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Mammal defaunation as surrogate of trophic cascades in a biodiversity hotspot

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ABSTRACT

Preserving large tracts of natural habitats is essential to maintain biodiversity. Nevertheless, even large areas may still suffer from less “visible” impacts such as loss of ecological processes. Because mapping ecological processes over large scales is not practical, an alternative is to map surrogate species that are key for those processes. In this study, we chose four species of Neotropical large mammals (the largest apex predator: jaguar – *Panthera onca*; the largest herbivore: tapir – *Tapirus terrestris*; the largest seed predator: white-lipped peccary – *Tayassu pecari*; and the largest arboreal seed disperser: miquiri – *Brachyteles* spp.) in an ecosystem with an old history of human impact (the Atlantic Forest) to test whether areas with native forest still harbor ecological processes that may guarantee long-term ecosystem maintenance. We gathered 94 locations with recent presence of the four species to map current ranges and model suitable areas. Our results reveal that 96% of the remaining Atlantic Forest is depleted of at least one of the four surrogate species and 88% is completely depleted of all four surrogate species. We also found that only 16% is still environmentally suitable for all four, and 55% is completely unsuitable to all four of them. Our study highlights the importance of looking beyond land cover to fully depict intactness of natural areas, and suggests that ecosystems with a long history of human impact (such as the Atlantic Forest) may be suffering from ecological impacts not seen at a first glance.

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1. Introduction

Preserving large tracts of forest has been one of the main strategies to conserve biodiversity (Bruner et al., 2001; Peres, 2005). However, even large protected areas are suffering from human encroachment, logging, and hunting (Laurance et al., 2012) and in the long-term, some large natural areas may be unable to guarantee conservation of the entire biodiversity and ecosystem function due to loss of key ecological processes. One important step towards a more complete conservation strategy would be to identify preserved areas where key ecological processes are already missing. Yet, because directly mapping of ecological processes is not yet feasible, an alternative is to map surrogate species that may represent a more complete set of ecological interactions (because they have unique ecological roles, are the first to disappear from impacted areas, and are relatively easy to detect).

In Neotropical forests, one large species of carnivore and three groups of large herbivores (two species and one subfamily) fit all three criteria (unique ecological roles, first to disappear and easy to detect): the jaguar (*Panthera onca*), the tapir (*Tapirus terrestris*), the white-lipped peccaries (*Tayassu pecari*), and ateline primates

(Atelidae family; Atelinae subfamily). The jaguar is the largest top predator of the Neotropics (50–160 kg, Seymour, 1989), it is essential in regulating populations of large prey, particularly ungulates (Weckel et al., 2006), and its diet hardly overlaps with that of the second largest top predator, the puma (*Puma concolor* – Emmons, 1987; de Azevedo, 2008; Di Bitetti et al., 2010). The tapir is the largest Neotropical herbivore (150–250 kg; Padilla and Dowler, 1994), it is fundamental for long-distance seed dispersal of several large seeds as well as predation of seedlings (Fragoso, 1997; Galetti et al., 2001; Tobler et al., 2010), and its role does not overlap with that of other large seed dispersers such as ateline primates (Bueno et al., 2013) or seedling predators, such as the red-brocket deer (Bodmer, 1991). The white-lipped peccary (hereafter WLP) accounts for the largest vertebrate biomass of Neotropical forests (Kiltie and Terborgh, 1983), and it is an important seed predator with a unique role as ecosystem engineer (Beck, 2005; Keuroghlian and Eaton, 2009). Ateline primates (a subfamily represented by four genera – *Ateles*, *Brachyteles*, *Lagothrix*, and *Oreonax*) are responsible for the dispersal of one-quarter to fifty percent of Neotropical forests seeds, most of them large seeds (Stevenson, 2000; Dew, 2005; Russo et al., 2005; Link and Fiore, 2006; Martins, 2006). They have a very distinct foraging behavior and diet composition from Alouattine primates (howler monkeys – Martins, 2006, 2008), and produce a dispersal spatial pattern that differs from that

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of other dispersers of large seeds (Bueno et al., 2013). All four groups (jaguars, tapirs, WLP, and ateline primates) are also highly threatened by habitat loss, habitat disturbance and direct persecution (Peres, 1996, 2000; Conforti and de Azevedo, 2003; Jerozolinski and Peres, 2003; Zimmermann et al., 2005; Paviolo et al., 2008) and they are the first to disappear from hunted and fragmented areas (Chiarello, 1999; Peres, 2000; Michalski and Peres, 2007; Canale et al., 2012). Finally, where they still occur, their presence hardly goes unnoticed – either because of their negative impact on cattle and agriculture or because of their touristic charisma – and reports of their presence can be unmistakably checked by indirect methods (such as footprints, feces). Because of their key roles in structuring food webs, their high vulnerability to human impacts, and their relative easiness of detection, they are ideal to be used as surrogates of more complete food webs in Neotropical forests.

