

Mammals in São Paulo State: diversity, distribution, ecology, and conservation

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Abstract: Mammals are charismatic organisms that play a fundamental role in ecological functions and ecosystem services, such as pollination, seed dispersal, nutrient cycling, and pest control. The state of São Paulo represents only 3% of the Brazilian territory but holds 33% of its mammalian diversity. Most of its territory is dominated by agriculture, pastures, and urban areas which directly affect the diversity and persistence of mammals in the landscape. In addition, São Paulo has the largest port in Latin America and the largest offshore oil reservoir in Brazil, with a 600 km stretch of coastline with several marine mammal species. These human-made infrastructures affect the diversity, distribution, ecology, and the future of mammals in the state. Here, we answer five main questions: 1) What is the diversity of wild mammals in São Paulo state? 2) Where are they? 3) What is their positive and negative impact on human well-being? 4) How do mammals thrive in human-modified landscapes? 5) What is the future of mammals in the state? The state of São Paulo holds 255 species of native mammals, with four endemic species, two of them globally endangered. At least six species (two marsupials, Giant otter, Pampas deer, Brazilian dwarf brocket deer, and Giant armadillo) were extirpated from the state due to hunting and habitat loss. The intense human land use in the state forced many mammalian species to change their diet to cope with the intense fragmentation and agriculture. Large-scale monoculture has facilitated the invasion of exotic species such as wild boars (javalí)

and the European hare. Several “savanna-dwelling” species are expanding their ranges (Maned wolf, Brocket deer) over deforested areas and probably reflect changes towards a drier climate. Because the state has the largest road system, about 40,000 mammals from 33 species are killed per year in collisions causing an economic loss of 12 million dollars/year. The diversity of mammals is concentrated in the largest forest remnants of Serra do Mar and in the interior of the State, mainly in the regions of Ribeirão Preto and Jundiaí. Sampling gaps are concentrated throughout the interior of the state, particularly in the northwest region. Wild mammals play a fundamental role in many ecosystem services, but they can also be a concern in bringing new emergent diseases to humans. Although the taxonomy of mammals seems to be well known, we show that new species are continuously being discovered in the state. Therefore, continuous surveys using traditional and new technologies (eDNA, iDNA, drones), long-term population monitoring, investigation of the interface of human-wildlife conflict, and understanding of the unique ecosystem role played by mammals are future avenues for promoting sustainable green landscapes allied to human well-being in the state. The planting of forest or savanna corridors, particularly along with major river systems, in the plateau, controlling illegal hunting in the coastal areas, managing fire regimes in the Cerrado, and mitigating roadkill must be prioritized to protect this outstanding mammal diversity.

Keywords: *e-DNA; iDNA; extinction risk; Atlantic Forest; Cerrado; Araucaria mixed forest; stable isotopes; line transect; camera trapping.*

Mamíferos do Estado de São Paulo: diversidade, distribuição, ecologia e conservação

Resumo: Os mamíferos são organismos carismáticos que desempenham um papel fundamental na função ecológica e nos serviços ecossistêmicos, como polinização, dispersão de sementes, ciclagem de nutrientes e controle de pragas. O Estado de São Paulo representa apenas 3% do território brasileiro, mas detém 33% da diversidade de mamíferos. A maior parte de seu território é dominado pela agricultura, pastagens e áreas urbanas que afetam diretamente a diversidade e a persistência dos mamíferos na paisagem. Além disso, São Paulo possui o maior porto da América Latina e o maior reservatório de petróleo costeiro do Brasil, com 600 km de extensão de litoral com diversas espécies de mamíferos marinhos. Essas infraestruturas afetam a diversidade, distribuição, ecologia e o futuro dos mamíferos no estado. Aqui, respondemos cinco perguntas principais: 1) Qual é a diversidade de mamíferos silvestres no Estado de São Paulo? 2) Onde eles ocorrem? 3) Qual é o seu impacto positivo e negativo no bem-estar humano? 4) Como os mamíferos persistem em paisagens modificadas pelo homem? 5) Qual é o futuro dos mamíferos no estado? O estado de São Paulo possui 255 espécies de mamíferos nativos, com quatro espécies endêmicas, duas delas globalmente ameaçadas de extinção. Pelo menos seis espécies (dois marsupiais, ariranha, veado-campeiro, veado-cambuta e tatu-canastra) foram extirpadas do estado devido à caça e perda de habitat. O intenso uso humano da terra no estado forçou muitas espécies de mamíferos a mudar sua dieta para lidar com a intensa fragmentação e agricultura. A monocultura em larga escala facilitou a invasão de espécies exóticas, como porcos selvagens (javaporco) e a lebre europeia. Várias espécies de áreas abertas estão expandindo suas áreas de distribuição (lobo-guará, veado-catingueiro) sobre áreas desmatadas e provavelmente refletem mudanças em direção a um clima mais seco. Como o estado possui o maior sistema rodoviário do Brasil, cerca de 40 mil mamíferos de 33 espécies são mortos por ano em colisões, causando um prejuízo econômico de 12 milhões de dólares/ano. A diversidade de mamíferos está concentrada nos maiores remanescentes florestais da Serra do Mar e no interior do Estado, principalmente nas regiões de Ribeirão Preto e Jundiaí. As lacunas amostrais estão concentradas em todo o interior do estado, principalmente na região noroeste. Os mamíferos silvestres desempenham um papel fundamental em muitos serviços ecossistêmicos, mas também podem ser uma preocupação em trazer novas doenças emergentes para as populações humanas. Embora a taxonomia de mamíferos pareça ser bem conhecida, mostramos que novas espécies estão sendo continuamente descobertas no estado. Portanto, pesquisas usando tecnologias tradicionais e novas (eDNA, iDNA, drones), monitoramento populacional de longo prazo, a investigação da interface do conflito homem-vida selvagem e a compreensão do papel único no ecossistema desempenhado pelos mamíferos são um caminho futuro para promover uma paisagem verde sustentável aliada ao bem-estar humano no estado. O plantio de corredores florestais ou de cerrado, principalmente junto aos principais sistemas fluviais, no planalto, o controle da caça ilegal nas áreas costeiras, o manejo dos regimes de fogo no Cerrado e a mitigação dos atropelamentos devem ser uma prioridade para proteger essa notável diversidade de mamíferos.

