



Jaguars in their largest stronghold: spatial distribution of a generalist apex predator

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Communicated by Andreas Schuldt.

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Abstract

The jaguar (*Panthera onca*) is the largest Neotropical apex predator. It exhibits marked behavioral plasticity, including flexible prey use, allowing it to respond to different landscapes. The Amazon forest harbors the largest jaguar population and is key to the species' conservation, yet the drivers of its distribution across the biome remain poorly understood. Here, we compiled the most geographically extensive dataset of jaguar records for the Amazon to date, based on camera-trap data, totaling 2,694 records from 123 study areas spanning nine countries. This study represents the first large-scale assessment to explicitly incorporate prey composition and climate predictors while accounting for variation in sampling effort, allowing us to better distinguish ecological patterns from methodological differences among sites. After controlling for sampling effort, jaguar relative abundance was higher in areas dominated by ungulates and lower in areas dominated by pacas (*Cuniculus* spp.), potentially reflecting differences in habitat conditions, given the species' tolerance of disturbance. Relative abundance also decreased with increasing drought intensity, suggesting that drought may influence jaguar populations across the biome. By explicitly modeling differences in sampling effort, including the number of cameras deployed, camera-trap duration and sampled area, we reduced spurious spatial patterns arising from heterogeneous survey designs and strengthened biome-wide inference on jaguar ecology. Our results highlight the likely importance of prey composition and drought conditions in explaining variation in jaguar relative abundance across the Amazon, while also showing that the biome continues to support widespread jaguar populations and remains a major stronghold for the species. These findings provide a broader empirical basis for understanding jaguar distribution and informing conservation planning across the one of the world's largest tropical forest systems.

Keywords Amazon · Camera-trap · Jaguar · Prey · Spatial distribution

Introduction

Large carnivores exhibit remarkable ecological and behavioral flexibility, allowing them to inhabit a wide range of natural and human-modified environments. At large spatial scales, availability of different prey types remains a key driver of their spatial distribution (Rich et al. 2017), while at local scales, it is also influenced by interactions with other species (Harmsen et al. 2009) and by structural habitat components, such as vegetation type, which affect both resources and shelter availability (Svoboda et al. 2019). Human disturbances further shape their habitat use, often reducing occupancy in highly modified areas or altering their activity patterns (Mills et al. 2023). Although many large carnivores are opportunistic, most species exhibit preferences for large prey (Cruz et al. 2021; Metz et al. 2023), and are associated with extensive relatively undisturbed areas that support viable populations (Santini et al. 2016). Therefore, understanding the factors that affect spatial distribution are essential for developing effective conservation strategies, especially in the face of accelerated environmental change (Lapola et al. 2023).

The jaguar (*Panthera onca*) is the largest terrestrial Neotropical carnivore, widely distributed from southern USA to northern Argentina (Morato et al. 2016; De la Torre et al. 2018). It exhibits notable behavioral plasticity, particularly in habitat use across environmental gradients (Watkins et al. 2015; Morato et al. 2018). Despite their broad geographic

range, they have disappeared from over 50% of their historic distribution (Jędrzejewski et al. 2018). As apex predators, jaguars regulate mesopredators and herbivore populations, thereby helping to prevent overgrazing by large herbivores (Ordiz et al. 2021). Although considered a generalist predator, prey selection is shaped more by socio-ecological and behavioral factors, such as prey abundance and group size, than by prey morphology (Hayward et al. 2016). Jaguars often show a preference for large-bodied prey even when these are not the most abundant species available (Weckel et al. 2006; Ferretti et al. 2020), suggesting a tendency to select such prey when they are accessible (Eriksson et al. 2022). This balance between plasticity and selectivity plays a key role in how jaguars respond to changing landscapes and prey communities across their range.

Jaguar densities vary with environmental productivity, with individuals exhibiting smaller home ranges and higher abundances in more productive, humid habitats, such as the Amazon (Thompson et al. 2021). In contrast, in dry, low-productivity regions, jaguars maintain larger home ranges, reflecting lower densities and their dependence on prey availability, which in turn relies on primary productivity and herbivore abundance (Jędrzejewski et al. 2018). Their spatial distribution is influenced by forest cover, temperature, precipitation patterns (Jędrzejewski et al. 2018) and elevation (Morato et al. 2014; Astete et al. 2017), while at finer spatial scales, habitat use is shaped by vegetation structure and access to water (Morato et al. 2018; Thompson et al. 2023). Jaguars are well adapted to diverse environments, from Amazonian *várzea* forests, where they live in a flooded landscape by hunting and resting in trees during high-water periods (Ramalho et al. 2021), to savannahs and semi-open habitats, provided there is sufficient prey and water (Morato et al. 2023). While some studies show that low levels of human disturbance cause jaguar declines (Morato et al. 2016; Romero-Muñoz et al. 2025; Cristiano et al. 2025) by affecting their spatial and temporal movement patterns and behavior (Morant et al. 2025), others in low-density human settlements within sustainable-development reserves show little effect on space use (Montanarin et al. 2023), highlighting context-dependent effects of human activities on jaguar spatial distribution. Despite these advances, current knowledge is largely derived from local or regional studies that focus on a limited subset of potential drivers. Consequently, it remains unclear whether the factors identified in these studies consistently explain variation in jaguar abundance and space use across the Amazon, where environmental conditions, prey assemblages, and human pressures vary substantially across space.

The Amazon forest harbors the largest jaguar population (Tobler et al. 2013; De la Torre et al. 2018; Alvarenga et al. 2025) and is particularly important for the species' conservation, as this biome represents the majority of its current distribution (Jędrzejewski et al. 2023). However, the region faces rapid transformations driven by a development model based on overexploitation, characterized by deforestation, fires, land grabbing, and poorly planned infrastructure expansion, which threaten the future of many species while intensifying habitat loss and climate change (Nobre et al. 2016). These changes are expected to intensify drought conditions across the biome. Changes in precipitation, particularly during the dry season, are among the most critical determinants of the climatic fate of the Amazon (Malhi et al. 2008). Because climate change in Amazonia is neither gradual nor homogeneous, the region is experiencing rapidly increasing extreme temperatures and water deficits (Barlow et al. 2025). Consequently, droughts are projected to become a major driver of carbon emissions from forest degradation, highlighting the central role of climate change in shaping degradation dynamics (Lapola et al. 2023). Despite projections indicating clear increases

in both the annual frequency and intensity of droughts across the Amazon Basin, important gaps remain in our understanding of how drought affect Amazonian fauna (McTigue et al. 2026).

Many protected areas within the Amazon are increasingly affected by human pressure and degradation, both within their boundaries and in the surrounding landscapes, where conflicts and management challenges are often more pronounced (Bogoni et al. 2023; Cristiano et al. 2025). In the Amazon, approximately 55% of the current jaguar range lies within areas with some form of legal protection (Jędrzejewski et al. 2023), highlighting their relevance for conservation. However, the effectiveness of large protected areas and Indigenous territories remains a key determinant of their role in jaguar persistence, acting as demographic and functional refuges (Mena et al. 2020).