The Atlantic Forest is considered a global conservation priority as it contains one of the world's highest diversity of plants and vertebrates, high endemism, and many threatened species (Myers et al., 2000; Tabarelli et al., 2005). It also provides essential ecosystem services for one of the most populated areas of the world (Ditt et al., 2010). More importantly, due to its long history of human occupation (Dean, 1996), it is also invaluable in helping understanding long-term human effects on tropical systems (Laurance, 2009). In the present study, we use the jaguar, the tapir, the WLP, and the two ateline primates from the Atlantic Forest (*Brachyteles hypoxanthus* and *Brachyteles arachnoides*, hereafter mureiqui) as surrogate species to identify areas with more complete food webs. Jaguars, tapirs and WLP were historically broadly distributed throughout the entire biome (Eisenberg and Redford, 2000; Sanderson et al., 2002; Taber et al., 2008; Altrichter et al., 2012). Mureiquis have a more restricted geographic range, with a broad distribution within their range (Aguirre, 1971; Paglia et al., 2011). Our analyses accounts for that restriction. Identifying areas in the Atlantic forest where those four keystone and highly human-sensitive mammal species are not present anymore can be a strong indication of trophic downgrading (*sensu* Estes et al., 2011). It may also help understand long-term effects of human pressure that may go unnoticed where large blocks of natural habitat are still maintained.

2. Methods

2.1. Species presence records

We compiled information on recent presence records (later than 2000) of each of the four target species (jaguar, tapir, WLP, and mureiqui) using recently published reviews and National Action Plans (jaguar – Beisiegel et al., 2012; tapir – Medici et al., 2012; WLP – Keuroghlian et al., 2012; mureiqui – Paglia et al., 2011), references therein, and gray literature (such as unpublished theses and dissertations, and meeting abstracts) for the last 12 years, within Atlantic Forest biome limits. After a meticulous analysis of information gathered from each species, we only considered primary records (direct observations, vocalizations, feces, footprints, or fur) to ensure that records were indeed from the last decade or so. For each presence record, we gathered information on patch size and coordinates (latitude and longitude). We assumed that presence within a patch means that the species uses the entire patch. For modeling, we used coordinates of the record, when available; and patch centroid coordinates, when record coordinates were not available. We determined patch coordinates through figures and geographic references available from the source publication. Google earth imagery helped us to double-check location coordinates when needed. Because of the broad spatial scale of

our study (entire biome), and $\sim 1 \text{ km}^2$ resolution, we believe that patch coordinates were sufficiently accurate for our analyses.

2.2. Species potential current range

We modeled potential current range of each of the target species within the Atlantic Forest biome, considering the species presence as the dependent variable (presence points) and selected environmental variables as the predictors (Table 1). Range limits for jaguars, tapirs and WLP were the original limits of the Atlantic Forest biome, as the three species were originally distributed throughout the entire biome (Eisenberg and Redford, 2000; Sanderson et al., 2002; Taber et al., 2008; Altrichter et al., 2012). Range limits and analyses for mureiquis were restricted by mureiqui's historical geographic distribution (Aguirre, 1971; Hirsch et al., 2002) plus a 100-km buffer (to allow for possible locations beyond known boundaries that were never recorded).

Three groups of environmental layers were used: bioclimatic, altitude and landscape. Bioclimatic and altitude variables ($\sim 900 \times 900 \text{ m}$ spatial resolution) were obtained from the freely accessible global climate database WorldClim (www.worldclim.org, last accessed on December 20, 2012). The choice of bioclimatic variables was based on known natural history for the species.

Landscape variables were obtained from three sources: (1) the “human-density” layer was obtained from the freely accessible database of the Center for International Earth Science Information Network (www.ciesin.org, Gridded Population of the World v. 3, last accessed on December 20, 2012). (2) The “distance-to-road” layer was generated from a shapefile of existing roads, freely downloaded from the Brazilian Institute of Geography and Statistics (IBGE, www.ibge.gov.br, last accessed on December 20, 2012). (3) Finally, percentage of vegetation cover, and a set of multi-scaled functional forest amount maps that consider varying gap crossing capabilities ($n = 16$), were generated and are available for download at the Spatial Ecology and Conservation Lab (LEEC – UNESP/IB/Ecologia – Rio Claro, SP; www.rc.unesp.br/ib/ecologia/leec). Percentage of vegetation cover and functional forest amount were generated using a binary 50-m resolution forest map (0 = matrix, 1 = vegetation) as input. Percentage of vegetation was calculated by applying a moving window spatial filter of 900 m around each focal pixel. Functional forest amount layers were previously generated and analyzed by Ribeiro et al. (2009), and were calculated by summing all patches that were accessible from a focal patch, given a gap crossing capability of 0 to 1500 m, with steps of 100 m (see Martensen et al., 2008, 2012, and Appendix, Fig. A1 for details). That allowed us to include patch connectivity within the forest patch size variable to simulate dispersability. Input data on remaining vegetation were obtained from SOS Mata Atlantic foundation (2005, see Ribeiro et al., 2009 for details). To guarantee spatial consistence with other environmental layers, both the search radius for moving window, and the resolution for output maps of percentage of cover and functional forest amount were set to $\sim 900 \times 900 \text{ m}$.

