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Predicting poaching hotspots in the largest remnant of the Atlantic Forest by combining passive acoustic monitoring and occupancy models

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A R T I C L E I N F O

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A B S T R A C T

Poaching can have major impacts on wild animal populations and is pervasive in tropical regions. The spatial distribution of this furtive activity is particularly difficult to estimate in large natural areas, and this hinders the development of effective anti-poaching strategies. We used passive acoustic recorders in combination with occupancy models to develop a predictive map of poaching presence in the Upper Paraná Atlantic Forest of Argentina and Brazil. Poaching activity was measured by gunshots detected by the recorders that were active for 7 months (August 2018 to February 2019) on 90 sampling sites distributed in an area of 4637 km^2. A total of 15,936 h of landscape sounds were recorded, detecting gunshots at 43 sites. Using occupancy models, we evaluated eight variables that might influence poaching occurrence and detectability. Poaching was higher in areas with higher accessibility, with a higher proportion of rural areas, and far from control posts of park rangers. The detectability of gunshots was lower during periods of heavy rainfall. We validated the occupancy models through field surveys conducted in the same period resulting in a predictive capacity of 82% of our best model. Our results show that this region is under very high poaching pressure, even within the protected area's boundaries and that urgent actions must be taken. The methods we used for estimating poaching pressure and the predictive maps developed could serve as a tool for developing and implementing anti-poaching strategies to reduce this pervasive threat.

1. Introduction

Poaching can have major impacts on wild animal populations, leading to large population declines or even local or global extinction, representing one of the main threats to biodiversity conservation (Maxwell et al., 2016). This activity is widely practised in tropical and subtropical regions, where the abundance of medium and large mammals are especially affected by this threat (Ripple et al., 2016; Benítez-López et al., 2017; Bogoni et al., 2020). Rapid human population growth and increased road infrastructure have promoted access to previously inaccessible natural areas, favouring an increase in illegal activities such as wildlife poaching (Laurance et al., 2015). Human access enables both settlement and land-use changes, facilitating the exploitation of environments rich in natural resources (Sanderson et al., 2002; Gallego-Zamorano et al., 2020). In tropical regions, this process is aggravated due to increasing rural population density, especially in areas near forest

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remnants (Peres and Lake, 2003).

Protected areas are among the main strategies for biodiversity conservation (Watson et al., 2014), however, in many tropical and subtropical regions, poaching also occurs within the boundaries of protected areas (Sousa and Srbek-Araujo, 2017). Although these areas are legally protected, the resources required for their effective safeguard are often insufficient, in part due to their large area, and political and economic restrictions (Peres and Lake, 2003; Ferreguetti et al., 2018). Anti-poaching patrols are the most widely implemented tool to control poaching in these regions, but they are not always effective (Astaras et al., 2020). Therefore, understanding the spatial distribution of poaching is a key component of the management strategies for the effective protection of protected areas (Watson et al., 2013).

The portion of Atlantic Forest remaining in Argentina and adjacent areas of Brazil (hereafter referred to as the Green Corridor) constitute one of the largest fragments of continuous Atlantic Forest in the world (Di Bitetti et al., 2003; Paviolo et al., 2009b). Despite the large area of forest under legal protection in the Green Corridor, most of it has high levels of poaching, decreasing its effectiveness for wildlife conservation (Di Bitetti et al., 2008). Studies conducted on different mammal species in this region found a negative correlation between their presence with human accessibility (Di Bitetti et al., 2008; Paviolo et al., 2009b; Cruz et al., 2019a; Iezzi et al., 2019) and with rural population density (De Angelo et al., 2013). These measures were used as proxies for poaching pressure but, to date, no systematic and standardized surveys of poaching activities in the Green Corridor have been conducted.

The main objective of our study was to implement a new approach to survey and estimate poaching pressure in the Green Corridor and to generate a predictive map of poaching activity which will serve as a management tool to focus control and mitigation efforts. Following this aim, we conducted a systematic survey using passive acoustic recorders to identify poachers' gunshots. We analysed these records using occupancy models to estimate the detectability and probability of occurrence of poaching, testing different hypotheses about the influence of landscape-scale variables for predicting poaching. Mainly, we expected poaching occupancy to be higher in more accessible areas and areas surrounded by rural activity, but lower in the legally protected areas and areas closer to park rangers' control posts.

2. Material and methods

2.1. Study area

We conducted this study in the Green Corridor, selecting as study area the north of Misiones Province, Argentina, and the Iguaçu National Park in Brazil (Fig. 1A; 54.2585° W, 25.9312° S), covering an extensive area of 9512 km^2 across the border of the two countries. This area, along with a portion of the forest that extends to the south of Misiones, contains the world's largest continuous fragment of Upper Parana Atlantic Forest, a semi-deciduous subtropical forest ecoregion of the Atlantic Forest. The remaining part of this ecoregion shared by Argentina, Paraguay and Brazil, is distributed among several fragments that occupy only 17% of the original extent (WWF, 2017). Due to its high degree of fragmentation, most of the remaining Atlantic Forest is less than 250 m from non-forest areas (Ribeiro et al., 2009), being easily accessible to poachers.

