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Research Article

The Atlantic Forest as a barrier to invasive rodents: study of a seaport in southern Brazil

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Abstract

Invasive rats and mice typically arrive in novel regions through unintentional transportation aboard ocean-going vessels, which makes seaports the principal point of entry of these species. In this innovative study, we modeled the spatial distribution and abundance of two invasive rodent species (*Rattus norvegicus* and *Mus musculus*) in Paranaguá, a port city, in southern Brazil whose original vegetation cover was Atlantic Forest. Occupancy and abundance were estimated using live and pitfall traps during nine field campaigns (4,214 trap.nights) at 18 sampling sites distributed along a gradient of habitat between the port and the forest. The abundance and occupancy of both species were affected negatively by the percentage of forest cover within a radius of 1,000 m. The occupancy of *M. musculus* was also affected by the abundance of buildings within a radius of 100 m and by the distance to the nearest forest edge. The occupancy of *R. norvegicus* was related positively to the proximity of the access roads that link the port of Paranaguá with the rest of the state of Paraná. We conclude that, while the port is the point of entry for invasive rodents, neither study species was associated strongly with this area. The study identified the principal elements associated with rat and mouse occupancy, which provides the local authorities with important insights for the implementation of an effective invasive species management program in the municipality of Paranaguá. Overall, the Atlantic Forest reveals a remarkable ecosystem service and appears to act as a natural barrier to the dispersal of both rats and mice, being associated with a reduced abundance of these species and low occupancy probabilities.

Introduction

Rats and mice are among the most pervasive of the invasive mammals found around the world (Lowe et al., 2000). The Norway rat (*Rattus norvegicus*), ship rat (*Rattus rattus*), and house mouse (*Mus musculus*) have colonized all continents except Antarctica through accidental transportation aboard ocean-going vessels (Russell et al., 2008, 2007; Long, 2003). A global fleet of over 50,000 vessels currently transports more than 10.7 billion tons of cargo by sea each year (UNCTAD, 2018) and seaports are not only the focus of international trade, they are also key points of entry for invasive rodents (Russell et al., 2008; Hulme, 2009). Preventive measures, such as the inspection of docked ships, can reduce the risk of the introduction of exotic rodents to the area of the port, but if this fails and a species reaches land, the next step is to control its establishment and spread, and the potential for this will depend on the physical and biological characteristics of the region (Gren, 2008). The identification of the characteristics of the novel environment that will determine the capacity of the invasive rodent to occupy this environment can help to improve control measures in port cities, and thus minimize the spread of these rodents into the surrounding area. Several studies have analyzed rat and mouse distribution patterns in different parts of the world (Walker et al., 2019; Traweger et al., 2006; Lehtonen et al., 2001) and have shown that these invasive species may present distinct responses to different environmental contexts (King et al., 2011). However, the occupancy patterns of these animals have never been evaluated in a natural Brazilian environment.

Brazil is a megadiverse country that has approximately 9.5% of the world's species (Lewinsohn and Prado, 2005). Invasive rodents represent a threat to many species around the world, including plants, invertebrates, birds, and mammals (St Clair, 2011; Harris, 2009; Meyer and Butaud, 2009; Jones et al., 2008; Wanless et al., 2007) but despite this potential threat, studies of these invasive species in Brazil are still scarce (e.g., Richardson et al., 2017; Panti-may et al., 2016; Sarmento et al., 2014). While some, occasional reports of the capture of non-native rodents in Brazil have been published (e.g., Cherem et al., 2011; Tonini et al., 2010), few data are available on the occupancy patterns of these species in complex natural environment, such as the native forests. The Atlantic Forest covers the whole eastern coast of Brazil and is considered to be a biodiversity hotspot (Myers et al., 2000). This rainforest is the first natural environment that most invasive rats and mice will encounter after arriving at Brazilian ports, and understanding the degree of penetration of these rodents into the forest will provide important insights into the threat they pose to native Brazilian species.

In order to understand how the dispersal of invasive rats and mice is affected by the Atlantic Forest landscape, we evaluated the abundance and occupancy of the species in relation to the amount of forest cover and the distance to the forest edge. We also attempted to identify other factors potentially associated with the abundance and occupancy of rats and mice in the port city, such as the distance from the quays and the principal access roads. The findings of the study provide important insights for the improvement of measures for the control of the dissemination of invasive rodent populations in Paranaguá and, potentially, in other port cities on the Brazilian coast.

