Influence of Vegetation Cover on the Abundance of Peccaries in an Area of Reforestation in southern Brazilian Amazonia

Francesca Belem Lopes Palmeira (francesca@alumni.usp.br)
Universidade de São Paulo
Cristiano Trapé Trinca
Federal University of Paraíba
Stephen Francis Ferrari
Federal University of Sergipe

Research Article

Keywords: Camera trap, detection, Generalized N-mixture Model, Pecari tajacu, Tayassu pecari

Posted Date: October 18th, 2023

DOI: https://doi.org/10.21203/rs.3.rs-3455159/v1

Additional Declarations: No competing interests reported.

Influence of Vegetation Cover on the Abundance of Peccaries in an Area of Reforestation in southern Brazilian Amazonia

Francesca Belem Lopes Palmeira[a*], Cristiano Trapé Trinca[b] and Stephen Francis Ferrari[b,c]

[a] Graduate Program in Forestry, Forest Science Department, University of São Paulo (ESALQ/USP), Av Pádua Dias 11, CEP 13418-900, Piracicaba, SP, Brazil, ORCID 0000-0002-7597-1157, Email: francesca@alumni.usp.br

[b] Graduate Program in Biological Sciences (Zoology), Federal University of Paraíba (UFPB), CEP 58059-900, João Pessoa, PB, Brazil, ORCID 0000-0003-4791-2050, Email: cttrinca@yahoo.com.br

[c] Laboratory of Conservation Biology, Department of Ecology, Federal University of Sergipe, São Cristóvão, SE, Brazil, Av. Marechal Rondon s/n, Rosa Elze, CEP 49000-100, ORCID 0000-0003-0566-0000, Email: ferrari@academico.ufs.br

*Corresponding author. Email: francesca@alumni.usp.br

Abstract As spatial variation in vegetation cover may influence the abundance of species at a landscape scale, abundance estimates may clarify shifts in habitat use within a vegetation mosaic. In the present study, we used camera trapping and a dynamics mix model to estimate the abundance of the white-lipped (*Tayassu pecari*) and collared peccaries (*Pecari tajacu*) in a study area in southern Brazilian Amazonia. We focused on the variation between three vegetation types – primary forest, secondary forest, and forest plantation – as potential determinants of peccary abundance. The initial abundance (λ) of *T. pecari* was higher in primary forest in comparison with the secondary forest and plantation. By contrast, the λ of *P. tajacu* did not vary significantly with vegetation cover. The expected abundance of *T. pecari* correlated positively with the presence of primary forest, and negatively with secondary forest and plantation. No clear correlation was found between the abundance of *P. tajacu* and any type of vegetation cover, however. The results of the present study provide important insights into the influence of vegetation cover on the abundance and detection of peccaries, whose ecology is still relatively poorly understood.

Keywords Camera trap; detection; Generalized N-mixture Model; *Pecari tajacu*; *Tayassu pecari*

Acknowledgments We would like to thank the “Carbon Sink Project”, Peugeot-Citroën, and Office National des Forêts (ONF-International and ONF-Brasil) for their logistical support at Fazenda São Nicolau (FSN). We are also grateful to Idea Wild for providing camera traps and Nicole Williams (WCS) for facilitating their shipment to Brazil. Special thanks to Yves-Marie Gardet, Adeline Giraud, Cleide Arruda, and all the personnel at FSN whose efforts made this project a reality.

Funding This study was supported by Liz Claiborne and Art Ortenberg Small Grant (Panthera Foundation), the People's Trust for Endangered Species (PTES), the Jaguar Conservation Program (Wildlife Conservation Society – WCS), the Brazilian Coordination for Higher Education Personnel Training (CAPES), and the Brazilian National Council for Scientific and Technological Development, CNPq (process no. 303994/2011-8).

Contributions All the authors contributed to the conception and design of the study. F.B.L.P. and C.T.T. prepared the materials, and collected and analysed the data. F.B.L.P. wrote the first draft of the manuscript and all the authors reviewed and edited the subsequent versions.

Data availability The data and code are available from the GitHub repository of the first author, [https://github.com/fblpalmeira/Peccaries].

Ethics declarations

Competing interest The authors declare that they have no competing interests.

Introduction

The abundance of a species is a fundamental variable for the study of population ecology, given its potential for variation across both time and space (Kéry and Schaub 2012), which is nevertheless predictable, based on the habitat preferences and inter-specific relationships of the species (MacKenzie et al. 2006). Species that have an ample geographic distribution may inhabit a range of different types of vegetation, which may result in dynamic shifts in abundance determined by the composition and quality of local habitats. The spatial distribution and abundance of an animal will thus reflect both its habitat use and the diversity of the landscape. The theory of habitat selection predicts that the habitat spectrum will shift in line with population density — the occupation of sites of lower quality will become more viable as population density rises, while populations are more likely to endure in more suitable habitats (Fletcher et al. 2011).

A decline in population density, in particular in large, gregarious herbivores, may trigger a cascade effect in the ecosystem, including the loss of ecological processes, such as seed dispersal, and indirect facilitation within nontrophic networks (Ripple et al. 2015). In the Neotropics, peccaries play a vital role in the formation of the soil structure and have a significant influence on the distribution and demography of numerous species of palm. The local extinction of peccaries is thus likely to result in substantial ecological transformations in local forests (Beck 2006). These extinctions may have unforeseen impacts on the characteristics of the leaf litter, for example, and the abundance of terrestrial amphibians and reptiles (Beck et al. 2010; Reider et al. 2013; Ringler et al. 2015). The absence of peccaries may also contribute to an increase in seed predation by rodents (Galetti et al. 2015), which would eventually impact the recruitment of large-seeded trees and endanger carbon storage over the long term (Bello et al. 2015).