In the Green Corridor, hunting of wildlife is an illegal but culturally-rooted activity that is practised by a large number of local people living in rural areas and small towns (Giraudo et al., 2003). For most inhabitants in this region, hunting is a recreational activity, while for indigenous communities and low-income rural people, hunting can help to supplement their diets with protein (Giraudo and Abramson, 2000). Almost all hunting in this region is conducted with firearms, and hunting with snares or other techniques is very rare (Giraudo and Abramson,

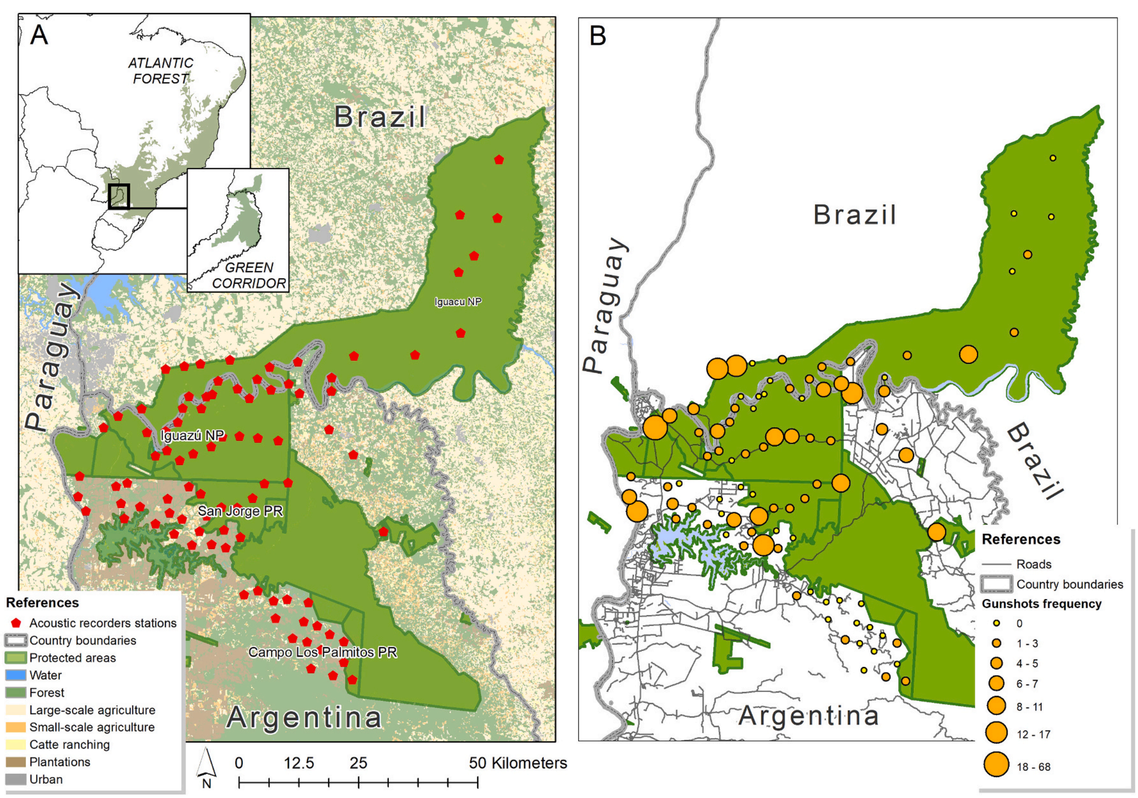

Fig. 1. A) The study area is located southwest of the Atlantic Forest, specifically in the main core areas of the Green Corridor, including northern Misiones province, in Argentina, and adjacent areas of Brazil. Land uses are shown in different colours and the location of the 90 survey stations is represented by red pentagons. NP = National Park, PR = Private Reserve. B) Distribution and number of gunshots recorded in each site surveyed in the Green Corridor of Misiones province in Argentina, and adjacent areas of Brazil. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2000; Paviolo et al., 2009a). A large proportion of the area included in this study corresponds to protected areas (3799 km^2); however, it also includes cities and towns, areas of degraded forests due to intense logging and areas replaced by tree plantations (pine and eucalyptus), agriculture (maize, tobacco, soy, yerba mate), and cattle ranching (Placci, 2000). We surveyed areas with different levels of legal protection such as the Iguazu National Park of Argentina (670 km^2), the Iguaçu National Park of Brazil (1850 km^2), the San Jorge (174 km^2) and Campo Los Palmitos (270 km^2) private Forest Reserves, and areas without protection (Fig. 1A). The study area also has a gradient of human accessibility and a variable proportion of rural areas in the surroundings.

2.2. Sound recorders and survey design

We used passive acoustic recorders to register the sounds of gunshots and study poaching activity in the area. We distributed 90 surveying sites in the north of the Green Corridor (Fig. 1A), comprising a minimum convex polygon of 4637 km^2. The location of sampling sites was selected using a systematic random design stratified by the cost of human access, the proportion of the rural areas, and the level of the legal protection of the forest. Based on an in situ gunshots recording test, we estimated the effective gunshot detection reach of the passive acoustic recorders to be 1.5 km (see also Dobbins et al., 2020), and therefore we considered the surveyed area by each recorder to be a circle of that radius (7.1 km^2). We used 20 passive acoustics recorders SM4 (Wildlife Acoustics®) and we organized the survey in five consecutive rounds. In each round, we selected the surveying sites by placing a grid of 2 by 2 km over a digital map of the study area and we randomly chose the ~20 grid cells to be surveyed in each round but considering a representative distribution of surveyed sites along with a range of the variables that we wanted to test. We deployed the passive acoustic recorders in the centre of each selected grid cell, ensuring that the surveyed sites were separated from one another by >3 km to avoid duplicated detection of gunshots. Distances were measured from where the recorder was located, which is the centre of the circular area covered by each device. The installation of the passive acoustic recorders at the surveying sites demanded an extensive field effort including the use of land vehicles (10,000 km), boats (130 km), and 16 flights in a helicopter (32h) to reach the most inaccessible places. At each site, we installed one recorder, approximately 4 m above the ground, and to avoid biases due to wind direction, all recorders were placed facing north. To optimize the battery and memory use of the recorders but maximize the gunshot detection, they were programmed to operate for 7.5 h/day during the periods of maximum poaching activity according to experienced local park rangers and anti-poaching authorities: one and a half hours at sunrise, and six hours at sunset. For the same reason, we ensured that each site was sampled at least during two weekends, which are the periods of the week with the greatest poaching activity in this region (Giraudo and Abramson, 2000). The recorders were moved to a different site every 20–25 days (mean = 22 days, min = 12 days, max = 48 days) until reaching 90 surveying stations, extending the complete field survey over 7 months (August 2018 to February 2019). We used a gunshot detection algorithm (De Almeida et al., 2017), to extract putative gunshots from the sound files obtained from each site, and subsequently assessed these records visually (i.e., through spectrographic analysis) and acoustically by trained people. As we mainly surveyed areas that were further than 1.5 km from urban settlements, we assumed that the detected gunshots indicated poaching activity, as other uses of firearms are uncommon in the surveyed areas.

