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EDITED BY
Eric Stolen,
University of Central Florida, United States

REVIEWED BY
Dipanjana Naha,
Cheetah Conservation Fund, Namibia
Milena Cambrero,
School for Field Studies, United States

*CORRESPONDENCE
Samantha Zwicker
✉ sjzwicker@hojanueva.org

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Persecuted mammals as indicators of moderate human disturbance in the Peruvian Amazon

Samantha Zwicker^{1*}, Dylan Singer¹ and Beth Gardner²

¹Hoja Nueva, Puerto Maldonado, Madre de Dios, Peru, ²School of Environmental and Forest Sciences, University of Washington, Seattle, WA, United States

Human population growth, land conversion, and hunting are accelerating defaunation in tropical forests. We asked how anthropogenic and ecological factors shape the site use (occupancy) of medium- to large-bodied mammals in an unprotected Amazonian landscape. From 2015–2022 we deployed camera traps at 293 stations across 12 spatially independent grids in four areas along the Las Piedras River, Madre de Dios, Peru. Using single-season, single-species occupancy models for 17 species, we evaluated anthropogenic covariates (distance to settlements, proximity to agriculture, land-use class: Conservation vs Mixed-Use) and environmental covariates (macrohabitat: floodplain vs terra firme, distance to river, Enhanced Vegetation Index, small/large prey indices). Detection was modeled with trail type (human vs wildlife trails/roads) and operable trap nights. We recorded 14,849 detections. Persecuted species showed strong responses to human disturbance: lowland tapir occupancy was lower near agriculture, and jaguar avoided agricultural sites. Environmental gradients were also important: for example, collared peccary occupancy increased near rivers, and ocelot and lowland tapir were more frequent in floodplain forest. Detection varied among species and was influenced by trail type—large felids were more often detected on human trails, whereas some prey were more frequently detected on wildlife trails. Both anthropogenic pressure and habitat features structure mammal assemblages in this unprotected region. Persecuted species provide sensitive indicators of ecosystem condition in mixed-use forests. Management should prioritize protecting riverine habitats and mitigating disturbance near agriculture, while tailoring actions to species-specific responses.

KEYWORDS

anthropogenic effects, biodiversity conservation, camera traps, defaunation, occupancy modeling, *Panthera onca*, prey dynamics, *Tapirus terrestris*

Introduction

Throughout the tropics, rapid human population growth has driven extensive land conversion, primarily fueled by resource-based economies in developing countries (Beaudrot et al., 2016). This conversion is largely due to agriculture, roads, and extractive activities, resulting in habitat loss and increased hunting pressure (Espinosa et al., 2014; Di Minin et al., 2016). Significant land-use change has occurred in Amazonian rainforests of Brazil and Peru, particularly near newly established road networks branching from the Interoceanic Highway (Chávez Michaelsen et al., 2013).

Subsistence hunting and slash-and-burn agriculture further affect mammal survival and distribution in tropical forests (Naughton-Treves et al., 2003; Peres, 2001). Human activities increase mortality through hunting, roadkill, and disrupted predation cues, altering species' foraging and activity patterns (Mendes et al., 2020). Wildlife abundance is often more affected by hunting patterns than by habitat size or forest type (Peres, 2000). Increased hunting accessibility reduces game species and apex predators like jaguars (*Panthera onca*), whose densities are significantly lower in accessible areas (Espinosa et al., 2018). Predator declines closely track prey declines due to habitat loss and hunting (Boron et al., 2019; Fuller and Sievert, 2001). Fine-scale habitat use of jaguars and pumas (*Puma concolor*) is best explained by prey availability, with larger prey determining predator carrying capacity (Palomares et al., 2016; Santos et al., 2019; Terborgh and Estes, 2010). Predicting wildlife spatial patterns requires integrating geographic, ecological, and anthropogenic factors.

Degradation can have complex biological effects beyond overt habitat loss. Even Amazonian forests with intact canopy cover may become “empty”—that is, functionally depauperate—through unsustainable hunting (Benítez-López et al., 2019). A pan-tropical synthesis shows that more than half of nominally intact forests exhibit significant mammal declines, indicating that defaunation can precede, and be more pervasive than, deforestation itself. This underscores the need to incorporate hunting pressure into assessments of ecosystem condition, not just visible indicators of land-use change.

Defaunation, driven by human activity, exacerbates biodiversity loss in tropical ecosystems (Beaudrot et al., 2016). Benítez-López et al. (2017) estimated that mammal abundance is, on average, 83% lower in hunted areas than in undisturbed sites. Persistent exploitation by human hunters has caused population declines and near-extinctions of large-bodied mammals, particularly in tropical ecosystems (Bush et al., 2015; Jorge et al., 2013). Defaunation can have far-reaching effects on ecosystem structure and function, including disruptions in dispersal mutualisms and biomass decline (Peres et al., 2016; Gil-Sánchez et al., 2021).

We use the term “persecuted species” to describe those facing high levels of human exploitation—intensive hunting for bushmeat, illegal wildlife trade, or retaliatory killings due to human-wildlife conflict, including real or perceived threats to humans, livestock, or agricultural production. This classification, informed by regional reports, expert interviews, field observations, and a synthesis of literature and expert opinion (e.g., Beck-King et al., 1999; Jędrzejewski et al., 2017; Morcatty et al., 2020; Peres, 2000; Reyna-Hurtado and Tanner, 2007),

differentiates these species from those experiencing lower hunting pressure. Examples include apex predators like jaguars and ocelots (*Leopardus pardalis*), often targeted for their pelts or seen as threats to livestock, and high-market-value prey species such as lowland tapirs (*Tapirus terrestris*) and white-lipped peccaries (*Tayassu pecari*).

Despite their ecological importance, the impacts of less visible threats like hunting and wildlife extraction remain poorly studied, particularly outside protected areas (Espinosa et al., 2018). Wildlife populations are typically higher in protected regions, underscoring their value for biodiversity (Benítez-López et al., 2017). However, monitoring wildlife in human-modified landscapes is crucial because ecological processes can degrade over time without apparent signs (Jorge et al., 2013). To address this challenge, we applied an occupancy modeling framework that accounts for imperfect detection while incorporating both environmental and anthropogenic covariates to estimate site use probability.

