



Long-term population trends of introduced mammals on an tropical island

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ABSTRACT

The introduction of species in areas with no top-down control is a recipe for ecosystem catastrophe. Theory predicts that introduced species in areas that lack predators may experience rapid growth and subsequently crash or stabilize around the carrying capacity. Impressively, there are very few studies on the population trend of tropical forest-dwelling mammals. In 1983, 100 individuals from 15 species of generalist mammals were introduced on an 828-ha tropical island in Southeast Brazil (Anchieta Island). Here, we present the status and population dynamics of the introduced species after 19, 21, 35, 38, and 39 years based on 611 km of line transects split into diurnal and nocturnal surveys. Among the introduced species, five were extinct and two species became super-abundant. The population of agouti has been fluctuating around 900 individuals and black-tufted marmoset around 600 individuals which may reflect the carrying capacity of the island. Our results showed that a tropical island, without top predators, resulted in a massive population explosion of 2 of the 15 introduced mammals, demonstrating that colonization and invasion processes are not straightforward to predict.

1. Introduction

We are currently undergoing an unprecedented biodiversity crisis and, combined with climate and land-use change, introduced

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species are one of the most detrimental drivers of global change, having increased drastically over the last few years (Dirzo et al., 2014; Fricke and Svenning, 2020; Galetti et al., 2021). Given the ubiquity of invasive species across the globe and the increased fragility of communities to their presence (Gaiarsa and Bascompte, 2022; Vollstädt et al., 2022), the Strategic Plan for Biodiversity (post-2020) of the CBD calls for urgent action to identify and estimate their degree of invasiveness to implement measures and prevent further introductions and invasions (CBD, 2022). One of the most significant challenges in providing subsidies for such actions is the scarcity of long-term studies on the population dynamics of introduced species. A comprehensive understanding of fluctuation patterns, the underlying drivers, and the invasion process is essential to direct attention towards species that are particularly susceptible to becoming problematic (Terborgh et al., 2002; Rich et al., 2014; Collins et al., 2020). Islands serve as valuable laboratories for studying population dynamics, primarily due to their isolation and limited size, which often results in distinctive population dynamics compared to the mainland. Within such conditions, populations are expected to exhibit higher and stable densities, displaying variations in reproductive rates and even morphological traits (e.g., body mass) (Benítez-López et al., 2021). Furthermore, the absence of top predators on islands allows for a clearer assessment of bottom-up intrinsic and extrinsic regulatory mechanisms, including dispersal, reproductive inhibition, disease, and trophic-level interactions (Erb et al., 2001). This phenomenon, commonly referred to as the island syndrome (Adler and Levins, 1994; Russell et al., 2011), renders islands highly susceptible to the impacts of introduced species (Gaiarsa and Bascompte, 2022; Vollstädt et al., 2022).

Long-term studies on population dynamics on island ecosystems are particularly relevant, given that introduced species fall into two broad categories: "true" exotic species, which are species not originally present in a region or biome, and native species introduced to areas where they were historically absent or have gone extinct (e.g., between the mainland and a nearby island) (Sax and Gaines, 2008). In the first case, when an introduced species encounters an entirely new environment, there are higher probabilities of extinction and a slower rate of population increase, particularly in the initial stages (Moran and Alexander, 2014). Conversely, in the other case, where the introduced or re-introduced species is already adapted to abiotic factors (e.g., climate), it is expected to be more adept at exploiting available food resources, leading to a quicker colonization process and higher, more stable population densities (Adler and Levins, 1994; Russell et al., 2011). However, this trend may become more evident with the introduction of a single species, as simultaneous multiple introductions can generate unpredictable patterns, particularly on an island without top predators (Bovendorp and Galetti, 2007). An experimental introduction of multiple species on islands provides a good tool to determine the establishment, persistence, and dynamics of island populations (Crowell, 1973; Schoener, 1983; Schoener and Spiller, 1995). However, such introductions will often be ethically or logistically impossible. Islands with past human-assisted introductions offer an unique opportunity to investigate the long-term population dynamics and invasion success (e.g. Blackburn and Duncan, 2001; Cassey et al., 2005; Bovendorp and Galetti, 2007).

