Research Article

Macro-ecological patterns of the endemic Afrosoricida and Rodentia of Madagascar

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Abstract

We examined the macro-ecological and species richness correlates of the endemic mammal fauna (Afrosoricida and Rodentia) of Madagascar. We divided the whole of Madagascar into 307, 50×50 km cells, and showed that there was a significantly uneven distribution of species across cells in both Afrosoricida and Rodentia, with a higher number of species per cell in the former taxon (peaks at around 19–21 species per cell in Afrosoricida versus 11–12 species in Rodentia). In each cell, the number of Afrosoricida species was positively correlated with the number of Rodentia species. Cell vegetation category affected species richness per cell in both Afrosoricida and Rodentia (evergreen forest cells had higher species richness than cells of any other type of vegetation). There was a significant effect of altitude category on species richness per cell in both Afrosoricida and Rodentia, with a confirmed Mid Domain Effect in both groups. Heterogeneity of habitat also influenced significantly and positively the species richness per cell in either Afrosoricida or Rodentia. About 15% of Afrosoricida and 28% of Rodentia are threatened according to IUCN. The distribution of threatened species of the two groups per cell showed (i) a low density of threatened species (just one species per cell in most cases) and (ii) distinct patterns for the two studied groups. Afrosoricida had two main regions where threatened species are concentrated (the evergreen forest belt in Eastern Madagascar and the deciduous broad-leaf forest in Central-Western Madagascar). Threatened Rodentia occur only in the portion of cells covered by evergreen forest, thus overlapping with part of the region where also threatened Afrosoricida occur.

Introduction

Madagascar is a unique geographical region in terms of endemism (e.g., Pearson and Raxworthy, 2009; Vences et al., 2009), and also one of the most important biodiversity hotspots because of the actual threatened status of most of its natural habitats (Myers et al., 2000). For instance, the whole Malagasy subcontinent has undergone large-scale deforestation during the last 50 years (e.g., Green and Sussman, 1009; Harper et al., 2007), and as a consequence heavy conservation threats have emerged towards its species-rich endemic fauna (e.g., Smoth et al., 1997; Andreone and Luiselli, 2003; Bollen and Donati, 2006).

Concerning mammals, the great majority of species is endemic (Garbutt, 1999, 2007), but studies exploring the macro-ecological correlates and the conservation implications of their distribution have been focusing mainly on lemurs and on other large-sized species (e.g., Smoth et al., 1997; Mittermeier and Nash, 2006; Mittermeyer et al., 2008; Gerber et al., 2010; but see also Lees et al., 1999). Studies of the same type concerning the endemic Afrosoricida and Rodentia of Madagascar are few (Lees et al., 1999). In this paper, we explore the geographical patterns of distribution of these two mammal groups. We emphasize on testing whether there are any specific nonrandom patterns explaining the current distribution of Afrosoricida and Rodentia, and on the conservation implications of the patterns observed. More specifically, we explore the habitat-related and altitude-related patterns of distribution of the various species, with an emphasis on the eventual differences between the two groups. In addition, we also offer the same type of analysis for the species which are currently listed as threatened by IUCN (2014.3; available at www.iucnredlist.org), in order to highlight whether there is any identifiable pattern that can have conservation and/or management implications.

Materials and methods

The geographical territory of Madagascar was divided into 307 cells of 50×50 km area, using Quantum GIS (Quantum GIS Development Team, 2015; freely available at http://www.qgis.org; Fig. 1). In each cell, the vegetation type was assigned by using the map available at http://www.wildmadagascar.org/maps/land_cover.html, and then transforming it to a raster and geo-referencing it. Although blocks of a given habitat were not so large than a 50×50 cell (and hence most of the cells included more than one habitat type), we assigned each cell to the vegetation type that was the most represented in the given cell. Habitat categories were categorized as follows: (1) savannah, (2) deciduous broad-leaf forest, (3) mixed forest, and (4) evergreen forest. Savannah was essentially grassy vegetation derived from pristine habitat alteration, including deforestation. Deciduous broad-leaf forest is a tropical dry forest ecoregion that is situated in the western part of Madagascar. This type of forest is characterized by high numbers of endemic plant and animal species; however it has suffered large-scale devastation due to clearance for agriculture. Mixed forests include divergent types of habitats such as spiny thickets, shrublands, and dry forests. Evergreen forests, widely distributed in the eastern side of Madagascar, consist of both broad-left and needle-leaf forest, which do not lose their leaves during the cold season.