Palavras-chave: *e-DNA; iDNA; risco de extinção; Mata Atlântica; Cerrado; Floresta de Araucária; isótopos estáveis; transecções lineares; armadilhas fotográficas.*

1. Introduction

Wild animals represent an insignificant part of the world's biomass when compared to plants and microbes. Plants make a whopping 81%, microorganisms 17% and wild animals only 0.001% of the world's living biomass (Bar-On et al. 2018). However, although wild animals represent small biomass, they are very important for the Earth's biodiversity and climate regulation (Malhi et al. 2022). Among wild animals, mammals play a fundamental role in ecosystem functioning and services, such as pollination, seed dispersal, and pest control. Mammals also play several disservices to humans, particularly when they raid crops, transmit zoonotic diseases, or prey upon livestock.

Brazil has 770 species of mammals (Quintela et al. 2020; Abreu et al. 2021), and São Paulo, which corresponds to less than 3% of the Brazilian territory, has 33% of those species. This high diversity lies in the considerable diversity of ecosystems and climate, such as savannas (Cerrado), dry and humid Atlantic Forests, Araucaria mixed forests, and the complex evolutionary history and diversification of the mammalian fauna (Vivo et al. 2011). The long history of research and network of protected areas (including the largest remaining area of Atlantic Forest) make São Paulo an ideal case where green sustainable landscapes, allied to economic growth and social benefits, are possible.

Here we review the diversity of mammal species in the State of São Paulo, their distribution, how they thrive in the human-modified landscapes, and discuss the future of mammal diversity. We summarize decades of research done in São Paulo, most of them supported by the Biota FAPESP program in the last 20 years.

What is the diversity of mammals in São Paulo state?

New inventories, catalogs, systematic revisions, and taxonomic studies continue to increase the number of mammal species recorded in São Paulo (Garbino 2016; Fegues et al. 2021). The increasing use of pitfall traps to sample small mammals have provided several new specimens of marsupials and rodents aiding in new species descriptions, species range delimitation, and small mammal community characterization (Bovendorp et al. 2017a). In addition, climate change and intensive land use change have created suitable habitats for colonizing "savanna-associated" species (Sales et al. 2020).

Vivo et al. (2011) listed 230 mammals (205 terrestrial and 25 marine species) with attested records in São Paulo state. After 11 years, we have increased our knowledge of the mammals present in the state, including recently described species with restricted distributional range (5 species – three rodents, one bat, and one marsupial), identity confirmation and taxonomic revalidation of nominal taxa previously included in the synonymy of other species (12 species), as well as new records of rarely sampled species in the state (13 species – five bats, five rodents, two felids and one canid), totaling 17 new terrestrial and 13 marine species for the list. Other species had their names excluded (*Monodelphis theresa*) or corrected (*Philander quica*), based on taxonomic approaches (17 species). On the other hand, some records (*Gardnerycteris crenulatum*, *Micronycteris brosseti* and *Uroderma bilobatum*) were removed from the list since they were not confirmed (Garbino, 2016). Therefore, São Paulo currently harbors 217 terrestrial and 38 marine species, totaling 255 mammalian native species (Supplementary Table S1), an impressive growth of 2.3 species/year.

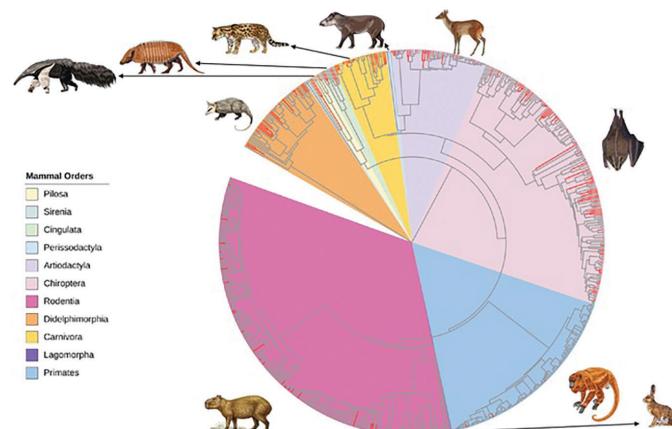


Figure 1. Phylogeny of the species of mammals in Brazil highlights the species found in São Paulo state.

Four species (Black-lion tamarin *Leontopithecus chrysopygus*, one terrestrial rodent *Akodon sanctipaulensis* and two arboreal rodents *Phyllomys kerri*, and *P. thomasi*) are endemic to the state. Two of these endemic species are Data Deficient and two are Endangered (www.iucnredlist.org).