Because there were 16 layers of functional forest amount (0 to 1500 m of gap crossing capability), we first modeled potential current range for each species using only the 16 layers of functional forest amount and chose the most important functional forest amount layer (the one with the highest contribution to the model's variation) to be used in the main analysis with all bioclimatic and landscape variables (Table 1).

For potential current range, we used the Maximum Entropy Software, Maxent 3.3.3 k (Phillips and Dudik, 2008). We chose to use MaxEnt for two main reasons: (1) we wanted to use a method that considered “presence-only” data as we felt uncomfortable in determining areas where the species were confirmed to be absent

Table 1

Variables used for the models of potential current range of muriqui (*Brachyteles* spp.), tapir (*Tapirus terrestris*), white-lipped peccary (*Tayassu pecari*), and jaguar (*Panthera onca*) using Maxent (version 3.3.3.k) within the Atlantic Forest biome.

Variable	Layer group	Source
Altitude	Relief	Global Climate Data www.worldclim.org
Annual mean temperature	Bioclimatic	Global Climate Data www.worldclim.org
Mean temperature diurnal range	Bioclimatic	Global Climate Data www.worldclim.org
Maximum temperature of the warmest month	Bioclimatic	Global Climate Data www.worldclim.org
Annual precipitation	Bioclimatic	Global Climate Data www.worldclim.org
Precipitation of the wettest month	Bioclimatic	Global Climate Data www.worldclim.org
Precipitation of the driest month	Bioclimatic	Global Climate Data www.worldclim.org
Percentage of vegetation cover	Landscape	LEEC – UNESP – Rio Claro (www.rc.unesp.br/ib/ecologia/leec)
Functional forest amount (16 layers: connectivity varying from 0 to 1500 m, with 100-m increments)	Landscape	LEEC – UNESP – Rio Claro (www.rc.unesp.br/ib/ecologia/leec)
Distance from nearest road	Landscape	Adapted from IBGE (www.ibge.gov.br)
Human density	Landscape	Center for International Earth Science Information Network (www.ciesin.org)

(we quote “presence-only” because although we input only presence records, MaxEnt’s algorithm randomly chooses background pixels as pseudo-absence to allow for modeling – Phillips, 2006); (2) among the “presence-only” methods, MaxEnt is currently the most widely used and seems to perform better than the alternatives (Elith and Graham, 2009).

To create the models for each species, we used 70% of the data for training and 30% for testing (Pearson, 2007). We sampled the data by bootstrapping with 10 random partitions with replacements and set the runs with a convergence threshold of 10^{-5} with 500 iterations, and with 10,000 background points. We used a logistic output format that resulted in continuous values for each grid cell from 0 (unsuitable) to 1 (most suitable). These values can be interpreted as the probability of presence of suitable environmental conditions for the target species (Veloz, 2009). The logistic threshold used to cut-off the models converting the continuous probability model in a binary model (0 = unsuitable, 1 = suitable) was the one that assumed the maximum test sensitivity plus specificity. Sensitivity is the probability that the model correctly predicts an observation of a species at a given site, and specificity is the probability that the model correctly predicts an absence (Liu et al., 2011). Maximizing the sum of sensitivity and specificity is equivalent to finding a point in the receiver operating characteristic curve (ROC) for which the tangent equals 1 (Cantor et al., 1999), or the areas with highest suitability (where the sum of sensitivity and specificity is maximized). We evaluated the models by their AUC values (area under the curve, or probability that a randomly chosen presence site will be ranked above a random site – Fielding and Bell, 1997), and omission error (Pearson, 2007). At the end of this step, we generated four binary maps (suitable or unsuitable), one per each target species (jaguar, tapir, white-lipped peccary and muriqui).

2.3. Suitability for all four species

We added the four resulting binary maps to generate the final map of potentially more complete food webs, so that the output final map varied from 0 (not suitable for any species) to 4 (suitable for all four species). Because muriqui has a more restricted historical geographic distribution than the other three species, we derived two final maps: one that included all four species and was delimited by muriqui’s historical geographic distribution (Aguirre, 1971; Hirsch et al., 2002) plus a 100-km buffer; and a second map, outside muriqui’s historical distribution, for which only the three other species (jaguar, tapir, and WLP) were accounted for.