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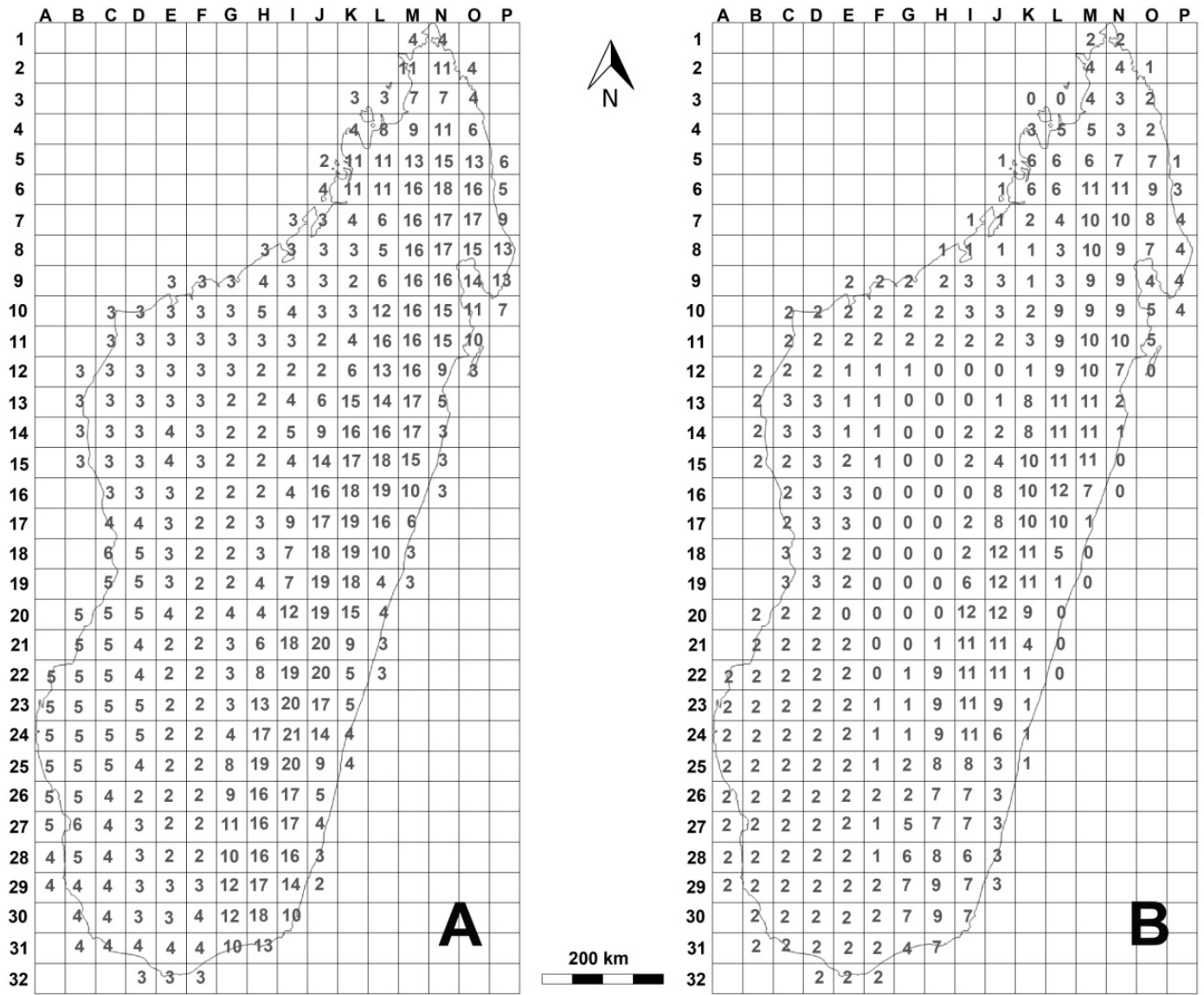*Email address:* giovanni.amori@uniroma1.it (Giovanni Amori)