From an evolutionary and conservation point of view, studies in population genetics are a critical key in illuminating the Evolutionary Significant Units (ESUs). For instance, tapirs inhabiting the large Atlantic Forest corridor are genetically different from the inland and coastal populations (Saranholi et al. 2022). It appears that even within large-sized mammals, fine-scale genetic differentiation may be more frequent than thought before, and this can be increased by landscape modifications, as also reported within *Puma concolor* (Saranholi et al. 2017).

Although the phylogenetic diversity of São Paulo mammals represents a subset of the diversity of Brazilian mammals, the state is well represented in all Orders, except Sirenia (Figure 1).

Where are the mammals in São Paulo state?

São Paulo has the best spatial information on its biodiversity in Brazil; with mammals being studied for over a century. A series of datasets on the distribution of Brazilian mammals are available and we used eight of them to compile a list of species for the state and species richness for 22 watersheds in the state: Atlantic Bats (Muylaert et al. 2017), Atlantic Camtrap (Lima et al. 2017), Atlantic Large Mammals (Souza et al. 2019), Atlantic Primates (Culot et al. 2019), Atlantic Small Mammals (Bovendorp et al. 2017b), Neotropical Carnivores (Nagy-Reis et al. 2020), and Neotropical Xenarthras (Santos et al. 2019) and summarized the species number information (richness) for the boundaries of the 22 hydrographic regions in the State of São Paulo (Figure 2).

These datasets provided information on 11,037 records, from 173 species. The number of species per Order was: Artiodactyla = 7 species, Carnivora = 23 species, Chiroptera = 48 species, Cingulata = 6 species, Didelphimorphia = 19 species, Lagomorpha = 3 species, Perissodactyla = 1 species, Pilosa = 3 species, Primates = 12 species, and Rodentia = 51 species. The regions of the state with the highest density of records are Parque Estadual Carlos Botelho, Parque

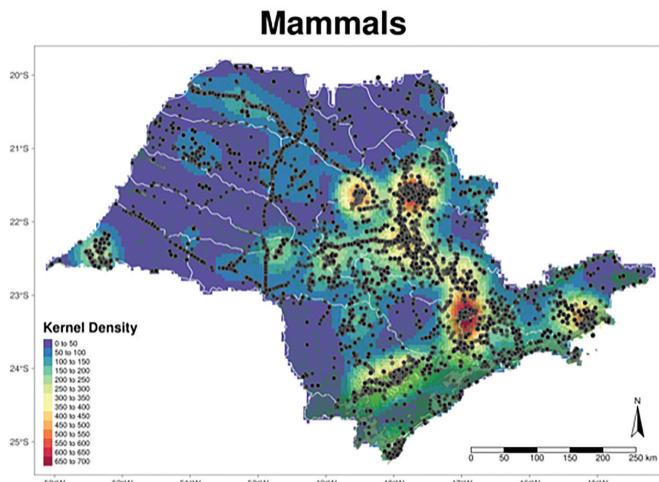


Figure 2. The distribution of records from mammals in São Paulo state shows the areas (red) with the highest number of records. Many records follow roads as the result of roadkill information.

Nacional da Serra da Bocaina, Serra do Japi, Área de Relevante Interesse Ecológico Cerrado Pé-de-Gigante, Estação Ecológica de Itirapina, and Parque Estadual do Morro do Diabo. The highest diversity in the humid coastal forests along the Serra do Mar massif and areas of the municipalities of Ribeirão Preto and Jundiaí, mainly associated with the remaining conservation parks, highlighting the role of these forests remnants as maintainers of the state's local and regional diversity (Figure 3). We created a Github repository with the information we used to generate Figures 2 and 3, as well as the figures in Appendix 2 of supplementary material: https://github.com/LEEClab/ms_mammals_sp_spatial_analysis. We also created an interactively spatial repository with the raw data of species records used in this paper, which can be accessed at <https://www.arcgis.com/apps/dashboards/11273a209cd44bba9826ce689fe04ac9>.

Although the distribution of mammals in São Paulo is relatively well studied, an estimate of their population size or abundance is much less known. One of the sites with the best information on population abundance in São Paulo is the Serra do Mar massif (Carlucci et al. 2021), also known as the Serra do Mar Biodiversity Corridor (*Corredor de Biodiversidade da Serra do Mar*, CBSM), located in the south and southeastern Brazil (Paraná and São Paulo states). CBSM encompasses the largest remaining block of Atlantic Forest (~16,040 km²), in the slopes and tops of the mountain range of Serra de Paranapiacaba, Serra do Mar, and Serra da Mantiqueira with its adjacent flat lowlands. Some of the largest protected areas in the Atlantic Forest biome are in the CBSM, of which ~7,276 km² are under strict protection. Part of these protected areas (State Parks, Ecological Stations, Environmental Protections Areas) is in the Serra de Paranapiacaba, with a 1,200 km² (Carlucci et al. 2021).

Two main methods have been used to estimate the abundance of medium and large-sized mammals in this region: camera trapping and line-transects (Galetti et al. 2017, Ferraz et al. 2022). Thirty medium and large-sized native mammal species were sampled by camera-trapping in eight protected areas (49,050 cameras/day; Ferraz et al. 2022, and 53,494 cameras/day; Silveira et al. 2010, Beisiegel and Nakano-Oliveira 2020), while 44 species were found in 4,090 km line transect in 13 regions along Serra do Mar Corridor (Galetti et al. 2009a, Galetti et al. 2017).

