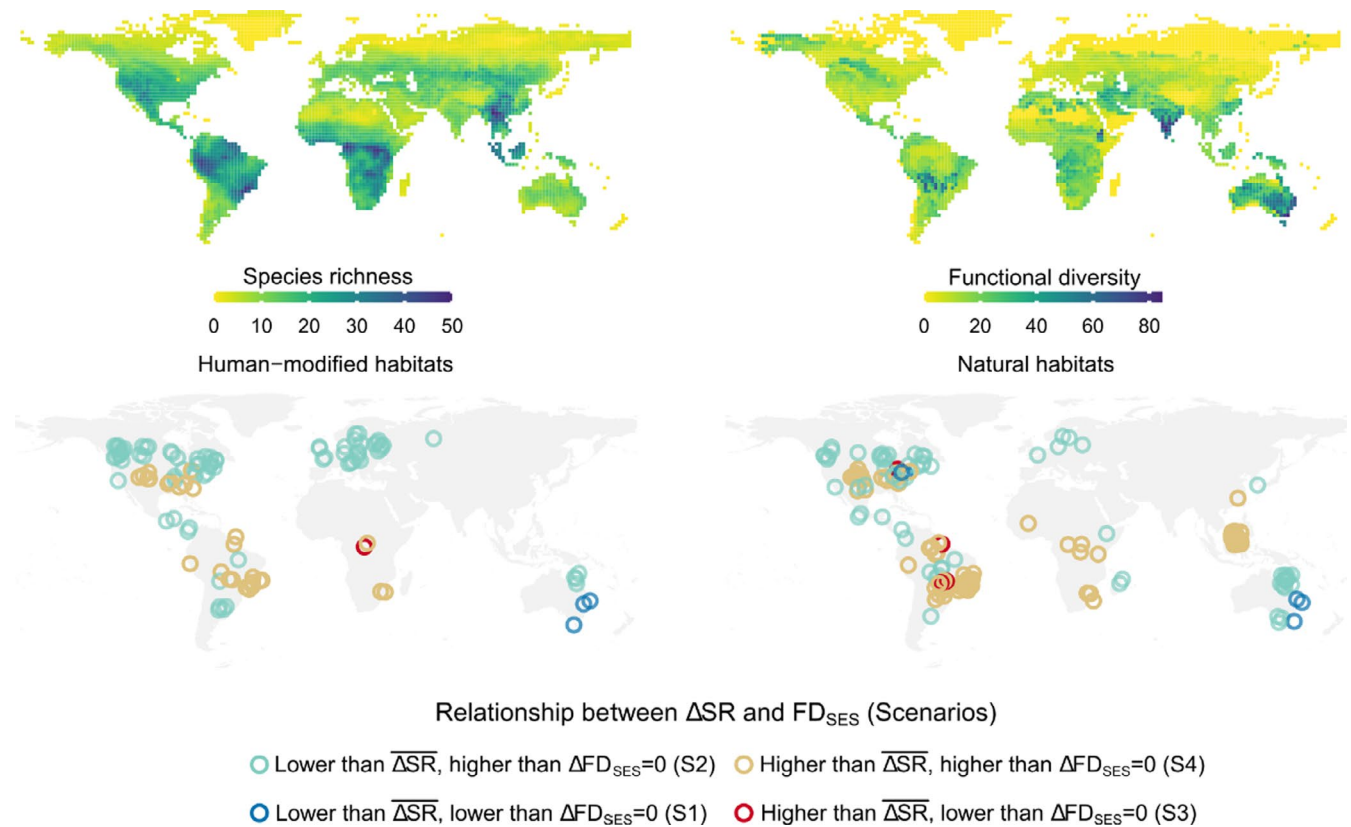

FIGURE 4 Geographical variation in the relationship between ΔSR and ΔFD$_{SES}$. The top panel are maps of potential species richness and functional diversity ($\overline{PFD}$, on square root scale) of the local probabilistic species pool (LPSP) at a resolution of 2 × 2-degree. Functional diversity is estimated by sampling $^i\psi_{DE}$ species from the LPSP based on their probability of occurrence. We repeated the procedure 100 times and then calculated an average potential hypervolume $\overline{PFD}$ for each grid cell. The unit of functional diversity, as measured by the n-dimensional hypervolume, is in standard deviations of transformed (centred and scaled) trait values, raised to the power of the number of traits. In the bottom panel, we present the studied sites with >1000 trap-nights and their respective scenario. FD, functional diversity; SR, species richness

