

Factors affecting space use by wild boars (*Sus scrofa*) in high-elevation tropical forests

T.A. Morais, C.A. Rosa, C.S. Azevedo, A.B. Viana-Junior, P. Santos, and M. Passamani

Abstract: The wild boar (*Sus scrofa* Linnaeus, 1758) is considered one of the 100 worst invasive species in the world and is present in the high-elevation forests in Brazil. Our objective was to understand how landscape and atmospheric conditions affect space use by wild boars. We hypothesized that wild boars would be more frequent at lower elevations, warmer and wetter forested areas, and away from human disturbances. After three years of data collection (2013–2016) using 16 camera traps, 881 independent records were obtained with a mean of 4.44 ± 9.25 pigs per record. Wild boar frequency of occurrence was higher at lower elevations, in more humid and warmer areas, and farther away human disturbance factors, corroborating our initial hypothesis. Understanding space-use patterns of wild boars is necessary for the design of management strategies that target areas of more intense usage, as well as for defining more effective population-control techniques.

Key words: Brazilian Atlantic forest, invasive alien species, introduced mammals, protected area, *Sus scrofa*, wild boar.

Résumé : Le sanglier (*Sus scrofa* Linnaeus, 1758) est considéré comme étant une des 100 pires espèces envahissantes dans le monde et est présent dans les forêts de haute élévation au Brésil. Notre étude visait à comprendre l'influence du paysage et des conditions atmosphériques sur l'utilisation de l'espace par les sangliers. Nous avions postulé que les sangliers seraient plus fréquents à faibles élévations, dans des zones boisées plus chaudes et humides et loin de perturbations d'origine humaine. Après trois années de collecte de données (2013–2016) à l'aide de 16 pièges photographiques, 881 registres indépendants ont été obtenus pour une moyenne de $4,44 \pm 9,25$ sangliers par registre. La fréquence de présences de sangliers était plus grande à faible élévation, dans des secteurs plus humides et chauds et plus loin de facteurs de perturbation d'origine humaine, ce qui corrobore notre hypothèse initiale. Une compréhension des motifs d'utilisation de l'espace des sangliers est nécessaire pour concevoir des stratégies de gestion qui ciblent les zones d'utilisation plus intense, ainsi que pour élaborer des méthodes efficaces de contrôle des populations. [Traduit par la Rédaction]

Mots-clés : forêt atlantique brésilienne, espèce non indigène envahissante, mammifères introduits, aire protégée, *Sus scrofa*, sanglier.

Introduction

Invasive species compete with native species for resources, causing biodiversity losses (McNeely 2001; Sampaio and Schmidt 2013; Spear et al. 2013; Gallien and Carboni 2017). High dispersal capacity and high reproductive rates contribute to establishment of invasive species (Arim et al. 2006; Flores-Moreno et al. 2013; Beckman et al. 2018). One invasive species with these characteristics is the wild boar (*Sus scrofa* Linnaeus, 1758), which is considered to be one of the most problematic invasive species (Lowe et al. 2000; Mapston 2012). Wild boars are native to Eurasia and North Africa (Oliver et al. 1993) and were intentionally introduced around the world for sport hunting and meat consumption in feral (boar) and domestic forms. It has become one of the invasive alien species with the largest geographic distributions (Massei and Genov 2004). This species can transmit several diseases to humans and domestic animals such as salmonellosis, brucellosis, leptospirosis, respiratory-stress syndrome virus, classical swine-fever

virus, etc. (Gisd 2010; Montagnaro et al. 2010; Mohamed et al. 2011; Mapston 2012), as well as alter the soil and vegetation when searching for food (Barrios-Garcia and Ballari 2012; Boughton and Boughton 2014).

