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# **Specific differences in habitat requirement drive responses to habitat loss and disturbance in Atlantic Forest small mammals**

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## **Abstract**

As deforestation proceeds, habitat is lost in the landscape and the human-created matrix augments. Species that differ in their habitat requirements and tolerance to disturbance should not be equally affected by habitat loss and degradation. Forest dependent species should be more affected by these effects than generalist species that can use more than one habitat type. On the other side, non-native species should benefit from environmental degradation. In this work, we compared the responses of three assemblages of small mammals (forest specialist, generalists and open area dwelling species) along a gradient of forest cover in five landscapes of the Atlantic Forest. We followed the responses of the assemblages in native forests and in non-forested matrices, observing diverse responses in adjacent environments within a forest-matrix system. As was expected, the specialists were the most affected by the loss of native habitat; they decayed considerably in richness and abundance below 35% of habitat in the landscape. Generalist species were not affected by the quantity of habitat in the forest but, conversely, they were positively affected by moderate levels of disturbance in the matrix. Open area species did not colonize the forest irrespective of coverage and they were the dominant assemblage in the disturbed, matrix environment.

**Keywords** extinction thresholds- specialization- forest- matrix- small mammals- Atlantic Forest

## Introduction

Destruction of habitat in a landscape results in loss of populations that depend on that habitat (Fahrig 2002). The number of individuals and species a region can support is a positive function of area; the species-area relationship (Williams 1964 and Simberloff 1976) and loss of species may occur as a direct consequence of area reduction or as an indirect consequence due to factors correlated with area reduction and, most importantly, fragmentation (Connor and McCoy 2004). As suitable habitat is lost in a landscape, different species will disappear at different points on the habitat loss gradient. The "extinction threshold" is the minimum amount of habitat required for a population of a particular species to persist in a landscape (Fahrig 2002). Extinction thresholds models in fragmented landscapes were derived from the theory of island biogeography (MacArthur and Wilson 1967) combined with models of metapopulations and landscape ecology. For ecological communities, such thresholds represent certain value of habitat amount below which further habitat loss leads to a disproportionate loss of species (Fahrig et al. 2003). Andrén (1994) proposed that this negative effect on biodiversity results from the interaction effect between habitat fragmentation and habitat amount when the proportion of suitable habitat in a landscape decreases below 10~30%. Above this proportion of habitat the negative effect over biodiversity could be counted as habitat loss *per se* (Andrén 1994; Trzcinski et al. 1999; Fahrig 2003).

A collateral effect of habitat loss is the rise of a new habitat (Andrén 1994). This new human-created habitat that surrounds the fragments of native vegetation is the matrix. Matrix habitat crucially influences the persistence of native species since it affects landscape connectivity (Fischer and Lindenmayer 2007). The matrix environment can act as a selective filter for the movements of species across the landscape and the type of vegetation in the matrix will determine its permeability. Matrices which are structurally similar to the original habitat are more permeable to crossing individuals than matrices with much modified vegetation structure (Gascon et al. 1999). As a result, processes leading to matrix effects can be modulated by the mobility, the migratory behavior, and the specific demands of the species involved (Dauber et al. 2003).

Consequently, not all the species present in an area are expected to be equally affected by human-induced environmental changes (Smart et al. 2006). Some species will decrease in abundance whereas others will increase. The concept of generalist and specialist strategies associated with niche breadth is a central concept in evolutionary ecology (Cockburn 1991) and the "specialization-disturbance hypothesis" (Vazquez and Simberloff 2002) predicts that specialists will be negatively affected by degradation of their habitat whereas ecological generalists should benefit from heterogeneous environments. Therefore, changes

in the landscape proportion of native habitat should affect distinctly the persistence of specialist and generalist species: as generalists use various habitat types in the landscape they should be less affected by habitat disruption than specialists which are more dependent on one or few habitat types (Krauss et al. 2004). Moreover, disturbance is usually believed to affect specialists negatively, while generalists are believed to benefit from it. Species that are habitat specialists are more susceptible to extinction (McKinney 1997) and increasing levels of habitat loss and fragmentation raise concerns about the future of many of these species (Tilman et al. 1994; Travis 2003).

Although two of the most classic theories in community ecology - Island Biogeography and Niche Theory - attempted to explain patterns of species distribution and abundance, they differ in the proposed explanation for the underlying mechanism structuring ecological communities. Island Biogeography theory assumes that all species are equal in terms of their chance of extinction and that local parameters - area and isolation of the islands - are the principal determinants of community diversity. In contrast, Niche theory considers that species are functionally different, species coexistence is facilitated by niche partitioning, and environmental heterogeneity is the principal factor determining community structure (Kadmon and Allouche 2007). The effects of habitat loss and fragmentation on species richness have usually been studied using the theory of island biogeography, however, real islands are different from fragmented landscapes in that the surrounding habitat isolating the fragments (i.e. the matrix) may be habitable to some extent (Andrén, 1994). Extinction threshold models combine ideas from landscape ecology through landscape configuration, connectivity and edges effects with classical aspects of communities in habitat islands to predict species richness and abundance. Surprisingly, only recently more attention has been paid to the development of models that integrate these theories in the understanding of species distribution patterns (for ex: Fox and Fox, 2000; Kadmon and Allouche 2007; Pardini et al. 2010; Franzén et al 2012).

The small mammals of the Atlantic Forest provide a reliable model to evaluate predictions from extinction threshold models and the effect of disturbance on species richness and abundance: they respond to habitat loss and fragmentation (Pires et al. 2002; Pardini 2004) and some small mammal species are clearly associated with mature forest, which makes them more sensitive to decline than those generalist species which can occupy altered habitat (Castro & Fernandez 2004; Utmetsu and Pardini 2007, Pardini et al 2009; 2010).

The aim of this study is to evaluate the response of small mammals along a gradient of habitat loss and disturbance integrating hypothesis derived from niche theory and extinction threshold models. To do

that, we compared three assemblages of species which vary in their habitat requirements and tolerance to disturbed habitats along a continuous gradient of vegetation cover. We classified the small mammal species by their degree of habitat specialization and we follow the curves of richness and abundance in response to changes in the proportion of forest-matrix areas at the landscape scale. We distinguished a priori three categories: specialists (an assemblage composed by tightly forest-dependent species); generalists (a group of forest species that can tolerate a certain degree of disturbance in their habitat); and a third assemblage composed by non-endemic species inhabitants of open areas.

For each assemblage, different responses to changes in the amount of suitable habitat and levels of disturbance are expected. For habitat specialist species, the hypotheses of specialization-disturbance predicts a negative response on abundance and richness as a function of forest cover decay and the extinction threshold hypotheses predicts a disproportionate response of these parameters when the amount of forest in the landscape is 10-30%. Generalist species, as they can compensate for the loss of original habitat by using the resources in the surrounding matrix (Andr n 1994; Krauss et al 2003), are expected to be less affected by habitat area than specialists (Krauss et al 2003), and have null or positive responses to habitat modification (Pardini et al 2009, 2010). Open area dwelling species, as they are invasive species from other biomes, should increase as deforestation proceeds and matrix area augments and be favored by environmental degradation and habitat disturbance (Marvier et al 2004). To evaluate these predictions, we analyzed the response of the assemblages in adjacent environments within a forest-matrix system, along a gradient of forest cover.

## **Methods**

This study is part of a multi-taxa, landscape scale project aimed to test the effects of the reduction in vegetation cover over eight ecological communities of the Atlantic Forest in the Brazilian state of Bahia. This project is carried out by a group of researchers from the Universidade Federal da Bahia-UFBA.