Over the past century, the white-lipped peccary (*Tayassu pecari*) has not only vanished from approximately 21% of its historical range, but has also declined in numbers and faces only a moderate chance of long-term survival in the remaining areas (Altrichter et al. 2012). While the collared peccary (*Pecari tajacu*) appears to be more tolerant of anthropogenic disturbance in comparison with *T. pecari* (Fragoso 1999; Altrichter and Boaglio 2004; García-Marmolejo et al. 2015), it is still vulnerable to impacts from deforestation and habitat fragmentation (Bodmer et al. 1993; García-Marmolejo et al. 2013).

In recent years, a growing number of studies have provided important insights into the impacts

of deforestation and habitat fragmentation on the Neotropical fauna (Offerman 1995). A knowledge gap nevertheless persists with regard to the ecological response of species to the restoration of degraded forests through reforestation programs. While the loss of biodiversity induced by deforestation in tropical regions may be partly offset by the expansion of secondary forests and the establishment of plantations (Barlow et al. 2007), the long-term potential of such strategies remain unclear. In the present study, we examine how vegetation cover impacts the abundance of both Amazonian peccary species, based on a four-year camera-trapping survey in an agricultural frontier region in the southern Brazilian Amazonia. An innovative aspect of this study was the use of a dynamic model that accounts for imperfect detection, an approach not used previously to estimate peccary abundance.

The study is based on the analysis of the relationship between peccary abundance and the distribution of three vegetation classes within an area impacted by past agricultural practises. We expected the two species to present differences in both abundance and detection in the different types of vegetation, related to their habitat requirements and distribution patterns. Our hypothesis was that the patterns of abundance and detection of the two peccary species are nonrandom, varying systematically among the vegetation classes, reflecting a hierarchical preference for habitats (primary forest > secondary forest > forest plantation).

Materials and Methods

Study area

The study area is located at the Fazenda São Nicolau (FSN), a 10,000-hectare farm on the left margin of the Juruena River in southern Brazilian Amazonia (Fig. 1). This site is located within the Tapajós-Madeira Rainforest ecoregion, as defined by Olson et al. (2001). The local climate is equatorial, warm and humid, with a three-month dry season. Approximately 70% of the property is covered with primary and secondary forests, while the other 30% consists of forest plantations and pasture.

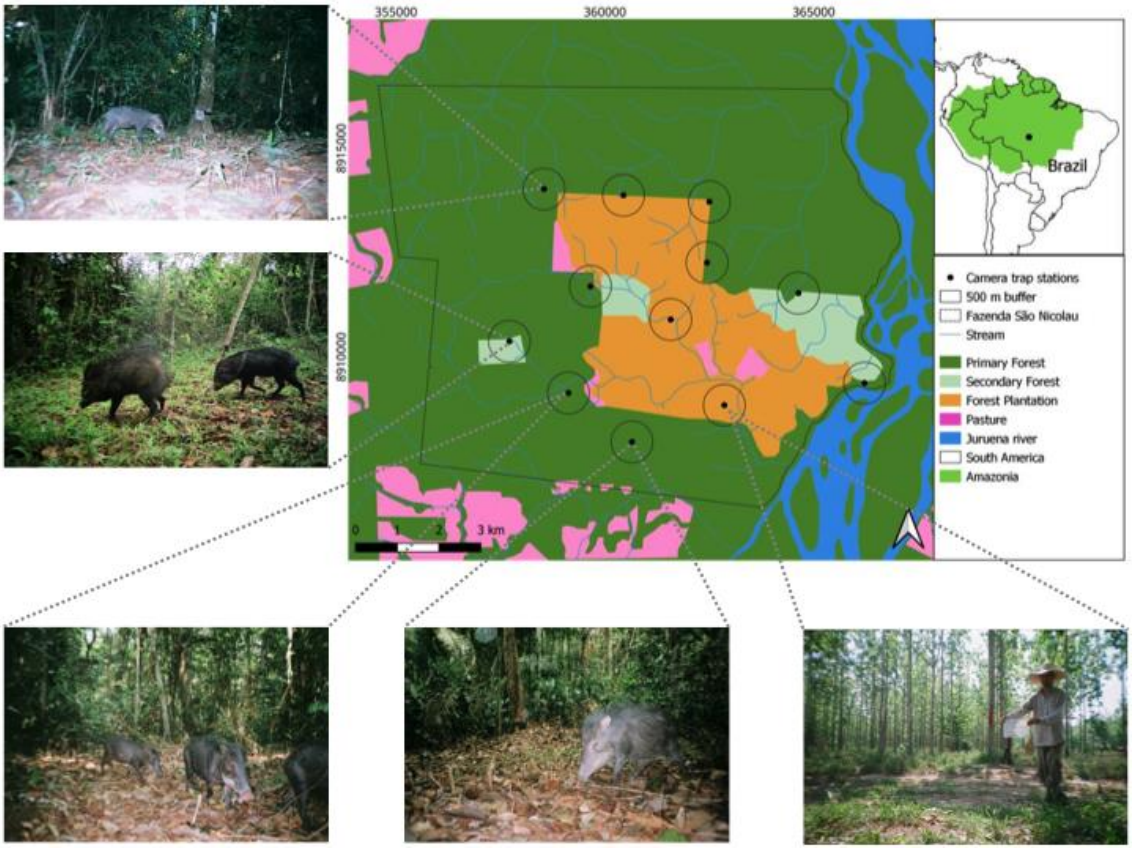

Fig. 1 Location of the camera trap stations used to monitor Amazonian peccaries at Fazenda São Nicolau in southern Brazilian Amazonia. Each station consists of a pair of cameras placed at a distance of 4–5 m from each other. The vegetation cover associated with each station was determined according to the proportion of each vegetation cover class observed within the 500-m buffer.