Peru has become a hotspot for wildlife trade in Latin America, with widespread exploitation and poorly regulated exportation of live animals and parts (D'Cruze et al., 2021). Community-based monitoring highlights how subsistence hunting and market demand for wild felids threaten local wildlife populations, with regional differences in hunting practices shaping local impacts (Valsecchi et al., 2023). The most commercially valuable bushmeat species include white-lipped peccary, collared peccary (*Pecari tajacu*), brocket deer (*Mazama* spp.), lowland tapir, paca (*Cuniculus paca*), and agouti (*Dasyprocta* spp.) (Espinosa et al., 2014). Hunters' prey choice often correlates with biomass and ease of capture, particularly as communities transition from traditional subsistence hunting to market-driven activities (Bodmer, 1995). Prior to CITES implementation in 1975, overexploitation across Latin America led to the harvest of 228,376 jaguar skins and 17,301 ocelot skins, decimating populations (Mena et al., 2021). Felid declines impact prey populations and trigger broader changes in ecosystem structure (Sandom et al., 2017).

Our study focused on the occupancy and probability of use of 17 mammal species within an unprotected landscape in Peru. Las Piedras, an unprotected river basin in Madre de Dios, Peru, provides a critical lens into the effects of moderate anthropogenic disturbance—characterized by selective logging, small-scale agriculture, and dispersed hunting pressure, but without the large-scale deforestation, industrial agriculture, or road density typical of high-impact frontiers—on Amazonian mammal communities. Unlike heavily fragmented frontiers or strictly protected parks, this region retains large tracts of forest under sustained pressure from nearby settlements, making it an ideal setting to study early-stage defaunation and species-specific responses. We incorporated environmental and anthropogenic covariates—such as distances between camera trap stations and settlements and agricultural areas—into an occupancy modeling framework that accounts for imperfect detection. Although the Las Piedras region experiences moderate deforestation compared to other areas in Madre de Dios, we hypothesized that mammal occupancy would still be shaped by anthropogenic threats. We predicted that highly persecuted species—particularly the two most persecuted cats (jaguar and ocelot) and the six prey species of the highest market value (lowland tapir, white-lipped peccary, brocket deer, collared peccary,

paca, and agouti)—would show the strongest responses to human disturbances. Our goal was to assess whether moderate human impact is accelerating defaunation in this biodiversity hotspot, potentially affecting ecosystem interactions across human-modified Amazonian landscapes. Although our study region is often described as a mosaic of Indigenous and non-Indigenous lands, our sampling was restricted to areas surrounding two non-Indigenous settlements—Puerto Nuevo and Puerto Lucerna. These communities differ in their cultural histories and land-use strategies, which are indirectly captured in our modeling via covariates such as proximity to agriculture and a land-use index.

Methods

Study area

The study was conducted in the Madre de Dios (MDD) region of the Peruvian Amazon, a biologically rich but increasingly fragmented area of lowland rainforest. Though official land-use

classifications designate areas for non-timber forest product extraction, native community use, and conservation, actual land use frequently diverges. Informal logging, subsistence hunting, and unregulated agricultural expansion have created a dynamic mosaic of forest cover, contributing to varying levels of anthropogenic pressure (Asner et al., 2010).

Our study spanned four distinct survey areas (Figure 1), together covering approximately 450 km² along the Las Piedras River. Area A, the Las Piedras Conservation Corridor, was surveyed across six field seasons and represents a relatively intact forest landscape under active protection by Hoja Nueva and its partners. Area B encompassed a network of selectively logged forests between the Interoceanic Highway and Puerto Lucerna. Area C focused on the forests surrounding the remote settlement of Puerto Nuevo, while Area D covered a deforested and fragmented cacao-producing region near the Lucerna agricultural association.

These four areas were deliberately chosen to represent a gradient of human disturbance along the Las Piedras River. Area A, the Las Piedras Conservation Corridor, serves as a low-

