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RESEARCH ARTICLE

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# Estimating species distribution from camera trap by-catch data, using jaguarundi (*Herpailurus yagouaroundi*) as an example

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## Abstract

**Aim:** Planning conservation action requires accurate estimates of abundance and distribution of the target species. For many mammals, particularly those inhabiting tropical forests, there are insufficient data to assess their conservation status. We present a framework for predicting species distribution using jaguarundi (*Herpailurus yagouaroundi*), a poorly known felid for which basic information on abundance and distribution is lacking.

**Location:** Mesoamerica and South America.

**Time Period:** From 2003 to 2021.

**Taxa:** *Herpailurus yagouaroundi*.

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Bart J. Harmsen and Sara Williams contributed equally to the study.

For affiliations refer to page 15.

**Methods:** We combined camera-trap data from multiple sites and used an occupancy modelling framework accounting for imperfect detection to identify habitat associations and predict the range-wide distribution of jaguarundis.

**Results:** Our model predicted that the probability of jaguarundi occupancy is positively associated with rugged terrain, herbaceous cover, and human night-time light intensity. Jaguarundi occupancy was predicted to be higher where precipitation was less seasonal, and at intermediate levels of diurnal temperature range. Our camera data also revealed additional detections of jaguarundis beyond the current International Union for Conservation of Nature (IUCN) range distribution, including the Andean foothills of Colombia and Bolivia.

**Main Conclusion:** Occupancy was predicted to be low throughout much of Amazonian lowlands, a vast area at the centre of jaguarundi known range. Further work is required to investigate whether this area represents sub-optimal conditions for the species. Overall, we estimate a crude global jaguarundi population of 35,000 to 230,000 individuals, covering 4,453,406 km$^2$ of Meso- and South America at the 0.5 probability level of occupancy. Our current framework allows for an initially detailed, well-informed species distribution that should be challenged and refined with improved habitat layers and additional records of jaguarundi detection. We encourage similar studies of lesser-known mammals, pooling existing by-catch data from the growing bank of camera-trap surveys around the world.

**KEYWORDS**
By-catch data, Camera trap, Felids, Neotropics, Occupancy modelling, Species distribution

## 1 | INTRODUCTION

Species conservation action and management require basic knowledge of the distribution and abundance of the target species. However, such basic information is lacking for the majority of mammalian species, and assessments of threats and extinction risks are often based on expert opinion or unvalidated field methods, rather than empirical data (e.g. the IUCN Red List, Burgin et al., 2018, IUCN 2023 accessed 1-Feb-2023). Data on abundance and distribution are notably scarce for many small- and medium-sized tropical mammal species (Bachman et al., 2019). A good example is the jaguarundi (*Herpailurus yagouaroundi*), an understudied small felid, ranging throughout Latin America (Caso & Oliveira, 2015). Here, we assess the habitat associations, predict the geographic range, and estimate global population abundance of the jaguarundi.

Despite jaguarundis being the most widespread small felid species in the Western Hemisphere (Caso & Oliveira, 2015), a review of the ecology and status of jaguarundis by Giordano (2016) highlighted the paucity of jaguarundi-specific studies and the lack of information regarding species status throughout its range. Jaguarundis lack the necessary traits to attract research focus: the species is small-sized (3–8 kg), not particularly charismatic, not associated with any economically important zoonosis, generally resides in range countries with limited economic capacity for ecological research, and individuals are not uniquely distinguishable from photo records (Caso & Oliveira, 2015; Giordano, 2016; Tensen, 2018). Evidence suggests that jaguarundis occur in a range of habitats with dense undergrowth, and are present in mixed landscapes with low intensity agriculture, frequently co-occurring with other carnivore species associated with human-disturbed lands (Giordano, 2016). However, the extent to which they use different habitats or tolerate human activities is poorly known (Giordano, 2016). As one of the few fully diurnal cat species (Giordano, 2016), they are sighted regularly, compared with sympatric cat species, giving the perception that they are common (pers. obs. B.H., R.F.). The most recent IUCN assessment of jaguarundi status and extinction risk indicated that, while the species may be Near Threatened, data were insufficient to make this judgement range wide (Caso & Oliveira, 2015). Therefore, the assessors listed the species as Least Concern, with the caveat that it should be regularly revised as more data become available.

The advent of camera traps has greatly facilitated the study of cryptic, terrestrial mammals, especially in the tropics (O'Connell et al., 2010), allowing the study of previously unknown species. Camera-trapping effort in the Neotropics has increased since the turn of the twenty-first century, most notably for monitoring jaguars (*Panthera onca*, e.g. Foster et al., 2020; Harmsen et al., 2017; Jędrzejewski et al., 2018; Silver et al., 2004) but also for keeping track of the forest mammal community in general (i.e. TEAM network, Ahumada et al., 2011). The wide deployment of camera grids for estimating jaguar density (see Foster et al., 2020 for an overview) has resulted in several range and region-wide assessments of jaguars within a single analytical framework (e.g. Jędrzejewski et al., 2018; Paviolo et al., 2016). Although mostly deployed for jaguars, these multitude of camera studies have detected many species beyond the largest cat of the Americas.

Camera traps log detections of all species that trigger the sensors, and thus provide considerable data on non-target species ("by-catch" data). Many of these species do not have visually unique individual features necessary for mark–recapture abundance estimation. In such cases, an occupancy modelling framework (MacKenzie et al., 2002), using presence/absence data and sampling effort, can provide a robust estimate of the species' probability of resource use across the landscape. This approach has allowed range-wide assessments of the habitat associations and distribution of previously understudied species, including two threatened species, the white-lipped peccary (*Tayassu pecari*, Thornton et al., 2020) and the Baird's tapir (*Tapirus bairdii*, Schank et al., 2020).

Detections of jaguarundis by camera traps are notably rare when compared with sympatric felids, white-lipped peccary or Baird's tapir (e.g. Carrera-Treviño et al., 2018; Di Bitetti et al., 2010; Gil-Sánchez et al., 2021; Maffei et al., 2007; Schank et al., 2020; Thornton et al., 2020). Recent efforts to assess jaguarundi abundance and distribution have been mainly restricted to local density estimates (Ecuador, Gil-Sánchez et al., 2021), and presence-only data that do not account for sampling effort (da Silva et al., 2016; Espinosa et al., 2018). Presence-only methods assume equal sample effort and detectability and are biased if these assumptions are not met. Grattarola et al. (2023) tried to account for this by modelling "presence-only" data in combination with an absence index with unknown search effort. Occupancy modelling explicitly accounts for detection probability and sampling effort (Guillera-Arroita et al., 2014). Failure to account for detection probability and sampling effort is compounded when records are sparse and detection probability is low (Guillera-Arroita et al., 2014).

In this study, we use an occupancy modelling framework and camera-trap data from across the species range, to predict relative probability of jaguarundi habitat use and distribution. Given the low detection records of jaguarundis in the literature, and the need to incorporate sampling effort to account for imperfect detection, we only include camera survey data with known sampling effort. This approach allows us to quantify the relative probability of occupancy and absence, allowing inference about jaguarundi habitat use, geographic range, and a first crude estimation of global population abundance based on our predicted area of occupancy (e.g. Steenweg et al., 2018, 2019). We consider our current effort the most thorough study, to date, on jaguarundi status across its range.