### *Studied biome: the Atlantic Forest*

The Atlantic Forest was one of the largest rainforests of the Americas, originally covering around 150 million ha from Brazil to Argentina. It presents highly heterogeneous environmental conditions with wide longitudinal, latitudinal and altitudinal ranges; characteristics that have favored high diversity and endemism in this biome (Ribeiro 2009). This tropical forest has been extremely reduced due to human activities and roughly 12% of the original vegetation remains (Ribeiro 2009). Most of the Atlantic Forest remnants are small

fragments (Ranta et al., 1998) isolated from each other and representing second-growth forests in early to medium stages of succession (Viana et al., 1997; Metzger 2000; Metzger et al. 2009). Due to its high biodiversity, endemism and a constant threat due to anthropogenic effects, nowadays it is considered one of the five hottest hotspots on a global scale (Myers 2000). The Atlantic Forest remaining in the state of Bahia (Brazil) is considered one of the five centers of regional endemism in the biome (Silva and Casteleti 2003). Currently, the Atlantic Forest remnants in Bahia are dominated by secondary-forest fragments surrounded by a matrix of pasture and intermixed with a variety of tree crops, including cocoa, rubber, bananas, palm oil, eucalyptus and coffee. Most of the forestland is privately owned (Saatchi et al. 2001).

#### *Studied landscapes: forest cover and anthropogenic matrix*

We sampled five landscapes located in the Atlantic Forests of Bahia state. Our sample units consisted of five areas of six-by-six kilometers with different proportions of native forest cover (5%, 15%, 25%, 35% and 45%). Each sample unit included secondary Atlantic rainforest in medium or advanced stages of regeneration and low permeability matrices (non-forested, herbaceous or shrubby areas). In order to select the sample units, we used the following procedure: first, we selected as our sampling universe the coastal strip of Atlantic Forest on the south of Todos os Santos Bay (N-S 13°00' -14°50' and E-W 39°00' - 39°30') (Fig 1), then we overlaid grids of 6x6 km<sup>2</sup> on this coastal strip and we created maps based on recent satellite images (2005-2008) from the “Atlas dos Remanescentes Florestais da Mata Atlântica” ([www.sosma.org.br](http://www.sosma.org.br) and [www.inpe.br](http://www.inpe.br)), which we used to calculate the percentage of forested area in each of the 6x6 km<sup>2</sup> squares.

In the search for our sampling areas, we controlled for some relevant variables that could potentially confound the effect of the amount of habitat on small mammals' biodiversity, including landscape variables, environmental variables, and biogeographical history. We calculated the proportion of forested and non forested area in the 6x6km landscape. At the landscape scale, we controlled the amount of forested area of the surroundings and the presence of large forest remnants, since both could act as sources of individuals, biasing abundance and richness in the sample. In all the cases we guaranteed that at least 80% of the matrix in the landscape is non-forested and non-urban, and that area covered by forest in the surroundings is equal or less than in the 6x6km landscape. That was checked for the 6x6km landscape and the 18x18km surrounding area to ensure structural similarities among scales. We also controlled for the effects of large remnants acting as source areas by using the Largest Patch Index (LPI; McGarigal and Marks, 1995), a

landscape index that informs the percentage of area in a landscape occupied by the largest patch. We discarded landscapes where the LPI index of the 18x18 km<sup>2</sup> square was higher than that of the 6x6 km<sup>2</sup> square. At the landscape scale, we controlled the permeability of the matrices involved by selecting low permeability matrices (considered as those dissimilar to the original vegetation) with no vertical strata or inferior to 2mt height, such as pastures and abandoned crops, and discarding tree plantations (cacao, pines, eucalyptus, seringueiras and capoeiras). We also controlled environmental variables that affect small mammals' community composition and capturability, such as altitude (we sampled below 800mt), seasonality (captures were restricted to dry season) and we randomized the spatial distribution of the sample units so there is no correlation between geographical position and percentage of forest cover. The biogeographical history of the small mammals' fauna was controlled by narrowing the geographical area sampled to encompass regional faunas with a common biogeographical history: latitudinally, we sampled the northern portion of the Atlantic Forest as the small mammals are a composite fauna northbound south (Costa 2003) and longitudinally it was controlled by restricting our sampling to the coastal strip, which is supposed to be a refugial area of diversity during the Quaternary (Carnaval and Moritz 2008).

That resulted in five areas of 6x6km ranging in a gradient of forest cover from 5% to 45% located in the following municipalities: Ilhéus (IOS, 5%), Presidente Tancredo Neves (PTN, 15%), Valença (VAL, 25%), Nilo Peçanha (NLP, 35%) and Camamú (CAM, 45%). Once the five areas were selected, we gridded the maps of 6x6 km<sup>2</sup> into 100 plots of 600x600 m<sup>2</sup> (Fig 2) and we classified them into forest and matrix plots. Then we raffled 8 plots of forest and 8 plots of matrix to be sampled. Prior to setting the trap lines, we validated our maps in the field. We conferred that every plot drawn in the map was in accordance with our methods criteria: forest habitat was secondary forest in medium or advanced stage of regeneration (primary forest did not occur in our landscapes) and matrix ambient was herbaceous or shrubby with no or reduced vertical structure. In the field, we gathered data to qualitatively characterize the forests we sampled: sub-canopy vegetation density, canopy height and successional stage of the forest. Density and height of the canopy not varied among landscapes (Supplementary material Appendix 1, Fig. A1 and A2), more advanced successional stages were present in more forested landscapes (Supplementary material Appendix 1, Fig. A3). We confirmed the absence of vertical structure in all the matrices. We guaranteed a minimum distance of 30mt from the trap line to the fragment edge in every case.

#### *Small Mammals captures and sampling*

We sampled rodents and marsupials in forested (For) and matrix (Mat) habitat using pitfall traps (35l) and medium size live traps similar to Sherman (8cm, 9x 9cm, 9x 23 cm) and Tomahawk (4.5cm, 9x14.5cm, 9x41cm). We extended a 100mt trap line in each sample point (sixteen by landscape, eight by habitat) with 10 pitfalls set in a serial and equidistant manner connected by a plastic drift fence of 50cm height. We placed 20 live traps on the ground (10 of each type) in a parallel line to the pitfalls in a distance of 5m. We baited the traps with a mixture of peanut butter, grains, soy, or dendê oil and sardines. We conducted one capture session of eight days in each landscape, performing a sampling effort of 3.840 trap x night per landscape and a total of 19.200 trap x night in the total study.

Trapping and handling were approved by IBAMA (license number 12023-3). All the specimens collected in this study were euthanized in a CO<sub>2</sub> chamber and will be deposited at the Museum of Zoology of UFBA. Euthanasia and handling methods followed the guidelines of the American Society of Mammalogists Animal Care and Use Committee. We identified small mammals to species-level following literature and consulting the specialists Yuri Leite and Leonora Costa from Universidade Federal do Espírito Santo.

### *Data Analysis*

#### *Species' classification*

For the subsequent analysis of the effect of habitat change on small mammals' distribution, we classified the species by the degree of habitat specialization according to the habitat use and tolerance to human-created disturbance. We follow the classification criteria of specialist and generalist species by Pardini et al (2009). This study classified small mammal's species as specialists and generalists using the criterion that specialist species are those dependent on humid forests and geographically restricted in relation to the major biomes, and generalists are species associated with anthropogenic habitats. This classification assumes that species that are restricted to forest at larger spatial scales are also more dependent on forest on a local scale. We followed this classification and included an additional criterion: the sensitivity to fragmentation and matrix tolerance that is still consistent with the former principles and might be useful to refine and better detect the effects of habitat change on each assemblage.

Therefore, we used information of species' biogeography (biome of endemism), habitat use (habitat of captures and abundances by habitat type), and tolerance to human-created disturbances (occupation and abundance in the matrix, fragment edges, degraded forests and open areas) to distinguish between the assemblages (See Online Resource S1). In all cases we used the information provided by the authors on



what type of habitat a species prefers (generally, preferred habitat is that where most captures occurred) and about its tolerance to fragmentation and anthropogenic matrix. Species' sensibility to fragmentation is considered by this literature to be directly related to data of presence/absence and abundance in small fragments and fragment edges, and matrix tolerance is measured as the capacity to traverse or occupy this habitat.

