



Landscape features lead to shifts in communities of medium- to large-bodied mammals in subtropical Atlantic Forest

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Defaunation is a key ecological issue that has only recently been given sufficient attention. As predicted, evidence so far indicates loss of larger species followed by medium-sized species, leading to cascading effects that propagate throughout entire communities and ecosystems. The Atlantic Forest is among the most important global biodiversity hotspots. These regions have historically been impacted by habitat loss and fragmentation, resulting in landscape changes and negative impacts upon animal communities. This study evaluates community characteristics of medium- and large-sized mammals in subtropical Atlantic Forest, southern Brazil. We gathered data on mammal occurrence using 108 camera traps located across 8 protected areas. We then tested whether landscape differences impact mammal richness, composition, and community complexity. Specifically, we used a regression tree to evaluate compositional differences as a function of landscape configuration. We analyzed data for 26 species in total, with the number of species per area ranging from 9 to 17. Changes in mammal composition at the landscape scale were most strongly associated with human occupation. Areas with strong human occupation had low species richness, with a predominance of medium-sized omnivores and insectivores species; these conditions led to high defaunation indices. Community complexity was greater in areas with low human occupation, where carnivores (Felidae) were more abundant. Differences in species composition were also linked to altitudinal bands and the ratio of period of time with protected status versus history of land exploitation in a particular area. Analysis of functional groups indicated that intense human occupation had negative effects on larger species, a process that may have impending consequences. Despite defaunation being a serious ecological issue, we assert that taking prompt action may limit or potentially reverse effects of defaunation before the most dramatic changes take place.

Defaunação é uma questão ecológica chave e que só recentemente tem recebido atenção suficiente. Como previsto, as evidências até agora indicam perda de espécies de maior porte, seguida por espécies de médio porte, levando a efeitos em cascata que se propagam em todas as comunidades e ecossistemas. A Mata Atlântica está entre os mais importantes *hotspots* de biodiversidade mundiais. Essa região tem sido historicamente impactada pela perda e fragmentação de habitat, resultando em mudanças na paisagem e impactos negativos nas comunidades animais. Este estudo avalia características de comunidades de mamíferos de médio e grande porte na Mata Atlântica subtropical, sul do Brasil. Nós reunimos dados sobre ocorrência de mamíferos utilizando 108 armadilhas fotográficas instaladas em oito áreas protegidas. Em seguida, avaliamos se as diferenças de paisagem impactam a riqueza, composição e a complexidade das comunidades de mamíferos. Especificamente, nós usamos uma análise de árvore de regressão para avaliar as diferenças na composição das comunidades em função da configuração da paisagem. Analisamos dados de 26 espécies no total, com o número de espécies por área variando 9 a 17.

As alterações na composição de mamíferos na escala da paisagem foram mais fortemente associadas à ocupação humana. As áreas com maior ocupação humana tiveram baixa riqueza de espécies, com predominância de espécies onívoras e insetívoras de médio porte, e, estas condições geraram índices de defaunação elevados. A complexidade das comunidades foi maior em áreas com baixa ocupação humana, onde carnívoros (Felidae) foram mais frequentes. As diferenças na composição de espécies também foram ligadas às quotas de altitude, assim como à razão entre o período de tempo com estatuto de proteção e o tempo de exploração de cada área. A análise com abordagem de grupos funcionais indicou que a maior ocupação humana teve efeitos negativos sobre as espécies maiores, um processo com consequências negativas iminentes. Apesar da defaunação ser uma importante questão ecológica, nós acreditamos que um conjunto de ações conservacionistas imediatas podem potencialmente limitar ou reverter os efeitos da defaunação antes que mudanças mais dramáticas aconteçam.

Key words: camera trapping, carnivores, communities, composition, defaunation, ecology, human occupation

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Biodiversity loss and effects of the recently conceptualized “Anthropocene defaunation” are consequences of human activities and key components of global environmental change (Cardinale et al. 2012; Galetti et al. 2013; Dirzo et al. 2014; Ceballos et al. 2015). Habitat loss, fragmentation, hunting, and forest conversion into extensive agricultural and urban areas are the principal human-driven causes of defaunation and compositional changes in local vertebrate communities, which may produce strong side effects upon ecosystem functions (Canale et al. 2012; Galetti and Dirzo 2013; Dirzo et al. 2014). Notably, gradual loss of mammal species can generate cascading effects across several spatial and temporal scales. In the short term, mammal loss affects the structure and dynamics of populations and communities (e.g., reduction in seed dispersal and predation, and changes in trophic webs), whereas in the long term, effects of mammal loss can escalate to generate evolutionary changes. Such changes at any scale are capable of disrupting important ecosystem functions (Galetti and Dirzo 2013; Kurten 2013).

Mammal populations have the greatest rates of decline in tropical regions (Dirzo et al. 2014), of which the Brazilian Atlantic Forest presents a particularly worrying scenario. It is 1 of the 5 most important centers of biodiversity and endemism in the world (Myers et al. 2000), with 298 known mammal species, 90 of which are endemic (~30%—Paglia et al. 2012). Human occupation has reduced the Atlantic Forest to small, disturbed, and isolated fragments mixed with agro-mosaic matrices, human settlements, and roads (Tabarelli et al. 2005, 2010; Ribeiro et al. 2009; Lira et al. 2012). Previous studies of Atlantic Forest regions indicate that fragmentation and habitat loss prevent the maintenance of natural mammal assemblies by promoting reduction in population sizes and changes in species composition and by driving cascade effects (Pardini et al. 2010; Dotta and Verdade 2011; Galetti and Dirzo 2013).

Studies of Atlantic Forest mammal communities have mainly focused on the Northeast (e.g., Canale et al. 2012) and Southeast (e.g., Chiarello 1999; Galetti et al. 2009; Jorge et al. 2013) regions of Brazil. Effects of landscape changes on mammal communities have rarely been addressed the southern, subtropical portion of the Atlantic Forest. A similar pattern

is expected for this region, including increased probability of local extinction for large-body-sized species due to reduction in fragment size and hunting activities (Silva and Pontes 2008; Galetti et al. 2009; Canale et al. 2012; Kurten 2013), with subsequent effects threatening most endemic or large species (Galetti et al. 2009; Canale et al. 2012).

Defaunation introduces nonrandom impacts on the functional space of communities. The subtropical Atlantic Forest region in the state of Santa Catarina contains 152 known mammal species, although none of the medium or large species is endemic (Cherem et al. 2004). Although some population studies have been carried out at reduced space–time scales (Mazzolli 1993; Mazzolli et al. 2002; Oliveira-Santos et al. 2008, 2009, 2012; Mazzolli and Benedet 2009), there have been few ecological or conservation-based studies of medium- to large-sized mammal communities in large areas with fragmented landscapes (Cherem et al. 2007; Goulart et al. 2009).