The Anchieta Island State Park in the Atlantic Forest of Brazil, created in 1977, has been highly impacted due to the long period of

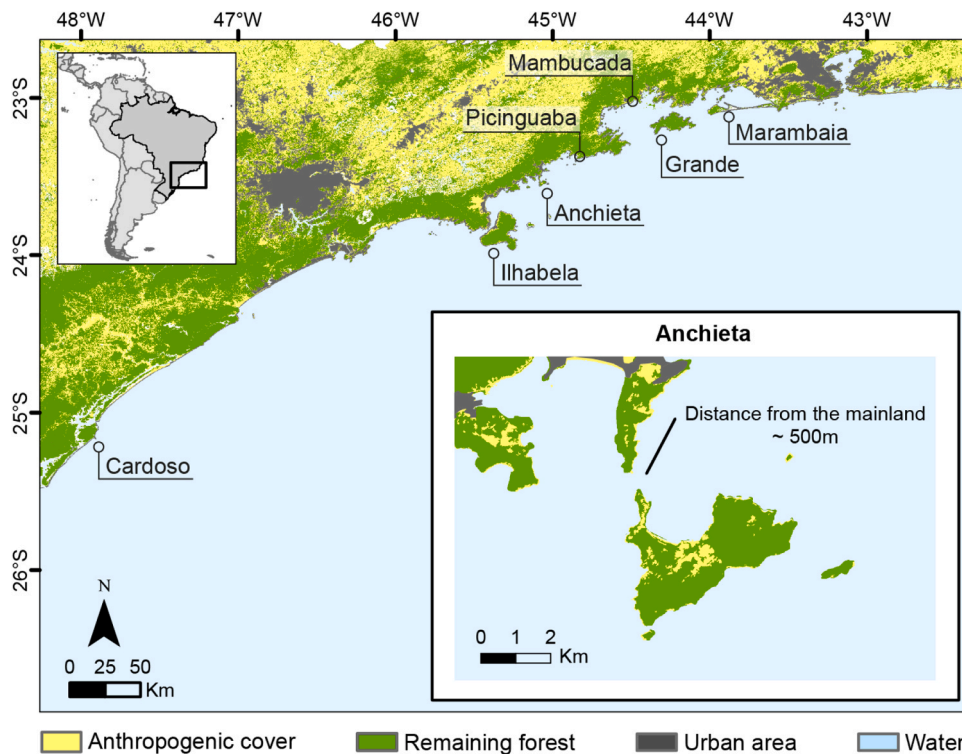


Fig. 1. Location of Anchieta Island and other major islands on the coast of São Paulo state, Brazil. Dark green is the rainforest and yellow pastures and agriculture.

human occupation and the intentional release of non-volant mammals (Bovendorp and Galetti, 2007). Little is known about the mammalian fauna of the island prior to human occupation. However, given its proximity to the mainland (500 m), it was probably composed by 30 terrestrial medium and large-sized mammalian species similar to the mainland, with the exception of large predators (e.g., jaguars and pumas) and ungulates (Rocha-Mendes et al., 2015; Gonçalves et al., 2018; Galetti et al., 2022). As a result of intense anthropogenic impact combined with the introduction of species, the last census conducted on the island revealed the highest density of terrestrial mammals worldwide (Bovendorp and Galetti, 2007). Such high densities were correlated with several trophic cascade effects (Fadini et al., 2009; Alvarez and Galetti, 2007; Gonçalves et al., 2020), highlighting the need to update the population status of these mammals to keep track of the ecological consequences of such introductions.

Here, using linear transect surveys, we evaluate the population trend of introduced mammals over a time series of 39 years on the Anchieta Island State Park, an tropical land-bridge island where approximately 100 individuals of 15 mammal species were intentionally introduced in 1983 (Bovendorp and Galetti, 2007). Leveraging the opportunities provided by multiple introductions and an extended time-span, our objective is to report whether all of these introduced species or only a subset conformed to the island syndrome pattern by attaining high and stable densities over time. Moreover, using two of the most abundant species as exemplars, we illustrated the various stages of the biological invasion process. Our findings offer practical recommendations for practitioners, funders, and decision-makers to effectively manage introduced species while simultaneously promoting conservation initiatives that extend beyond mere species release (Gonçalves et al., 2021).