Despite recent advances, standardized data covering large portions of the Amazon remain limited (Alegre et al. 2025), challenging our ability to understand how large carnivores respond to environmental changes. This gap is particularly concerning given the absence of a comprehensive understanding of the ecological drivers of jaguar space-use across their range. Although important progress has been made, most models still focus on species occurrence (Alegre et al. 2025) rather than abundance, mainly due to limited access to standardized data, especially at large spatial scales. However, species abundance is often more sensitive than occurrence-based data for detecting ecological and anthropogenic effects on species distributions, as it captures variation in population density that may not be reflected in presence-only records (Rovero and Marshall 2009; Maxwell et al. 2019). Methodological constraints such as differences in sampling effort and design can also affect model results and lead to conflicting conclusions (Montanarin et al. 2023), therefore it is critical to ensure robust and comparable inferences across heterogeneous datasets.

Although jaguars are widely used as flagship species for conservation, to date no study has evaluated the relative influence of prey composition, environmental conditions and anthropogenic pressures simultaneously across broad spatial extents in the Amazon. We compiled the largest and most geographically extensive standardized dataset of jaguar records ever assembled for the Amazon, enabling robust comparisons across heterogeneous landscapes while controlling for methodological variability. Using camera-trap data from 123 study areas and 5,830 coordinates, our dataset comprises 2,694 jaguar records distributed across nine countries, providing an unprecedented opportunity to disentangle the biotic and abiotic drivers of jaguar distribution at a biome-wide scale. This is the first large-scale study to explicitly incorporate information on potential prey species detected by camera traps as a covariate across all sites. We hypothesized that variation in jaguar records across Amazonia would be associated with broad-scale differences in prey composition, environmental conditions, and anthropogenic disturbance among sites. Specifically, we predicted higher jaguar records in areas characterized by prey communities containing a greater proportion of large-bodied species, greater vegetation cover, greater environmental productivity, and proximity to watercourses. Conversely, we predicted lower jaguar records in areas exposed to stronger anthropogenic pressures and climatic stressors.

Methods

Study area

The Amazon harbors the largest tropical rainforest and the most extensive river basin in the world, covering approximately 40% of South America (Malhi et al. 2008). Pan-Amazonia spans about 6.7 million km² across nine countries: Brazil, Bolivia, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname, and Venezuela; extending from the Atlantic Ocean to the Andes Mountains and from the Guiana Shield to the Brazilian Highlands (Junk et al. 2015; RAISG 2020). This biome is heterogeneous and supports exceptional biodiversity, making it one of the most complex and ecologically significant regions on Earth. Additional details on ecosystem diversity, hydrology, and soils are provided in *Appendix A. Study area description*.

Dataset

This study is based primarily on the Amazonia Camtrap dataset (Antunes et al. 2022), which comprises 122,534 camera-trap records compiled from 42 studies distributed across 143 sites throughout the Amazon, spanning eight countries and the period 2001–2020. It includes 289 terrestrial vertebrate species and represents the most comprehensive spatially explicit dataset currently available for the Amazon forest. To expand its coverage, we incorporated 33 additional datasets obtained through collaborations with researchers and institutions, particularly the National Center for Research and Conservation of Carnivorous Mammals (CENAP) and the Brazilian Biodiversity Monitoring Program (Monitora Program) of the Instituto Chico Mendes de Conservação da Biodiversidade. These complementary data extend the geographic scope to new areas such as Colombia and Guyana and fill gaps in the original compilation with further records from Suriname and Brazil (see Data availability).

Data preparation

We defined the sampling units for our analyses as spatial clusters of camera-trap stations. Clusters were identified using a distance-based clustering procedure and refined according to spatial-independence criteria (see *Appendix B. Data preparation*). For each sampling unit ($n = 123$), we estimated its spatial extent using a convex hull and calculated the total area (km²), mean number of camera-days, and total number of camera stations. Hereafter, these sampling units are referred to as clusters.

Jaguar records

For each camera-trap station, the original data consisted of jaguar photographs. Photograph series were grouped into independent records, defined as one or more jaguar detections within a short temporal interval (e.g., detections of the same animal within a 30-min window count as a single independent record; see *Appendix C. Variable details*). When more than one jaguar was photographed simultaneously (e.g., an adult with a cub), each observed animal contributed separately to the record count. Independent records were then summed

across all camera-trap stations within each cluster to obtain the response variable used in the analyses.

Predictor variables

To determine how the number of jaguar records in the Amazon is affected by prey composition, environmental, and anthropogenic factors, we selected key variables shown to be important for jaguar persistence in previous studies (Jędrzejewski et al. 2018; Thompson et al. 2021; Morato et al. 2023).

Prey composition: Jaguars have a varied diet, including a wide range of prey species. Because detections of prey taxa were widespread across camera-trap stations, we focused on six commonly detected species: collared peccary, tapir, white-lipped peccary, spotted paca, deer, and armadillos. These taxa encompass a substantial proportion of the terrestrial prey community detectable by camera traps and were used to characterize spatial variation in prey composition across study areas. Due to taxonomic variability in detectability and identification, prey species were classified at different hierarchical levels: species level (*Dicotyles tajacu*, *Tapirus terrestris*, *Tayassu pecari*), genus level (*Cuniculus*), family level (Cervidae), and order level (Cingulata). Detailed taxonomic composition of grouped categories is provided in *Appendix C. Variable details*. Based on this classification, we evaluated how the proportions of records for each taxon varied across clusters. As these prey-related variables were highly correlated, we summarized variation using a Non-metric Multidimensional Scaling (NMDS) analysis in two dimensions. The NMDS biplot showing study sites and taxa scores is provided in the Supplementary Material (Fig. S1), and the corresponding ordination scores are provided in Table S1. To visualize spatial patterns, we generated Poncho graphs (Dambros 2013). Details are given in *Appendix D. Analyses*.

Environment: We extracted the vegetation indices NDVI (Normalized Difference Vegetation Index) and EVI (Enhanced Vegetation Index), and productivity metrics Gross Primary Productivity (GPP), Net Primary Productivity (NPP), and the NPP Quality Control Layer from the MODIS product. We characterized forest structure using canopy-height data from GEDI (2019) and tree-cover percentage from Hansen et al. (2013), and elevation derived from the SRTM dataset. To extract these variables, we applied a 1-km buffer around each camera-trap station and averaged the values within each cluster. We then calculated the mean of all extracted variables for each cluster. Given the collinearity among environmental variables, we applied a Principal Component Analysis (PCA) to reduce dimensionality. The first two axes explained 73.2% of the cumulative variance (Supplementary Fig. S2). PC1 (57% of the variance) was associated with NDVI, forest cover, EVI, and GPP, while PC2 (16%) was associated with NPP and elevation.

Distance to watercourses: This was derived from the open-water class in the MapBio-mas Pan-Amazonia land-use and land-cover dataset, a water-related attribute consistently mapped across the entire study region and corresponding to features detectable by the normalized difference water index (NDWI). The original MapBio-mas water raster is provided

at a 30 m spatial resolution. This was aggregated to 90 m using a majority rule. For the group of 90 m cells in each polygon, we report the mean of distances to the nearest open water. It is important to note that small artificial impoundments and small- to intermediate-size streams are detectable in deforested landscapes, whereas the former are absent and the latter are hidden from view by flooded forests in areas with little or no deforestation. This reduces the distance to water for polygons in or near deforested regions.

Seasonality: We used annual maximum cumulative water deficit (MCWD) data provided by Barlow et al. (2025), originally derived from CHIRPS precipitation data following the methodology of Aragão et al. (2007). MCWD is a widely used indicator of forest water stress and drought intensity in tropical forests. For each site, we calculated the mean MCWD over the period 2000–2024 to represent long-term exposure to water deficit where more negative values indicate higher drought intensity.

