



Effects of human-induced habitat changes on site-use patterns in large Amazonian Forest mammals

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ABSTRACT

The Amazon is one of the most diverse biomes around the globe, currently threatened by economic and industrial development and climate change. Large mammals are keystone species, playing an important role in ecosystem structure and function as ecological engineers, while being highly susceptible to deforestation, habitat degradation, and human exploitation. Using a unifying hierarchical Bayesian spatial approach, we examine the site-use patterns of four large Amazonian Forest mammals and their relationships to anthropogenic factors at a biome-wide scale. Our results showed that species' patterns of site use are correlated with human induced habitat changes, and that this correlation is species-specific. The white-lipped peccary shows highest site-use estimates within strict protected areas, affected by proximity to urban areas and benefiting from indigenous territories, the tapir responding slightly to proximity to burned forested areas, while the giant armadillo and the jaguar were primarily affected by vegetation cover loss; disturbances related to the colonization of the Amazon. Our findings

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contribute to the understanding of how human-induced environmental changes influence the site-use patterns of these four large mammals, and inform future conservation and land use planning. Transboundary conservation efforts, empowering and integrating native (indigenous and non-indigenous) communities in land governance schemes, involving the private sector and securing the commitment of developed countries are important paths for the protection and sustainability of the globally-crucial Amazon rainforest.

1. Introduction

Species distributions are the result of historic environmental changes and the species' intrinsic capacity to adapt to them. These have been heavily influenced by direct and indirect environmental impacts of anthropogenic activities (Boivin et al., 2016, 2017). Understanding how human-induced changes impact and threaten the way in which species persist, move, and occupy shared and heterogeneous environments is key to the design and implementation of long-term programs seeking to integrate the wildlife conservation, land-use planning, and socio-economic development.

With an area of roughly 6.7 million km², the Amazon rainforest is the largest tropical rainforest on the globe, and is an important major wilderness area (Mittermeier et al., 1998; Myers et al., 2000). Despite being recognised as a continuous natural ecosystem with low levels of habitat fragmentation and isolation (Crooks et al., 2011; Rabinowitz and Zeller, 2010), this biodiversity hotspot is under threat. It is currently subjected to high and increasing deforestation rates (Escobar, 2019, 2020; Silva Junior et al., 2021) because of economic and industrial development; including fossil fuel extraction, large-scale agriculture (e.g., soybean, cattle ranching), mining (legal and illegal), hydroelectric dams, infrastructure development (e.g., roads) and recent colonization (Alvarez-Berrios and Aide, 2015; Fearnside, 2017; Laurance et al., 2004; Sontger et al., 2017). Moreover, wildfires, commercial hunting and logging intensify with ongoing economic development and exert drastic negative impacts on wild vertebrate populations (Brando et al., 2020; Escobar, 2019; Espinosa et al., 2018; Peres, 2001).

Large mammals are keystone species, playing important roles in ecosystem structure and function, either by maintaining ecosystem equilibrium while stabilizing prey species populations, or as ecological engineers by changing the composition and structure of the surrounding vegetation (Beck, 2005; Crooks and Soulé, 1999; Estes et al., 2011; Marquis, 2010; Ripple et al., 2014; Terborgh et al., 1999). They are highly susceptible to human activities, such as deforestation, habitat degradation and fragmentation, direct exploitation and persecution (Bogoni et al., 2020; Cardillo et al., 2004; Ceballos and Ehrlich, 2002; Chiarello, 1999; Milner-Gulland et al., 2003; Ripple et al., 2015). Thus, large threatened terrestrial forest-dwelling mammals have been used as indicator species of human-induced biodiversity loss, and as biological models for designing range-wide conservation strategies (Morrison et al., 2007; Ray, 2005, 2010; Soares-Filho et al., 2006; Steneck, 2005; Zeller and Rabinowitz, 2011).

While site-use patterns of large mammals based on field observation data have been described at local and regional scales in the Amazon (e.g., Abrahams et al., 2017; Espinosa et al., 2018; Fragoso, 2004; Whitworth et al., 2019), we are not aware of any studies that have attempted to test for the effect of human-related habitat changes at a biome-wide scale (Peres and Lake, 2003). This is particularly important because, despite major local and regional conservation actions, protecting the integrity of the Amazon rainforest and its associated biodiversity requires landscape-scale conservation efforts; these should be informed by understanding of the distribution patterns of wide-ranging species at meaningfully large-scales (Laurance, 2005; Peres, 2005).

Here, we examine the patterns of site-use of four exemplar wide-ranging species at a landscape scale, in relation to anthropogenic factors. Our main objective is to reveal which, and to what extent, anthropogenic variables best account for the occurrence of these four large forest-dwelling mammals throughout the Amazon rainforest. To

accomplish this, we used a unifying hierarchical Bayesian spatial approach, constructed upon the largest known detection/non-detection dataset for each and all the study species. We hypothesized that all four species will be particularly affected by human presence and habitat degradation due to agro-industrial expansion and colonization (i.e., fires), energy industry and infrastructure. Also, since all four species are forest-dwellers, we expect their use of sites to be less in areas subjected to deforestation, or otherwise lacking forest cover. Additionally, we expect the presence of game species, such as the white-lipped peccary and tapir, to be negatively related to proximity to indigenous territories, human settlements and roads, since these features are correlated to hunting pressure (Espinosa et al., 2018; Peres and Lake, 2003; Peres and Nascimento, 2006; Soares-Filho et al., 2006).

2. Material and methods

2.1. Study area

The study area comprises the Amazon Biome, which is located in central and northern South America, and extends across nine countries (Brazil, Bolivia, Peru, Ecuador, Colombia, Venezuela, Guyana, French Guiana and Suriname). It is characterized by a matrix of tropical moist broadleaf forest, with small proportions of tropical savannahs and shrublands mostly restricted to the southern and northern periphery (Olson et al., 2001). The rainforest matrix is represented by a mosaic of distinct and unique ecosystems, broadly including swamps, palm forests, seasonally white and blackwater flooded forests (i.e., *varzea* and *igapó*, respectively), and lowland and montane unflooded forests (i.e., *terra firme*) (Junk et al., 2011; WWF, 2020). Air temperature is nearly constant throughout the year, with a mean annual temperature fluctuating around 22–34 °C. The timing and duration of the dry season, including precipitation events, differ regionally within the Amazon, but in general there is a distinct dry season lasting four to five months (from around July to around January), and mean annual rainfall varies from 1000 to 4000 mm (Sombroek, 2001). However, in some areas is not that long and distinct, such as eastern Ecuador.

2.2. Study species

The jaguar (*Panthera onca*), apex predator of America, is listed as Near Threatened by the IUCN, while the white-lipped peccary (*Tayassu pecari*), giant armadillo (*Priodontes maximus*), and lowland tapir (*Tapirus terrestris*) are listed as Vulnerable; all are facing rapid and continuous populations decline (Anacleto et al., 2014; Keuroghlian et al., 2013; Oshima et al., 2021; Quigley et al., 2017; Varela et al., 2019). Throughout the Amazon rainforest, these species are mostly threatened by deforestation, habitat degradation, human settlement, road infrastructure, legal and non-legal extraction and retaliatory persecution (Abrahams et al., 2017; Anacleto et al., 2014; Dias et al., 2019; Espinosa et al., 2018; Ferreguetti et al., 2017, 2018; Morato et al., 2018; Pfeifer et al., 2017; Varela et al., 2019; Zimbres et al., 2018). Besides their conservation status, and their particular susceptibility to habitat transformations, we selected these four large mammals as study species because they are mainly forest-dwellers, ecologically distinct, with large energetic requirements due to their size, and are used by local communities, making them biological models for landscape planning.