The main human-induced change at the landscape scale is the conversion of native vegetation, which can destabilize key ecosystem properties and promote loss of resilience (Pardini et al. 2010). In addition to deterioration of natural vegetation, the remaining natural landscapes typically experience indirect effects of human activities, such as climate change (Barnosky et al. 2012). The resulting decrease in availability of suitable habitat reduces the population sizes of many animal species (Andr n 1994; Pardini et al. 2010; Dirzo et al. 2014) with potentially widespread effects due to climate change further reducing available habitat (de Chazal and Rounsevell 2009). Hence, we expect that many species will be lost under the current landscape configuration, which may result in functional changes in mammal communities (Brooks et al. 2002; Pardini et al. 2010; Estavillo et al. 2013).

The intricate relationships between historical conditions, the extent and intensity of landscape changes, and the legacy of previous human activities call for consideration of several factors when evaluating associations between wildlife habitat use and tolerance to landscape changes (Davidson et al. 2009; Morris and Rowe 2014). Although environmental determinants of species distribution and abundance patterns remain poorly understood at large spatial scales, species are generally sorted

by forest type at smaller scales (Galetti et al. 2009; Mathur et al. 2010). Changes at the habitat scale in the Northeast and Southeast Atlantic Forest have reduced species richness and decreased body size of remaining species, often resulting in the sole persistence of generalist or matrix-tolerant mammals (Chiarello 1999; Galetti et al. 2009; Canale et al. 2012; Jorge et al. 2013). We thus expect that subtropical Atlantic Forest landscapes with major native vegetation coverage, will have greater complexity in mammal communities due to the occurrence of large carnivores and large herbivores, and along distinct coverage types will occur species turnover. Conversely, landscapes with intense human occupation and a long history of human exploitation should be detrimental to large and specialized species, being less detrimental to and potentially favoring omnivores and medium-sized species. Current landscape conditions are much different than conditions prior to intensive human occupation, hence we expect mammal community composition to be most strongly influenced by land use, with variation in native vegetation or historical conditions showing only secondary effects on species distribution patterns.

Our main goal was to assess differences in the distribution of medium- to large-bodied mammal species and to evaluate potential changes in the functional composition of communities across distinct land uses and environmental gradients. We also investigated whether distinct landscape characteristics reduce mammal community complexity in subtropical Atlantic Forest areas where defaunation is highest and determined which species contribute most to deviations in defaunation values. We hypothesized that in the current landscape scenario human activities have an overwhelming effect upon communities, surpassing the ability of additional predictors to explain differences in mammal community structure and complexity.

MATERIALS AND METHODS

Study area.—We sampled mammal composition using 108 sample points distributed among 9 subtropical Atlantic Forest sites in Santa Catarina state, southern Brazil (26°27′–28°33′S; 48°48′–52°34′W). These points lie within 8 protected areas: 4 points in the Parque Estadual das Araucárias (PEA); 7 points in the Parque Estadual da Serra do Tabuleiro-A (PTA); 13 points in the Parque Estadual da Serra do Tabuleiro-B (PTB); 26 points in the Reserva Particular do Patrimônio Natural (RPPN) Caraguatá (RCA); 16 points in RPPN Chácara Edith (RCE); 6 points in the Reserva Biológica Estadual do Aguai (REA); 13 points in RPPN Leão da Montanha (RLM); 11 points in RPPN Rio das Furnas (RRF); and 12 points in RPPN Serra da Farofa (RSF; Fig. 1 and Supporting Information S1). All sites are now located within protected areas; however, they differ in period of time with protected status, and the length of time is affected by human exploitation.

The study region falls within the humid subtropics (Cfa) according to the Köppen–Geiger classification (Peel et al. 2007). In general, the seasons are well defined, and rainfall is evenly distributed throughout the year with an annual average of 1,700 mm. Temperatures vary greatly during the year,

ranging between -10°C and 40°C with an annual average between 11°C and 19°C (Monteiro 2001; Peel et al. 2007). The vegetation in the study region is Araucaria moist forest (Mixed Ombrophilous Forest [FOM]), including cloud forest and altitudinal grassland (in PEA, PTB (transition area), RLM, RRF, and RSF) and, to a lesser extent, dense rainforest (Dense Ombrophilous Forest [FOD]; in PTA, RCA (transition area), RCE and REA—IBGE 1992; (Supporting Information S1).

Mammal sampling.—We mounted 1 camera trap (Models: Tigrinus 6.0C, Tigrinus 6.0D and Bushnell) at each sampling point at different times between 2005 and 2011. Duration of camera sampling at each point ranged from 30 to 365 days, and our total sampling effort was 11,998 trap-days. In forest patches, we attached camera traps without baits to tree trunks at 30–40 cm height, intentionally placed on trails and paths naturally used by mammals. Camera traps were placed at an average distance of 1,521 ($\pm 1,110$) m, with a density of approximately 0.16 (± 0.38) camera traps per ha. Traps were active for approximately 111 (± 107) days at each point ($\sim 2,664$ h) with an average of 1,330 ($\pm 1,338$) camera trap-days (Supporting Information S2). Cameras operated autonomously for approximately 1,600 h, with verification of operation and maintenance performed nearly every 30 days. One exception was the PEA site, in which cameras were verified and maintained every 3 months (in this case, sampling effort was considered as only the days of operation between the first and last mammal record, varying from 30 to 339 days). For all analogical traps ($n = 62$, model Tigrinus 6.0C), trapping time was considered from the day of installation until the end of the photographic film.

We excluded both exotic and invasive species recorded if their presence was improbable in the sampled environments, including *Lontra longicaudis* and *Myocastor coypus* (associated with water bodies), and *Sapajus nigritus* and *Guerlinguetus ingrani* (tree-dwelling species). We also excluded small rodents (family Cricetidae) from all analyses, because they are certainly under-sampled using camera traps and because identification based on available data is prohibitively difficult. However, we opted to keep 1 small mammal (*Philander frenatus*) in the analysis due to ease of identification using photographic records and wide distribution (Costa et al. 2011). The only invasive species used in the analyses was *Lepus europaeus*, a species introduced to South America long ago (1888 in Argentina and 1896 in Chile, dispersing throughout the continent thereafter) and, to our knowledge, with no reported major impacts upon native fauna (Grigera and Rapoport 1983; Parera 2002; Reis et al. 2006). Next, we grouped and organized the species by dietary habit (carnivore, herbivore–frugivore, or omnivore–insectivore) and by body size (large, medium, or small) based on the literature (Parera 2002; Magioli et al. 2015).