Land tenure and human disturbance: From Protected-areas classification, we generated a binary raster (1 = protected, 0 = non-protected) at a 1-km spatial resolution. We then calculated the proportion of each cluster that overlapped with protected areas based on this raster. We used the Human Footprint Index (HFI) from Venter et al. (2018) with a 10 km buffer around the cluster to represent anthropogenic influence. Protected areas, including Indigenous lands, were classified according to RAISG (2023), distinguishing between protected and non-protected areas. For more detailed information on variable-selection data processing, see *Appendix C. Variable details*.

Methodological covariates: To account for differences among clusters (our sampling units), we considered three variables describing sampling effort: the mean number of trap-deployment days, the total number of camera-trap stations, and the area covered by camera traps within each cluster. All environmental and methodological covariates are summarized at the level of the sampling unit.

Analyses

To determine whether the number of jaguar records is influenced by prey composition, habitat, climate and anthropogenic factors, we used a Generalized Linear Model (GLM) with a negative binomial distribution and a log-link function, appropriate for count data with overdispersion and a high proportion of low values. This framework was selected to evaluate broad-scale ecological relationships while accounting for methodological differences among studies, rather than focusing on occupancy or absolute density estimation.

The response variable was the total number of independent jaguar records per cluster, used as a measure of relative abundance. We opted not to standardize records per trap-night, a common practice in camera-trap studies (Rovero and Marshall 2009), which combines distinct components of sampling effort into a single value, because this metric assumes a strictly proportional relationship between records and effort — an assumption not supported by our data. Instead, we explicitly modeled sampling effort as a multidimensional factor, incorporating mean number of trap-deployment days, the number of camera-trap stations,

and the study-area size. Each of these components influenced detectability in distinct and potentially non-linear ways, meaning that two surveys with identical trap-night values could yield different detection probabilities depending on how effort was temporally or spatially distributed. By treating these variables separately rather than collapsing them into a single standardized index or offset, our analyses capture their unique contributions and reduce the risk of bias. In addition, trap-nights represent cumulative effort, calculated as the number of cameras multiplied by the mean number of days they were deployed, but this metric does not explicitly reflect the number of cameras nor the spatial extent they cover — that is, the effective size of the study area sampled, both of which can strongly influence detection probability. Although the number of cameras and the area covered were correlated, they affected detectability in distinct ways, warranting their inclusion as separate covariates rather than merging them into a single standardized rate. To further evaluate the assumption underlying trap-night standardization, we tested the relationship between records and the three effort components by adding a quadratic term to linear models; the significance of this term indicated deviations from linearity (Table S2; Snedecor and Cochran 1967), which is an assumption of the GLMs.

We modeled the number of independent jaguar records using a negative binomial error distribution using GLM, including methodological variables as covariates to represent the multidimensional structure of sampling effort. We had to log-transform and standardized these variables to meet the linearity assumptions of the model. With this approach, we preserved the statistical properties of count data, accommodated heterogeneous sampling designs, and avoided imposing unsupported assumptions of proportionality between effort and detections.

Magnitudes of effects and patterns of distribution

We calculated pseudo- R^2 values based on deviance, following the expression:

$$R^2_{deviance} = 1 - (model\$deviance / model\$null.deviance).$$

First, we fitted a model including only methodological variables to isolate their contribution and obtained R^2_{method} . Next, we fitted the complete model, which included methodological, prey, environmental, and anthropogenic variables, and obtained R^2_{total} . To estimate the proportion of variance explained by ecological variables independent of methodological variables, we used:

$$\begin{aligned} & \text{Explained by prey, environmental, and anthropogenic predictors} \\ &= (R^2_{total} - R^2_{method}) / (1 - R^2_{method}) \end{aligned}$$

This approach allowed us to quantify the relative contribution of methodological factors versus predictors of interest to the overall patterns observed.

To visualize broad-scale spatial variation in jaguar-record intensity while reducing the influence of uneven sampling effort, we modeled the number of jaguar records per cluster using a GLM with a negative binomial distribution. The model included the following methodological predictors: the mean number of trap-deployment days, the total number of camera-trap stations, and the size of the study area, allowing us to isolate and remove variation attributable to sampling factors. We then extracted the model residuals, which capture variation unexplained by methodological variables, and adjusted them to a positive scale by adding the absolute value of the most negative residual for visualization purposes. Although these residuals are useful for visualization, they should not be used for statistical analyses in a two-step procedure (Jackson 2022). These adjusted residuals were used to generate a spatial distribution map and represent broad-scale variation in jaguar-record intensity across space while reducing bias associated with heterogeneous sampling effort. As residuals represent variation remaining after accounting for methodological factors, they may also reflect spatial variation in relative abundance. The use of residuals is a common procedure when the effect of one variable hides the effect of another or the target variable cannot be measured directly (Kugler 1983).

In addition, to evaluate whether these residuals could be interpreted as an index of relative density, we compared deviations in the number of jaguar records from those expected based solely on sampling effort with independent density estimates reported by Alvarenga et al. (2025) for 13 sites in common across the Amazon. Specifically, residuals were calculated as the difference between observed and expected counts from the generalized linear model including only effort-related covariates for our entire data set, thus representing departures from the values predicted by sampling effort alone. We then fitted a linear regression to assess the relationship between these residuals and jaguar densities estimated using spatially explicit capture–recapture methods. In a further attempt to calibrate the relationship between the number of records in camera traps and estimate of density, we used all sites ($n=22$) investigated by Alvarenga et al. (2025) and the results are reported in Supplementary Material—An attempt at calibration of density indices (Fig. S7).

We also conducted alternative analyses frequently used in the literature using approaches that do not fully account for the structure of our data and basic statistical principles. Although these approaches are subject to heightened type-II errors, they did not alter any of our principal conclusions. We provide the results for these in Supplementary Material—Alternative analyses and additional details. All analyses were performed in R version 4.4.2 (R Core Team 2024).

Spatial autocorrelation in model residuals was assessed using Moran's I (Bivand 2022). Spatial relationships among sampling sites were defined using a k -nearest neighbors approach based on site centroid coordinates ($k = 5$), with row-standardized spatial weights. Moran's I was calculated on residuals from the final model, and significance was assessed using permutation tests. The test indicated only weak and statistically non-significant spatial autocorrelation (Moran's I = 0.0063, $p = 0.389$). (Fig. S3). Model adequacy was assessed using DHARMA residual diagnostics, which indicated no significant deviations from uniformity, dispersion, or zero inflation (Supplementary Fig. S4).

Multicollinearity was evaluated using Variance Inflation Factors (VIF) in R (package car). It was not necessary to account for multicollinearity, as all VIF values were low (< 2.563).

