Assessing the Most Irreplaceable Protected Areas for the Conservation of Mammals in the Atlantic Forest: Lessons for the Governance of Mosaics

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Abstract: We have gathered 21,353 records of 40 different medium- and large-sized species of mammals existing in the Atlantic Forest conservation units of Brazil, including full protection and sustainable use types of management. We have classified the conservation units by their irreplaceability in terms of their role in the protection of mammalian species. Most irreplaceable conservation units are concentrated in the southern and southeastern regions of Brazil, mainly in the states of Rio de Janeiro, São Paulo and Paraná. Our data show that over and above the area of the conservation unit or its type of use, protection of its surroundings appears to be of most consequence. Therefore, it is essential to develop effective mosaic governance mechanisms that include protected areas and different types of land use. However, it is also necessary to establish common ground that allows the coexistence of human economic demands and wildlife preservation.

Keywords: Atlantic Forest; wildlife; protected areas; irreplaceability; governance of mosaics; SDG 15

1. Introduction

The recent loss of biodiversity caused by anthropogenic activity has reached alarming levels, to the point of resembling the great extinctions of the past. Several authors have referred to it as the sixth extinction wave [1–3], an event that “has happened only five times in the past 540 million years” [1]. However, focusing only on the extinction of species is to ignore the decline in populations before their complete disappearance [4,5]. These extirpations lead to the loss of ecological interactions [6,7], which inevitably leads to changes in ecosystem functions [2,8,9] and may have short- and long-term implications [10,11]. Janzen [12] was the first to point out that the extinction of ecological interactions is of paramount importance for conservation, since it encompasses the loss of ecosystem services [13].

In the face of this scenario, biodiversity hotspots have become the center of investigations that assess the status of their populations. In this study we focused on the Brazilian Atlantic Forest, one of the world’s hottest biodiversity hotspots [14]. This is partially the result of its wide latitudinal, longitudinal and altitudinal range, which has favored high diversity and endemism [15], and partially due to its extensive past deforestation, which left only a few large fragments in inaccessible places [16], isolated from one another. Even today, this biome continues to suffer increasing anthropogenic pressure [17–19], such as the expansion of agriculture [20].

Here, we chose mammals as a study group to evaluate how irreplaceable a conservation unit is. Vertebrates generally receive considerable attention from researchers and are a good proxy for less...
well studied groups [21]. Mammals in particular are among the vertebrates that have suffered the most anthropogenic threats [2,4], and countless studies show that their loss may entail strong trophic cascades in both top-down and bottom-up senses [22–24]. In a fragmented landscape like the Atlantic Forest, the consequences to the ecosystem of loss of mammals can cause additional biodiversity losses, making the study of this group even more urgent.

In Brazil, a national system has been established to create different types of nature conservation units [25]. Basically, all 12 types of unit can be separated into two major groups: full protection (FP), with more restricted land use as regards humans, and those of sustainable use (SU), with more flexibility of use. Our study aimed to critically assess where the populations of medium and large mammals still exist, by observing the type of conservation units in which they occur. We focused on a wide variety of mammal species, and addressed the entire Brazilian Atlantic Forest, which is rare among studies [26,27]. Therefore, we intend to reveal some general patterns that could guide authorities, or even alert them as to what kinds of government measure should be taken with a view of optimizing fauna conservation.

2. Materials and Methods

2.1. Study Area

The Atlantic Forest is distributed through Argentina, Paraguay and Brazil, which holds 90% of this biome [28]. In Brazil, the forest borders with other biomes, such as Pampas in the south, Cerrado and Pantanal in the mid-west and Caatinga in the northeast. Since the arrival of Europeans in 1500, the original landscape has undergone intense conversion due to diverse types of exploitation [29]. Nowadays less than 12% of its original coverage remains, distributed mostly in forest remnants of less than 50 ha [15]. We focused here on the Brazilian portion [30] of this biome, using data from 14 states that have sufficient up-to-date information on the areas of occurrence of the species understudy.

2.2. Species Studied

A survey was carried out on 40 medium- and large-sized mammals that occur in this biome. We followed the definition proposed by Emmons and Feer [31] regarding the classification of mammalian body-size pattern, considering medium-sized mammals (those weighing 2–7 kg; although two species below 2 kg were also included) and large-sized mammals (those weighing more than 7 kg). We chose to work with medium- and large-sized mammals not only because they can be good indicators, but also due to their comparatively easy identification, allowing more accurate estimates in relation to other groups. However, due to taxonomic and biogeographic uncertainties, for Conepatus (Conepatus chinga and Conepatus semistriatus) and Dasyprocta we chose to work at genus rather than species level, since species of these genera are difficult to distinguish in areas where their distributions overlap. All other taxonomic references were based on Wilson and Reeder [32].