Landscape characterization.—To describe coarse geographic characteristics among areas, we obtained altitude data (A) using GPS and relief data (R) obtained as the coefficient of altitudinal variation, using the ratio between the altitudinal average and sampling point standard deviation at each area, weighted according to variability (Supporting Information S3). We also obtained land use data by manual decomposition of

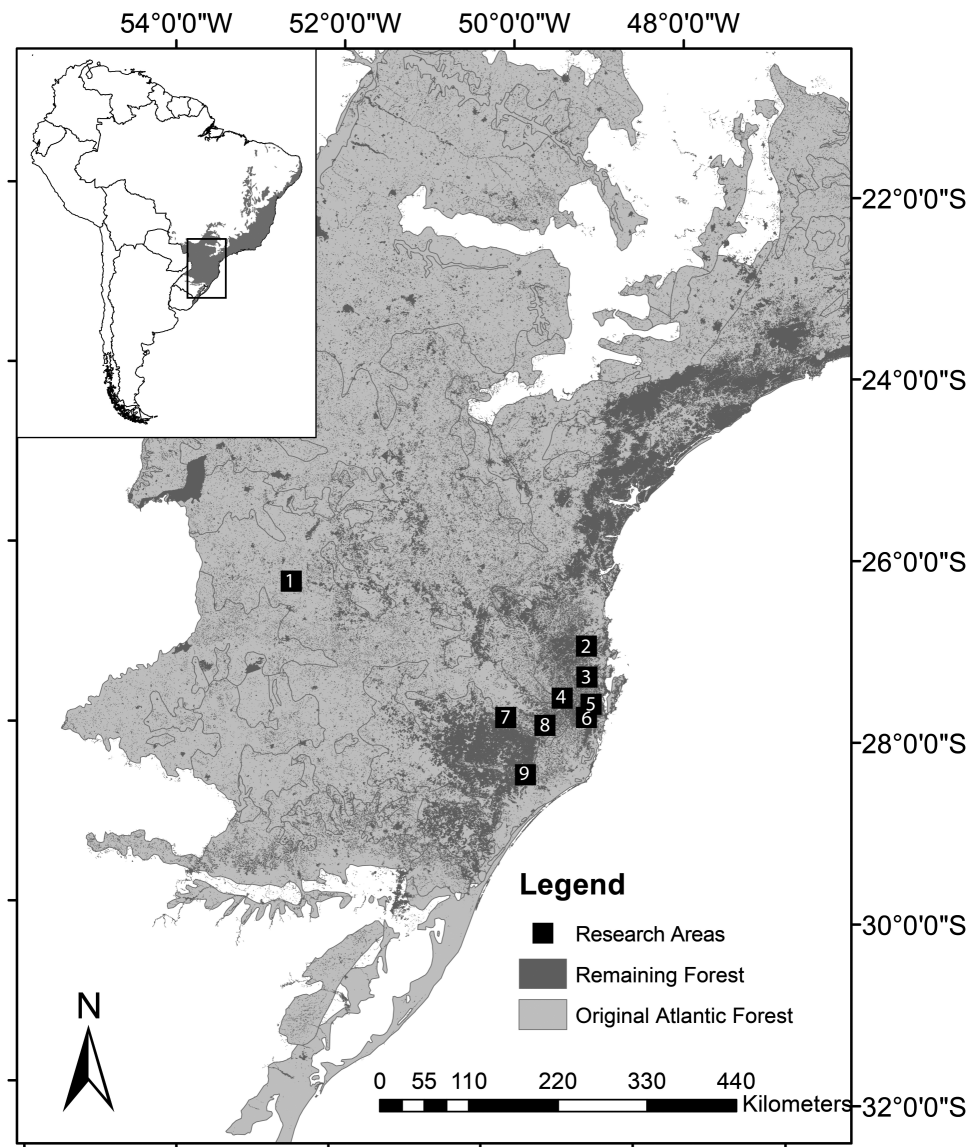


Fig. 1.—Location of research areas in Brazilian subtropical Atlantic Forest. Dark gray areas indicate remaining forest areas, and light gray areas indicate original forest areas. Areas are: 1: Parque Estadual das Araucárias (PEA); 2: RPPN Chácara Edith (RCE); 3: RPPN Caraguatá (RCA); 4: RPPN Rio das Furnas (RRF); 5: Parque Estadual da Serra do Tabuleiro (PTA); 6: Parque Estadual da Serra do Tabuleiro (PTB); 7: RPPN Serra da Farofa (RSF); 8: RPPN Leão da Montanha (RLM); and 9: Reserva Biológica Estadual do Aguai (REA).

high-resolution satellite images into 1 ha pixels (Estavillo et al. 2013). We applied this method to satellite images from 2010 and 2011, available in *Google Earth* (Google Earth 2014). We drew each landscape as an area of 36 km², including the extent of each area, combining surrounding lands and covering 324,000 ha in total. For each pixel, we verified the prevailing land cover class. We categorized the land cover into one of the following types: native forest (N) under any successional stage; native open areas (O), especially grasslands (considering vegetation formation, altitudinal profile, satellite images, and field observations); nonnative open areas (nO); using the same previous criteria); water bodies (W); human occupation (H; buildings and roads); and silviculture (S; monoculture of exotic species, especially *Pinus* sp. and *Eucalyptus* sp.). Based on this classification, we generated 1 chorological matrix for each

area showing land use in protected and adjacent areas, with the exception of grouping native and nonnative open areas. This matrix allowed us to obtain the full percentages of land cover type (Supporting Information S4).

We also calculated the median connectivity (C) of areas obtained by the percentage of native forest coverage by analyzing the perimeters of delimited area (36 km²). We then calculated fragment size (F) by the delimitation of a polygon along fragment perimeters, and isolation (I) as the distance from the edge of the sampled fragment (protected area) to the edge of the nearest fragment (Vieira et al. 2009) ignoring fragments smaller than 50 ha. Even though smaller fragments may serve as stepping stones between larger fragments (Haddad et al. 2003), we chose this size threshold because small fragments are generally less likely to be used by larger mammals, and because small

and large forest remnants vary widely in the number of species they contain (Canale et al. 2012).

Lastly, we obtained the (P:E) ratio between time under protection and time being exploited. Protection time was considered the number of years in each area from the legal establishment of “protected” status and 2015. Exploitation time was the number of years between the initiation of logging activities in each region (Eduardo 1974) and the legal establishment of protected status.