Results

Factors associated with jaguar relative abundance

The number of jaguar records was strongly influenced by methodological variables. Records increased with the mean number of trap-deployment days, the total number of

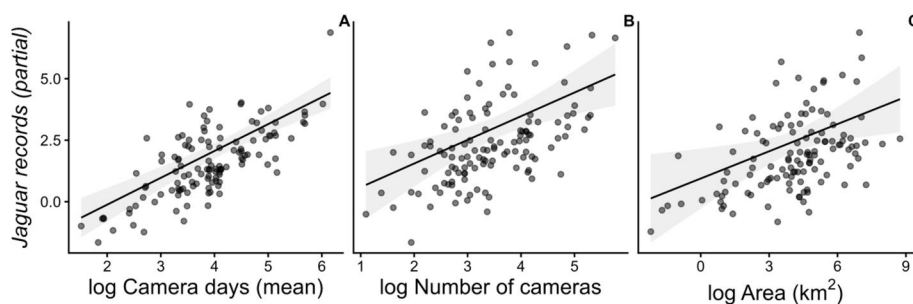


Fig. 1 Partial relationships between log-transformed sampling-effort variables and the response variable (number of records of jaguar). Black dots ($N=122$) indicate observed values of the variable after taking into account the other variables, while the black trend line shows the model's fitted function. The grey shaded area represents the 95% confidence interval, reflecting model uncertainty. (A) The X-axis represents the log-transformed mean camera days, while the Y-axis shows the model's fitted response. (B) The X-axis shows the log-transformed number of cameras. (C) The X-axis describes the log-transformed sampled area (km^2)

Table 1 Negative binomial GLM results for the number of independent jaguar records across 122 Amazonian sites. The model tested effects of methodological variables (mean trap-deployment days, number of cameras and study-area size), prey composition (NMDS axes), environmental conditions (principal components PC1 and PC2), distance to watercourses (m), maximum cumulative water deficit (MCWD), human footprint (HFP) and protected areas. Bold values indicate statistically significant effects ($P < 0.05$). Jaguar relative abundance increased with sampling effort, varied with prey composition, and decreased with MCWD

Predictor	Estimate	Std. Error	Pr(> z)
(Intercept)	-4.539	0.809	<0.001
Log Camera days (mean)	1.091	0.143	<0.001
Log Number of cameras	0.654	0.184	<0.001
Log Area km^2	0.263	0.101	0.009
NMDS1	-0.792	0.292	0.007
NMDS2	0.665	0.345	0.054
PC1	-0.061	0.072	0.400
PC2	-0.158	0.133	0.233
Distance to water	-0.000	0.000	0.471
MCWD	0.003	0.001	0.019
HFP	-0.073	0.051	0.152
Protect Areas (IL)	-0.303	0.296	0.305

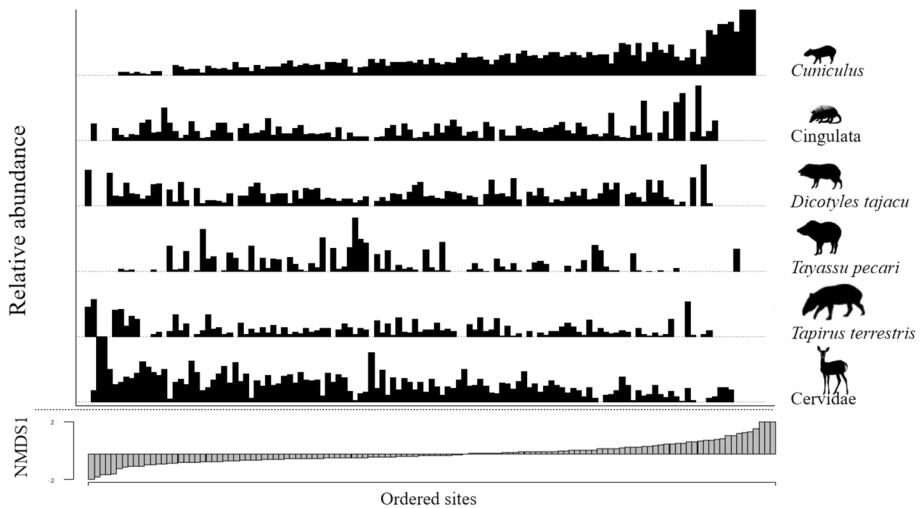


Fig. 2 Distribution of prey taxa across sites, ordered by the first NMDS axis (NMDS1—associated with small-bodied prey). The upper panels show bar plots of within-species relative abundance for each prey taxon (*Tayassu pecari*, *Tapirus terrestris*, *Dicotyles tajacu*, *Cuniculus*, *Cingulata*, and *Cervidae*) across sites, arranged by NMDS1 score (X-axis). The Y-axis indicates relative abundance for each taxon. The lower panel displays the corresponding NMDS1 values for the same sites, ranging from negative (left) to positive (right), illustrating the compositional gradient that structures prey distribution

camera-trap stations, and the size of the study area (Fig. 1). The relationships were linear only on a logarithmic scale (Table S2), and the magnitude of effects varied among variables. Together, these effort-related variables explained most (59%) of the variance in jaguar records (pseudo- $R^2 = 0.594$).

After accounting for the strong effects of methodological predictors (Table 1), the remaining variables explained only 10% of the variance not captured by the methodological model (pseudo- $R^2 = 0.096$). This value was calculated as the difference between the pseudo- R^2 of the full model (0.633) and that of the model including only methodological variables (0.594), divided by the variance unexplained by the latter ($1 - 0.594$). Prey composition and maximum cumulative water deficit (MCWD) were the only variables associated with jaguar records and together explained 7.1% of the variance that remained unexplained after accounting for methodological variables.

Jaguar relative abundance was associated with gradients in prey community composition summarized by NMDS axes. NMDS1 reflected variation in prey assemblages, with paca contributing strongly to the positive end of the gradient, whereas NMDS2 captured a gradient toward assemblages characterized by large-bodied prey, particularly white-lipped peccaries and tapirs (Figs. 2 and 3). Jaguar relative abundance decreased significantly along NMDS1 (Table 1; Fig. 4A), whereas it showed a marginally positive association with NMDS2 (Table 1; Fig. 4B). Jaguar records decreased with more negative mean MCWD values, with lower records associated with more severe drought conditions (Table 1; Fig. 4C).

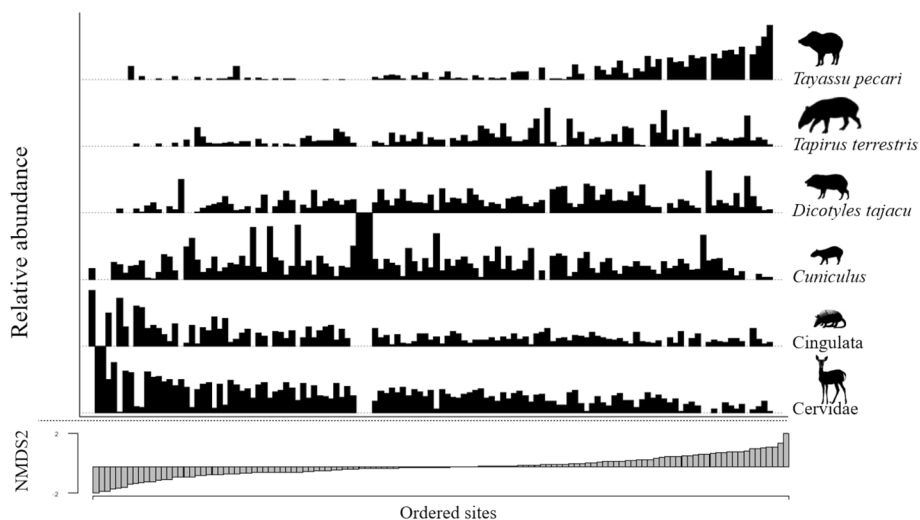


Fig. 3 Distribution of prey taxa across sites, ordered by the second NMDS axis (NMDS2—associated to large-bodied prey). The upper panels show bar plots of within-species relative abundance for each prey taxon (*Tayassu pecari*, *Tapirus terrestris*, *Dicotyles tajacu*, *Cuniculus*, *Cingulata*, and *Cervidae*) across sites arranged according to their NMDS2 scores (X-axis). The Y-axis indicates relative abundance for each taxon. The lower panel displays the corresponding NMDS2 values for the same sites, ranging from negative (left) to positive (right), illustrating the compositional gradient that structures prey distribution