Finally, since the four surrogate species are demanding in terms of spatial requirements and highly vulnerable to anthropogenic effects, we looked at our results within large and protected patches of Atlantic Forest’s remaining area. For large, we chose patches that

were equal to or larger than the smallest patch size where the most spatially demanding species (jaguar) can still be found (i.e. 100 km²; Fig. 1d). For protected, we considered strictly protected reserves (National Parks, State Parks, Ecological Stations, Biological Reserves, and Wildlife Refuges). Shapefiles of the post-processed remaining patches were obtained from the Spatial Ecology and Conservation Lab (LEEC – UNESP/IB/Ecologia – Rio Claro, SP). Shapefiles of the protected areas were freely obtained from the Brazilian Ministry of Environment website (www.ibama.gov.br, last accessed on July 01, 2012).

3. Results

3.1. Recent presence records

We gathered 94 localities with information about recent presence records of the four focal species (muriqui: 43; tapir: 58; white-lipped peccary: 32; and jaguar: 21 – Table A1, Fig. A2). Together, all 94 localities encompass 2.4 million ha, or only 12% of Atlantic Forest’s remaining area (considering Ribeiro et al., 2009). In other words, 88% AF’s remaining area is completely depleted of all four species. Furthermore, only five localities (or 4% of AF’s remaining area) still harbor all four (or all three) species together; therefore 96% of AF’s remaining area is depleted of at least one of the four surrogate species. Considering patches that are larger than 10,000 ha and protected, 58% of AF’s remaining area harbors at least one of the four large mammals, but only 20% harbors all four species. Therefore, 80% of the large and protected remaining AF is depleted of at least one of the four large mammals and 42% of the large and protected remaining AF is depleted of all four species.

Considering localities within muriqui’s historical range (hereafter WMR: 80 out of 94), 50 localities harbor one of the four species, 15 localities harbor two species, 13 localities harbor three species, and only two localities (or 3% of the remaining area) still harbor all four species. One is within the Serra do Mar continuum, which is the largest Atlantic forest remnant, and together with Serra da Bocaina National Park, encompasses over 500,000 ha of AF, only cut by roads. The other is Juréia-Itatins Ecological Station, which encompasses above 100,000 ha of native forest, and is located southwest of the Serra do Mar continuum, but disconnected from it by rural and urban development. Outside muriqui’s historical range (hereafter OMR – 14 localities total), four localities harbor one species, seven harbor two species, and only three localities (or 1% of AF’s remaining area) still harbor all three large mammals.

Muriqui can be found in fewer areas than tapir (43 vs. 58), but it is less restricted by fragment size (Fig. 1a), as it was recorded in very small patches (17 ha), up to patches larger than 500,000 ha. Its current area of occupancy is approximately 900,000 ha (or