Fazenda São Nicolau participates in the Carbon Sink Forest Project, which began in 1998, following the Kyoto Protocol. The primary objective of this project is to investigate carbon sequestration using a variety of tree species. Over more than a decade, large tracts of pasture have been transformed through reforestation, although some areas of pasture still remain. Reforestation began in 1999, and was based on the planting of a mixture of native and exotic tree species, including teak (*Tectona grandis*), jambolan (*Syzygium cumini*), white fig (*Ficus* sp.), and pink ipé (*Handroanthus impetiginosus*). The plantations include both single- and mixed-species stands, with trees reaching heights of approximately 15–20 meters.

The study area was partially deforested between 1981 and 1996 for the planting of cattle pasture. The remaining primary forest has been subject to some limited selective logging, although many mature

mahogany trees (*Swietenia macrophylla*) are still standing. Currently, the only exploitation of forest resources is the collection of Brazil nuts (*Bertolletia excelsa*) by residents of the local rural settlements. Apart from the development of the plantations, which was initiated in 1999, the study area has not been impacted by human activities, including hunting, for more than 25 years.

Camera trapping

We sampled a total of 12 sites (Fig. 1), deploying camera traps for a total of 3 months (94±4 days) per station between 2008 and 2011, with a total of 3556 camera days being registered (Table 1). A camera trap station consisted of a pair of camera traps, which were fixed to supports (trees or fenceposts) at a height of 40 cm above the forest floor, inclined slightly downward, to avoid being triggered by vegetation moving in the wind. The traps at each station were deployed facing each at a distance of approximately 4–5 meters. The undergrowth within the field of view of each camera was cleared during the deployment of the traps, and cleared at regular intervals throughout the duration of the study period.

Sampling effort at each station during a given period was defined by the total number of camera days during the period, minus the number of days on which the camera was inoperable. We established eight sampling occasions, at intervals of 7–14 days (mean ± standard deviation of 11.5 ± 2.9 days), for each year. We collected three months of continuous sampling, based on the capture-recapture assumption for camera trapping (Noss et al. 2013), and restricted the sampling to the dry season months due to better visibility and logistics, and to protect the cameras from humidity.

Table 1 Summary of the sampling effort employed in the present study to survey Amazonian peccaries. Each year (primary period) was sampled on eight occasions (7-14 days of continuous sampling). The variation among the years in the number of camera trap stations was due to the fact that station 3 was not sampled in the first year, and sites 5 and 10 were excluded in the three subsequent years. The number of camera days refers to the actual sampling effort, that is, the number of field days minus the days of camera malfunction

Period	Camera trap stations	Camera days	Number of records of: *Tayassu pecari*	Number of records of: *Pecari tajacu*
August 9th–November 1st, 2008	11	904	161	136
July 25th–October 31st, 2009	10	973	232	98
September 23rd–December 29th, 2010	10	840	119	138
September 18th–December 16th, 2011	10	839	202	176
Total	12	3,556	714	548

We selected the sampling points considering a minimum distance of 1.8 km between sites. We used 35-mm and digital camera traps from different manufacturers (Night Hawk, Stealth Cam, Deer Cam, Cuddeback, and Bushnell), which were programmed to take photographs with day/time data and a delay of 1 minute. We combined cameras of different brands at each trap station to calibrate their performance and ensure the collection of samples with at least one camera, even when the other camera had suffered a malfunction. During each occasion, we took a test photograph to ensure that the equipment was operational.

Selection of the variables

Using a digitised map, we established a buffer with a radius of 500 meters around each trapping station to calculaste the vegetation cover at each site, which was incorporated in the models as a site covariate (Fig. 1). A 500-m radius was established for the buffers as it provided the best fit for the compilation of the data in comparison with buffers of 100 m, 1000 m or 1500 m. We used three vegetation cover classes: (i) primary forest, (ii) secondary forest and (iii) forest plantation (Table 2). To ensure a lack of collinearity among these classes, we applied Spearman's nonparametric correlation coefficient, rho (Zar 2010), and found no significant association ($p > 0.05$) in any case. We also included the years (primary periods), date and hour (secondary periods) as covariates.

Table 2 Explanatory variables used as parameters to estimate the initial abundance (λ) and the probability

of detection (*p*) of the two peccary species. While initial abundance varies among sites, the detection probability depends on the site, survey, and season.

Covariate	Fixed effect	Description	Range	Parameter
Site	Primary forest	Percentage (%) of primary forest	0–100	l, *p*
	Secondary forest	Percentage (%) of secondary forest	0–51.81	l, *p*
	Forest plantation	Percentage (%) of plantation	0–100	l, *p*
Survey	Hours	Sampling effort converted into hours after subtracting periods of camera malfunction	24–509 h	*p*
	Date	Sampling occasion converted to Julian date	2454679–2455905 d	*p*
Season	Year	Sampling year (primary period)	1–4 y	*p*

We sampled a smaller proportion of sites in the plantation and secondary forest because these classes represented less than 30% of the total vegetation cover. We also omitted pasture from the model because it covered a negligible (< 6%) of the study area. To maximize the probability of detecting the target species, we placed some traps at the limit between vegetation classes (Fig. 1).