4 | DISCUSSION

Using ΔSR and ΔFD—which quantify how far communities are from their potential—we showed that human-modified habitats are closer to their potential richness than natural habitats. However, they are not closer to the functional diversity potential. Communities can undergo compositional changes while species richness is maintained, resulting in species replacement over space and time, and no systematic loss of richness (Blowes et al., 2019; Dornelas et al., 2014; Sax et al., 2005). We found a prominence of scenario 2 in human-modified habitats—ΔSR is lower than the global average of ΔSR, and ΔFD$_{SES}$ is higher than zero— depicting no change in richness but loss of functional diversity relative to community potential. However, we found S4 most prevalent in natural habitats—ΔSR and ΔFD are both

higher than global ΔSR average and zero, respectively—depicting loss of richness and functional diversity relative to community potential. We also found a variation of the most prevalent scenario across biomes, reinforcing that human influence on local community diversity shows geographical variation (Blowes et al., 2019; Brodie et al., 2021). These two main observations directly question whether a simple increase in species richness in human-modified habitats still contributes to ecosystem functioning and habitat intactness (sensu Newbold, Hudson, Arnell, et al., 2016; Steffen et al., 2015).

Changes in species composition, or even an increase in species richness with human influence, usually did not coincide with a similar change in functional diversity (Dornelas et al., 2014; Mouillot et al., 2013; Sax et al., 2005; Sobral et al., 2016). More specifically, such an accrual of species did not expand the functional hypervolume or

TABLE 2 Contingency table showing geographical variation in the observed and expected (in parentheses) number of sites in different scenarios (S1, S2, S3 and S4—Figure 1), biomes and habitats, considering the dataset of >1000 trap-nights effort

Biome × habitat	S1	S2	S3	S4	Total
Temperate forest					
Natural	5 (1.64)	37 (29.66)	0 (1.46)	11 (21.68)	54
Human-modified	3 (2.33)	64 (42.29)	1 (1.02)	10 (30.92)	77
Tropical forest					
Natural	0 (2.09)	18 (37.90)	1 (1.31)	50 (27.70)	69
Human-modified	0 (0.79)	10 (14.28)	1 (0.49)	15 (10.44)	26
Temperate grassland					
Natural	0 (0.36)	3 (6.59)	0 (0.23)	9 (4.81)	12
Human-modified	0 (0.15)	4 (2.75)	0 (0.09)	1 (2.00)	5
Tropical grassland					
Natural	0 (0.61)	9 (10.98)	2 (0.38)	9 (8.03)	20
Human-modified	0 (0.03)	0 (0.55)	0 (0.02)	1 (0.40)	1
Total	8	145	5	106	264

increase the functional diversity. Instead, it results in a dense packing of functionally redundant species within a combination of traits already existing in the community (Aros-Mualin et al., 2021; Mouillot et al., 2013; Pigot et al., 2016). Functionally redundant species colonizing human-modified habitats could compete with resident and ecologically similar species, or further promote specialization for resource exploitation and partitioning among the species that profit under human influence (Mouillot et al., 2013; Pigot et al., 2016). Independent of the underlying process, community functional diversity is maintained at low levels, which can weaken the capacity of whole ecosystems to withstand growing anthropogenic pressures and ensure ecosystem services (Cooke et al., 2019; Mouillot et al., 2013), with potential consequences for ecosystem functioning and nature contribution to people (Díaz et al., 2019).

4.1 | Predominance of the scenarios in natural and human-modified habitats

The high prevalence of scenario 2 (71% of the cases) of no change in richness but loss of functional diversity relative to community potential could be explained by the intense and permanent management of human-modified habitats. Such a management often leads to local extinctions of 'loser' mammals: those with narrow range (Newbold et al., 2018), small litter size and slow life history (Carmona et al., 2021; Cooke et al., 2019; Flynn et al., 2009), and specialized diet (Brodie et al., 2021; Flynn et al., 2009; Hurst et al., 2014) and life habits (Fleming et al., 2014). For instance, species with litter size smaller than 2.25 individuals per litter/individual, and diet based on fish, fruit, seeds or nuts, might not persist with agriculture intensification and natural habitat loss (Brodie et al., 2021; Flynn et al., 2009; Hurst et al., 2014). Also, specialized digging mammals have been shown to decline under habitat loss and introduction of exotic species (Fleming et al., 2014). The loss of these unique community components is a global-wide process (e.g. Brodie et al., 2021;