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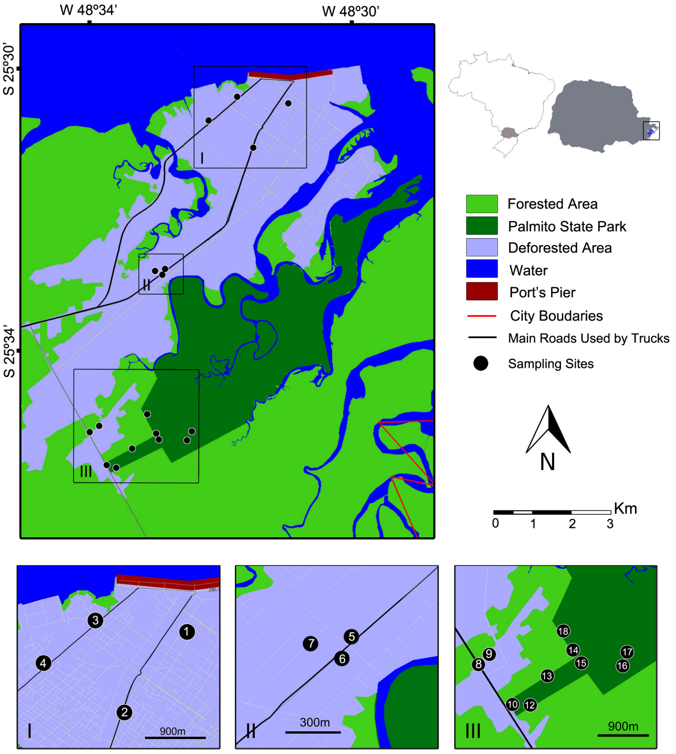

Figure 1 – Location of the study area in Paranaguá, Paraná state, Brazil. Only the area where the vessels dock is represented as port. In III, sampling site 10 and 11 are overlapped.

Materials and methods

Study area

The study was conducted in Paranaguá (25°31′ S, 48°30′ W), a seaport with a population of 153600 inhabitants and a municipal area of 827 km^2, located in the state of Paraná, southern Brazil (Fig. 1). The city of Paranaguá is surrounded by a continuous tract of Atlantic Forest (Dense Ombrophilous Forest) and 21.7% of the territory of the municipality is covered by five protected areas. The port, began as a dock in 1872, and was established officially in 1935. The shipping terminal has a total area of 425 km^2 and is the third most important seaport in Brazil, shipping primarily solid bulk cargo (32 million tons in 2018), but also liquid bulk and containers (APPA, 2019; ANTAQ, 2018). Paranaguá is the most important port in South America for the export of soybean, soymeal, and corn (ANTAQ, 2018).

To estimate the abundance and occupancy of invasive rodents in Paranaguá, we selected 18 sampling sites within the municipality along a gradient of increasing distance from the port in the direction of the forest. Given its proximity to the urban zone of Paranaguá, the forest sampling points were located within Palmito State Park (PSP). The PSP is an integral protection conservation unit, comprising 1782 hectares of native vegetation composed of dense lowland ombrophilous forest, and secondary formations with marine or fluvial-marine influence (mangrove).

Data collection

Data were collected between January 2017 and July 2018 in nine field campaigns at the 18 sampling points within the study area. The rodents were collected in five types of live trap, including three models of Sherman trap (9 cm×9 cm×25 cm; 9.5 cm×9.5 cm×31 cm; 40 cm×21 cm×21 cm) and two models of Tomahawk trap (18 cm×14.5 cm×35 cm; 13 cm×13 cm×22 cm).

These traps were distributed differently at the sampling points, depending on the spatial configuration of the habitat: (i) at sampling sites 1 and 12–18, traps were placed at 10 m intervals along line transects, and (ii) at sampling sites 2–11, the traps were distributed randomly within a mean area of 452 m^2 (SD=85). As the urban conditions of some sites impeded the daily installation of traps, sampling effort ranged from 35 to 1069 trap nights per site (Tab. 1). The traps were baited with a mixture of banana, cornflour, peanut butter, and fish oil.

Rodents were also collected at two forest sites (17 and 18) using pitfall traps. These traps were installed along linear transects, with 10 buckets (60 L) spaced at 10-m intervals. All captured individuals were processed following the procedures approved by UFPR Ethics Committee (CEUA n.1211) and by the Brazilian federal environment agency (license n.23102-1 SISBIO).

Covariates and associated hypotheses

We used seven covariates to model the abundance and occupancy probability of the three invasive rodent species considered in the present study. In order to test our hypothesis that the abundance and occupancy probability of invasive rodents is associated with the forest, we measured the distance from the forest edge (covariate: edge) and the percentage of forest cover within a radius of 1000 m of each point (covariate: forest). To test whether the port plays a significant role in the access of rodents to the region, the distance from the port was also used as a covariate (covariate: port). To test whether dispersal routes influence rodent occupancy, the distance from the two principal access roads used by cargo trucks was also determined (covariate: truck), as was the distance from the nearest road (covariate: road). The abundance of buildings within a radius of 100 m (covariate: building) and the distance from the nearest building (covariate: building_edge) were also used to evaluate the degree of association between human agglomerations and the study species.

In the case of the forest edge covariate, negative values were attributed to sites located within the forest and positive values to those located outside the forest. The "nearest forest" referred to any fragment with an area of at least 5 hectares. To measure the abundance of buildings within a radius of 100 m and the distance of the sampling point from the nearest building, we considered only residences and other buildings, which are presumed to be occupied by the human population. Other infrastructure, such as roads, trucking yards, and vacant lots, were not counted in this evaluation.