2.3. Model variables

To understand the effects of environmental and anthropogenic factors that can affect the occurrence of poaching in this region, we considered variables that spatially represent the main hypotheses to be tested (Table 1). All these variables were quantified using a GIS for the

Table 1

Hypotheses and a priori predictions about the influence of spatial variables on poaching occupancy (ψ) and detectability (p) in the Green Corridor. Variables used for each prediction are in italics.

Hypotheses and justification	Variables and alternatives	Predictions
Cost of access: Poaching activity is directly related to how accessible is this area to poachers. Human access enables both settlement and land-use changes, facilitating the human exploitation of natural environments (Sanderson et al., 2002; Gallego-Zamorano et al., 2020). Ferreguetti et al. (2018) found a negative relationship between the occurrence of poachers and the nearest human settlement. In the Green Corridor, several studies found positive relationships between the presence of mammal species persecuted by poachers and the cost of access (Di Bitetti et al., 2008; Paviolo et al., 2009a; De Angelo et al., 2013; Iezzi et al., 2018; Cruz et al., 2019a, 2019b; Iezzi et al., 2019).	We built 3 alternative variants of a variable that represents the cost of access for poachers from the nearest inhabited locations or access points to each sample station: 1.a. *access*: represented by the time that a person would need to reach the sampling station from the nearest town or city. To build this variable we used estimates of mean human speed when traversing different kinds of roads (i.e., by car or motorcycle) or land uses (i.e., by walk). A detailed explanation of the methodology used to estimate this variable can be found in De Angelo et al. (2011) and Iezzi et al. (2018). 1.b. *roads*: Euclidean distance to the closest main road (Ferreguetti et al., 2018) 1.c. *localities*: Euclidean distance to the closest town or city present in the study area (Ferreguetti et al., 2018).	The poaching occurrence will be negatively related to the cost of human access (*access, roads* or *localities*).
Legal protection: Protected areas are among the main strategies for biodiversity conservation (Watson et al., 2014). Variations in the levels of protection of natural areas affect the abundance and behaviour of mammal species in the Green Corridor (Di Bitetti et al., 2008; Paviolo et al., 2009a).	To represent the levels of legal protection we built an ordinal variable: 2. *protection*: we selected the boundaries of the protected area and we assigned values of 0 to the areas without any protection, 1 to private reserves, and 2 to national or provincial reserves.	Increasing protection levels (*protection*) will reduce the occurrence of poaching.
Park rangers control posts: Anti-poaching patrols are the most widely implemented tool to control poaching in tropical regions (Astaras et al., 2020). In the Atlantic Forest, poaching levels increase when control and vigilance efforts by anti-poaching patrols decrease (Sousa and Srbek-Araujo, 2017).	We used the same accessibility model used to develop the variable *1. a* but selecting the park rangers and other safeguard posts as the points of origin instead of the towns or villages. 3. *p_ranger*: it represents the time it would take a park ranger to reach each sample station from the control posts where they are normally based. This variable has the same units cost that the variable *1. a*.	There will be a positive relationship between the time from park ranger control posts (*p_ranger*) and poaching occurrence.
Proportion of rural areas: Poaching activity is higher in areas with a more rural population. The rapid growth of human population	We mapped the distribution of small-scale agricultural or livestock-grazing areas (Izquierdo et al., 2008; Martinez Pardo, 2020) and we	Poaching occurrence will be positively related to the proportion of rural areas (*rur_2km, rur_5km*, or *rur_9km*)

(*continued on next page*)

Table 1 (*continued*)

Hypotheses and justification	Variables and alternatives	Predictions
density near forest remnants in tropical regions has increased accessibility and facilitated harvesting and poaching activities (Peres and Lake, 2003; Laurance and Vasconcelos, 2009). In the Green Corridor, hunting of wildlife is a culturally-rooted activity that is practised by a large number of local people living in rural areas (Giraudo and Abramson, 2000).	constructed three alternative variables, each one representing different distances that poachers may use to travel from rural areas to the hunting sites in this region (2, 5, and 9 km; Pereira, 2003). These distances were used as the radii in a neighbourhood analysis to calculate these variables as the proportion of rural areas in the surrounding of each site: 4. a. *rur2km*: proportion of rural areas within a radius of 2 km. 4. b. *rur5km*: proportion of rural areas within a radius of 5 km. 4. c. *rur9km*: proportion of rural areas within a radius of 9 km.	
Game species availability: Poachers chose areas where they know that some of their preferred mammalian species would be found more often, thus increasing the cost-benefit balance of the poaching expeditions (Ferreguetti et al., 2018). These game species in the region are the paca (*Cuniculus paca*), the agouti (*Dasyprocta azarae*), armadillos (*Dasypus novemcinctus* and *Euphractus sexcinctus*), peccaries (*Tayassu pecari* and *Pecari tajacu*), brocket deer (*Mazama americana, Mazama nana,* and *Mazama gouazoubira*) and the tapir (*Tapirus terrestris*) (Giraudo and Abramson, 2000).	We predicted the occupancy of these species for each sample station using the models created by Paviolo et al. (2018) and then, we built three alternatives of the availability of the game species variable by modifying the relative weights of the different species: 5.a. *game_sp1*: sum of the probability of occupancy of all game species 5.b. *game_sp2*: sum of the probability of occupancy of larger game species only (peccaries + brocket deer + tapir). 5. c. *game_sp3*: sum of the probability of occupancy of all game species but weighting larger species twice as much as smaller ones.	Areas with greater availability of the game species preferred by poachers (*game_sp1, game_sp2,* or *game_sp3*) will have a higher poaching occurrence.
Water: Water resources represent favourable areas for poachers, both logistically (good places to camp) and as a source of resources used by wildlife (Pereira, 2003, Ferreguetti et al., 2018).	6. *water*: Euclidean distance to rivers, streams, and lakes measured in meters.	The poaching occurrence will be higher near water resources (*water*).