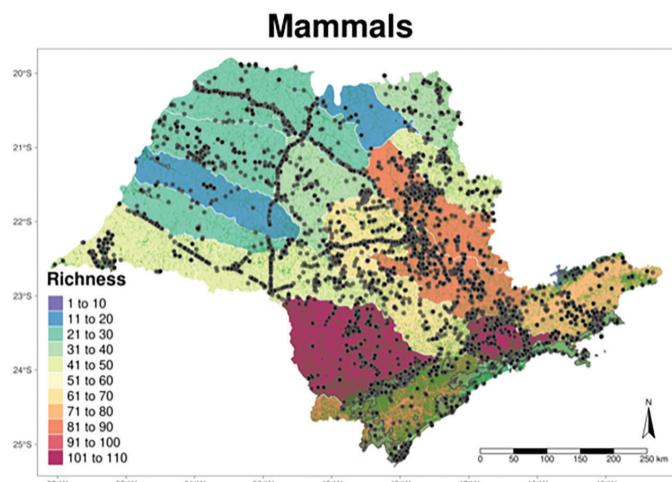


Figure 3. The distribution of mammalian diversity in São Paulo state.

The density and biomass of mammals varied 16 and 70-fold among sites and a biomass decline of 98% in sites where hunting is frequent (lowland Atlantic Forest; Galetti et al. 2017, Figure 4). The Serra do Mar Corridor holds populations of mammals that are on the verge of extinction in other states' ecosystems, such as the muriqui (*Brachyteles arachnoides*) (Jerusalinsky et al. 2011), the bush dog (*Speothos venaticus*) (Beisiegel and Ades 2004), and the jaguar (*Panthera onca*) (Beisiegel and Nakano-Oliveira 2020).

The population status of mammals in dry forests and Cerrado vegetation is less known, but regions with higher forest cover and connected by forest corridors hold more species than regions with small, isolated fragments immersed in pastures and agriculture fields (Magioli et al. 2015, Magioli et al. 2016, Paolino et al. 2018, Versiani et al. 2021). While forest cover and connectivity explain mammal diversity in fragmented landscapes, hunting pressure, and altitude (which is also related to forest productivity) are the main drivers that explain mammal diversity and abundance in large continuous forests of Serra do Mar (Galetti et al. 2009b, Ferraz et al. 2022). The outbreak of yellow fever in the last few years is likely to have caused the local extinction of howler monkeys in some forest remnants and population decline in many protected areas (Berthet et al. 2021).

Although São Paulo waters have a high diversity of cetacean species, just six species are residents year-round (20% of the species), four species are seasonal visitors in migration to reproductive areas (13%), two species are random visitors (7%), and 19 were strays from their original distribution (60%) (Figueiredo et al. 2020). A resident population of Guiana dolphins, the target of longitudinal investigations since 1995 and with a population estimated at 400 individuals (de Mello et al. 2019), can be found year-round in the Iguape-Cananeia estuarine waters, at the southern edge of São Paulo state. They can be also found along the shoreline, mainly close to estuarine and riverine discharges. La Plata (*Pontoporia blainvilliei*), Atlantic spotted (*Stenella frontalis*), Common bottlenose (*Tursiops truncatus*), and Rough-toothed (*Steno bredanensis*) dolphins, added to Bryde's whales (*Balaenoptera edeni*) are found in relatively high numbers, but data on their abundances are not yet available – the same can be applied to the seasonal visitors. Recent investigations have shown that the coast of São Paulo is a