Generalised N-mixture models

We fitted eight candidate models, each representing distinct biological hypotheses on the spatial patterns in the use of habitats Amazonian peccaries (Table 3). We used explicit hierarchical models for open populations (Dail and Madsen 2011), which is a generalisation of the N-mixture model, combining the Poisson and binomial distributions (Royle 2004). These models can be extended to describe population dynamics, such as recruitment (g) and apparent survival (w), initial abundance (l), and the probability (*p*) of species detection (Kéry and Schaub 2012). In the present study, population dynamics (γ, ω) were not modelled with site- or year-specific covariates, so their estimates were omitted from the results. However, constant values (~1) were assigned to these dynamics in the candidate models. Given this, we focused solely on the λ and p parameters for estimation and prediction, taking advantage of the model's potential to analyse the entire 4-year dataset and provide robust insights into the site-specific

parameters that may influence peccary abundance.

Table 3 The formulas and number of parameters (*K*) used in the set of candidate models developed in the present study for Amazonian peccaries. A value of "~1" indicates a constant value for initial abundance (l), recruitment (g), apparent survival (w) and detection (*p*). The parameters of population dynamics received a constant value in all the candidate models and were excluded from the results due to the wide-ranging behaviour of the species among the different vegetation classes. The year is a time-dependent parameter, with the value in the first year providing the baseline for the values of the subsequent years (Year – 1)

Candidate Fit Model (FM)	Model formula	*K*
(FM1) Null model – All parameters (abundance, recruitment, survival and detection) with constant (~ 1) values, which means that there is no dependence on site, survey or season	l (~ 1), g (~ 1), w (~ 1), *p* (~ 1)	4
(FM2) Initial abundance, recruitment and survival all constant, with detection dependent on the survey (time and date of the samples) and season (full time-dependence)	l (~ 1), g (~ 1), w (~ 1), *p* (~ Hours + Date + Year – 1)	9
(FM3) Initial abundance, recruitment and survival all constant, with detection dependent on primary forest, survey and season	l (~ 1), g (~ 1), w (~ 1), *p* (~ Primary + Hours + Date + Year – 1)	10
(FM4) Initial abundance, recruitment and survival all constant, with detection dependent on secondary forest, survey and season	l (~ 1), g (~ 1), w (~ 1), *p* (~ Secondary + Hours + Date + Year – 1)	10
(FM5) Initial abundance, recruitment and survival all constant, with detection dependent on the plantation, survey and season	l (~ 1), g (~ 1), w (~ 1), *p* (~ Plantation + Hours + Date + Year – 1)	10
(FM6) Initial abundance dependent on primary forest, with	l (~ Primary), g (~ 1), w (~ 1), *p* (~	11

recruitment and survival constant, and detection dependent on primary forest, survey and season	Primary + Hours + Date + Year – 1)	
(FM7) Initial abundance dependent on secondary forest, with recruitment and survival constant, and detection dependent on secondary forest, survey and season	l (~ Secondary), g (~ 1), w (~ 1), *p* (~ Secondary + Hours + Date + Year – 1)	11
(FM8) Initial abundance dependent on plantation, with recruitment and survival constant, and detection dependent on plantation, survey and season	l (~ Plantation), g (~ 1), w (~ 1), *p* (~ Plantation + Hours + Date + Year – 1)	11

To incorporate imperfect detection, we assumed that the sampling occasions were independent of one another. We extracted the probability of detection (1 = detected, 0 = undetected) for each species from the historical photocapture data of the eight sampling occasions (J = 8) across the 12 sampling sites (n = 12). We converted the site and survey covariates to a mean of zero and variance of one. We used two link functions, the log of the local l (N_i) and g described by a Poisson distribution, and logit of the *p* and w described by a binomial distribution. To reduce the bias caused by malfunctions, we incorporated the sampling effort of each site per occasion as a survey covariate that might affect the probability of detection. We compared the models using Akaike's Information Criterion (AIC), using the top delta score ($\Delta < 2$) and highest weights (*w*) (Burnham and Anderson 2002). We fitted and selected the best models by Maximum Likelihood Estimation (MLE) using the 'unmarked' package in the R environment (Fiske and Chandler 2011). All parameter estimates were expressed as the mean ± standard error (SE). We verified the significance of the parameters based on the 95% confidence interval (CI).

As occupancy can be considered to be a proxy for abundance, these parameters tend to coincide at a fine scale, when the selected site is so limited that only one individual or a pair can inhabit the site, as observed in certain bird species (Kéry and Schaub 2012). For species such as peccaries, however, which form large herds that occupy extensive areas, abundance is a more reliable descriptor of finer-scale habitat use than occupancy.

Results

The white-lipped peccary (*Tayassu pecari*) was documented at nine camera trap stations, while the

collared peccary (*Pecari tajacu*) was observed at all 12 sites. No records of *T. pecari* were obtained during 218 of the observations, and no records of *P. tajacu* in 190 observations. In both cases, 60 of the instances were designated "not available" (NA), which indicates missing data due to equipment malfunction.

Based on the top delta value of less than 2 ($\Delta < 2$) and the highest weight (*w*), the models supported for both species indicate that abundance (l) may be dependent on site covariates, and that detection (*p*) may be dependent on the site, season and survey covariates (Table 4).