study area and the ArcGIS 10.3 software. In some cases, we considered alternative options of predictor variables to represent the same hypothesis (cost of access, proportion of rural areas, game species availability; Table 1). We also measured environmental features and weather conditions that could have affected the probability of poaching or its detectability during the surveys (Ferreguetti et al., 2018; Moore et al., 2018; Tables 1 and 2).

2.4. Data analysis

We analysed how poaching pressure varies in this landscape with single-species single-season occupancy models with a likelihood-based approach using PRESENCE 2.12.9 program (Hines, 2006; MacKenzie, 2006). These models provide an unbiased estimate of the probability that a species or a phenomenon (in this case, poaching) occurs in an area (ψ) when detection probability (p) is <1 while modelling the effects of predictive variables on ψ or p (MacKenzie and Kendall, 2002; MacKenzie et al., 2006). The probability of detection (p) is estimated by repeated sequential samplings of a specific area (MacKenzie et al., 2006). To increase the per-occasion probability of detection, we combined three consecutive sound-recorder days into a recording occasion, reaching up to 16 sampling occasions.

Table 2
Hypotheses and a priori predictions about the influence of the precipitation and the moonlight on poaching detectability (p) in the Green Corridor. Variables used for each prediction are in italics.

Hypotheses and justification	Variables and alternatives	Predictions
Rain: Precipitation reduces the detectability of gunshots and poaching occurrence. The noise generated by rain can affect how far a recorded can register a gunshot in the forest. Additionally, poachers ́ activity may be discouraged during rainy days and seasons (Astaras et al., 2020).	7. *rain*: the average rainfall (in mm/day) during the period that each sample station was active, obtained from http://www.meteomanz.com (accessed in March 2019).	The amount of rain accumulated in a survey site (*rain*) will be negatively related to poaching detectability.
Moonlight: Poaching activity is lower during moonlight hours reducing its detectability. Some of the game species preferred by poachers are less active on full moon nights (Kotler et al., 2010; Mori et al., 2014). Local poachers seem to avoid hunting on full or nearly full moon nights because they associate lunar illumination with a lower probability of hunting success (Pereira, 2003).	We built a variable that represents the percentage of the moon's illumination: 8. *moon*: the average of the percentage of brightness value for each sample station on the days it was active. We obtained these values from the website https://www.timeanddate.com/moon/@3435588 (accessed in March 2019).	Moon luminosity (*moon*) will reduce poaching detectability.

We included, as variables affecting ψ (Table 1): (1) the cost of human access, using “access”, “roads” and “localities” as alternatives, (2) the level of legal protection (“protection”), (3) the time from a park ranger control post (“p_ranger”), (4) the proportion of rural areas, using as alternatives “rur2km”, “rur5km”, and “rur9km”, (5) the occupancy of game species, using “game_sp1”, “game_sp2” and “game_sp3” as alternatives, and (6) the distance to water resources, “water”. Variables considered as potentially affecting p were (Table 2): (7) precipitation (“rain”) and (8) the brightness of the moon (“moon”). We tested for collinearity among the variables with Spearman correlations using the Infostat program (Di Rienzo, 2009).

For the occupancy models, we used a three-step approach (Estevo et al., 2017; Cruz et al., 2019b) (Fig. A.1, Suppl. Info.). To reduce the number of models to be compared (Burnham and Anderson, 2002; Johnson and Ommland, 2004; Burnham et al., 2011), we first assessed which of the alternatives for the variables cost of access, proportion of rural areas, and game species occupancy had the highest influence on the probability of poaching (Estevo et al., 2017; Nagy-Reis et al., 2017; Di Bitetti et al., 2020). Also, given that “protection” was highly correlated with “game_sp” ($r > 0.70$; Table A.1 Suppl. Info), we used this first step to select the one that best explained the data. We ran all potential full models that included only one of the alternatives for each variable and one of the correlated variables, keeping fixed the variables of ψ with no alternatives (“water” and “p_ranger”), and the two variables considered for p (MacKenzie, 2006; Nagy-Reis et al., 2017; Table A.2, Suppl. Info). We selected the alternative for each variable and the correlated variable (i.e., "protection" or "game_sp") that were present in the best-ranked model (Paviolo et al., 2018; Cruz et al., 2019a; Di Bitetti et al., 2020) (Table A.2, Suppl. Info).

During the second step, we analysed the effect of variables that may affect p (MacKenzie et al., 2006; Nagy-Reis et al., 2017) by including the three variables selected in the previous step plus "water" and "p_ranger" affecting ψ and running all possible combinations of the two variables that can affect p (Table A3, Suppl. Info). Models were ranked using the AIC value. Then, we estimated the relative importance of each variable by adding the AIC weight (AIC wgt) of each model where the variable was present. We considered important those variables that had an accumulated AIC wgt > 0.5 (Burnham and Anderson, 2002; MacKenzie et al., 2006). During the third step, we modelled all the possible combinations of variables that can affect ψ (the three variables selected in the first step plus "water" and "p_ranger") keeping fixed the variables affecting p selected in the second step (Table A.4, Suppl. Info), and we applied the same criteria used in the second step to identify important variables (AIC weight > 0.5). We evaluated our models and analysed potential overdispersion through the MacKenzie and Bailey goodness-of-fit tests of the most parameterized models (MacKenzie and Bailey, 2004).