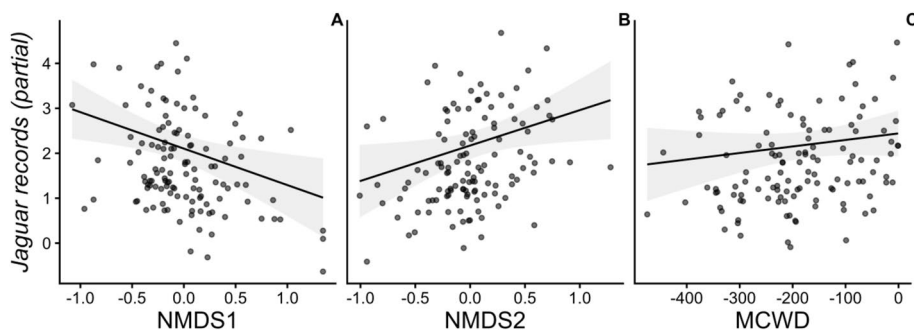


Fig. 4 Partial regression plots from the negative binomial model relating jaguar records to prey composition and climatic conditions. Black dots represent observed sampling units ($n = 122$) after controlling for the effects of all other predictors in the model. Black trend lines indicate fitted effects and grey shaded areas represent 95% confidence intervals. **(A)** Jaguar records decreased with increasing NMDS1 of prey composition ($\beta = -0.792 \pm 0.292$ SE, $P = 0.007$). **(B)** Jaguar records showed a positive trend with increasing NMDS2 of prey composition ($\beta = 0.666 \pm 0.345$ SE, $P = 0.054$). **(C)** Jaguar records increased with increasing mean cumulative water deficit (MCWD; $\beta = 0.003 \pm 0.001$ SE, $P = 0.019$), i.e., less negative values

None of the environmental variables, including the two PCA axes (PC1 and PC2) and distance to water, or anthropogenic variables, such as the Human Footprint Index and protected area, showed a statistically significant association with jaguar records (Table 1; Supplementary Fig. S5A–E).

Patterns of jaguar distribution

After controlling for variation in sampling effort (Fig. S6), the adjusted model residuals—used here as proxies for relative jaguar abundance—highlight areas with higher or lower detections than expected by sample effort (Fig. 5). Across most sites, relative abundance did not vary greatly from expected, although the lowest values were generally observed in the far southern and central-western locations.

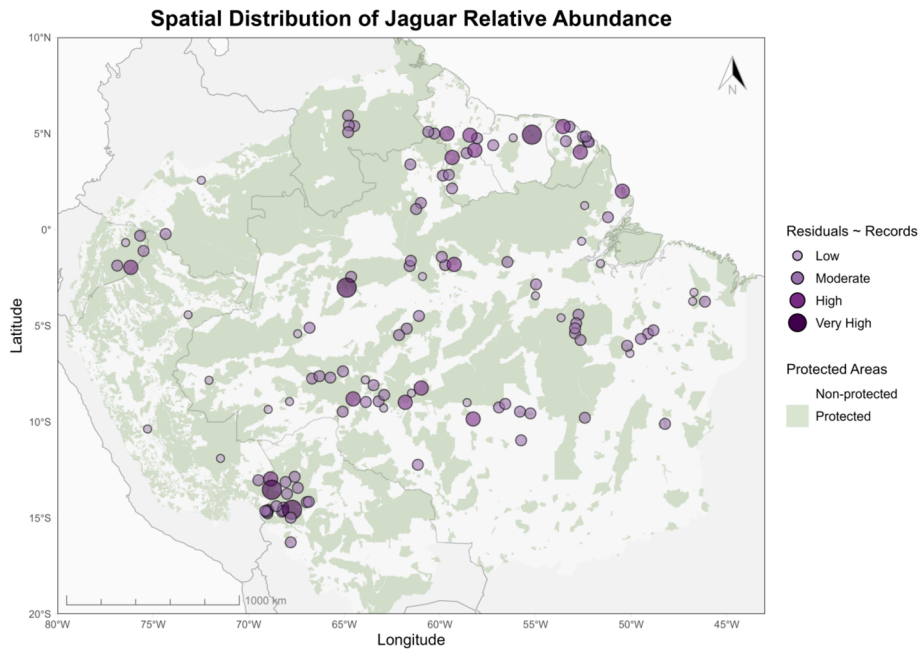


Fig. 5 The map illustrates the spatial distribution of jaguar relative detection-corrected density across the Amazon after accounting for methodological variables. Each circle represents a sampling unit ($n = 123$), with the circle's size indicating the magnitude of deviation from the number of records expected given the sampling effort. Larger and darker circles correspond to higher residual values (i.e., more records than expected), and smaller, lighter circles correspond to lower residual values (i.e., fewer records than expected). Green areas correspond to protected areas

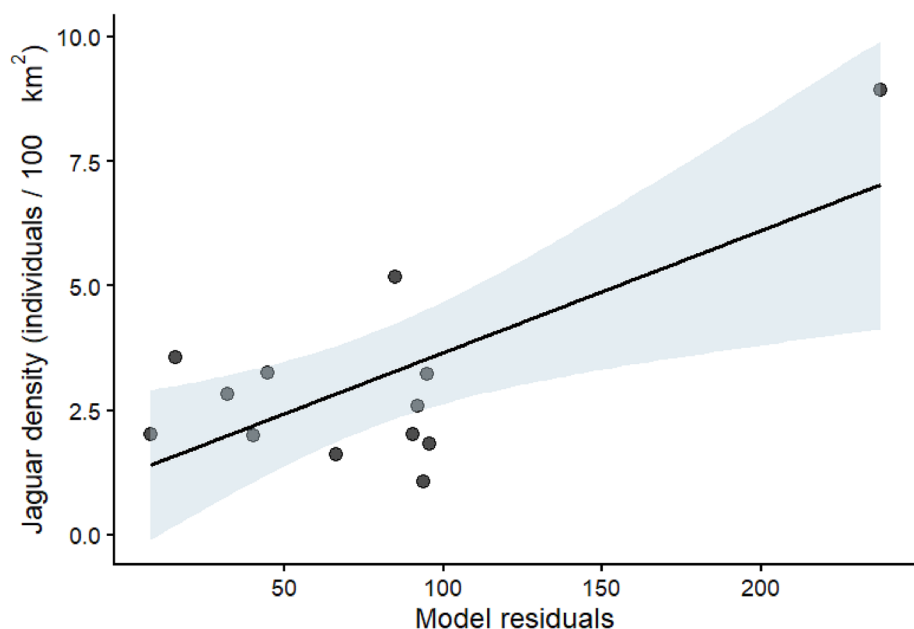


Fig. 6 Relationship between the residuals of jaguar records (observed – predicted, after controlling for days of camera operation, number of cameras, and sampled area) and estimated jaguar densities (individuals/km²) from Alvarenga et al. (2025). Each point represents a study area ($n = 13$). The black line shows the linear-model fit (Density ~ Residual), with the shaded blue area indicating the 95% confidence interval. The relationship is positive and statistically significant ($\beta = 0.024$, $p = 0.008$, $R^2 = 0.47$), but is driven only by the influence of one point

There was a positive relationship between model residuals and independent jaguar-density estimates across 13 Amazonian sites ($R^2 = 0.47$; Fig. 6). However, this relationship was strongly influenced by the Mamirauá site and was not retained when this site was excluded. We also compared the residuals with the larger set of density estimates reported by Alvarenga et al. (2025), but the large confidence intervals around these estimates precluded a precise calibration of the residual index (Supplementary Fig. S7).