2.3. Data collection and preparation

We analysed data from 25 independent camera trap surveys (i.e., study sites) conducted between 2011 and 2018 in Brazil, Ecuador, Guyana and Peru (Fig. 1). The study sites varied in terms of dominant land use and the camera trap surveys differed in terms of the area covered, survey time-period, as well as in the brand, technical configuration and number and spacing of camera traps used. In general, stations (i.e., sampling sites) consisted of a single camera trap, set perpendicular to human or animal trails at around 30 to 50 cm above the ground, mainly as part of terrestrial vertebrate monitoring studies. In total, the 25 study sites covered an approximate area of 20,000 km², comprised of 1,191 single camera trap stations, and with a total effort of

nearly 86,500 trap-days.

Occupancy models are constructed upon repeated binary (i.e., detection/non-detection) observations, while accounting for imperfect detection to reduce bias in the estimation of the species' occupancy parameter and facilitating more precise ecological inferences than those available using traditional species distribution models (Kéry and Schmidt, 2008; MacKenzie et al., 2002). It involves two important assumptions: 1) the closure assumption states that the latent state (i.e., the occupancy state of a camera site) does not vary within the surveyed period (i.e., the primary sampling period), and 2) that the probability of detecting a species is independent among sites (MacKenzie et al., 2002). Regarding the former, and as stated by MacKenzie et al. (2006), parameter estimation is unbiased if changes in the latent state occur

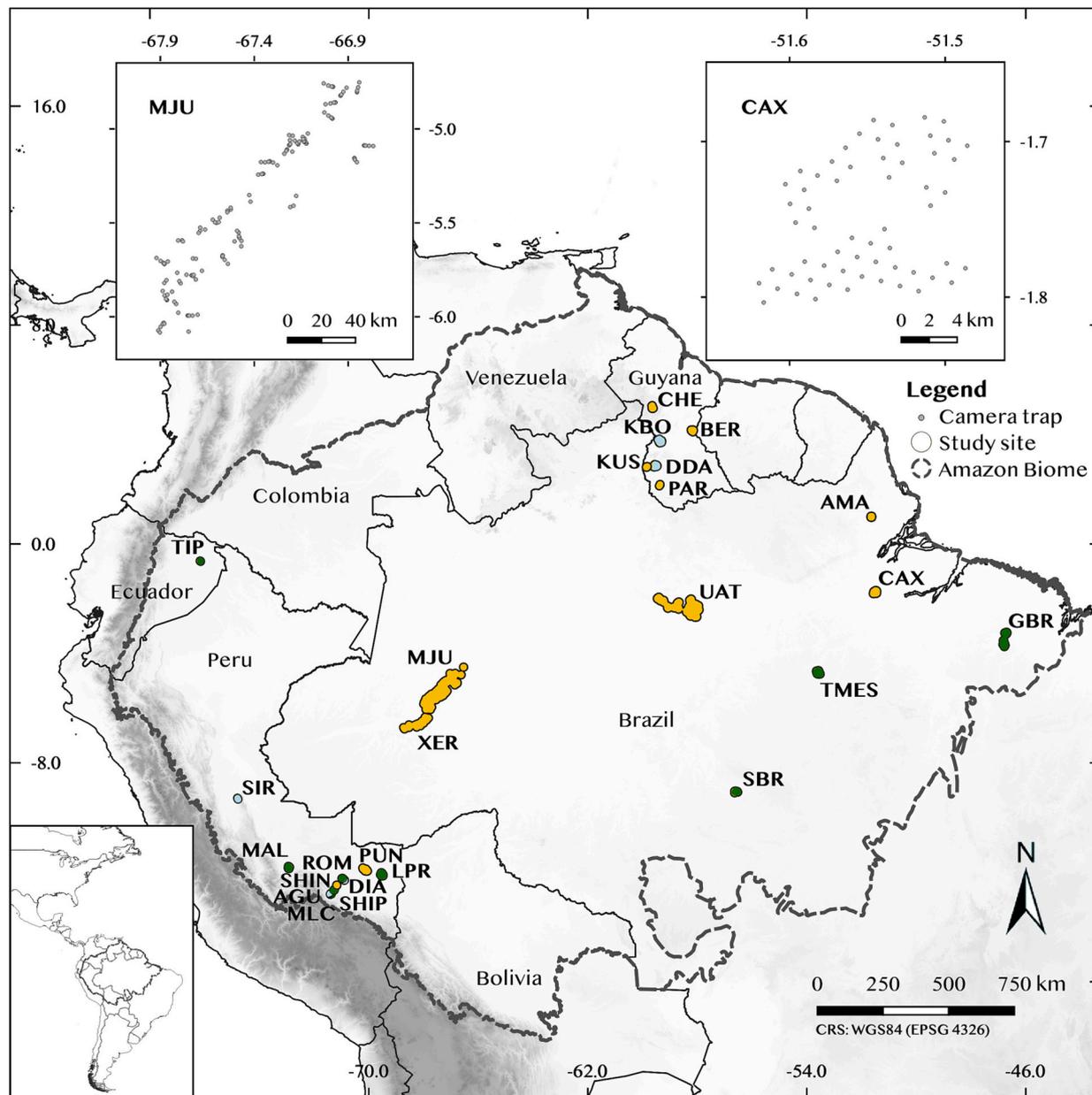


Fig. 1. Map showing the 25 camera trap study sites used to model the site-use of the four study species, located in Brazil ($n = 8$), Ecuador ($n = 1$), Guyana ($n = 6$) and Peru ($n = 10$). The extent showed for each study site is for visualization purpose only and corresponds to a 16 km dissolved buffer surrounding the camera trap stations. Colours represent land-use types, where dark green depict public and private natural reserves with strict protection, orange to community land with sustainable use and light blue to productive community lands. Small upper maps depicting camera trap deployment at two study sites in Brazil (MJU and CAX), as representatives of opposite extremes in terms of survey design. All the studies sites within Guyana represent the “GUY” study area, while in Peru, LPR and PUN conform the “SAM” study area, and AGU, MLC, SHIN, SHIP, DIA and ROM integrates the “AND” study area (see text for details). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

randomly, in which case occupancy should be interpreted as site ‘use’ rather than site ‘occupancy’. Regarding the assumption of independence, and to resolve issues with multicollinearity and confounding spatial effects, [Johnson et al. \(2013\)](#) proposed a unifying hierarchical spatial occupancy model based on a ‘probit’ mixture framework which is particularly effective over large spatial extents and heterogeneous data

sets. These authors introduce a random spatial effect into the model by considering the realization of a Gaussian process, which takes account of the spatial autocorrelation (SAC, i.e., non-independence) among sampling units in terms of covariates, reducing the bias and the inflation of uncertainty on the estimated parameters.

To standardise the data across the different study sites (i.e., surveys),

Table 1

Detailed information of the study sites and camera trap surveys included in this study.