## 2 | METHODS

### 2.1 | Study area

All authors in this study contributed raw data from 182 surveys in 13 range countries (Mexico, Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Guyana, Suriname, and Brazil). Surveys were conducted between 2003 and 2021. Sampling was highly skewed towards Mesoamerica, with higher survey effort compared to other regions (Table 1; Figure 1). Our study concerned prediction of jaguarundi range, and thus covered the known Neotropical jaguarundi range of Meso- and South America, however our sample lacked representation from the Amazon region, which may be considered the spatial core of jaguarundi distribution range (Caso & Oliveira, 2015, Figure 1).

### 2.2 | Data preparation

All data were collapsed into a single data-frame, where each row represented: a camera location with associated World Geodetic System (WGS 84) lat–long coordinates, name of survey, country of origin, and detection or non-detection of jaguarundi within a single 24 h day (detection =1, non-detection = 0). Each row contained covariate information relating to habitat type, climate conditions, and human disturbance. As camera-trap researchers usually do not gather habitat or environmental information around camera locations in a standardised fashion, we were limited to the use of range-wide remote-sensing data, overlaying map data with camera locations. As this was an exploratory analysis, we used an extensive array of spatial covariates ($n = 19$) that we expected would influence carnivore or mammal occupancy based on previous studies (e.g. Jędrzejewski et al., 2018, see Tables 2 and S1). Additional information about the covariates (i.e. annual variation, data source, abbreviated name notations) is provided in Tables 2 and S1. The habitat, climate, and human influence conditions around the camera locations did not represent the full range of conditions found across the known range of the species. For comparison, we provide in Table S2 the covariate range values across the sampled sites, together with the range values across the IUCN jaguarundi distribution range (IUCN distribution map from Caso & Oliveira, 2015). Figure S1 provides a visual "heat map" representation, showing how the covariates vary across the continents.

We overlaid the area with a sampling grid of 6 × 6 km cells (36 km$^2$, hereafter we shall use the term "site" to refer to a sample grid cell). Within occupancy modelling, the choice of site cell size can be somewhat arbitrary. Some studies have based cell size on the conservative lower end of home range size of the target species (e.g. 36 km$^2$ for white-lipped peccary (Thornton et al., 2020) or 10 km$^2$ for jaguars (Petracca et al., 2018)). To date, range size estimation for jaguarundi has been anecdotal and highly variable, and we chose 6 × 6 km to reflect a reasonable home range size for a small Neotropical cat (Sunquist & Sunquist, 2002). We pooled all camera data within a site and used the site as the sampling unit. As the number of stations and sampling effort (number of trap-nights) varied between sites, we used these as covariates when modelling detection probability.

### 2.3 | Analysis

None of the surveys included here were originally designed to monitor jaguarundis specifically. Furthermore, the dataset combined

**TABLE 1** Camera-trapping sampling effort across 13 countries included in range-wide occupancy analysis of jaguarundis (ordered by latitude).

| Country | Camera stations | Sites[a] | Trap-nights | Jaguarundi detections | Detection rate (unique detections/100 nights) | Year range | Years surveyed | Distinct surveys | Survey length range (days) |
|---|---|---|---|---|---|---|---|---|---|
| Mesoamerica | | | | | | | | | |
| Mexico | 314 | 80 | 24,442 | 47 | 0.192 | 2015–2018 | 3 | 3 | 97–114 |
| Belize | 688 | 93 | 143,140 | 347 | 0.242 | 2003–2020 | 18 | 46 | 56–464 |
| Guatemala | 25 | 11 | 1418 | 5 | 0.353 | 2014–2017 | 4 | 5 | 40–82 |
| Honduras | 83 | 33 | 4530 | 26 | 0.574 | 2011–2019 | 7 | 18 | 12–126 |
| El Salvador | 136 | 9 | 5360 | 7 | 0.131 | 2019–2019 | 1 | 3 | 74–210 |
| Nicaragua | 101 | 41 | 9326 | 12 | 0.129 | 2009–2012 | 4 | 1 | 1093–1093 |
| Costa Rica | 526 | 97 | 40,155 | 109 | 0.271 | 2011–2020 | 10 | 9 | 114–296 |
| Panama | 265 | 24 | 28,324 | 36 | 0.127 | 2011–2020 | 9 | 49 | 19–267 |
| South America | | | | | | | | | |
| Colombia | 518 | 57 | 28,509 | 92 | 0.323 | 2012–2018 | 6 | 11 | 49–228 |
| Venezuela | 525 | 95 | 23,157 | 31 | 0.134 | 2011–2014 | 4 | 13 | 28–240 |
| Guyana | 307 | 51 | 11,659 | 10 | 0.086 | 2011–2015 | 5 | 8 | 39–174 |
| Suriname | 16 | 3 | 23,898 | 56 | 0.234 | 2013–2017 | 5 | 5 | 195–365 |
| Brazil | 352 | 68 | 41,990 | 106 | 0.252 | 2017–2021 | 5 | 11 | 57–822 |
| Total | 3856 | 662 | 385,908 | 884 | | 2003–2021 | 81 | 182 | 12–1093 |

[a] Site" refers to $6 \times 6\,\text{km}^2$ grid cell containing at least one camera-trap station.

FIGURE 1 Location of camera-trap stations (blue triangles) used for estimating jaguarundi occupancy overlaid with the current predicted jaguarundi range in beige (Caso & Oliveira 2015); red line indicates country borders.

projects with disparate survey efforts in both space and time, with considerable variation in timing and duration (i.e. surveys were conducted throughout the year and varied in duration, ranging between 30 and 365 days). Therefore, we explored a variety of modelling approaches using extensions to the standard single-season occupancy model (MacKenzie et al., 2002), including stacked (e.g. Fuller et al., 2016; Linden & Roloff, 2013), autologistic (e.g. Tingley et al., 2016), continuous-time multiscale (Emmet et al., 2021), dynamic multi-season models (MacKenzie et al., 2003), and spatial occupancy models (Doser et al., 2022).

### 2.3.1 | Occupancy analysis

We found that the stacked occupancy model implementation best accommodated our constraints and survey variability. This

TABLE 2 Nineteen different covariates hypothesised to affect jaguarundi occupancy: seven variables describing general plant growth and productivity (noted as (P) behind abbreviation), one human influence variable (noted as (H) behind abbreviation), eight bioclimatic variables (noted as (C) behind abbreviation), and three terrain variables (noted as (T) behind abbreviation).

| Category | Full covariate name | Abbreviated name for figures | Description | Varies across years |
|---|---|---|---|---|
| Surface vegetation and ground cover | Perc. tree canopy | Veg % Tree (P) | Amount of pixels classified as treed | Yes |
| | Perc. non-tree vegetation | Veg % Bush (P) | Amount of pixels classified as vegetation but non-treed | Yes |
| | Perc. non-vegetated | Veg % Bare (P) | Amount of pixels classified as bare ground | Yes |
| | Forest cover | Veg % Forest (P) | Forest canopy closure vegetation taller than 5 m | Yes |
| Greenness and production | Enhanced vegetation index | Prod EVI (P) | Quantifies vegetation greenness while correcting for atmospheric conditions and background canopy | Yes |
| | Normalised difference vegetation index | Prod NDVI (P) | Quantifies vegetation greenness | Yes |
| | Net primary productivity | Prod NPP (P) | Difference between the amount of carbon produced through photosynthesis (gross primary production (GPP)) and the amount of energy that is used for respiration | Yes |
| Human development | Harmonised global night-time light intensity | Human light (H) | Measure of human activities associated with electricity consumption and urbanisation | Yes |
| Bioclimatic variables | Rainfall per year | Rain per year (C) | mm | Yes |
| | Annual mean temp. (1970–2000) | Temp µ year (C) | BIO 1 – Mean of average monthly temperatures | No |
| | Annual mean diurnal temp. range (1970–2000) | Temp range1 (C) | BIO 2 – Mean of the monthly temperature ranges (monthly maximum minus monthly minimum) | No |
| | Annual temp. range (1970–2000) | Temp range2 (C) | BIO 7 – Range of temperatures from minimum temperature of the coldest month to maximum temperature of the warmest month | No |
| | Temp. seasonality (1970–2000) | Temp Season (C) | BIO 4 – Temperature variation based on the standard deviation of monthly temperature average | No |
| | Isothermality (1970–2000) | Temp isoth. (C) | BIO 3 – Day-to-night temperature variation relative to the summer-to-winter temperature variation | No |
| | Annual precip. (1970–2000) | Rain year (C) | BIO 12 – Sum of monthly precipitation | No |
| | Precip. Seasonality (1970–2000) | Rain season (C) | BIO 15 – Variation in monthly precipitation totals | No |
| Terrain | Elevation | Elevation (T) | Elevation above sea level | No |
| | Slope | Slope (T) | Ratio of vertical change to horizontal change | No |
| | Terrain ruggedness index | Ruggedness (T) | Variance in elevation between a central pixel and surrounding pixels | No |