A central point of each area or transect was chosen for the collection of the data on environmental parameters at each sampling site. All the covariates were measured using satellite images taken in 2018, available in the Google Earth Pro software (version 7.3.2.5491). As more than one type of trap was used to collection the rodents, we included the size and model of the traps as additional covariate to cover any potential variation in detection rates that may be related to trap type.

Table 1 – Trap effort per sampling site. Applied and general environmental context of each sampling site. LT = Line Transect, RDA = Randomly Distributed in the Area.

Sampling Site	Trap Method	Trap Effort	Context of the Site
1	Live-trap/LT	71	Urban environment
2	Live-trap/RDA	156	Urban environment
3	Live-trap/RDA	45	Urban environment
4	Live-trap/RDA	57	Urban environment
5	Live-trap/RDA	45	Urban environment
6	Live-trap/RDA	121	Urban environment
7	Live-trap/RDA	142	Urban environment
8	Live-trap/RDA	158	Edge
9	Live-trap/RDA	1069	Edge
10	Live-trap/RDA	386	Edge
11	Live-trap/RDA	35	Edge
12	Live-trap/LT	38	Forest
13	Live-trap/LT	253	Forest
14	Live-trap/LT	273	Forest
15	Live-trap/LT	312	Forest
16	Live-trap/LT	351	Forest
17	Pitfall	362	Forest
18	Pitfall	340	Forest
Total		4214	

Table 2 – Royle/Nichols Occupancy Model (Royle and Nichols, 2003). Selection for mean sampling site abundance (λ) for both rodent species *Mus musculus* and *Rattus norvegicus* based on AICc values for Paranaguá/PR. AICc = Akaike's Information Criterion, ΔAICc = difference in AICc relative to the smallest value, AICcw = AICc weight, K = number of parameters.

Model	AICc	ΔAICc	AICcw	K
Mus musculus				
λ(forest)r(.)	258.25	0	0.82	3
λ(.)r(.)	263.54	5.29	0.09	2
λ(forest)r(forest)	265.36	7.11	0.02	4
λ(.)r(forest)	269.12	10.87	0.01	3
Rattus norvegicus				
λ(forest)r(.)	159.42	0	0.82	3
λ(.)r(.)	164.25	4.83	0.09	2
λ(forest)r(forest)	167.52	8.1	0.02	4
λ(.)r(forest)	169.69	10.27	0.01	3

Data analysis

We performed Moran's I (Dormann et al., 2007) to verify spatial autocorrelation. Moran's I is widely used in ecology, to determine whether neighboring areas are more similar than expected by chance. Moran's I is a correlation coefficient which measures the overall spatial autocorrelation in the dataset. In other words, it measures the degree to which a given site is similar to the adjacent sites. If sites are influenced by their neighbors (attracted or repelled), their data are not considered to be independent (Dormann et al., 2007). Values of Moran's I range from -1 (indicating perfect dispersion) to +1 (perfect correlation). Moran's I was computed using a permutation-based test (99 permutations at a 5% significance level, using the `moran.cp` function in the `spdep` package of the R platform).

Occupancy modelling accounts for imperfect detection by interpreting a series of detection/non-detection events based on the assumption that these events are determined by the interaction between the probability of patch occupancy (Ψ) of a species and its detection probability (P) (Mackenzie et al., 2018). A detection event occurs when both the site was occupied and the species was detected ($\Psi \times P$). A non-detection occurs because either (i) the species was present but not detected ($\Psi \times [1 - P]$), or (ii) the species was not present and therefore, not detected ($1 - \Psi$) (Mackenzie et al., 2018). The maximum likelihood method, used in this occupancy modeling approach, was considered to provide the least biased estimates of occupancy and detection probabilities, based on the evaluation of a series of alternative methods (Wintle et al., 2004).

We implemented the Royle-Nichols occupancy model in the PRESENCE program (Royle and Nichols, 2003) to estimate the abundance of both rodent species (*Mus musculus* and *Rattus norvegicus*). This model assumes that the heterogeneity in detection among sites is the result of underlying differences in abundance (Royle and Nichols, 2003). This analysis estimates an index (λ) of mean abundance per site, which permits the evaluation of the variation in the abundance of the two species among the 18 sampling sites. The Royle/Nichols occupancy model assumes that: (i) the number of animals at a site follows a defined spatial distribution, for which $\hat{\lambda}$ indicates the mean abundance across all transects, and (ii) the probability of detecting an animal at each site is related to the species' inherent detection probability, $\hat{r}$, and its total abundance.