2. Material and methods

2.1. Study area

The study was carried out at Anchieta Island State Park (hereafter Anchieta Island, 23°27'S; 45°03' W), an 828-ha land-bridge island in Ubatuba, north coast of São Paulo State, south-east Brazil (Fig. 1). The island is 500-meters away from the mainland and has a long history of human occupation including a settlement of Tupimambá Indigenous tribe and a prison at the beginning of the 20th century (Guillaumon et al., 1989). The prison and all infrastructures were expropriated, and the island was transformed into a protected area in 1977. In March 1983, the São Paulo Zoo Foundation introduced about 100 individuals of 15 mammal species (see Table S1) onto the island with the intention of “restoring” the local fauna (Guillaumon et al., 1989). The vegetation on the island includes the ombrophilous dense Atlantic forest type, covering around 77% of the island’s surface and presenting different successional stages, as a result of the long period of human occupation. The remaining surface is occupied by open fields invaded by ferns (*Gleichenia* sp.) (17%) and the other 6% is divided between salt marsh, beaches, rocky shores, buildings, and mangroves (Fleury et al., 2014). The climate is classified as a humid subtropical Climate, with rainfall (1818–2000 mm annually) concentrated between December and March, and a marked dry season from May to August (Bovendorp and Galetti, 2007; Fleury et al., 2014).

2.2. Mammal census

We estimated the abundance, density, and population size of introduced mammals using the distance sampling method (Thomas et al., 2010). We surveyed six transects, ranging from 0.35 to 2.7 km in length (Fig. S1), that were walking at a constant speed of 1 km/h between 6:30 and 11:30 h and between 17:30 h and midnight. For every animal detected during our sampling, we measured the perpendicular distance between the animal and the transect and the number of individuals (in the case of groups). For groups, we measured the perpendicular distance by the most centralist animal in the group. The transects were sampled by previously trained researchers, in order to avoid sampling errors such as responsive movements before detection and inaccurate estimation of the distance between the animal and observer in the transect (Thomas et al., 2010). The surveys were carried out in the dry season during the months of July and August of 2002 (42 km), May and July of 2004 (96 km), July of 2018 (72 km), July of 2021 (221 km) and July of 2022 (178 km), for a total of 611 km (369 km diurnal and 242 km nocturnal). The raw data from 2002 and 2004 are from Bovendorp and Galetti (2007) and were re-analyzed and incorporated into an open dataset (GitHub: LEEClab/anchieta_mammals). We split diurnal and nocturnal surveys according to each species’ dominant activity period. For example, we used only the data obtained during the diurnal sampling for the agouti and the marmoset, and nocturnal sampling for the opossum. As our sampling period was relatively short, we assumed population closure, i.e., no births, deaths, permanent immigration, emigration or movement on and off a study area between detection occasions.

Two species of agoutis were introduced in 1983, *Dasyprocta azarae* that are a typical species from the South American dry forest (Catzeflis, 2016), and *Dasyprocta leporina* which is a species from the coastal Atlantic forest and Amazon forest (Silvius and Fragoso, 2003; Ferregueti et al., 2018). Because both species are known to produce hybrids in captivity, we consider this population as *Dasyprocta* spp. A full genetic study is highly desirable to elucidate if the individuals on Anchieta Island are hybrid or from one single species.

2.3. Data analysis

The study was carried out during both the rainy, at various periods between censuses, and in the dry season, which is limited to the month of July in almost all censuses. To ensure consistency and avoid potential heterogeneity that could influence the detection probability and population estimates, we focused our analysis on the data collected during the dry season. We used the Conventional Distance Sampling (CDS) modelling to estimate the relative abundance, density and population size of the mammal species on

Anchieta Island (Thomas et al., 2010). Conventional distance sampling is a mix of design-based and model-based methods. Models are proposed for the detection function $g(y)$, which is the probability of detection of an animal, expressed as a function of its distance y from the line or point. These are fitted to the distance data using maximum likelihood methods. This component of estimation is therefore model-based. However, the likelihood maximized is not the full likelihood, but a conditional likelihood: the likelihood of the distances y , conditional on the number n of animals detected. To estimate it, the program uses the perpendicular distances of the detected animals. It calculates the observer's effective strip width (ESW) to select the model of probability detection function of the animals, because transects sampled with no detected animals (days of intense rainfall and high climate instability, for example), can inflate data (Thomas et al., 2010). As detection is generally not perfect on the transect, we need a formulation to allow for detectability to decrease with distance from the central line. This detection bias can be modelled via a loglink using a generalized linear mixed model (GLMM) with a Poisson distribution error structure. Thus, we applied the model to predict the probability of a detection event occurring each year, even when it has a high likelihood of happening but becomes rare in actual occurrences. In cases where the coefficient of variation (CV) was above 20%, which corresponds to the maximum recommended value for an accurate density estimate (Thomas et al., 2010), we estimated only the relative abundance (individuals or groups observed per 10 km walked) and their respective 95% confidence intervals estimated by Distance 7.5 (Fig. 2). To be very conservative, we successfully estimated the population density and size of two species, the agouti (*Dasyprocta* spp.) and the marmoset (*Callithrix penicillata*). To ensure accuracy, we meticulously excluded non-habitat areas, such as buildings, rocky shores, beaches, open fields, and mangroves (Fleury et al., 2014). Our study focused on 634 ha of suitable habitat for both species, providing valuable insights into their ecological dynamics. Additionally, the regressions provided by Distance for each year indicate that cluster size was not related to distance from the transect line (since all Pearson Correlations were less than -0.3). Therefore, for population estimates of marmoset, we used cluster size data input without the need to make adjustments. The analysis was conducted using the software Distance 7.5 (Thomas et al., 2010).