2.3. Survey of Data

We compiled a database that included only presence information for 40 species of medium and large mammals, based on a literature review of works published from 1986 to 2016. The survey consisted of scientific articles and so-called gray literature, which includes monographs, dissertations, theses, congress abstracts and technical papers. These data were further supplemented by museum records, personal sightings and databases, such as GBIF (Global Biodiversity Information Facility), SpeciesLink (http://splink.cria.org.br/), Portal da Biodiversidade (https://portaldabiodiversidade.icmbio.gov.br/portal/) and Urubu System. The Urubu System database lists records of vertebrate roadkills (http://cbee.ufla.br/portal/sistema_urubu/). In order to guarantee the quality of information acquired, all searches were limited to primary sources. Furthermore, in addition to the species name, each data entry in our database contained the type of record (camera trap, sighting, vocalization, carcass, feces, tracks and hair), geographical coordinates, locality and the year in which it was obtained. We always
tried to use the precise coordinates for each record, but when this was not possible, the centroid of the forest remnant was used.

2.4. Estimating Area Occupied by Species

It was assumed that each record would imply the existence of at least one population in the area sampled. From the database, we generated a kernel density map (0.02684 bandwidth) to estimate the area currently occupied by each species, plus the lower and upper bounds of the confidence interval for these estimates. We then applied the Kernel Utilization Distribution model from ‘adehabitatHR’ package in R software [33], considering the entire utilization distribution.

Nonetheless, as the smoothing parameter ($h$) has a substantial effect on kernel estimates [34–36] we used a protocol proposed by Kie [36] to obtain a suitable value. Starting with the estimated $h_{ref}$, we decreased it sequentially by 0.01, and calculated the relation between the different $h$ values and the areas estimated for each one. Next, through the predict function in R software, we plotted the occupation area of *Panthera onca* in the Atlantic Forest (37,825 km$^2$ [37]) to retrieve its specific ad hoc $h$ value.

As kernel tends towards oversmoothing when estimating the area of occurrence of a species with low density, leading to a Type I error (false positive [36]), *Panthera onca* was used to estimate a conservative ad hoc $h$. *Panthera onca* is a large-sized species with low density, but it has been well sampled for multiple reasons: its size makes it conspicuous; it is the object of study of many researchers, including a working group of ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade) and its charisma increases the chance of sightings being reported. Therefore, its occurrence in the Atlantic Forest is relatively well known, making its estimated area of occurrence more accurate than most, if not all, other species [38]. As we do not know the actual area of occurrence for every studied species, *Panthera onca* was used as a model, and the same value of ad hoc $h$ was applied to all species.

Adjustments in the estimated areas were made in order to eliminate parts of the projections that exceeded the limits of the Atlantic Forest. We also excluded areas where it was known the studied species would be absent or had very low probability of occurrence, such as cities and mountain peaks. The same went for rivers and lagoons, which were excluded from the areas of occurrence of terrestrial species, being kept only for *Lontra longicaudis*.

All estimates of distributions were made on the basis of data from the last 30 years. This approach assumes that 30 years is enough time to cover a wide variety of sources of information on the occurrence of species in the same area, diminishing the probability of not recording a species in an area where it occurs. We also assumed that any site where a species had not been recorded for over 30 years could no longer be considered as part of its current area of occurrence.

All maps were georeferenced in the Albers equal area conic projection using the QGIS [39] program, and the current occupied area of each species was calculated in km$^2$.

2.5. Data Analysis

As protected areas are distributed throughout the Atlantic Forest, we evaluated the species distributions in different categories of conservation units in the Atlantic Forest. In order to assess the influence of size and category (full protection or sustainable use) on species richness, generalized linear models (GLM) were applied with Poisson error distribution corrected for overdispersion. We used the glm function in the Stat package within the R language [40]. Species richness was estimated by summing the number of species that had at least a portion of its area of occurrence inside the conservation unit according to the maps generated by kernel, as explained in the section above.

The importance of protected areas for biodiversity conservation was further assessed by means of the species coverage indicator (SCI) [41], used in this study to evaluate the importance of each conservation unit and what we called the Conservation Irreplaceability Index (CII). This indicator was originally proposed as a species irreplaceability indicator, but we adapted it to quantify the value of a protected area according to the species present in it. In this test, each species was scored using the
fraction \(1/n\), where \(n\) represents the number of protected areas in which a species occurs. Following this, the contribution of each conservation unit was taken as the sum of the values of \(1/n\) for all the species found there. The higher the value, the more irreplaceable the reserve is.

Moreover, once species are not restricted inside conservation units, it is plausible that proximal protected areas could form a biologically connected mosaic. In the context of this paper, we define ‘mosaic’ as a contiguous set of different, interacting land uses, which includes protected areas and land used for different purposes, but which have as a common aim the maintenance of ecosystem functionality for the benefit of both human economy and wild life preservation. In order to assess which conservation units could be united as part of any one mosaic, a buffer of 10 km was created around their limits, using the criterion suggested by Crouzeilles and Curran [42]—a meta-analysis that found that mammals respond to changes in the landscape occurring up to 10 km around their occurrence areas. When the buffer areas of two neighboring conservation units overlapped, we considered them part of the same mosaic. Therefore, if we consider the conservation units located at the limits of a mosaic, we would see that they are more than 20 km apart (considering the buffers of two bordering conservation units) from the surrounding units not included in the same mosaic.