Discussion

Variation in the number of independent jaguar records was largely explained by methodological factors related to sampling effort. However, after accounting for effort-related variation within the model, prey composition and MCWD variables explained additional, independent variation in jaguar detections. Our results suggest that some prey groups, including larger-bodied or more gregarious species, may influence jaguar records, corroborating previous studies (Weckel et al. 2006; De Thoisy et al. 2016; Azevedo et al. 2022). Jaguars were more frequently recorded in areas with prey assemblages dominated by species typically classified as large-bodied, mostly notable *Tayassu pecari*, and less frequently in areas with higher representation of smaller-bodied prey, such as *Cuniculus*. These patterns are consistent with previous studies reporting jaguar associations with medium- to large-bodied prey

across ecosystems (Tirelli et al. 2019; Foster and Harmsen 2022; Entringer et al. 2022), while shifting to smaller species in overhunted or heavily deforested landscapes (Miranda et al. 2018; Metz et al. 2023). Notably, the large-bodied prey species most strongly associated with higher jaguar relative abundance (e.g., *T. pecari*, *T. terrestris*) are also among the least resilient to human pressures. Thus, our findings likely reflect not only prey composition but also the disproportionate impacts of anthropogenic activities, ranging from indirect effects such as prey overhunting to direct effects on jaguars, including retaliatory killing (Inskip and Zimmermann 2009). In some areas, higher proportions of pacas may indicate more degraded habitats, as this medium-sized prey species tolerates disturbance and readily adapts to fragmented landscapes (León et al. 2016), which are typically associated with lower jaguar records.

Covariation among prey community composition, human pressures, and environmental conditions makes it difficult to isolate the influence of individual prey species on jaguar distribution, and these relationships are likely to be strongly context-dependent. Moreover, aquatic and semi-arboreal prey (e.g., fish, caimans, sloths, and primates) were not included in our analyses due to methodological constraints, despite evidence that these resources can represent key components of jaguar diets in highly productive landscapes, such as seasonally flooded protected areas (Rabelo et al. 2019; Ramalho et al. 2021; Eriksson et al. 2022). In such systems, aquatic resources may play a disproportionate role in shaping jaguar space use and can contribute to unusually high population densities, as documented in several Amazonian floodplain environments (Eriksson et al. 2022, 2025; De Barros 2025; Alvarenga et al. 2025). Consequently, differences in the availability of aquatic resources across Amazonian landscapes may help explain regional variation in jaguar distribution patterns that are not fully captured by terrestrial-prey metrics alone.

None of the environmental PCA axes showed a significant association with jaguar relative abundance. This included gradients summarizing vegetation and productivity indices, despite previous studies reporting positive associations between jaguar density and vegetation structure, such as tree cover (Jędrzejewski et al. 2018; Morato et al. 2018), and productivity (e.g., NPP; Alvarenga et al. 2025). Elevation has also been identified as a limiting factor for jaguar distribution in the Caatinga (Morato et al. 2014; Astete et al. 2017) and in different regions of Mexico (Rodríguez-Soto et al. 2011). However, most of these analyses are based on a limited number of locations within the Amazon or on a few ecoregions across the species' range (Thompson et al. 2021), and environmental associations may therefore vary among ecosystems and spatial scales. In dry environments, such as the Caatinga and the Cerrado, jaguars occur at lower densities and use space more extensively, as individuals require larger areas to meet energetic demands under lower resource availability (Thompson et al. 2021). At local scales, habitat use may also be weaker in highly productive environments. For instance, jaguars exhibit no clear habitat preference in várzea forests (Montanarin et al. 2023), suggesting that in resource-rich systems selection may become less sensitive to habitat heterogeneity (Gaudry et al. 2018). In contrast, more recent multi-site evidence indicates that jaguars consistently select productive, heterogeneous, and well-preserved forests, regardless of human activity levels (Morant et al. 2025). These contrasting findings suggest that relationships between jaguar abundance and environmental conditions may depend on spatial scale and ecological context. As the vegetation-related variables explained only about 4% of the variance not accounted for by the methodological variables, our main conclusion is that jaguars in the Amazon are highly generalist in habitat use.

Although jaguar habitat use can be influenced by access to water (Morato et al. 2018; Thompson et al. 2023), proximity to watercourses was not a significant predictor of jaguar records in our analyses. In the Amazon biome, water is generally not a limiting resource, given the high density of rivers, streams, and seasonally flooded areas (Junk et al. 2011; Ribas et al. 2025), which results in relatively low spatial variation in water availability among sampling units. Across the jaguar's distribution, resource-selection studies indicate that selection for watercourses occurs mainly in regions where water is scarce or spatially heterogeneous (Morato et al. 2018). In contrast, in landscapes with widespread water availability, habitat selection becomes largely independent of proximity to water (Montanarin et al. 2023). Consistently, individuals located closer to water sources show no detectable selection for watercourses, suggesting that water ceases to be a discriminating factor under high availability (Thompson et al. 2021).

Used as a proxy for the average intensity of the dry season, MCWD was positively associated with jaguar records, indicating that jaguar records were lower in drier areas. Although dry periods can drive substantial changes in mammal communities, their effects on jaguars appear to be strongly context- and scale-dependent. Such climate-driven changes may alter resource availability and animal movements, with potential consequences for jaguar space use (Sepulveda et al. 2026). Expected climatic changes and increasing aridification may therefore have strong direct and indirect effects on jaguars (Jędrzejewski et al. 2017). Studies from the Pantanal indicate that jaguars can persist during short drought periods, potentially because access to aquatic prey may buffer them against drought-related impacts (Eriksson et al. 2025). Seasonal hydrological changes may also concentrate aquatic prey in areas near water, potentially maintaining prey availability for jaguars during dry periods. However, successive drought events over short time intervals can lead to population declines (Burrage et al. 2020), while increasing aridification may increase jaguar extinction risk, as arid and less productive habitats are associated with higher extirpation rates (Jędrzejewski et al. 2017). As extreme droughts intensify, understanding their temporal effects and species-specific ecological responses will become increasingly important (de Barros et al. 2025). These concerns are particularly relevant in Amazonian floodplains, where jaguar populations can occur at high densities but are increasingly exposed to extreme climate events (Sepulveda et al. 2026). The Amazon faces increasing threats from extreme climate events, yet remains overlooked in large-scale conservation planning.