Status of mammals in São Paulo

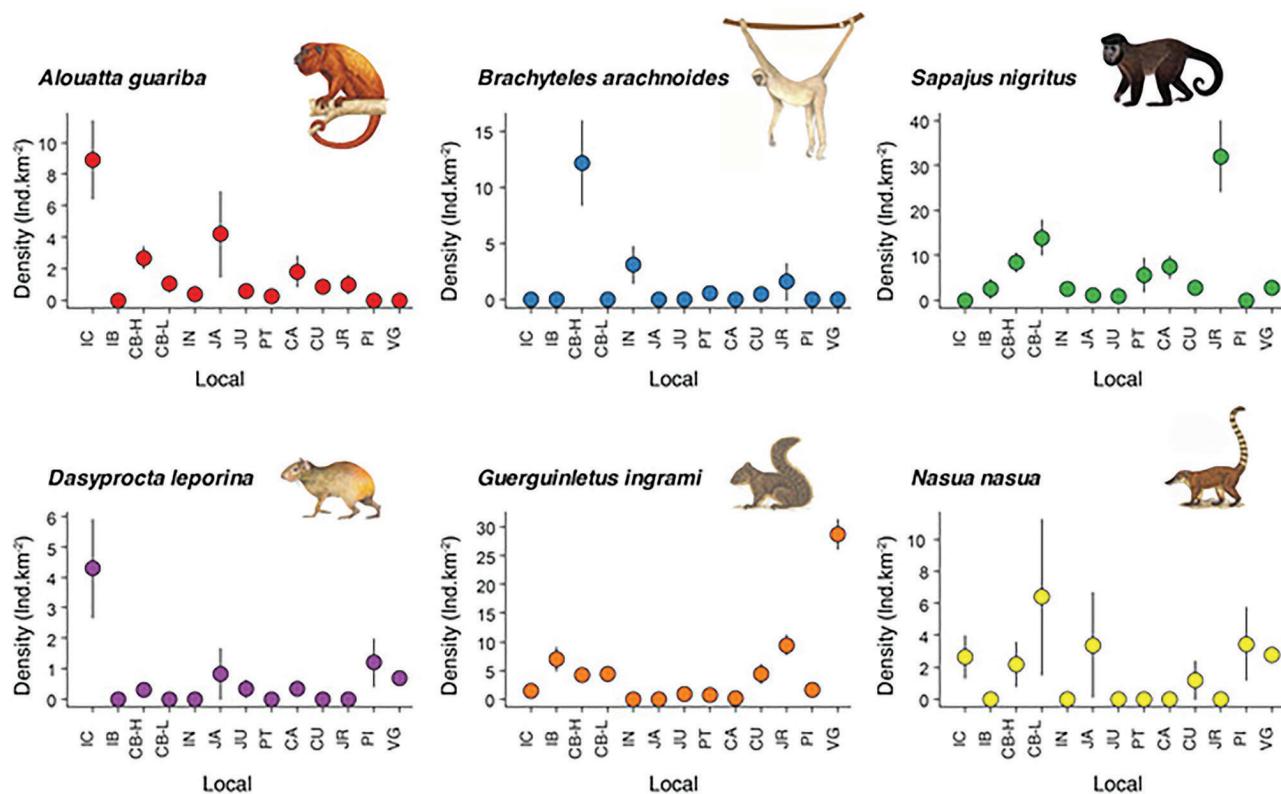


Figure 4. Density (ind./km²) of diurnal mammals based in line transects sampling in the Serra do Mar, São Paulo (Sites: IC=Ilha do Cardoso, IB=Ilhabela, CB-H=Carlos Botelho highlands, CB-L=Carlos Botelho Lowlands, IN=Intervales, JA=Jurupará, PT=Petar, CA=Caraguatatuba, CU=Cunha, JR=Juréia, PI=Picinguaba, VG=Vargem Grande (see Galetti et al. 2017).

hotspot to investigate La Plata, Atlantic spotted, and Common bottlenose dolphins (Paschoalini and Santos 2020).

What are the services and disservices provided by mammals?

Humans have always had a relationship of love and hate with mammals. Humans have domesticated dogs, cats, pigs, sheep, cows, horses, and many other mammal species for pleasure, food, use in transport, and material resources for millennia. At the same time, we were responsible for the extinction of species or local populations that we could not domesticate or that we fear (e.g., predators). In daily life, our urban society sees wildlife mostly in TV documentaries, with a poor understanding of how close and dependent we are on wild mammals. Mammals are known to play important ecosystem services that are hardly acknowledged. For instance, bats eat thousands of tons of insects, preying on at least 237 potential pest species (Ramirez-Francel et al. 2022) in agricultural landscapes, saving >3.7 million USD/year in pest control just in the USA. Bats also pollinate several important crops, such as banana, mango, and guava, and are essential in forest regeneration (Ramirez-Francel et al. 2022). Small, medium, and large mammalian predators play an important role in controlling rodent populations (Cruz et al. 2022).

Mammals also play an important role in seed dispersal and indirectly are important for mitigating human-induced climate change (Bello et al. 2015, Bello et al. 2021). By dispersing large-seeded trees that

produce large hardwood trees, with higher carbon storage capacity, large mammals are fundamental for the maintenance of above-ground carbon storage. Large herbivorous mammals (particularly tapirs and white-lipped peccaries) are also important for mediating plant composition and diversity (Villar et al. 2020), plant biomass (Villar et al. 2022), nutrient cycling (Villar et al. 2021), and plant life growth form (Souza et al. 2022) in the Atlantic Forest. By experimentally fencing part of the vegetation, scientists have found that by feeding or trampling plants, large mammals promote an increase in plant beta diversity (i.e. create a mosaic of areas of low and high diversity) (Villar et al. 2022) and are fundamental in adding carbon and other nutrients to forest's soil, particularly in areas rich in palms (*Euterpe edulis*) (Villar et al. 2021) (Figure 5). Large mammals are also important in maintaining the diversity of plant growth forms, a vital component of the 3-dimensional diversity of the Atlantic Forest (Souza et al. 2022).

Nevertheless, mammals can play disservices and cause major economic loss when overabundant, particularly in the transmission of zoonoses (Keesing et al. 2010, Luz et al. 2019) or when feeding on agricultural crops (Ferraz et al. 2003) or predation on livestock (Palmeira et al. 2015). An estimate of 40,000 viruses occurs in the bodies of mammals, of which a quarter could conceivably infect humans; and climate change associated with habitat loss will continue to force many species to relocate to habitats near humans, increasing the chances of virus spillover into humans (Carlson et al. 2022, Winck et al. 2022). The intense monoculture of sugar cane has facilitated the expansion and population growth of the introduced wild boars (javalí or