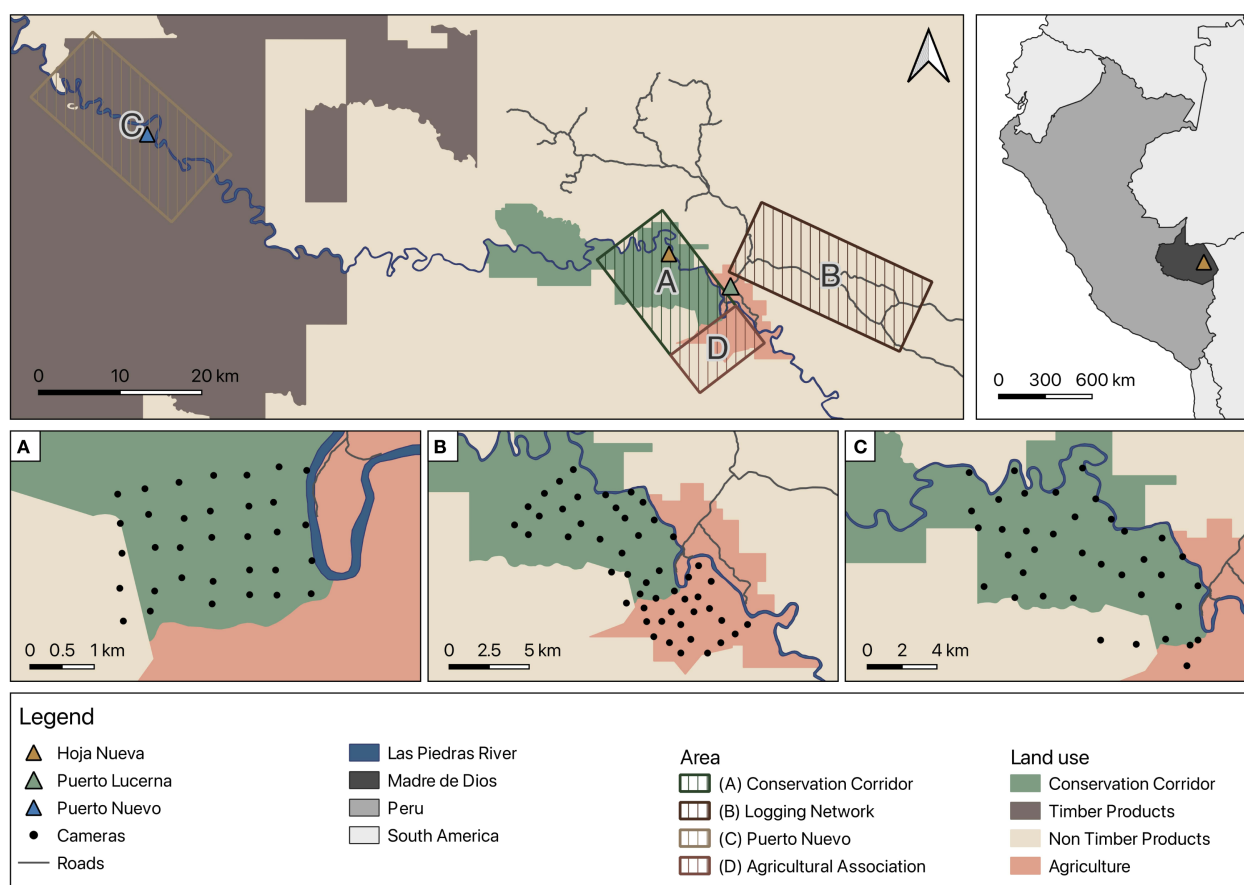


FIGURE 1

The study was conducted across four distinct areas along the Las Piedras River in the Madre de Dios region of Peru (Southern Hemisphere UTM Zone 19, Easting: 408473, Northing: 8665291). The Las Piedras Conservation Corridor (Area A), was surveyed six times between 2018 and 2022 with a total of 170 camera trap stations. Area B, a logging road network, was sampled in 2015 with 27 stations; Area C, a remote Indigenous settlement, was sampled in 2017 with 46 stations; and Area D, a cacao agricultural association, was sampled between 2018 and 2021 with 50 stations. Two settlements are indicated with triangles: Puerto Nuevo (an Indigenous subsistence hunting settlement) and Lucerna (a migrant agricultural settlement). Insets show example spatial layouts: (A) one of the 2022 margay-focused grids (reduced spacing), (B) a 2021 standard grid targeting ocelots, and (C) a 2019 standard grid used for large felids.

disturbance reference site due to its continuous forest cover, minimal human presence, and active protection. Area B represents moderate disturbance, where selective logging and canopy openings occur along a network of access roads. Area C is influenced primarily by subsistence hunting pressure from the settlement of Puerto Nuevo, with little agricultural clearing, placing it in the low-to-moderate disturbance category. Area D reflects the high-disturbance end of the gradient, with extensive small-scale agricultural conversion—primarily cacao and papaya—resulting in fragmented forest and reduced canopy integrity. By capturing this disturbance spectrum, our study areas allow direct comparison of mammal occupancy across varying intensities and types of human impact, improving interpretation of species-specific responses to both habitat alteration and direct exploitation.

The two communities adjacent to our study areas—Puerto Nuevo and Puerto Lucerna—differ markedly in cultural origin and land-use intensity. Puerto Nuevo was established in the early 2000s by families migrating from the Yine Indigenous community of Monte Salvado. It remained without formal land tenure until 2022 and is characterized by dispersed bushmeat hunting and timber extraction with minimal farming. In contrast, Puerto Lucerna is a migrant agricultural settlement composed largely of people from Ayacucho, who have engaged in substantial forest clearing for small-scale cacao and papaya cultivation. These divergent land-use strategies are reflected in the spatial patterns of disturbance across our study grids, with Area C experiencing localized hunting pressure and Area D showing broad-scale habitat conversion. The research was conducted from a permanent field station operated by Hoja Nueva along the Las Piedras River, located approximately 70 km northwest of Puerto Maldonado.

Focal species

In conservation science, indicator species reflect specific environmental conditions, such as habitat quality or ecosystem health (Caro, 2010). These species help monitor biodiversity and ecosystem processes, providing an efficient way to detect ecological shifts. Traditional indicators often respond to natural environmental gradients like water quality, forest structure, or habitat connectivity. Building on this concept, we propose *human impact indicators*—species whose distribution and abundance reveal patterns of anthropogenic stress, such as hunting pressure and proximity to agriculture. The persecuted species in our study serve as human impact indicators in tropical ecosystems, similar to large mammals used to assess global human impacts (Morrison et al., 2007). Monitoring these species provides a critical measure of anthropogenic disturbance, ecosystem health, and resilience.

Our study focused on five felid species and 12 prey species, many of which are either data deficient or threatened with extinction locally or globally (Table 1). The five sympatric felid species in our region include the jaguar, puma, ocelot, jaguarundi (*Herpailurus yagouaroundi*), and the margay (*Leopardus wiedii*). The 12 terrestrial prey species we included in our study included the lowland tapir, giant armadillo (*Prionomys maximus*), giant anteater

(*Myrmecophaga tridactyla*), white-lipped peccary, brocket deer, collared peccary, *Dasypus armadillos* (*Dasypus* spp.), paca, agouti, common opossum (*Didelphis marsupialis*), green acouchi (*Myoprocta pratti*), and the Brazilian rabbit (*Sylvilagus brasiliensis*).

We classified eight species as persecuted species in our study area due to documented high levels of hunting, conflict, and wildlife extraction in Madre de Dios including jaguar, ocelot, lowland tapir, white-lipped peccary, brocket deer, collared peccary, paca, and agouti. During intensive logging in the Las Piedras River basin, structured interviews and field surveys documented an estimated monthly harvest of 41,282 kg of bushmeat—primarily large-bodied mammals such as peccaries, tapir, brocket deer, agouti, and paca—across 231 logging camps, of which 176 were operating inside protected areas (Schulte-Herbrüggen and Rossiter, 2003, unpublished report). Jaguars are also targeted directly or killed in retaliation, with ongoing livestock depredation and poaching pressures driving the implementation of regional conflict response programs in Madre de Dios (WWF-Peru, 2023). These documented patterns are consistent with observations from local communities, markets, and hunting camps in the Las Piedras and Puerto Maldonado regions (S. Zwicker, pers. comm.), where these same species remain the most common wild meats sold and the primary sources of human-wildlife conflict. Rescue center records further corroborate these trends, with a disproportionately high number of orphaned individuals from these taxa entering the wildlife trade compared to non-persecuted species.