#### *Analysis of curves of response*

To assess the effects of changes in the proportion of suitable habitat on small mammals' species we followed the curves of abundance and richness of the assemblages of generalist, specialist, and open area-dwelling species along a gradient of native forest decay (45% to 5%). Abundance is considered to be the number of individuals. Richness is analyzed as number of species recorded.

## **Results**

#### *Trapping results and species assemblages*

A total of 242 individuals of 24 different species were captured: 10 species of marsupials (69 individuals) and 14 species of rodents (173 individuals). Marsupials were more abundant in the forest (54 individuals) than in the matrix (15 individuals) and the opposite occurred for rodents (55 and 118 individuals respectively). Six out of 24 species were captured exclusively in the forest: *Hylaeamys laticeps*, *Metachirus nudicaudatus*, *Trinomys setosus*, *Didelphis aurita*, *Rhipidomys mastacalis* and *Micoureus demerarae*; while eight species were captured exclusively in the matrix: *Necomys lasiurus*, *Cerradomys vivoi*, *Criptonanus agricolai*, *Monodelphis domestica*, *Nectomys squamipes*, *Pseudoryzomys simplex*, *Holochilus brasiliensis* and *Cavia aperea*. Ten species were captured in both habitats: *Akodon cursor*, *Didelphis albiventris*, *Oxymycterus dasythrycus*, *Oligoryzomys nigripes*, *Marmosa murina*, *Monodelphis americana*, *Euryoryzomys russatus*, *Marmosops incanus*, *Gracilinanus microtarsus* and *Rattus rattus*. (Fig 2).

Our records include 14 of the 20 species of small mammals previously recorded in preserved forests of the Una Biological Reserve, in the state of Bahia (Pardini 2004), two species that were not recorded by that study (*T. setosus* and *O. dasythrycus*), plus eight species found exclusively in matrix habitats with no or rare records in forest fragments in the region (Moura 2003; Pardini 2004). The species captured were classified as specialists (seven species, 88 individuals), generalists (ten species, 73 individuals) and open area dwellers (seven species, 81 individuals) (Table 1, Fig 2) following the criteria mentioned above (Supplementary material, Appendix 2).

### *Comparison of the assemblages' responses in forest and matrix environments*

Although our sample numbers are small to fit in statistical analysis, conveniently, our sampling design is patronized and symmetrical allowing us to make comparisons through the curves of response.

In the forest, abundance of specialist species declined as function of forest cover reduction and dropped rapidly in a range of 45-25% to reach a stable plateau of low abundance at low forest cover (25-5%) (Fig 4A). Richness showed a similar pattern along the gradient (Fig 4B), although the decrement in the number of species started in 35%, to reach a stable plateau of low richness at 15-5%. Thus, the number of specialist individuals began to decline before the number of species by the effect of the reduction in habitat amount. In a range of 20% of forest cover, abundance of specialists dropped almost four times (from 34 to 9 individuals) (Fig4A) and the number of species declined three times (from 6 to 2 species) (Fig 4B). Generalist species in the forested habitat showed no effect in abundance or richness as function of forest cover (Fig 4A and 3B). Indeed, the number of individuals and species remained low and constant along the gradient of forest cover. Open area-dwelling species were absent in the native habitat and did not penetrate into the forest independently of coverage (Fig 4A and 3B). This result is notable, since indicates the adjustment of our species' classification and the strong association of these species to habitats in open areas. In fact, this assemblage was clearly segregated from forest-dwelling species.

In the matrix we found a different response: the assemblage of specialists were less rich and abundant, being present only in the matrices of more forested landscapes (35-45%) and absent in matrices of low forested landscapes (5-25%) (Fig 4C and 4D). Furthermore, the presence of specialists in the matrix coincides with the portion of the habitat axis where the assemblage retains high values of richness and abundance in their native habitat (35-45%, Fig 4A and 4B). Below 35% of remaining habitat, no individuals were found in the matrix. In addition, when we compared the curves of response of specialists in the matrix (Fig 4C and 4D) and in the forest (Fig 4A and 4B), we found largely lower values of abundance and richness in the matrix (6 individuals, 2 species) relative to the forest (82 individuals and 6 species), suggesting that the disturbed habitat environment resulted in a less suitable habitat for this assemblage. When the degree of disturbance increased (low forested landscapes) specialists resided only in the forests (Fig 4C and 4D).

The assemblage of generalist species was more abundant in the matrix (46 individuals) than in the forest (27 individuals), and the same occurred for richness (maximum number of species in the matrix was 6 and in the forest was 3). Thus, the total numbers of generalists in the disturbed environment augmented when compared to native habitat, revealing that the matrix can harbor abundant and rich assemblages of

generalist species. Contrary to what happened in the forest, where generalists were not affected by forest loss (Fig 4A and 4B), abundance and richness of generalists in the matrix responded along the gradient (Fig 4C and 4D). We found that the number of species and individuals of generalists in the matrix declined at low forest cover, where almost no generalists persisted, whereas the matrices of intermediary and high levels of forest (25-45%) harbored specious and abundant assemblage of generalists. Moreover, the observed curve of richness in the matrix presents an interesting result (Fig 4D): the number of species of generalists reached a maximum value at intermediate coverage (35%), with low number of species both at low (5%) and high (45%) forest cover. Therefore, the richness of generalists was the highest in the matrix of moderately disturbed landscapes. For abundance, this result was less pronounced due to high numbers of individuals in the matrix of 45% (Fig 4D), although this value corresponds to a unique species (*A. cursor*).

In conclusion, there are two remarkable observations regarding the response of generalists in the matrix: first, the assemblage was affected by landscape forest cover and level of disturbance in the anthropogenic matrix, whereas in the native habitat they showed no effect. Second, there was a peak of richness in the matrix of intermediate forest cover (and moderate disturbance). With respect to open area-dwelling species, they were the most abundant and rich assemblage present in the matrix (Fig 4C and 4D), which reveals that these introduced and non-endemic species were successful in colonizing open areas of the Atlantic Forest. The curves of abundance and richness appeared to fluctuate along the gradient, showing a less defined pattern.

#### *Richness and abundance across landscapes*

Considering the small mammal assemblages independently of habitat type (Fig 5A and 5B), we observed that total numbers of individuals and species were low in low forested landscapes (5-15%) and then increased as function of the amount of forest (25-45%), reaching a peak in richness and abundance at intermediary forest cover (35%). When we analyze the response of each assemblage along the gradient, considering the whole landscape and disregarding matrix and forest environments, the curves indicate that i) specialists were the most negatively affected by the loss of forest, ii) generalists showed a pattern of maximum richness and abundance at intermediary forest amount, and iii) open areas species were not affected along the gradient.

As a general result, when we consider all the species of small mammals across the portion of Atlantic forest sampled by this study, the community was sensitive to habitat loss and disturbance along the gradient, responding negatively to the decrement in native habitat proportion and positively to the increment

of landscape diversity at intermediary coverage. Remarkably, some information may remain veiled when responses in natural and disturbed environments are not differentiated (ex: the response of generalists differed among habitats).

## DISCUSSION

In this work we show the responses of three assemblages of small mammals to changing levels of habitat loss and disturbance and the interaction of these species with an adjacent environment in a forest-matrix system. We integrate the responses of species that vary in their habitat requirements and tolerance to disturbance in a whole-landscape approach. We see that the effect of the reduction of native habitat varies among assemblages and environments (Fig 4). As was expected, specialists were the most affected by the loss of native habitat; they declined considerably in richness and abundance below 35% of habitat in the landscape. Generalist species were not affected by the quantity of habitat in the forest, but conversely, they were positively affected by moderate levels of disturbance in the matrix. Open area species did not colonize the forest irrespective of coverage and they were the dominant assemblage in the disturbed, matrix environment.