Data analysis.—We initially compared species richness among areas. We used only independent photographic records by area, excluding photographs of the same species at the same point at intervals shorter than 1 h (Gómez et al. 2005; Di Bitetti et al. 2006; Oliveira-Santos et al. 2008, 2009). Next, we used rarefaction curves with 95% confidence intervals (Magurran 2004; Colwell et al. 2012) to compare species richness among areas using both a minimum value of independent records and independent records relative to sampling effort (the ratio between the number of independent records and camera traps/day/area).

We then calculated the defaunation index (D—Giacomini and Galetti 2013) for each area for both independent records and species presence–absence only. We set reference areas (RA) as the ones with highest species richness and numbers of independent records. We checked for defaunation under 2 different scenarios: D_{bs} , species importance value (ω) indicated by body size (average species mass, obtained from Parera 2002; Oliveira and Cassaro 2005; Paglia et al. 2012; Giacomini and Galetti 2013) elevated to the power of $\frac{3}{4}$ (Brown et al. 2004; Hansen and Galetti 2009; Giacomini and Galetti 2013), and D_{eq} , where all species had the same importance ($\omega = 1$ —Giacomini and Galetti 2013). We assessed whether defaunation index decreased because of increasing species richness using Pearson linear correlations. We further calculated the defaunation index by deconstructing communities into trophic guilds, adopting the same criteria as above. Afterwards, we performed a canonical correspondence analysis (CCA—Borcard et al. 2011) to rank sites and species depending on defaunation index values obtained from independent records and presence–absence data, thereby assessing the main species contributing to the ordination in the CCA space. For the CCA, independent record asymmetries were Hellinger transformed (Borcard et al. 2011), and presence–absence data were not transformed.

To determine whether a set of candidate variables was able to explain differences in mammal composition among areas (e.g., species occurrence in the same place at same time [Fauth et al. 1996; Magurran 2004]), we analyzed data with multivariate regression trees using the information from replicated points in each area as sampling units (De’ath 2002). Regression trees aim to select variables amenable to grouping sampling units such that groups are homogeneous, and the differences between groups are maximized. We included as predictors the proportion of the 6 distinct land cover types described above, as well altitude (A), connectivity (C), relief (R), fragment size (F), isolation (I), and the ratio between protection and exploitation time (P:E). We set maximal tree size interactively by cross-validating

the results, then using classification error and its standard error to indicate the ideal number of splits. We showed the resulting classification with a PCA (correlation) on species by area (De’ath 2002; Borcard et al. 2011; De’ath 2014). We performed analyses in R (R Core Team 2015) using vegan (Oksanen et al. 2013) and mvpart (De’ath 2014) packages.

RESULTS

Mammal richness and defaunation index.—We sampled 2,165 mammals, with 1,595 independent records. We recorded 26 species in total, ranging from 9 to 17 species per area (all independent records, including species not considered in our analyses, are listed in Supporting Information S5). Rarefaction curves and confidence intervals confirmed that species richness follows an increase in mammal richness among areas, with differences in the extreme values yet overlapping intervals, even when considering differential sampling effort. However, when independent records are made relative to sampling effort, the curve did not stabilize in some areas (RSF, RLM, and PTB) despite those areas having large sampling effort (Supporting Information S2 and S6).

The defaunation index showed that the area with greatest defaunation is PTA (independent records: $D_{bs} = 0.79$, $D_{eq} = 0.72$; presence–absence: $D_{bs} = 0.55$, $D_{eq} = 0.31$; Supporting Information S7). Species richness was negatively correlated with defaunation (D_{bs} : $r = -0.87$, $P < 0.01$; D_{eq} : $r = -0.99$, $P < 0.01$, both based on presence–absence data; Fig. 2). The greatest extent of defaunation was in PTA and PEA for carnivores, in PTA and REA for herbivores, and in PTA and RRF for omnivores (Supporting Information S7).

The CCA showed that, for independent records, 56.4% of variation was explained by axis 1 and 31.1% by axis 2, with herbivore defaunation explaining the bulk of the variation on axis 1 and carnivore defaunation on axis 2 (Supporting Information S8). The main species that contributed to the values in axis 1 were *Mazama nana*, *Mazama americana*, and *Cuniculus paca*, and *Puma concolor* and *Puma yagouaroundi* on axis 2. Results from the CCA using presence–absence data showed that axis 1 accounted for 23.8% of the total variation and axis 2 accounted for 15.8%. The 1st axis is connected more strongly to defaunation values for omnivores and herbivores, and the 2nd axis to defaunation values for herbivores and carnivores (Supporting Information S8). The most common species in the analysis using presence–absence data were *Tayassu pecari*, *Lycalopex gymnocercus*, *Tapirus terrestris*, *Mazama americana*, *Mazama nana*, *Mazama gouazoubira*, *Puma concolor*, and *Leopardus pardalis*.

Mammal composition across landscapes.—The regression tree analysis resulted in 6 groups and explained 24.1% of the total variation in mammal composition (Fig. 3A; error = 0.773, cross-validation relative error = 0.883 [± 0.036]; Supporting Information S9). The 1st split explained 6.7% of the differences in mammal composition and was a function of land use, with a threshold around 15% human occupation (H). Points with land use under 15% human occupation (H) were next grouped by