Camera trapping

We placed 293 camera trap stations in four study areas from 2015 to 2022. In total, we conducted 12 spatially independent grid deployments (Table 2): six in Area A, one in Area B, one in Area C, and four in Area D. The Las Piedras Conservation Corridor (Area A) was sampled six times with 170 unique station locations, and the fragmented agricultural region (Area D) was surveyed in four separate grid deployments between 2018 and 2022, with 50 unique station locations in total (Table 2). The logged forest (Area B) was sampled once in 2015 with 27 stations, and the remote Indigenous settlement of Puerto Nuevo (Area C) was sampled once in 2017 with 46 stations.

Primary inter-station spacing for standard grids targeting medium-large felids ranged from ~0.93–1.54 km (locations in Figure 1; design details in Table 2), following established guidelines for surveying medium-sized felids—particularly ocelots—to ensure adequate coverage while minimizing spatial autocorrelation (Maffei and Noss, 2008). This design aligns with ocelot home-range studies in tropical forests (males $\approx$ 38.8 km²; females $\approx$ 17.4 km²; Crawshaw, 1995) and the principle that grids should encompass at least one average home-range diameter. In 2022, we used reduced spacing (~0.43–0.44 km) in two margay-focused grids to increase detections of this smaller, more arboreal, low-density felid (Zwicker et al., 2024).

We aimed to operate cameras for roughly three months during the dry or dry-wet transition season (July–December) to minimize

TABLE 1 Data for all 17 focal species including their weight range, ecological role, IUCN red list status, and Peru Red Book status.

Species	Weight range (kg)	Ecological role	IUCN status	Peru red book status	Citations
Jaguar (<i>Panthera onca</i>)	30 - 120	Hypocarnivore/Apex Predator	Near Threatened	Near Threatened	(Emmons and Feer, 1999; IUCN, 2022; SERFOR (Servicio Nacional Forestal y de Fauna Silvestre), 2018)
Puma (<i>Puma concolor</i>)	22 - 80	Hypocarnivore/Apex Predator	Least Concern	Near Threatened	(IUCN, 2022; Moreno et al., 2006; SERFOR (Servicio Nacional Forestal y de Fauna Silvestre), 2018)
Ocelot (<i>Leopardus pardalis</i>)	8 - 18	Hypocarnivore/Mesopredator	Least Concern	Unlisted	(IUCN, 2022; Moreno et al., 2006)
Jaguarundi (<i>Herpailurus yagouaroundi</i>)	4.5 - 9	Hypocarnivore/Mesopredator	Least Concern	Unlisted	(IUCN, 2022; Santos et al., 2019)
Margay (<i>Leopardus wiedii</i>)	3 - 8	Hypocarnivore/Mesopredator	Least Concern	Data Deficient	(IUCN, 2022; Santos et al., 2019; SERFOR (Servicio Nacional Forestal y de Fauna Silvestre), 2018)
Lowland Tapir (<i>Tapirus terrestris</i>)	150 - 250	Herbivore/Seed Disperser	Vulnerable	Near Threatened	(IUCN, 2022; Padilla and Dowler, 1994; SERFOR (Servicio Nacional Forestal y de Fauna Silvestre), 2018)
Giant Armadillo (<i>Priodontes maximus</i>)	28 - 44	Insectivore/Ecosystem Engineer	Vulnerable	Vulnerable	(IUCN, 2022; SERFOR (Servicio Nacional Forestal y de Fauna Silvestre), 2018; Silveira et al., 2009)
Giant Anteater (<i>Myrmecophaga tridactyla</i>)	27 - 39	Insectivore	Vulnerable	Vulnerable	(IUCN, 2022; Medri and Mourão, 2005; SERFOR (Servicio Nacional Forestal y de Fauna Silvestre), 2018)
White-Lipped Peccary (<i>Tayassu pecari</i>)	25 - 35	Omnivore/Seed Predator/Ecosystem Engineer	Near Threatened	Near Threatened	(Kiltie and Terborgh, 1983)
Brocket Deer (<i>Mazama</i> spp.)	11.4 - 30	Herbivore/Seedling Predator	Data Deficient	Data Deficient	(Emmons and Feer, 1999; IUCN, 2022; Richard-Hansen et al., 1999; SERFOR (Servicio Nacional Forestal y de Fauna Silvestre), 2018)
Collared Peccary (<i>Pecari tajacu</i>)	15 - 25	Herbivore/Seed Predator/Ecosystem Engineer	Least Concern	Unlisted	(IUCN, 2022; Kiltie and Terborgh, 1983)
Armadillo (<i>Dasypus</i> spp.)	3 - 13	Insectivore/Ecosystem Engineer	Data Deficient	Unlisted	(IUCN, 2022; Richard-Hansen et al., 1999)
Paca (<i>Cuniculus paca</i>)	5.2 - 9.5	Herbivore/Seed Predator	Least Concern	Unlisted	(IUCN, 2022; Richard-Hansen et al., 1999)
Agouti (<i>Dasyprocta variegata</i>)	3 - 5.8	Herbivore/Seed Predator	Least Concern	Unlisted	(IUCN, 2022; Richard-Hansen et al., 1999)
Common Opossum (<i>Didelphis marsupialis</i>)	0.6 - 2	Omnivore/Scavenger	Least Concern	Unlisted	(IUCN, 2022; Richard-Hansen et al., 1999)
Green Acouchi (<i>Myoprocta pratti</i>)	0.6 - 1.8	Herbivore/Seed Predator	Least Concern	Unlisted	(IUCN, 2022; Richard-Hansen et al., 1999)
Brazilian Rabbit (<i>Sylvilagus brasiliensis</i>)	0.7 - 1	Herbivore	Least Concern	Unlisted	(IUCN, 2022; Richard-Hansen et al., 1999)

trap loss; when cameras remained in the field longer, we truncated effort to 100 days per station to standardize sampling across sites. Although grid locations and spacing varied among years due to logistics and target species, we mitigated potential temporal and spatial bias by restricting sampling to consistent seasonal windows. Because most grids were not re-sampled annually and grid size varied, we fit single-season occupancy models but included Year and Grid in the candidate model set to account for temporal and spatial structure where supported by the data.