Table 4 The best-fit models for the Amazonian peccaries monitored during the present study, determined using Akaike's Information Criterion (AIC), considering the top delta value ($\Delta < 2$) and the greatest weight (*w*). In all the models supported for both species, the abundance (l) was found to be influenced by the site, while detection (*p*) was influenced by the site, survey, and season

Species	Best fit model	AIC	D	*w*
Tayassu pecari	(FM6) l (~ Primary), g (~ 1), w (~ 1), *p* (~ Primary + Hours + Date + Year – 1)	2071.67	0	1
Pecari tajacu	(FM5) l (~ 1), g (~ 1), w (~ 1), *p* (~ Plantation + Hours + Date + Year – 1)	1682.69	0	0.52
	(FM8) l (~ Plantation), g (~ 1), w (~ 1), *p* (~ Plantation + Hours + Date + Year – 1)	1684.53	1.84	0.21
	(FM3) l (~ 1), g (~ 1), w (~ 1), *p* (~ Primary + Hours + Date + Year – 1)	1684.67	1.98	0.19

The abundance of *T. pecari* was dependent on primary forest, whereas that of *P. tajacu* was relatively constant among the different vegetation classes. The probability of detection of *T. pecari* was also dependent on primary forest, while that of *P. tajacu* may be dependent on the presence of plantation habitats or primary forest. For both species, the probability of detection varied among surveys and seasons, and decreased progressively over the years of the study period (Table 5).

Table 5 Summary of the estimates of initial abundance (l) and detection (*p*) of the best-fit models for Amazonian peccaries. The estimates, together with their standard errors (SE) and 95% confidence intervals, were computed on log and logit scales, and then transformed back to their original unit

Species	Best fit model	Fixed effect	Estimate	SE	95% CI
Tayassu pecari	FM6	l - Intercept	2.58	1.31	1.52–4.40
		l - Primary	6.01	1.28	3.69–9.78
		p - Primary	0.49	0.52	0.44–0.54
		p - Hours	0.58	0.5	0.56–0.6
		p - Date	0.89	0.66	0.67–0.97
		p - Year 1	0.82	0.71	0.45–0.96
		p - Year 2	0.28	0.58	0.17–0.42
		p - Year 3	0.01	0.59	0.009–0.04
		p - Year 4	0.005	0.72	0.0007–0.03
Pecari tajacu	FM5	l - Intercept	8.77	1.16	6.55–11.75
		p - Plantation	0.62	0.53	0.55–0.68
		p - Hours	0.53	0.51	0.51–0.55
		p - Date	0.94	0.68	0.77–0.98
		p - Year 1	0.87	0.73	0.5–0.98
		p - Year 2	0.21	0.58	0.12–0.36
		p - Year 3	0.02	0.6	0.009–0.05
		p - Year 4	0.002	0.74	0.0003–0.02
	FM8	l - Intercept	9.07	1.18	6.46–12.75
		l - Plantation	0.94	1.15	0.71–1.24

	p - Plantation	0.63	0.54	0.55–0.7
	p - Hours	0.53	0.51	0.51–0.55
	p - Date	0.94	0.68	0.77–0.98
	p - Year 1	0.87	0.73	0.49–0.98
	p - Year 2	0.21	0.58	0.11–0.35
	p - Year 3	0.02	0.6	0.009–0.05
	p - Year 4	0.002	0.74	0.0003–0.02
FM3	1 - Intercept	8.21	1.15	6.22–10.85
	p - Primary	0.37	0.53	0.30–0.44
	p - Hours	0.53	0.51	0.51–0.55
	p - Date	0.94	0.68	0.78–0.98
	p - Year 1	0.89	0.73	0.53–0.98
	p - Year 2	0.22	0.58	0.12–0.37
	p - Year 3	0.02	0.6	0.01–0.05
	p - Year 4	0.002	0.74	0.0003–0.02

The parameter estimates for the different vegetation classes varied considerably between the two peccary species. The initial abundance of *T. pecari* was notably higher in primary forest, in comparison with secondary forest and plantation (Fig. 2a). By contrast, the initial abundance of *P. tajacu* was relatively similar among the vegetation classes (Fig. 2c). The detection of *T. pecari* was also similar among the vegetation classes, whereas the detection of *T. pecari* was much higher in the areas of plantation (Fig. 2b), followed by the secondary and then the primary forest (Fig. 2d).