*Note*: For nine variables, we used year-specific data to the closest year of the camera survey when surveys were conducted at particular sites (noted with "Yes" in the column "Varies across years"), while "No" in this column indicated the value was considered constant. For the climate variables, only Rainfall varied per year, all other bioclimatic variables were averages of the annual records from 1970 to 2000.

model allowed us to include the multi-year surveys conducted at several sites within a single-season occupancy model. Here, a single-season occupancy model is fit but the combination of site and year (hereafter "site-year") becomes the sample unit used for occupancy probability, with each year represented as a separate survey (site-year). We used year-specific values per site-year for nine of the covariates, matching environmental conditions with the year a survey was conducted (see Table 2). A random effect for site was incorporated in the model to avoid artificially deflating variance and account for non-independence between repeated surveys that occur at the same site. We used a 7-day sampling occasion (i.e. collapsed 7 days into one encounter occasion), such that the first day of the first sampling occasion began on whatever calendar date a camera became operational at any given site. For 11 covariates, we hypothesised that a quadratic relationship, rather than linear, might have a better fit, with a peak in occupancy at an intermediate value of the covariate (e.g. minimal occupancy at temperature extremes, maximal occupancy at mid-level temperatures). We therefore assessed the quadratic relationship for 11 climatic, elevation-derived, and human development covariates. We centred and scaled all covariates before model fitting, using a Z transformation, using R (R Core Team., 2022), resulting in all covariate values having a mean of 0 and a standard deviation (SD) of 1.

We used a multi-stage process to determine the final model. We first tested if sampling effort (i.e. the number of trap-nights per sample occasion) and the number of camera stations in each occasion (both log-transformed) had an effect on the probability of detection by fitting models with detection covariates but constant occupancy (i.e. the null model Pr(occ) ~ 1). Using the best-fit detection model, we ran models for each occupancy covariate individually (single covariate models). For the covariates listed above, we assessed both a linear relationship and a quadratic relationship and compared these models using expected log pointwise predictive density (ELPD), with higher values of ELPD indicating a more supported model (Vehtari et al., 2017). We considered a difference of 4 points to be significant for these comparisons and otherwise chose the more parsimonious (linear) model. We then retained covariates, either linear only or linear and quadratic depending on the best fit, for which the posterior distribution did not cross 0 and were not highly correlated (> 0.6) at the 90% credible interval (CI) for the global model. Figure S2 provides additional information on how all the 19 covariates were correlated with each other across the continent.

To assess the robustness of our model outcome, we equally ran an alternative model set up, using a spatial occupancy model implementation, using the spOccupancy package in R (Doser et al., 2022; R Core Team, 2022). While our stacked model accounted for autocorrelation, using a random effect for site, the spOccupancy package allows the inclusion of spatial random effect. We used the same workflow as described above and provide results in a supplementary section (see Supplement: spatial occupancy results).

### 2.3.2 | Prediction

Using our global model, we predicted the probability of jaguarundi occupancy using mean point estimates for occupancy and covariate coefficient parameters. As we created prediction maps outside our study area with covariate values sometimes exceeding or falling below the values found within our surveyed areas, we capped the covariate values to the maximum or minimum as found in our surveyed areas to avoid overprediction when extrapolation to areas where values exceeded or went below the maximum or minimum values for our survey areas. We used an external dataset to validate our predicted occupancy probability across jaguarundi range as predicted from our final model. The recently published dataset by Nagy-Reis et al. (2020) contains presence records from a variety of Neotropical carnivores. We filtered this external dataset to include only camera surveys and used only one record of jaguarundi per unique coordinate location ($n = 1262$). We binned our prediction layer into 10 quantiles and extracted the categorised predicted probability of occupancy for each observed jaguarundi occurrence from the external dataset. We evaluated Spearman's rank correlation (rho or $r_s$) based on the number of occurrences that fell within each predicted probability bin.

We used three probability thresholds (0.6, 0.75, and 0.8) to assess the jaguarundi range boundary. Within each predicted range, we excluded small ($\leq 36\,\text{km}^2$) and highly isolated areas that could not support multiple jaguarundis and estimated the total area of predicted jaguarundi occupancy for each of the three thresholds. We then calculated a simple estimate of the number of male and female jaguarundis that may be supported in the total area of occupancy, assuming two jaguarundis (one male and one female) per $36\,\text{km}^2$.

All models were fit and predicted using "ubms" (unmarked Bayesian models with Stan) (Kellner et al., 2022) via program R (ver. 4.1.3; R Core Team, 2022) using the *stan_occu* function. We ran all models (both single covariate and global models) for three chains of 15, 000 iterations each and otherwise used the default settings. To assess general model convergence, we visually assessed trace plots and posterior distributions and checked that all R-hat convergence diagnostic values were < 1.05 (Vehtari et al., 2021) for both the individual covariate models and the global model.

## 3 | RESULTS

The combined dataset included 385,908 trap-nights from 662 unique sites, which encompassed 3856 camera stations (Table 1). The number of surveyed sites varied widely among countries, from three in Suriname to 97 in Costa Rica (median = 51). The number of sampling occasions per site-year ranged from 1 to 53 (median = 11). The majority of surveys were conducted after 2010, with only Belize and Nicaragua having eight surveys conducted in previous years (Table 1). There were 884 unique jaguarundi detections (jaguarundis detected at a single camera station within

24 h) falling within 727 independent sampling occasions at 215 sites (naïve occupancy = 0.325). Seventy-seven detections fell outside of the current IUCN jaguarundi range map showing jaguarundi occurrence in north-eastern El Salvador, central northern and southern Honduras, and the northern Andes of Colombia. Detection frequencies varied widely across sites and countries. Across all sampled sites, unique detections of jaguarundi ranged from 5 to 347 (median = 36, see Table 1) and capture rates ranged from 0.086 to 0.574 detections / 100 trap-nights (median = 0.237; see Table 1).

## 3.1 | Occupancy analysis

Both effort (i.e. the total number of trap-nights) and number of camera stations for each site-year had a positive and supported influence on detection probability (Figure 2). As such, these parameters were included in the detection model for all occupancy models.