Country	Study area*	Study site	Study site name	Main use of land	Surveyed year	Surveyed area (km ²)**	Number of stations	Trap density (traps/km ²)	Minimum trap spacing mean (min. - max.)	Total effort (trap-days)
Brazil	AMA	AMA ¹	Floresta Nacional de Amapá	Protected area with sustainable use	2016	41	30	0.732	949 (890–997)	1,342
Brazil	CAX	CAX ²	Floresta Nacional de Caxiuanã	Protected area with sustainable use	2013	205	60	0.293	1,365 (1,265–1,410)	2,783
Brazil	GBR	GBR	Gurupi Biological Reserve	Natural reserve (strict)	2017	233	65	0.279	1,325 (1,246–1,437)	4,568
Brazil	MJU	MJU ³	Medio Jurua & Uacari Reserves	Extractive reserve	2013	7,741	148	0.019	1,511 (271–9,409)	4,762
Brazil	SBR	SBR	São Benedito River	Natural reserve (strict)	2017	68	22	0.324	1,432 (1,264–2,688)	1,527
Brazil	TMES	TMES	Terra do Meio Ecological Station	Natural reserve (strict)	2016	152	59	0.388	1,322 (1,113–1,445)	3,526
Brazil	UAT	UAT ³	Uatumã Biological Reserve	Natural reserve (sustainable use)	2014	4,341	94	0.022	1,150 (258–5,211)	2,785
Brazil	XER	XER	Xerua (multiple sites)	Extractive reserve	2011	1,313	41	0.031	1,764 (406–8,485)	3,576
Ecuador	TIP	TIP	Tiputini Biodiversity Station	Private natural reserve (strict)	2016	21	10	0.476	741 (617–1,074)	604
Guyana	GUY	BER	Berbice	Sustainable small-scale logging concession	2014	73	28	0.384	1341 (658–1,574)	1,390
Guyana	GUY	CHE	Chenapau	Indigenous community land	2014	54	38	0.704	676 (540–1291)	1,242
Guyana	GUY	DDA	Dadanawa	Productive community land	2012	134	42	0.313	1,475 (1,118–2,026)	1,478
Guyana	GUY	KBO	Karanambo	Productive community land	2011	141	63	0.447	1,060 (282–2,193)	1,911
Guyana	GUY	KUS	Kusad	Indigenous community land	2013	27	20	0.741	486 (377–591)	913
Guyana	GUY	PAR	Parabara	Indigenous community land	2013	21	18	0.857	491 (441–522)	519
Peru	AND	AGU ⁴	Aguanos & Adanrayo	Productive community land	2016	12	10	0.833	510 (389–664)	1,171
Peru	AND	DIA ⁴	Diamante	Indigenous community land	2016	14	10	0.714	515 (262–700)	1,169
Peru	AND	MLC ⁴	Manu Learning Centre	Private natural reserve (strict)	2016	15	10	0.667	685 (445–997)	1,181
Peru	AND	ROM ⁴	Romero Rainforest Lodge	National Park (strict)	2016	16	9	0.563	577 (524–655)	1,080
Peru	AND	SHIN ⁴	Shintuya Community Reserve	Indigenous community land	2015	16	9	0.563	684 (597–958)	1,021
Peru	AND	SHIP ⁴	Shipetiari Community Reserve	Indigenous community land	2016	11	10	0.909	540 (489–633)	1,091
Peru	MAL	MAL	Malvinas	Private natural reserve (strict)	2018	81	42	0.519	1,172 (291–2,978)	4,979
Peru	SAM	LPR	Las Piedras River	Private natural reserve (strict)	2018	131	32	0.244	1,394 (681–2,010)	3,253
Peru	SAM	PUN	Puerto Nuevo	Productive community land	2017	173	47	0.272	956 (347–2,316)	2,897
Peru	SIR	SIR ⁵	Sira Communal Reserve	Indigenous community land	2015	17	15	0.882	305 (254–426)	1,680
Total	14	25			2011–2018	15,055	932	0.062	989 (305–1,764)	52,448

* Defined as a detection covariate. See text for details.

** Minimum convex polygon (MCP) at 1 km buffer from each camera trap station.

¹ [Michalski et al. \(2015\)](#); [Paredes et al. \(2017\)](#).

² [Santos et al. \(2019\)](#).

³ [Abrahams et al. \(2017\)](#).

⁴ [Whitworth et al. \(2019\)](#).

⁵ [Pillco Huaracaya et al. \(2019\)](#).

data processing was required before conducting data analysis. Firstly, paired stations (~ 5 %) were reduced to one camera-trap detection history by selecting the one with the larger number of trap-days, or, if both were deployed for the same duration, by randomly selecting one of them. Secondly, stations that were closer than 250 m from one another were deleted, retaining the highest possible number of stations after deletion. To minimize the chance of violating the closure assumption and to avoid bias in the parameter estimations (MacKenzie et al., 2006; Rota et al., 2009), all detection non-detection histories were reduced to a maximum of 120 days (Penjor et al., 2018; Tan et al., 2017; Wang et al., 2019). Moreover, survey periods were limited to the dry seasons from 2011 and 2018, since lateral movements of mammal species have been shown to be driven by flood pulses in the study area (Costa et al., 2018), affecting the sites' availability for some of the study species, and causing non-random changes in the state parameter. Finally, detection histories were collapsed into 20-day intervals, for a maximum of 6 sampling occasions per site, to increase both the temporal independence among occasions, and the overall detection probability. If the latter is too low, it may prevent model convergence (Dillon and Kelly, 2007) leading to spurious parameter estimations (MacKenzie et al., 2002; Welsh et al., 2013). After this standardisation of the data, the total number of sampling sites (i.e., stations) was 932, covering a total area of 15,055 km², for an overall mean camera trap density of 0.47 trap/km² (min. 0.02, max. 0.91), and an average minimum distance between stations of 989 m. The total sampling effort is 52,448 trap-days, collapsed into 3,020 20-day sampling occasions, and representing the largest known dataset for all, and each, of the study species (Table 1).

Among occupancy models, detection probability corresponds to the probability of detecting a particular species in a particular sampling site, given that it is present. We are mindful that there may be differences between teams (i.e., camera trap surveys) in terms of each study's main objectives, researcher's expertise, and survey protocols, with implications in principle for detection probabilities. Thus, we tested for the effect of study area on the species' detection probability. To do so and avoid over-parameterization of the model when including all study sites as a detection covariate, we converted the 25 study sites into 14 study areas, by grouping the camera trap surveys that were conducted as part of the same study. This was: 1) all study sites from Guyana (BER, CHE, DDA, KBO, KUS and PAR) were grouped as the "GUY" study area; 2) from Perú, the five study sites from Whitworth et al. (2019) were collapsed into the "AND" study area, 3) while two others (LPR and PUN) were combined as the "SAM" study area (Table 1). Overall, each sampling occasion corresponded to a 20-days interval. However, for those sites with a total effort of <120 days, the last sampling occasion might include a shorter time interval (e.g., for a 110-days deployed camera trap, the last sampling occasion will correspond to a 10-days interval). Since the longer a camera trap is active, the higher the chance of detecting a particular species; we included effort as a detection covariate, expressed as the number of days that comprises each sampling occasion, being different from 20 days only for the last occasion at some sampling sites.

2.4. Estimation of site-use covariates

Because our main goal was to explore and identify the human-induced habitat changes that influence the site-use of all four target species in the Amazon at a landscape scale, we selected the following seven covariates: distance to boundary of nearest strict protected area, distance to boundary of nearest indigenous territory, distance to nearest energy industry (mining, hydroelectric or fossil fuels), distance to nearest road, distance to fires, distance to nearest urban area and proportion of non-forested/deforested areas.

Proportion of non-forested/deforested cover was calculated using the updated Global Forest Change 30 m raster layers (GFC; Hansen et al., 2013), which enabled setting different tree cover thresholds to consider a pixel as forest or no-forest. We subjectively set four different threshold

values (30 %, 50 %, 75 % and 90 %, following Tan et al., 2017) to create annual forest/no-forest raster layers, upon which we conversely calculated the mean value of the proportion of non-forested cover and areas with forest loss (i.e., no-forest pixels that were classified as forest in previous years). In each case we used the GFC layers corresponding to the year of each survey. This was done using the "gfcanalysis" R package and following (Zvoleff, 2014). Distance to urban areas was calculated based on the 2015 ESA CCI Land Cover layer, at 300 m resolution (<https://www.esa-landcover-cci.org/>), while the remaining covariates were calculated based on the Amazon Geo-referenced Socio-environmental Information Network (<https://www.amazoniasocioambiental.org>). Details and sources for each variable are shown in Table A1. All polyline and polygon vector layers were rasterized at a 250 m resolution using QGIS version 3.6 (QGIS Development Team, 2019). Environmental covariates, such as water availability (e.g., proportion/density), distance to water sources, land cover type, elevation, or slope, are known to influence the site-use of the focal species throughout the study area (see references cited in the introduction). Thus, to avoid confounding effects, we tested for correlation among these and the seven tested human-induced variables, for which none was correlated ($r < |0.7|$; Table A2).

