Apex Predators & Prey Co-occupancy Drivers in the Tropics

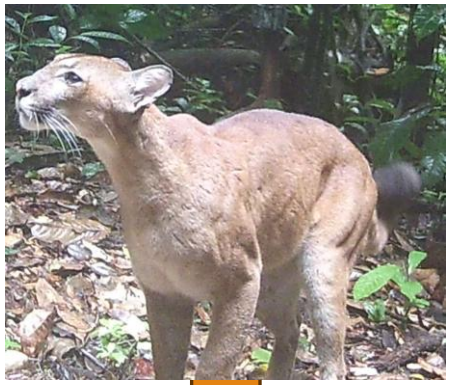
Yeamin Faria Chowdhury

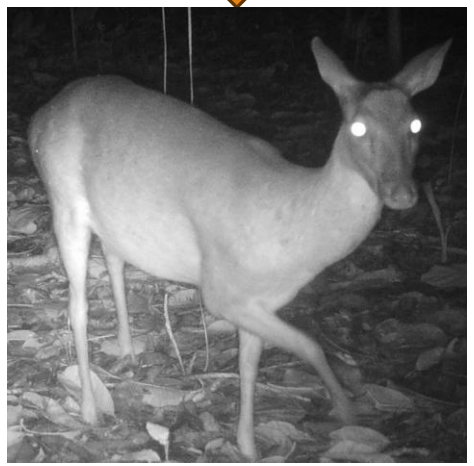
Apex predators' interactions

Apex predators are species at the top of the food chain and play a critical role in the function of the ecosystem balance by controlling prey populations (Brook et al. 2012), structure community composition (Burgos et al. 2024).

Jaguars (*Panthera onca*) and pumas (*Puma concolor*) coexist through dietary segregation, spatial partitioning, and behavioral differences—jaguars specializing on peccaries and pumas on deer (Oliveira, 2002; Cascelli de Azevedo, 2008; Iriarte et al., 1990).

Studies across Latin America show that jaguar and puma habitat use and activity are shaped by prey availability, vegetation, and human disturbance (Alegre et al. 2025; Ávila–Nájera et al. 2020; Ávila-Nájera et al. 2016).





Threats to mammalian habitats

Habitat fragmentation:

"**A large expanse of habitat is transformed into a number of smaller patches of smaller total area, isolated from each other by a matrix of habitats unlike the original**" (Wilcove et al., 1986).

Effects of habitat fragmentation on mammals:

- lower probability of species presence (Chad et al., 2025)
- shift their daily activity patterns (Gaynor et al., 2018; Lee et al., 2024)
- alter predator–prey relationships (Chad et al., 2025)
- increase interspecific competition (Manlick and Pauli, 2020)

Brazilian Amazon photographed by Georg Gerster

How do we study the mammals?

- Camera Trapping as a tool.
- Use of photographic trapping rate (i.e., the number of independent photographs/number of days camera was active) as a proxy to estimate species abundance (Carbone et al., 2001; Debata & Swain, 2018).
- Information on presence-absence data correlates well with population size and can be used to track population trends (Joseph et al., 2006; Pollock, 2006; Ewing & Gangloff, 2016).
- Animal activity involves quantifying how species distribute their behavior across different times of the day.

Problem statement

- Wildlife may not completely avoid human presence and face tradeoffs in allocating their time.
- Fragmented habitats restricts apex predators' movement and disrupt ecosystem functions and services they play (Banks-Leite 2020).
- Most studies have concentrated on protected areas or heavily disturbed sites (e.g. Paemelaere et al., 2025; Harris et al., 2023; Pierre et al., 2020; Pickles et al., 2011).
- There are at least two gaps in understanding…
  - How different external factors affects mammalian behaviors.
  - How different factors are influencing apex predators' presence with their prey
  - How different human presence affect the mammalian behavior and distribution.

To develop conservation strategies that respect cultural traditions while ensuring species sustainability.

To assess their behavioral adaptations and coexistence.