To generate a map of potential poaching pressure, we extrapolated the best occupancy model to the entire study area of Argentina and Brazil (9512 km^2) using the ArcMap 10.3 Raster Calculator tool. With this same software, we calculated the percentage of the surface of the protected areas that are under high (ψ >0.68), medium (ψ between 0.33 and 0.67), and low (ψ <0.34) poaching pressure.

2.5. *Validation of occupancy models through field surveys*

To validate the predictions of the occupancy models generated with the recorder's survey, we also conducted field surveys of poaching activity during the same period in 86 of the 90 sample sites. This survey consisted of an intensive search for poachers' evidence by experienced park rangers. After a recorder was removed from one survey site, the park rangers conducted four 30-min intensive surveys in a 1.5-km buffer around each station looking for any evidence of hunting, such as spent shotgun cartridges, hunting camps or poaching platforms. A total of 331 km was walked during 338 half-hour walks.

From the evidence found in this survey, we constructed a confusion matrix (Fielding and Bell, 1997) and compared the data from sites that the model identified as having a high probability of being occupied (ψ >0.5) or unoccupied (ψ < 0.5) by poaching, with the presence/absence data of poaching signs found in the field surveys. We calculated the sensitivity of the model (total of observed presences correctly predicted/total of observed presence values), which gives the probability that, given a positive observation (poaching evidence), the model will classify its site as a positive observation (occupied). We also calculated the negative predictive power (total of observed absences correctly predicted/total of predicted absence values), which estimates the probability that, given a negative prediction (unoccupied), the evidence will also be negative (no-poaching evidence).

3. Results

During a total of 15,936 h of effort gunshots were detected in 43 of the 90 sites (48%), and the number of gunshots per station ranged from 1 to 68 (Fig. 1B). Stations with gunshots were distributed along most of the study area, including stations located far from roads and in areas with different protection levels (Fig. 1B).

Through the first step, "access" was selected as the best alternative for cost of access as it was not only present in the best-ranked model but also in all the models with a ΔAIC ≤2 (Table A.2, Suppl. Info). The different alternatives for proportion of rural areas had similar support from the data, and the same occurred with "protection" and the three alternatives of "game_sp" (Table A.2, Suppl. Info), but to reduce the number of variables only "rural_5km" and "protection" were kept for the following steps as they were in the best-ranked model (Table A.2, Suppl. Info).

The best-ranked model for detectability (p) included "rain" exclusively (Table A.3, Suppl. Info). The second-ranked model also included "moon", but "rain" obtained the highest weight in the models (AIC wtg = 0.74) while "moon" had an AIC weight < 0.50 (AIC wtg = 0.43; Table A.3, Suppl. Info). Therefore, we retained "rain" as an important variable in the next modelling step and excluded "moon". No overdispersion and a good model adjustment were observed for the full model in this step ($\chi2$ = 17,344.89; P = 0.25; c-hat = 0.52).

In the third step, considering the AIC weight, the important variables to predict occupancy by poachers were the cost of access (AIC wtg = 0.81), the proportion of rural areas (AIC wtg = 0.68), and the distance from the park rangers' control posts (AIC wtg = 0.62) (Table 3). The mean probability of poaching occurrence for the study area using this model was 61%. As we predicted, poaching occurrence decreased with the cost of access (Fig. 2A; Table A.4. Suppl. Info.), and as the proportion of rural lands ("rur5km") increased, so did the probability of occurrence of poaching (Fig. 2B; Table A.5. Suppl. Info.). However, this increase occurred only in the first 0–10% range of rural areas where the poaching probability sharply increased, but then it rises to an asymptote at levels close to the maximum probability (Fig. 2B). The time from the park-ranger control posts ("p_ranger") had a positive relationship with poaching occurrence (Fig. 2C; Table A.5. Suppl. Info.). No overdispersion and a good model adjustment were observed for the full model in this step ($\chi2$ = 20,936.07; P = 0.19; c-hat = 0.97).

The extrapolation of the final model into the study area shows that poaching pressure was higher at lower cost access locations and those surrounded by rural areas (Fig. 3). Also, the model estimated that within the boundaries of the protected areas, 47.8% of their area (1814 km^2) had a high poaching pressure, 20.6% (782 km^2) had medium pressure, and only 31.7% (1204 km^2) had low poaching pressure.

Poachers' evidence was detected at 44 of the 86 sites field surveyed for signs (Fig. B.1, Suppl. Info.). The evidence of poaching found during these surveys corresponded to poaching activities practised with firearms (hunting campsites, artificial salt licks, poaching platforms, gunshots heard, spent shotgun cartridges) and no evidence of other poaching techniques was found (e.g., snares or poison). Sampling sites with poaching evidence in the field surveys had a probability of poaching occupancy greater than 0.5 in 82% of cases (sensitivity), while 70% of the sites with <0.5 predicted poaching occupancy had no hunting evidence (negative predictive power) (Table B.1, Suppl. Info.).

4. Discussion

The most important determinants of poaching occurrence in the

Table 3
Single-species single-season best models for predicting poaching presence in the Green Corridor. Models were ordered according to the lowest value of AIC. Only models with ΔAIC≤2 are presented (see Appendix A for details). Only the additive effects of the variables were considered. Variables' abbreviation: access = cost of access; rur5km = percentage of rural areas within 5 km radius; protection = legal protection level of the area; water = presence of watercourses; p_ranger = time from park rangers control posts; rain = precipitation.