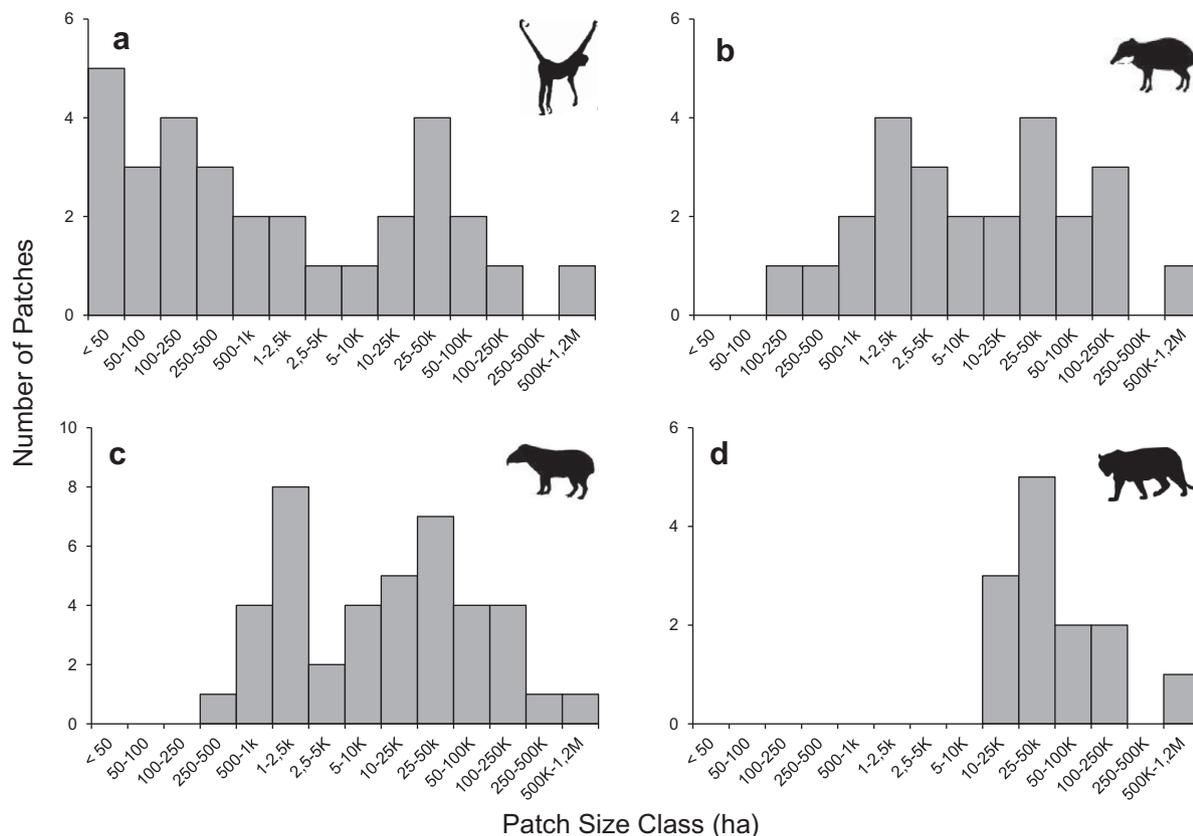


Fig. 1. Patch size distribution of the four surrogate species of the Atlantic forest: (a) murreti (*Brachyteles* spp.); (b) white-lipped peccary (*Tayassu pecari*); (c) tapir (*Tapirus terrestris*); (d) jaguar (*Panthera onca*).

10% of AF's remaining area WMR). White-lipped peccary (hereafter WLP) is more sensitive to fragment size (Fig. 1b). The smallest patch where it can be found is 166 ha, but less than 10% of the records (3/32) are in patches smaller than 1000 ha, whereas more than 30% (10/32) are in patches larger than 100,000 ha. Its current area of occupancy is approximately 1.3 million ha (8% of AF's remaining area). Tapir is even more sensitive to patch size than WLP (Fig. 1c), but was recorded in more areas than both murreti and WLP (58 vs. 32 and 43). Less than 7% of the records (4/58) are in patches smaller than 1000 ha, whereas almost 35% (20/58) are in patches larger than 100,000 ha. Its current area of occupancy is approximately 2.2 million ha (13% of AF's remaining area). The most sensitive species to patch size is jaguar, for which all 21 records are in patches larger than 10,000 ha and almost half (10/21) are in patches larger than 100,000 ha (Fig. 1d). Its current area of occupancy is approximately 1.15 million ha (7% of AF's remaining area).

3.2. Species potential current range

Resulting models for all four species had high average test AUCs (murreti: 0.988 ± 0.005 ; tapir: 0.981 ± 0.006 ; WLP: 0.976 ± 0.010 ; jaguar: 0.971 ± 0.014) and very low omission errors for the threshold of maximum test sensitivity plus specificity (murreti: 0; tapir: 0.012; WLP: 0.010; jaguar: 0.025).

For murreti, the four most important variables to explain the variation in the species probability of occurrence were: (1) forest amount with functional connectivity of 200 m (45%); (2) forest amount with functional connectivity of 1100 m (24%); (3) precipitation of the driest month (12%) and; (4) percentage of vegetation cover (7%). Collectively they explained 88% of the variation (Fig. A3a). The logistic threshold of maximum test sensitivity plus

specificity (0.132) resulted in a model that suggests that 40% of the remaining AF is still suitable for the species (WMR), with the main suitable regions being: (1) Serra de Paranapiacaba (SP) down to Serra do Mar of Paraná (PR); (2) northern part of Serra do Mar (SP); (3) Serra dos Orgãos (RJ); (4) central Espírito Santo; and (5) and northeast Minas Gerais (MG) (Fig. A4a).

For tapir, the four most important variables to explain the variation in the species probability of occurrence were: (1) forest amount with functional connectivity of 0 m (68%); (2) percentage of vegetation cover (15%); (3) precipitation of the driest month (6%) and; (4) distance to the nearest road (3%). Collectively they explained 92% of the variation (Fig. A3b). The logistic threshold of maximum test sensitivity plus specificity (0.083) resulted in a model that suggests that 37% of the remaining AF is still suitable for the species, with the main suitable regions being: (1) the entire Serra do Mar continuum, going from northern Santa Catarina (SC) to northern São Paulo (SP), and connecting with Serra da Bocaina (PJ); (2) Serra dos Orgãos (RJ); (3) Southern Bahia (BA); and (4) Iguazu NP (PR – Fig. A4b).