Camera trap stations were placed along wildlife trails, human trails, and roads. Across all areas, 153 stations were positioned on human-made trails/roads and 140 on wildlife trails; wildlife trails were used at grid points only when a human-made trail or road was unavailable within 100 m. Following Kelly et al. (2012), trail placement was used to enhance detection probabilities, particularly for medium-to-large carnivores that use trails as movement corridors, while recognizing potential bias toward species that preferentially use trails (Harmsen et al., 2010). Each

TABLE 2 Sampling areas, dates sampled, the number of stations during each, and the average camera spacing.

Area	Dates	Stations (n)	Average spacing
A	September 2018 – January 2019	25	1466m
A	September – December 2019	32	1426m
A	July – October 2021	27	1283m
A	November 2021 – January 2022	25	1038m
A	July – September 2022	33	428m
A	October 2022 – January 2023	28	443m
B	August – November 2015	27	1417m
C	August – October 2017	46	928m
D	October 2018 – January 2019	8	1129m
D	September – December 2019	6	1540m
D	July – October 2021	22	1042m
D	October 2021 – January 2022	14	1334m

station consisted of one or two Browning BTC-5/BTC-6 cameras mounted ~40–50 cm above ground and configured to capture videos.

Covariates

To evaluate how bottom-up habitat features and human disturbance shape mammal site use, we modeled two detection covariates and eight occupancy covariates. Continuous predictors were z-scored before analysis, and pairwise correlations were low ($|r| < 0.70$).

Anthropogenic covariates (occupancy):

- Distance from settlement (km; continuous) — Euclidean distance from each site to the nearest settlement centroid (Puerto Lucerna or Puerto Nuevo), derived with ArcGIS *Near* using mapped GPS coordinates (mean = 6.775 km; range = 1–22 km) (Esri, 2015). Greater distances index lower hunter accessibility (e.g., Nagy-Reis et al., 2017).
- Proximity to agriculture (categorical) — ≤ 500 m ($n = 35$) vs > 500 m ($n = 258$) from any mapped farm > 4 ha (handheld-GPS mapping of active fields). We used a categorical threshold to (i) reflect expected non-linear edge/human-use effects around fields and homesteads and (ii) reduce spatial error from boundary mapping; 500 m captured the observed zone of frequent human use in our system.

- Land-use index (categorical) — Conservation ($n = 159$): inside the Las Piedras Conservation Corridor (LPCC); Mixed-use ($n = 134$): outside the LPCC where settlements, farms > 4 ha, and Brazil-nut concessions occur and where we recorded vehicles, hunting, or timber extraction.

Environmental covariates (occupancy):

- Macrohabitat (categorical) — Floodplain ($n = 119$) vs terra firme ($n = 174$), classified from a local DEM and detailed transition-zone mapping.
- Small-prey index (continuous) — captures of prey < 5 kg per trap-night (mean = 0.312; range = 0–2.438).
- Large-prey index (continuous) — captures of prey > 5 kg per trap-night (mean = 0.496; range = 0–2.475).
- Enhanced Vegetation Index (EVI; continuous) — MOD13A1 v6 (Didan, 2015; USGS EarthExplorer) extracted within a 500-m neighborhood around each site; imagery taken the week prior to each grid's survey (mean = 0.595; range = 0–1).
- Distance to river (km; continuous) — distance to the GPS-mapped Las Piedras River main channel; the river course was GPS-tracked three times to build a high-accuracy river layer prior to computing distances with ArcGIS *Near* (mean = 2.362 km; range = 0.03–15.4 km).

Detection covariates:

- Trail type (categorical) — On-trail ($n = 153$) cameras on human trails/roads vs Off-trail ($n = 140$) on wildlife trails.
- Trap nights operable (continuous) — number of nights a camera was functional (mean = 75; range = 10–100).

For interpretation, we distinguish LPCC (Conservation) from the surrounding matrix (Mixed-use)—a mosaic with agriculture, settlements, and extractive activities—because species responses often differ sharply between these land-use regimes.

Occupancy analysis

All data analyses were carried out using R (R Core Team, 2022) in RStudio (RStudio Team, 2020). Encounter histories were generated from camera trap footage using the “camtrapR” package (Niedballa et al., 2016) based on predetermined sampling occasions (5 or 10 days). Sampling occasions were tailored by species to reflect detectability and movement ecology. We used 10-day occasions for low-detectability or infrequently recorded species (e.g., jaguarundi, giant armadillo, giant anteater) and 5-day occasions for species with higher per-occasion detections (e.g., jaguar, puma, ocelot, margay and most prey). This design balanced detection and precision across taxa with differing ecological traits. We combined all 293 camera trap stations in one analysis and

treated each as a sampling unit, hereafter "site," for the purposes of occupancy modeling. Each site was considered closed to changes in occupancy during the time it was operational. Due to repeated sampling within study areas and over years, we also considered these covariates in the candidate model set; however, they were correlated with one another and other variables, thus we only included them in a limited set of models and not within the same model.

We used the "unmarked" package (Fiske and Chandler, 2011) to fit single-season, single-species occupancy models (MacKenzie, 2006) for 17 mammal species. Candidate models were defined *a priori* based on ecological predictions for each species or species group (e.g., predators, mesopredators, and prey).

For felids, the global occupancy model was formulated as:

$$\psi_i = \text{logit}^{-1} (\beta_0 + \beta_1 \cdot \text{distanceRiver}_i + \beta_2 \cdot \text{EVI}_i + \beta_3 \cdot \text{preyIndex}_i + \beta_4$$

$$\text{proximityAgriculture}_i + \beta_5 \cdot \text{landUse}_i + \beta_6 \cdot \text{distanceSettlement}_i + \beta_7 \cdot \text{macroHabitat}_i + \beta_8 \cdot \text{area/year}_i).$$

with detection modeled as:

$$p_{ij} = \text{logit}^{-1} (\alpha_0 + \alpha_1 \cdot \text{trail}_{ij} + \alpha_2 \cdot \text{operableNights}_{ij})$$

For large felids (i.e., jaguars and pumas), the preyIndex was the large prey index and for small felids (i.e., margays, ocelots, jaguarundis), the preyIndex was the small prey index, and for all prey species, the preyIndex was excluded. Candidate model sets included up to 18 models representing competing hypotheses (e.g., anthropogenic-only, environmental-only, forage availability, and combined models), allowing us to evaluate the relative importance of human disturbance versus natural environmental drivers. When convergence issues arose for species with limited detections (e.g., white-lipped peccary), the model set was reduced appropriately to avoid overfitting.