3. Results

3.1. The winners and losers

Of the 15 species introduced in 1983, nine species were observed during line transect census and ad libitum walks from 2002 to 2022. Five species (*Cabassous tatouay*, *Mazama gouazoubira*, *Myocastor coypus*, *Euphractus sexcinctus*, and *Bradypus variegatus*) were

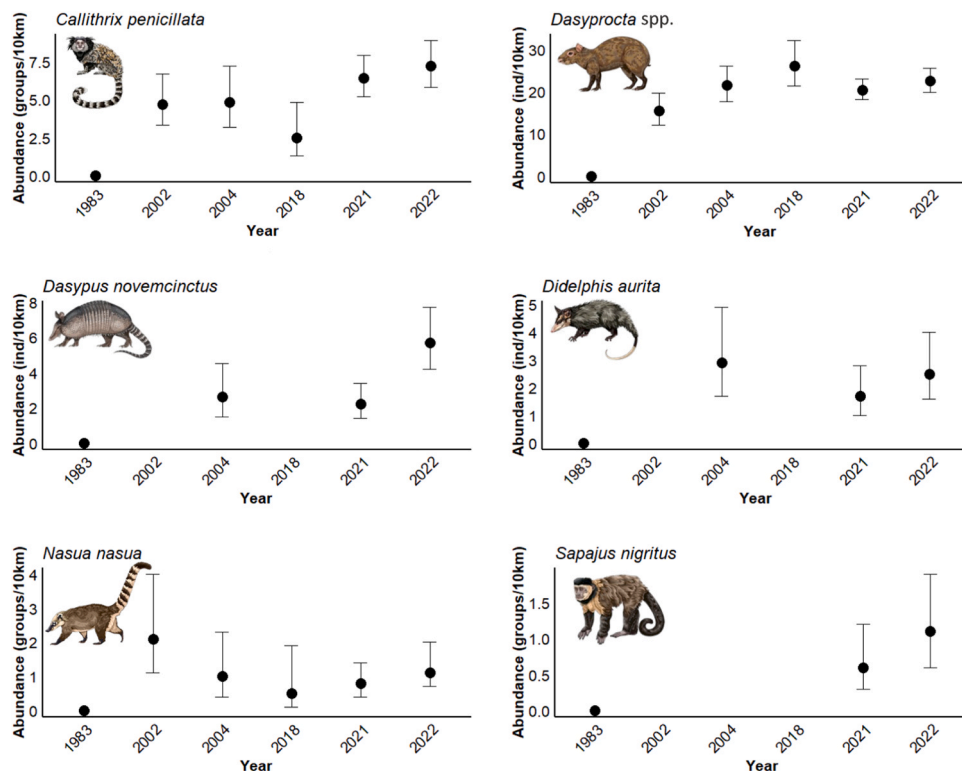


Fig. 2. The abundance (individuals-groups/10 km) of six mammalian species since their introduction in 1983 on Anchieta Island, São Paulo, Brazil. *Dasybus novemcinctus* and *D. aurita* were recorded exclusively during nocturnal sampling and are potential native species on Anchieta Island. The dots represent the estimated abundance, and the lines indicate their respective 95% confidence intervals (CI). Please observe the varying scales used for each species in the figure.

never recorded and we considered these species extinct. Along the 611 km walk (diurnal and nocturnal), we obtained 1050 sightings. *Dasybus novemcinctus*, *Didelphis aurita*, *Cuniculus paca*, *Tamandua tetradactyla*, *Hydrochoerus hydrochaeris*, and *Sphiggurus villosus* were rarely recorded in transects. No other species of non-volant mammals that occur on the mainland near Anchieta Island were recorded (Rocha-Mendes et al., 2015; Gonçalves et al., 2018; Galetti et al., 2022).