The wild boar has wide ecological plasticity, being able to apply diverse strategies in the use of space and time to exploit a variety of resources available in an area (Mayer and Brisbin 2009). The species can rapidly adapt its behavior in response to structural and functional features of the landscape such as elevation, proximity to rivers, and forest cover, as well as to varied atmospheric conditions (temperature, rainfall, and humidity) (Virgós 2002; Lemel et al. 2003; Podgórska et al. 2013; Brivio et al. 2017). Wild boars occur most often in open habitats and agricultural fields close to natural forest remnants both in and outside their native range (Cordeiro et al. 2018; Lewis et al. 2017). While forests function as shelter from intense heat, resting areas, and hiding place from predators, open areas are used for feeding (Choquenot and Ruscoe 2003; Huynh et al. 2005).

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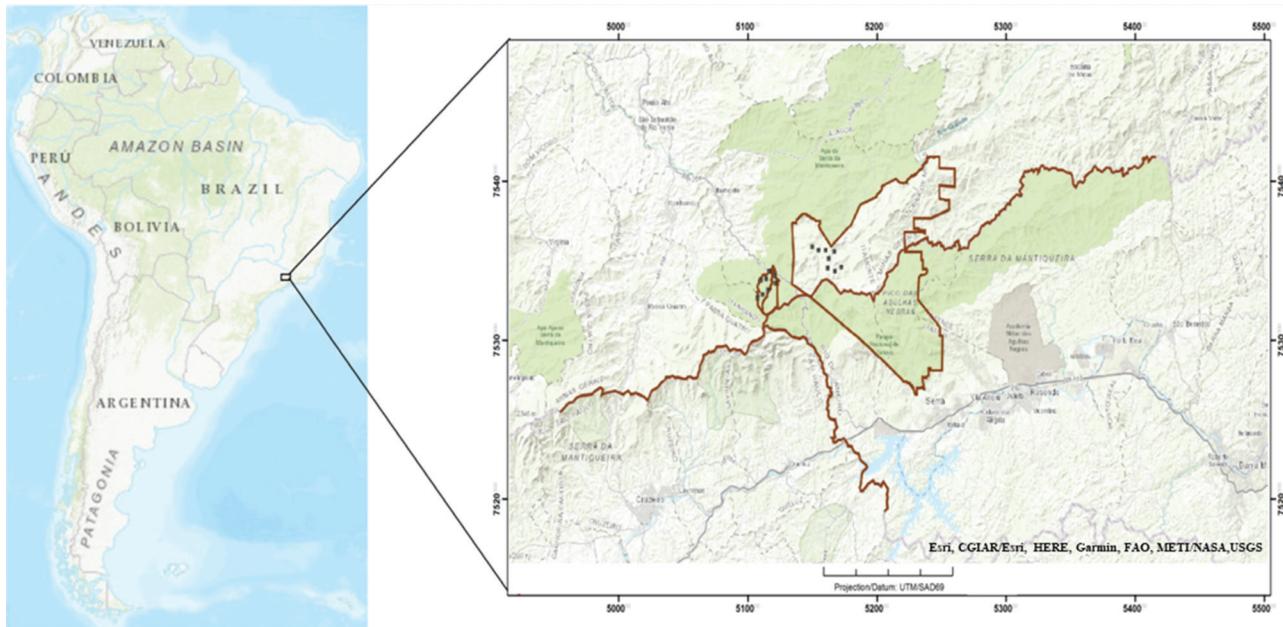
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Fig. 1. The study area in two protected areas: Itatiaia National Park (INP) and Alto-Montana Natural Heritage Private Reserve (NHPR). The black circles represent sampling points in the INP and NHPR. The brown lines indicate state borders (Rio de Janeiro, São Paulo, and Minas Gerais) and the borders of the protected areas. Color version online.



Local characteristics such as temperature, humidity, precipitation, and soil cover are the main abiotic and biotic factors affecting animal behavior (Taraborelli et al. 2009; Wingfield 2013; Hall and Chalfoun 2019). Normally, wild boar feeding rates and general activity diminish with increased temperature, humidity, and precipitation (Rosell et al. 2004; Huynh et al. 2005; Olczak et al. 2015). Also, in areas with more forest cover and less human impact, wild boars tend to exist in larger numbers and behave differently than in areas with more human presence (Santilli and Varuzza 2013; Stillfried et al. 2017). Wild boar hunting is less efficient in habitats with dense forest cover (Merli et al. 2017). Precipitation and forest cover also affect the global distribution of wild boars; more precipitation and forest cover are associated with higher wild boar densities (Lewis et al. 2017). Thus, it is expected that at local scales, areas with more forest cover and lower temperature, precipitation, and humidity will be used more by wild boars.