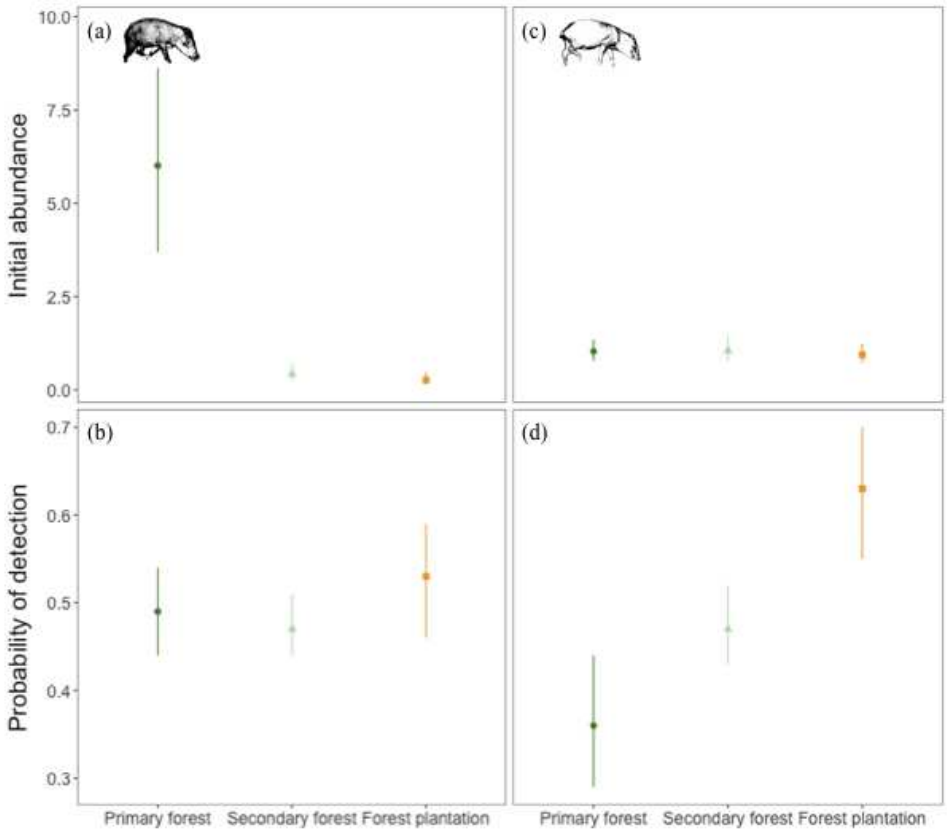

Fig. 2 Estimates of the initial abundance (a) and detection (b) of *Tayassu pecari*, and the initial abundance (c) and (d) detection of *Pecari tajacu*. The dots represent the estimated coefficients, and the error bars represent the 95% confidence intervals.

The influence of each vegetation class on the parameter estimates also varied between the two peccary species. The expected abundance of *T. pecari* had a positive relationship with primary forest cover, but a negative correlation with secondary forest and plantation (Fig. 3a). On the other hand, the expected abundance of *P. tajacu* did not vary significantly with vegetation cover (Fig. 3c). In terms of detection, *T. pecari* had a positive relationship with primary forest, but correlated negatively with secondary forest and plantation (Fig. 3b). In the case of *P. tajacu*, detection was related negatively to primary forest, while having a slightly negative association with secondary forest, but a positive correlation with plantation (Fig. 3d).

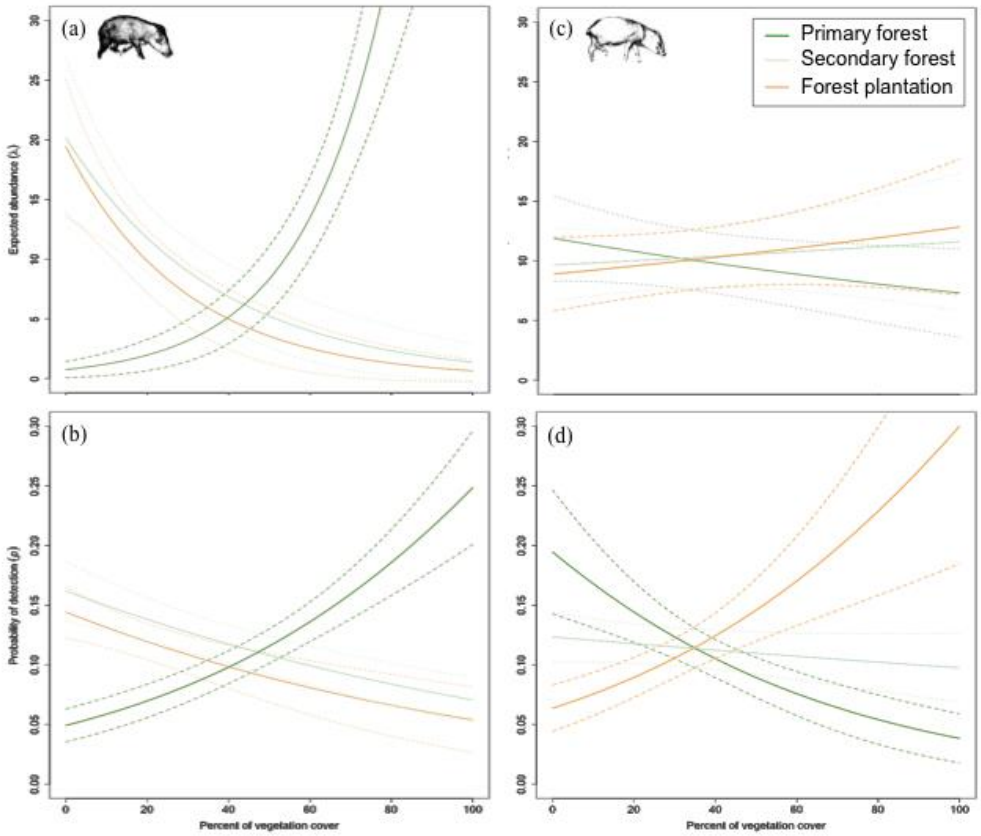

Fig. 3 Influence of each vegetation cover class on the expected (a) abundance and (b) detection of *Tayassu pecari*, and the expected (c) abundance and (d) detection of *Pecari tajacu*. The shaded areas represent the 95% confidence intervals for the respective parameter.

Discussion

The results of the present study indicate that the white-lipped peccary (*Tayassu pecari*) was more abundant in the primary forest > secondary forest > plantation, whereas the abundance of the collared peccary (*Pecari tajacu*) was virtually constant among the different vegetation classes. Primary forest was pivotal to the abundance of *T. pecari*, whereas *P. tajacu* was affected more at a landscape scale. *Tayassu pecari* varied in its use of distinct forest types based on fruit availability, with primary forest having the highest availability (Altricther et al. 2001; Carrillo et al. 2002). This nonrandom preference for habitats in *T. pecari* underscores the importance of a diverse array of forest types and their associated fruiting species (Keuroghlian et al. 2009). *Tayassu pecari* avoided agricultural environments (Hofman et al. 2016), secondary forests, and forest plantations (Vindolin et al. 2009), focusing on forested areas, including riparian zones, in which the availability of water shapes its patterns of habitat use significantly

(Fragoso 1999; Keuroghlian and Eaton 2008; Reyna-Hurtado et al. 2009), in particular during the dry season (Moreira-Ramírez et al. 2016). The herds of *T. pecari* were observed traveling longer distances and more frequently in dry habitats (Reyna-Hurtado et al. 2012). Similarly, *P. tajacu* favored landscapes with forest cover (García-Marmolejo et al. 2015), but did not present any clear preference for either primary or secondary forest (Romero et al. 2013), which may reflect its adaptability to a wider range of conditions in comparison with other peccary species (Altrichter and Boaglio 2004).