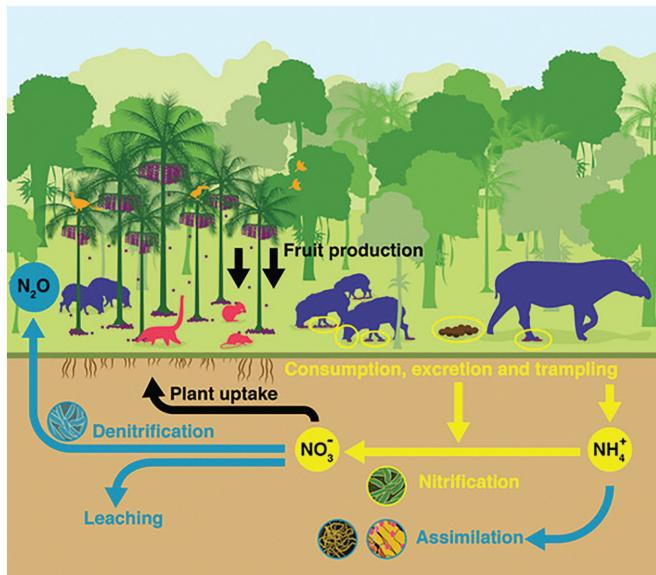


Figure 5. Mammals play a fundamental role in carbon and nitrogen soil cycling. Mammal excrements promote fertilization of forest soil and are fundamental for microbes (bacteria, and mycorrhizal fungi) in the soil. The density of palms attracts mammals and creates positive feedback on soil fertilization due to mammal foraging (from Villar et al. 2021).

javaporco) whose 70% of their diet is composed of corn or sugar cane (Pedrosa et al. 2021). The increase in wild boar populations may lead to an increase in rabies cases because they are today the main prey of vampire bats (Galetti et al. 2016, Gonçalves et al. 2021).

How do mammals survive in a human-modified landscape?

There has been a common misunderstanding that most of the mammal species that we see in agricultural landscapes are exotic

species such as livestock (cow, horse, pigs) or invasive species, such as European hares (*Lepus europaeus*; Pasqualotto et al. 2021) and wild pigs (*Sus scrofa*; Pedrosa et al. 2015). Recent evidence has shown that even largely human-modified landscapes dominated by agriculture and pastures hold a considerable diversity of native mammals (Magioli et al. 2016, Beca et al. 2017). How species persist, and even thrive, in human-modified ecosystems is becoming a recurrent question in ecology.

Several studies have found that medium and large mammals are coping with land-use modification by changing their feeding behavior and incorporating resources from agricultural crops. Carbon and nitrogen stable isotopes analysis found that mammals are incorporating more agricultural crops (C_4 -rich resources, such as corn) and nitrogen-rich food items (probably due to the intense crop fertilization) when forest resources are scarce (Magioli et al. 2014, Magioli et al. 2019, Magioli et al. 2022, Pedrosa et al. 2021). The analyses of stable isotopes have provided important evidence of the plasticity of mammals in human-dominated landscapes and in continuous forests where defaunation has modified trophic food webs (Galetti et al. 2015, Gonçalves et al. 2020) (Figure 6).

Habitat degradation, overfishing, noise and chemical pollution, incidental captures in fishing operations, collisions with boats and the lack of a national and a regional policy to protect cetaceans are the main threats to their survival along the coast of São Paulo (Santos et al., 2010; Figueiredo et al. 2017). The larger port in Latin America, added to the largest oil plant on land in Brazil, and the increase in a 3-order in the number of leisure boats in the past two decades (CODESP, 1992; Zanardi-Lamardo et al. 2013; Figueiredo et al. 2017) are responsible for an extremely high boat and ship traffic, posing cetaceans at risk. The number of the southern right whale (*Eubalaena australis*) visits has been decreasing over the last four decades (Santos et al. 2001; Figueiredo et al. 2017), meanwhile, its population abundance has been growing in the southern hemisphere (Cooke & Zerbini, 2018). The way resident cetaceans and seasonal visitors are reacting to the quoted impacts should be urgently addressed.

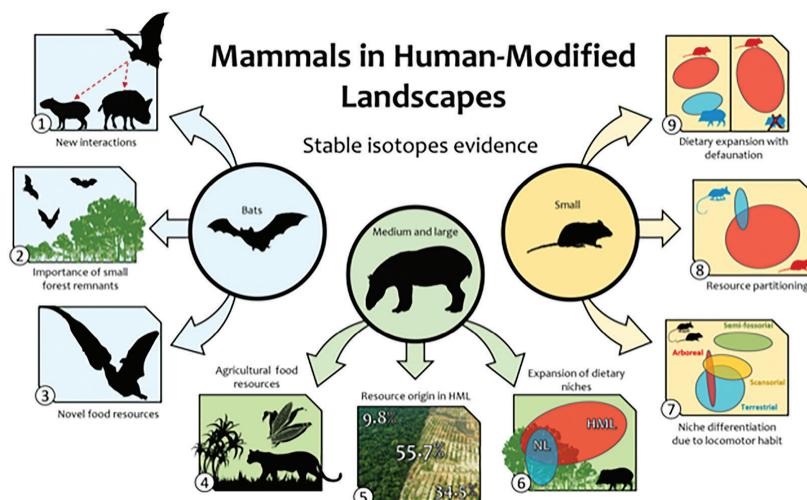


Figure 6. The use of stable isotopes has elucidated how mammals are thriving in human-modified landscapes 1) Galetti et al. (2016b) and Gonçalves et al. (2020); 2) Kruszynski et al. (2022); 3) Kruszynski et al. (2016); 4) Magioli et al. (2014); 5) Magioli et al. (2019); 6) Magioli et al. (2022); 7 and 8) Galetti et al. (2016a) and Bovendorp et al. (2017); 9) Galetti et al. (2015). Ellipses in panels 6–9 represent the bidimensional isotopic niche space of stable carbon and nitrogen isotopes; HML = human-modified landscape; NL = natural landscape.