Invasion by wild boars in Brazil began in the southern region in 1989, when animals crossed the border from Uruguay; intentional and non-intentional introductions intensified the process (Deberdt and Scherer 2007; Pedrosa et al. 2015). As a result, the wild boar is currently concentrated in the southern and southeastern regions of the country (Pedrosa et al. 2015; Rosa et al. 2017). Given the environmental and economic damage that the wild boar has generated in Brazil in the past 30 years (Salvador 2012; Pedrosa et al. 2015), since 2013, the Brazilian government has authorized its control in the entire country by any citizen who acquires a license. The most common methods used to control wild boar populations since the regulations were issued are hunting with dogs, stand hunting, and trapping (Rosa et al. 2018).

Brazilian tropical forests are megadiverse and serve as refuges for many endangered and endemic species (Myers et al. 2000). Therefore, the wild boar invasion of Brazil's Atlantic domain, which is considered a biodiversity hotspot, is especially concerning (Myers et al. 2000; Le Saout et al. 2013). Only 12% of the original cover of Atlantic domain remains, mainly in the form of forest remnants smaller than 100 ha (Ribeiro et al. 2009). One of the most threatened forest formations in the domain is the araucaria forest (*Araucaria angustifolia* (Bertol.) Kuntze), listed by IUCN as "critically endangered" (Thomas 2013). Araucaria forests occur at elevations

above 500 m. The araucaria seed, a type of pinyon nut, is a key food resource for several mammals, for example, Azara's agouti (*Dasyprocta azarae* Lichtenstein, 1823), Ingrami's squirrel (*Sciurus ingrami* Thomas, 1901), and the striped Atlantic Forest rat (*Delomys dorsalis* (Hensel, 1872)) (Solórzano-Filho 2001; Iob and Vieira 2008; Vieira and Iob 2009), but wild boars reduce the food supply to native species by consuming pinyons (Sanguinetti and Kitzberger 2010; Shepherd and Ditgen 2013). As these forests are of concern for conservation, understanding how wild boars use this habitat is essential for the development and improvement of management techniques and the control of wild boar populations. The objective of our study was to determine which landscape features and atmospheric conditions influence the frequency of occurrence of wild boars in conservation areas in high-elevation forests. We hypothesized that wild boars would be more frequent in more forested areas away from human disturbances such as roads and buildings, because they would be safer from hunters in these areas. We also analyzed whether wild boar frequency of occurrence is higher in lower elevation areas, where the climate is milder and the araucaria forests are denser, providing abundance of food and shelter. Understanding how landscape ecology affects wild boar occurrence in an environment characterized by a strong spatial heterogeneity and how weather conditions affect wild pig seasonal patterns of activity is necessary to developing wild boar management strategies to prevent habitat damage and loss of biodiversity, both in the Atlantic domain and in similar areas across the globe.

Materials and methods

Our study was conducted in the Itatiaia National Park (INP), one of the largest protected areas in the Mantiqueira Mountain Range, and in the Alto-Montana Natural Heritage Private Reserve (NHPR) (Fig. 1). The INP covers 28 084 ha at elevations between 600 and 2791 m. The NHPR covers 672 ha at elevations between 1300 and 2100 m ($22^{\circ}21'08''\text{N}$, $44^{\circ}48'04''\text{W}$). According to local residents, six boars that had been held captive in a commercial breeding site were intentionally released next to the INP and the NHPR in 2006. The vegetation in both protected areas is Montane Semideciduous

Table 1. Mean values of landscape, anthropic, and atmospheric variables used in the investigation of habitat use by wild boars (*Sus scrofa*) in preserved areas in high-elevation Atlantic Forests of Brazil.