3.2. Temporal trends in the abundance, densities, and population sizes

Based on the abundance of individuals from six species sighted in at least four out of five censuses, our results provided a comprehensive overview of each population's status (Fig. 2). Apart from the ring-tailed coati, all other species exhibited a remarkable increase in abundance during the last three censuses (Fig. 2). Among these, the agoutis (*Dasyprocta* spp.), the sole species found in all sampled transects, were sighted 659 times. Their abundance showed a rising trend until 2004, followed by a stable period until 2018, and then a notable surge in the years 2021 and 2022. Despite typically being solitary, in transects with a high density of palm trees, we observed groups of up to six agoutis foraging simultaneously.

In 2022, the black-tufted marmoset (*Callithrix penicillata*) was sighted 221 times, displaying the highest average abundance on the island (7.2 groups/10 km). The species showed a slight decline in 2018 but experienced an increase in both 2021 and 2022. The largest group observed comprised 10 individuals, while single individuals were also sighted in the transects (Fig. 2). The black-horned capuchin monkey (*Sapajus nigritus*) was sighted 23 times and has a relatively low abundance, since the introduction of 33 individuals in 1983. The species had estimated abundance only in the years 2021 and 2022 (Fig. 2). The largest group sighted has 7 individuals.

The ring-tailed coati (*Nasua nasua*) was sighted 40 times in 2002, with an abundance of 2.1 groups per 10 km. It experienced slight declines in sightings in both 2004 and 2018, followed by increases in 2021 and 2022. The largest observed group consisted of 11 individuals, with several single-individual sightings (Fig. 2). The nine-banded armadillo (*Dasybus novemcinctus*) was sighted 71 times, exhibiting relatively low abundance in both 2004 and 2021 but increasing in 2022. Notably, no individuals were sighted in the transects in 2018 (though some were eventually sighted near the buildings). In 2021, the detection rate was 2.2 individuals per 10 km, which significantly increased to 5.7 individuals per 10 km in 2022 (Fig. 2). The black-eared opossum (*Didelphis aurita*) was sighted 36 times, showing a relatively low abundance throughout the entire study period (Fig. 2). *Dasybus novemcinctus* and *D. aurita* were recorded exclusively during nocturnal sampling and are potential native species on Anchieta Island.

Based on these results, we noted that the encounter rate for *C. penicillata* and *N. nasua* was the lowest in 2018, whereas *Dasyprocta* spp. showed the highest encounter rate. Meanwhile, *D. novemcinctus*, *D. aurita*, and *S. nigritus* exhibited consistent, average encounter rates with no significant changes in abundance across the years 2002, 2004, and 2018 (Fig. 2).

Due to the limited relative abundance of other mammal species, the sample sizes were insufficient to obtain statistically robust estimates. Nonetheless, we successfully achieved reliable densities and population size estimates (CV < 20%; see Table S2 and S3) for two species: the black-tufted marmoset and agouti (Fig. 3).

4. Discussion

Studies of the long-term population trend are needed to tackle the main objectives in conservation biology and better define management strategies and evaluate the impacts of introduced species (Carrillo et al., 2000). Additionally, such data may be used as a template to better understand and predict the cascading effects at trophic and spatial levels on different ecological processes affecting vegetation dynamics such as herbivory and seed dispersal (Bueno et al., 2021). On Anchieta Island, where the top predator is no longer present, it was expected that the island syndrome would be observed in all the introduced species (Adler and Levins, 1994). However, during our observations, we noticed a significant population explosion in two out of the 15 introduced mammal species, highlighting that colonization and invasion processes are not straightforward to predict. Similarly, determining the most effective conservation