Model selection was based on Akaike's Information Criterion corrected for small sample sizes (AICc), and models with $\Delta\text{AICc} < 2$ were retained as the top models (Akaike, 1973). For each species, model-averaged predictions for occupancy (ψ) and detection probabilities (p) were computed by using the AIC weights of the top models. The delta method (Burnham and Anderson, 2002) was used to calculate unconditional standard errors and variances for model-averaged parameter estimates. This approach ensures that model uncertainty is preserved when generating estimates and confidence intervals.

For detection probabilities, predictions were averaged across survey occasions to yield a single detection estimate per site. Site-level occupancy estimates were averaged across all 293 camera trap stations to derive species-level means. For species with large home ranges (e.g., jaguars and pumas), occupancy was interpreted as the probability of site use rather than true occupancy, as independence among sites may not be fully met for wide-ranging species. Conversely, for species with smaller home ranges (e.g., agoutis), occupancy estimates likely reflect true occupancy due to minimal overlap between sites.

As described in the Camera Trapping section, sampling was restricted to the dry and dry-wet transition seasons to mitigate potential temporal bias arising from interannual differences in grid

locations and spacing. By standardizing the sampling period and maintaining consistent environmental conditions across seasons, we ensure that our results reflect meaningful patterns of species occupancy and detection while adhering to the assumptions of a single-season occupancy modeling framework.

Results

Out of the 17 mammal species studied, we recorded a total of 14,849 detections across all sampling grids. The most frequently captured species were agouti (1469 captures) and brocket deer (1604 captures), while the least frequently captured were white-lipped peccary (26 captures) and jaguarundi (32 captures). Sample occasions ranged from 50 to 100 days across study sites. Model-averaged mean occupancy ranged from 0.17 (Brazilian rabbit) to 0.93 (brocket deer), and mean detection probabilities varied between 0.054 (giant armadillo and white-lipped peccary) and 0.40 (agouti and brocket deer). Model-averaged coefficients for occupancy from the top model(s) for all species are provided in Table 3.

Model-averaged coefficients for persecuted species revealed distinct responses to environmental and anthropogenic covariates, highlighting key drivers of occupancy across species (Table 3). Jaguars were negatively associated with proximity to agriculture ($\beta = -1.58$, SE = 0.96, $p = 0.10$) and positively associated with mixed-use areas ($\beta = 1.90$, SE = 0.87, $p = 0.03$), suggesting some tolerance for moderate levels of human disturbance in matrix habitats. Lowland tapirs showed a significant decrease in occupancy within 500 m of agricultural areas ($\beta = -0.99$, SE = 0.48, $p = 0.04$), likely reflecting the combined effects of hunting pressure and reduced habitat quality near farmland.

Environmental predictors, with the exception of prey index, were more often included in the top model overall than anthropogenic covariates. Distance to river was the most commonly included covariate in the top model across species (included for 12 out of 17 species). Puma, ocelot, collared peccary, *Dasybus* armadillo, and Brazilian rabbit had lower occupancy with increasing distance from river ($p < 0.05$); giant armadillo and giant anteater showed the same pattern ($p < 0.1$). Macro-habitat preferences varied across species. Ocelots had higher occupancy in floodplain forest over terra firme forest ($\beta = -1.19$, SE = 0.47, $p = 0.01$) as did lowland tapir ($\beta = -1.42$, SE = 0.45, $p < 0.01$), which may be due to denser vegetation cover in floodplain areas that support these species. In contrast, *Dasybus* armadillos had increased occupancy in terra firme forest (*Dasybus* armadillos: $\beta = 0.71$, SE = 0.36, $p = 0.05$), which may offer refuge from hunting pressure concentrated in lower-elevation floodplain habitats.

EVI, a measure of vegetation greenness, was also an important covariate in determining occupancy probability. EVI had a significant positive effect on the occupancy of giant anteaters ($\beta = 0.76$, SE = 0.26, $p < 0.01$) and lowland tapirs ($\beta = 0.36$, SE = 0.17, $p = 0.03$). Margay occupancy also increased with higher EVI values ($\beta = 0.35$, SE = 0.19, $p = 0.08$), although this relationship was not as strong.

TABLE 3 Single-species occupancy results for the 17 focal species including total captures from camera trap stations, individual sample occasions used in detection histories, covariate estimates for occupancy in each top model (on the logit scale), and the model-averaged mean detection and model-averaged mean occupancy.

Species	Total captures	Agriculture	Settlement	EVI	Terra firme	Prey	River	Mixed-used	Year	Area	Mean detection	Mean occupancy
Jaguar	186	-1.58*	-0.33					1.90	–		0.07	0.61
Puma	366					0.29*	-0.37				0.13	0.64
Ocelot	787				-1.19		-0.39				0.21	0.82
Jaguarundi	32					0.56					0.08	0.19
Margay	123			0.35*	-0.23		0.29		**	–	0.06	0.46
Lowland Tapir	852	-0.99	0.10	0.36	-1.42		0.07	0.00			0.26	0.79
Giant Armadillo	75				-1.76		-0.74*				0.05	0.63
Giant Anteater	97			0.76	-0.23		-0.44*				0.08	0.55
White-Lipped Peccary	26		-0.44	0.34	0.55		-0.15	-0.76			0.05	0.28
Brocket Deer	1604	-0.99*	-0.07	0.37	0.93		0.51	-1.48			0.40	0.93
Collared Peccary	1030	-0.32	0.44	0.15			-0.62	-0.63		**	0.35	0.85
Armadillo	266			0.22	0.71		-0.54		**		0.14	0.43
Paca	740						-0.11			*	0.27	0.61
Agouti	1469								**		0.40	0.82
Common Opossum	588								**	**	0.22	0.58
Green Acouchi	264									**	0.16	0.34
Brazilian Rabbit	123	0.49		-0.36			-1.00	1.19			0.15	0.17

Bolded values indicate a p-value < 0.05, values with an * indicate a p-value < 0.10; for year and area, ** indicates at least one of the category estimates had a p-value < 0.05, * indicates at least one of the categories had a p-value < 0.10 and - indicates the parameter was in the top model.