	Mean	SD	Maximum value	Minimum value
% Araucaria cover	41.05	25.84	100	3.67
% Stream cover	1.58	0.79	3.28	0.088
% Forest cover	79.30	20.54	100	31.11
Elevation	1779.44	254.03	2334	1410
Human activity index (HAI)	0.45	0.81	4.04	0
Distance from road (km)	0.241	0.002	0.064	0.018
Distance from buildings (km)	0.083	0.061	0.023	0.009
Annual mean temperature (°C)	20.28	3.29	28	16
Annual mean humidity (%)	71.32	13.56	90	40
Annual accumulated rainfall (mm)	109.16	84.21	450	10

Seasonal Forest with *A. angustifolia* and high-elevation grasslands (Veloso et al. 1991; Oliveira-Filho and Fontes 2000). Human activities in the NHPR are low because only research activities and organized, low-impact ecotourism are allowed (mean of 300 visitors per year). Human activity in the INP is intense due to disorganized tourism (more than 85 000 visitors per year; Barros 2003). There is no extensive monoculture in the region, only small cultivation areas and home vegetable gardens mostly planted for subsistence or local sales.

The NHPR and high-elevation INP climate where wild boars occur is Cwb type (high-elevation tropical) (Köppen 1936) with dry winters and mild, rainy summers. The annual mean temperature in the region varies between 17 and 19 °C, with annual rainfall of 1749 mm in the NHPR and up to 2400 mm in the INP (Arthur and Pégas 2013). Frost, hailstorms, and occasional snow events occur in winter in the INP (Fundação Brasileira para o Desenvolvimento Sustentável (FBDS) 2000; Instituto Chico Mendes de Conservação da Biodiversidade (ICMBIO) 2013).

Wild boars have an estimated life-span of 10 to 14 years, a home range varying from 100 to 7000 ha, and a mean range span of 4–5 km, but they may cover 15 km in one year (Keuling et al. 2018). The density of these animals can range from 1 to 80 individuals·km⁻², depending on the environment and the available resources (Hone 2002; Long 2003). In our study area, it is known that in the years of 2013 and 2014, there were wild boar densities of about 8.5 and 15.8 individuals·km⁻² in the INP and NHPR, respectively (Gonçalves 2015).

We installed eight motion-activated camera traps in each area (NHPR and INP) (Bushnell HD, Bushnell Outdoor Products, California, U.S.A.). Within each area, camera traps were installed in the places most visited by wild boars (near water and on trails used by animals and visitors), evidenced by marks in the environment (Srbek-Araújo and Chiarello 2013). Previous studies in the areas helped to locate the sites most used by the boars (Gonçalves 2015; De Abreu 2016). The distance between cameras was 1 km to maintain the independence of each sampling station (Goulart 2008; Harmsen et al. 2010; Gatti et al. 2014; Gonçalves 2015). This distance is recommended (Gatti et al. 2014) and is commonly used for the study of medium- and large-sized mammals (body mass of adults greater than 1 kg) (Emmons 1987) with large home ranges (Crawshaw et al. 2004; Silveira 2004; Chiarello et al. 2008). Cameras were distributed within an area of approximately 3.5 km² in each area.

The camera traps were active between October 2013 and September 2016. We checked the cameras every one or two months for cleaning, changing batteries, and collecting data. Thus, sampling effort was calculated considering only the days in which the camera functioned during the entire time. The camera traps were programmed to trigger when the animals passed in front of them, taking three consecutive photos; traps triggered another three photos only 30 s after activation by motion. No baits were used to

avoid attracting animals and to confirm the assumption of equal capture (Karanth and Nichols 2002).