The model proposed by Royle and Nichols (2003) uses the Poisson distribution as the theoretical distribution to model abundance at the observed sites, based on the parameters r and λ. The inherent detection probability, r, varies by species but is constant for all the individuals of

Table 3 – Single-season occupancy and detectability models for *Mus musculus* and *Rattus norvegicus* in Paranaguá, Brazil. Covariates include: distance from forest edge (edge); distance from truck access (truck); forest cover (forest); distance from the closest road (road); abundance of human edifications (edification). Ψ = occupancy, p = detection, ΔAICc = difference in AICc relative to the smallest value, AICcw = Akaike weight, K = number of parameters.

Model	ΔAICc	AICcw	K
Mus musculus			
Ψ(edification;edge) p(.)	0.00	0.25	4
Ψ(edge;forest) p(.)	1.02	0.23	4
Ψ(edification;edge;forest) p(.)	1.26	0.21	5
Ψ(edge) p(.)	3.69	0.18	3
Ψ(edification;forest) p(.)	6.25	0.08	4
Ψ(.) p(.)	8.17	0.03	2
Ψ(edification) p(.)	10.63	0.01	3
Ψ(edification;edge;forest;road) p(.)	13.45	<0.01	6
Ψ(forest) p(.)	14.25	<0.01	3
Ψ(edification;edge;road) p(.)	14.67	<0.01	5
Rattus norvegicus			
Ψ(truck; forest) p(.)	0	0.72	4
Ψ(truck) p(.)	3.69	0.12	3
Ψ(forest) p(.)	5.56	0.08	3
Ψ(truck;road) p(.)	9.25	0.05	4
Ψ(truck;forest;road) p(.)	11.25	0.02	5
Ψ(truck;forest;edification) p(.)	13.65	<0.01	6
Ψ(truck;edification) p(.)	15.25	<0.01	4
Ψ(forest;road) p(.)	15.68	<0.01	4
Ψ(.) p(.)	18.25	<0.01	2
Ψ(truck;forest;road;edification) p(.)	18.36	<0.01	6

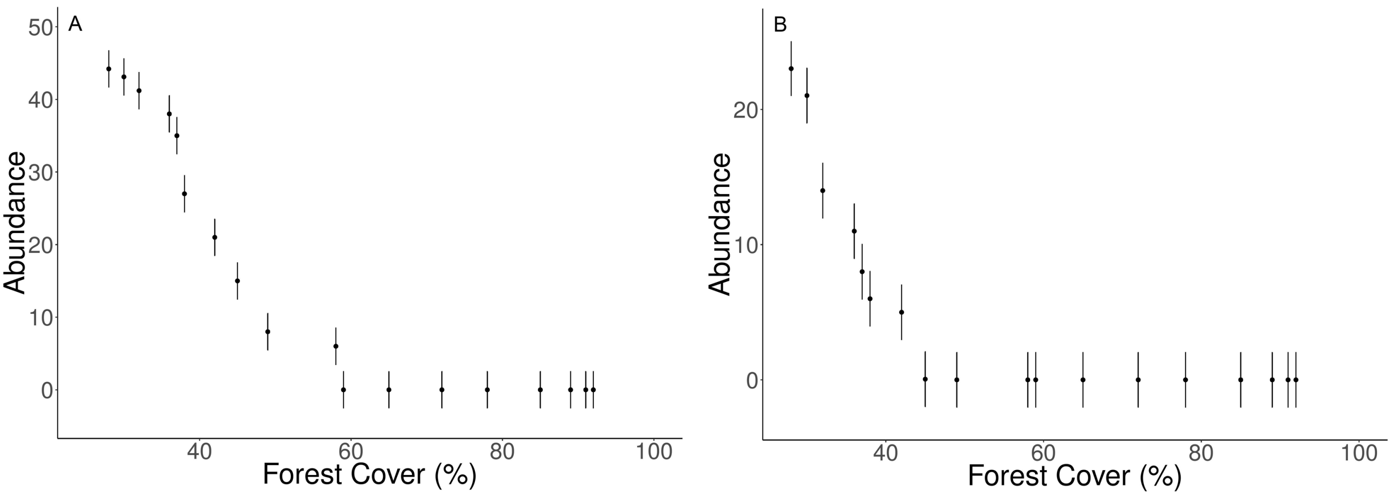

Figure 2 – Variation of abundance as function of the best-fit covariate according to Royle/Nichols model. *Mus musculus* abundance in relation to percentage of forest cover within a 1000 m radius (A); *Rattus norvegicus* abundance in relation to percentage of forest cover within a 1000 m radius (B).