We found that year entered the top models for a minority of species and showed no consistent increasing or decreasing trend. Year was the only parameter retained in agouti top models and occupancy probability was lowest in year 2022 ($p < 0.05$). Margay occupancy was lowest in 2018 ($p < 0.05$), while small armadillo was highest in 2018 ($p < 0.05$). Opossum had the highest occupancy in years 2019 and 2020 and the lowest in years 2015 and 2017; however only area B was sampled in 2015 and area C in 2017, which may reflect a difference in the features of the areas as opposed to a direct effect of year. Jaguar included year in the top model, but none of the years differed significantly in occupancy probability.

Area was included in the top model set for 5 of 17 species. For green acouchi, area was the only parameter retained in top models; with area C having significantly lower occupancy probability than other areas ($p < 0.05$). For opossum, Areas B and C had significantly lower occupancy than Area A ($p < 0.05$), which is consistent with our results for the year effect. Similarly, we found collared peccaries had significantly lower occupancy Areas B and D than Area A ($p < 0.05$). Paca had lower occupancy in Area B ($p < 0.10$), while margay models included area but showed no significant effects.

For some species, covariates did not yield significant results, but these patterns still offer insights into their ecological preferences and responses to human activity. White-lipped peccaries were recorded in only 26 instances, and none of the covariates significantly explained their site use. This low detection rate and small sample size limit the interpretability of these results, suggesting potentially low population density or movement patterns that reduce detectability. Similarly, jaguarundis showed no clear association with macrohabitat or anthropogenic covariates, except for a strong relationship with small prey abundance ($\beta = 0.56$, $SE = 0.23$, $p = 0.02$). Other species, such as Brazilian rabbits and brocket deer, exhibited varied responses to mixed-use and agricultural areas, indicating a complex interplay between tolerance to disturbance and habitat preference.

Detection results (final wording). Detection probability varied widely among species and was strongly influenced by trail type; trail placement was a significant predictor for 10 species ($p < 0.05$). Large felids were much more likely to be photographed on human trails/roads: jaguar ($\beta = 0.89$, $SE = 0.21$, $p < 0.01$), puma ($\beta = 1.74$, $SE = 0.18$, $p < 0.01$), and ocelot ($\beta = 1.47$, $SE = 0.11$, $p < 0.01$). Several prey/generalist species also showed higher detection on human trails—lowland tapir, agouti, and common opossum (all $p < 0.05$). In contrast, paca, white-lipped peccary, and brocket deer were more frequently detected on wildlife trails (i.e., lower detection on human trails; $p < 0.01$). These patterns are consistent with many taxa using linear openings as movement routes, while certain prey avoid larger, human-made paths.

The number of camera nights operable also had a significant impact on detection probability for 3 species. Longer operability periods increased detection for green acouchis ($\beta = 0.20$, $SE = 0.11$, $p = 0.07$). Conversely, operable nights had a negative coefficient for collared peccary ($\beta = -0.16$, $SE = 0.05$, $p < 0.01$) and tapir ($\beta = -0.18$, $SE = 0.05$, $p < 0.01$). Often, a longer camera deployment leads to more detections; however, there are some cases when animals may be detected less due to changes in movement over time or other

factors. The relatively low detection probabilities for species such as white-lipped peccaries and giant armadillos highlight the challenge of monitoring these species using camera traps, as their low densities and wide-ranging behavior may reduce the likelihood of encounters with cameras. Across all 17 species, model-averaged detection probabilities ranged from 0.05 for white-lipped peccary to 0.40 for agouti, reflecting substantial interspecific variation in detectability.

Discussion

Our study revealed that mammal occupancy patterns in the Peruvian Amazon are shaped by both anthropogenic and environmental factors, with species responding differently based on their ecological roles and sensitivity to human activities. Persecuted species can act as reliable indicators of ecosystem degradation, guiding conservation in human-modified landscapes. Some showed significant responses to human disturbance, while others were more influenced by proximity to rivers and macrohabitat type. These findings underscore the importance of using indicator species to monitor ecosystem health, particularly in regions where subsistence hunting and habitat fragmentation have synergistic impacts on forest vertebrates (Peres, 2001). Persecuted species offer valuable insights into the intensity and spatial extent of anthropogenic pressures, providing an early-warning tool for conservation efforts in highly impacted landscapes.

Lowland tapirs showed a significant negative relationship with agricultural proximity, consistent with studies linking agricultural expansion to reduced habitat quality through hunting pressure, habitat loss, and restricted water access (Burs et al., 2023; Medici and Desbiez, 2012). Tapirs are frequently targeted by subsistence hunters near agricultural areas, where spotlighting is particularly effective. Forest fragmentation also reduces the abundance of herbaceous plants crucial to their diet (Williams-Linera, 1990). However, their occupancy in mixed-use areas suggests they may persist in less-disturbed matrix habitats with forest connectivity and essential resources.

Jaguars showed a higher probability of using mixed-use areas but avoided agricultural sites. These results suggest that jaguars may use mixed-use areas for movement or as secondary habitat (McBride and Thompson, 2018), while agricultural areas may pose higher risks due to habitat loss and increased human-wildlife conflict (Amador et al., 2013). Agricultural plots often lack sufficient vegetation cover and prey availability, and the presence of livestock without protection increases the likelihood of retaliatory killing by farmers. Mixed-use areas, despite some human disturbance, may retain enough forest cover and prey species to support jaguar persistence (Morato et al., 2018). Similar to findings from other studies, our results emphasize the need for proactive conflict mitigation measures in areas bordering protected forests (Foster et al., 2010; Zeilhofer et al., 2014). Although we did not explicitly include community identity as a covariate in our models, several anthropogenic variables—such as distance from settlements, proximity to agriculture, and a mixed-use land classification—

reflect the spatial influence of local land-use practices. Puerto Nuevo is characterized by low-intensity, dispersed hunting and timber harvesting, while Puerto Lucerna engages more intensively in agriculture-driven forest clearing. These differences help explain spatial patterns in human pressure across our study areas and are captured by our land-use index, which distinguishes between protected and mixed-use zones. We also did not include interaction terms among covariates or species in the modeling framework; however, interactions—particularly between land use, proximity to settlements, and river corridors—may reveal more complex habitat relationships and should be considered in future work.