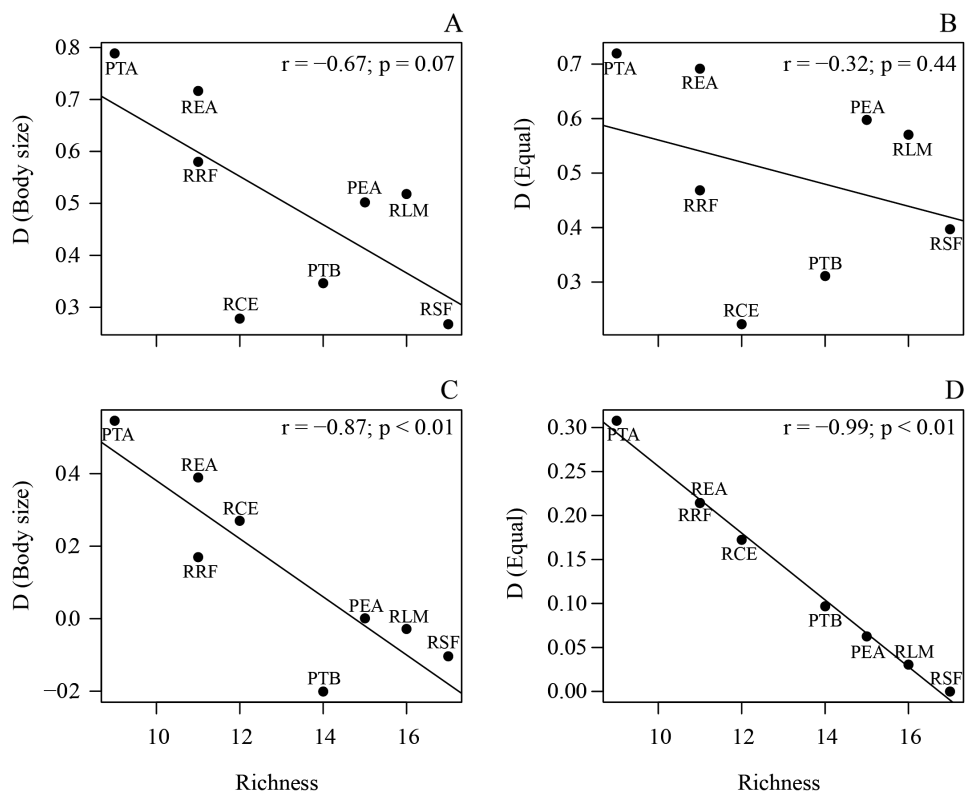


Fig. 2.—(A) Correlation between defaunation index (with independent records) by richness and weighted body size; (B) correlation between defaunation index (with independent records) with nonweighted body size and richness; (C) correlation between defaunation index (with presence–absence) by weighted body size and richness; (D) correlation between defaunation index (with presence–absence) by nonweighted body size and richness. PEA: Parque Estadual das Araucárias; RCE: RPPN Chácara Edith; RCA: RPPN Caraguatá; RRF: RPPN Rio das Furnas; PTA: Parque Estadual da Serra do Tabuleiro-A; PTB: Parque Estadual da Serra do Tabuleiro-B; RSF: RPPN Serra da Farofa; RLM: RPPN Leão da Montanha; and REA: Reserva Biológica Estadual do Aguaf.

altitude (A), with a threshold of 1,299 meters above sea level (m.a.s.l.) explaining 5.9% of the residual deviation. Points over 1,299 m.a.s.l. were then grouped by the ratio between protection and exploration time (P:E) with a threshold of 0.15, explaining 4.3% of the residual deviation. Points with P:E > 0.15 were split based on native forest cover (N) with a threshold of 42%, explaining 2.9% of the residual deviation. Finally, areas with N > 42% were split regarding the extent of relief variation (R) with a threshold of 50%, explaining 2.9% of the residual deviation. All multivariate regression estimates, node splits, and the ordination in PCA space were similar after removing *Philander frenatus* from the analysis.

Species scores (indicating the chance of species occurrence within groups resulting from the regression trees) show displacement of foraging guilds (bars in Fig. 3A; Supporting Information S10). Guild composition under higher human occupation showed prominence of omnivores and insectivores species. Under both low human occupation and high altitude (> 1,299 m.a.s.l.), guild composition was more even and diverse than in all other groups. Under low P:E ratios (short protection time versus exploitation time), there was a decrease in proportional presence values for many species, without a specific bias to any trophic guild. For P:E ratios below 0.15, native forest cover (N) and relief (R) account for additional differences in relative guild occurrence. First, areas with less than

42% native vegetation cover showed higher evenness between guilds, but with a lower number of carnivores. Second, in areas with greater vegetation cover, guild composition responded to relief variation with a greater number of carnivores, omnivores, and insectivores in areas with rough terrain and, remarkably, increased numbers of herbivores and frugivores in flatter areas.

The ordination explained 39.53% and 24.28% on the first 2 axes, adding up to 63.8% of the total variation in the species matrix (Fig. 3B). The 1st axis was explained mostly by human occupation and altitude and the 2nd axis by P:E ratio and marginally altitude (Fig. 3B). The 2nd ordination axis indicated replacement of medium-sized and generalist species (axis 1) by large-sized or more specialized species (Fig. 3B). The 1st group (G1) included the 5 species with the highest overall relative occurrence; the 2nd (G2) included 1 species; the 3rd (G3), 6 species; the 4th (G4), 9 species; the 5th (G5), 4 species; and the 6th (G6), 3 species. *Puma yagouaroundi*, *Dasyprocta azarae*, *Cerdocyon thous*, *Cabassous tatouay*, and *Didelphis aurita* had the greatest probability of presence in areas with higher human occupation (G1), although additional species had high importance scores (*Nasua nasua* and *Procyon cancrivorus*). *Lycalopex gymnocercus* was more likely to occur in areas with less human occupation and higher altitude (G2). *Puma concolor*, *Leopardus wiedii*, *Mazama gouazoubira*, *Lepus europaeus*, *Nasua nasua*, and *Philander frenatus* tend