3. Results

A total of 21,353 records were collected between 1986 and 2016, excluding repeated points and recordings in more than one source, such as two articles mentioning the same record. The so-called gray literature provided most records (11,753) followed by databases (5431), scientific articles (3405), and museums (2932). This result demonstrates the importance of using unconventional sources to survey species, always taking the necessary care in relation to data collection. One good example was the number of records obtained through the Urubu System (2349), a cellphone application developed by the Federal University of Lavras, Minas Gerais that registers Brazilian road kills. This was an important source of data that reduced sampling bias, since the information collected by citizens was not concentrated in the localities where there is an infrastructure for researchers. Before any data is publically provided by this application, the photograph sent by the citizen is analyzed by taxonomy experts to identify the species. These photographs are also available to anyone that uses the application, so that taxonomic confirmations are constantly being made. Each record includes a photograph of the animal with the geographic coordinates and the date on which it was taken.

*Ceirdocyon thous* was the most registered species \( (n = 2158)\), while *Speothos venaticus* had the fewest sightings \( (n = 20)\). The largest mammal, *Tapirus terrestris*, and the smallest, *Silvulagus brasiliensis*, had average weights of 281 and 1.2 kg, respectively [43]. *Tayassu pecari*, *Panthera onca*, *Tapirus terrestris* and *Myrmecophaga tridactyla* were infrequently sighted in the northeastern states, except for southern Bahia, with sightings of *P. onca* and *T. terrestris* in Rio Grande do Sul, in Turvo State Park and *T. pecari* in isolated conservation units of Rio de Janeiro.

Only a small percentage of the geographical range of each species is covered by some sort of conservation unit (Table 1). Aside from four species—the two *Brachyteles*, *Priodontes maximus* and *T. pecari*—all other species presented a larger percentage of occupied areas in the sustainable use than in the full protection category, although *T. terrestris* presented similar values for the two categories. Most mammals had less than 20% coverage for each type of conservation unit. Within full protection, only *Brachyteles arachnoides*, *Brachyteles hypoxanthus*, *P. maximus* and *T. pecari* were above this value (Table 1), while sustainable use had five species, four of them which were different from those found for full protection—*B. arachnoides*, *S. venaticus*, *Leopardus emiliae*, *P. onca*, and *L. longicaudis*. In addition, the average percentage of occupied areas was slightly higher in the sustainable use conservation units, even though this category and that of full protection were similar in species composition (Table 1).
| Taxa                        | FP  | SU  | Taxa                        | FP  | SU  | Taxa                        | FP  | SU  |
|----------------------------|-----|-----|----------------------------|-----|-----|----------------------------|-----|-----|
| Alouatta belzebul          | 4.3 | 6.7 | Cerdocyon thous            | 5.5 | 10.6| Nasua nasua                | 8.7 | 12.9|
| Alouatta guariba           | 12.2| 14.8| Chrysocyon brachyrurus     | 7.2 | 15.2| Potos flavus               | 9.7 | 11.1|
| Brachyteles arachnoides    | 45.2| 30.9| Speothos venaticus         | 19.4| 26.1| Procyon cancrivorus        | 6.7 | 11.7|
| Brachyteles hypoxanthus    | 26.7| 2.2 | Leopardus guttatus         | 10.2| 12.4| Tapirus terrestris         | 18  | 18.2|
| Bradypus torquatus         | 6.1 | 14  | Leopardus pardalis        | 9.6 | 15  | Mazama americana           | 12.3| 12.8|
| Bradypus variegatus        | 11.4| 16.6| Leopardus emiliae         | 2.3 | 21.8| Mazama gouazoubira         | 9.1 | 13.9|
| Myrmecophaga tridactyla    | 9.6 | 12.6| Leopardus wiedii          | 10.4| 11.9| Pecari tajacu              | 13.1| 17.1|
| Tamandua tetradactyla      | 5.9 | 10.1| Panthera onca             | 17.9| 20  | Tayassu pecari             | 24.2| 14.9|
| Cabassous tatouay          | 7.8 | 9.2 | Puma concolor            | 13.6| 16.3| Dasypus                  | 11.6| 16.2|
| Cabassous unicinctus       | 6.9 | 11.8| Puma yagouroundi         | 8.6 | 12.2| Hydrochoerus hydrochaeis    | 8.3 | 14.4|
| Dasypus novemcinctus       | 7.9 | 13.6| Conepatus                 | 5.5 | 7.2 | Cuniculus paca            | 9.5 | 13.9|
| Dasypus septemcinctus      | 6.4 | 10  | Eira barbara             | 8.5 | 11.8| Sylvilagus brasiliensis     | 7.8 | 13.1|
| Euphractus sexcinctus      | 5.3 | 10.9| Galictis cuja            | 6.3 | 11  | Mean                      | 11.3| 14.1|
| Priodontes maximus         | 23  | 10.5| Lontra longicaudis        | 8   | 26.4| SD                        | ± 7.8| ± 5.3|