Carmona et al., 2021) that may hamper critical ecosystem processes such as the rate of predation, dispersal and recruitment of seeds, and the structure, dynamics and chemistry of soils (Bovendorp et al., 2019; Fleming et al., 2014; Flynn et al., 2009; Hurst et al., 2014; Santos-Filho et al., 2016). While these losers decline, generalists and widespread 'winner' species can increase in number without adding ecological functions (Newbold et al., 2018; Sobral et al., 2016). Small mammals known to profit from human disturbances are usually terrestrial, small-sized, omnivores or insectivores, and prolific breeders under a wide range of environmental conditions (Castro, & Fernandez, 2004; Luza et al., 2015; Pfeifer et al., 2017), which may explain why scenario 2 is prevalent in most human-modified habitats. More than half (52%) of the sites with natural habitat showed high ΔSR and ΔFD, indicating that species richness and functional diversity are lower than their community potential. The prevalence of scenario 4 in natural habitats indicates that the local extinction of specialist and narrow-ranged 'losers' are not counterbalanced by generalist and widespread 'winner' small mammals (Newbold et al., 2018). There are two possible explanations for this result: (1) human influence in the surrounding landscape is influencing natural habitats, causing local extinctions and preventing compensatory immigrations (Bogoni et al., 2018; Bovendorp et al., 2019; Pfeifer et al., 2017); (2) the probabilistic species pool only includes dispersal and environmental filters, but neglects any potential biotic interactions (Karger et al., 2016; Lessard et al., 2016). For example, predator release in modified landscapes results in an increase in biomass of a few generalists which, in turn, leads to an increase in interspecific competition for limited resources and microhabitats (Bogoni et al., 2018; Bovendorp et al., 2019).

Scenarios which predict either a community under low rates of extinction and colonization (S1) or gains in functional diversity (S3) are almost absent in our data. It makes clear that human influence without changes in functional diversity is unlikely, and that a loss of functional diversity is the most likely outcome of human influence on non-volant small mammal communities.

4.2 | Differences between habitat types

Communities from human-modified habitats under intense management, such as clear-cuts and forest edges, showed the highest functional loss (observed ΔFD was higher than null ΔFD, producing positive ΔFD_{SES}). Clear-cuts, which result from forest logging and are rapidly transformed into crop fields, artificial pastures and tree monocultures (Laurance et al., 2014), presented a richness closer to the potential—lower ΔSR—than forests and grassland, and a functional diversity farther from their potential—higher ΔFD_{SES}—than crop fields. A similar functional deficit was found for forest edges. Forest edges are often formed through forest loss and fragmentation (Pfeifer et al., 2017). As these edges are in close contact with the surrounding matrix, generally composed by environmentally and structurally contrasting habitats such as crop fields and artificial pastures, they differ in fundamental microhabitat conditions (e.g. temperature and humidity) relative to forest-core habitats (Castro, & Fernandez, 2004; Pfeifer et al., 2017). Edge formation has therefore promoted declines in abundance and local extinction of forest-core species while fostering the colonization of edge-tolerant, matrix-tolerant and gap-crossing species into edge habitats (Castro, & Fernandez, 2004; Umetsu et al., 2008). Consequently, communities from these severely disturbed habitats are well below their potential functional diversity.

4.3 | Geographical variation in scenarios

Rates of biodiversity change are heterogeneous across regions (Blowes et al., 2019; Brodie et al., 2021; Davidson et al., 2017; Dornelas et al., 2014). Temperate and tropical forest biomes that still maintain extensive areas of natural habitats (Newbold, Hudson, Arnell, et al., 2016) and are under slow rates of biotic change (Blowes et al., 2019) could present scenario 1, whereas temperate and tropical grasslands and savannas that are severely modified by humans (Newbold, Hudson, Arnell, et al., 2016; Veldman et al., 2015) and likely under fast rates of change could present scenario 4. We found a single prevalent scenario in the different states of human modification within a biome but variation in scenarios among biomes, except for temperate grasslands. The predominance of just one scenario per biome is expected due to its homogeneous species pool (Olson et al., 2001; Penone et al., 2016). However, more than one scenario can occur when the intensity of use and the degree of land-cover change compete with environmental filters in explaining regional biodiversity (Kehoe et al., 2017).

Scenario 2 of no change in richness but loss of functional diversity relative to community potential predominated in temperate forests, a biome under long-standing human influence (Blowes et al., 2019; Newbold, Hudson, Arnell, et al., 2016; Newbold et al., 2018; Song et al., 2018) and—as we did not observe richness loss—with enough time for species to adapt to novel conditions and immigrate into modified habitats (Newbold et al., 2018). Furthermore, biologic

invasions are a major driver of local biodiversity change in temperate ecosystems (Murphy, & Romanuk, 2014). Although invaders competitively exclude local species in temperate forests, recent time-series analyses also show local gains of richness through immigration (e.g. Blowes et al., 2019). Our results add to this and show that such richness gains do not necessarily add functional diversity to non-volant small mammal communities from temperate forests.