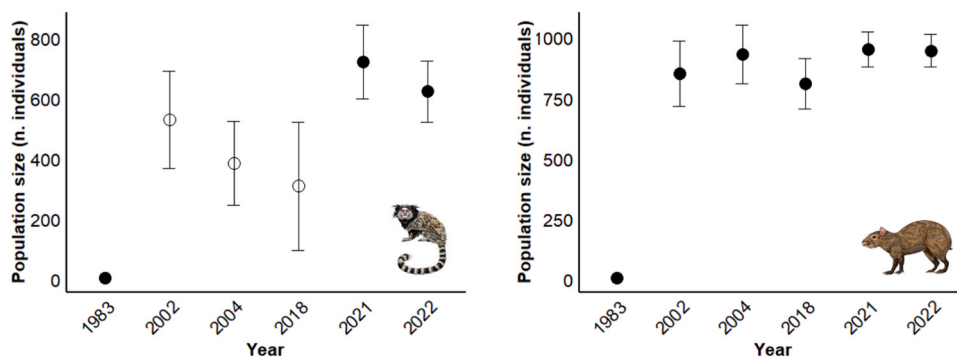


Fig. 3. The population size of black-tufted marmoset (*C. penicillata*) and agouti (*Dasyprocta* spp.) since their introduction in 1983 on Anchieta Island, São Paulo, Brazil. Full dots show the estimated population size and their respective standard error (SE) in lines. Open dots represent estimates with a coefficient of variation higher than 20%.

strategy is not simple. For instance, deciding whether to control or promote specific species or to conduct new introductions can be challenging. Therefore, studies like ours play a crucial role in understanding community dynamics and the interconnected biological and anthropogenic impacts over the long term, especially following multiple species introductions.

The mammal community at Anchieta Island reflects part of disturbed communities in the mainland Atlantic forest that suffer from strong human pressure, with a high population size of rodents (agoutis) and mesopredators (marmosets) (Pires and Galetti, 2022). Out of the 15 species introduced, only nine thrive on Anchieta Island. The introduction of mammals led to fast population growth of two species, agouti (*Dasyprocta* spp.) and black-tufted marmoset (*C. penicillata*) with different ecological attributes. The black-horned capuchin monkey population grew rapidly in fragments without top predators (Portela and Dirzo, 2020), but on Anchieta, the population of capuchin monkeys tend to remain around the same number of individuals. Furthermore, ring-tailed coatis are often preyed on by big cats (Hass and Valenzuela, 2002) and an increase in their density is mainly attributed to the absence of a top predator combined with generalist feeding habits (Terborgh, 1992). However, its population does not seem to increase on Anchieta Island. It is likely that male competition for females may be regulating the population of coatis on the island (Hirsch, 2011). For these cases, other studies are necessary to understand the factors that are limiting the population growth of a free-predator species.

The estimated density of agouti on Anchieta Island (149.4 ind/km²) is the highest density of the genus *Dasyprocta* detected in studies conducted on islands in the Neotropical realm and the third highest compared to mainland studies (Table 1). In the protected areas with relative proximity to Anchieta Island, such as the Serra do Mar State Park, PESM-Vargem Grande, Picinguaba and Caraguatatuba (Fig. 1), agoutis occur with an average density of 0.73 ind/km², 204 times lower than on Anchieta Island. This is a clear example of the island syndrome, where populations reach high and stable densities after introduction (Adler and Levins, 1994), and the same pattern was also reported on isolated fragments in the mainland (Chiarello and Arruda, 2017).

Agoutis are more abundant in forests larger than 20,000 ha, likely due to the increased availability of palm fruits, which serve as a preferential food source (Chiarello, 1999; Galetti et al., 2006). The remarkably high density of agoutis could have significant ecological consequences. For example, agoutis are considered seed predators that occasionally act as important seed dispersers, as they have the habit of burying seeds in the soil (Silva and Tabarelli, 2001; Galetti et al., 2006). However, as competition for resources intensifies at high densities, an increased number of individuals may engage in resource theft, leading to a potential increase in seed predation (Mittelman et al., 2021; Guimarães et al., 2006). This could subsequently result in a decrease in the recruitment capacity of the island's native flora (Fadini et al., 2009; Fleury et al., 2014). Furthermore, Ferreguetti et al. (2018) found a strong correlation between the presence of agoutis and the proximity of water resources, with nearly zero occurrences observed in areas located more than one kilometer away from water sources. On Anchieta Island, water availability is widespread across a significant portion of its territory. As a result, the detection of agoutis in all trails may be strongly associated with their proximity to water sources and the water regime

Table 1
Population density estimates of genus *Dasyprocta* in the Neotropical realm.