Figure 1 – Map of Madagascar showing the cells used for our analyses, and the number of species present in each cell (A = Afrosoricida; B = Rodentia).
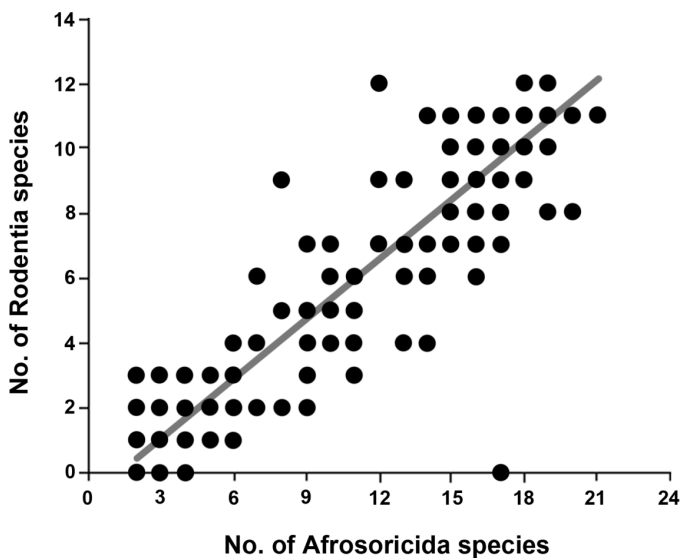

Figure 2 – Relationship between the number of Afrosoricida per cell and number of Rodentia species per cell. For statistical details, see the text.

For each cell, we also assigned the most representative category of altitude by using GIS vector data available at http://www.diva-gis.org/gdata. The categories (m a.s.l) were as follows: (1) -8–548, (2) 549–1105, (3) 1106–1660, and (4) 1661–2218. These categories were derived after exploring the frequency distribution of the various elevational zones, and considering the discontinuities as the various thresholds. Habitat heterogeneity was determined by calculating the number of habitat types within each cell, using the habitat types available in the FAO map of Madagascar available at http://www.wildmadagascar.org/maps/land_cover.html.

The list and distribution of species was compiled using Garbutt (2007) and IUCN red list maps (www.iucnredlist.org), and using also Wilson and Reeder (2005) as an integration. A few other recently described species (*Microgale grandidieri*, *M. jenkinsae*, *M. jobihely*, *Macrotarsomys petteri*, and *Vohalavo anthsabensis*) were omitted from our calculations because they are presently known from less than 5 specimens, and therefore their distribution range is not known. Also, we did not include in calculations the introduced species (e.g., *Rattus rattus*, *Rattus norvegicus*, *Mus musculus*, and *Suncus murinus*).

Inter-cell differences in the species richness for the two studied taxa were assessed by a Monte Carlo procedure of χ^2 test, with 9999 iterations. Differences inside each cell in the species richness of the two groups were assessed by Wilcoxon paired test. Correlations between number of Afrosoricida species per cell and number of Rodentia species per cell were assessed by Pearson's correlation coefficient. The
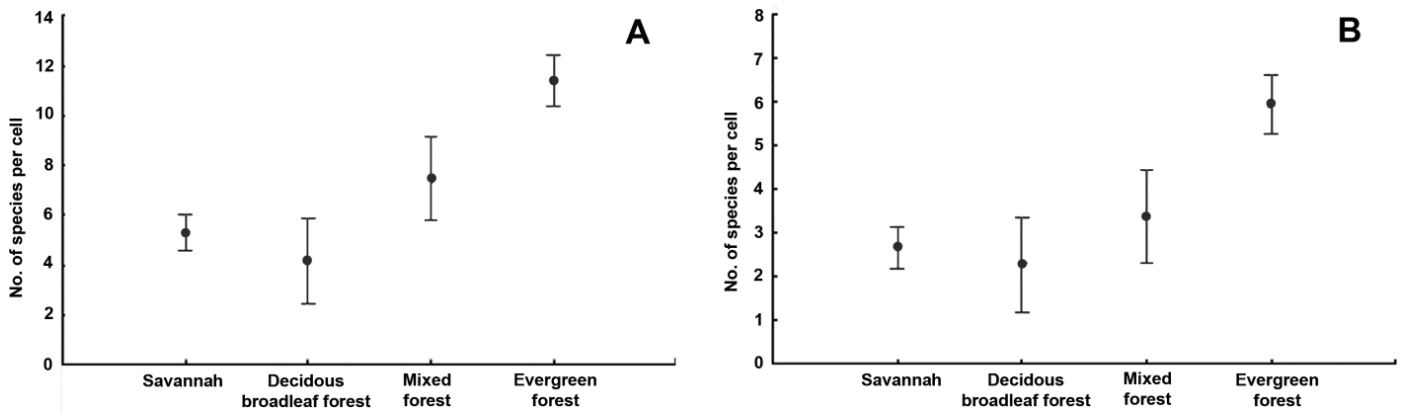
Figure 3 – Mean (and dispersion measures) of species richness per cell in relation to vegetation category in Madagascar. (A) Afrosoricida; (B) Rodentia.