Two scenarios predominated in the different states of human modification in temperate grasslands. This is globally the biome most influenced by humans as it is mechanistically easy to convert into other land uses, and is naturally suitable for cattle raising (Medan et al., 2011; Newbold, Hudson, Arnell, et al., 2016; Veldman et al., 2015). For instance, temperate grasslands are one of the regions presenting the highest agricultural yields in the world (Kehoe et al., 2017). Severe land-use change and landscape homogenization along the last centuries explain the predominance of scenario 2 in human-modified habitats of temperate grasslands, such as crop fields. This scenario reveals the functionally redundant, depauperated community of small mammals occupying these habitats subjected to severe temporal variation in resource availability and microclimates due to the planting and harvesting of annual crops (Bilenca et al., 2007; Medan et al., 2011). In turn, the prevalence of scenario 4—richness and functional diversity loss—in natural grasslands of temperate regions can be explained by the too intensive grazing and burning regimes applied on grasslands used to cattle raising, which can be detrimental to the local biodiversity of these ecosystems (Andersen et al., 2012; Luza et al., 2015).

In turn, scenario 4 of richness and functional diversity loss relative to community potential predominated in tropical forests and grasslands, where human influence has been more recent but not less pervasive (Newbold, Hudson, Arnell, et al., 2016; Song et al., 2018). Habitat loss and harvesting (hunting and poaching) are the main causes of mammal population declines in the tropics (Bogoni et al., 2018; Brodie et al., 2021), with an extinction probability especially high for narrow ranged and functionally unique species that do not occur anywhere else (Brodie et al., 2021; Gibson et al., 2011; Newbold, Hudson, Hill, et al., 2016; Newbold et al., 2018). Furthermore, community and ecosystem impoverishment and biodiversity losses are expected in the coming decades whether actions to conserve tropical environments and species are not met (Brodie et al., 2021; Song et al., 2018).

4.4 | Shortfalls of SDMs and data

The probabilistic pools included in this study only account for ~33% of the global number of non-volant small mammal species. The size of the LPSP, and also ΔSR and ΔFD_{SES}, could therefore be underestimated (Karger et al., 2020). Omitting these species could bias our results towards the most optimistic scenario (S1), as we could omit severely threatened species experiencing human influence throughout their range (Newbold et al., 2018). We minimized these drawbacks by adding all species locally observed to the LPSP, including recently

described and small-ranged species. Results suggest that such errors might be homogeneous over space, as neither scenario 1 predominate nor potential richness and functional diversity maps differ from existing ones (e.g. Oliveira et al., 2016). Finally, it is noteworthy that most data are from the Neotropics and Nearctic, while the Indo-Malay region and the eastern Palaearctic are underrepresented in the datasets we used here (Hudson et al., 2017; Luza et al., 2019). These regions have high richness and functional diversity of non-volant small mammals (Figure 4), and are currently under high rates of land-use change (Laurance et al., 2014; Song et al., 2018). As such, they are expected to behave like other tropical forest and grassland regions—that is, present the scenario S4 of richness and functional diversity loss relative to community potential—although data are needed to confirm this hypothesis.

5 | CONCLUSION

Human modification of habitats can have multiple effects on species richness and functional diversity. For non-volant small mammal communities, a larger species richness in human-modified habitats did not result in larger functional diversity. Rather there seems to be an increase in functional redundancy, as the species which profit from human modification do not bring new functions into human-modified habitats. An increase in species richness is often seen as a positive aspect, but if this increase in species richness did not coincide with an increase in ecological function, a higher species richness could instead weaken the capacity of habitats to withstand growing anthropogenic pressures, weakening ecosystem services and diminishing nature contribution to people.

CONFLICT OF INTEREST
We have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT
The community data of Luza et al. (2019) are available on https://doi.org/10.1016/j.dib.2019.103842, and of Hudson et al. (2017) on https://doi.org/10.1002/ece3.2579. Ensemble of species distribution modelling and occurrence data, as well R codes and results are available on Zenodo (https://zenodo.org/record/5230562#.YSjVMo5KjIU). R codes for the analyses are also freely available on GitHub (https://github.com/andreluza/Probabilistic_pool_project.git).

ORCID
André Luís Luza https://orcid.org/0000-0003-0302-529X
Dirk Nikolaus Karger https://orcid.org/0000-0001-7770-6229