Effects of environmental variables on species habitat selection is both species-specific and scale-dependent (Macdonald et al., 2019; McGarigal et al., 2016; Pitman et al., 2017; Stevens and Conway, 2019; Sunarto et al., 2012; Timm et al., 2016; Wiens, 1989). To assess for scale-specific relationships between species' site-use and non-forested/deforested cover, we converted this site variable into seven multi-scale covariates, by calculating the mean value at a 250 m, 500 m, 1 km, 2 km, 4 km, 8 km, and 16 km buffer around each of the camera trap stations, at each of the four cover thresholds tested (see above). The chosen buffers allows us to account for the possible effect of surrounding areas on a local site at different spatial scales, and has been used for other large mammal species (Macdonald et al., 2019). This was done using the raster calculator tool in QGIS 3.6 (QGIS Development Team, 2019). Prior to analysis, all covariates were z-standardized ($\mu = 0$, $SD = 1$), allowing comparison of the effect among covariates and facilitating model convergence (Stanton et al., 2015).

2.5. Data analysis

Spatial autocorrelation (SAC) was addressed in all stages of the data analysis to account for the detection heterogeneity and non-independence of covariates among sampling sites (e.g., overlapping buffer areas between stations when estimating the proportion of non-forested/deforested areas). We applied single-season single-species Bayesian hierarchical spatial occupancy models (Johnson et al., 2013), using the "stocc" package 1.30 (Johnson, 2015) in R 3.6.2 (R Core Team, 2017). The SAC parameter was specified by the usage of the restricted spatial regression model (RSR), which uses an efficient Gibbs sampler Markov chain Monte Carlo (MCMC) method to infer detection and occupancy parameters based on a 'probit' link function instead of a traditional *logit* link function (Johnson, 2015). In comparison to the 'logit' link function, the 'probit' model increases computational efficiency and flexibility through a data augmentation approach (Dorazio and Rodríguez, 2012; Johnson et al., 2013). As recommended by Hughes and Haran (2013), we set the 'moran.cut' parameter as $0.1 * \text{number of sampling sites}$, which represents the cut-off for selecting the spatial harmonics used in the RSR model and which might be interpreted as analogous to correlation in the site-use probability across sampling sites (Johnson et al., 2013). The threshold component is used as a distance threshold in which all sites within the specific range are considered as neighbours of each site, and it was set as the radius of the species' average home range reported in the literature for the study area (Table A3). Default package's priors were chosen for all parameters, and specifically, the scalar precision parameter (τ) of the spatial process was set as $\tau \sim \text{Gamma}(0.5, 0.0005)$ (Hughes and Haran, 2013; see Johnson et al., 2013 for details). "The shape and rate parameters chosen for the τ

prior heavily weight large values that a priori imply less spatial autocorrelation. Therefore, any observed spatial effect in the posterior implies strong evidence of spatial autocorrelation” (Johnson et al., 2013 pg. 805). RSR model selection was based on the posterior predictive loss criterion (PPLC), which can be interpreted as a penalized deviance criterion representing a combination of a weighted goodness-of-fit measure and a weighted penalty term (Gelfand and Ghosh, 1998; Hooten and Hobbs, 2015). It is similar to information criteria used in classic (i.e., maximum-likelihood) methods, such as the Akaike Information Criterion (AIC), and can be interpreted analogously; where lower values of PPLC represents lower expected loss in predicting new data, based on the posterior model parameters (Gelfand and Ghosh, 1998; Hooten and Hobbs, 2015; Johnson, 2015).

2.6. Model selection and evaluation

Prior to undertaking the spatial site-use modelling, we tested for the goodness-of-fit of the global non-spatial occupancy model (MacKenzie and Bailey, 2004) for each of the species, to evaluate 1) the plausibility of the model being correct ($p > 0.05$), and 2) how adequately the model described the observed data, determined by the over dispersion statistic (\hat{c}) (MacKenzie and Bailey, 2004). Construction of the non-spatial occupancy model was done using the “unmarked” R package (Fiske and Chandler, 2011) and the goodness of fit test was done by specifying 1,000 simulations within the ‘mg.gof.test’ function in “AICcmodavg” R package (Mazerolle, 2017). We removed those sites that inflated the chi-squared value and were mainly responsible for the lack of fit of the global non-spatial model, following Meredith’s (2008) suggestion. One sampling site was removed accordingly, corresponding to a site within the XER study area with an unexpectedly high number of jaguar’s encounters. Goodness-of-fit test results are shown in Table A4.

The spatial site-use modelling was done in three steps. Firstly, we modelled the detection probability accounting for each or both detection covariates (i.e., effort and study area) while excluding all site covariates and keeping the site-use probability constant (MacKenzie et al., 2006). Secondly, and to identify the best-supported scale for each focal species of the non-forested/deforested occupancy covariate, we tested univariate models for each of the scales and thresholds while fixing detection covariates based on the results of the previous step. Thirdly, to reduce the number of covariates, we ran univariate RSR models and discarded those covariates for which 1) the null model performed better (i.e., lower PPLC), and had no apparent effect on site-use probability (i.e., 95 % credible intervals include zero), or 2) the MCMC chain did not reach convergence after a single run (see below the details of the control parameters of the MCMC). Afterwards, we ran all possible RSR multivariate models and selected the best based on PPLC. It is unknown how well the PPLC performs in hierarchical models, seemingly being biased towards complex ones (lower PPLC estimates; Broms et al., 2014). Nonetheless, this was not invariably the case for our dataset, insofar as in many cases simple models were selected over more complex ones (Table A8). Furthermore, while PPCL includes a goodness-of-fit component in its calculation, its value does not quantify whether the model actually fits the data (Broms et al., 2014). However, and as shown by Broms et al. (2014), model selection using PPCL was consistent with other model selection criteria used in Bayesian inference, resulting in similar patterns and parameter estimations. Therefore, we limited our analysis to the use of restricted spatial regression models.

For each univariate RSR model, we ran a single MCMC chain for 50,000 iterations, with a burn-in of 10,000 and thinning rate of 5, for a total posterior sample of 8,000 datapoints (Johnson et al., 2013). Model’s convergence among posterior samples was checked at all stages by visual inspection of the trace plots and using the output of the Geweke’s diagnostic test. This step was done using the package “coda” version 0.19–3 (Plummer et al., 2006) in R 3.6.2 (R Core Team, 2017).

After identifying the best performing multivariate spatial model, we ran three MCMC chains for 175,000 iterations each, with a burn-in of

75,000 and thinning rate of 5, to increase the effective posterior sample size, and check for consistency on the parameters estimates. This was done by visual inspection of the trace plots and estimating the R-hat convergence diagnostic, using the R package “wiqid” version 0.2.3 (Meredith, 2020). The median untransformed beta coefficients and 95 % credible intervals (CRI) estimates were calculated for each MCMC single-chains and the average median upon the three MCMC single-chains was used to examine the strength and direction of the effect of each covariate on the species’ site-use probability. We considered site-use covariates as important if the 95 % CRI excluded zero.

3. Results

Among all four study species, tapir was, by far, the species with the highest number of independent detections, as well as being detected at the highest proportion of sampling sites (e.g., naïve occupancy) throughout the study area. This is followed in decreasing order by jaguar, white-lipped peccary, and giant armadillo (Table 2). Parameter estimates obtained from the best performing SRS model for each species where consistent and reached convergence in all cases (Fig. A1).