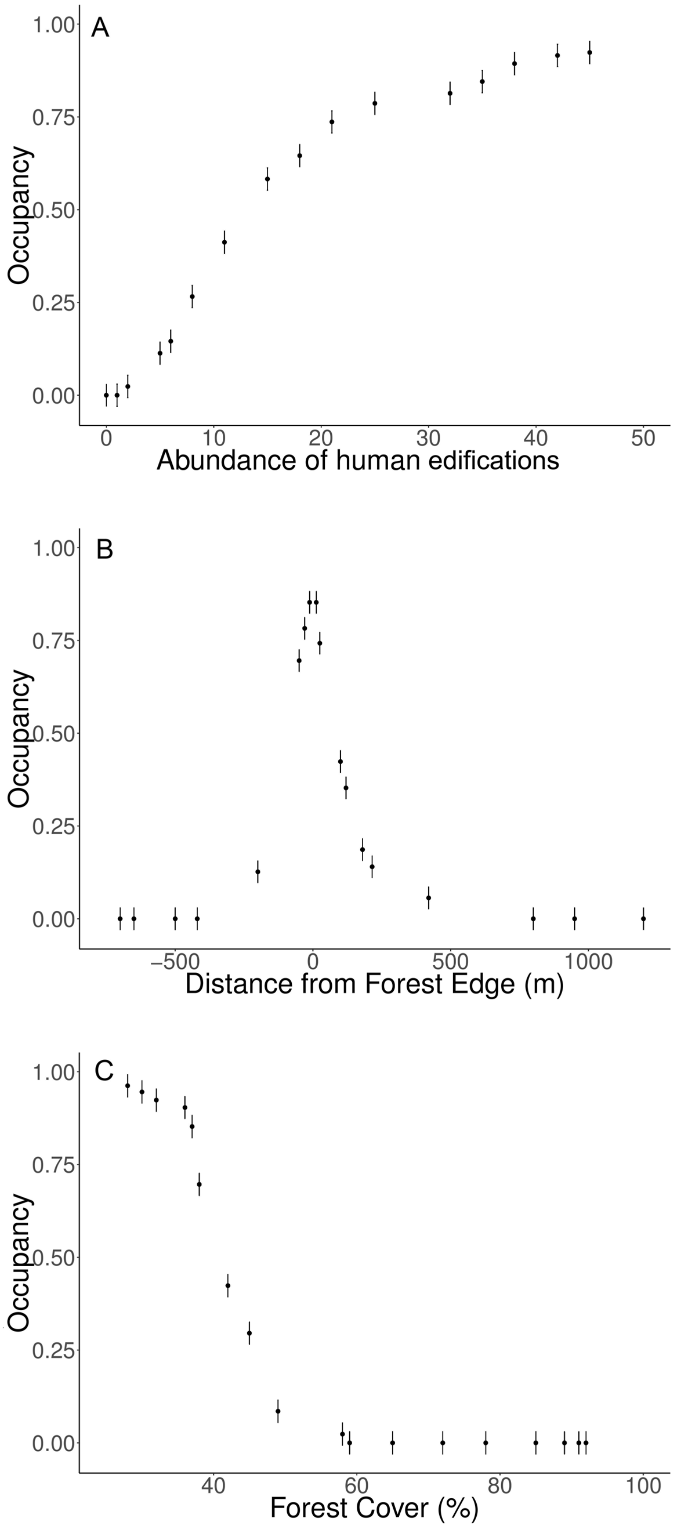

Figure 3 – Occupancy probability by *Mus musculus* according to the best-fit models. Relation between occupancy and the abundance of human edifications within radius of 100 m (A), relation between occupancy and distance from forest edge (B), negative values were attributed to sampling sites inside the forest and positive values to those outside of it; relation between occupancy and percentage of forest cover within radius of 1,000 m (C).

the same species. With N animals at a site, the probability of observing one or more animals at a site (and thus demonstrating that the site is occupied) is p=$1-(1-r)^N$. The distribution of N across sites is assumed to follow a Poisson distribution with a mean of λ, which is equal to the variance. The / value represents the probability that a site is occupied and is thus also the probability estimated from the Poisson distribution that one or more animals occur on the site. The principal assumption of the Royle-Nichols model is related to the initial assumption, that is, that the probability of detection of the target species at any site is a function of the abundance of animals at this site. The probability of detection at the site can thus be estimated by the formula:

$$p = 1 - (1 - r)N_i \tag{1}$$

where p is the site detection probability, r is the inherent detection probability, and N_i is the abundance of the species at site i.

We also investigated in how the habitat covariates affected the occupancy and detectability of each species. For this, single-species, single-season occupancy models were created for each species using the `unmarked` package in the R platform (Fiske and Chandler, 2011). We classified each campaign as an occasion, totalizing nine occasions, based on the detection history approach of Mackenzie et al. (2018). We constructed a set of candidate models for each species, which were selected by a priori hypotheses based on three different approaches: (i) considering occupancy probability and detectability as constant across all sites, (ii) considering the variation in occupancy as a function of the study covariates, and (iii) considering only detectability as a function of the study covariates. The top models were selected using Akaike's Information Criterion adjusted for small sample size (AICc). All the models with a ΔAICc value of less than 2 were considered to be more likely to estimate the parameters more reliably (Burnham and Anderson, 2002). We also considered the weight (AICcwt) of each model, that is, the amount of evidence that supports it, to select the best model, which was used to test the hypotheses.