Vegetation cover promoted distinct effects on the abundance and detection of the two peccary species. An increase in primary forest cover had a positive influence on both the abundance and detection of *T. pecari*, although no similar pattern was found in the case of *P. tajacu*. On the other hand, secondary forest and plantation cover did not favor the abundance or detection of *P. tajacu*. Even though areas of natural regeneration and even plantations of exotic trees can provide some supplementary ecosystem services, primary forests play a crucial role in the maintenance of tropical biodiversity (Barlow et al. 2007). Presumably, a more favourable resource base is available for peccaries in primary forest, in comparison with secondary forest and plantation. Even so, *P. tajacu* did not present a clear preference for primary forest, although Romero et al. (2013) did note that the herds of this species tended to be larger in primary forest. Large herds of *T. pecari* may also divide into smaller sub-herds according to the availability of resources during different seasons (Keuroglian et al. 2004). The habitat requirements of this species within a large-scale landscape mosaic of vegetation types may account for its susceptibility to local extinction (Fragoso 1999).

The variation found in the probability of detection among surveys and between seasons may be attributed to the heterogeneity in the capture of the animals (MacKenzie 2006). The declining probability of detection over the years may be linked to the movement patterns reported for Amazonian peccaries, where fluctuations in the food supply regulate the use of space by both species (Mendes Pontes and Chivers 2007).

The present study determined the influence of vegetation cover on the abundance and detection of peccaries, which are still relatively poorly understood. The landscape of the study site may have contributed positively to the estimates due to the proximity of the secondary forest and plantations to the primary forest. The cover of natural habitats within the landscape is a critical factor determining the occurrence of peccaries in plantation forests (Begotti et al. 2017). Parameters such as patch size and location, the distance from primary forests, the percentage of modified habitats, the levels of degradation,

structural similarities between the plantation and natural vegetation, and the type of habitat converted to plantation all influence the value of this habitat for the peccaries (Hartley 2002). Older plantations are also more likely to provide more valuable habitat for a greater diversity of organisms (Brockerhoff et al. 2008). The carbon sequestration project in the study aims to maintain these older plantations, which are less intensely managed, and thus more beneficial for biodiversity. Given this, estimating the local abundance of the two peccary species will be fundamental for the monitoring of the quality of the regenerating secondary forests and plantations over time. Peccaries can provide essential ecosystem services, such as the enhancement of soil structure, seed dispersal, facilitating the accessibility of resources, and contributing to the preservation of local diversity.

References

Altrichter M, Carrillo E, Sáenz J, Fuller TK (2001) White-lipped peccary (*Tayassu pecari*, Artiodactyla: Tayassuidae) diet and fruit availability in a Costa Rican rain forest. Rev de Biol Trop 49:1183-1192

Altrichter M, Boaglio GI (2004) Distribution and relative abundance of peccaries in the Argentine Chaco: associations with human factors. Biol Conserv 116:217-225

Altrichter M, Taber A, Beck H, Reyna-Hurtado R, Lizarraga L, Keuroghlian A, Sanderson EW (2012) Range-wide declines of a key Neotropical ecosystem architect, the Near Threatened white-lipped peccary *Tayassu pecari*. Oryx 46:87-98

Barlow J, Gardner TA, Araujo IS, Ávila-Pires TC, Bonaldo AB, Costa JE, Esposito MC, Ferreira LV, Hawes J, Hernandez MIM, Hoogmoed MS, Leite RN, Lo-Man-Hung NF, Malcolm JR, Martins MB, Mestre LAM, Miranda-Santos R, Nunes-Gutjahr AL, Overal WL, Parry L, Peters SL, Ribeiro-Junior MA, da Silva MNF, da Silva Motta C, Peres CA (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. PNAS 104:18555-18560

Beck H (2006) A review of peccary-palm interactions and their ecological ramifications across the Neotropics. J Mammal 87:519-530

Beck H, Thebpanya P, Filiaggi M (2010) Do Neotropical peccary species (Tayassuidae) function as ecosystem engineers for anurans? J Trop Ecol 26:407-414.

Bello C, Galetti M, Pizo MA, Magnago LFS, Rocha MF, Lima RAF, Peres CA, Ovaskainen O, Jordano P (2015) Defaunation affects carbon storage in tropical forests. Sci Adv 1:e1501105

Begotti RA, Pacífico ES, Ferraz SFB, Galetti M (2017) Landscape context of plantation forests in the

conservation of tropical mammals. J Nat Conserv 41:97-105

Bodmer RE, Sowls LK (1993) The collared peccary (*Tayassu tajacu*). In: Oliver WLR (ed) Pigs, peccaries, and hippos. IUCN/SSC Pigs and Peccaries and IUCN/SSC Hippos Specialist Group. Kelvyn Press, Broadview, pp 7-13

Brockerhoff EG, Jactel H, Parrotta JA, Quine CP, Sayer J (2008) Plantation forests and biodiversity: oxymoron or opportunity? Biodivers Conserv 17:925-951

Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach. Springer-Verlag, New York

Carrillo E, Saenz JC, Fuller TK (2002) Movements and activities of white-lipped peccaries in Corcovado National Park, Costa Rica. Biol Conserv 108:317-324