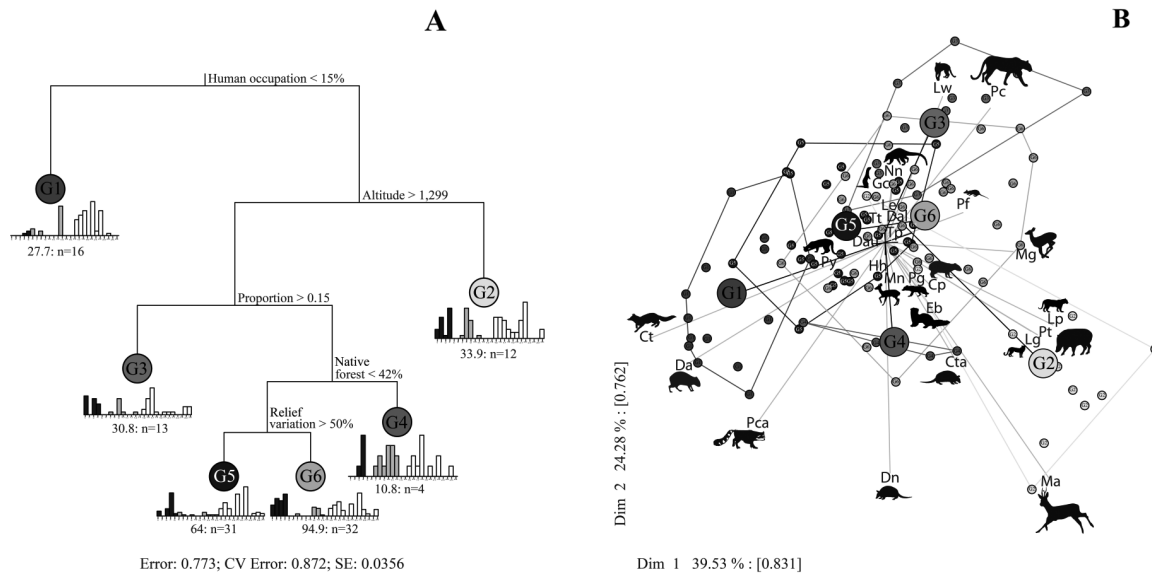


Fig. 3.—(A) Regression tree for responses in mammal composition due to different thresholds of land cover in protected Atlantic Forest areas in Santa Catarina state, Brazil. The bars below the final junctions represent changes in mammal species, and height describes the probability of occurrence of each mammal species in that particular land cover condition (i.e., proximity to a value of “1” and including hierarchical effects from superior groups) based on recursive partitioning of the regression tree. Black bars represent the carnivore guild; gray bars represent herbivores/frugivores; and white bars represent omnivores/insectivores. The order of species in the bars are in the Table 1. The values below the bars represent the similarity between all sampling units within the unfolding compared to a split with the same number of observations (N), being a measure of residual variation (unexplained variation). Example interpretation for the variation of mammal composition in different conditions is presented in Supporting Information S6. (B) Principal component analysis (PCA) spatially ordering the different sample points and their species occurring under certain conditions, according to the junctions formed by regression tree analysis. The groupings represent, hierarchically: (G1): areas and their respective points where human occupancy (H) is greater than or equal to 15%; (G2): areas where the altitude (A) is higher than 1,299 meters above sea level (m.a.s.l.); (G3): areas where the proportion of time between protection and exploitation (P:E) is less than or equal to 0.15; (G4): areas where native forest cover is less than 42%; (G5): areas where the relief variation is less than 50%; and (G6): areas where the relief variation is greater than 50%. Species names abbreviations in Table 1.

to occur in areas with low human occupation, low altitude, and low P:E ratios (G3). *Leopardus guttulus*, *Hydrochoerus hydrochaeris*, *Mazama americana*, *Mazama nana*, *Cuniculus paca*, *Pecari tajacu*, *Eira barbara*, *Procyon cancrivorus*, and *Galictis cuja* were more likely to occur under low human occupation, low altitude, high P:E ratios, and low native forest cover (G4). *Tapirus terrestris*, *Tayassu pecari*, *Dasypus novemcinctus*, and *Didelphis aurita* frequently occurred in areas with low human occupation, lower altitude, higher proportion time, low forest cover, and low relief variation (G5). *Leopardus pardalis*, *Didelphis albiventris*, and *Didelphis aurita* were more likely with low human occupation, low altitude, high P:E ratios, low forest cover, and high relief variation (G6; Table 1).

DISCUSSION

Current gaps in knowledge limit our understanding of the range of impacts associated with the Anthropocene defaunation (Dirzo et al. 2014), and the loss of species we currently face is much greater than the natural background loss (Ceballos et al. 2015). After analyzing historical, geographical, and land use aspects, our results show that anthropogenic alteration has become a more important factor for explaining mammal distribution than solely environment. Thus, with a continuum decrease of species richness between areas, we found high defaunation indices for

most areas, with land use differences shifting mammal composition and, more importantly, promoting functional alterations across communities (mostly due to the absence of large species with restricted diets). Reduction in the distribution of larger species is probably leading to yet unknown effects upon ecosystem functions and serves as additional evidence for widespread defaunation leading to dramatic future global ecological changes, with potential to exacerbate current mass extinction events (Dirzo et al. 2014; Ceballos et al. 2015). Our study adds to the growing body of evidence indicating that after natural and anthropogenic changes, shifts in species composition are not functionally random (Galetti et al. 2009). Despite extinction risk likely resulting from a combination of body size and additional ecological traits (Davidson et al. 2009; Smith and Lyons 2011), theoretical and empirical data indicate that human populations can drive local extinctions (Foley et al. 2005; Canale et al. 2012; Cassano et al. 2012; Tabarelli et al. 2012), decrease population sizes, and impact species composition in communities (Foley et al. 2005).

Large mammals and carnivores are generally lost first (Canale et al. 2012; Dirzo et al. 2014), and hunting may be a decisive factor contributing to these local extinctions (Mazzolli 2008). Carnivores, especially large-sized animals, use extensive areas to search for prey (Peters 1983; Mazzolli 2008; Mazzolli and Hammer 2008), and landowners may pursue

Table 1.—Relative presence of mammals and landscape conditions in each group formed in the regression tree of protected areas located in Atlantic Forest at Santa Catarina state, Brazil. TG—Trophic Guild: C—Carnivores, H/F—Herbivores/Frugivores, O/I—Omnivores/Insectivores; BS—Body Size: L—Large, M—Medium, S—Small; N In—number of points (in 108) where a species is recorded; N—species number; SA—species abbreviation. See meaning of the color groupings in the legend of Fig. 3A. Values in bold representing the highest probability of occurrence of the species for the regression tree grouping.