REFERENCES
Andersen, A. N., Woinarski, J. C. Z., & Parr, C. L. (2012). Savanna burning for biodiversity: Fire management for faunal conservation in Australian tropical savannas. *Austral Ecology*, 37(6), 658–667. https://doi.org/10.1111/j.1442-9993.2011.02334.x
Aros-Mualin, D., Noben, S., Karger, D. N., Carvajal-Hernández, C. I., Salazar, L., Hernández-Rojas, A., Kluge, J., Sundue, M. A., Lehnert, M., Quandt, D., & Kessler, M. (2021). Functional diversity in ferns is driven by species richness rather than by environmental constraints. *Frontiers in Plant Science*, 11, 615723. https://doi.org/10.3389/fpls.2020.615723
Bilenca, D. N., González-Fischer, C. M., Teta, P., & Zamero, M. (2007). Agricultural intensification and small mammal assemblages in agroecosystems of the Rolling Pampas, central Argentina. *Agriculture, Ecosystems & Environment*, 121(4), 371–375. https://doi.org/10.1016/j.agee.2006.11.014
Bischoff, A. (2005). Analysis of weed dispersal to predict chances of recolonisation. *Agriculture, Ecosystems & Environment*, 106(4), 377–387. https://doi.org/10.1016/j.agee.2004.09.006
Blonder, B., Lamanna, C., Violle, C., & Enquist, B. J. (2014). The n-dimensional hypervolume. *Global Ecology and Biogeography*, 23(5), 595–609.
Blowes, S. A., Supp, S. R., Antão, L. H., Bates, A., Bruelheide, H., Chase, J. M., Moyes, F., Magurran, A., McGill, B., Myers-Smith, I. H., Winter, M., Bjorkman, A. D., Bowler, D. E., Byrnes, J. E. K., Gonzalez, A., Hines, J., Isbell, F., Jones, H. P., Navarro, L. M., ... Dornelas, M. (2019). The geography of biodiversity change in marine and terrestrial assemblages. *Science*, 366(6463), 339–345.
Bogoni, J. A., Pires, J. S. R., Graipel, M. E., Peroni, N., & Peres, C. A. (2018). Wish you were here: How defaunated is the Atlantic Forest biome of its medium- to large-bodied mammal fauna? *PLoS One*, 13(9), e0204515. https://doi.org/10.1371/journal.pone.0204515
Bovendorp, R. S., Brum, F. T., McCleery, R. A., Baiser, B., Loyola, R., Cianciaruso, M. V., & Galetti, M. (2019). Defaunation and fragmentation erode small mammal diversity dimensions in tropical forests. *Ecography*, 42(1), 23–35. https://doi.org/10.1111/ecog.03504
Bowman, J., Jaeger, J. A., & Fahrig, L. (2002). Dispersal distance of mammals is proportional to home range size. *Ecology*, 83(7), 2049–2055.
Brodie, J. F., Williams, S., & Garner, B. (2021). The decline of mammal functional and evolutionary diversity worldwide. *PNAS*, 118(3), e1921849118. https://doi.org/10.1073/pnas.1921849118
Carmona, C. P., Tamme, R., Pärtel, M., de Bello, F., Brosse, S., Capdevila, P., González, M. R., González-Suárez, M., Salguero-Gómez, R., Vásquez-Valderrama, M., & Toussaint, A. (2021). Erosion of global

functional diversity across the tree of life. *Science Advances*, 7(13), eabf2675. https://doi.org/10.1126/sciadv.abf2675

Castro, E. B. V., & Fernandez, F. A. S. (2004). Determinants of differential extinction vulnerabilities of small mammals in Atlantic Forest fragments in Brazil. *Biological Conservation*, 119(1), 73–80. https://doi.org/10.1016/j.biocon.2003.10.023

Cooke, R. S. C., Eigenbrod, F., & Bates, A. E. (2019). Projected losses of global mammal and bird ecological strategies. *Nature Communications*, 10, 2279. https://doi.org/10.1038/s41467-019-10284-z

Corbelli, J. M., Zurita, G. A., Filloy, J., Galvis, J. P., Vespa, N. I., & Bellocq, I. (2015). Integrating taxonomic, functional and phylogenetic beta diversities: Interactive effects with the biome and land use across taxa. *PLoS One*, 10(5), e0126854. https://doi.org/10.1371/journal.pone.0126854

Cornell, H. V., & Harrison, S. P. (2014). What are species pools and when are they important? *Annual Review of Ecology, Evolution, and Systematics*, 45, 45–67. https://doi.org/10.1146/annurev-ecolsys-120213-091759

Davidson, A. D., Shoemaker, K. T., Weinstein, B., Costa, G. C., Brooks, T. M., Ceballos, G., Radeloff, V. C., Rondinini, C., & Graham, C. H. (2017). Geography of current and future global mammal extinction risk. *PLoS One*, 12(11), e0186934. https://doi.org/10.1371/journal.pone.0186934

Diaz, S., & Cabido, M. (2001). Vive la difference: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, 16, 646–655.

Díaz, S., Settele, J., Brondízio, E. S., Ngo, H. T., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., … Zayas, C. N. (2019). Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science*, 366(6471), eaax3100. https://doi.org/10.1126/science.aax3100

Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., & Magurran, A. E. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science*, 344(6181), 296–299.