### *Effects of Habitat Loss and Disturbance on Specialist Species*

In Atlantic Forest landscapes, low forested areas harbored considerably fewer species and individuals of tightly forest dependent small mammals. Along a continuous gradient of habitat loss, habitat specialists dropped abruptly in richness and abundance when the percentage of habitat decayed below 35%. Habitat specialist small mammals were capable of spilling out from the forest into the matrix when the assemblage is still rich and abundant (45-35%), but below 35% of forest cover the assemblage declines and the remaining specialists persist only in the forests. This abrupt response of specialists at 35% of forest cover is in accordance with a critical threshold of 30% habitat cover proposed by Andr  n 1994.

If species' abundance is only affected by the amount of habitat in the landscape, then those species should decline in exact proportion to habitat loss (Swift and Hannon 2010). The pattern of decline of specialist small mammals revealed that when 20% of the habitat is lost at critical levels of habitat coverage (25-45%) the abundance and richness of specialist species declined disproportionately, populations became four times smaller, and only one third of the species persists. Several studies on extinction thresholds had proposed that this disproportionate effect should result from the complementary effects of habitat loss and

fragmentation at low levels of habitat. Critical thresholds in habitat proportion are of relevance for biodiversity conservation (Lindermayer and Luck 2005) and the effectiveness of management projects for enhancing biodiversity should be greatest at intermediate of vegetation cover (Pardini et al 2010).

#### *Effects of Habitat Loss and Disturbance on Generalist Species*

In our work, generalist small mammals presented interesting responses. This group of species responded differently to forest reduction and disturbance: while they showed no effect in richness or abundance along the gradient of forest cover in the native environment, they responded positively to intermediate levels of disturbance in the anthropogenic matrix. As it has been hypothesized, generalists should be strongly affected by surrounding landscape diversity (Jonsen & Fahrig, 1997), whereas specialists should be more affected by habitat area (Krauss et al. 2003). Indeed, previous studies predict for generalist species to be not affected or positively affected by habitat loss (Pardini 2010) or to benefit from heterogeneous environments (Futuyma and Moreno 1988, Kassen 2002, Marvier et al. 2004). This study supports those predictions and showed that generalist small mammals can respond in both manners: that was unveiled when we separate the responses in adjacent environments within the forest-matrix system.

As was noted above, generalist species should benefit from heterogeneous environments. In a multi-taxa study aimed to evaluate the role of forested low-contrast matrix habitats in the Atlantic Forest, Pardini et al (2009) found that the conversion of mature forest results mainly in a proliferation of disturbance-adapted native species. In our study, the response of generalists in the matrix concurs with those results: generalists proliferated in the disturbed environment and this response was more pronounced for richness at intermediary levels of vegetation cover, where landscapes can be structurally more heterogeneous (see below). As a corollary, our results are aligned with the prediction that generalists should be less affected by habitat degradation than specialists (Krauss, et al 2003; Brouat et al. 2004; De Victor et al 2008); habitat heterogeneity could have a more important role in regulating generalist species than native habitat amount.

#### *Effects of habitat loss and disturbance on open area-dwelling species*

In this work, open area-dwelling species were all non-endemic species, strongly associated to open country areas and highly tolerant of human-created disturbances (Supplementary material, Appendix 2). Most of these species are endemic to open Brazilian biomes like Cerrado and Caatinga or cosmopolitan species (*R. rattus*). Open area dwelling species were the dominant assemblage in the matrix environment of

Atlantic Forest landscapes, whilst they were not recorded in native forests. High numbers of species and individuals of these species in human-created open areas indicate that they proliferated in modified landscapes. Theory pointed out that the proportion of matrix in a landscape should control the propagation of disturbances and invading species (Turner et al.1989), However, our results indicate that the amount of matrix has no effect over these species which showed a oscillating pattern in richness and abundance along the gradient. We suggest that other factors than matrix area could be regulating these populations.

We found that open area-dwelling species did not penetrate into the forest, independent of the amount of forest in the landscape. This result is unexpected since invasive species are considered a major threat to the persistence of endemic species and their presence in native habitat are often a symptom of additional conservation problems such as habitat destruction, disturbance, and fragmentation (Marvier et al 2004). Certainly, we found a strong segregation among open area and forest dwelling species. This strong segregation in assemblages concur with the finding of Umetsu and Pardini (2007) and other studies suggesting that a strong habitat association and a clear segregation between open habitats and forests may be the rule among tropical small mammal assemblages.

#### *All species responses along gradients of habitat loss and disturbance*

In his seminal work, Andrén (1994) predicted that the total species diversity across habitats in a landscape may increase when new patches of habitat are created since new species may be found in these new habitats, even if they are human-made. Although we have not measured habitat configuration, in real landscapes (Fig 2) the process of fragmentation and habitat loss would come together. As habitat is lost in the landscape, the process of habitat fragmentation goes on, resulting in more patches of smaller area and more isolated from each other (Andrén 1994; Fahrig, 2003). Landscapes at intermediary coverage retain more number of patches and total area of edges than either low or high covered landscapes, due to the non-linear relationship among habitat amount and landscape geometry (Andrén 1994; Fahrig, 2003). In this way, landscapes intermediately forested have more structural diversity, including more number of different habitat types or more equally represented types of habitat (Jonsen and Fahrig, 1997). Therefore, our results may fit Andrén's prediction (Fig 5): the number of small mammals' species was the highest at intermediary forest cover where the number and types of habitat in the landscape is elevated and well represented.

## CONCLUSIONS

Our work follows the guidance of those studies that highlight the importance of integrating approaches to understand the effects of human-induced changes on biodiversity. Here we recognize how processes in the matrix contribute to patterns of species responses in the whole system. In Atlantic Forest landscapes, the effect of deforestation affected primarily habitat specialist small mammals and disturbance favored generalists when the amount of forest cover in the landscape is at intermediary levels.

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Supplementary material (Appendix 1 and 2 at <[www.oikosoffice.lu.se/appendix](http://www.oikosoffice.lu.se/appendix)>). Appendix 1–2.