The occurrence of a high diversity of mammals in human-modified landscapes does not mean that they are healthy. Recent studies on terrestrial and marine mammals have found high contamination by pesticides and other toxic chemicals in mammalian populations (Yogui et al. 2010, Medici et al. 2014).

What is the future of mammal diversity in São Paulo State?

São Paulo state has the paradox of having the largest human population in Brazil, the largest road network, and the largest industrial section, but also has the largest remnants of the Atlantic Forest in Brazil. In the last 10 years, forest coverage in São Paulo State increased 5% thanks to the State Restoration Program, Sustainable Agricultural Program, and increasing investment in law enforcement, but we need a more audacious environmental agenda to avoid the extinction of the endemic species, avoid the extirpation of large-sized species that have lost their habitats (Marsh deer, Pampas deer) or species that are continuously being persecuted (Jaguars), control invasive species (particularly the wild boar) and promote the persistence and the connectivity of mammal populations in the much-altered landscapes of São Paulo.

Although the intensive studies in the last two decades have provided an immense bulk of information about the mammals in São Paulo, there are many regions that are poorly sampled. In addition to traditional surveys, the use of new technologies such as the environmental DNA (eDNA) or ingesta or invertebrate-derived DNA (iDNA) can also be a powerful tool for assessing vertebrate (mammal) communities (Carvalho et al. 2021).

About 15% of the mammal species are threatened by extirpation, and six have already disappeared in the state (two marsupials, the giant otter, the giant armadillo, the Pampas deer, and the Brazilian dwarf brocket deer) and at least two large-sized species are on the verge of state's extirpation (Jaguar, Marsh deer). All four state's endemic species are not safe from extinction. For example, the Black lion tamarin *Leontopithecus chrysopygus* survives in 15 localities in the state of São Paulo, but only the subpopulation of the Morro do Diabo State Park, with 1,200 individuals, has been considered demographically and genetically viable in the long term (Rezende et al. 2020). Nevertheless, the species occurs in high densities in the degraded riverine forest in the upper Paranapanema watershed, including eucalyptus plantations where the understory was allowed to regenerate (as in Buri municipality). The restoration of larger areas of riverine forest and legal reserves connecting areas such as Capão Bonito National Forest and forest fragments in the municipalities of Buri and São Miguel Arcanjo would greatly increase the resilience of the species (Garcia et al. 2022). The Giant Atlantic Tree Rat *Phyllomys thomasi* is endemic to São Sebastião island (Ilhabela) with no individuals in captivity. The status of this species is unknown (Olmos 1997), but recent records have been made in secondary forests in low-elevation areas (F. Olmos pers. obs.). Most of the island is part of a state park, except areas below 100 m asl where a rapid urbanization process is occurring. The protection of the low-elevation (sea-level to 100 m asl) belt from Saco do Sombrio to Castelhanos, Caveira, and Poço beaches, either by adding it to Ilhabela State Park or by creating a new protected area, would include areas where *P. thomasi* have been recorded.

Cerrado species, especially those from open savannas (*campo limpo, campo cerrado*), are particularly vulnerable to local extinction because most of the protected areas are too small and poorly managed. In the absence of controlled fires and herbivory, many open savannas are becoming dominated by trees (transitioning into *cerradão*), a phenomenon known as the “wood encroachment” (Stevens et al. 2017). Specialists in open savannas such as the Pampas Deer, Marsh Deer, and the rodents *Clyomys laticeps*, *Cerradomys scotti*, and marsupials such as *Cryptonanus chacoensis* are negatively affected by increasing wood encroachment (Furtado et al. 2021).

Some large-bodied species are on the verge of extinction due to illegal hunting, including the Jaguar (*Panthera onca*), which also suffers from competition with humans for its favored prey (peccaries). Recent estimates suggest that less than 50 jaguars live in São Paulo state, distributed in only two isolated populations (Paviolo et al. 2016). The conservation of this species will require the reestablishment of healthy populations of prey species such as peccaries in the Atlantic Forest, increasing the likelihood of suitable habitat being colonized and the translocation of individuals from other populations. The conservation of Jaguars (and many other species) would be greatly enhanced if broad forest corridors more in line with scientific recommendations, than the meager belts required by the Forest Code, are created along the shores of the reservoirs that now make up most of the Paraná, Paranapanema, Tietê and Grande rivers.

The situation of most deer species in São Paulo state is worrisome. The Marsh deer is critically endangered in the state with only two natural sub-populations (Rio do Peixe and Rio Aguapeí) and one introduced (Rio Mogi-Guaçu) and probably less than 200 individuals left in the wild (Duarte et al. 2012). The Brazilian dwarf brocket deer (*Mazama nana*) is likely to be one of the extirpated species in the state, the small brocket deer (*Mazama jucunda*, formerly *M. bororo*) vulnerable and *Mazama rufa*, a recently revalidated species, is likely to be critically endangered (Peres et al. 2022; M.B.Duarte, unpublished data).