Fleming, P. A., Anderson, H., Prendergast, A. S., Bretz, M. R., Valentine, L. E., & Hardy, G. E. S. J. (2014). Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function? *Mammal Review*, 44(2), 94–108. https://doi.org/10.1111/mam.12014

Flynn, D. F. B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B. T., Lin, B. B., Simpson, N., Mayfield, M. M., & DeClerck, F. (2009). Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters*, 12(1), 22–33. https://doi.org/10.1111/j.1461-0248.2008.01255.x

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J. A., Laurance, W. F., Lovejoy, T. E., & Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 478, 378–381. https://doi.org/10.1038/nature10425

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, 8(9), 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Hastie, T. J., & Tibshirani, R. J. (1986). Generalized additive models. *Statistical Science*, 1(3), 297–310.

Hudson, L. N., Newbold, T., Contu, S., Hill, S. L. L., Lysenko, I., De Palma, A., Phillips, H. R. P., Alhusseini, T. I., Bedford, F. E., Bennett, D. J., Booth, H., Burton, V. J., Chng, C. W. T., Choimes, A., Correia, D. L. P., Day, J., Echeverría-Londoño, S., Emerson, S. R., Gao, D. I., … Purvis, A. (2017). The database of the PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) project. *Ecology and Evolution*, 7(1), 145–188. https://doi.org/10.1002/ece3.2579

Hurst, Z. M., McCleery, R. A., Collier, B. A., Silvy, N. J., Taylor, P. J., & Monadjem, A. (2014). Linking changes in small mammal communities to ecosystem functions in an agricultural landscape. *Mammalian Biology*, 79, 17–23. https://doi.org/10.1016/j.mambio.2013.08.008

IUCN. (2017). *The IUCN Red List of Threatened Species. Version 2017-3.* www.iucnredlist.org

Jackson, S. T., & Sax, D. F. (2010). Balancing biodiversity in changing environment: Extinction debt, immigration credit and species turnover. *Trends in Ecology and Evolution*, 25, 153–160.

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4, 170122. https://doi.org/10.1038/sdata.2017.122

Karger, D. N., Cord, A. F., Kessler, M., Kreft, H., Kühn, I., Pompe, S., Sandel, B., Sarmento Cabral, J., Smith, A. B., Svenning, J.-C., Tuomisto, H., Weigelt, P., & Wesche, K. (2016). Delineating probabilistic species pools in ecology and biogeography. *Global Ecology and Biogeography*, 25(4), 489–501. https://doi.org/10.1111/geb.12422

Karger, D. N., Wüest, R. O., König, C., Sarmento-Cabral, J., Weigelt, P., Zimmermann, N. E., & Linder, H. P. (2020). Disentangling the drivers of local species richness using probabilistic species pools. *Journal of Biogeography*, 47(4), 879–889. https://doi.org/10.1111/jbi.13763

Kehoe, L., Senf, C., Meyer, C., Gerstner, K., Kreft, H., & Kuemmerle, T. (2017). Agriculture rivals biomes in predicting global species richness. *Ecography*, 40(9), 1118–1128. https://doi.org/10.1111/ecog.02508

Koenig, C., Karger, D. N., Patric, W., Sandel, B., & Cabral, J. S. (2018). *Package 'probpool': An implementation of probabilistic species pools. Version:0.0.0.91.* https://rdrr.io/github/ChrKoenig/probpool/

Laurance, W. F., Sayer, J., & Cassman, K. G. (2014). Agricultural expansion and its impacts on tropical nature. *Trends in Ecology and Evolution*, 29(2), 107–116. https://doi.org/10.1016/j.tree.2013.12.001

Lessard, J.-P., Weinstein, B. G., Borregaard, M. K., Marske, K. A., Martin, D. R., McGuire, J. A., Parra, J. L., Rahbek, C., & Graham, C. H. (2016). Process-based species pools reveal the hidden signature of biotic interactions amid the influence of temperature filtering. *The American Naturalist*, 187(1), 75–88. https://doi.org/10.1086/684128

Lewis, R. J., de Bello, F., Bennett, J. A., Fibich, P., Finerty, G. E., Götzenberger, L., Hiiesalu, I., Kasari, L., Lepš, J., Májeková, M., Mudrák, O., Riibak, K., Ronk, A., Rychtecká, T., Vitová, A., & Pärtel, M. (2017). Applying the dark diversity concept to nature conservation. *Conservation Biology*, 31(1), 40–47. https://doi.org/10.1111/cobi.12723

Luza, A. L., Gonçalves, G. L., & Hartz, S. M. (2015). Phylogenetic and morphological relationships between nonvolant small mammals reveal assembly processes at different spatial scales. *Ecology and Evolution*, 5(4), 889–902. https://doi.org/10.1002/ece3.1407

Luza, A. L., Graham, C. H., & Hartz, S. M. (2019). A global database on non-volant small mammal composition in natural and human-modified habitats. *Data in Brief*, 23, 103842. https://doi.org/10.1016/j.dib.2019.103842