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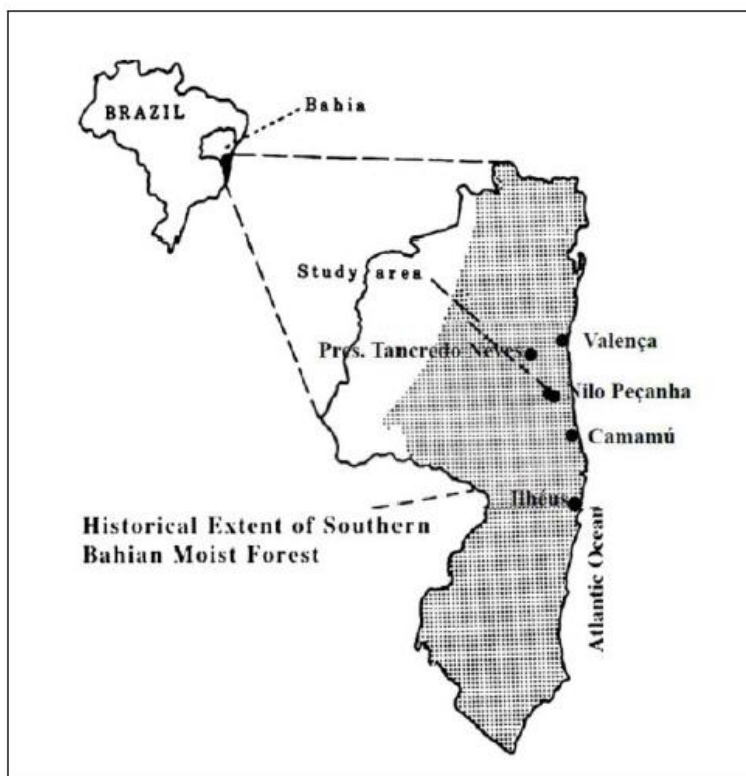
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SPECIES	ORDER	Endemism to Atlantic Forest Biome	Habitat use
FOREST SPECIALISTS			
<i>Trinomys setosus</i>	Rodentia	endemic	forest dweller
<i>Marmosops incanus</i>	Didelphimorpha	endemic	forest dweller
<i>Monodelphis americana</i>	Didelphimorpha	endemic	forest dweller
<i>Euryoryzomys russatus</i>	Rodentia	endemic	forest dweller, preference for preserved areas
<i>Hylaeamys laticeps</i>	Rodentia	endemic	forest dweller
<i>Oxymycterus dasythrycus</i>	Rodentia	endemic	forest dweller
<i>Metachirus nudicaudatus</i>	Didelphimorpha	nonendemic	forest dweller
FOREST GENERALISTS			
<i>Didelphis albiventris</i>	Didelphimorpha	nonendemic	open areas, urban centers, disturbed forests
<i>Rhipidomys mastacalis</i>	Rodentia	endemic	forests and plantations
<i>Akodon cursor</i>	Rodentia	nonendemic	open areas, degraded forests
<i>Holochilus brasiliensis</i>	Rodentia	nonendemic	open areas and forests
<i>Oligoryzomys nigripes</i>	Rodentia	nonendemic	open areas, plantations, forests
<i>Gracilinanus microtarsus</i>	Didelphimorpha	endemic	forests and open areas
<i>Micoureus demerarae</i>	Didelphimorpha	nonendemic	forests and disturbed areas
<i>Marmosa murina</i>	Didelphimorpha	nonendemic	forests and disturbed areas
<i>Nectomys squamipes</i>	Rodentia	nonendemic	forest and disturbed areas
<i>Didelphis aurita</i>	Didelphimorpha	endemic	forests and disturbed areas
OPEN AREA DWELERS			
<i>Cryptonanus agricolai</i>	Didelphimorpha	nonendemic	open areas
<i>Monodelphis domestica</i>	Didelphimorpha	nonendemic	open areas
<i>Necomys lasiurus</i>	Rodentia	nonendemic	open areas
<i>Cerradomys vivoi</i>	Rodentia	nonendemic	open areas
<i>Cavia aperea</i>	Rodentia	nonendemic	open areas
<i>Pseudoryzomys symplex</i>	Rodentia	nonendemic	open areas
<i>Rattus rattus</i>	Rodentia	nonendemic, introduced	open areas, urban centers
TOTAL SPECIES: 24			

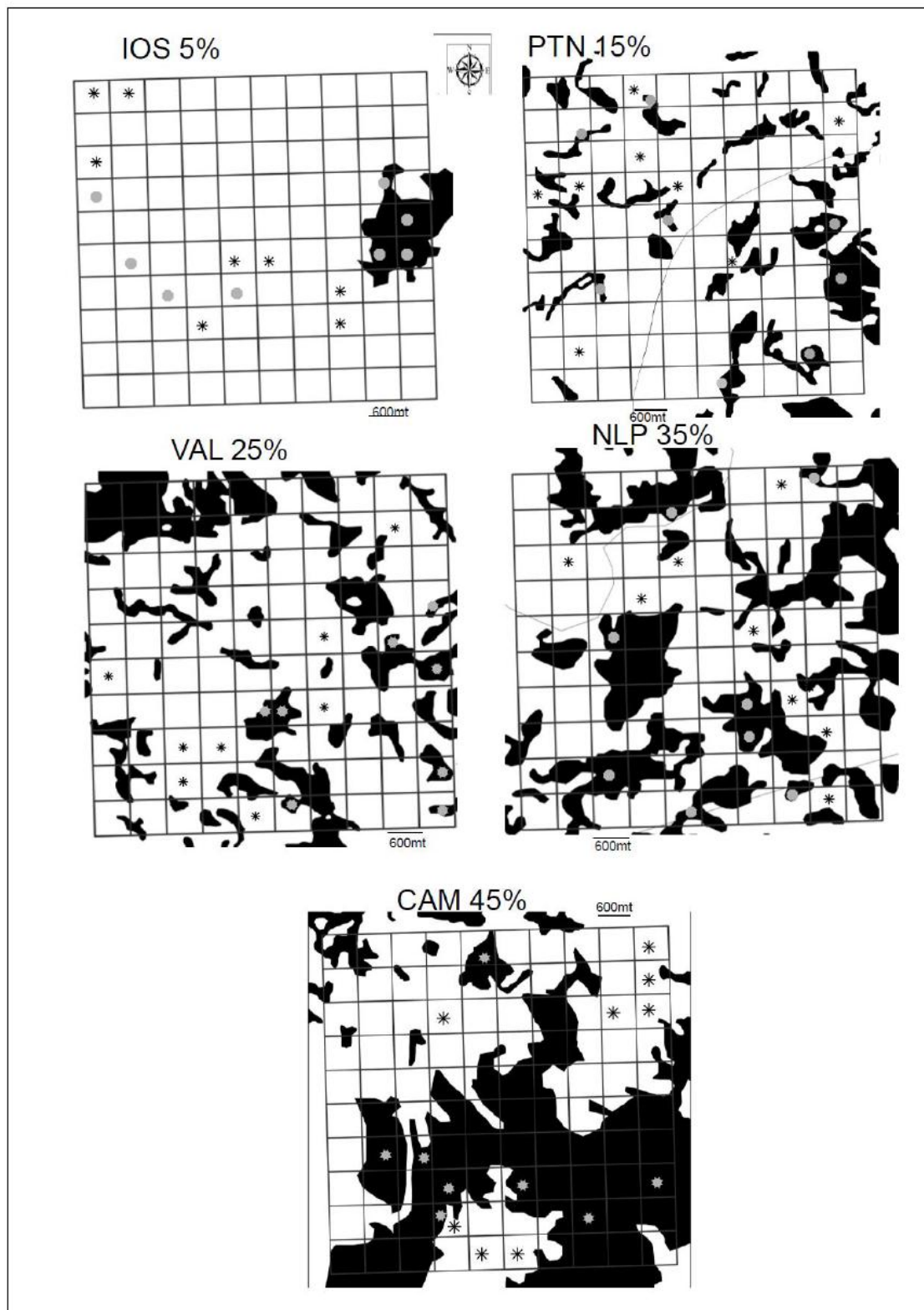
Table 1: List of species recorded in this study. Species were classified into specialists, generalists and open area-dwelling species according to their habitat use, tolerance to human-induced disturbances and endemism (see text and S1 for more details).