All single covariate models reached convergence, having sufficient support to be considered in a final model, with Figure S3 showing single peak normal distributions and Figure S4 showing trace plots remaining within a narrow and consistent band with each iteration. However, only six covariates influenced jaguarundi occupancy substantially enough to meet our criteria for final model inclusion (Table 3; Figure S5): annual mean diurnal temperature range, precipitation seasonality, harmonised night-time light intensity, percent non-tree vegetation, slope, and terrain ruggedness index. Slope and ruggedness were highly correlated (>0.6, see Figure S2), so we dropped slope from the global model as ruggedness had the larger magnitude of influence (Figures S3; Table S3). For the remaining five variables, only annual mean diurnal temperature better fit the data as a quadratic rather than a linear relation (Figures S3b and S4b; Table S4). Our final model comprised five environmental variables modelled as fixed effects on occupancy probability, a random effect for site, and two variables for detection probability (Figure 2; Table 3, with Figure S6 showing trace plots for final model).

In our final model, detection probability was low (mean = 0.078, 90% CI: 0.071, 0.085 on the real probability scale; mean = −2.725, 90% CI: −2.936, −2.515 on the logit scale) when the number of trap-nights and the number of camera stations were held at their mean and median values, respectively (23.5 trap-nights and 4 camera stations per occasion). Occupancy variance (sigma) was relatively large compared to covariate effects (mean = 2.133, 90% CI: 1.501, 2.890, Table 3), indicating variance among sites was not fully explained by the range-wide covariates. With all covariates held at their means and ignoring group-level random effects, baseline probability of occupancy (the intercept) in our global model was 0.516 on the real probability scale (90% CI: 0.408, 0.627; mean = 0.064, 90% CI: −0.370, 0.519 on the logit scale).

Percent non-tree vegetation, harmonised global night-time light intensity, and terrain ruggedness index all had a positive influence on occupancy probability (Table 3; Figure 2; Figures S5 and S6). In contrast, there was evidence that precipitation seasonality had a negative influence on occupancy, although the 90% CI overlapped marginally with 0 in the global model (Table 3; Figure 2b; Figures S5 and S6). For the annual mean diurnal temperature range, occupancy had a bell-shaped quadratic relationship, rising then falling with increasing temperature range (Table 3; Figure 2b; Figures S5). Ruggedness had the highest absolute magnitude relative to the other spatial covariates (mean = 0.478, CI (90%) = 0.105–0.901) followed by the diurnal temperature range (mean = − 0.431, CI = −0.679 – −0.194), percent non-tree vegetation (mean = 0.426, CI = 0.073–0.812), light intensity (mean = 0.336, CI = −0.01 – 0.722), and precipitation seasonality (mean = −0.231, CI = −0.643 – 0.162). See Figure S5 for visual inspection of posterior distribution of the included variables in the final model. See Figure S7 for visual inspection on where values were capped for the five model covariates included in the final model.

The spatial occupancy implementation (see Supplement: spatial occupancy results) gave similar results as our stacked model, indicating that our occupancy implementation was robust.

## 3.2 | Prediction

Our model predicted low probability of jaguarundi occupancy throughout much of Mexico, primarily in the desert, temperate sierras, and southern semi-arid highlands and the Yucatan Peninsula (Figure 3). Throughout the rest of Mesoamerica, our model predicted a high likelihood of jaguarundi occupancy (Figure 3). In South America, we predicted high probability throughout the northern Andes of Ecuador, Colombia, and Venezuela, with pockets of high probability of jaguarundi occupancy in Guinian Highlands, Ilanos of Colombia, and the Cerrados (Figure 3). Probability occupancy was also high in north-eastern Caatinga and throughout the Atlantic forests of Brazil and Paraguay, the humid Chaco of Paraguay, central Bolivia, and eastern Argentina (Figure 3). However, the probability of jaguarundi occupancy was predicted to be low throughout much of the rest of the Amazonian–Orinocan lowland, particularly in the Amazon and coastal lowlands and the moist forests of the Brazilian Shield, as in the Central Andes (Figure 3). The area of occupancy covered 4,453,406 km$^2$ at the lowest probability threshold (0.5),

FIGURE 2 (a) Influence of trap effort on detection probability of jaguarundi (upper graph), and influence of number of camera stations on detection probability of jaguarundi within a site (6 × 6 km$^2$ grid cell; lower graph). The data are centred with mean = 0 and log-transformed. The grey shading around the graph line represents the 90% CI. (b) Influence of the five covariates, included in the final model, on occupancy probability of jaguarundi. Effects of each covariate on range-wide jaguarundi occupancy are shown while holding all other four covariates at their median, with 90% CI indicated in grey.

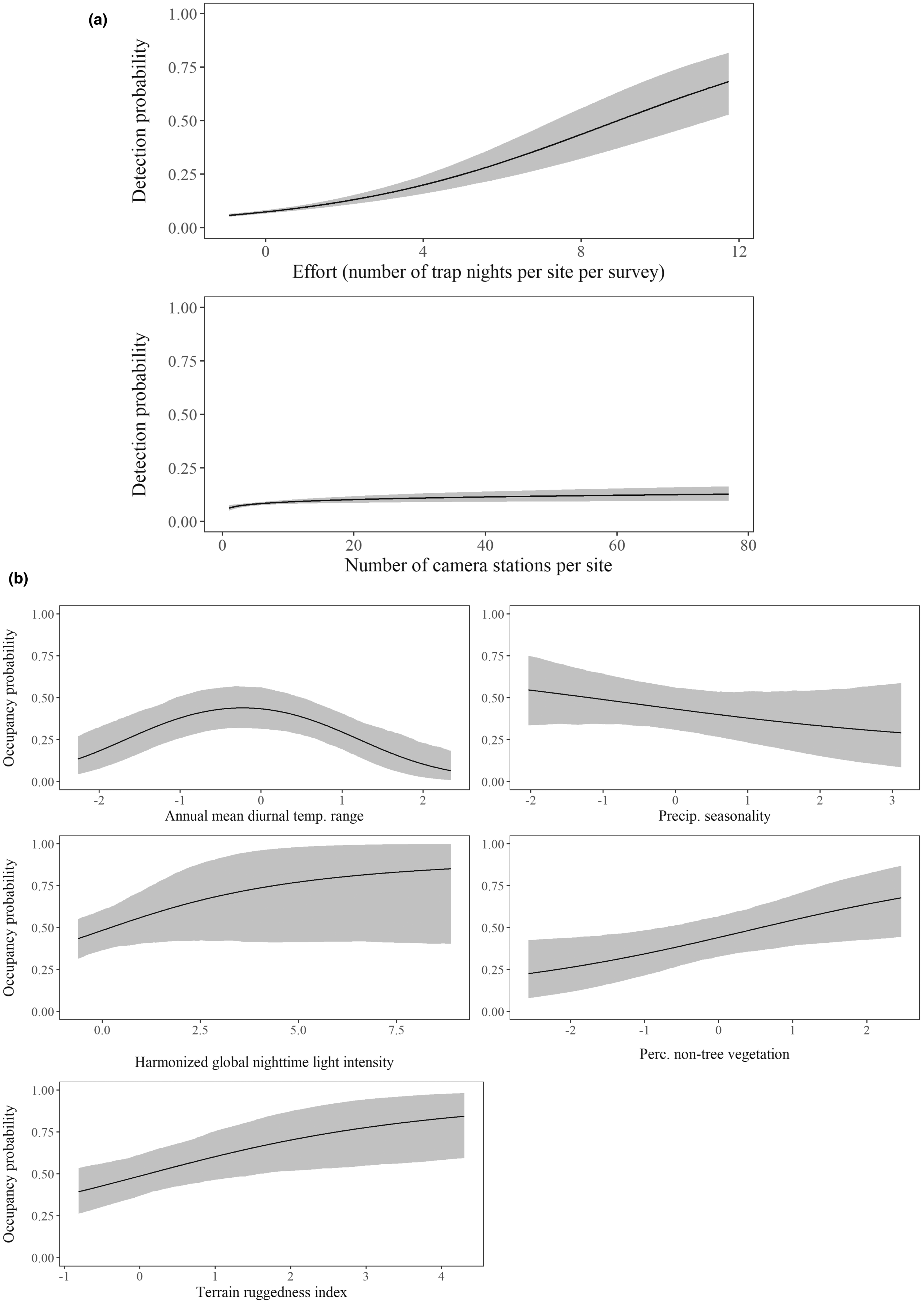
(a)
Detection probability
1.00
0.75
0.50
0.25
0.00
0
4
8
12
Effort (number of trap nights per site per survey)
Detection probability
1.00
0.75
0.50
0.25
0.00
0
20
40
60
80
Number of camera stations per site
(b)
Occupancy probability
1.00
0.75
0.50
0.25
0.00
-2
-1
0
1
2
Annual mean diurnal temp. range
-2
-1
0
1
2
3
Precip. seasonality
Occupancy probability
0.0
2.5
5.0
7.5
Harmonized global nighttime light intensity
-2
-1
0
1
2
Perc. non-tree vegetation
Occupancy probability
-1
0
1
2
3
4
Terrain ruggedness index