For WLP, the four most important variables to explain the variation in the species probability of occurrence were similar to those for tapir: (1) forest amount with functional connectivity of 0 m (37%); (2) percentage of vegetation cover (35%); (3) precipitation of the driest month (9%) and; (4) distance to the nearest road (6%). Collectively they explained 87% of the variation (Fig. A3c). The logistic threshold of maximum test sensitivity plus specificity (0.158) resulted in a model that suggests that 35% of the remaining AF is still suitable for the species, with the main suitable regions very similar to the ones for tapir (Fig. A4c).

For jaguar, the four most important variables to explain the variation in the species probability of occurrence were: (1) forest amount with functional connectivity of 0 m (41%); (2) percentage

of vegetation cover (30%); (3) human density (9%) and; (4) distance to the nearest road (7%). Collectively they explained 86% of the variation (Fig. A3d). The logistic threshold of maximum test sensitivity plus specificity (0.154) resulted in a model that suggests that 24% of the remaining AF is still suitable for the species, with the main suitable regions being: (1) the southern region of Serra do Mar continuum, going from São Paulo (SP) down to northern Santa Catarina (SC); (2) the northern region of Serra do Mar (SP/RJ), connecting with Serra dos Orgãos (RJ); (3) Ivinhema basin (PR/MS); and (4) Iguazu NP (PR – Fig. A2d).

3.3. Suitable, large and protected

The combined model reveals that 45% of AF's remaining area can harbor at least one of the four (WMR) or three (OMR) species. Yet, only 16% of AF's remaining area is suitable for all four species (WMR), and 15% is suitable for all three species (OMR). Within muriqui's range (WMR), those areas encompass: (1) Serra da Par-

anapiacaba, in southern São Paulo (SP) and northern Paraná (PR); (2) Juréia-Itatins Massif; (3) the northern part of Serra do Mar, SP; (4) Serra dos Orgãos (RJ); and (5) Morro do Diabo, SP. Outside muriqui's range (OMR), the areas suitable for all three species are: (6) Iguazu NP (PR), and (7) parts of Santa Catarina's eastern region (Fig. 2). Among those, the only two that may indeed have all four species at present are Juréia-Itatins and the Serra do Mar continuum.

Considering patches that are protected and larger than 10,000 ha, 95% of AF's remaining area is suitable for at least one of the four species. Yet, only 65% is suitable for all four species (WMR) and 85% is suitable for all three species (OMR).

4. Discussion

Only 12% of the Atlantic forest remains (Ribeiro et al., 2009). Our study reveals that 88% of what remains is completely defau-