Luza, A. L., Gonçalves, G. L., Pillar, V. D., & Hartz, S. M. (2016). Processes related to habitat selection, diversity and niche similarity in assemblages of non-volant small mammals at grassland–forest ecotones. *Natureza & Conservação*, 14(2), 88–98. https://doi.org/10.1016/j.ncon.2016.09.003

Medan, D., Torretta, J. P., Hodara, K., de la Fuente, E. B., & Montaldo, N. H. (2011). Effects of agriculture expansion and intensification on the vertebrate and invertebrate diversity in the Pampas of Argentina. *Biodiversity and Conservation*, 20(13), 3077–3100. https://doi.org/10.1007/s10531-011-0118-9

Mori, A. S., Shiono, T., Haraguchi, T. F., Ota, A. T., Koide, D., Ohgue, T., Kitagawa, R., Maeshiro, R., Aung, T. T., Nakamori, T., Hagiwara, Y., Matsuoka, S., Ikeda, A., Hishi, T., Hobara, S., Mizumachi, E., Frisch, A., Thor, G., Fujii, S., … Gustafsson, L. (2015). Functional redundancy

of multiple forest taxa along an elevational gradient: Predicting the consequences of non-random species loss. *Journal of Biogeography*, *42*(8), 1383–1396. https://doi.org/10.1111/jbi.12514

Mouillot, D., Graham, N. A., Villéger, S., Mason, N. W., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, *28*(3), 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Murphy, G. E. P., & Romanuk, T. N. (2014). A meta-analysis of declines in local species richness from human disturbances. *Ecology and Evolution*, *4*(1), 91–103. https://doi.org/10.1002/ece3.909

Nelder, J. A., & Wedderburn, R. W. M. (1972). Generalized linear models. *Journal of the Royal Statistical Society. Series A (General)*, *135*(3), 370–384. https://doi.org/10.2307/2344614

Newbold, T., Hudson, L., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., Palma, A. D., Diaz, S.-G., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., … Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*, 45–50. https://doi.org/10.1038/nature14324

Newbold, T., Hudson, L. N., Arnell, A. P., Contu, S., Palma, A., Ferrier, S., Hill, S. L. L., Hoskins, A. J., Lysenko, I., Phillips, H. R. P., Burton, V. J., Chng, C. W. T., Emerson, S., Gao, D. I., Pask-Hale, G., Hutton, J., Jung, M., Sanchez-Ortiz, K., Simmons, B. I., … Purvis, A. (2016). Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science*, *353*(6296), 288–291.

Newbold, T., Hudson, L. N., Contu, S., Hill, S. L. L., Beck, J., Liu, Y., Meyer, C., Phillips, H. R. P., Scharlemann, J. P. W., & Purvis, A. (2018). Widespread winners and narrow-ranged losers: Land use homogenizes biodiversity in local assemblages worldwide. *PLoS Biology*, *16*(12), e2006841. https://doi.org/10.1371/journal.pbio.2006841

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Gray, C. L., Scharlemann, J. P. W., Börger, L., Phillips, H. R. P., Sheil, D., Lysenko, I., & Purvis, A. (2016). Global patterns of terrestrial assemblage turnover within and among land uses. *Ecography*, *39*(12), 1151–1163. https://doi.org/10.1111/ecog.01932

Oliveira, B. F., Machac, A., Costa, G. C., Brooks, T. M., Davidson, A. D., Rondinini, C., & Graham, C. H. (2016). Species and functional diversity accumulate differently in mammals. *Global Ecology and Biogeography*, *25*(9), 1119–1130. https://doi.org/10.1111/geb.12471

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., & Kassem, K. R. (2001). Terrestrial ecoregions of the world: A new map of life on Earth. *BioScience*, *51*(11), 933–938.

Pacifici, M., Santini, L., Di Marco, M., Baisero, D., Francucci, L., Grottolo Marasini, G., Visconti, P., & Rondinini, C. (2013). Generation length for mammals. *Nature Conservation*, *5*, 89–94. https://doi.org/10.3897/natureconservation.5.5734

Penone, C., Weinstein, B. G., Graham, C. H., Brooks, T. M., Rondinini, C., Hedges, S. B., Davidson, A. D., & Costa, G. C. (2016). Global mammal beta diversity shows parallel assemblage structure in similar but isolated environments. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1837), 20161028. https://doi.org/10.1098/rspb.2016.1028