**TABLE 3** Final model parameter estimates of jaguarundi occupancy and detection, using a Bayesian analysis framework.

| | Mean | SD | LCI | UCI | R-hat |
|---|---|---|---|---|---|
| Occupancy probability | | | | | |
| Intercept | 0.064 | 0.270 | −0.370 | 0.519 | 1.00 |
| Annual mean diurnal temp. range | −0.198 | 0.196 | −0.523 | 0.121 | 1.00 |
| Annual mean diurnal temp. range (quadratic) | −0.431 | 0.148 | −0.679 | −0.194 | 1.00 |
| Precip. seasonality | −0.231 | 0.246 | −0.643 | 0.162 | 1.00 |
| Harmonised global night-time light intensity | 0.336 | 0.224 | −0.010 | 0.722 | 1.00 |
| Perc. non-tree vegetation | 0.426 | 0.225 | 0.073 | 0.812 | 1.00 |
| Terrain ruggedness index | 0.478 | 0.244 | 0.105 | 0.901 | 1.00 |
| Sigma (site random effect) | 2.133 | 0.022 | 1.501 | 2.890 | 1.00 |
| Detection probability | | | | | |
| Intercept | −2.725 | 0.129 | −2.936 | −2.515 | 1.00 |
| Camera trap-nights | 0.285 | 0.034 | 0.230 | 0.341 | 1.00 |
| No. of stations | 0.181 | 0.068 | 0.070 | 0.293 | 1.00 |

*Note*: The results are for the six variables for which the 90% posterior distribution (CI) did not include 0, using single covariate occupancy models. We include both the quadratic and the linear results for annual mean diurnal temperature range. Presented are the mean, standard deviation (SD), the lower boundary of the 90% credible interval (LCI), upper boundary of the 90% credible interval (UCI), and the R-hat convergence diagnostic.

2,030,093 km$^2$ at the intermediate threshold (0.65), and 652,002 km$^2$ at the most conservative threshold (0.8), see Figure 4. Figure S8 shows a similar prediction map as Figure 4, clearly indicating which areas were affected by capping values.

External validation data (see Figure 3) indicated that our model predicted the probability of occurrence well ($r_s = 0.9154$, $p$-value <.001, see Figure 3 for distribution of external validation points). Substantially more occurrences fell within our higher predicted probability bins; 46.9% of the external observations fell within our top third of predicted occupancy probability (bins 8–10; Figure 5). Using our simple equation of abundance estimate, multiplying the number of occupied cells of 36 km$^2$ by 2, we estimate the global jaguarundi populations as 36,222 individuals at the most conservative occupancy threshold (0.8), 112,783 individuals at an occupancy probability threshold of 0.65, and for the lowest threshold of occupancy probability (0.5), we estimate 247, 411 individuals.

## 4 | DISCUSSION

Although the range of the jaguarundi is known to span the Western Hemisphere, from Mexico to Argentina (Caso & Oliveira, 2015), we noted new records in southwestern Mexico, southern Guatemala, north-eastern El Salvador, central northern and southern Honduras, the northern Andes of Colombia, and the central Andes of Bolivia (this study and Nagy-Reis et al., 2020). Pooling camera-trap data from multiple sites across the region and using occupancy modelling, we found positive associations between jaguarundi occupancy and level of: non-tree vegetative cover (undergrowth and shrub habitat), human land-use (measured as night-time light intensity), intermediate diurnal temperatures, and rugged terrain, while seasonal variation in precipitation had a negative association with occupancy.

Despite almost 400,000 trap-nights, detection rates were consistently low, ranging from 0.09 detections per 100 trap-nights in Guyana to 0.57 in Honduras. These results compare similarly with the few published detection rates of jaguarundi in other camera-trap studies across the Neotropics, ranging from 0.03 to 0.81 detections per 100 trap-nights (Boron et al., 2020; Carrera-Treviño et al., 2018; Di Bitetti et al., 2010; Gil-Sánchez et al., 2021; Maffei et al., 2007; Santos et al., 2019). In most of these studies, camera traps were deployed to optimise the detection of larger felids (jaguars and pumas, *Puma concolor*), thus were potentially sub-optimal for smaller species, resulting in low detection rates of jaguarundis (see Harmsen et al., 2021).

Negative biases in occupancy estimates can arise due to the effects of unmodelled heterogeneity in the probability of detection ('detectability'; Mackenzie & Royle, 2005). Although our model accounted for heterogeneity in effort between the sample sites, there likely remains unexplained heterogeneity in detectability within sites between camera stations, associated with factors such as camera height, trail width, camera placement, camera model, and variation in micro-habitat around cameras. The influence of this kind of heterogeneity on occupancy estimates may be exacerbated if the species has low detectability (Mackenzie & Royle, 2005), as jaguarundis seem to have across their range. The chance of detecting jaguarundis in an area increased with trapping effort. Jaguarundis were more likely to be detected at sites with more camera stations and more sampling occasions, indicating that knowledge of