3.1. Detection probability

Based on the best performing models, species’ detection probability was set differently for each of the species. For the giant armadillo, it was set as constant (i.e., no detection covariate), while for the white-lipped peccary, tapir and jaguar, sampling effort, as the total number of days comprising each sampling occasion, was included as detection covariate. For the latter two species, study area was also supported as a detection covariate (Table A5). Sampling effort, as the number of days included in the last sampling occasion (max. 20-days), consistently exhibited a positive effect on species detection probability (Table 3). In relation to study area, a comparatively lower detection probability was estimated for the tapir in Brazil_XER, and a higher detection probability was estimated in GBR and SBR in Brazil, and in SAM and SIR in Peru. For the jaguar, the lowest detection probabilities were estimated in Brazil at the GBR, SBR, TMES, UAT and XER study sites (Table 3).

3.2. Site-use probability

In terms of the site-use covariates, and particularly in relation to the proportion of non-forested/deforested areas (DEF), both the threshold of forest/no-forest and the scale were species-dependent. For the giant armadillo and the tapir, we used the DEF at a 75 % threshold and at a 1 km and 500 m scale, respectively, while for the remaining species, we used a 90 % threshold at a 250 m scale (Table A6). For the multivariate spatial occupancy models, we discarded those covariates that did not exhibit an apparent effect on the species’ site-use and did not increase the predictive performance of the model relative to the null model (Tables A7 and A8).

For each study species, the best performing model provided strong evidence of spatial autocorrelation, being the scalar precision parameter

Table 2

Summary of the detection history and naïve occupancy estimates for each focal species.

Focal species	Total sampling sites	20-days sampling occasions	Total detections	Naïve occupancy
<i>Tayassu pecari</i>	932	3,020	133	0.14
<i>Priodontes maximus</i>	932	3,020	104	0.11
<i>Tapirus terrestris</i>	932	3,020	294	0.32
<i>Panthera onca</i>	931	3,015	180	0.19

Table 3

Parameter estimates, standard errors, and 95 % CRI based on the best restricted spatial regression (RSR) model for each species. In bold are depicted the parameters for which the estimated 95 % CRI excluded zero.

	<i>Tayassu pecari</i>			<i>Priodontes maximus</i>			<i>Tapirus terrestris</i>			<i>Panthera onca</i>		
	Mean	SE		Mean	SE		Mean	SE		Mean	SE	
Site-use probability (ψ)	0.197	0.091		0.369	0.088		0.612	0.113		0.572	0.148	
Modelled parameters	β^*	2.5 %	97.5 %	β^*	2.5 %	97.5 %	β^*	2.5 %	97.5 %	β^*	2.5 %	97.5 %
Site-use covariates												
Intercept	-1.527	-1.825	-1.254	-0.510	-0.882	-0.061	0.325	0.073	0.623	0.221	-0.302	1.079
PA	NA	NA	NA	NA	NA	NA	0.305	-0.037	0.652	0.146	-0.201	0.503
Indigenous	0.287	0.019	0.587	NA	NA	NA	NA	NA	NA	0.154	-0.499	0.755
Energy	–	–	–	–	–	–	0.039	-0.327	0.407	0.213	-0.173	0.976
Roads	–	–	–	–	–	–	0.046	-0.238	0.323	-0.096	-0.594	0.312
Fires	–	–	–	–	–	–	0.217	0.002	0.452	NA	NA	NA
Urban	0.415	0.184	0.653	0.280	0.097	0.475	–	–	–	NA	NA	NA
DEF**	NA	NA	NA	-0.751	-1.249	-0.340	–	–	–	-0.358	-0.961	-0.050
Detection covariates												
Intercept	-1.631	-2.157	-1.121	-1.244	-1.468	-1.016	–	–	–	–	–	–
SA XER***	–	–	–	–	–	–	-1.882	-2.586	-1.231	-1.861	-2.469	-1.254
SA AMA	–	–	–	–	–	–	-0.479	-1.267	0.374	-0.668	-1.541	0.226
SA AND	–	–	–	–	–	–	0.366	-0.246	1.058	0.075	-0.423	0.595
SA CAX	–	–	–	–	–	–	-0.090	-0.746	0.583	-0.635	-1.471	0.432
SA GBR	–	–	–	–	–	–	0.801	0.176	1.496	-0.818	-1.403	-0.175
SA GUY	–	–	–	–	–	–	-0.578	-1.196	0.091	0.004	-0.574	0.647
SA MAL	–	–	–	–	–	–	0.184	-0.471	0.908	-0.158	-0.698	0.402
SA MJU	–	–	–	–	–	–	0.143	-0.469	0.731	-0.523	-1.063	0.004
SA SAM	–	–	–	–	–	–	0.764	0.160	1.439	0.097	-0.411	0.621
SA SBR	–	–	–	–	–	–	0.769	0.081	1.523	-1.386	-2.462	-0.390
SA SIR	–	–	–	–	–	–	0.738	0.024	1.497	0.493	-0.061	1.070
SA TIP	–	–	–	–	–	–	0.134	-0.786	1.209	0.011	-0.745	0.803
SA TMES	–	–	–	–	–	–	0.595	-0.048	1.303	-0.853	-1.463	-0.218
SA UAT	–	–	–	–	–	–	-0.101	-0.780	0.623	-0.946	-1.676	-0.221
Effort	0.066	0.040	0.094	–	–	–	0.056	0.040	0.073	0.059	0.036	0.083
Spatial variance parameter (τ)	0.096	0.028	0.164	20,388	0.048	40,776	17,354	0.080	34,708	46,483	2,217	90,749

Site-use covariates: distance to boundary of nearest strict protected area (PA), to boundary of nearest indigenous territory (Indigenous), to nearest energy industry (Energy; mining, hydroelectric or fossil fuels), to nearest road, to forest fires, to nearest urban area, and proportion of non-forested/deforested areas (DEF).

Detection covariates: SA stands for study area. AND includes the study sites AGU_MLC, DIA, ROM, SHIN and SHIP from Peru; GUY includes all study sites in Guyana (BER, CHE, DDA, KBO, KUS AND PAR); and SAM includes LPR and PUN study sites from Peru. Effort corresponds to total number of trap-days considered in each sampling occasion.

* Median untransformed beta coefficient.

** DEF at different GFC thresholds and scales based on the best-fitting univariate RSR model. *T. pecari*: 90 % threshold at 250 m buffer; *P. maximus*: 75 % threshold at 1 km buffer; *Tapirus terrestris*: 75 % threshold at 500 m buffer; *P. onca*: 90 % threshold at 250 m buffer.

*** XER was used as intercept when accounting for study area as a detection covariate.

(τ) in all cases different from zero (i.e., 95 % CRI did not include zero, Table 3, Fig. A1). Among all surveyed areas, the mean site-use probability estimated from the best performing spatial model followed the same pattern as the naive occupancy analysis, with the exception that the lowest value was estimated for the white-lipped peccary rather than for the giant armadillo (Table 3). Mean site-use probability among all surveys was estimated to be nearly 20 %, 37 %, 57 % and 61 %, for the white-lipped peccary, giant armadillo, jaguar, and tapir, respectively (Table 3). When considering each survey site separately, there was no apparent geographic pattern in the estimated site-use probability for any of the species (Fig. 3). In general, the highest site-use probabilities were estimated at TMES in Brazil and TIP in Ecuador, corresponding to a public and private strict nature reserves, respectively.