Models	ΔAIC	AIC wgt	#parameters
ψ (access, rur5km, p_ranger), p(rain)	0	0.16	6
ψ (access, p_ranger), p(rain)	0.75	0.11	5
ψ (access, rur5km, water, p_ranger), p(rain)	1.59	0.07	7
ψ (access, rur5km, protection, p_ranger), p (rain)	1.74	0.07	7
ψ (access, rur5km), p(rain)	1.97	0.06	5
ψ (.). p(.)	14.66	<0.01	2

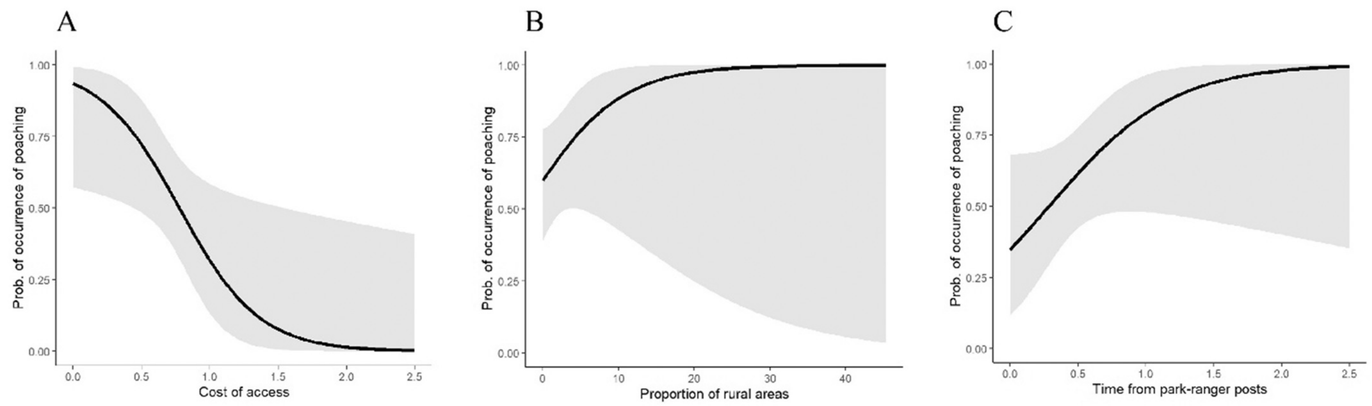

Fig. 2. Estimated effect of (A) cost of access, (B) proportion of rural areas, and (C) time from park rangers' control posts on the probability of occurrence of poaching in the Green Corridor. The variables plotted in Figs. A and C are calculated in the same units (cost units). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

north of Misiones Province and Iguaçu National Park were the distance to control posts of park rangers, the proportion of rural areas surrounding a location and, with the highest importance, the cost of access from human settlements. This was reflected in that poaching pressure was particularly higher in areas with easier access from towns and cities, probably because poachers prefer to hunt in nearby, easily accessible areas. However, the records of poaching in more remote areas show that some poachers also travel to inaccessible sites with higher prey availability and less hunting competition. While there is an important gradient in poaching intensity and this variation is explained by a few variables, poaching is pervasive in the study area, even in remote areas within the best-protected areas.

Ferreguetti et al. (2018) developed different variables as proxies for the cost of access in a protected area in the Atlantic Forest eco-region and they also found that the cost of access to natural areas by poachers is a key factor affecting the distribution of poaching pressure. Euclidean distance to roads and towns are variables often used to represent the effect of accessibility or direct human impact (Naves et al., 2003; Titeux et al., 2007; Ferreguetti et al., 2018; de Matos Dias et al., 2020). However, these variables were excluded in our model selection while "access", based on the accessibility model generated by De Angelo et al. (2011), showed a better fit in our poaching occupancy models. Accessibility modelling has the advantage of combining several factors in one single variable (e.g., distance from towns, the effect of different types of roads and land covers, slopes, etc.), allowing to weigh the effect of these different factors according to their location in the landscape (e.g., main roads will have a greater impact when they are closer to a potential source of poachers than when they are located far from towns or cities; De Angelo, 2009, De Angelo et al., 2011). Several studies included the cost of access as a proxy for hunting pressure and showed the importance of including this variable when modelling different aspects of threatened mammal species in this region (Cruz et al., 2014; Paviolo et al., 2016; Paviolo et al., 2018; Iezzi et al., 2019). Although accessibility modelling demands more parameters and a more complex calculation than simple Euclidian distances, our results show that this variable is a very good predictor of poaching pressure.

One potential limitation of the variable cost of access is that it was estimated from towns and cities, mainly representing the potential effect of poachers accessing from those sources. However, poaching activity by rural people who do not depend on using traditional access roads for their hunting expeditions may not be well represented in this variable. This different source of poaching activity was also supported by our results, showing that the presence of small-scale agricultural or livestock production areas occupied by rural residents surrounding natural areas is an important prediction of poaching activity. In zones dominated by rural areas, such as in the northeast of the study area, ψ values were close to 1, agreeing with previous anthropological studies, which observed that poaching is a very culturally rooted activity among local people in this region of the Atlantic Forest (Giraudo and Abramson, 2000; Ferrero, 2008).

Anti-poaching patrols have been demonstrated as an effective tool for reducing poaching activity (Jenks et al., 2012; Moore et al., 2018), and although the patrolling resources available in this region are limited, our results show that the presence of park ranger posts seems to be effective in reducing poaching in the north of the Green Corridor. The presence of park ranger posts combined with more resources for ranger patrolling may expand their local effect to larger areas. Nevertheless, our results highlight the importance of control activities conducted by law enforcement authorities to mitigate poaching, as was previously observed in other areas of the Atlantic Forest eco-region (Sousa and Srbek-Araujo, 2017).