TG	BS	N	SA	Species	N	Relative presence (Range 0 to 1) in Groups (G)						
						In	G1	G2	G3	G4	G5	G6
						108	Red	Yellow	Green	Purple	Dark Blue	Light Blue
C	L	1	Pc	<i>Puma concolor</i>	24	0.00	0.26	0.54	0.00	0.13	0.31	
C	M	2	Lp	<i>Leopardus pardalis</i>	23	0.00	0.25	0.00	0.00	0.00	0.50	
C	S	3	Lw	<i>Leopardus wiedii</i>	29	0.06	0.30	0.46	0.25	0.19	0.44	
C	S	4	Lg	<i>Leopardus guttulus</i>	59	0.13	0.62	0.31	1.00	0.61	0.63	
C	S	5	Py	<i>Puma yagouaroundi</i>	5	0.19	0.02	0.00	0.00	0.06	0.00	
H/F	L	6	Tt	<i>Tapirus terrestris</i>	3	0.00	0.03	0.00	0.00	0.10	0.00	
H/F	L	7	Hh	<i>Hydrochoerus hydrochaeris</i>	8	0.13	0.07	0.08	0.25	0.03	0.06	
H/F	L	8	Ma	<i>Mazama americana</i>	12	0.00	0.13	0.00	0.50	0.00	0.00	
H/F	M	9	Mg	<i>Mazama gouazoubira</i>	14	0.00	0.15	0.46	0.25	0.03	0.00	
H/F	M	10	Mn	<i>Mazama nana</i>	4	0.00	0.04	0.08	0.75	0.00	0.00	
H/F	M	11	Cp	<i>Cuniculus paca</i>	12	0.00	0.13	0.00	0.75	0.00	0.25	
H/F	S	12	Da	<i>Dasyprocta azarae</i>	25	0.81	0.13	0.00	0.50	0.10	0.22	
H/F	S	13	Le	<i>Lepus europaeus</i>	3	0.00	0.03	0.08	0.00	0.03	0.03	
O/I	L	14	Tp	<i>Tayassu pecari</i>	1	0.00	0.01	0.00	0.00	0.03	0.00	
O/I	L	15	Pt	<i>Pecari tajacu</i>	18	0.00	0.20	0.15	0.25	0.03	0.22	
O/I	M	16	Eb	<i>Eira barbara</i>	38	0.44	0.34	0.46	0.50	0.19	0.31	
O/I	M	17	Nn	<i>Nasua nasua</i>	50	0.56	0.45	0.77	0.25	0.35	0.41	
O/I	M	18	Pca	<i>Procyon cancrivorus</i>	30	0.69	0.21	0.08	1.00	0.19	0.16	
O/I	M	19	Pg	<i>Lycalopex gymnocercus</i>	2	0.00	0.02	0.00	0.00	0.00	0.00	
O/I	M	20	Ct	<i>Cerdocyon thous</i>	48	0.94	0.36	0.08	0.25	0.58	0.34	
O/I	M	21	Cta	<i>Cabassous tatouay</i>	9	0.13	0.08	0.08	0.00	0.00	0.00	
O/I	M	22	Dn	<i>Dasytus novemcinctus</i>	71	0.69	0.65	0.08	0.50	0.77	0.66	
O/I	M	23	Dal	<i>Didelphis albiventris</i>	6	0.00	0.07	0.00	0.00	0.00	0.19	
O/I	M	24	Dau	<i>Didelphis aurita</i>	5	0.06	0.04	0.00	0.00	0.06	0.06	
O/I	S	25	Gc	<i>Galictis cuja</i>	7	0.00	0.08	0.23	0.25	0.10	0.00	
O/I	S	26	Pf	<i>Philander frenatus</i>	14	0.00	0.15	0.23	0.00	0.06	0.19	

these predators due to actual or perceived risk of predation upon domestic animals (Mazzolli et al. 2002; Marchini et al. 2011). Predation upon domestic animals by carnivores is enhanced by the reduced availability of important prey species in the natural environment (Mazzolli and Hammer 2008; Martins et al. 2008). The 1st issue regarding the loss of large animals, including predators or primary consumers, involves effects on trophic webs (Galetti and Dirzo 2013) in which communities can be rearranged by changes in seed dispersal, seed predation, and herbivory (Kurten 2013). Changes in the abundance and distribution of organisms, especially consumers, may cause ecosystem changes; this notion is supported by evidence in the literature showing top-down cascading effects (Hairston et al. 1960; Fretwell 1987; Power 1992; Estes et al. 2011).

Areas with the highest human impact were dominated by medium-bodied omnivores–insectivores (e.g., *Cerdocyon thous*, *Nasua nasua*, and *Procyon cancrivorus*), small herbivores–frugivores (e.g., *Dasyprocta azarae*), and 1 small carnivore (*Puma yagouaroundi*). These species are common in disturbed landscapes and are mainly generalists with strong plasticity in habitat and resource use (Parera 2002; Reis et al. 2006; Dotta and Verdade 2011; Canale et al. 2012). Physiological responses showed that *Chrysocyon brachyurus* (medium-sized omnivore), although sensitive to disturbance,

makes use of landscape matrix mosaics that are highly modified (converted to farmland) in the Cerrado (Vynne et al. 2014). Because areas located at higher altitudes have also lower human density, there is a cumulative effect from decrease in both human land occupation and additional human-driven impacts. Consequently, these areas showed the highest species and structural complexity, with particularly high probability of finding carnivore and herbivore species that were uncommon elsewhere. Despite altitude being a proxy for spatial processes such as dispersal limitation, lack of adaptation to increased seasonality, and lower availability and quality of food (Bonvicino et al. 1997; Geise et al. 2004), we suggest that lower human impact made these areas into refuges for sensitive species. Specifically, lower population density and harsher terrain may limit species disturbance in these areas by virtue of being less accessible to hunters (Canale et al. 2012), and due to reduction of usable land for domestic livestock (Mazzolli 1993).

Historical factors and their legacy can also explain patterns in regional species pools and local communities (Ricklefs 2006). Areas located at higher altitudes are also those that have been legally protected for less time, showing that even recent changes in policy and conservation priorities in the region may have benefited carnivores (e.g., *Puma concolor* and *Leopardus wiedii*) that were more abundant in these areas. Poorly explained distribution

or atypical placement of species in the regression tree and ordination may be due to either undersampling or other unaddressed factors in this study. For example, *Hydrochoerus hydrochaeris* and *Lycalopex gymnocercus* are associated with water bodies and open fields, respectively (Reis et al. 2006). Because camera traps were placed in forest patches, the probability of detecting these species was low. Conversely, despite *Didelphis* spp. being generalist in habitat use, tolerant to disturbed environments, and with semiarboreal habits (Parera 2002; Cáceres et al. 2009; Oliveira et al. 2014) the pattern obtained in this study suggest that were likely undersampled. Additionally, *Tayassu pecari* and *Tapirus terrestris* have been intensely hunted and require large areas for population maintenance (Redford and Robinson 1987; Jorge et al. 2013), possibly explaining the rarity and suggesting low population densities. Many of these species have similar values in all groups of the regression tree, indicating that they occur in many distinct areas, except for *Tayassu pecari* and *Tapirus terrestris*. Despite using presence–absence data to avoid problems with abundance information due to different detection probabilities, 1 potential concern is that differences in sampling effort can still bias presence–absence data. Even areas with the highest sampling effort may have been incompletely sampled, as indicated by their rarefaction curves. However, the additional effort required to sample additional, potentially rare species increases steeply, limiting the ability to obtain complete samples (Colwell et al. 2012).

Our finding that land use differences along with historical and geographic constraints change mammal communities is becoming increasingly well documented, adding to the known effects of habitat loss and fragmentation (e.g., Peres and Palacios 2007; Silva and Pontes 2008; Canale et al. 2012 for medium and large species, and Vieira et al. 2009; Estavillo et al. 2013 for small species). Such filtering of species due to changes in habitat and landscape characteristics can modify interspecific competition and agonistic interactions, which can amplify differences in community composition prior to and after changes (Palomares and Caro 1999; Oliveira et al. 2010). Thus, historical differences in exploitation, changes in land use, and the introduction of exotic species can drive to changes in species interactions and in community composition - perhaps favoring numerically some species over others.