For the white-lipped peccary, we discarded distance to protected areas and proportion of non-forested/deforested areas from the posterior multivariate spatial analyses. Among the 32 possible models, the model with the best predictive performance included distance to urban areas and to indigenous territories (Table A8). To urban areas it showed a positive effect, meaning that the species' site-use probability increases as it gets further from these. In relation to indigenous territories, slightly higher site-use probabilities were predicted inside the territories, decreasing steadily further from their boundary (Table 3, Fig. 2). The estimated mean site-use probability was highly variable between survey sites, fluctuating between 2 % and 92 %. In general, particular high values were estimated on strict public and private nature reserves (e.g., TMES, and SBR in Brazil, TIP in Ecuador, and MAL in Peru), while lowest

values at two protected areas with sustainable use in Brazil (AMA and UAT), and two indigenous community-owned lands in Peru with an influence of colonisers, with extractive practices of natural resources, one with foreign agricultural practices as well (SHIN, and SIR, respectively; Fig. 3).

For the giant armadillo, we discarded distance to protected areas, to indigenous territories and to energy industry. The model with the best predictive performance included the distance to urban areas and proportion of non-forested/deforested areas as covariates affecting the species' site-use probability (Table A8). Proximity to urban areas exhibited a negative effect (i.e., higher probability further from urban areas), while higher site-use probability was estimated at sites with a low proportion of unforested/deforested areas (Table 3, Fig. 2). Site-use probability among survey sites was variable, fluctuating between 0.02 and 0.65. Particularly high values were estimated at sites sparsely distributed along the Amazon with different land-uses, such as the TMES in Brazil, an indigenous land in Guyana (PAR), and a small-scale productive community land in Peru (PUN). Low estimates were obtained for three productive small-scale community lands, one of Andean immigrants practicing clearance agriculture in Peru (AGU, see Serrano-rojas et al., 2022) and two, characterized by a predominant natural savannah land cover, in Guyana (DDA and KBO; Fig. 3).

For tapir, only distance to indigenous territories was discarded from the posterior multivariate spatial analyses. The model with the best predictive performance included distance to protected areas, to energy industry, to roads and to fires (Table A8). Based on the posterior

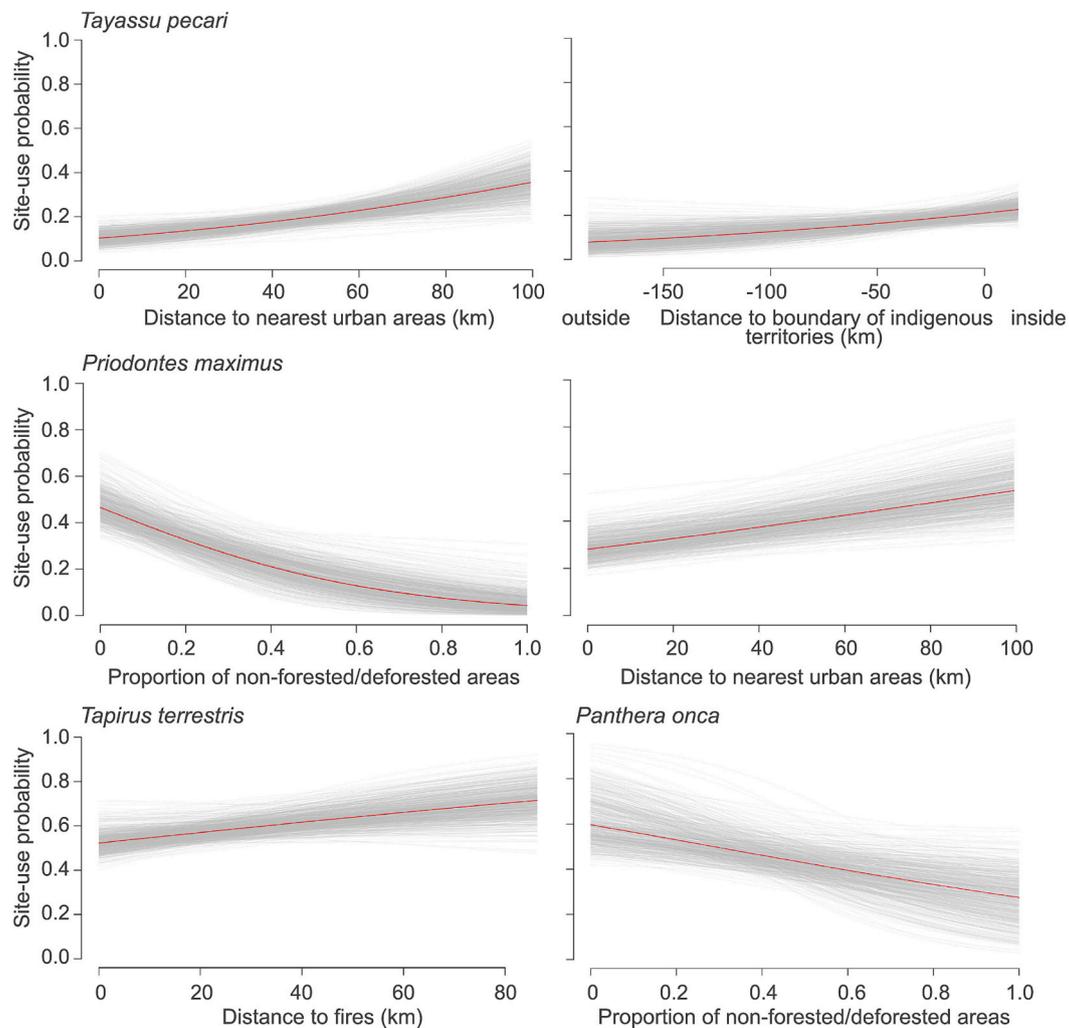


Fig. 2. Relationship of the site-use probability and the meaningful occupancy covariates for each focal species along the Amazon rainforest, based on the parameter estimation from the best performing restricted spatial regression (RSR) model. Red continuous lines correspond to the posterior median of the beta estimate, and grey lines correspond to 800 random posterior samples obtained from the three MCMC single chains. Each figure was created considering one covariate at a time. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

parameter estimates, only proximity to forest fires exhibited a marginally significant effect on the species' site-use probability; predicting a slightly higher probability further from recently burned areas (Table 3, Fig. 2). In general, tapir exhibited the highest site-use estimates and the lowest variation in site-use probability among survey sites, fluctuating between 0.41 and 0.82. Again, particularly high mean values were obtained at the TMES strict nature reserve in Brazil, as well as at the community land of PUN in Peru (Fig. 3).

Finally, for the jaguar distance to fires and to urban areas were discarded from posterior multivariate spatial occupancy modelling. Among all possible models, the one with the best predictive performance was the one considering all the other five site-use covariates (Table A8). Among these, only the proportion of unforested/deforested areas had a significant, and negative effect, estimating higher site-use probabilities at sites with high forest cover at a narrow scale (Table 3, Fig. 2). For jaguar, the variation in the estimated site-use probability between and within sites was high, fluctuating from 24 % to 78 %. Particularly low estimates were obtained at sampling sites within a highly forested indigenous community land with increasing influence of colonisers and selective logging activities, located within the Manu Biosphere Reserve in Peru (DIA; Fig. 3).

4. Discussion

Here we examined the site-use patterns of four forest-dwelling large mammals and their relationships to anthropogenic factors throughout the Amazon biome. Our results revealed that site-use patterns of four study species are correlated with human induced habitat changes, and that this correlation may differ with species. Highest site-use probability of the white-lipped peccary were estimated in strict private and public protected areas, decreasing towards urban areas and increasing slightly inside indigenous territories in comparison to the unprotected forest matrix; the site-use of giant armadillo decreased with increasing proportion of unforested/deforested areas and towards urban areas; the site-use of the lowland tapir showed a slight decrease towards burned areas; and jaguar's site-use probability decreased with increasing proportion of unforested/deforested areas.