We established a 500 m buffer around each camera trap, where we registered landscape features (elevation, percentage of forest, percentage of araucarias, and percentage of streams) using georeferenced images (UTM 23S, WGS 84) of the RapidEye satellite with spatial resolution of 5 m (Gonçalves 2015). We analyzed the images in ArcGIS 9.3 software (Environmental Systems Research Institute, Inc., <http://webhelp.esri.com/arcgisdesktop/9.3/index.cfm?TopicName=welcome>). We obtained the variables relating to human disturbance (distance from road, distance from buildings) by taking measurements in a straight line (in metres) from each camera trap to the road or nearest buildings using Google Earth (© Google 2019). Additionally, we quantified human activities as the number of independent records (at each hour of day) obtained with camera traps related to human activities (presence of people, domestic cats (*Felis catus* Linnaeus, 1758), domestic dogs (*Canis lupus familiaris* Linnaeus, 1758), cars, motorcycles, trucks, tractors, bicycles, domestic horses (*Equus ferus caballus* Linnaeus, 1758), or domestic cattle (*Bos taurus* Linnaeus, 1758)). We calculated the human activity index (HAI) based on these data (HAI = NXO/MNXO + NYO/MNYO + ...), in which NXO represents the number of a given human activity observed at a given sampling point and MNXO represents the mean of the numbers of a given human activity observed at the 16 sampling points. We based the calculations on data of presence and absence of the individuals as it was not feasible to individually identify wild boars. We obtained atmospheric variables (mean temperature in the region, mean humidity in the region, and accumulated rainfall in the region) from the INMET (National Meteorology Institute) website based on daily measures (Table 1).

We used the frequency of occurrence of wild boars as the response variable. We used photos separated by at least 1 h in each trap season as independent records, as have other studies that used camera traps (Srbek-Araújo and Chiarello 2013). Wild boars living in social groups tend to follow a dominant animal, so we considered photos of wild boar groups as single records (Graves 1984; Kaminski et al. 2005; Morelle et al. 2015).

To determine which landscape and atmospheric condition variables affect the spatial and temporal patterns of use by wild boars, we used the model selection approach based on Akaike's information criterion adjusted for small samples (AIC_c) to choose the best predictive and plausible model among all candidate models (Burnham and Anderson 2002). The effect of the explanatory variables on the response variable was inferred based on the subset of models that differed by two or less units of AIC_c as the best model (AAIC_c). Model averaging was applied to this subset of models to build a final model that included all variables with averaged coefficients that did not include zero within their standard-error range.

Table 2. Results of selection of landscape and atmospheric condition models of wild boar (*Sus scrofa*) frequency of occurrence in the Itatiaia National Park and Alto-Montana Natural Heritage Private Reserve.

Models	Terms	K	Adjusted R ²	AIC _c	ΔAIC _c	Akaike weight	Sum of Akaike weight
Itatiaia National Park							
Landscape	<i>Elevation + distance from buildings</i>	4	0.79	52.66	0.00	0.55	0.55
	<i>Altitude + distance from buildings + HAI</i>	5	0.80	56.59	3.93	0.07	0.62
Atmospheric condition	<i>Temperature</i>	6	0.15	155.7	0.00	0.30	0.30
	<i>Humidity + temperature</i>	7	0.19	156.6	0.93	0.2	0.48
	<i>Rainfall + temperature</i>	7	0.16	158.3	2.57	0.1	0.56
Alto-Montana Natural Heritage Private Reserve							
Landscape	<i>Elevation + distance from buildings</i>	4	0.79	52.66	0.00	0.55	0.55
	<i>Altitude + distance from buildings + HAI</i>	5	0.80	56.59	3.93	0.07	0.62
Atmospheric condition	<i>Temperature</i>	6	0.15	155.7	0.00	0.30	0.30
	<i>Humidity + temperature</i>	7	0.19	156.6	0.93	0.2	0.48
	<i>Rainfall + temperature</i>	7	0.16	158.3	2.57	0.1	0.56

Note: The models that best explain the frequency of wild boar are in italic type. Akaike weight is the probability that the present model is the best in the set of candidates. AIC_c, Akaike's information criterion adjusted for small samples; ΔAIC_c, relative difference of AIC_c between models; K, number of model parameters; HAI, human activity index.