effect of cell vegetation and altitude categories on species richness per cell were assessed by GLM with Poisson error structure, since counts for species richness were used, and this variable was not continuous. The correlations between heterogeneity of habitat and species richness per cell were assessed by Spearman's rank correlation coefficient. In all cases, alpha was set at 5%, and the tests were two-tailed. Analyses were performed with Statistica version 10.0 version and PAST 3 softwares.

Results

Overall, our analyses are based on a total of 27 species of Afrosoricida, 1 of Soricomorpha (*Suncus madagascariensis*) and 25 of Rodentia. As expected, there was a significantly uneven distribution of species across cells in both Afrosoricida (Monte Carlo χ^2=563.9, p<0.0001) and Rodentia (Monte Carlo χ^2=405.3, p<0.001). The number of species per cell was generally higher for Afrosoricida than for Rodentia, with peaks at around 19–21 species per cell in Afrosoricida versus 11–12 species per cell in Rodentia (Fig. 2). Indeed, deeper inspection of data revealed that, in each cell, there was a significant difference in species richness of the two groups (Wilcoxon paired test: Z=14.6, p<0.0001). The number of Afrosoricida and Rodentia species per cell were positively correlated (r=0.91, p<0.0001; Fig. 2).

Species richness per cell in Afrosoricida (Fig. 3A) was higher in evergreen forest cells than in cells with any other type of vegetation. Mixed forest cells had higher species richness than cells with savannah and deciduous broad-leaf forests. A GLM model revealed that vegetation type significantly affected species richness (mean square=677.06, df=3, F=9.081, p<0.005), as well as the interaction term vegetation type × altitude (mean square=134.66, df=11, F=10.284, p<0.0001),

whereas elevation alone did not influence species richness (mean square=235.49, df=5, F=2.84, p=0.062). Concerning Rodentia, a similar pattern was also observed (Fig. 3B). In this case, only evergreen forest cells had higher species richness than cells of any other type of vegetation, whereas all other vegetation types were similar in terms of their species richness per cell. A GLM model revealed that vegetation type significantly affected species richness (mean square=233.12, df=3, F=39.206, p<0.001), as well as the interaction term vegetation type × altitude (mean square=47.45, df=11, F=7.767, p<0.0001), whereas elevation alone did not influence species richness (mean square=71.55, df=5, F=2.396, p=0.094).

For Afrosoricida, the species richness per cell was significantly higher at 549–1105 and 1106–1660 m a.s.l. than all other categories (Tukey test, all p<0.0001; Fig. 4A), and that the 1661–2218 m altitude category cells contained significantly less species than all other elevation categories (Tukey test, all p<0.001). For rodents, the same trend was confirmed: species richness per cell was significantly higher at 549–1105 and 1106–1660 m a.s.l. than at other elevations, and lowest in cells situated at 1661–2218 m (Tukey test, all p<0.001; Fig. 4B).

Heterogeneity of habitat also influenced significantly and positively the species richness per cell in either Afrosoricida (Spearman's r=0.20, n=308, p<0.001) or Rodentia (Spearman's r=0.16, n=308, p<0.01).