Five areas showed high defaunation indices (PTA, REA, PEA, RCE, and RRF) for both mammal communities as a whole and based on trophic guilds. We found no support for a single driver of defaunation in these areas except that all areas were undergoing landscape changes due to various factors, indicating that different sources of change can lead to similar results, namely defaunation and potential functional imbalances. Specifically, RCE is within a nearly impermeable landscape matrix because of its highly occupied surroundings; PEA has very small fragments and low native forest cover interspersed among farming crops; and PTA's northern borderlines fall near a highway with high traffic density (BR-282), which can potentially negatively impact animal dispersal and cause road kills. Further, some species may be absent in these areas due to either hunting or lacking the required habitats. These conditions are partly explained by

the species that contributed most to the defaunation values in our study, which were large and medium herbivores (*Mazama* sp. and *Cuniculus paca*) and large- and medium-sized carnivores (*Puma concolor* and *Leopardus pardalis*), and by rare species (*Tayassu pecari*, *Tapirus terrestris*, and *Lycalopex gymnocercus*). Guild defaunation indices are obviously related to the corresponding guild richness in these areas. In general, guild defaunation indices decreased with increasing richness, and the few negative defaunation values found indicate that some species may have been favored by either reintroductions or changes to their protection status (Giacomini and Galetti 2013). The few negative defaunation rates were linked to 3 species with single records and species recorded in few areas (e.g., *Leopardus pardalis* and *Mazama americana*). *Tapirus terrestris* in particular was part of a reintroduction program in the 1980s. The offspring of the reintroduced individuals still inhabits some Restinga areas of the Parque Estadual da Serra do Tabuleiro, where this species was recorded (Brusius 2009), in semicaptive conditions. *Tapirus terrestris* and *Tayassu pecari* are regionally endangered (EN) and critically endangered (CR), respectively (Santa Catarina 2011). *Leopardus pardalis* and *Mazama americana* are regionally endangered, and the threatened status may have had positive effects by means of directed conservation efforts and monitoring.

As defaunation and changes in mammal communities become common phenomena, large-bodied and endemic species will likely continue to be affected; the consequences of those effects are becoming increasingly evident (Jorge et al. 2013). While populations of large-sized species decrease, medium-sized mammals are becoming important targets for hunters and are thus predicted to be the next group to decrease to critical values as fragmentation and habitat destruction continue (Redford 1992; Kurten 2013). Moreover, it is clear that even currently common species can no longer thrive in landscapes dominated by humans (Pereira and Novaro 2014). Degree of habitat specialization is an important determinant of species vulnerability to landscape changes (e.g., fragmentation and habitat loss) and can determine capacity for dispersal and thus the degree of isolation of populations (Püttker et al. 2013). Under the current landscape scenario, the spatial arrangement of habitat patches is important, and small fragments can assist in functional connectivity of the landscape, acting as stepping stones for several species (Andr n 1994; Haddad et al. 2003).

Consequently, 2 important questions arise: Is there a way to prevent or reverse defaunation? And what is the financial burden of protecting the Atlantic Forest? Several conservation plans have been proposed to mitigate defaunation, including reintroduction and reinforcement, assisted colonization, and rewilding (Seddon et al. 2014). Yet, the most straightforward methods appear to be increasing the size and number of protected areas or reducing the intensity of human impacts on landscapes. Astonishingly, costs to preserve 30% of the Atlantic Forest area in Brazil were recently estimated at 198 million dollars per year or 0.0092% of the annual Brazilian GDP, by government payments to landowners to keep ecological set-asides (Banks-Leite et al. 2014). Reversing or slowing down defaunation in the Atlantic Forest is

thus possible and practical, although largely dependent on financial and political decisions (Galetti et al. 2010).

In summary, variation in species richness was low across landscapes, with only a 7 species difference between landscapes with the lowest and highest richness. We found defaunation indices associated with the loss of large herbivores and carnivores, and important shifts in species composition associated with landscape characteristics. We discovered key effects of anthropogenic impacts upon landscapes, increasing concerns about the threats to the Atlantic Forest. We suggest that mammal community composition is deeply linked to both current and historical landscape changes. Chiefly, intensive human land use changes mammal distribution and selects different trophic guilds and larger species. These phenomena further predict cascading effects with consequences for entire communities. Although defaunation is a key ongoing ecological issue, we believe that prompt action may prevent more dramatic scenarios by directing specific funding toward increasing the extent of ecological refuge.

ACKNOWLEDGMENTS

This study was funded by scholarships to JAB (CAPES, DS) and post-doctoral fellowships to ELHG (PNPD, CAPES). We thank M. Galetti and another anonymous referee for excellent considerations; R. W. Coffin and FATMA for allowing field research at the Reserves; F. V. B. Goulart for his help in fieldwork; and Conservation International—Brazil, RPPN Caraguatá, Klabin S.A., and FUNPESQUISA/UFSC for logistical support.

SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Political, historical, geographical, landscape, and land use of 9 Conservation Units located in subtropical Atlantic Forest, Brazil.

Supporting Information S2.—Details of mammals sampling effort in each area researched in subtropical Atlantic Forest, Brazil.

Supporting Information S3.—Formula to determine the variability of topography in 9 Atlantic Forest areas located in 8 protected areas in Santa Catarina, Brazil.

Supporting Information S4.—(A) Percentage of landscape coverage (uniting native open areas/grasslands and nonnatives as open areas) in areas of subtropical Atlantic Forest, Brazil. (B) Chorological matrix demonstrating the spatial distribution of each coverage type in each area and altitudinal profile.

Supporting Information S5.—Species list of mammals recorded (number of independent records and between parenthesis the proportion of points that were recorded) in 9 subtropical Atlantic Forest areas.

Supporting Information S6.—Rarefaction curves for medium- to large-bodied mammals registered in 9 Atlantic Forest areas located in 8 protected areas in Santa Catarina, Brazil.

Supporting Information S7.—Defaunation indexes for 9 Atlantic Forest areas located in 8 protected areas in Santa Catarina, Brazil.

Supporting Information S8.—Canonical correspondence analysis (CCA) for the defaunation index (by trophic guild) in 9 Atlantic Forest areas located in 8 protected areas in Santa Catarina, Brazil.

Supporting Information S9.—Sizes and x values of relative error at regression tree analysis for spatial data and medium- to large-bodied mammals records in 9 Atlantic Forest areas located in 8 protected areas in Santa Catarina, Brazil.

Supporting Information S10.—Example for interpreting variation in the composition of mammals generated under different conditions in the regression tree.

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Submitted 25 March 2015. Accepted 23 December 2015.

Associate Editor was Marcus V. Vieira.