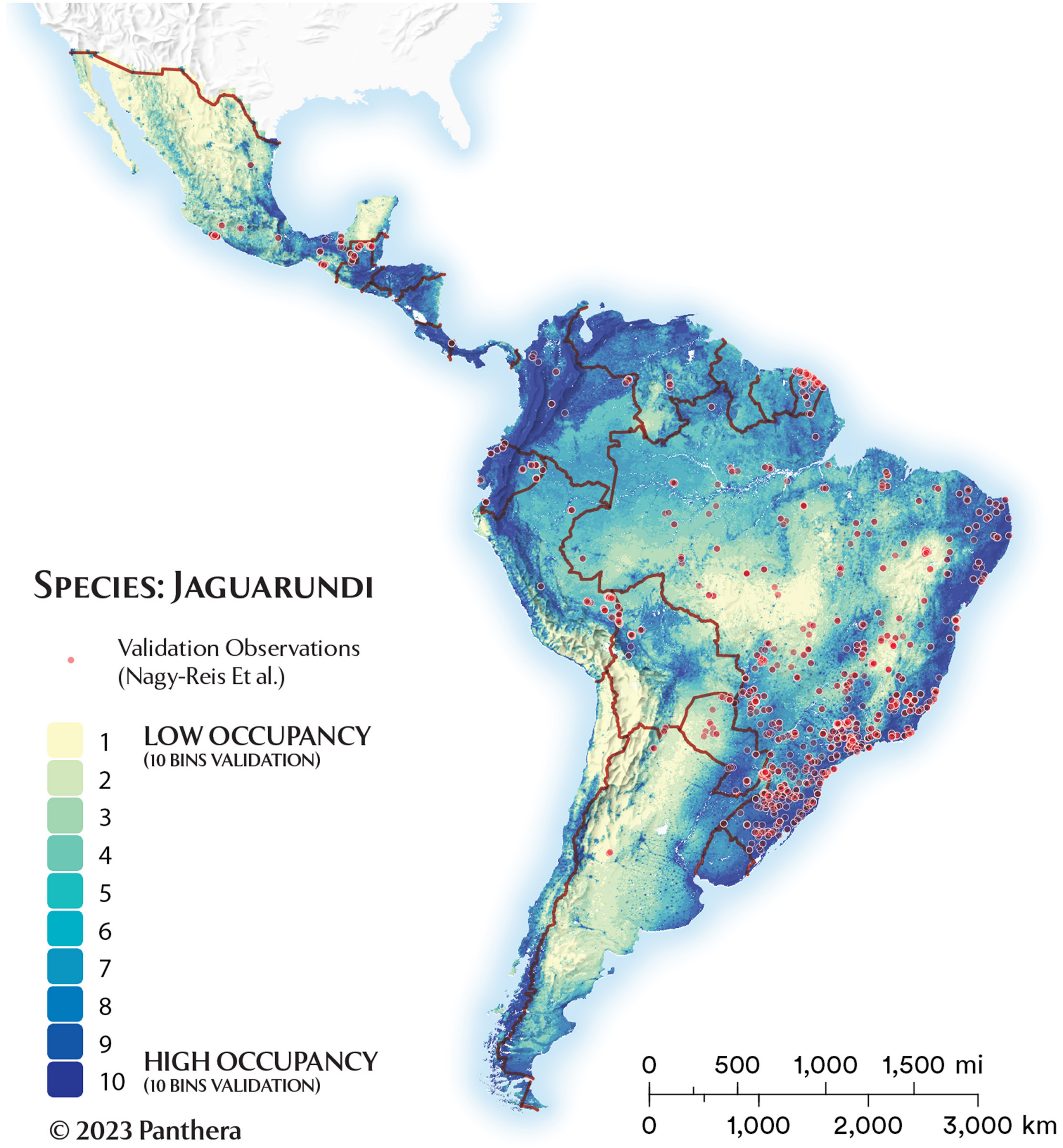

FIGURE 3 Predicted probability of occurrence across jaguarundi range, derived from our final occupancy model. The probability of occupancy is shown as 10 separate bin colours, varying from low chance of occupancy (yellow) to high chance of occupancy (dark blue), using green as an intermediate. The red dots in the map indicate locations where jaguarundi were detected, using the database of Nagy-Reis et al. (2020).

sample effort is vital to understand occupancy and presence. In the absence of validation, we caution against the use of models making impactful statements about species distribution. For example, Grattarola et al. (2023) described a sizable change in jaguarundi distribution across the last two decades. Using a published dataset (Nagy-Reis et al., 2020), they described a north–south species range contraction, and an overall east–west expansion within the last decade, comparing the periods 2000–2013 and 2014–2021. Such a statement implies considerable environmental change and/or perturbation on the species, coinciding with extensive extinction and colonisation events across this latter decade. However, their models did not include sample effort, instead using presence-only and an

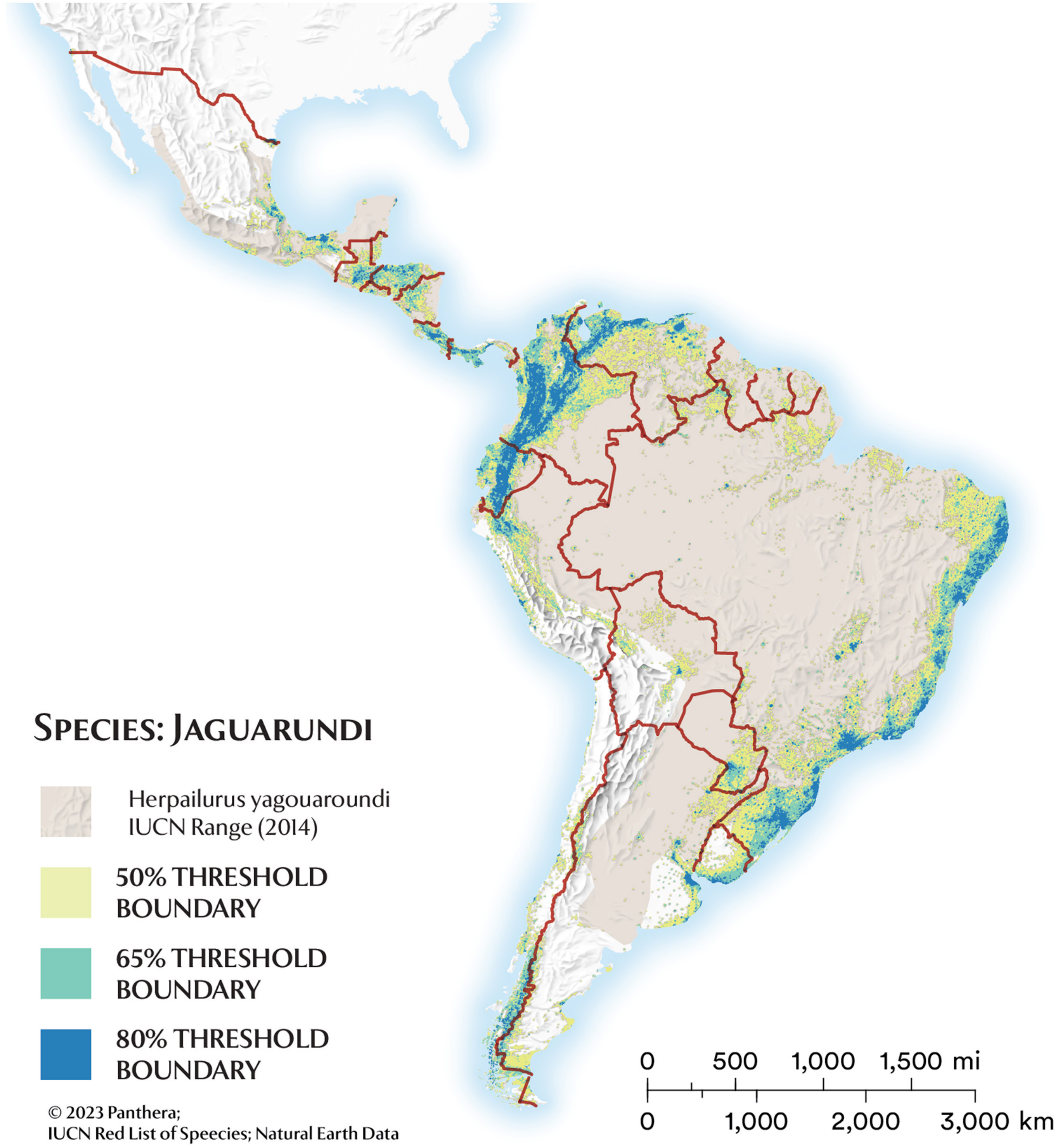

FIGURE 4 Predicted probability of occurrence across jaguarundi range, derived from our final occupancy model. We show three threshold levels of occupancy, in three colours, from high threshold to low: probability of occurrence: 0.5 (yellow), 0.65 (green) and 0.8 (blue). The original assessed IUCN red list jaguarundi range is overlaid in beige (Caso & Oliveira, 2015).

absence index based on the overall non-reporting of jaguarundi. On close inspection of the Nagy-Reis et al. (2020) dataset, the reported survey activity was highly variable across space, between the two decades, contracting along the North–South axis and expanding on the West–East axis, seemingly following the pattern of extinction and colonisation reported by Grattarola et al. (2023).