Landscape models

Before constructing the models, we tested for collinearity between all predictive variables to define which could be inserted into the global model. Variables with >0.7 correlations were excluded (e.g., percentage of araucaria, correlation of 0.71 with percentage of forest). We initially built a global model including all candidate models. We calculated a monthly mean of the records for each of the 16 camera traps in the study areas (NHPR, n = 8; INP, n = 8). Thus, the global model was $Y = \mu + \text{elevation} + \% \text{ stream cover} + \% \text{ forest cover} + \text{distance from road} + \text{distance from buildings} + \text{HAI} + \text{site} + \varepsilon$ (model residual). We ran the analyses in the statistical software R version 3.2.2 (R Core Team 2015) using the MuMIn package (Barton 2016).

Atmospheric-condition models

We used linear mixed-effects models (LME) to determine the effects of atmospheric conditions on patterns of wild boar activities because the data repeatedly collected at the same point configure temporal pseudo-replication (Hurlbert 1984) and these models are best adjusted for this type of data (Verbeke et al. 2010). Linear mixed-effects models are ideal for repeated-data measures because their structure accepts the inclusion of fixed- and random-effects variables (Verbeke et al. 2010). All data from all sampling points were added (n = 16) for a single month, and 49 repeated measures were obtained for the region. The global model was $\log(Y + 1) = \mu + \text{temperature}(x_1) + \text{humidity}(x_2) + \text{rainfall}(x_3) + x_1:x_2 + x_1:x_3 + x_2:x_3 + \varepsilon$. The syntax “~1|Area/Year/Sampling month” was used as a random-effect variable representing a temporally repeated sample of the points in the months within the year in each protected area (NHPR and INP) (Chaves 2010, Bates et al. 2015). We built the models in R version 3.2.2 (R Core Team 2015) using the lme4 package (Bates et al. 2015).

Results

In 1095 sampling days, with an effort of 17 520 trap-nights in both sampling areas, we obtained a total of 881 independent records of wild boars, 86.5% in Alto-Montana NHPR and 13.5% in INP, with a mean of 4.44 wild boars per independent record.

Elevation and distance from buildings were the explanatory variables in the most parsimonious models for spatial activity of wild boars, while temperature alone was the most parsimonious explanatory variable for temporal activity, although temperature together with humidity were also plausible (Table 2; Supplementary Table S1¹). Elevation had a negative effect, while distance

from buildings had a positive effect on wild boars, indicating that more records were obtained at lower elevations away from buildings (Fig. 2A). Temperature and humidity had positive effects on wild boars, with more records obtained in warmer and more humid times of the year (Fig. 2B).

Discussion

The results of our study show that wild boars were more frequent in areas at lower elevation (between 1100 and 1500 m) and at greater distance from buildings (beyond 1 km), as well as on more humid and warmer days (above 24 °C and 70% humidity), corroborating our hypothesis. The negative effect of elevation on space use by wild boars has also been observed in the United States (Singer et al. 1981; Schlichting et al. 2016), where the species is also invasive. This is normally associated with low food availability in high-elevation areas (Hone 1988; Keyling 2010), which can also result in increased interactions in the competition for food and expansion of the home range (Massey et al. 1997; Keuling et al. 2008; Morelle et al. 2015; Schlichting et al. 2016).