Poaching activity was less detectable during days with higher levels of rainfall, which could be due, in part, to the ambient noise generated by the heavy rainfall that decreases the ability of the recorders to detect gunshots. This is mainly because the precipitation hit the foam surrounding the microphones, making it more difficult to identify the shots in the recordings. However, rainfall can also reduce detectability because it impedes hunting by making stream crossings dangerous, animal spotting difficult, and gun use challenging (Astaras et al., 2020), thus decreasing the possibility of poachers being willing to go out on a hunting expedition under those conditions. The inclusion of the effect of rain on the detectability shows an increase of ~25% in the estimation of poaching in the area and supports the usefulness of models that incorporate detectability factors, like occupancy models, for a better estimation of poaching pressure (Ferreguetti et al., 2018; Moore et al., 2018; de Matos Dias et al., 2020). This enhances the importance of this modelling approach not only for studying species occupancy, but also for a better understanding of other processes with imperfect detection like poaching, human-wildlife conflicts (e.g., Goswami et al., 2015), illegal trade (e.g., Barber-Meyer, 2010), or other human-wildlife interactions (e.g., Waldron et al., 2013).

Besides this detectability correction of poaching probability, our estimates may still underestimate the real impact of poachers in this area. Although the large effort that was deployed for surveying an extensive area in many sites, our recorders were not active for 24 h, and therefore we were unable to detect gunshots that occurred when the recorders went off. However, the recording schedule was developed with the aid of experienced park rangers to optimize the recordings during time windows of higher poaching detection probability. Additionally, we acknowledge that our detection method only recorded poachers using not silenced firearms and that other poaching methods were not registered. This is an important issue to be considered for

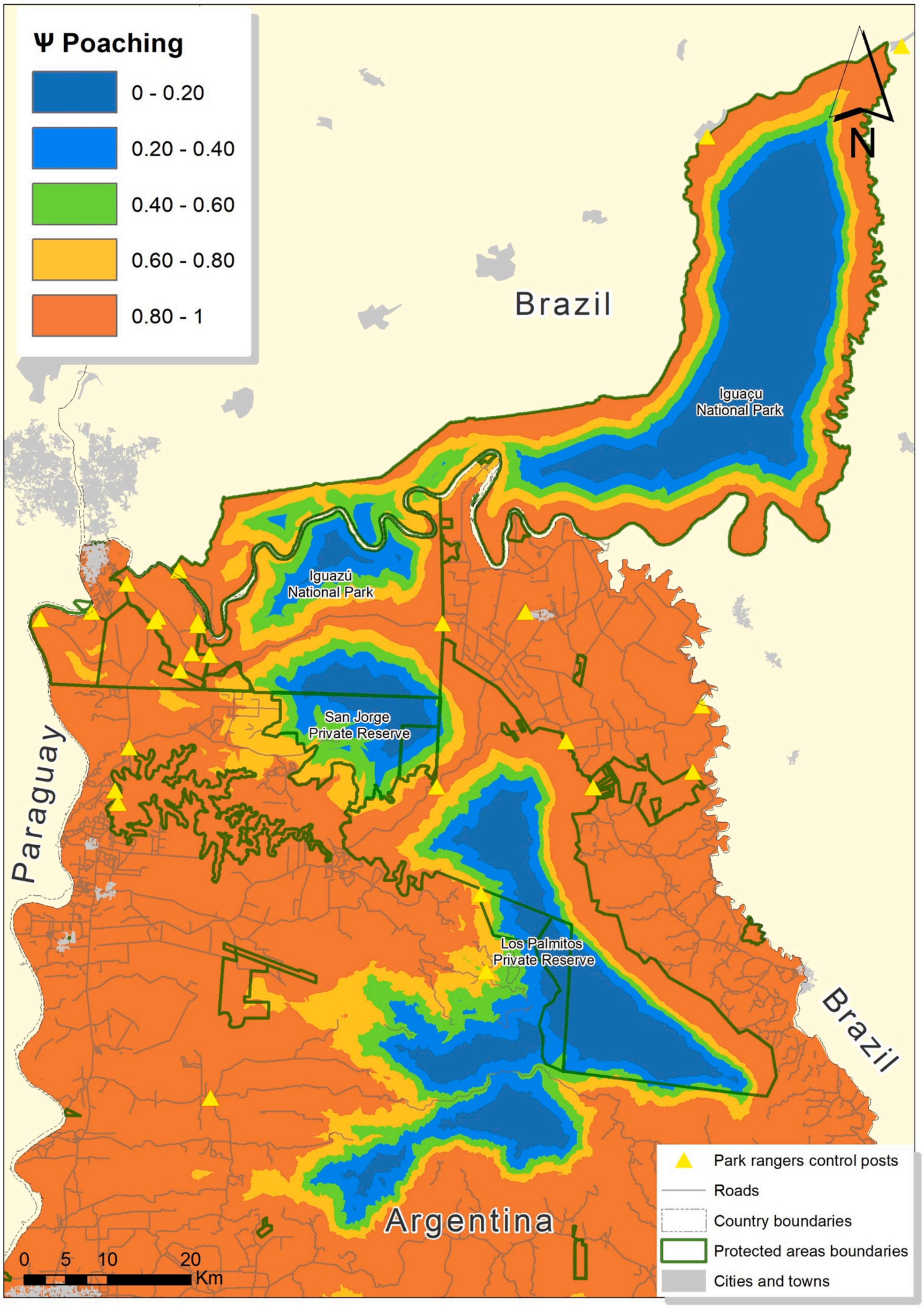

Fig. 3. Predictive map of poaching occurrence (Ψ) for the study area according to the selected predictive model. The blue areas represent the lowest occurrence of poaching activity (probability less than 20%) and the red areas present the highest occurrence of poaching activity (probability greater than 80%). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

applying our survey method in other areas where, for example, snares or other traps (e.g., O'Kelly et al., 2018), poison (e.g., St John et al., 2011), or firearms with silencers (e.g., Carlson et al., 2015), are common hunting methods. In these situations, a complementary survey technique should be implemented (e.g., Dobbins et al., 2020). As our validation surveys demonstrated, in the Green Corridor firearms are the most common hunting method used by poachers (see also Pereira, 2003), and silencers are still rare in our region and only reported by anti-poaching patrols on the Brazilian side of our study area and other regions of the Brazilian Atlantic Forest (Sousa and Srbek-Araujo, 2017).