A relatively low percentage of species is threatened according to latest IUCN data (about 15% in Afrosoricida and 28% in Rodentia). The distribution of threatened species of the two groups per cell (Fig. 5) showed (i) a low density of threatened species (just one species per cell in most cases) and (ii) distinct patterns for the two studied groups. Indeed, Afrosoricida had two main regions where threatened species are concentrated, i.e. a large area characterized by evergreen forest,
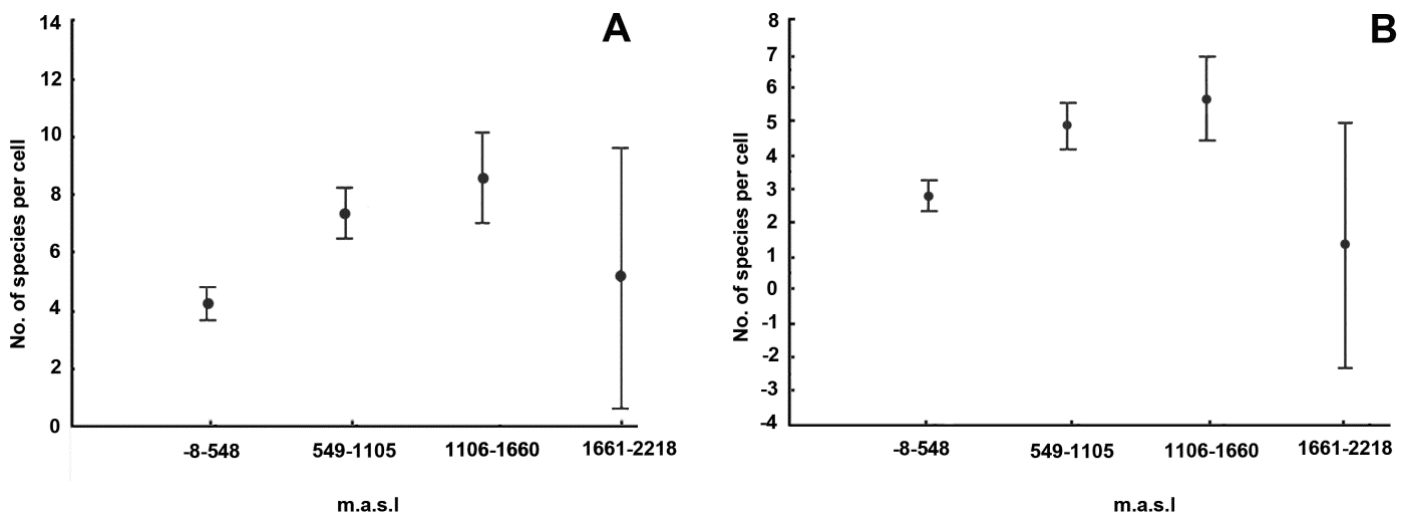