Results

A total effort of 4214 trap.nights (Tab. 1) rendered 33 captures of *Rattus norvegicus*, 16 of *Mus musculus*, and one of *Rattus rattus*. Due to the low detection rate of *Rattus rattus*, this species was excluded from the analyses. None of the exotic species was captured inside the forest environment, and we found no spatial autocorrelation in the residuals (Moran's I=-0.59). This means that neighbouring sites are not more similar to each other than expected by chance. Similarly, the type of trap (model and size) had little influence on the best-fit models for the description of abundance and occupancy, which eliminates possible variation in the efficiency of the traps as a potential source of bias.

Royle-Nichols occupancy models

The Royle/Nichols model with the forest cover as a covariate provided the best explanation for the mean abundance of both rodent species at the different sites (wi=0.82; Tab. 2). The estimated population size ($\hat{N}$) of *M. musculus* in the study area as a whole was 140±12 individuals (95% CI=128–152 individuals), while that of *R. norvegicus* was 82±9 individuals (95% CI=73–91 individuals). The estimated mean abundance of both species was affected negatively by the forest cover, with $\hat{\lambda}$ declining among sites with increasing forest cover with estimate β values of -1.21 for *M. musculus* and -1.39 for *R. norvegicus* (Fig. 2).

Single-species occupancy models

For clarity, we only present the top 10 occupancy models for each species here, based on the ΔAICc (Tab. 3). *Mus musculus* was observed at only three of the 18 sampling sites, resulting in a naïve occupancy probability of 0.17. The estimated mean occupancy probability was 0.51±0.06 and the mean detection probability was 0.35±0.03. The best-fit models described the occupancy probability as an additive function of the site's abundance of buildings, distance from the forest edge, and forest cover, with the detection probability as a constant (Tab. 3).

The occupancy of *M. musculus* was higher at sites with more buildings (Ψ decreasing from 0.97±0.03 [mean±SE] to 0±0.02; Fig. 3A) and at sites closest to the forest edge (Ψ decreasing from 0.89±0.03 to 0±0.04; Fig. 3B). Occupancy was negatively affected by the forest cover, with probabilities ranging from Ψ=0.98±0.03 to Ψ=0±0.03 (Fig. 3C). We observed *R. norvegicus* at 6 of the 18 sampling sites, resulting in a naïve occupancy probability of 0.34. The estimated mean occupancy probability was 0.42±0.04 and the mean detection probability was 0.24±0.03. The best-fit model described occupancy prob-

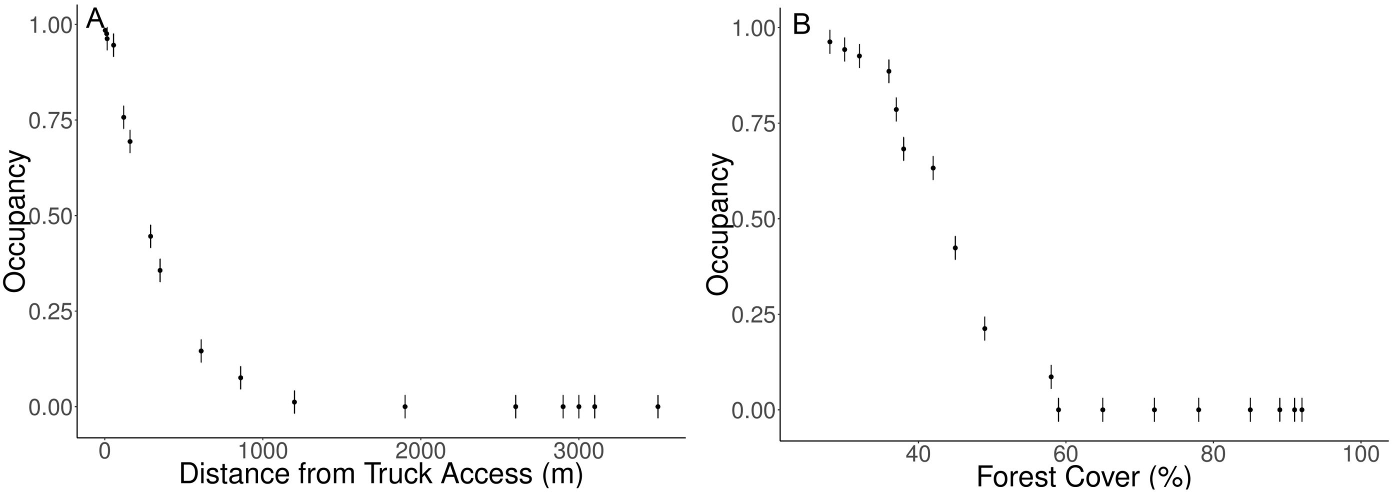

Figure 4 – Occupancy probability by *Rattus norvegicus* according to the best-fit models. Relation between occupancy and distance from road used by trucks to access the port (A), relation between occupancy and percentage of forest cover within radius of 1,000 m (B).

ability as a function of the distance from access roads and the forest cover. Detection was best modeled as a constant with the covariates having no effect. Occupancy was higher (Ψ=0.98±0.02) at sites closest to access roads (Fig. 4A) and at sites with the lowest forest cover (Ψ=0.96±0.03) (Fig. 4B).