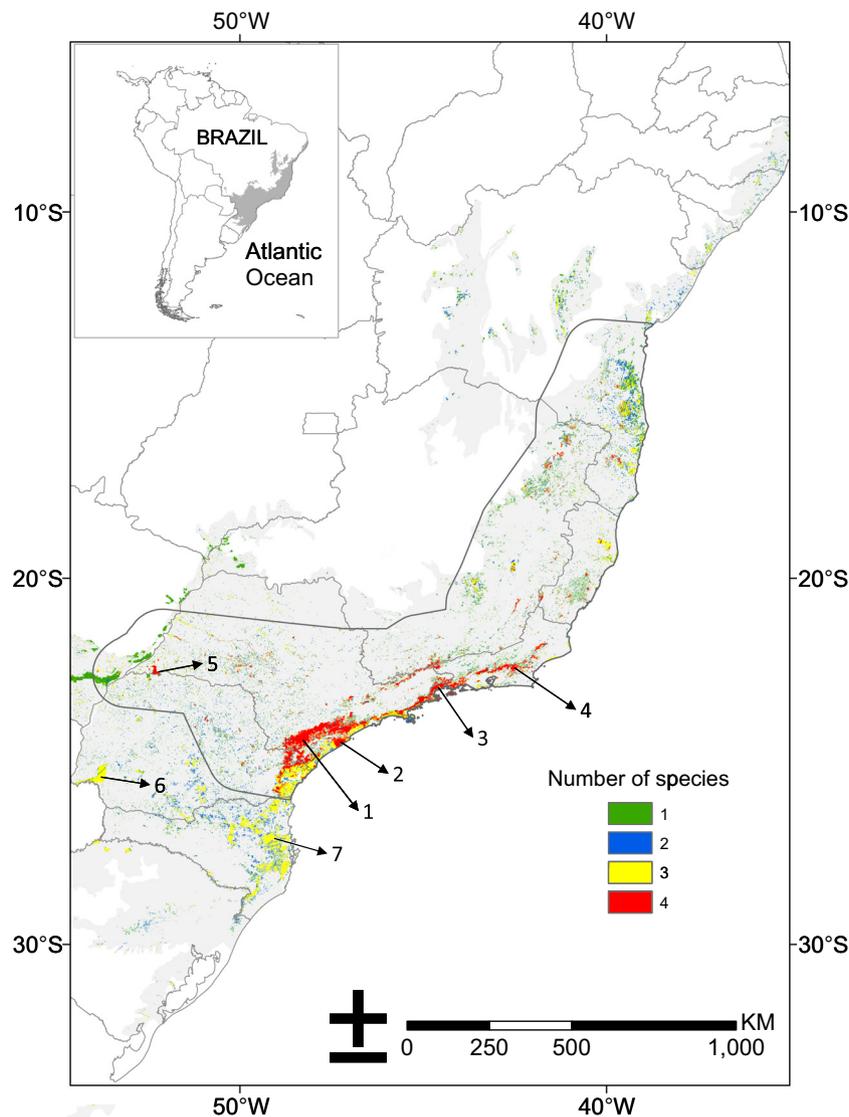


Fig. 2. Combined suitability of the four surrogate species derived from species potential current range models of each species. The gray area is the original extent of the Atlantic Forest biome, which includes all centers of endemism and transitional regions proposed by da Silva and Casteleti (2003), except Brejos Nordestinos. The dark black line defines the area within muriqui's range plus a 100-km buffer. Within the black line limits, the maximum expected number of species is four (red); outside the black line limits, the maximum expected number of species is three (yellow). Numbers refer to the large blocks suitable for four or three species, within and outside muriqui's range, respectively: (1) Serra da Paranapiacaba, in southern São Paulo and northern Paraná; (2) Juréia-Itatins Massif; (3) the northern part of Serra do Mar; (4) Serra dos Orgãos; (5) Morro do Diabo State Park; (6) Iguazu National Park; and (7) parts of Santa Catarina's eastern region. See text for explanation of threshold values and combined model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Percent of remaining Atlantic Forest (AF) area where each of the four surrogate mammal species (muriqui, tapir, white-lipped peccary and jaguar) are currently absent and where potential trophic cascade effects can be expected.

Species (ecological role)	% of remaining AF area where species is currently absent (unsuitable)	Ecological role	Potential effects		Source
			Direct trophic cascade effects	Indirect trophic cascades effects	
Muriqui (arboreal seed disperser)	90% (60%) ^a	Dispersal of large-seeded plants	Changes in dispersal (shorter dispersal distance, lower germination rates, clumped deposition) of large seeds; some large-seeded species (>1 cm) undispersed	Decline of plant diversity	Martins (2006) Martins (2008) Bueno et al. (2013)
		Pollination	Low seed set		Ferrari and Strier (1992) Culot et al. (this issue)
		Feces as resource for dung beetles		Decline in diversity of dung beetles associated to primates	
Tapir (terrestrial seed disperser/herbivore)	87% (63%)	Disperser of large-seeded plant species (>2.5-cm wide)	At least 50 large-seeded plant species undispersed	Decline of plant diversity	Galetti et al. (2001)
		Long-distance disperser of large-seeded plants	No long-distance dispersal of large-seeded plants		Fragoso (1997)
		Herbivory of >50 plant species Feces as resource for dung beetles	Lack of herbivory	Decline in diversity of dung beetle associated to tapirs	Hibert et al. (2011) Culot et al. (this issue)
White-lipped peccary (terrestrial seed predator/herbivore)	92% (65%)	Predator of large and hard palm-nuts	No predation of large hard palm-nuts		Silman et al. (2003) Keuroghlian and Eaton (2008)
		Ecosystem engineering (soil rooting, clearing and redistributing litter, uprooting and trampling seedlings)	No soil rooting, no litter clearing or redistribution, no trampling	Decline in plant diversity	Keuroghlian and Eaton (2009) Beck (2005) Beck et al. (2010)
Jaguar (apex predator)	93% (76%)	Controls populations of large mammals	Increase in abundance of herbivores (e.g. deer, peccary, capybara) Increase in abundance of mesopredators (e.g. opossum, tayra, coati, jaguaroundi)	Increase in herbivory, lime and other diseases transmitted by ungulates Decline in abundance of birds, small mammals, reptiles	Emmons (1987) Aranda and SanchesCordero (1996) Taber et al. (1997)

^a Within muriqui's historical range + 100-km buffer (see text for details).