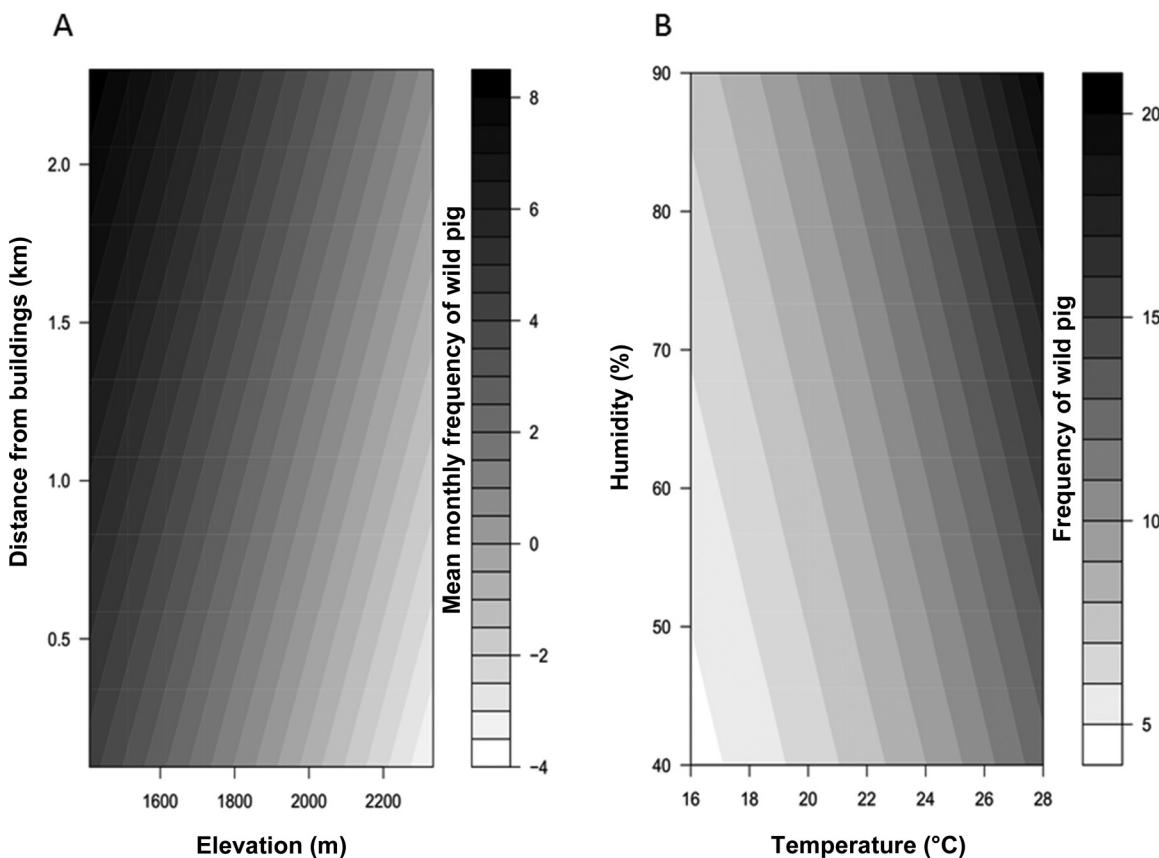
Wild boars also tend to occupy open habitats, especially when associated with agricultural fields that can be used for feeding (Herrero et al. 2006; Thurfjell et al. 2009; Ballari and Barrios-García 2014) or with forest areas that provide shelter and protection against predators, hunters, and heat (Bertolotto 2010; Saito et al. 2012; Lewis et al. 2017). In our study areas, forest cover and the frequency of araucaria trees decrease with elevation increases, especially above 1900 m, where relief becomes steeper, soils are shallower, and the vegetation is dominated by herbaceous plants (Oliveira-Filho and Fontes 2000; Ribeiro et al. 2007). There is also no agricultural activity above 1900 m.

Araucaria seeds are an important food resource for wild boars (Sanguinetti and Kitzberger 2010; Shepherd and Ditgen 2013; Brocardo et al. 2018). Although wild boars have a generalist diet, feeding on more roots and bulbs of herbaceous plants and grasses at high elevations (Baubet et al. 2004), the combination of high elevation, absence of forested areas, and low resource availability may have contributed to the lower frequency of wild boars in high-elevation areas in both the NHPR and INP (FBDS 2000; Geise et al. 2004; Martins 2011; Pompeu 2011).

Lower elevation areas have higher temperature and humidity than high-elevation areas in our study (INMET 2017, Massena Station 2018), apparently favoring the use of these habitats by wild boars. The higher areas in this study (>2000 m) are concentrated

¹Supplementary table is available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2019-0130>.