Discussion

Occupancy and abundance

The percentage of forest cover was inversely related to the occupancy rate and abundance of both invasive rodent species. Forest cover appears to have a strongly negative effect on *R. norvegicus*, given that its abundance drops to zero when forest cover reaches 45%. The abundance of *M. musculus* was less affected, with zero abundance being reached at a forest cover of 59%. The occupancy probability of both species was zero when the forest cover within a radius of 1000 m was 59% or more. Gatto-Almeida et al. (2016) surveyed the mammal species in a second state park on the southern coast of Paraná, which has ecological characteristics similar to the present study area (i.e. Atlantic Forest in close proximity to an urban environment), and also recorded no invasive species within the forest, including a disused landfill site located within the reserve, despite a considerable sampling effort, of 6,633 trap.nights.

In Salzburg, Austria, by contrast, Traweger et al. (2006) recorded a positive association between *R. norvegicus* and patches of multi-layer vegetation (undergrowth, shrubs, and trees), and obtained low trapping success in patches with no vegetation. Similarly, *M. musculus* has been recorded amply in the forests of New Zealand, although the species is more common in disturbed habitats (Walker et al., 2019; King et al., 1996). Our analysis indicates, however, that a number of factors have a strong negative influence on the occurrence of the two species in areas with greater forest cover in the Atlantic Forest domain.

King et al. (2011) proposed that the presence of the red squirrel, *Sciurus vulgaris*, is responsible for the absence of *R. rattus* from Britain's forests, whereas the absence of specialist arboreal rodents in New Zealand permitted the colonization of its forests by the ship rat. As the Atlantic Forest has a high diversity of small mammals (Paglia et al., 2012), interspecific competition may be a primary factor determining the absence of invasive rodents from the forests of Paranaguá, although this does not explain why they are so rare in areas near the forest.

One additional factor here is the presence of predators. *Rattus norvegicus* has shown to present avoidance behavior toward a number of different mammals (Yin et al., 2011). In Paranaguá, greater forest cover is likely related to the presence of a larger number of potential predators, which reduce the density of mice and rats, and inhibit their occupancy. In fact, bone fragments of *M. musculus*, *R. rattus*, and *R. norvegicus* are commonly identified in the pellets of the Barn Owl (*Tyto furcata*) in Brazil (Lemos et al., 2015; Scheibler and Christoff, 2004). *Rattus rattus* and *M. musculus* are also known to be among the prey of the Crab-eating fox, *Cerdocyon thous*, a small South American canid that is common in forest edges and anthropogenic habitats (Dotta and Verdade, 2007; Gatti et al., 2006; Pedó et al., 2006). Both these predator species will hunt in areas adjacent to forests, and may thus contribute to a reduction in the density of invasive rodents in the areas surrounding a forest. There are also a number of other potential predators of rats and mice in the Atlantic Forest, including five native felines (Paglia et al., 2012) and around 70 birds of prey (ARB, 2019) that present a potential threat to invasive rodents in the forest habitat.

A second covariate that was associated positively with mice occupancy was the distance from the forest edge. Mice preferred areas closer to the edge of the forest, with a bell curve distribution that peaked (Ψ=0.85±0.03) 12 m from the edge of the forest, and 12 m into the vegetation. This does not contradict the findings on forest cover, given that the covariate "edge of the forest" does not reflect the amount of forest but rather, the proximity of natural shelters. Paranaguá has a lot of small fragments of forest with irregular edges that were considered to be the closest edge to a sampling site in many cases in the present study, although these forests were often too small or degraded to have any major population of predators. This finding reinforces the hypothesis that the negative association with forest cover is more closely related to the presence of predators than the capability of the species to colonize forest environments. This also suggests that *M. musculus* is a potential bioindicator of edge effects.

The occupancy analysis also indicated that *M. musculus* preferred more built-up areas, with more buildings within a 100-m radius. In contrast with *R. norvegicus*, which typically nests in underground burrows (Varnham, 2010; Traweger et al., 2006), *M. musculus* tends to spend more time in complex, ground-level habitats, or at least in places with overhead cover in open areas where no ground-level structures are available (Jensen et al., 2003), the type of cover that may be provided by either trees or buildings.

The occupancy analysis of *R. norvegicus* also indicated a positive association with the access roads. Like ships, trucks can transport rats accidentally (Sanu and Newport, 2010), and this type of dispersal may be especially frequent in and around ports, where trucks are constantly loading cargo and containers that may be infested by rodents brought from overseas. It is important to here that the distance to any road was included as a covariate in the analysis, although only the access roads (highlighted in Fig. 1) presented a significant association. In Paranaguá there are two main access roads that are used by trucks to reach the area of the port. Large amounts of grain, in particular soybean and corn often fall from the backs of trucks onto the roadside along these routes (Fig. S1), providing rodents with a potentially important feeding resource.