Location	Country	Species	Density (ind/km ²)	Method	Study
Island					
Anchieta Island State Park	Brazil	<i>Dasyprocta</i> spp.	149.4	Distance sampling	This study
Barro Colorado Island	Panamá	<i>D. punctata</i>	100	Capture-Mark-Recapture	Aliaga-Rossel et al. (2008)
Coiba Island	Panamá	<i>D. coibae</i>	73.3	Occupancy models	Duquette et al. (2017)
Central Range Wildlife Sanctuary	Trinidad	<i>D. leporina</i>	8.38	Distance sampling	Nelson et al. (2011)
Cardoso Island State Park	Brazil	<i>D. leporina</i>	4.29	Distance sampling	Galetti et al. (2016)
Mainland					
Natural History Museum and Botanic Garden (Urban fragment)	Brazil	<i>D. prymnolopha</i>	368.5	Distance sampling	Chiarello and Arruda (2017)
Tikal National Park (disturbed area)	Guatemala	<i>D. punctata</i>	160.24	Distance sampling	Hidinger (1996)
Kayapó Reserve (A'Ukre)	Brazil	<i>D. leporina</i>	43.3	Distance sampling	Peres and Nascimento (2006)
La Selva Biological Station	Costa Rica	<i>D. punctata</i>	37.7	Distance sampling	Romero et al. (2016)
Linhares	Brazil	<i>D. leporina</i>	21	Distance sampling	Ferreguetti et al. (2018)
Tikal National Park (preserved area)	Guatemala	<i>D. punctata</i>	14.48	Distance sampling	Hidinger (1996)
Kayapó Reserve (Pinkaiti)	Brazil	<i>D. leporina</i>	12.5	Distance sampling	Peres and Nascimento (2006)
Iwokrama Forest	Guyana	<i>D. leporina</i>	10.5	Distance sampling	Bicknell and Peres (2010)
Pantanal (forest)	Brazil	<i>D. azarae</i>	10	Distance sampling	Desbiez et al. (2010)
Pantanal (cerrado)	Brazil	<i>D. azarae</i>	6.22	Distance sampling	Desbiez et al. (2010)
Manu National Park (Cocha Cashu)	Peru	<i>D. punctata</i>	3.47	Distance sampling	Endo et al. (2010)
Manu National Park (Lower Panagua)	Peru	<i>D. punctata</i>	1.88	Distance sampling	Endo et al. (2010)
Manu National Park (Pakitza)	Peru	<i>D. punctata</i>	1.82	Distance sampling	Endo et al. (2010)
Manu National Park (Cumerjali)	Peru	<i>D. punctata</i>	1.72	Distance sampling	Endo et al. (2010)
Manu National Park (Tayakome)	Peru	<i>D. punctata</i>	1.64	Distance sampling	Endo et al. (2010)
Pantanal (floodplain)	Brazil	<i>D. azarae</i>	1.2	Distance sampling	Desbiez et al. (2010)
PESM Picinguaba	Brazil	<i>D. leporina</i>	1.19	Distance sampling	Galetti et al. (2016)
Manu National Park (Upper Panagua)	Peru	<i>D. punctata</i>	0.99	Distance sampling	Endo et al. (2010)
PESM Vargem Grande	Brazil	<i>D. leporina</i>	0.67	Distance sampling	Galetti et al. (2016)
PESM Caraguatatuba	Brazil	<i>D. leporina</i>	0.34	Distance sampling	Galetti et al. (2016)
Jurupará State Park	Brazil	<i>D. leporina</i>	0.33	Distance sampling	Galetti et al. (2016)
Carlos Botelho State Park	Brazil	<i>D. leporina</i>	0.3	Distance sampling	Galetti et al. (2016)

throughout the year. Additionally, the abundance of palm trees on the island contributes to this relationship, as these trees are considered essential food resources for species in the Atlantic forest (Donatti et al., 2009; Galetti et al., 2010; Pires and Galetti, 2012).

The estimated density of black-tufted marmosets on Anchieta Island, the only known Brazilian island with the presence of the genus *Callithrix*, is significantly higher compared to mainland studies (Table 2), with the exception of an urban fragment in northeastern Brazil (de Andrade et al., 2020). In nearby protected areas (Cunha-Itamambuca, Vargem Grande and Cunha-Santa Virgínia), the average density is approximately 10 ind/km², while on Anchieta Island, the density of marmosets is approximately 98.4 ind/km², which is approximately 10 times greater (Table 2).