Table 1. Percentage of current occupied area for each taxon within full protection (FP) and sustainable use (SU) conservation units in the Atlantic Forest. Standard deviation—SD.
Interestingly, even though full protection units presented less variation and smaller area than sustainable use ones, they still showed slightly higher species richness (the highest values for species richness found in conservation units were 33 and 31 species for FP and SU, respectively). In any case, richness was significantly related to area for both category types ($p < 0.01$, $pR^2 = 0.089$; Figure 1). Here, we considered that a conservation unit with more than 25 species of medium- and large-sized mammals could be viewed as a unit with high richness, while units with fewer than 10 species were considered to have low richness.

![Figure 1. Quasi-Poisson regression model relating species richness to area of conservation unit. Full protection (black circle) and sustainable use (gray circle).](image)

When focusing on irreplaceable conservation units, it can be observed that for units classified as full protection, there is large amplitude in area, ranging from 35.6 km$^2$ in the Augusto Ruschi Biological Reserve to 3222.9 km$^2$ in the Serra do Mar State Park (Table 2). However, when we look at species richness, there is no such discrepancy, with values lying around 30 species. The Murici Ecological Station was an exception, since despite having a low species richness value, it proved to be one of the 20 most irreplaceable conservation units (Table 2) due to its harboring a species of high irreplaceability value, *Alouatta belzebul*. Other conservation units presented high species richness because they form part of large blocks of forested areas, such as Itatiaia National Park, Intervales State Park and even Iguaçu National Park, which is part of a large continuum of protected forest in Argentina, in the Misiones region.
Table 2. The top 20 full protection (FP) conservation units in the Brazilian Atlantic Forest, according to their Conservation Irreplaceability Index (CII) value, along with their area (km$^2$) and species richness. At the end of each conservation unit name we highlight the Brazilian state(s) where it is located: AL - Alagoas, BA - Bahia, ES - Espírito Santo, MG - Minas Gerais, MS - Mato Grosso do Sul, PR - Paraná, RJ - Rio de Janeiro, SP - São Paulo.

| Type | Conservation Unit                  | Area  | Species Richness | CII  |
|------|------------------------------------|-------|------------------|------|
| FP   | Itatiaia National Park RJ          | 280.9 | 31               | 0.247|
| FP   | Pedra Selada State Park RJ         | 80.4  | 30               | 0.242|
| FP   | Murici Ecological Station AL       | 61.3  | 5                | 0.212|
| FP   | Sooretama Biological Reserve ES    | 278.6 | 30               | 0.200|
| FP   | Rio Doce State Park ES             | 359.5 | 24               | 0.188|
| FP   | Serra do Mar State Park SP         | 3222.9| 33               | 0.187|
| FP   | Carlos Botelho State Park SP       | 401.4 | 31               | 0.185|
| FP   | Nascentes do Paranapanema State Park SP | 222.1 | 30               | 0.177|
| FP   | Serra da Bocaina National Park RJ-SP| 1038.7| 31               | 0.175|
| FP   | Intervales State Park SP           | 406.5 | 28               | 0.168|
| FP   | Iguaçu National Park PR            | 1697.0| 28               | 0.165|
| FP   | Campos Gerais National Park PR     | 213.0 | 26               | 0.153|
| FP   | Una Wildlife Refuge BA             | 232.6 | 28               | 0.140|
| FP   | Pau Brasil National Park BA        | 189.3 | 28               | 0.139|
| FP   | Lagamar de Cananeia State Park SP  | 407.1 | 23               | 0.137|
| FP   | Bom Jesus Biological Reserve PR    | 341.8 | 26               | 0.135|
| FP   | Augusto Ruschi Biological Reserve ES| 35.6  | 28               | 0.133|
| FP   | Una Biological Reserve BA          | 187.2 | 27               | 0.131|
| FP   | Ilha Grande National Park MS-PR    | 761.4 | 27               | 0.124|
| FP   | Serra do Gandarela National Park MG| 312.7 | 26               | 0.123|

Augusto Ruschi Biological Reserve presented the smallest size, but with high species richness, and more importantly, it shelters irreplaceable species. Found in Carlos Botelho State Park are $S$. venaticus and $B$. arachnoides, two endangered and highly irreplaceable species. Una Biological Reserve and Una Wildlife Refuge, home to the endangered species $B$. hypoxanthus, may thus also be considered highly important. Itatiaia National Park and Pedra Selada State Park lie in a high position in the irreplaceability ranking because they are the only conservation units to have both Brachyteles species.