Despite its wide distribution, the vulnerable white-lipped peccary is a rare species, highly susceptible to habitat degradation and direct persecution and hunting (Ferreguetti et al., 2018; Fragoso, 2004; Whitworth et al., 2022; Zimbres et al., 2018). Hunting pressure has been shown to be the major cause of population depletion at regional and wider scales (Bogoni et al., 2020; Peres, 1996; Peres and Palacios, 2007), so we were expecting the species site-use to be lower closer to both urban areas and indigenous territories, but this was not true for the

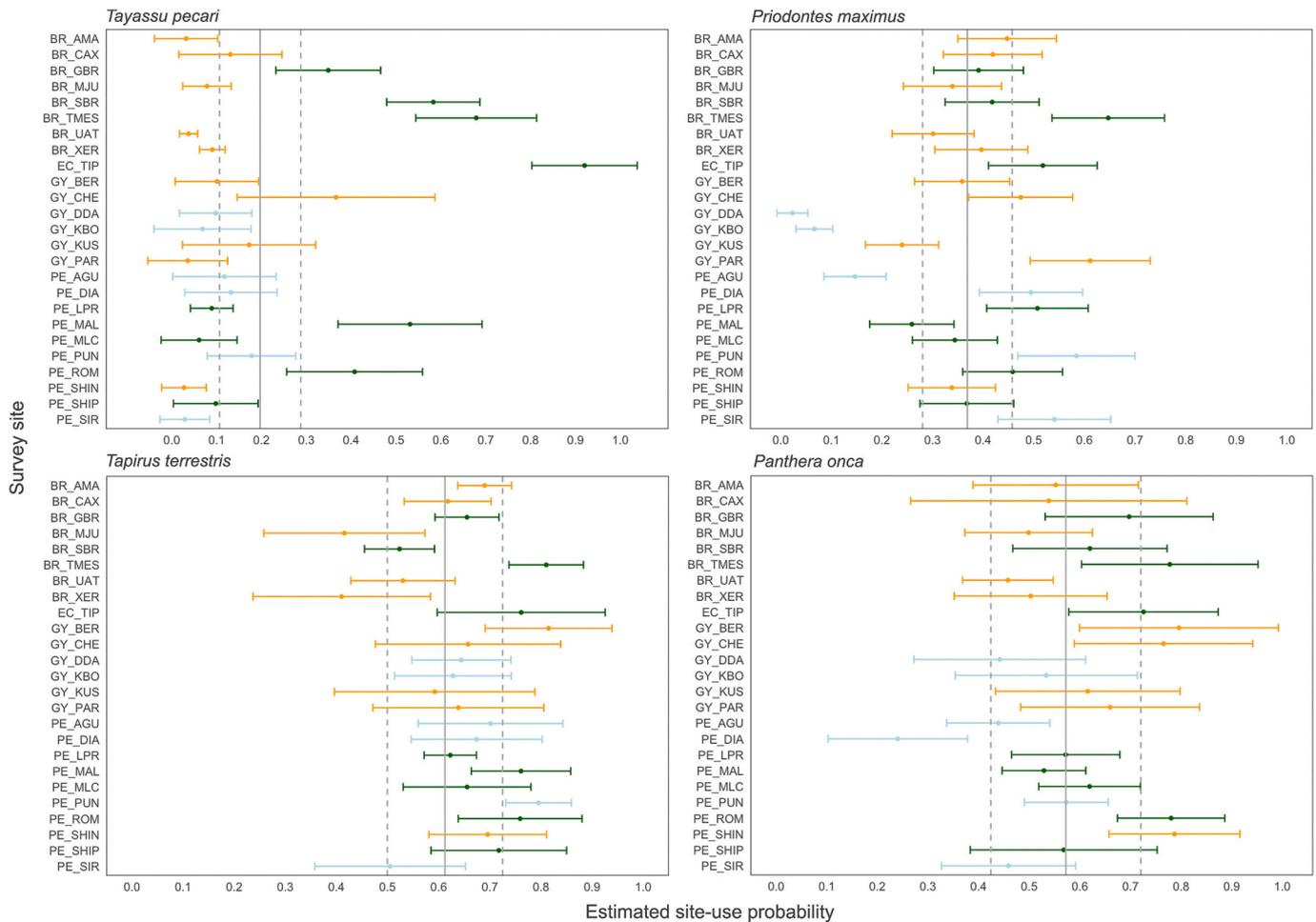


Fig. 3. Estimated site-use probability (mean and 95 % CRI) for each of the 25 study sites. Study sites are ordered alphabetically by country (Brazil-BR, Ecuador-EC, Guyana-GY and Peru-PE). Colours represent land-use types, where dark green depict public and private natural reserves with strict protection, orange to community land with sustainable use and light blue to productive community lands. Grey vertical lines correspond to the mean (continuous) and the 95 % CRI (dashed) of the overall estimated site-use probability for each species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

latter. Unlike urban areas, indigenous lands tend to be a matrix of natural habitat, with low human densities and small-scale farming, and shown to be efficient in reducing deforestation rates in the Amazon (Nepstad et al., 2006). Additionally, indigenous traditional hunting practices include selective hunting which might reduce the negative impacts of hunting. For example, indigenous groups in Guyana avoid killing the herd leader, who plays a significant role in group cohesion and orientation, and, therefore, in herd survival (Nogueira et al., 2015).

Besides the effect of hunting, other plausible, but not excluding, explanations for the opposing species site-use pattern in relation to the proximity to rural areas and indigenous territories include competition with livestock and epizootic disease (Fragoso, 2004), which might be higher closer to urban areas, and land accessibility. Peres and Lake (2003) argued that non-overexploited core populations of peccaries inside protected areas and indigenous reserves are in general larger than those distributed across the entire Amazon basin as a result of these areas being less accessible than the unprotected forest matrix. Within indigenous lands, contrasting trends in peccaries' populations have been evidenced at local and regional scales (Abrahams et al., 2017; De Souza-Mazurek et al., 2000; Peres, 1996; Shaffer et al., 2017) that might be explained by differences in land management, governance, human density, and traditional practices of wildlife-use among Amazon tribes. Such differences were not addressed here and needs further attention.

Apart from the latter, it is worth mentioning that there is evidence of very high abundances of peccaries in forested areas associated with

agriculture expansion, where the species has been considered a pest (Lima et al., 2019), and that natural large-scale boom-bust population cycles have been documented for the species during the last century, seemingly being a major cause of the sudden disappearance and drastic fluctuations of wild populations throughout the continent (Fragoso et al., 2020).

The vulnerable giant armadillo has been described as a forest specialist, exhibiting low population densities and rarely encountered (Anacleto et al., 2014; Noss et al., 2004; Silveira et al., 2009). While this species is positively associated with natural open areas at a National Park within the Cerrado biome (Anacleto et al., 2014; Silveira et al., 2009), our results indicate that, throughout the Amazon biome, the species is a forest dweller, and its occurrence is negatively impacted by the proportion of unforested/deforested areas. Moreover, and congruent with other studies, proximity to urban areas manifests as a negative factor for giant armadillos, possibly because of direct hunting (Abrahams et al., 2017; Trujillo and Superina, 2013). While at a local scale the species might benefit from protected areas (Silveira et al., 2009), proximity to these did not appear as an important site-use predictor at a landscape scale. In summary, our results suggest that the giant armadillo in the Amazon rainforest is rare, restricted to primary forest, and primarily threatened by deforestation, and possibly by habitat degradation, human perturbation and hunting pressure coming from urban people. Indigenous people, at least those from Guyana, mentioned that the species was usually seen and hunted in savannahs and natural open

areas. Therefore, its tight association with forested areas in the Amazon seems to be a behavioural response to reduce vulnerability, rather than an ecological response; but this needs further studies.