Figure 4 – Mean (and dispersion measures) of species richness per cell in relation to altitude category in Madagascar. (A) Afrosoricida; (B) Rodentia.
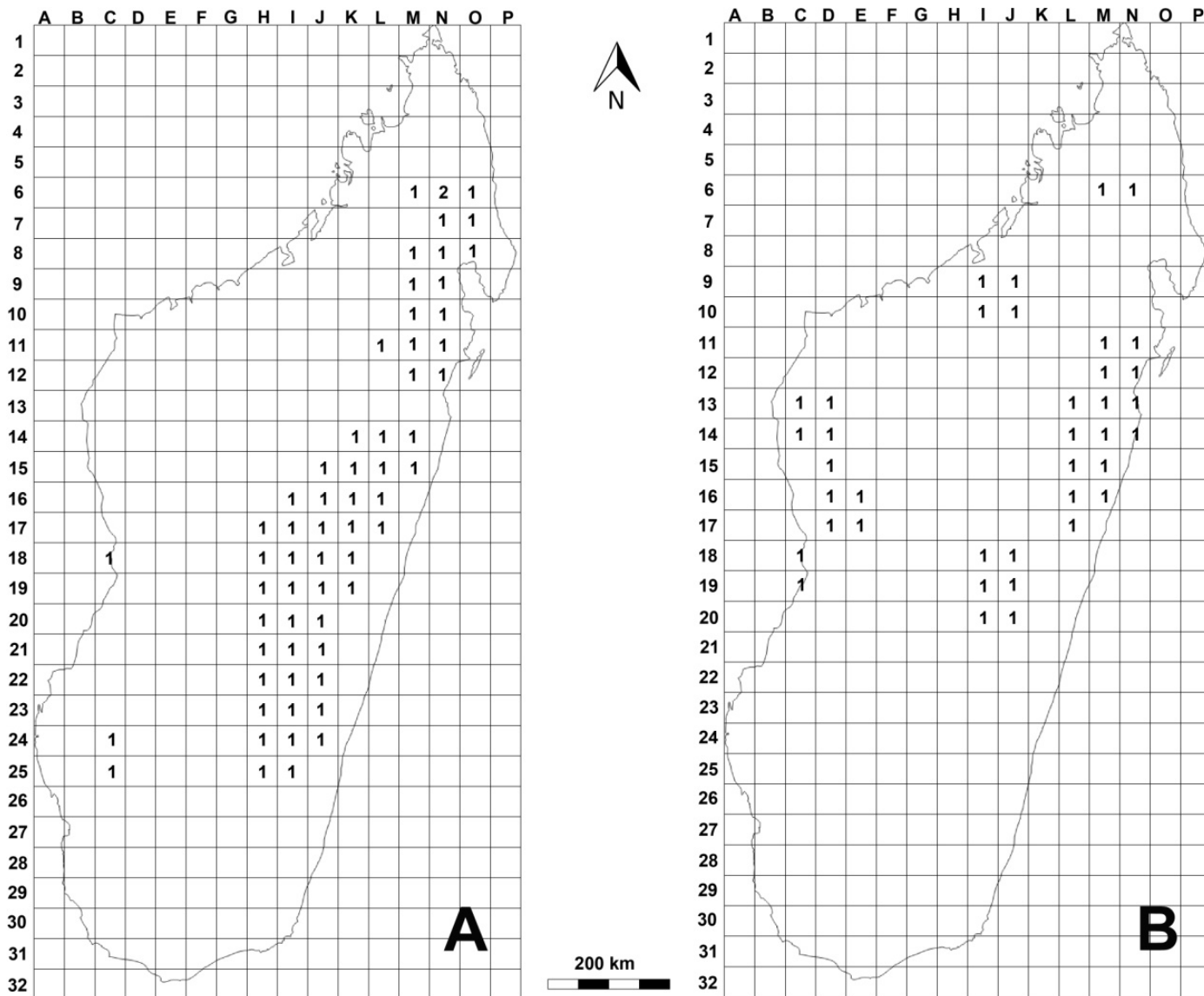
Figure 5 – Map of Madagascar showing the number of threatened species present in each cell (A = Afrosoricida; B = Rodentia). Threatened species were counted by following IUCN Red List www.iucnredlist.org.

and another main area in Central-Western Madagascar with deciduous broad-leaf forest. Conversely, threatened Rodentia occur only in the portion of cells covered by evergreen forest, thus overlapping with part of the region where threatened Afrosoricida occur (Fig. 5).

Discussion

Our study revealed several non-random macro-ecological patterns for Malagasy Afrosoricida and Rodentia, some of them being expected on the basis of available literature on other Malagasy vertebrates, but also being rather unexpected (see below). To begin with, our study showed that, despite the total species richness of Afrosoricida and Rodentia was similar at the overall scale of Madagascar (e.g., Garbutt, 1999, 2007), the number of Afrosoricida was significantly higher in each cell. This pattern may arise from the remarkable differences in the average range size of the two groups, with rodents showing significantly narrower ranges than Afrosoricida species (Amori et al., unpublished data), and, consequently, with several Afrosoricida being habitat generalists (e.g., *Tenrec ecaudatus*, *Setifer setosus*, etc). On the contrary, most of the endemic rodents of Madagascar are specialized forest-dwelling species (e.g., *Nesomys rufus*, *Brachytarsomys albicauda*; see Garbutt, 2007).