Most irreplaceable conservation units are concentrated in the southern and southeastern regions of Brazil, mainly in the states of Rio de Janeiro, São Paulo and Paraná. The northeast region was represented only by four conservation units: Murici Ecological Station, Pau Brasil National Park, Una Wildlife Refuge and Una Biological Reserve, the last two forming a continuous block of forested area. Also, Ilha Grande National Park in the states of Mato Grosso do Sul and Paraná may be influenced by individuals coming from the Cerrado biome.

The top 20 sustainable use conservation units were more heterogeneous than the full protection units, with a wide range in area (0.02 to 4312.8 km$^2$) and species richness (1 to 31 species), although only two units presented low richness: Mata da Estrela Natural Heritage Private Reserve and Lagoa do Jequiá Marine Extractive Reserve (Table 3). These two conservation units hold Alouatta belzebul, a rare and widely dispersed species concentrated in the north of the Brazilian Atlantic Forest, thus increasing the importance and irreplaceability of these units. Most of the lowest area values were found in Natural Heritage Private Reserves, such as Agulhas Negras and Chalé Club do Alambary (Table 3), which may have high irreplaceability values due to their proximity to other, larger conservation units. In fact they are part of mosaic 3, as discussed below (as can also be observed in the Supplementary Material, Figure S3).
Table 3. The top 20 sustainable use (SU) conservation units in the Brazilian Atlantic Forest, according to their Conservation Irreplaceability Index (CII) values, along with their area (km$^2$) and species richness. At the end of each conservation unit name we highlight the Brazilian state(s) where it is located: AL - Alagoas, ES - Espírito Santo, MG - Minas Gerais, PR - Paraná, RJ - Rio de Janeiro, RN - Rio Grande do Norte, SP - São Paulo.

| Type   | Conservation Unit                                      | Area  | Species Richness | CII  |
|--------|--------------------------------------------------------|-------|------------------|------|
| SU     | Murici Environmental Protection Area AL               | 1295.2| 21               | 0.278|
| SU     | Serra da Mantiqueira Environmental Protection Area MG-RJ-SP | 4312.8| 31               | 0.247|
| SU     | Natural Heritage Private Reserve Agulhas Negras RJ    | 0.2   | 30               | 0.242|
| SU     | Natural Heritage Private Reserve Chalé Club do Alambary RJ | 0.02  | 30               | 0.242|
| SU     | Natural Heritage Private Reserve Dois Peões RJ         | 0.6   | 30               | 0.242|
| SU     | Natural Heritage Private Reserve Mata da Estrela RN   | 20.4  | 4                | 0.206|
| SU     | Natural Heritage Private Reserve Santo Antonio SP     | 5.4   | 29               | 0.205|
| SU     | Lagoa do Jequiá Marine Extractive Reserve AL          | 102.0 | 1                | 0.200|
| SU     | Serra do Timóteo Environmental Protection Area MG      | 58.2  | 23               | 0.185|
| SU     | Recanto das Antas Environmental Protection Area ES     | 22.5  | 29               | 0.183|
| SU     | Serra do Mar Environmental Protection Area SP         | 4196.6| 30               | 0.177|
| SU     | Natural Heritage Private Reserve Mutum Preto ES       | 3.8   | 27               | 0.176|
| SU     | Marinha do Litoral Norte Environmental Protection Area SP | 3164.6| 31               | 0.175|
| SU     | Cairuçu Environmental Protection Area RJ              | 326.1 | 30               | 0.169|
| SU     | Escarpa Devoniana State Environmental Protection Area PR | 4147.8| 30               | 0.168|
| SU     | Engenheiro Fassos Environmental Protection Area RJ    | 26.8  | 29               | 0.166|
| SU     | Guaraqueçaba Environmental Protection Area PR         | 2824.4| 28               | 0.161|
| SU     | Goytacazes National Forest ES                         | 14.3  | 23               | 0.159|
| SU     | Cananéia-Iguape-Peruíbe Environmental Protection Area SP | 2023.1| 28               | 0.158|
| SU     | Guaratuba State Environmental Protection Area SP      | 1993.7| 26               | 0.143|

Table 4 lists the 30 top conservation units that presented high values both for richness and CII. Among them there were 17 full protection and 13 sustainable use units. The most frequently mentioned state on the list was Rio de Janeiro, with 10 units, seven of these with full protection. Rio de Janeiro was followed by São Paulo, with nine units, five also being full protection. Of the 10 conservation units in Rio de Janeiro, only six reached the top 25, while all nine conservation units of the state of São Paulo are included in the list. The listed conservation units were more concentrated in the southeastern region, and only Bahia, Mato Grosso do Sul and Paraná represented the northeast, the mid-west and the south of Brazil, respectively. The two states with fewest conservation units in this list were represented only by full protection ones, Bahia having three and Mato Grosso do Sul having only one unit.
Table 4. Relation between the 30 main conservation units that combine high species richness and high irreplaceability values in the Brazilian Atlantic Forest. When the conservation unit is included in a mosaic, the table indicates which mosaic it belongs to. FP—full protection conservation unit. SU—sustainable use conservation unit. CII—Conservation Irreplaceability Index. Area is in km². At the end of each conservation unit name we highlight the Brazilian state(s) where it is located: BA - Bahia, ES - Espírito Santo, MG - Minas Gerais, MS - Mato Grosso do Sul, PR - Paraná, RJ - Rio de Janeiro, SP - São Paulo.