## FIGURES



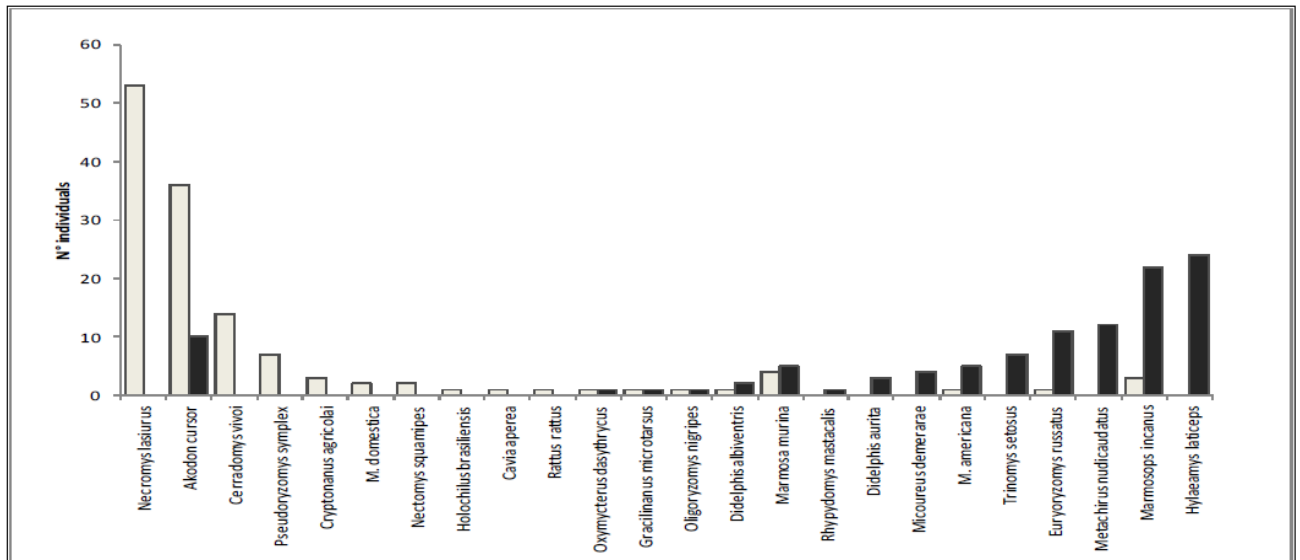
**Figure 1**

Figure 1: Map of Brazil, showing the state of Bahia and detailed map of coastal Bahia with the six localities sampled (from north to south, localities and forest cover by landscape): Valença 25%, Presidente Tancredo Neves 15%, Nilo Peçanha, 35%, Camamú 45% and Ilhéus 5% (modified from Saatchi et al 2001)



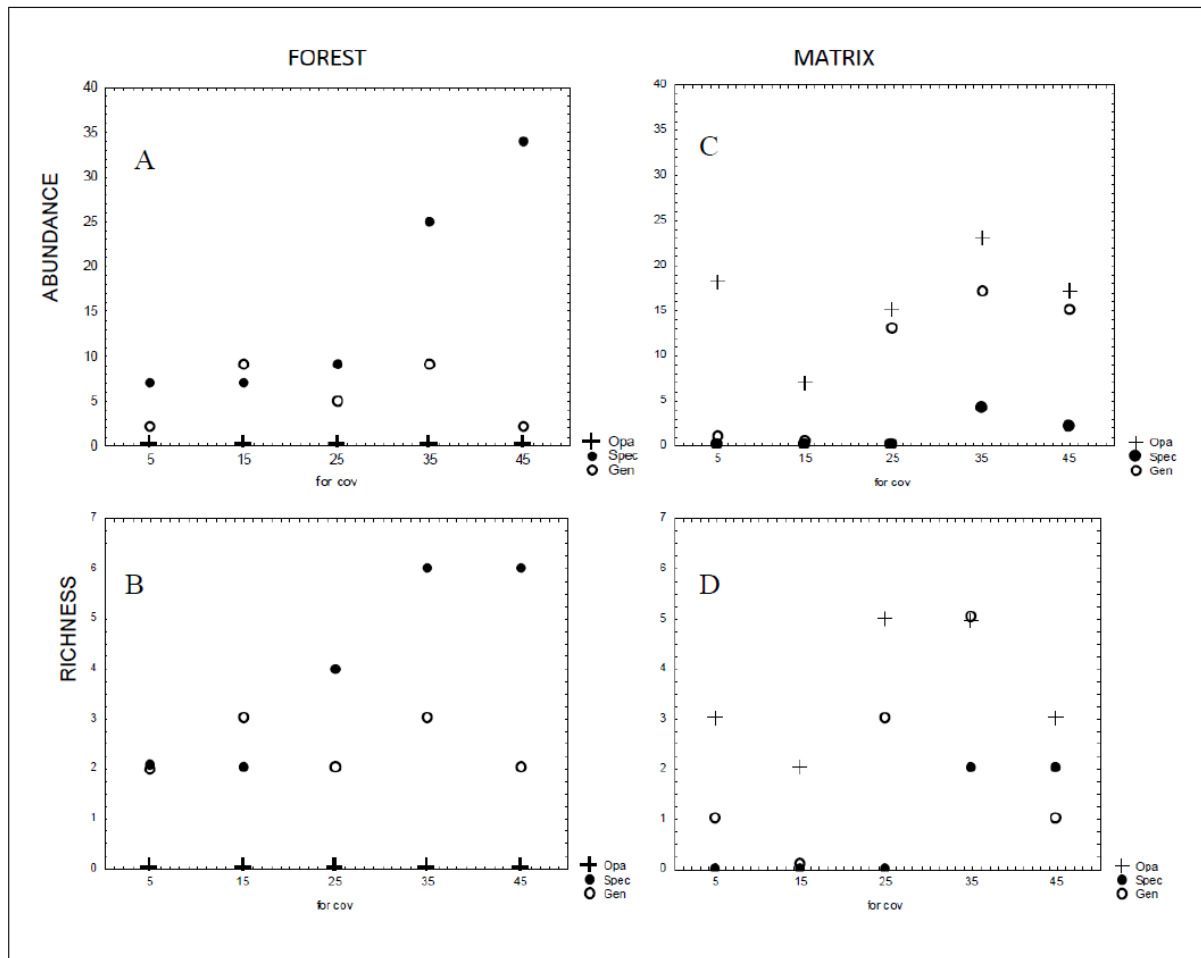
**Figure 2**

**Figure 2:** Maps of the six sampled landscapes showing forest remnants (in black) and matrix (in white). Sampling points of each landscape are shown, eight for the forest (gray dots) and eight for the matrix (black stars).



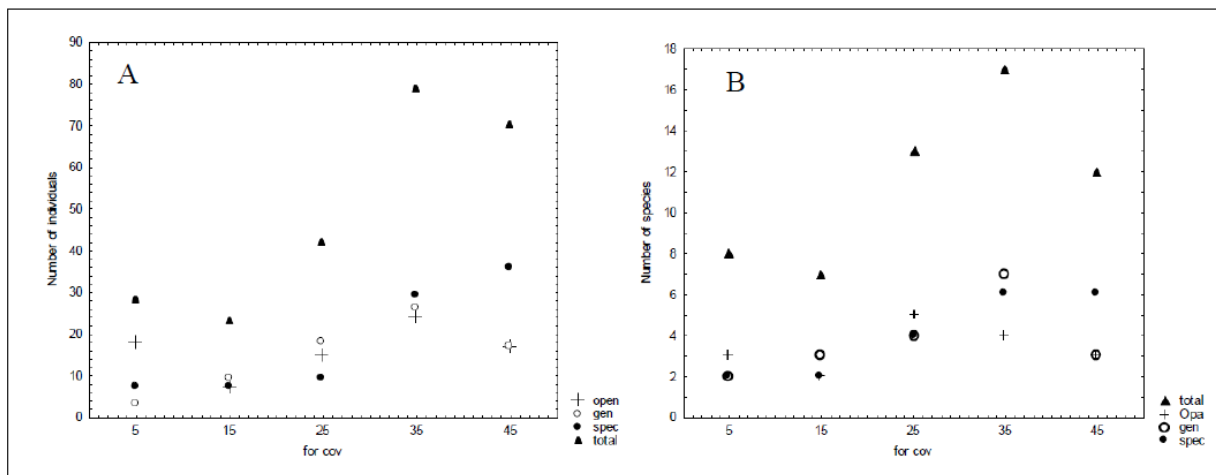
**Figure 3**

**Figure 3:** Number of individuals of each species captured in the forest (black bars) and in the matrix (open bars). The axis of the species was ordered by abundance per habitat so the species more common in the matrix are stacked on the left side of the x axis and species common in the forest are on the right



**Figure 4**

**Figure 4:** Number of individuals and species by landscape and habitat of the three assemblages of small mammals along a gradient of forest cover. Specialists (Spec) black dots; Generalists (Gen) white dots; Open area dwellers (Opa): crosses. A: abundance in the forest habitat; B: richness in the forest habitat; C: abundance in the matrix and D: richness in the matrix



**Figure 5**

**Figure 5:** Number of individuals (A) and species (B) of small mammals present by landscape along a gradient of forest cover (irrespective of the habitat of occurrence). Specialists (Spec) black dots; Generalists (Gen) white dots; Open area dwellers (Opa): crosses: Total: black triangles.