Fig. 2. (A) Simultaneous effect of elevation and distance from human settlements over the monthly frequency of occurrence of wild boars (*Sus scrofa*) in the Itatiaia National Park (INP) and Alto-Montana Natural Heritage Private Reserve (NHPR); (B) Simultaneous effect of temperature and humidity over the monthly frequency of occurrence of wild boars in INP and NHPR.



in the INP, where temperatures below 0 °C are frequent even on summer nights; in winter, intense frost and occasional brief snowfalls occur and temperatures can be cold enough to cause the lakes in the region to freeze (FBDS 2000). Although wild boars tend to be more active at temperatures below 10 °C (Barrett 1978; Coblenz and Baber 1987; Cuevas et al. 2012), their activity is reduced to about 1.5 h per day when temperatures are below -5 °C (Blasetti et al. 1988; Keuling et al. 2008). In areas with milder temperatures, where air temperature is never higher than 20 °C, wild boars increase activity on the warmest nights (Brivio et al. 2017). However, when temperatures are higher than 20 °C, activity of wild boars and other ungulates tends to be reduced (Shi et al. 2006; Brivio et al. 2016). Therefore, the occurrence of wild boars is higher in the NHPR, where mean annual temperatures are mild (between 15 and 19 °C, not higher than 22 °C in the warmest months) (Arthur and Pégas 2013; ICMBIO 2013) and where most of the lower elevation areas in our study are concentrated. The absence of poaching also favors the presence of wild boars in the NHPR.

In the areas sampled, both temperature and elevation are related to humidity. Forest habitats located at elevations up to 2000 m in the NHPR and INP are under the influence of a phenomenon called “hidden rain”, common in forests on slopes and at elevations above 1600 m (Pereira et al. 2016). Cloud water condensing upon contact with vegetation (tree trunks and crowns) constitutes an additional or even dominant water supply, with humidity equivalent to rainfall (Barbosa 2007; Pompeu 2015). Wild boar activity tends to increase in more humid areas or areas subject to high rainfall (Cuevas et al. 2012; Brivio et al. 2017) because humidity increases the efficiency of the sense of smell of wild boars (Lemel et al. 2003), favoring activities such as foraging (the more

humid the soil, the softer and easier to root and nuzzle), orientation (wild boar use their sense of smell to find their way back to the nest), social interactions, and detection of predators (Bueno et al. 2009; Kittawornrat and Zimmerman 2010; Morelle et al. 2015), besides reducing body temperature due to the increase of heat dissipation, as wild boars are physiologically limited by the lack of sudoriferous glands (Lemel et al. 2003; Swaminathan et al. 2016).

Habitat use by wild boars was associated with human factors, as well as landscape features and atmospheric conditions. The frequency of wild boars increased with distance from human activities, as has been observed in Argentina, where the species is also invasive (Gantchoff and Belant 2015). Although fragmentation and food scarcity may induce wild boars to live even in urban areas (Kotulski and König 2008; Cahill et al. 2012), they tend to temporally and spatially avoid peopled areas, preferring remote places away from human interference, which avoids conflict and risk of death due to hunting (Kotulski and König 2008; Cahill et al. 2012; Thurfjell et al. 2013; Morelle and Lejeune 2015). Distance from buildings associated with forest cover, which provides shelter and food (Freemark and Merriam 1986; Gerard et al. 1991; Virgós 2002; Honda 2009; Rosvold et al. 2010), and with a mild climate favor colonization and invasion by wild boars even more in uninhabited tropical forest areas in the Atlantic domain with these characteristics.

This is the first study to be conducted on wild boars in the high-elevation tropical forests. Control of the wild boar is urgent in these tropical forests, and the species' space-use behavior shown by this study has elucidated spatial priorities for population control and monitoring native biota potentially affected by wild boar invasion. We observed that wild boars occur more fre-

quently at lower elevations where temperatures and humidity are higher. To reduce possible damage in the short term and successfully control wild boar populations in the mid and long terms, control actions in high-elevation tropical forests would be best carried out in areas of elevations between 1100 and 1500 m during the summer months, when temperature and humidity are higher and wild boars more active. In addition, agricultural crops and pinyon (araucaria seeds) in forest habitats are scarce during the summer, which increases the success of baiting (in traps or stand hunting) in the control of wild boars.

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