| Type     | Conservation Unit                              | Area  | Mosaic | Species Richness | CII    | State       |
|----------|-----------------------------------------------|-------|--------|------------------|--------|-------------|
| FP       | Carlos Botelho State Park                     | 401.4 | 2      | 31               | 0.185  | SP          |
| FP       | Pedra Selada State Park                       | 80.4  | 3      | 30               | 0.242  | RJ          |
| FP       | Serra do Mar State Park                       | 3222.9| 1      | 33               | 0.187  | SP          |
| FP       | Intervales State Park                         | 406.5 | 2      | 28               | 0.168  | SP          |
| FP       | Nascentes do Paranapanema State Park          | 222.1 | 2      | 30               | 0.177  | SP          |
| FP       | Serra da Bocaina National Park                | 1038.7| 1      | 31               | 0.175  | RJ, SP      |
| FP       | Serra do Gandarela National Park              | 312.7 | -      | 26               | 0.123  | MG          |
| FP       | Ilha Grande National Park                     | 761.4 | -      | 27               | 0.124  | PR, MS      |
| FP       | Iguaçu National Park                          | 1697  | 4      | 28               | 0.165  | PR          |
| FP       | Itatiaia National Park                        | 280.9 | 3      | 31               | 0.247  | RJ          |
| FP       | Campos Gerais National Park                   | 213   | -      | 26               | 0.152  | BA          |
| FP       | Pau Brazil National Park                      | 189.3 | -      | 28               | 0.139  | BA          |
| FP       | Una Wildlife Refuge                           | 232.6 | -      | 28               | 0.14   | BA          |
| FP       | Augusto Ruschi Biological Reserve             | 35.6  | -      | 28               | 0.133  | ES          |
| FP       | Bom Jesus Biological Reserve                  | 341.8 | 2      | 26               | 0.135  | PR          |
| FP       | Sooretama Biological Reserve                  | 278.6 | -      | 30               | 0.2    | ES          |
| FP       | Una Biological Reserve                        | 167.2 | -      | 27               | 0.131  | BA          |
| SU       | Cairuçu Environmental Protection Area         | 326.1 | 1      | 30               | 0.169  | RJ          |
| SU       | Cananeia-Iguape-Paruibe Environmental Protection Area | 2023.1 | 1,2  | 28               | 0.158  | SP          |
| SU       | Engenheiro Passos Environmental Protection Area | 26.8  | 3      | 29               | 0.166  | RJ          |
| SU       | Guaraqueçaba Environmental Protection Area    | 2824.4| 2      | 28               | 0.161  | PR          |
| SU       | Devonian Escarpment State Environmental Protection Area | 4147.8 | - | 30 | 0.168 | PR |
| SU       | Marinha do Litoral Norte Environmental Protection Area | 3164.6 | 1 | 31 | 0.175 | SP |
| SU       | Serra da Mantiqueira Environmental Protection Area | 4312.8 | 3 | 31 | 0.247 | MG, RJ, SP |
| SU       | Serra do Mar Environmental Protection Area    | 4196.6| 1      | 30               | 0.177  | SP          |
| SU       | Natural Heritage Private Reserve Agulhas Negras | 0.2  | 3      | 30               | 0.242  | RJ          |
| SU       | Natural Heritage Private Reserve Chalé Club do Alambary | 0.02  | 3 | 30 | 0.242 | RJ |
| SU       | Natural Heritage Private Reserve Dois Póeis   | 0.6   | 3      | 30               | 0.242  | RJ          |
| SU       | Natural Heritage Private Reserve Recanto das Antas | 22.5 | - | 29 | 0.183 | ES |
| SU       | Natural Heritage Private Reserve Santo Antônio | 5.4  | 3      | 29               | 0.205  | RJ          |

To create the mosaics, we chose to exclude sustainable use units, primarily due to the weak conservation efforts in environmental protection areas (EPA), which are the type of unit that presents larger observed surface areas. EPAs are loosely protected and Brazilian governance allows the installation of cities, roads, pastures, plantations and other anthropic interventions. Although many preserved areas may persist inside their limits, when included in the analysis the highly variable nature of EPAs leads to an overestimation of the actual protected area of a mosaic.

Nonetheless, when mosaics were formed, parts of sustainable use conservation units were seen to lie between full protection units, working as important connectors (see Supplementary Material). However, although an EPA may lie between two mosaics, if it contains a city it does not necessarily mean that these two mosaics are biologically connected, since the city may act as a barrier to biological connectivity.