## Online Appendix 2

### **Review of Small Mammal species of the Atlantic Forest: endemism, geographical distribution, habitat preference and sensitivity to human-induced disturbances**

#### ***Euryoryzomys russatus:***

This rodent species is endemic to the Atlantic Forest. It is distributed from Brazil to Argentina and occurs in the Atlantic Forest and transitional areas of Cerrado and Pampas. It is a forest species, being abundant in continuous forest and scarce in fragments and is absent in degraded landscapes, fragment edges and plantations. The species is negatively affected by fragmentation (Rossi et al 2011), as was less common in fragmented than in continuous forest (Umetsu and Pardini 2007). Because of its negative response to anthropic disturbs, low capacity to occupy altered areas and high abundance in continuous forests, it has been pointed out by Rossi (2011) as an environmental indicator, since its presence indicates rich communities. They feed on fruits and invertebrates, nocturnal, with terrestrial habits.

#### ***Hylaeamys laticeps:***

This is an endemic rodent species to the Atlantic Forest. The geographic distribution of the species is narrow, occupying a portion of Atlantic Forest from Bahia to Rio de Janeiro. The species was formerly known as *Oryzomys laticeps*. Weksler et al. (2006) recently reviewed the genus *Oryzomys* and ten new genera arose, including *Hylaeamys spp.* which is considered as one of the most complex of the Sigmodontinae subfamily. In fragmented landscapes of the Atlantic Forest, its abundance was lower in the forested matrix compared to mature forest (Pardini et al 2004). It is cited in the IUCN Red List as Near Threatened because is confined to an altered piece of the Atlantic Forest.

#### ***Marmosops incanus:***

This species is endemic to the Atlantic forest. It is considered as a member of the forest fauna and also may occur in areas of Cerrado and semideciduous forest. It is strongly associated to forests, with no records of captures in open areas. This marsupial is abundant in continuous forest and fragments. It is common forest interiors and its abundance decreased at edges (Pardini et al 2004). This species was pointed out as an

excellent environmental indicator by Rossi (2011) since it responds negatively to deforestation and fragmentation, has a low capability to occupy disturbed areas and high abundance in continuous forests. They are insectivorous-omnivorous with escansorial habits.

### ***Oxymycterus dasytrichus***

This rodent is endemic to the Atlantic Forest. Occurs in the Atlantic Forest region of Brazil, including Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo states, but it was also registered in transitional areas of Cerrado. It was present in continuous and secondary forest with no records in open areas, disturbed ambient or fragment edges. Rossi et al (2011) classified this forest species as sensible fragmentation due to its absence in degraded forest. They feed on insects and have semi-fossorial habits.

### ***Monodelphis americana***

This marsupial species is endemic to the Atlantic forest. The species occurs in eastern Brazil from Pará to Santa Catarina (Wilson and Reeder 2005). It is common in forested areas of the Atlantic forest and gallery forest of Cerrado (Johnson et al. 1999). This species is clearly associated with mature Atlantic Forest being more abundant in mature forest than corridors (Pardini et al 2005). In the Atlantic Forest landscapes its abundance was lower at edges compared to interiors (Pardini et al 2004), and was more common in continuous compared to fragmented forest (Umetsu and Pardini 2007). The species is sensible to fragmentation and absent in degraded forest (Rossi et al 2011). They are insectivorous-omnivorous, semi fossorial and probably diurnal.

### ***Trinomys setosus***

This rodent species is endemic to the Atlantic Forest. In Brazil is distributed from the state of Sergipe to Espírito Santo and east of Minas Gerais. It occurs in Bahia coastal and interior forests. Aspects of the biology and distribution of the species are poorly known, but for the genus *Trinomys* available information indicates that they are typical of the Atlantic Forest biome being absent in degraded and isolated forest fragments (Attias et al, 2009). They are nocturnal, solitary and terrestrial, with a diet based on seeds, fruits, fungi and insects.

### ***Rhipidomys mastacalis***

This species is an endemic rodent to the Atlantic Forest. Occurs from north-eastern Brazil to Espírito Santo, in the Atlantic forest and transitional areas of Atlantic Forest and Cerrado. In the Atlantic Forest it was more abundant at edges than forest interiors and more common in forested matrices than mature forest fragments (Pardini 2004). They are nocturnal, frugivores and arboreal, but they can use all forest strata.

***Metachirus nudicaudatus:***

This marsupial occurs in the Atlantic forest, Amazonia and Cerrado (Reis et al 2011). It is widely distributed throughout South America, from Mexico to Argentina. It occurs in primary and secondary evergreen forests, occasionally in deciduous forests. Studies of *Metachirus* in Brazil suggest that the species is locally rare in the forests where it occurs. They prefer mature forest with open undergrowth (Emmons, 1999), although, due to their capacity to transverse long distances, Pires et al (2002) considered them as matrix tolerant. In the Atlantic Forest, Stevens & Husband (1998) did not find the species within 80m of forest edge and they avoided farmland matrix. They are affected by fragmentation (Reis et al 2011). They are nocturnal, terrestrial and solitary with omnivorous diet, preponderantly insectivorous. The taxonomy of this species needs revision since molecular data can reveal more than one species for the genus (Brito, 2004).

***Didelphis aurita:***

This is a marsupial endemic to the Atlantic Forest, with a wide distribution across the biome. It occurs in coastal Brazil, from Bahia to Rio Grande do Sul, eastern Paraguay and northeastern Argentina. It is characteristic of Atlantic Forest, but it also occurs in Cerrado. It is found in primary and secondary forests, is abundant in fragments and degraded forests. In Atlantic Forest landscapes, although not captured in matrix habitats, increased in abundance in low forested and high altered habitats (Umetsu et al 2008). They can use resources associated with human activities and benefit from altered habitats (Umetsu et al 2008). It is a habitat generalist species with no clear preference on forest quality and is tolerant to disturbed ambient. They are nocturnal, use different vertical strata and have an omnivorous and opportunistic diet.

***Marmosa murina:***

This marsupial occurs in the Atlantic Forest, Amazonia, Pantanal and Cerrado biomes (Fonseca et al 1996). It is distributed from Colombia to Bolivia. The systematic of *M. murina* is imperfectly known. It is strongly

associated with moist habitats and tropical evergreen forests. Found in dense rain forests and also in weedy areas, being especially common in swampy and modified areas. In the Amazonia, it was captured in pastures by Silva et al (2008) and was considered an opportunistic species. It tolerates secondary growth and disturbed areas. In the Atlantic Forest, Pardini et al (2004) found this species to be significantly more common in the forested matrix compared to mature forest; it was abundant in secondary forest and edges. They are arboreal, nocturnal and insectivorous, but versatile in habitat exploitation.

***Micoureus demerarae:***

This species occurs in the Amazonia, Atlantic Forest, Cerrado, Pantanal (Fonseca et al., 1996) and Caatinga (Oliveira et al., 2004). It is distributed throughout the Amazon and the central Brazilian forests, reaching the Atlantic Forest in coastal Brazil (Costa 2003). The species lives in tropical humid forests and it is relatively abundant in second growth and disturbed areas, frequently found in plantations (Gardner, 2007). It is common in forest but it was also found in Eucalyptus plantations (Stallings, 1989). In the Atlantic Forest, it was mostly captured in fragment edges (Stevens and Husband, 1998) and it was common in the matrix (Pardini et al 2004). *M. demerarae* forms an atypical metapopulation where only the males migrate (Brito and Fernandes 2000) They are nocturnal, solitary and feed mostly on insects, preferentially arboreal but versatile.