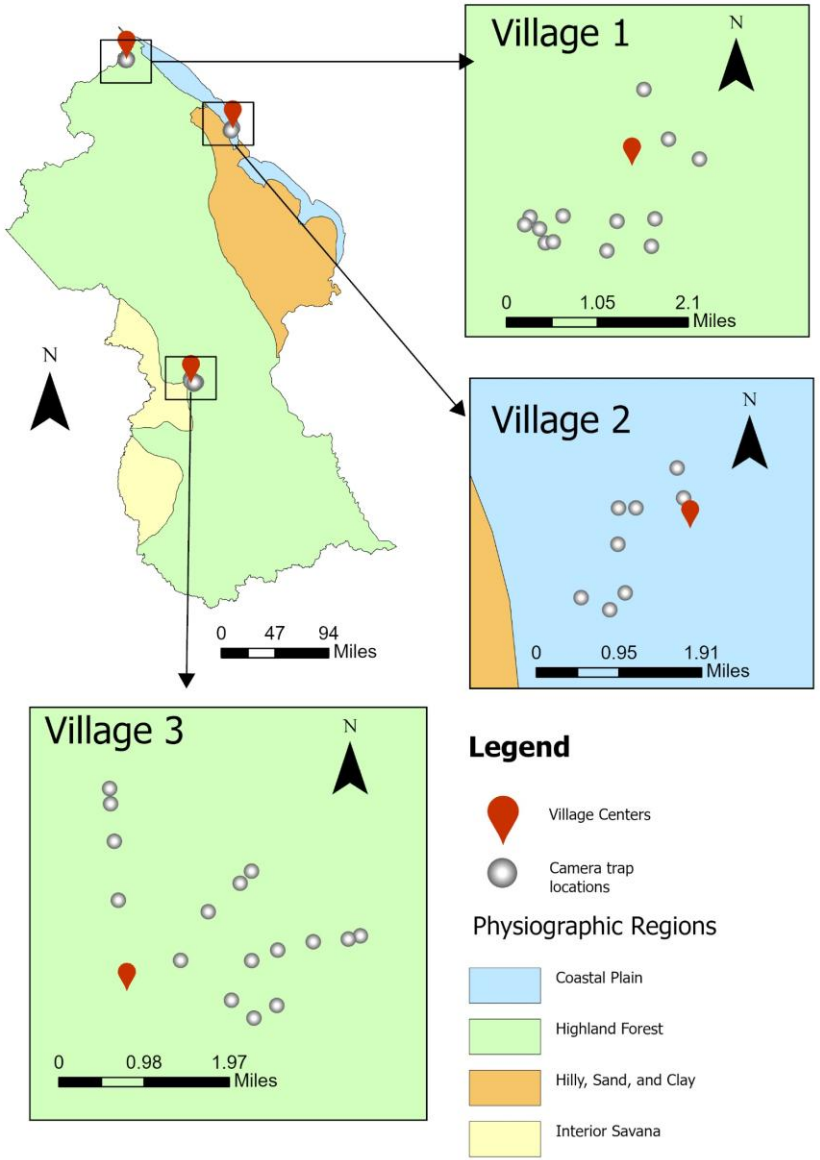
Animal behavior often provides the first warning signs of environmental degradation.

Forests in Guyana

- Guyana has 94% of its total land covered by forest (FAO, 2020).
- Guyana's forests remain largely intact and undisturbed (Guyana Forestry Commission, 2007).

Study areas peoples

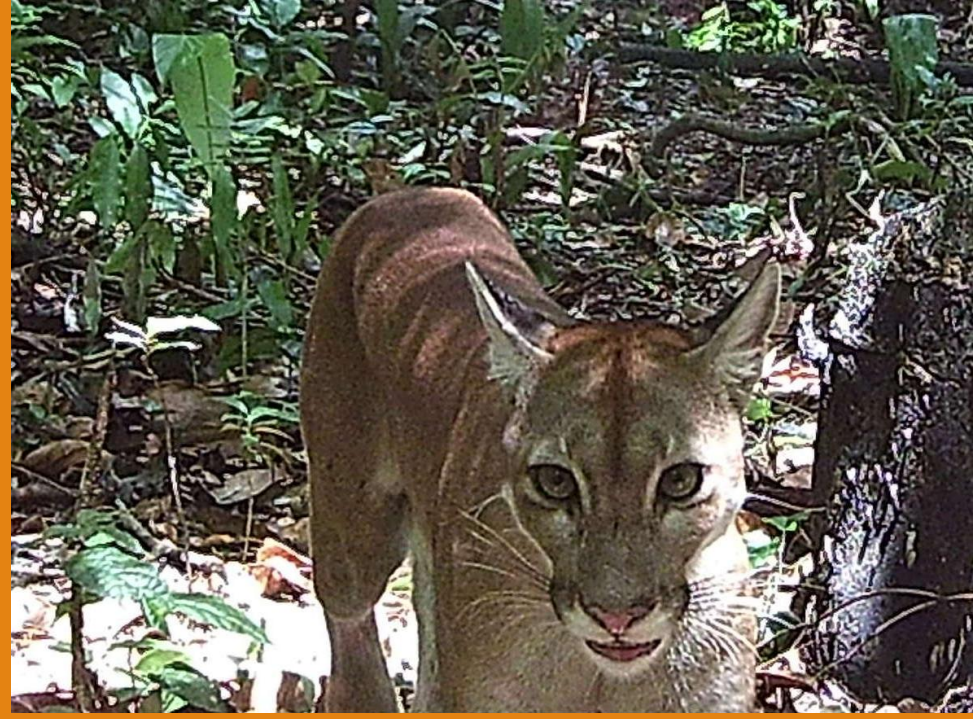
- The rainforests are central to the lives of Guyana's nine Indigenous groups, also referred to as Amerindians, the pre-colonial inhabitants of the region.
- The Indigenous groups practice traditional lifestyles such as subsistence farming, hunting, and fishing.
- The subsistence farming method practiced by indigenous groups, referred to as swidden agriculture (Cummings et al., 2017; Arwida et al., 2024).
- Intensification from shortened fallow periods has raised concerns over habitat degradation and biodiversity loss (Henley, 2011; Li et al., 2014; Finch et al., 2022).
- Guyana's interior, rich in timber and minerals, drives extraction and road expansion, increasing human access. (Guyana Lands and Surveys Commission, 2013; Pierre et al., 2020).