nated of four of the largest Neotropical mammals (jaguars, tapirs, white-lipped peccaries, and muriquis), and 96% is defaunated of at least one of those four species. Due to their unique ecological roles, and their position at the top of the body mass distribution within trophic groups (the largest top predator; the largest arboreal and terrestrial frugivores, and the largest biomass of seed predator), our results indicate that 88–96% of what remains in the Atlantic Forest is likely to be suffering from trophic cascade effects, such as changes in patterns of seed dispersal, herbivory and plant recruitment (*sensu* Nunez-Iturri et al., 2008; Bueno et al., 2013), changes in community structure (*sensu* Peres, 2000), density compensation (*sensu* Peres and Dolman, 2000), and mesopredator release (*sensu* Levi and Wilmers, 2012) that may reverberate onto many other organisms (such as rodent, amphibian, reptile, and insect diversity – McCauley et al., 2006; Nichols et al., 2009; Culot et al., this issue), and ecosystem processes (such as ant–plant mutualisms – Palmer et al., 2008) (Table 2).

All areas where the four surrogate species still co-occur are large blocks of continuous and protected forest, which reinforces the idea that large and protected areas are fundamental to ensure the maintenance of the most sensitive species and to guarantee all necessary elements that maintain ecosystem functioning and long-term conservation efficiency (Peres, 2005; Andam et al., 2008; Canale et al., 2012; Laurance et al., 2012). Nevertheless, our study reveals that even some of the largest and most protected forest patches are already defaunated. If we consider only patches that are larger than 10,000 ha, and federally or state-wise protected, 42% of the remaining Atlantic Forest's area does not harbor any of the four species, and 80% is depleted of at least one of them.

Many reasons may explain the lack of our four surrogate species in the largest and most protected patches of this global hotspot. The Atlantic Forest is a biome that suffers from intense harvesting of natural resources (including overexploitation of wildlife) from the very first centuries of European occupation (Dean, 1996). Such an old history of human-driven unsustainable harvesting eliminated more sensitive wildlife populations (or brought them to dangerously low numbers) even before some of the largest areas were set aside for protection. More recently, there is still ongoing illegal hunting inside reserves (Chiarello, 1999; Cullen et al., 2001; Melo et al., 2004; Zimmermann et al., 2005; Paviolo et al., 2008; Galetti et al., 2009), many times associated with illegal harvest of Juçara palm-hearts (*Euterpe edulis*, Galetti and Fernandez, 1998). Continued agricultural development has also resulted in increased isolation of some of the large and protected patches (e.g. Morro do Diabo State Park – SP, Rio Doce State Park – MG), which may increase chance of extinction and decrease chance of recolonization. Finally, wildlife contact with domestic animals (dogs, cats and livestock that invade reserves through their edges) brings new diseases that may further jeopardize wildlife populations (Lafferty and Gerber, 2002). For instance, the disappearance of white-lipped peccary populations from many large parks in the last two decades (de Azevedo and Conforti, 2008; Keuroghlian et al., 2012) reinforces the hypothesis that even in large and protected areas, large mammal species are still highly susceptible to ongoing negative anthropogenic effects.

Our suitability models reveal that there are opportunities for improvement. Forty-five of the remaining Atlantic Forest is still suitable for at least one of the four surrogate species (compared to 12% that is currently occupied), and 16% and 15% is suitable for all four or three species, within muriqui's and outside muriqui's range, respectively (compared to 4% that is currently occupied). Within large and protected patches, 95% is suitable for at least one of the four species (compared to 58% currently occupied), and 67% and 85% is suitable for all four or all three species, within muriqui's and outside muriqui's range, respectively (compared to 20% currently occupied).

Assuming that suitable areas indicate potential for recolonization, 15–16% of Atlantic Forest's remaining area (and 67–85% of largest and most protected areas) still has the potential to harbor a more complete set of the mammalian community and their food webs, and conservation efforts should be directed to those areas. On the other hand, 55% of the Atlantic Forest's remaining area is already unsuitable for all four species, and conservation efforts towards restoring those areas should first be directed to mitigate factors that make those areas unsuitable, such as small forest amount, low percentage of native vegetation, and proximity to roads, as those were the main factors that explained probability of occurrence of the four species (jaguars, tapirs and WLPs).

The importance and ecological uniqueness of large mammals on ecological processes and community structure is well-documented in other ecosystems (e.g. Campos-Arceiz et al., 2012; Estes et al., 2011). Our study highlights the importance of looking at ecological elements to fully depict intactness of natural areas; and suggests that ecosystems with long history of human impact (such as the Atlantic Forest) may be suffering from widespread ecological impacts not seen at a first glance. Unfortunately, defaunation is a global phenomenon that affects tropical ecosystems throughout the world (Corlett, 2007; Fa et al., 2002; Peres, 2010). A large-scale mapping effort of defaunation and an analysis of habitat suitability in the other ecosystems may help better delineate conservation programs to restore ecological processes in depleted natural areas.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2013.04.018>.

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