***Gracilinanus microtarsus:***

This marsupial species is endemic to the Atlantic forest, although they occur in Cerrado biome (Geise and Astua 2009). It ranges from Paraná state to Rio de Janeiro, occupies dense ombrophilous forest and deciduous forest and gallery forest of Cerrado. It is predominantly a forest species but it also can be caught in agriculture open areas and cacao plantations. It has no clear preference for forests in different stages of regeneration and apparently is not prejudiced by fragmentation (Rossi 2011). In the Atlantic Forest, *G. microtarsus* displayed little sensitivity to disturbance and was present in vegetation corridors (Rocha et al 2011) and eucalyptus plantations (Umetsu and Pardini 2007). They are arboreal, nocturnal, escansorial and feed on invertebrates and fruits.

***Didelphis albiventris:***

This marsupial occurs in the Atlantic Forest, Cerrado and Caatinga. It is widely distributed throughout South

America, from Ecuador to Argentina, occurring in a variety of biomes and habitats. It is encountered on plains, marshes, grasslands and marginal and rain forests. It is present in open areas, urban centers and disturbed forests. Is a generalist species, associated to open areas, commonly found in secondary forest, disturbed forest and urbanized areas (Bonvicino et al. 2002; Monteiro-Filho 2007). *D. albiventris* is not affected by fragmentation (Rossi 2011). The diet is omnivore including invertebrates, fruits, seeds and small vertebrates. Habits are terrestrial.

#### ***Akodon cursor:***

This rodent occurs in the Atlantic Forest, Campos do Sul, Caatinga and Cerrado biomes. It occupies a geographical range from southeastern and central Brazil through Uruguay, Paraguay, and northeastern Argentina (Gardner 2007). This is one of the most common species in forests and forest grasslands throughout its distribution (Eisenberg and Redford, 1999). It is found in several varieties of habitats, from semi-deciduous areas, forest-grassland ecotones to forests. In the Atlantic Forest it was more common at the edges and forested matrix than in continuous forest (Pardini 2004). The species is characteristic of disturbed habitats (Vieira 1999, Pardini 2004) and apparently benefited from forest fragmentation (Feliciano et al., 2002). They are insectivorous-omnivorous including in their diet arthropods and seeds.

#### ***Oligoryzomys nigripes***

This rodent occurs in Atlantic Forest, Caatinga, Pantanal, Campos Sulinos, Chaco and Cerrado. It is distributed throughout Paraguay, Argentina, Brazil and Uruguay (Weksler and Bonvicino, 2005). Across its distribution it occupies altered areas, grasslands, eucalyptus and other plantations, continuous forests, secondary and initial stages of regeneration and also forest fragments. It is a disturbance-adapted species (Pardini 2004), was found in native forest and anthropogenic habitats by Umetsu and Pardini (2007). This species is not affected by fragmentation (Pardini 2004), and was considered one of the most habitat generalist species by Weskler (2005).

#### ***Nectomys squamipes***

This species occurs in Atlantic Forest, Chaco and Cerrado biomes. It is widely distributed in South America, including Brazil, Paraguay and Argentina. It is associated to flooded forest, gallery forests and riparian forests. Widespread and abundant in the Atlantic Forest (Vieira 1999). Trapping records for the species

indicate that it can occupy different habitats like forest fragments, secondary forests, disturbed and anthropic areas. The water rat *N. squamipes* seems to be negatively affected by the reduction of its preferential habitat, the flooded forest (Viveiros and Fernandes 2004); yet it occurs in fragments and crosses open areas (Pires et al., 2002). It is a semi-aquatic and insectivorous rodent, strongly associated to water courses inside forest.

### ***Cryptonanus agricolai***

This species is commonly found in xeric habitats from Caatinga and open formations of the Cerrado in east-central Brazil (Gardner 2008). The marsupial genus *Cryptonanus* was rediscovered by Voss et al in 2005, and includes five species formerly grouped in the genus *Gracilinanus*. In Cerrado, they occurred in open, grasslands habitats (Bezerra et al 2009), although the authors reported little habitat information for the species. The species is recognized by the IUCN and listed as Data Deficient.

### ***Monodelphis domestica***

This marsupial is occurs in Cerrado, Pantanal and Atlantic Forest. It is distributed in eastern and central Brazil, Bolivia, Paraguay and north Argentina (Gardner 2007). It is primarily found in xeric situations, trapped in grassy areas and bushes (Eisenberg and Redford 1999). It is characteristic of open areas and could be tolerant to fragmentation (Fernandez and Pires 2006) and to man-made clearings (Eisenberg and Redford 1999). It is a predator, feeding on invertebrates.

### ***Holochilus brasiliensis:***

This rodent occurs in Atlantic Forest, Chaco, Caatinga and Cerrado biomes. It is distributed across Brazil, Uruguay and Argentina. In Brazil, it occurs from Bahia state to Rio Grande do Sul, Minas Gerais and Mato Grosso do Sul. This is a semi aquatic rodent occurring in low marshy areas and gallery forests where it feeds tender parts of plants (Eisenberg and Redford, 1999). It can be found in open areas and forests, and can become very abundant in cultivated fields (Herskovitz 1955). It is common along the canals and rivers in agricultural areas, especially common in sugarcane plantations in Argentina (Mares et al. 2000). They can become pests for rice crops (Valencia et al. 1994).

### ***Cavia aperea***

This rodent occurs in the Atlantic Forest, Cerrado and Caatinga. It is widely distributed across South America, occurring in Colombia, Ecuador, Venezuela, Guyana, Brazil, Bolivia, north Argentina, Uruguay, and Paraguay. This species primarily is associated with savannas and other open habitats (Voss *et al.*, 2001) and can occur in disturbed areas. They are diurnal and crepuscular and live in burrows.

### ***Pseudoryzomys simplex***

This rodent is considered endemic of the Cerrado biome (Fonseca *et al.* 1996). It is widely distributed in tropical and subtropical lowlands of South America including Bolivia, central and eastern Brazil, Paraguay and northern Argentina. It inhabits areas with strong seasonal rainfall characterized by palm savannas and thorn scrub (Eisenberg and Redford, 1999) and it is found in humid and dry environments. It is considered characteristic of open (unforested) tropical and subtropical lowland habitats (Voss and Myers, 1991). The species is uncommon in surveyed areas, so it may be rare or difficult to catch. It is considered an open area dwelling species, with records in unforested tropical and subtropical lowland habitats.

### ***Cerradomys vivoi*:**

This is a novel species of rodent described by Percequillo *et al* in 2008. Apparently, it inhabit the Caatinga domain and penetrated the Atlantic rainforest, the remaining congeneric species are typical open-area inhabitants. It is distributed in the Brazilian states of Minas Gerais, Bahia and Sergipe. In the Cerrado-Caatinga transitional areas inhabits secondary semi-deciduous and gallery forests. In the Atlantic Forests it was absent or very rare in mature forests including the edges, and apparently, is more common in open areas (Percequillo *et al*, 2008).

### ***Necomys lasiurus*:**

This rodent occurs in the Atlantic rainforest, Caatinga, Cerrado, Pantanal, and Amazon biomes (Eisenberg and Redford 1999). It is widely distributed throughout central South America, from Peru to Argentina, Brazil, Paraguay and Bolivia. In Brazil it occurs in Cerrado, Caatinga, Amazonia, Pantanal and Atlantic Forest biomes. The species is usually found in open areas like grassland and savannas and occasionally in forests' edges. They can occupy cultivated or abandoned fields. In a study in the Atlantic forest, it was restricted to areas of agriculture and benefited from matrix habitat (Umetsu and Pardini 2007). Due to *N. lasiurus* positive response to anthropic disturbs and high abundance in altered forest areas it was pointed as indicator species

of degraded forests (Rossi 2011). They have an omnivore diet and terrestrial habits.

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