In addition to ecological drivers, jaguar relative abundance showed a negative association with Human Footprint levels, although this relationship was not statistically supported ($\beta = -0.073$, $SE = 0.051$, $p = 0.152$). The lack of a detectable association does not necessarily indicate an absence of responses to anthropogenic pressure, which may vary with the intensity and context of human disturbance. At larger spatial scales, jaguars exhibit human-avoidance behavior regardless of population density (Morato et al. 2018), and may adopt compensatory strategies such as increasing the distance traveled to locate suitable habitats and avoid disturbance (Morato et al. 2016). In human-modified and fragmented landscapes, jaguars may also expand their home ranges (Thompson et al. 2021) or modify their activity patterns in response to anthropogenic pressures (Morant et al. 2025). At local spatial scales, however, responses to human presence can be context-dependent. In the Atlantic Forest, jaguars concentrate in primary forests and dense marshes and avoid disturbed habitats (Cullen Junior et al. 2013), whereas in highly productive Amazonian flooded forests (várzeas) within a Sustainable Development Reserve, jaguars may tolerate rather than avoid

human settlements, likely reflecting lower levels of anthropogenic pressure (Montanarin et al. 2023). Thus, anthropogenic pressure may influence jaguar ecology through responses that are not necessarily reflected in relative abundance, particularly given the predominance of protected areas in our dataset.

Notably, protected areas did not show a significant association with jaguar records in our models. This likely reflects the relatively low variation in deforestation and habitat conditions within Amazonian protected areas in our dataset, where many sites remain comparatively intact, limiting our ability to detect differences attributable to protection status. However, this does not imply that protected areas are sufficient on their own to ensure jaguar persistence, as their effectiveness is strongly influenced by surrounding landscape conditions, edge effects, and matrix quality (Woodroffe and Ginsberg 1998). Protected areas remain essential components of jaguar conservation and act as key refuges across their range (Mena et al. 2020; Menezes et al. 2021), but their role is context-dependent and may vary across biomes. In more heavily modified systems such as the Atlantic Forest and Cerrado, where habitat loss and fragmentation are more severe, jaguar persistence is expected to depend more strongly on the presence and effective management of protected areas and the surrounding landscape context.

Although our analyses indicate that jaguars are adaptable and do not show strong spatial variation in abundance across sites, this pattern must be interpreted in light of our sampling context: most sites were in continuous forest. Jaguars fare much worse in landscapes with open vegetation, deforestation, or higher human densities (Ribeiro-Souza et al. 2024). Climate models further warn of the potential for large-scale forest dieback (Nobre et al. 2009). Should this occur, jaguars in Amazonia are likely to become as vulnerable as those in other biomes.

Methodological and monitoring considerations

Camera traps are widely used in wildlife monitoring due to their non-invasive nature and capacity for long-term, large-scale data collection (O'Connell et al. 2011). However, despite calls for standardized survey designs (Kelly 2008; Sunarto et al. 2013), standardization remains uncommon because of heterogeneous research objectives, logistical constraints, and habitat variability. To address these challenges, we incorporated key methodological covariates as analytical controls, improving comparability across studies with differing designs. In doing so, our study also contributes to reducing the geographic bias in camera-trap research, as the Amazon remains underrepresented despite its high biodiversity and increasing anthropogenic pressures (Oliver et al. 2023; Mugerwa et al. 2024). Our study therefore refines methodological interpretation and helps fill a critical gap in geographic knowledge of one of the world's most ecologically significant tropical-forest systems.

Our results suggest that using the residual variation after accounting for sampling effort was an appropriate choice, as it provides a potentially meaningful index of jaguar relative abundance and reveals relationships that cannot be detected using only presence=absence data. The positive relationship observed between our residuals and independent jaguar density estimates from Alvarenga et al. (2025), who estimated jaguar densities at 13 of our sites using mark-recapture methods, provides some support for this interpretation. However, this relationship was driven exclusively by one site in várzea habitat and was not retained when this site was excluded. An additional comparison using all 22 sites investigated by Alva-

renga et al. (2025) provided limited evidence for a consistent relationship (Supplementary Fig. S7), while the large confidence intervals associated with several of the independent density estimates prevented precise calibration of our residual index against density. Despite this limitation, the observed relationship is consistent with the possibility that residual variation captures ecological differences in local jaguar abundance rather than simply random noise, as reported for some ungulates (Rovero and Marshall 2009). Although our residuals were not designed to estimate density, their potential to capture relative variation in abundance may make them useful for comparative analyses and meta-analyses where standardized density estimates are scarce or unavailable (Rovero and Marshall 2009). Nevertheless, differences in sampling design, data quality, and spatial coverage between studies, together with the relatively small number of sites and the correlative nature of the comparison, warrant caution in interpreting the residuals as an index of local abundance. More precise independent density estimates will be needed to establish the relationship between camera-trap-based indices and true jaguar density in Amazonian forests.

The lack of significant spatial autocorrelation suggests that the variable of interest is not strongly clustered or over-dispersed across space at the scale of our study. This indicates that the observed patterns are unlikely to be driven by spatially structured processes, supporting the use of standard statistical models that assume independent observations. After accounting for variation in sampling effort among studies, jaguar relative abundance showed only moderate variation across most sites, and the remaining factors explained only 10% of the variance not explained by our measures of effort. The main spatial pattern evident in the distribution map was the lower relative abundance of jaguars in the west, particularly in the former Pebas system, indicating that jaguars are very adaptable; a conclusion in line with previous studies (Watkins et al. 2015; Morato et al. 2023).

Caveats

We found three limitations that highlight avenues for future research. 1) Although our model identified methodological variables as strong predictors of jaguar relative abundance, environmental and prey-related variables showed limited predictive power across the Amazon. This may partly reflect the species' generalist behavior and the relatively low variability in these covariates across our study sites, particularly given that most of our data come from protected areas, many of which remain relatively intact. Thus, the influence of these variables may be difficult to detect at the broad spatial scale considered here. 2) We were unable to assess the availability of other prey groups, such as aquatic species (e.g., fish, caimans, turtles) and domestic animals in areas with human presence, which may also influence jaguar distribution. We modelled prey composition, but prey abundance could be important too, although getting abundance for species such as peccaries and tapir are hard given their low densities and large territories. 3) Because our sampling was biased toward protected lands, we cannot draw firm conclusions about the effectiveness of protection status alone in securing viable populations. Broader sampling outside protected areas is needed to clarify these patterns.

Conclusion

Our results highlight prey composition as an important predictor of jaguar spatial patterns, reinforcing the well-established link between apex predators and prey distribution while extending this evidence to a biome-wide Amazonian context using standardized camera-trap data. Accounting explicitly for methodological variation proved essential to distinguish ecological signals from sampling-related effects, as ignoring effort-related covariates can generate biased spatial patterns and misleading inferences. Consistent with previous assessments, our findings support the view that the Amazon remains one of the main strongholds for jaguar populations, supported by extensive areas of continuous forest, including protected areas and Indigenous lands. As most study sites were located within protected areas, the lack of a detectable association between jaguar relative abundance and human footprint does not necessarily indicate that anthropogenic pressures have no influence on jaguar populations. Further large-scale studies, particularly outside protected areas, are therefore needed to better understand how jaguars respond to varying levels of anthropogenic pressure and to inform conservation strategies under ongoing environmental change. Finally, the association between jaguar relative abundance and drought intensity further suggests that climatic conditions may also shape jaguar populations across the biome. As climate change is expected to increase drought and aridification in parts of the Amazon, understanding how these changes affect jaguars, both directly and through their effects on prey and habitat, will be important for anticipating future changes in jaguar populations across one of the world's most important ecosystems for jaguar conservation.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10531-026-03461-2>.