Jaguarundis are commonly associated with areas of dense shrub or undergrowth which provide den sites, shade during diurnal activity, shelter, cover for ambush hunting, and likely support abundant populations of rodents and birds, their main vertebrate prey (Giordano, 2016). Accordingly, we found that the probability of jaguarundi occupancy increased with non-tree vegetative cover,

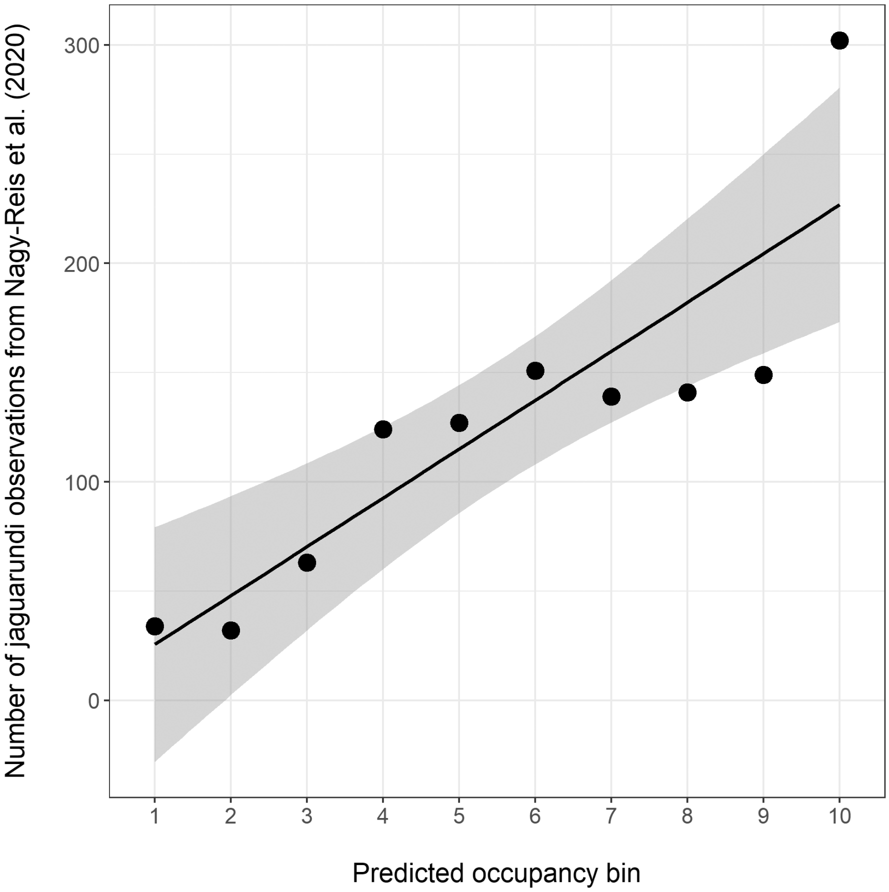

**FIGURE 5** Number of jaguarundi occurrences from the validation dataset of Nagy-Reis et al. (2020) that fell within 10 quantile bins of predicted probability of occupancy, as derived from our final occupancy model. The 90% confidence interval is shown in grey.

suggesting a preference for grasslands, savannas, and shrublands, and potentially agricultural lands, rather than forest interiors or bare ground. Additionally, jaguarundi occupancy increased with the terrain ruggedness. Potentially, their elongated body form, long tail, and comparatively short legs allow jaguarundis to exploit rough areas that are less accessible to their competitors. In carnivores, active selection for rugged terrain may provide refugia from interspecific competition and predation (Durant, 1998), for example safe denning sites (e.g. Eurasian lynx, *Lynx lynx*; White et al., 2015), as well as giving an advantage when stalking prey (e.g. dhole, *Cuon alpinus*, and puma, *Puma concolor*; Grassman et al., 2005; Smith et al., 2019). Both terrain ruggedness and non-tree vegetation cover had the strongest effects on jaguarundi occupancy, each having approximately twice the effect compared to the next strongest covariate. For both covariates, we did not sample the upper extent of ruggedness and non-tree vegetative cover present within the prediction area (e.g. the peaks of the Andes, and the Argentine Pampas, respectively). It is however difficult to predict the effect of ruggedness beyond our sampled data. We would expect a cut-off point when high ruggedness becomes a barrier to jaguarundi movement and we know this point was not reached within our sampled datasets. Furthermore, the majority of our sites were located within non-tree vegetative cover, sampled natural herbaceous cover, rather than agricultural lands (pastures and croplands). As our covariate layer did not distinguish between natural cover and agricultural uses, our model may overestimate the probability of jaguarundi occupancy in extensive farmland lacking patches of dense natural undergrowth or shrubs. Notably, our model predicted a high probability of jaguarundi occupancy throughout Uruguay, where despite extensive camera trapping and research effort spanning 115 years (da Silva et al., 2016; Espinosa et al., 2018; Nagy-Reis et al., 2020), there is only one confirmed detection of a jaguarundi (Grattarola et al., 2023). Approximately 80% of land in Uruguay is dedicated to agriculture uses, primarily livestock (The World Bank, 2020). We suspect that this area is devoid of jaguarundis and that the high probability of occupancy estimated by our model is an artefact of the positive association with natural herbaceous cover applied to extensive pasture and arable land.

Using night-time light intensity as a proxy for human impact, we found that jaguarundi resource use increased with human activity. However, our sampling was confined to natural areas within sparsely populated rural communities. Above some threshold where light intensity reaches levels associated with urbanisation, we expect a negative relationship, with occupancy declining to zero in densely populated areas. Considering also the positive association with non-tree vegetative cover, these results suggest that jaguarundis tolerate some human activity and have an affinity for habitats associated with rural human populations. However, the extent to which they make use of human-modified landscapes is unclear (Giordano, 2016). Although jaguarundis occur in mixed agricultural areas with remnants of forest fragments, several studies suggest a negative association with croplands and pastures, a positive association with natural herbaceous cover, and a positive association with proximity to native forest, which become more important as the proportion of crop and pasture increases (Boron et al., 2020; Costa et al., 2022; Cruz et al., 2019). The negative effect of croplands and pastures on jaguarundis versus the positive effect of natural herbaceous cover may be associated with prey availability. Thus, in agricultural landscapes we expect that jaguarundis are more successful around rural small-holdings, where they can supplement their diet with domestic species, particularly poultry (Giordano, 2016), and human-associated rodent populations. In contrast, expansive monocultures are less hospitable (e.g. Boron et al., 2020) and may lack sufficient prey. Living in human-modified landscapes exposes jaguarundis to additional threats. As predators of domestic fowl (Giordano, 2016), they are commonly blamed for attacks on poultry and suffer retaliatory killings by people (Foster, 2018). Because the diurnal activity pattern of jaguarundis coincides with human activities, roads pose a particular risk, disrupting their behaviour and increasing mortality (Gil-Sánchez et al., 2021). Indeed, in a global assessment on the fragmenting effect of roads and highways on mammalian carnivore species, jaguarundis were listed in the top 5% of species most vulnerable to road expansion (Ceia-Hasse et al., 2017). Understanding the limitations of jaguarundi tolerance to human activity will be pivotal for its conservation in the coming decades.