Pfeifer, M., Lefebvre, V., Peres, C. A., Banks-Leite, C., Wearn, O. R., Marsh, C. J., Butchart, S. H. M., Arroyo-Rodríguez, V., Barlow, J., Cerezo, A., Cisneros, L., D'Cruze, N., Faria, D., Hadley, A., Harris, S. M., Klingbeil, B. T., Kormann, U., Lens, L., Medina-Rangel, G. F., … Ewers, R. M. (2017). Creation of forest edges has a global impact on forest vertebrates. *Nature*, *551*, 187–191. https://doi.org/10.1038/nature24457

Pigot, A. L., Trisos, C. H., & Tobias, J. A. (2016). Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1822), 20152013. https://doi.org/10.1098/rspb.2015.2013

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Santini, L., Di Marco, M., Visconti, P., Baisero, D., Boitani, L., & Rondinini, C. (2013). Ecological correlates of dispersal distance in terrestrial mammals. *Hystrix*, *24*(2), 181–186.

Santos-Filho, M., Bernardo, C. S. S., Da Silva, D. J., Ignácio, A. R. A., & Canale, G. R. (2016). The importance of considering both taxonomic and habitat guild approaches in small mammal research. *Austral Ecology*, *41*, 854–863. https://doi.org/10.1111/aec.12380

Sax, D. F., Kinlan, B. P., & Smith, K. F. (2005). A conceptual framework for comparing species assemblages in native and exotic habitats. *Oikos*, *108*(3), 457–464. https://doi.org/10.1111/j.0030-1299.2005.13402.x

Sobral, F. L., Lees, A. C., & Cianciaruso, M. V. (2016). Introductions do not compensate for functional and phylogenetic losses following extinctions in insular bird assemblages. *Ecology Letters*, *19*(9), 1091–1100. https://doi.org/10.1111/ele.12646

Song, X.-P., Hansen, M. C., Stehman, S. V., Potapov, P. V., Tyukavina, A., Vermote, E. F., & Townshend, J. R. (2018). Global land change from 1982 to 2016. *Nature*, *560*, 639–643. https://doi.org/10.1038/s41586-018-0411-9

Steffen, W., Richardson, K., Rockstrom, J., Cornell, S. E., Fetzer, I., Bennett, E. M., Biggs, R., Carpenter, S. R., de Vries, W., de Wit, C. A., Folke, C., Gerten, D., Heinke, J., Mace, G. M., Persson, L. M., Ramanathan, V., Reyers, B., & Sorlin, S. (2015). Planetary boundaries: Guiding human development on a changing planet. *Science*, *347*(6223), 1259855. https://doi.org/10.1126/science.1259855

Stekhoven, D. J., & Buehlmann, P. (2012). Package MissForest—Nonparametric missing value imputation for mixed-type data. *Bioinformatics*, *28*(1), 112–118. https://doi.org/10.1093/bioinformatics/btr597

Thuiller, W., Guéguen, M., Renaud, J., Karger, D. N., & Zimmermann, N. E. (2019). Uncertainty in ensembles of global biodiversity scenarios. *Nature Communications*, *10*, 1446. https://doi.org/10.1038/s41467-019-09519-w

Umetsu, F., Metzger, J. P., & Pardini, R. (2008). Importance of estimating matrix quality for modeling species distribution in complex tropical landscapes: A test with Atlantic Forest small mammals. *Ecography*, *31*(3), 359–370. https://doi.org/10.1111/j.0906-7590.2008.05302.x

Veldman, J. W., Buisson, E., Durigan, G., Fernandes, G. W., Le Stradic, S., Mahy, G., Negreiros, D., Overbeck, G. E., Veldman, R. G., Zaloumis, N. P., Putz, F. E., & Bond, W. J. (2015). Toward an old-growth concept for grasslands, savannas, and woodlands. *Frontiers in Ecology and the Environment*, *13*(3), 154–162. https://doi.org/10.1890/140270

Whitmee, S., & Orme, C. D. (2013). Predicting dispersal distance in mammals: A trait-based approach. *Journal of Animal Ecology*, *82*(1), 211–221. https://doi.org/10.1111/j.1365-2656.2012.02030.x

Wilson, J. W., Stirnemann, R. L., Shaikh, Z. S., & Scantlebury, M. (2010). The response of small mammals to natural and human-altered edges associated with Afromontane forests of South Africa. *Forest Ecology and Management*, *259*(5), 926–931. https://doi.org/10.1016/j.foreco.2009.11.032

BIOSKETCH

André Luís Luza is currently a post-Doc researcher at the Universidade Federal de Santa Maria, and is interested in macroecology, macroevolution and hierarchical modelling. This study is part of his PhD thesis. The authors combine an interest in understanding the factors that shape biodiversity and community composition.

Author Contributions: ALL, CHG, SMH and DNK contributed to the conception and design of the study; ALL and DNK collected and analysed the data; ALL wrote the first version of this manuscript; CHG, SMH and DNK contributed critically to the revision of the preliminary versions and the final version of this manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.