The tapir is the largest terrestrial herbivore throughout the Amazon, and while tolerant to some habitat degradation, it is susceptible to deforestation, road infrastructure, human settlements and direct persecution, being one of the most hunted mammals for meat (De Souza-Mazurek et al., 2000; Espinosa et al., 2018; Ferregueti et al., 2017; Peres and Nascimento, 2006; Varela et al., 2019). The tapir's site-use was not correlated to proximity to urban areas, roads nor indigenous territories, but rather, distance to forest fires was revealed as an important factor affecting the species' occurrence in the Amazon. The impact of forest fires on wild populations merits further research (Adeney et al., 2009; Schroeder et al., 2005). However, a recent study designed to evaluate the role of the lowland tapir in dispersing seeds to a recurrently burned and undisturbed Amazonian forest bordering a soybean field, suggested that the species uses this twice as often as undisturbed forested areas, as a consequence of greater availability of palatable plants during early-successional stages (Paolucci et al., 2019). In contrast, our findings suggest that tapirs are responding negatively to proximity to burned areas. This seems explicable insofar as, broadly speaking, wildfires along the Amazon are inextricably linked to deforestation processes, preceding agro-industrial expansion and colonization (Adeney et al., 2009; Escobar, 2019), rather than forest successional regeneration.

The jaguar is the apex terrestrial predator in the Amazon and has been thought to be continuously distributed throughout this vast rainforest. Congruent with other studies, our results showed that forest cover is a main factor influencing the species-habitat association (De Angelo et al., 2011; de la Torre et al., 2017). Previous research revealed that jaguar site-use varies as a function of forest availability, avoiding more strongly unforested areas in forested landscapes (Morato et al., 2018). Forest cover has been shown to be a main factor shaping the site-use patterns of other large felids (Macdonald et al., 2019; Sunarto et al., 2012; Tan et al., 2017), possibly due to the availability of prey and shelter (Santos et al., 2019; Schuette et al., 2013). In sum, results showed that, throughout the Amazon biome, deforestation at a site scale represents a major threat to this forest-dwelling species (Haag et al., 2010; Olsoy et al., 2016).

The probability of detecting a species primarily depends on the time invested in searching, the expertise in terms of knowledge of the species ecology and the sampling method used, as well as the species' density/abundance. The likelihood is that the better one understands a species, the more effective the effort to detect it becomes. As expected, species' detection probabilities were maximized by complete sampling occasions (i.e., 20-days), decreasing proportionately to the reduction in days. This was true for all but the secretive giant armadillo whose occurrence has been described as rare and sporadic (Aguilar, 2004). Detection probability of tapir and jaguar also varied as well in relation to study area. Besides differences in trapping protocols and sampling design among these areas, variation in detection probabilities might also be the result of differences in species abundances among areas, which could be tested by modelling count data. Unfortunately, when testing for the effect of study area as an observation covariate, the RSR models gave spurious estimates as a result of overparameterization and non-convergence due to the low detection rates among these two species.

In all cases, the predicted site-use probability was significantly higher than the naïve occupancy, supporting the hypothesis of imperfect detection among all study species and reinforcing the benefit of using occupancy models over traditional species distribution models in studying species-habitat relationships. Moreover, and in agreement with other studies (Penjor et al., 2018; Poley et al., 2014; Tan et al., 2017; Wang et al., 2019), our results showed a strong spatial effect on the species-habitat associations and thus, highlight the need to explicitly account for spatial autocorrelation to avoid violating the independence assumption of spatial modelling based on large and heterogenic

datasets, such as the ones included here. Essentially, as species home range size increases, the scale of non-independence increases, clearly evidenced by the jaguar which exhibits the largest home ranges of these four study species and for which the RSR model estimated a notably large spatial variance parameter (Tables 3 and A3); a benefit of treating species independently compared to ad-hoc or by-catch multispecies models that assume cameras are independent for all species, especially for studies that have not achieved independence in their design.

Our findings contribute to understand how human-induced environmental changes influence the site-use patterns of these four large mammals. Even though all four are forest-dwelling mammals, each responded differently to these changes. This study was mainly restricted to areas under strict protection, such as national protected areas and private reserves, to indigenous lands with sustainable hunting and logging, and to native community lands under small-scale agriculture, and no clear site-use pattern was observed in this respect, except for the white-lipped peccary exhibiting the highest site-use probabilities within strict protected areas (public and private). Private reserves, through their strict land protection, and indigenous and local communities, through their traditional land-use practices, have been shown to be efficient in reducing deforestation and contributing to the conservation of biodiversity (Adeney et al., 2009; Dawson et al., 2021; Gadgil et al., 1993; Guerrero-Pineda et al., 2022; Nepstad et al., 2006; Rylands and Brandon, 2005; Schwartzman et al., 2000); as supported by our results. Research initiatives away from remote wilderness areas, such as those under economic land concessions or industrial agriculture, are urgently needed and would be hugely informative. Additionally, there is a need for landscape-level sustainable-use plans to prevent, rather than merely to mitigate, biodiversity loss throughout the Amazon rainforest, for which the next steps will be to expand our approach to the other major mammal species in the system and to identify common core areas for conservation and corridors to be prioritized.

Great efforts have been devoted to the creation of strict protected areas and natural reserves in the Amazon rainforest; however, isolated and scattered natural protected areas are insufficient (Soares-Filho et al., 2006; Sobral-Souza et al., 2018), and as a whole, these may not be configured to deliver wild population connectivity and genetic diversity for protecting the integrity of the Amazon rainforest. As stated by Peres and Terborgh (1995), even if public reserves throughout the Amazon are decreed on paper, due to weak capacity of the national governmental agencies, ineffective law enforcement, and lack of financial and human resources, too many of these reserves are far from fulfilling the conservation goals for which they were created. This could explain why, at a biome scale, proximity to strict protected areas showed to be irrelevant to the site-use patterns of these four species.

Conserving the integrity of the Amazon rainforest requires the holistic integration of a huge network of strategically located expansive protected areas (> 1 million ha; Laurance, 2005; Peres, 2005) connected by viable biological corridors. The success of such a landscape-scale conservation strategy will depend heavily on transboundary protection measures (DeMatteo and Loiselle, 2008; Thornton et al., 2020), political will (Laurance, 2005) and strong governance. Indigenous people play an important role in the protection of forests and, consequently, in wildlife conservation. Therefore, conceding the land rights to native communities, and recognizing them as environmental authorities within their ancestral territories can contribute to strengthening governance in the Amazon (Dawson et al., 2021; Guerrero-Pineda et al., 2022; Schwartzman and Zimmerman, 2005).

Colonization implies fires, deforestation, and human settlement (Laurance et al., 2004), all of which were identified as detrimental to these forest dwelling species, and represents a latent and major threat to the Amazon Biome. Therefore, land acquisition and economic development need to be limited and oriented by the UN sustainable development goals to ensure the long-term protection of the Amazon. Social, environmental and economic benefits coming from the standing forests needs to be encouraged and prioritized among private properties (e.g.,

REDD+/carbon credits), rather than those coming from land transformation, industrialization and the exploitation of natural resources (Soares-Filho et al., 2006).

To meet the Amazonian countries' financial needs to deliver these environmental goals, investment from the private sector and from developed countries will be required. The latter might necessitate the direct payment for the global ecosystem services provided by the Amazon (i.e., water regulation, carbon capture and storage, climatic stability), and remission of national foreign debts in recognition of, or against pledges of, steps to protect and restore the Amazon ecosystems. All these interventions must be informed by socio-ecological data.

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.

Data availability

Data will be made available on request.

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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.2023.109904>.

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