Evergreen forest cells clearly showed a higher richness of species of both orders than cells with any other type of vegetation category. However, for interpreting the above-mentioned pattern, it should be reminded that in a 50×50 km cell different habitat types can occur, thus

the results based on our method to assign habitat type must be considered with some caution. This result is clearly expected on the basis of the available literature, as tropical evergreen forests are in general among the most species-rich habitats of the whole world (e.g., Gentry, 1988; Phillips et al., 1994; Barlow et al., 2007 and later literature), and the same was also true in Madagascar. For instance, Malagasy evergreen forests represented the main species richness hotspots for such distinct animals as butterflies, frogs, chameleons and lemurs (Lees et al., 1999).

Concerning distribution along the elevation gradient of the two mammal groups, we found clear evidence that the peaks of species richness tend to occur in mid-elevation cells, especially in conjunction with forest ecosystems. We interpret this pattern as a case of mid-domain effect. According to general theory, a mid-domain effect occurs where landmass boundaries such as oceans and mountaintops limit species ranges and the simple overlap of many, variously sized ranges, create a peak in species richness at mid-elevation (Colwell and Hurtt, 1994; Colwell and Lees, 2000; McCain, 2004). Similar cases of mid-domain effect in small mammals were also documented for, e.g., the Philippines (Heaney, 2001), Borneo (Md. Nor, 2001) and in Taiwan (Yu, 1994).

Heterogeneity of vegetation per cell also affected positively the species richness per cell in both Afrosoricida and Rodentia. Also in this case, our pattern can be reconducted to an explicit theoretical ecological model that is the edge effect (Lidicker, 1999; Lettinen et al.,

2003), with the linear trend in high heterogeneity peaks supporting a hypothesis of a suite of interacting climatic/microhabitat variables influencing the pattern of biodiversity at a larger scale. As alternative hypothesis, since 2500 km² is a very large scale compared to small mammals average range size, it is possible that a cell with two different habitats should host more species than a cell with a single habitat type simply because, to the number of species common to both habitats, it can be summed the number of species living only in the first or in the second habitat.

This result is somewhat counterintuitive if we think that the evergreen forests are the most species-rich vegetation type in Madagascar, and that, therefore, cells dominated by only (large-sized) evergreen forest habitat would have been predicted to be more species rich than those with a suite of habitats (including smaller patches of evergreen forest). We think that this pattern indirectly shows that forest-specialist Afrosoricida and Rodentia do not need large forest patches to survive, but also can occur in small and fragmented patches, thus being found also in cells with a low percentage of territory being actually covered by evergreen forest.

The correlation between the number of species of the two groups per cell was likely dependent on the fact that the same main environmental variables (and especially the main vegetation zones) drive the species richness of the two groups. Indeed, evergreen forests contained by far the higher number of species per cell.

Concerning the threatened taxa, the figures relative to Afrosoricida and to Rodentia presented opposite patterns. On the one hand, there was a remarkably lower percentage of threatened taxa among Malagasy Afrosoricida (about 15% of the species) than among the whole representatives of this order (31.5%, see Amori et al., 2014). On the other hand, Malagasy rodents were remarkably more threatened in Madagascar (about 28% of the total number of species) than overall (15.9%, see Amori et al., 2014). We interpret that also these differences may reside in the higher specialization for forest habitats of Malagasy rodents compared to Afrosoricida, thus resulting in a higher global threatening risk due to the current alteration status of the Malagasy forests (e.g., Green and Sussman, 1009; Lowry et al., 1997; Harper et al., 2007). However, a shared pattern between Afrosoricida and Rodentia resides in that almost invariably only one threatened species of each group occurs in a single cell, with many cells across Madagascar housing a threatened species. The consequence of this pattern is that there is no single area of specially high conservation priority for the two investigated groups. Nonetheless, there is a need of widespread and de-centered conservation effort in order to maintain and protect the threatened Afrosoricida and Rodentia of Madagascar. In particular, it would be necessary to concentrating field efforts in evergreen forests, not only in large but also in smaller patches, in order to better explore the ecological correlates of richness distribution in these two groups of mammals. ✍

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