Environmental variables, particularly proximity to rivers and macrohabitat type, significantly influenced species occupancy. Puma and ocelot occupancy were higher near rivers, likely due to prey availability and access to water, similarly *Dasypus* armadillos and collared peccary occupancy decreased with increasing distance from rivers, reflecting their reliance on riverine habitats for forage and water (Keuroghlian and Eaton, 2008). Seasonal inundations in floodplain forests are critical for determining ungulate habitat use (Bodmer, 1990), with similar patterns observed across Neotropical systems (Boron et al., 2019; Dias et al., 2019). Given the ecological importance of riverine habitats for both wildlife and human communities, future conservation strategies should prioritize protecting these areas from further encroachment.

Macrohabitat type also played a key role in shaping species distributions. Ocelots preferred floodplain forests, which may offer increased prey availability and denser understory for cover (Di Bitetti et al., 2010). Although ocelots avoided agricultural areas, they appeared to tolerate moderate disturbance in mixed-use zones, demonstrating their adaptability in fragmented landscapes. These findings align with research in the Peruvian Amazon showing that ocelots shift their activity patterns temporally to avoid human presence without significantly altering their spatial distribution (Zwicker and Gardner, 2024). Similarly, *Dasypus* armadillos favored terra firme forests, consistent with their preference for well-drained soils (Gonçalves et al., 2022). Jaguarundis were the only predator species positively associated with small prey availability, suggesting a potential prey dependence. Although their cryptic nature and low number of detections complicate definitive conclusions, their habitat associations underscore the importance of diverse ecosystems for supporting predator-prey dynamics and maintaining overall biodiversity.

The strong responses of highly persecuted species—such as jaguar, lowland tapir, white-lipped peccary, brocket deer, collared peccary, and agouti—to anthropogenic pressures demonstrates their sensitivity to ecosystem degradation. Jaguar, lowland tapir, and brocket deer avoidance of heavily altered areas reflects broader patterns of tropical forest degradation, where the loss of apex predators and large herbivores can disrupt ecological balance and trigger cascading effects. Jaguars, as apex predators, can reflect broader ecosystem changes, while brocket deer and lowland tapir offer insights into prey availability and hunting pressure. The loss of large carnivores like jaguars can trigger significant trophic cascades, reshaping entire ecosystems and altering prey dynamics (Ripple et al., 2014). Their persistence is critical for maintaining ecological balance and

biodiversity and they can aid in identifying areas of concern and guiding targeted conservation efforts. Integrating persecuted species data into land-use planning not only helps prioritize critical areas for intervention but also enhances community-led initiatives by providing tangible, locally relevant conservation targets. Similar to the use of large mammals as indicators of global human impacts (Morrison et al., 2007), these persecuted species act as sentinels of ecosystem health in tropical forests. Each of these species displayed significant responses to anthropogenic or environmental covariates, providing early-warning signals of ecosystem degradation. Lowland tapirs and white-lipped peccaries are particularly valuable indicators due to their sensitivity to habitat disturbance and hunting pressure (Fragoso, 2004; Medici and Desbiez, 2012).

White-lipped peccaries were recorded at very low rates and we had no detections in 2018 or 2019. Though a number of covariates were included in the top model for occupancy probability, none were considered significant. This could be attributed to factors such as low population density, recent recolonization following a decline, or wide-ranging movement patterns that reduce detectability in camera trap grids. Previous studies have documented large-scale movements and temporary population declines driven by hunting pressure, disease, and natural cycles (Fragoso, 2004; Fragoso et al., 2022). Our results suggest that more data are required to tease apart factors influencing their occupancy; however, we did find that white-lipped peccaries were less likely to be detected on trails, indicating they are less likely to use human made paths. The variation in detection of white-lipped peccaries, including years with no detections, highlights the importance of long-term monitoring to distinguish short-term fluctuations from long-term trends. Understanding white-lipped peccary population dynamics is crucial given their role as ecosystem engineers and key prey for top predators.

By monitoring these species, conservation practitioners can detect early signs of defaunation and habitat degradation. Protecting riverine habitats and establishing buffer zones around agricultural areas will help mitigate human-wildlife conflict and reduce hunting pressure. Community involvement in conservation initiatives is key to ensuring long-term success. Programs that engage local communities in wildlife monitoring and sustainable land management can help build local capacity and increase stewardship. Developing policies that integrate scientific findings into land-use planning and conflict mitigation can further support these efforts. Collaborative approaches that incorporate both ecological and social perspectives will be essential for balancing conservation priorities with the needs of local communities.

Our study highlights the complex relationships between human activities, habitat characteristics, and mammal occupancy in the Peruvian Amazon. By focusing on persecuted species as human impact indicators, we contribute to a growing body of evidence supporting the use of sensitive species to monitor ecological change and human influence. This approach provides an effective framework for addressing biodiversity loss while fostering sustainable management practices. Targeted strategies addressing specific anthropogenic pressures, coupled with adaptive management and long-term monitoring, will help maintain resilient and biodiverse tropical ecosystems. Future research should continue to refine this framework, incorporating both ecological and social dimensions to

balance conservation goals with community needs. Given the global significance of tropical forests for biodiversity and climate resilience, coordinated international efforts are critical to protect these landscapes before further irreversible losses occur.

Data availability statement

The data that support the findings of this study are openly available in Zenodo at <http://doi.org/10.5281/zenodo.14848173>, reference number 14848173.

Ethics statement

The animal study was approved by Servicio Nacional Forestal y de Fauna Silvestre - SERFOR. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

SZ: Funding acquisition, Investigation, Conceptualization, Software, Visualization, Resources, Writing – review & editing, Project administration, Validation, Writing – original draft, Methodology, Supervision, Formal analysis, Data curation. DS: Funding acquisition, Conceptualization, Resources, Investigation, Writing – review & editing, Writing – original draft, Project administration, Methodology, Visualization. BG: Supervision, Writing – review & editing, Resources, Writing – original draft, Validation, Project administration.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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