Mosaic 1 had significantly more EPAs in its composition than the other mosaics. If we consider the 10 largest conservation units of this mosaic, seven are EPAs, and the three remaining units are composed...
of state and national parks and an ecological station. This mosaic is composed of 76 conservation units, being the richest and most extensive of the four mosaics formed. Mosaic 2 presented 45 conservation units, the 10 largest being slightly different than the previous mosaic. In mosaic 2 we found only five EPAs and the other main units are composed only of state and national parks, a full protection type of conservation unit. Mosaic 3 was formed by 18 conservation units, only seven of which presented more than 10 km². These seven consist of three EPAs, three state parks and one state wildlife refuge.

We observed the repetition of EPAs between mosaics. For example, Cananéia-Iguape-Peruíbe and Serra do Mar Environmental Protection Areas were present in mosaics 1 and 2, while Bacia do Paraíba do Sul Environmental Protection Area was in mosaics 1 and 3. Although this does not mean that the three mosaics are biologically connected to each other, this leaves room for an easier increase in the real protected area. If more investments were made towards the conservation of these EPAs, it would substantially enhance the protected area, connecting large mosaics and forming one large forested block. Once these conservation units are established, human impact on these landscapes must be restricted and enforced (for more details see the Supplementary Material).

4. Discussion

Our results suggest that several important mammal species are dependent on land adjacent to protected areas, thereby revealing their fragile conservation status given current protection regimes. Table 1 shows that the percentage occupied area inside conservation units is rather small for nearly all species, indicating that in general these species currently occupy regions where they are not protected from human threats. This scenario is aggravated for species that are extremely dependent on a minimum size of forested area, and for species that are endemic to those portions of the Atlantic Forest that receive the lowest conservation priority.

*Pecari tajacu*, *Tapirus terrestris* and *Tayassu pecari* are examples of forest specialist species, recorded by Beca et al. [19] only in areas with more than 45% forest cover, possibly a minimum threshold for their occurrence. For the first two species in particular, this may be one probable reason for their low area of occurrence, further impacted by hunting pressure. This lack of large forested areas may also explain the absence of most large-sized mammals from the northeastern region, where deforestation was more intense due to the earlier colonization and narrower distribution of this biome [29,44]. Similarly, *Speothos venaticus* had only 20 records, concentrated mostly in the state of São Paulo and some in Paraná. This low number may not only be because the bush dog is a cryptic species [45], but mostly because it needs forested areas to survive [46].

For the same reason, *Alouatta belzebul*, a species endemic only to the northern portion of the Atlantic forest, presented here an alarmingly small occupied area in this biome. The distribution of *L. emiliae* in the Atlantic Forest is also limited to the northern portion, and presented a slightly larger occupied area, probably because it is not as dependent on forest habitat as *A. belzebul*, but it should be closely watched and managed in order to prevent the same fate. As these species are distributed in small, sparse fragments, they suffer greatly from the edge effect, apart from having more contact with human threats, such as hunting pressure [10,44,47]. An exception in the northern Brazilian Atlantic Forest is located in southern Bahia, where we can find the ‘cabruca agroforest’, composed of a mixture of cacao and taller native forest trees, which provides better conditions to sustain higher richness. Although constituting the last relict shelter for large mammals in the north of this biome [44,47], this vegetation is not ideal, as hunting and other human pressures are more intense in this area than they would be in protected conservation units [48].

An interesting indicator of the degree of transformation this biome is undergoing due to fragmentation and the deforestation processes is the fact that the two species which are most adapted to open environments (*Chrysocyon brachyurus* and *Mazama gouazoubira*) have expanded their distributional range to include the Atlantic Forest. These two species are habitat generalists, and the changes that are modifying this biome into something more similar to the Cerrado biome [19,49,50] have given them
an advantage over specialist species [51,52]. The more recurrent presence of these two species in the Atlantic Forest emphasizes the urgent need for more investment in conservation units.

The remnant populations of Panthera onca, which could be considered a flagship species, and more importantly, an umbrella species in the Atlantic Forest, are alarmingly constricted to southern Bahia and to the states of São Paulo, Minas Gerais, Espírito Santo, Paraná and Rio Grande do Sul, with only one record in the last state, in Turvo National Park, located on the border with Argentina. As the structure and size of this park cannot sustain a viable population of Panthera onca, it is likely that this individual came from Argentina. This critical framework is in line with de la Torre [38], who found that the jaguar’s global area of occurrence has shrunk by 55% from its historical range, and proposed that most subpopulations should be considered endangered or critically endangered. The Brazilian Atlantic Forest populations are extremely isolated in a fragmented landscape, which may exacerbate this species’ situation even further.