The spatial extrapolation of the poaching occupancy model allowed us to estimate the pressure of poaching in a very extensive area and to generate a predictive map that can be useful as a landscape conservation tool. The validation of this model with independent empirical evidence also gives reliability to this extrapolation. In the resulting map, we found that a large surface of the study area is under very high poaching pressure. What is more concerning is that a large proportion of the protected areas (48%) also have very high poaching pressure. This result partially explains why the variable "protection" was not retained in the final model. Considering that the study area includes some of the best implemented protected areas of the Atlantic Forest (Paviolo et al., 2008) the extensive occurrence of poaching is worrisome. According to the results of previous studies in the Green Corridor, areas with high poaching pressure have abundances of large felids and ungulates that are between two to five times lower than in well-protected areas (Di Bitetti et al., 2008; Paviolo et al., 2008, 2009a, 2009b; Cruz et al., 2014). Therefore, it is very likely that the role of protected areas in maintaining healthy populations of large mammals and their ecosystem functions is being seriously threatened.

To achieve the effective protection of these areas, it may not be enough to increase the intensity of the park rangers' patrols (Astaras et al., 2020). Considering the restrictions of funding and personnel of the protected areas in this region, the optimization of patrols to the areas where this threat is most critical is a priority. In this scenario, the information generated from this work could be very useful, but the monitoring of poaching pressure and the effectiveness of patrols must be periodically performed (Ferreguetti et al., 2019). In environments such as the one studied here, where firearms are the main poaching practice, passive acoustics recorders and occupancy models showed to be effective for monitoring this threat (Dobbins et al., 2020), and their combination with a systematization of patrols efforts and results (e.g., through the Spatial Monitoring and Reporting Tool, SMART http://smartconservationtools.org; or the ArcGIS Solutions for Protected Area Management, https://www.esri.com/en-us/industries/sustainability/conservation/protected-area-management) can be very promising to combat poaching more effectively.

5. Conclusions

Human accessibility, the presence of rural areas surrounding native forests, and the distance to park ranger posts determine the spatial distribution of poaching pressure in this portion of the Atlantic Forest. We determined the effect of these factors through the combination of passive acoustic surveys and occupancy modelling, estimating the spatial distribution of poaching pressure across a very large and heterogeneous area. The next step is to use this information for prioritizing and focusing mitigation efforts against this threat.

Poaching is a pervasive activity in this region despite being one of the best-preserved fragments of the Atlantic Forest (Di Bitetti et al., 2003). The lowest values of poaching occurrence within the study area correspond to the core areas of the main blocks of continuous forest, which are the areas with the highest cost of access in this region. However, these large forest fragments are undergoing a process of fragmentation, mainly caused by the conversion to productive land uses and by the construction of roads, becoming increasingly accessible to poachers (Ribeiro et al., 2009; Martinez Pardo, 2020; Rodrigues, 2021). Under this scenario, it is essential to focus on management strategies that improve the effective protection of natural areas and on environmental protection laws to mitigate the pressure of poaching (Benítez-López et al., 2017; Sousa and Srbek-Araujo, 2017). The spatial distribution of poaching pressure is the first step that we have addressed in this work, but it is necessary to complement it with other management measures. According to our results, management efforts should be focused on reducing the accessibility of poachers to natural areas through the effective presence of control and monitoring mechanisms. Also, we believe that the improvement of the socio-economic situation of rural people and the implementation of education and awareness activities focused on the effects of poaching are fundamental to reduce both the impact on the inhabitants of urban areas who engage in this activity (Giraudo and Abramson, 2000; Paviolo et al., 2009a) and the rural inhabitants who live near the forest areas, whose effect was also evident in the models evaluated here.

CRediT authorship contribution statement

Julia Martínez Pardo: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing - Original Draft, Writing - Review & Editing, Visualization, Supervision, Project administration; **Paula Cruz:** Software, Formal analysis, Investigation, Conceptualization, Methodology, Writing - Original Draft, Writing - Review & Editing, Visualization; **Sergio Moya:** Software, Formal analysis, Investigation, Conceptualization, Methodology, Writing - Original Draft; **Esteban Pizzio:** Data curation, Conceptualization, Methodology; **Fernando Foletto:** Data curation, Conceptualization, Methodology; **Facundo Robino:** Data curation, Writing - Original Draft; **Jesica Aquino**: Data curation, Writing - Original Draft; **Sebastian Costa:** Data curation, Writing - Original Draft; **Yara Barros:** Writing - Original Draft, Resources, Visualization, Funding acquisition; **Falcao Cleo:** Data curation, Conceptualization; Mario Di Bitetti: Conceptualization, Methodology, Formal analysis, Writing - Original Draft, Writing - Review & Editing, Visualization, Funding acquisition; **Maria Eugenia Iezzi**: Methodology, Formal analysis, Writing - Original Draft, Writing - Review & Editing, Visualization; **Agustín Paviolo:** Funding acquisition, Conceptualization, Methodology, Data curation, Writing - Original Draft, Writing - Review & Editing, Visualization; **Carlos De Angelo:** Conceptualization, Methodology, Formal analysis, Funding acquisition, Writing - Original Draft, Writing - Review & Editing, Visualization, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109600.

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