The black-tufted marmoset (*C. penicillata*) is native to the South American dry forest (Rylands and Faria, 1993) and has been introduced in several areas of Brazil (Gestich et al., 2023). Compared to other primates, marmosets are more generalist in their behavior, which can lead to ecological impacts when they are introduced or relocated. These impacts may include competition with native species (Ruiz-Miranda et al., 2006), predation on small vertebrates and eggs (Alexandrino et al., 2012; Begotti and Landesmann, 2008; Galetti et al., 2009), and hybridization with other species of the genus *Callithrix* (Malukiewicz, 2019). The black-tufted marmoset (*C. penicillata*) also possesses morphological adaptations in their teeth and digestive system that enable them to dig into tree trunks and consume expelled gum (Hershkovitz, 1977). This species is particularly specialized in gum foraging (Hershkovitz, 1977), relying significantly on gum as a primary food source in their diet. Tree gum is rich in carbohydrates and available almost throughout the year (Hershkovitz, 1977), allowing the marmoset to meet its energy needs even during periods of resource scarcity, such as limited fruit and insect availability (Ferrari et al., 1993). Furthermore, the Anchieta Island's black-tufted marmoset population, when at high density, poses a threat to tree trunks, even leading to individual tree mortality, as reported for specific tree species (Genini et al., 2009). This dense concentration of marmosets near tourist areas (edification areas) is likely linked to the availability of human food and people's behavior, as they persistently feed the animals, despite legal prohibitions. Moreover, during periods of food scarcity in the forest, black-tufted marmosets, coatis, black-horned capuchin monkeys, and black-eared opossums forage for food in edifications and trash bags (V. Zipparro pers. commun.). Nevertheless, despite this human-food interaction, stable isotope analysis suggests that human food does not significantly impact the dietary patterns of mammals on the island (Gonçalves et al., 2020).

The population sizes of agouti and marmosets have exhibited exponential growth since their introduction in 1983, continuing until the first census in 2002. Additionally, both species have been reported to achieve high population densities in urban fragments (Chiarello and Arruda, 2017; de Andrade et al., 2020). Indeed, biological invasions often progress through four distinct stages: (1) the introduction of a species, (2) the establishment period, (3) the population growth phase, and (4) the eventual demographic balance with fluctuations in populations (Andersen et al., 2004; With, 2002). The high estimated population sizes observed after 21 years of introduction (in 2002 and 2004) indicate that both agouti and marmosets have entered the third stage, characterized by continuous population growth. Moreover, the further increase in population size during the censuses of 2021 and 2022, after 39 years of introduction, suggests that these species have likely reached the final stage of the invasion process, where a demographic balance is achieved with fluctuations in their populations. Based on our study findings, it can be concluded that agouti and marmoset populations on the island have exhibited a clear island syndrome pattern. However, it is evident that their population growth is constrained by density-dependent controls, such as interspecific competition and diseases, even as early as 20 years after their introduction. These factors are likely playing a crucial role in shaping and regulating the population sizes on the island.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: A co-author of this study is one of the Co-Editors-in-Chief of Global Ecology and Conservation (Mauro Galetti, PhD).

Table 2
Population density estimates of genus *Callithrix* in Brazil.

Location	Country	Species	Density (ind/km ²)	Method	Study
Island					
Anchieta Island State Park	Brazil	<i>C. penicillata</i>	98.4	Distance sampling	This study
Mainland					
Mata do Buraquinho (Urban fragment)	Brazil	<i>C. jacchus</i>	250	Distance sampling	de Andrade et al. (2020)
Universidade Federal da Paraíba (Urban fragment)	Brazil	<i>C. jacchus</i>	200	Distance sampling	de Andrade et al. (2020)
Linhares	Brazil	<i>C. geoffroyi</i>	37.8	Distance sampling	Chiarello and de Melo (2001)
Sooretama	Brazil	<i>C. geoffroyi</i>	31.8	Distance sampling	Chiarello and de Melo (2001)
Córrego do Veado	Brazil	<i>C. geoffroyi</i>	18.5	Distance sampling	Chiarello and de Melo (2001)
PESM Cunha-Itamambuca	Brazil	<i>C. aurita</i>	11.4	Distance sampling	Galetti et al. (2016)
PESM Vargem Grande	Brazil	<i>C. aurita</i>	11	Distance sampling	Galetti et al. (2016)
PESM Cunha-Santa Virgínia	Brazil	<i>C. aurita</i>	7.55	Distance sampling	Norris et al. (2011)
Putiri	Brazil	<i>C. geoffroyi</i>	3.8	Distance sampling	Chiarello and de Melo (2001)
Córrego da Onça	Brazil	<i>C. penicillata</i>	3.2	Distance sampling	Henriques and Cavalcante (2004)
Córrego Grande	Brazil	<i>C. geoffroyi</i>	2.6	Distance sampling	Chiarello and de Melo (2001)

Data Availability

Associated data is also available in GitHub github.com/LEECIab/anchieta_mammals.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02623](https://doi.org/10.1016/j.gecco.2023.e02623).

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