Our results showed that despite being significant, their size does little to explain the richness found in the conservation units. We observed that most of the largest units were of the sustainable use type, especially environmental protection areas (EPA), a very poorly-preserved type of conservation unit where there is a lack of government control and the establishment of cities is permitted without sufficient restrictions. Also, since sustainable use and full protection units are spatially very close, sometimes with adjoining borders or even overlapped areas, it is difficult to identify which species can be maintained by each conservation unit type alone. Therefore, what may seem to be a rich EPA may simply be the result of other, smaller full protection units nearby that are supplementing them with individuals and leading to a high richness value. In this scenario, we may find large sustainable use and small full protection conservation units which are spatially close and have similar richness values. Nonetheless, we do not suggest that conservation unit size does not matter. In fact, larger preserved areas lead to a higher protection status because the species have a larger portion of occupied area not in contact with humans [44,53]. Excluding EPAs, our results even indicated that the largest conservation units like the full protection units Serra do Mar State Park (3,223 km²), Iguaçu National Park (1,697 km²) and Serra da Bocaina National Park (1,039 km²) presented high values for species richness (33, 28 and 31 species, respectively). It is worrying that the 20 largest conservation units that composed the mosaics, except for six units, are all EPAs, showing that the total area of preserved land in the Atlantic Forest is not so large (Supplementary Material, Table S1).

One way to achieve larger protected areas is the establishment of buffer zones around conservation units, especially in tropical habitats [54], thus providing additional habitat for species to access [42]. For instance, it has been suggested that a requirement of at least 30% of forested area in the landscape would maintain a healthy community of vertebrates [52,55], and the implementation of these buffer areas may be sufficient to achieve that. Our top 30 main conservation units in the Atlantic Forest (Table 4) are good examples of the importance of the surroundings in determining species richness. Many of these units are embedded in large forest mosaics, which are not entirely legally protected, but where forest cover extends far beyond the conservation unit area. Thus, these large forested blocks are important in ensuring enough resources to maintain a species [47,56], and still shelter large and threatened species, such as Brachyteles spp., P. onca, P. maximus, T. pecari and T. terrestris. Iguaçu National Park in Brazil is an example, embedded as it is in an enormous forest mosaic that still encompasses part of the Argentinian province of Misiones (Supplementary Material, Figure S4).

These somehow preserved surrounding areas are also the reason why many small reserves were considered irreplaceable. Some of them are Natural Heritage Private Reserves (NHPR), like Agulhas Negras, Dois Pêoes and Chalé Club Alambary in the state of Rio de Janeiro, which despite their small size presented high richness because of their closeness to a much larger, well managed conservation unit, Itatiaia National Park, and they form part of a mosaic (Supplementary Material, Figure S3 and Table S1). These NHPR function as satellite protected areas, supporting and being supported by large conservation units nearby, and they are probably vital in adding more resources and available area for species that live in the vicinity.
Finally, we should note that high species richness does not necessarily indicate that a protected area is well preserved, since there may be an ‘extinction debt’ effect manifested by a reduction in population number of several of the species still present [57]. In addition, it has been observed that conservation units at higher altitudes have lower population abundances [58], which is a matter of concern in the Atlantic Forest, where most protected areas are concentrated in mountainous terrain not yet fully occupied by humans. This makes these populations even more sensitive to extinction, and gives further reason for keeping and enhancing surrounding forested areas, connecting conservation units, and enhancing functional diversity [26,54,59]. If it is not possible to increase the size of the protected area or decrease the number of people living outside it [53,60], conservation measures should be stricter on both sides of a conservation unit border [61].

We believe that maintaining hope for a more sustainable Atlantic Forest is not a naïve idea. If our goal is restoration of 30% of forest cover, this would mean a cost of only 6.5% of Brazil’s annual expenditure on agricultural subsidies; that is, 0.0092% of the Brazilian annual GDP [55]. This amount would be further reduced to 0.0026% once regeneration has been initiated. Therefore, we do have the ways and the means to save what is left of the Atlantic Forest.

Given that this work has shown that the irreplaceability value of a conservation unit is not linked to its size, the most important lesson learned towards achieving sustainability objectives is that mechanisms of participatory governance of entire mosaics must be strengthened. We should include all actors in the socio-ecosystem and establish a tolerant dialogue on different land uses. Despite inevitable clashes of interests, the common ground of sustainability must be maintained. We could then achieve coexistence with human demands, prevent extinction and, consequently, ensure the functionality of this unique ecosystem.

Supplementary Materials: The following are available online at http://www.mdpi.com/2071-1050/11/11/3029/s1, Figure S1: Map of the Mosaic 1 representing full protection (FP - dark gray) and sustainable use conservation units (SU - light gray), Figure S2: Map of the Mosaic 2 representing full protection (FP - dark gray) and sustainable use conservation units (SU - light gray), Figure S3: Map of the Mosaic 3 representing full protection (FP - dark gray) and sustainable use conservation units (SU - light gray), Figure S4: Map of the Mosaic 4 with the conservation units that compose it, Table S1: List of conservation units, with their type of protection (full protection or sustainable use) and total coverage area (km$^2$) in each mosaic of the Brazilian Atlantic Forest.

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