While some species are declining, other species seem to be expanding in the state, particularly carnivore-generalist species, such as the maned-wolf (*Chrysocyon brachyurus*; Coelho et al. 2018), the Pampas fox (*Lycalopex gymnocercus*; Magioli et al. 2016), the brown brocket deer (*Mazama gouazoubira*; Duarte et al. 2012) and the Pantanal cat (now *Leopardus braccatus*; Breviglieri et al. 2018). All these species are taking the opportunity of the previously forested areas being transformed into savanna-like environments, represented mostly by anthropogenic land-cover types, a phenomenon named “fauna savanization” (Sales et al. 2020). Generalist rodent species (e.g. *Akodon montensis*, *Oligoryzomys nigripes*) are other species that are rapidly increasing in the state (Umetsu and Pardini 2007). In addition, anthropogenic land use is also benefiting the invasion of exotics, such as the wild boar and the European hare (Pedrosa et al. 2015, Pasqualotto et al. 2021). What we know is that this expansion of some species is not due to long movements from populations from more pristine Cerrado. For instance, the Maned wolves of São Paulo are genetically differentiated from the western Mato Grosso do Sul populations and show reduced genetic variation, probably caused by the extensive landscape modifications across the São Paulo state (Rodriguez-Castro et al. 2022).

Most of the native vegetation or recovering areas in the Atlantic Forest region are in areas occupied formerly by savanna or

semideciduous forests and we need to create new ways to protect the remaining forest patches without burdening agricultural lands. Focusing on the restoration and promoting connectivity between patches of riparian forest in the savanna area is crucial to maintaining the movement of mammals and restoring their genetic diversity (Saranholi et al. 2017, Saranholi et al. 2022). Some important remnants in the Cerrado and semideciduous forests deserve priority of conservation because they maintain several endangered species and can act as source individuals for the smaller fragments nearby (e.g., Fazenda Barreiro Rico/Bacury) (Antunes and Eston 2009, Beca et al. 2017).

The coexistence between humans and wild mammals requires an integrative social and ecological agenda focusing on turning ‘conflicts’ into win-win solutions. Hunting, animal-vehicle collisions, and the spillover of zoonotic disease are among the conflicts most challenging for the São Paulo state. For instance, about 40,000 individuals of medium and large-sized mammals are road-killed per year on highways in the state of São Paulo affecting at least 33 different species (Abra et al. 2021). Road mortality can be considered one of the most important mortality risks, overtaking poaching, animal trafficking, and big fires (Galetti et al. 2021). In São Paulo state, about 156 Maned wolves, 149 Giant anteaters, and 47 Pumas are road-killed per year (Abra et al. 2021). Collisions with animals on highways in São Paulo state represent 3% of all collisions, totaling more than 2,600 animal-vehicle crashes per year, of which 18.5% of these resulted in human injuries or fatalities. The losses that include material, aesthetic, moral damages, and health treatments from human victims burden São Paulo society with 56 million reais annually (or 12 million US dollars) (Abra et al. 2019).

Hunting (particularly wild boars), a common practice in São Paulo state, can increase the spillover of zoonoses to humans (Winck et al. 2022). Potential new diseases may emerge and re-emerge from wild and invasive mammals, as they carry thousands of known and unknown viruses (Holmes 2022). Wild boars, for instance, may host dozens of viruses and bacteria and are one of the main preys of vampire bats (Schneider et al. 2009, Stoner-Duncan et al. 2014, Galetti et al. 2016). Illegal hunting can only be controlled by equipped park rangers in the protected areas and the adequate management of invasive species should be done by professional wildlife managers, not armed civilians.

Most of the protected parks in the state are badly understaffed, and hunting and palm-heart harvesting negatively impact several species (Valverde et al. 2021). Ecotourism is an obvious strategy to help protect those areas, create jobs, and develop a sustainable economy based on having positive (non-lethal) experiences with wildlife the way many developing countries, from bird-watching hub Costa Rica to gorilla-haven Rwanda, have managed. Despite decades-old, positive experiences in Intervales State Park such as being one of the biggest consumer markets of bird watchers and wildlife photographers in the country, most protected areas in São Paulo still lack proper ecotourism programs that look at wildlife as an economic asset. Better infrastructure and security, standard rules across the protected area system, partnerships with local businesses, granting tourism concessions, training for local guides and rangers, and start-ups that ally conservation to economic viability is major gaps, only partially filled by private enterprises such as the ones taking enthusiasts to watch Black Lion Tamarins in Buri, Muriquis in Carlos Botelho State Park and São Francisco Xavier and Tapirs in São Miguel Arcanjo and Tapirai municipalities.

The state of São Paulo has started a payment of ecological services program and is planning to scale it up in the coming years, including bonuses to those preventing human-wildlife conflicts. This policy has the potential of reducing retaliatory killing and may contribute to the conservation of the Jaguar. Using schemes based on payments for environmental services and carbon markets to restore large areas currently occupied by the degraded pasture of low economic output in the Paraíba river valley, the interior slopes of the Serra do Mar, and lower areas of the Mantiqueira range would not only increase the available habitat to many mammalian species and connect currently isolated populations but also increase the resilience of watersheds that supply water to a large percentage of the Brazilian population. Therefore, the conservation of the mammalian diversity in São Paulo relies on strategies that connect forests within São Paulo and between São Paulo and neighboring states, curb illegal hunting, control invasive wild boar, create green roads, and provide incentives for ecotourism.

Supplementary Material

The following online material is available for this article:

Appendix 1 – Checklist of the Mammals from São Paulo State.

Appendix 2 – Distribution of each mammalian order in São Paulo state.

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Conflicts of Interest

There is no conflict of interest.

Ethics

This study did not involve human beings and or clinical trials that should be approved by one Institutional Committee.

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