Considering climatic conditions, our model predicted higher probabilities of jaguarundi occupancy where precipitation was less seasonal, and at intermediate levels of diurnal temperature range. We hypothesise that highly seasonal rainfall may influence jaguarundis directly, and indirectly via an impact on prey availability. Flooding may reduce accessibility to refuges and hinder movement across the landscape for both jaguarundis and their prey, while seasonal drought conditions may reduce food resources and thus prey abundance. In areas where climatic variation is even more extreme than the capped values, our model may have overestimated the probability of jaguarundi occupancy in areas of higher seasonality in precipitation and more variable diurnal temperatures, and underestimated it in capped areas where precipitation is not seasonal.

Our model predicted the occupancy of jaguarundi without accounting for possible effect(s) of prey availability, a key driver of the spatial distribution of obligate carnivores. In the case of Neotropical felids, prey abundance was more important than interspecific competitors or habitat complexity in explaining the occupancy of jaguars, pumas, and ocelots (Santos et al., 2019). In the Brazilian Caatinga, prey occurrence had a positive effect on habitat use of oncillas and jaguarundis (Dias et al., 2019), and in the High Andes of Bolivia, the occupancy of the Andean cat (*Leopardus jacobita*) and Pampas cat (*Leopardus colocolo*) increased with prey availability (Huaranca et al., 2022). Given that jaguarundi diet encompasses several classes of small terrestrial vertebrate, estimating and including prey availability in our model was beyond the scope of this study, however we infer that the majority, if not all, of the covariates in our final model are direct predictors of suitable prey abundance and availability (e.g. Moreno-Sosa et al., 2022).

Our model did not incorporate the distribution or abundance of potential predators or interspecific competitors, which might be important explanatory variables of felid distribution. The jaguarundi is sympatric with at least seven other felid species, overlapping most extensively with jaguars, pumas, ocelots, and margays (de Oliveira et al., 2015; Nielsen et al., 2015; Paviolo et al., 2015). High dietary overlap exists between jaguarundis and the other sympatric small felids (e.g. Migliorini et al., 2018; Silva-Pereira et al., 2011; Zuercher et al., 2022). Although this may indicate the potential for competitive exclusion and effects of interspecific competition on distribution, coexistence is likely facilitated by their differing activity patterns rather than spatial segregation (e.g. Dias et al., 2019; Fox-Rosales & de Oliveira, 2023; Giordano, 2016; Santos et al., 2019). Based on size differences and range overlap, jaguars, pumas, and ocelots are all capable of killing jaguarundis (de Oliveira & Pereira, 2014). However, although intraguild predation occurs, it is not commonly detected among these species (Crawshaw, 1995; Magioli & Ferraz, 2018; Martins et al., 2008). Indeed, empirical data from the Brazilian Caatinga showed no evidence of spatial segregation, intraguild competition, or predation between jaguarundis and jaguars, pumas, ocelots, or oncillas (Dias et al., 2019; Fox-Rosales & de Oliveira, 2023). It would be worthwhile that future analyses include occupancy and/or detection of competing meso-carnivores within the analytical framework to assess impacts of competition.

Our model predicted jaguarundi area of occupancy ranging from 652,002 km$^2$ to 4,453,406 km$^2$ (using the 0.8 to 0.5 occupancy thresholds). This is more conservative than previous range estimates of: at 14, 900,000 km$^2$, based on expert opinion Caso and Oliveira (2015); at 14, 700, 000 km$^2$ based on presence-only data and temperature as a measure of habitat suitability (Espinosa et al., 2018); or at 12,000,000 km$^2$, based on annual temperature range, precipitation seasonality, elevation, and net primary productivity (NPP) (Grattarola et al., 2023). In contrast to the latter model, our model indicated a negative relation with seasonal precipitation, rather than a positive relation with jaguarundi occupancy.

Our model predicted low probability of jaguarundi occupancy throughout much of Mexico, with high occupancy throughout most of Mesoamerica. In South America, we predicted high probability throughout the more rugged northern part of the continent in the Andes, Llanos, and Cerrados areas (Ecuador, Colombia, Venezuela, and Brazil), while equally along the eastern part of the continent in the more humid areas of Chaco, Caatinga, and Atlantic forest (Brazil, Bolivia, Paraguay, and Argentina). However, the probability of jaguarundi occupancy was predicted to be low at the core of their known range within the Amazonian–Orinocan lowland, particularly in the Amazon and coastal lowlands and the moist forests of the Brazilian Shield. This region is often considered the core range of other sympatric pan-Neotropical felids, e.g., the ocelot (*Leopardus pardalis*) (Paviolo et al., 2015), and the margay (*Leopardus wiedii*) (Oliveira et al., 2015). Although it is widely recognised for its high biodiversity value in conservation prioritisation studies, our model suggests that this region represents sub-optimal conditions for jaguarundis.

External validation, using the Nagy-Reis et al. (2020) dataset, showed that our model predicted the probability of jaguarundi occupancy well; however, we note several areas where our model predicts high jaguarundi occupancy, while extensive research across these ranges have never detected a jaguarundi and they are likely absent (e.g. Nagy-Reis et al., 2020). In particular, our model predicted a high probability of occupancy throughout the southern Andes of Chile and the southern tip of Patagonia, which we suspect was an artefact associated with the positive relationship with ruggedness and the negative relationship with precipitation seasonality. Likewise, the probability of occupancy was unexpectedly high in the Pampas of Uruguay and the coast of Argentina, likely associated with the high levels of herbaceous cover in this region. Conversely, the likelihood of jaguarundis occupying the Western Dry Chaco of northern/central Argentina was notably low, while historically this has always been part of the jaguarundi species range (Caso & Oliveira, 2015). This may be an artefact of the model, associated with the highly variable daytime temperatures in this area.

Despite its limitations, the occupancy modelling framework is a robust approach to predict species distribution, indicated by similar results from both the stacked and spatial occupancy implementations (see Supplement: spatial occupancy results). We used these models to provide baseline estimates of global jaguarundi occupancy and habitat associations. The models could be refined by sampling sites across the total extent of covariate values, reducing the need for capping, while equally refining the covariates by distinguishing between natural and agricultural land-cover, and expanding the covariates by incorporating data on potential competitor and prey species. Using the estimated area of occupancy, we estimate the global population with a probability of occupancy of 0.8 to 0.5 to range from 36, 222 to 247, 411 individuals, respectively. However, if we exclude the southern Andes of Chile and the southern tip of Patagonia, knowing that jaguarundis are not present, these estimates would drop to 34,645 to 230,034. This initial assessment provides a starting point, which should be updated as more data become available and the model refined with different covariate layers.

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As this study concerns the use of pre-existing by-catch data, the field research was funded and implemented for monitoring other wildlife (e.g. jaguars). All co-authors volunteered to assist with formatting and resolve questions to ensure the creation of a single, high-quality dataset. The use of this dataset does not require permission or authorisation from any funding body, as such there was no particular funding for this study. The final dataset was formatted and analysed by the core analytical team who were all salaried by the Panthera Corporation under the general mandate of the organisation to expand knowledge on distribution and abundance for all 40 species of felids.

## CONFLICT OF INTEREST STATEMENT

The main authors and co-authors do not have any conflict of interest, and all co-authors contributed data with the sole purpose of expanding knowledge on the habitat use and distribution of an understudied and unknown felid species.

## PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13831.

## DATA AVAILABILITY STATEMENT

We will make the dataset available upon publication at a publically available siteup, allowing reproduction of analyses.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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