Management implications

As shown by King et al. (2011), the results of the present study indicate that rats and mice, which have been able to adapt to most regions around the world, may be relatively less successful at colonizing some environments, depending on the characteristics of the local habitats and the species they encounter in the region. Understanding how these invasive species interact with the local environment may be the key to the development of effective programs of control and eradication, which reinforces the need for studies of this type in other regions of the world.

We found that both *R. norvegicus* and *M. musculus* had lower prevalence and abundance in forest proximities, but unfortunately, few Brazilian cities have large remnants of Atlantic forest in close vicinity to the urban environment, as observed in Paranaguá. Brazilian environmental legislation (federal law n. 12651/2012) requires that any rural property located within the Atlantic Forest biome maintains at least 20% of its area as native vegetation, although our findings indicate that even this amount of forest cover would be inadequate to control invasive rodent populations.

Rezende et al. (2018) recently reviewed the remote sensing data on the vegetation cover of the Brazilian Atlantic Forest and found 28% of native vegetation cover, in contrast with the 11–16% estimated in previous studies. This apparent increase in forest cover was due to the identification of fragments and secondary forests not mapped previously. A fragmented landscape is probably not as efficient at controlling the dispersal of populations of invasive rats and mice, but reinforces the need for the natural regeneration of the forest cover. If all rural properties restored their legal debt (20% minimum of native forest cover), the Atlantic Forest could reach up to 33–35% of its original area (Rezende et al., 2018), and create a natural barrier to the invasion of exotic rodents along the Brazilian coast.

Brazil has a considerable species richness of small mammals (Paglia et al., 2012), and the traditional bait-poisoning method used to control rat populations (Courchamp et al., 2003) represents a potential threat to the native species found in contact areas. In this context, the Atlantic Forest may provide an extremely important ecosystem service that has been largely overlooked in studies that estimate the value of these services (e.g. Groot et al., 2012; Costanza et al., 2014, 1997). Our data have shown, for the first time, that this tropical forest has a considerable negative impact on the occupancy and abundance of two invasive rodents, and may thus represent a valuable alternative (or complementary) tool for the control of invasions. Rats cause billions of dollars of economic losses every year (Pimentel et al., 2000), and their natural control, by the Atlantic Forest, would be an ecological service of considerable value, that should be considered systematically in future valuation studies, and in the development of conservation policies.

Regarding *R. norvegicus* positive association with the main roads used by trucks to access the port. This indicates that the areas in the vicinity of these access roads, where the highest occupancy probabilities were recorded, should be given priority in any measures implemented by the local authorities for the control of rat populations. As this characteristic of the access roads is unlikely to be exclusive to Paranaguá, it would be advisable for other port cities to prioritize their access roads for rodent monitoring and control measures.

Finally, the distance from the quay was not a significant covariate, which means that the hypothesis of higher occupancy and abundance nearer to the port, where the rodents arrive, was rejected. If the port is actually a point of entry for invasive rodents, this finding may reflect two factors: (i) the new immigrants do not prefer to occupy areas in the vicinity of the quay, and/or (ii) the control measures adopted in the area of the port are highly effective (and should thus be extended to the rest of the city). What we know is that *M. musculus* and *R. norvegicus* are found throughout the city, and even though prevention measures to minimize the risk of new introductions are important, the results of the present study indicate emphatically that the competent authorities of the municipality of Paranaguá should focus on the implementation of comprehensive and continuous measures for the reduction of the local population of invasive rodents.

Relatively little South American research has focused on non-native species (Speziale et al., 2012) and in Brazil, only 15 of the 143 papers published on this topic between 1999 and 2015 referred to studies of mammals (Zenni et al., 2016). The present study is the first evaluate the abundance and distribution of invasive rodents in a Brazilian city. The methods adopted in the present study are typically used in research on native mammals, in particular for the definition of population parameters to support conservation initiatives (Wolff et al., 2019; Ferreguetti et al., 2018, 2017; Thorn et al., 2011). The present study was thus the first time that occupancy modeling has been used to evaluate the abundance and distribution of invasive rodents in a Brazilian urban zone.

Conclusion

Paranaguá has a privileged ecological context, in which the city is surrounded by a continuous tract of forest that appears to be confining the local rat and mouse populations to the urban environment, restricting the spread of these species beyond the urban zone. In particular, the present study has shown that rats are found primarily at some distance from the the forest and close to the main port access roads, which thus appear to be the priority areas for the implementation of control measures. The preference of *M. musculus* for the forest edge reinforces the need to maintain the integrity of the forest, emphasizing the ecosystem service provided by the Atlantic Forest as a natural barrier to the populations of these rodents. Further research in the study area should focus on the identification of the possible contact zones between the exotic and native rodent species found within the study area, and a more precise definition of the distribution patterns of the populations of the invasive species, in order to better understand their behavior and further refine management strategies.

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Figure S1 Fallen grains along one of the main roads used by trucks to access port area.