Dail D, Madsen L (2011) Models for estimating abundance from repeated counts of an open metapopulation. Biometrics 67:577-587

Fletcher RJ, Young JS, Hutto RL, Noson A, Rota CT (2011) Insights from ecological theory on temporal dynamics and species distribution modeling. In: Drew CA, Wiersma YF, Huettmann F (ed). Predictive species and habitat modeling in landscape ecology: concepts and applications. Springer, New York, pp 91-107

Fiske IJ, Chandler RB (2011) unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. J Stat Software 43:10.18637/jss.v043.i10

Fragoso JMV (1999) Perception of scale and resource partitioning by peccaries: behavioral causes and ecological implications. J Mammal 80:993-1003

Galetti M, Bovendorp RS, Guevara R (2015) Defaunation of large mammals leads to an increase in seed predation in the Atlantic forests. Global Ecol Conserv 3:824-830

García-Marmolejo G, Chapa-Vargas L, Huber-Sannwald E, Weber M, Rosas-Rosas OC, Martínez-Calderas J (2013) Potential distributional patterns of three wild ungulate species in a fragmented tropical region of northeastern Mexico. Trop Conserv Sci 6:539-557

García-Marmolejo G, Chapa-Vargas L, Weber M, Huber-Sannwald E (2015) Landscape composition influences abundance pattern and habitat use of three ungulate species in fragmented secondary deciduous tropical forests, Mexico. Global Ecol Conserv 3:744-755

Hartley MJ (2002) Rationale and methods for conserving biodiversity in plantation forests. For Ecol Manage 155:81-95

Hofman MP, Signer J, Hayward MW, Balkenhol N (2016) Spatial ecology of a herd of white-lipped peccaries (*Tayassu pecari*) in Belize using GPS telemetry: challenges and preliminary results. THERYA 7:21-37

Kéry M, Schaub M (2012) Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Waltham

Keuroghlian A, Eaton DP, Longland WS (2004) Area use by white-lipped and collared peccaries (*Tayassu pecari* and *Tayassu tajacu*) in a tropical forest fragment. Biol Conserv 120:411-425

Keuroghlian A, Eaton DP (2008) Importance of rare habitats and riparian zones in a tropical forest fragment: preferential use by *Tayassu pecari*, a wide ranging frugivore. J Zool 275:283-293

Keuroghlian A, Eaton DP, Desbiez AL (2009) The response of a landscape species, white-lipped peccaries, to seasonal resource fluctuations in a tropical wetland, the Brazilian Pantanal. Int J Biodivers Conserv 1:87-97

MacKenzie DI (2006) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, San Diego

Mendes Pontes AR, Chivers DJ (2007) Peccary movements as determinants of the movements of large cats in Brazilian Amazonia. J Zool 273:257-265

Moreira-Ramírez JF, Reyna-Hurtado R, Hidalgo-Mihart M, Naranjo E, Ribeiro MC, Garcia-Anleu R, Mérida M, Ponce-Santizo G (2016) Importance of waterholes for white-lipped peccary (*Tayassu pecari*) in the Selva Maya, Guatemala. THERYA 7:51-64

Morrison JC, Sechrest W, Dinerstein E, Wilcove DS, Lamoreux JF (2007) Persistence of large mammal faunas as indicators of global human impacts. J Mammal 88:1363-1380

Noss A, Polisar J, Maffei L, Garcia R, Silver S (2013) Evaluating jaguar densities with camera traps. Jaguar Conservation Program, Latin America and Caribbean Program, Wildlife Conservation Society, New York

Offerman HL, Dale VH, Pearson SM, Bierregaard Junior RO, O'Neill RV (1995) Effects of forest fragmentation on Neotropical fauna: current research and data availability. Environ Rev 3:191-211

Reider KE, Carson WP, Donnelly MA (2013) Effects of collared peccary (*Pecari tajacu*) exclusion on leaf litter amphibians and reptiles in a Neotropical wet forest, Costa Rica. Biol Conserv 163:90-98

Reyna-Hurtado R, Rojas-Flores E, Tanner GW (2009) Home range and habitat preferences of white-lipped peccaries (*Tayassu pecari*) in Calakmul, Campeche, Mexico. J Mammal 90:1199-1209

Reyna-Hurtado R, Chapman CA, Calme S, Pedersen EJ (2012) Searching in heterogeneous and limiting environments: foraging strategies of white-lipped peccaries (*Tayassu pecari*). J Mammal 93:124-133

Ringler M, Hödl W, Ringler E (2015) Populations, pools, and peccaries: simulating the impact of ecosystem engineers on rainforest frogs. Behav Ecol 26:340-349

Ripple WJ, Newsome TM, Wolf C, Dirzo R, Everatt KT, Galetti M, Hayward MW, Kerley GIH, Levi T, Lindsey PA, Macdonald DW, Malhi Y, Painter LE, Sandom CJ, Terborgh J, VanValkenburgh B (2015) Collapse of the world's largest herbivores. Sci Adv 1:e1400103

Romero A, O'Neill BJ, Timm RM, Gerow KG, McClearn D (2013) Group dynamics, behavior, and current and historical abundance of peccaries in Costa Rica's Caribbean lowlands. J Mammal 94:771-791

Royle JA (2004) N-mixture models for estimating population size from spatially replicated counts. Biometrics 60:108-115

Vidolin GP, Biondi D, Wandembruck A (2009) Seletividade de habitats pela anta (*Tapirus terrestris*) e pelo queixada (*Tayassu pecari*) na Floresta com Araucária. Scientia Forestalis 37:447-458

Zar JH (2010) Biostatistical analysis, 5th edn. Pearson Prentice Hall, New Jersey