Acknowledgements AM This study was financed in part by the Fundação de Amparo à Pesquisa do Estado do Amazonas – Brasil (Fapeam). We thank Daniel Bastos Pimenta for providing technical support in generating the raster of protected areas. We thank the Wildlife Conservation Society (WCS) and the MONITORA Program (ICMBio) for providing substantial datasets that were fundamental to this study. We are also grateful to all collaborators and institutions involved in the collection, management, and sharing of the raw camera-trap data that enabled this research. ACA thanks German Research Foundation (DFG—FZT 118, 202548816). FB thanks CNPq grant #312878/2023-0. CRF thanks CNPq, Bolsa de Produtividade (308657/2023-3). ABC thanks Bolsa de doutorado—CNPq. AGM thanks PPBio Amazônia Ocidental (CNPq, processos nº 441260/2023-3 e 441228/2023-2), INCT-CENBAM (CNPq, processo nº 406474/2022-2). CAP is supported by a Frontiers Planet Prize from the Frontiers Research Foundation. CD thanks Instituto Chico Mendes de Conservação da Biodiversidade—ICMBIO. CR is supported by CAPES/FAPEAM (grant 88887.174942/2025-00), INCT-SinBiAm (grant CNPq Nº 406767/2022-0), INCT-CENBAM (grant CNPq Nº 406474/2022-2) and PPBio (grant CNPq 441260/2023-3 and 441228/2023-2). DGR This study was made possible through financial and logistical support from the Instituto de Desenvolvimento Sustentável Mamirauá (IDSM), the National Geographic Society, the Horodas Family Foundation for Conservation Research, the Explorers Club, the Alongside Wildlife Foundation, and the Hellman Foundation. We are grateful to the managers and staff of Corumbiara State Park (SEDAM-RO), Samuel Ecological Station, Guaporé Biological Reserve, and Pousada Cumaru for logistical assistance, as well as to the Polícia Ambiental de Rondônia for their support during fieldwork in the Guaporé region. We thank numerous field assistants, park rangers and community members for their invaluable help in the field. We are especially indebted to the people of the Ubim and Baré communities for their hospitality and support. D.G. Rocha received a scholarship from CAPES/Doutorado Pleno no Exterior (grant no. 88881.128140/2016-01). Finally, we acknowledge ICMBio/SISBIO (permits 52720-1, 54457-1, 76292) and SEDAM-RO (permit 0028.385509/2019-21) for granting access to protected areas. DJR thanks PPBio (process N. 441228/2023-2 e 441260/2023-3 and INCT—CENBAM Process N. 406474/2022-2). EMV thanks CNPq productivity grant number #308543/2021-1. EARDJC thanks fieldwork was supported by Programa Áreas Protegidas da Amazônia—ARPA. EADP thanks Funding: LCAOF (Liz Claiborne Art Ortenberg Foundation), Global Wildlife Conservation, WWF-

Guianas, USFWS; Field assistants: Chico Mendoza, Diana Fernandes, Angelbert Johnny, Nick Carter, Frank Carter, Rupert Williams, Dexter Torres, Edmund Torres, Huichang Yang, Anupana Puran, Christopher Li. FM receives a productivity scholarship from the CNPq (Process 310573/2021-1). GDSFN thanks The Rufford Foundation (20754-1). HDOBD thanks Pós graduação em Biodiversidade Tropical (PPGBio) Universidade Federal do Amapá (UNIFAP). Programa Nacional de Cooperação Acadêmica da Amazônia (PROCAD-AM/CAPES, no. 88887.200472/ 2018-00). Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). Instituto Chico Mendes para conservação da Biodiversidade (ICMBio) e WWF-Brasil. JAC thanks Monitores de Umancia Eroinano J+kanua Uai (Resguardo Indígena Predio Putumayo) and Mesa de Gobernanza Corredor del Jaguar Guaviare. JTT thanks the National Council for Scientific and Technological Development (CNPq) for financial support: Universal (#409827/2021-5 and #459735/2014-4) and Pro-Amazônia (#444350/2024-1). J.J.T. was supported by CNPq with a Research Productivity Scholarship (#316281/2021-2). LP thanks Biologists and Parabiologists who made possible the data collection: Biologists: Antonio Belandria, Isabel Villamil, Carlos Valeris, Igor Castillo, Luis Sibira. Parabiologists: Elso Espinoza, Williams Sarmiento, Orlando Rodriguez. MB thanks CNPq productivity for the grant 304189/2022-7. PAJ thanks TEAM data were provided by the Tropical Ecology Assessment and Monitoring (TEAM) Network, a collaboration between Conservation International, the Smithsonian Institution and the Wildlife Conservation Society. PO thanks Research at Brownsberg was financially supported by the Belgian Directorate-General for Development Cooperation (DGDC) and the Flemish Interuniversity Council (VLIR-UOS)(2015-2016), and by WWF-Guianas (2021-2022). IUCN Netherlands funded the jaguar research at Kabalebo (2021-2022). RRH thanks the National Council for Scientific and Technological Development—CNPq (process: 302928/2025-1). RBW thanks Wildlife Conservation Society (given that a large 24% of the camera trap data was provided by WCS). RF thanks National Council for Scientific and Technological Development (PELD-POPA; project numbers 441443/2016-8; 445954/2024-8); Coordination for the Improvement of Higher Education Personnel (PROCAD-Amazônia, project number 88887.200472/2018-00). RGM thanks FAPESP (#08461-8/2017). SE thanks Estación Científica Yasuni, Pontificia Universidad Católica del Ecuador. TOL thanks para os dados da região do: Parque Nacional do Monte Roraima Agradecimentos ao Conselho do Povo Indígena Ingarikó, e as pessoas das comunidades Karumambatei, Mapaé e Pipi do Manalai, que permitiram e apoiaram o monitoramento da fauna em seus territórios ancestrais. Parque Nacional do Viruá e Estação Ecológica de Maraca;Agradecimentos aos gestores, auxiliares de campo, agentes temporários ambientais e monitores do Programa Monitora. WEM was supported by CNPq grants Bolsas de Produtividade em Pesquisa 406474/2022-2 and INCT da Biodiversidade Amazônica 01.02.016301.02394/2024-50, and FAPEAM grants INCT da Biodiversidade Amazônica 152/2024 and Projeto:Análise da distribuição e impacto de mudanças climáticas em mamíferos neotropicais 01.02.016301.01102/2023-80.

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Funding The Article Processing Charge (APC) for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614). Fundação de Amparo à Pesquisa do Estado do Amazonas.

Data availability A subset of the dataset generated and analyzed during the current study is publicly available through Zenodo (<https://doi.org/10.5281/zenodo.6325578>) and corresponds to Antunes et al. (2022) – AMAZ ONIA CAMTRAP: A dataset of mammal, bird, and reptile species recorded with camera traps in the Amazon. However, due to the sensitive nature of species occurrence data and to protect the locations of threatened species, the full datasets are not publicly available. These data can be made available by the corresponding author upon reasonable request.

Declarations

Conflicts of interest No conflicts of interest.

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