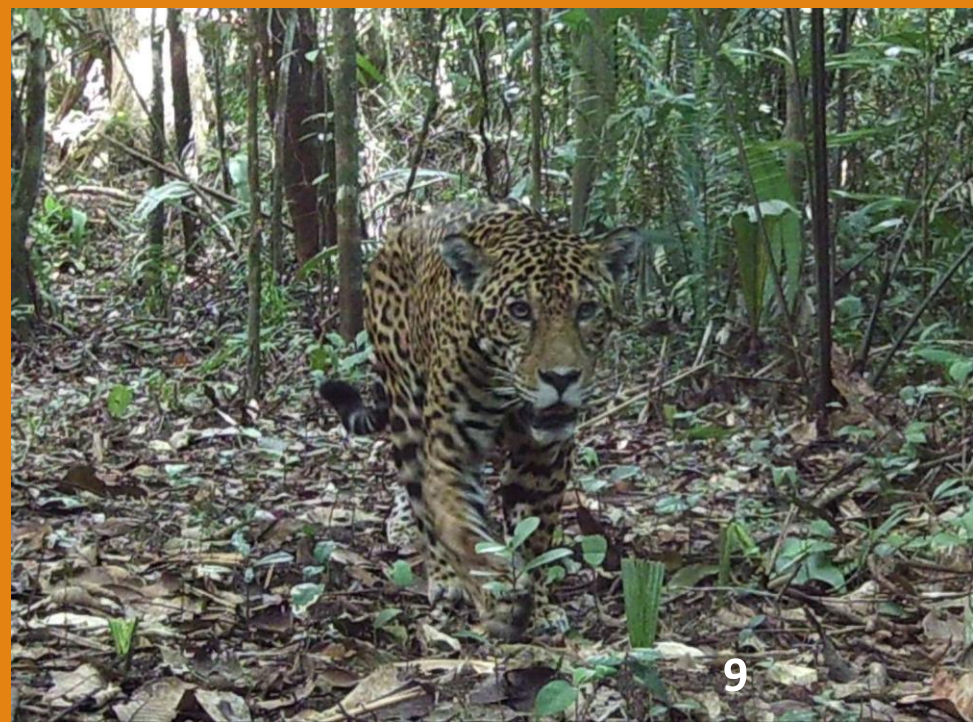


Study Area

- Village 1: Mix of commercial agriculture + traditional swidden cassava cultivation.
- Village 2: High human influences — commercial pineapple, logging, and gold mining.
- Village 3: Low influences — traditional swidden cassava farming for subsistence.

What are the drivers of apex predator-prey co-occurrences?





Chapter 3: Spatial interaction

Data preparation

- Repeated surveys
- Binary detection matrix

Model specification

- Four models (2 predators, 2 prey species)
- R package 'unmarked'
- Variables were tested for multicollinearity, and the final selected variables had variance inflation factors (VIF) below 5.

Local Neighborhood Effects

- Addresses spatial autocorrelation

Model components

- Detection probabilities
- Conditional occupancy
- Second-order interactions

Covariates used in multispecies model

Independent variable

Environmental Variable

- NDVI (Source: Open Topography website, Google Earth Engine)
- Elevation
- Slope
- Hillshade
- Roughness
- Aspect

Anthropogenic Variable

- Distance from road (Source: Humanitarian OpenStreetMap)
- Distance from farms (Source: Research team)

Climate variables

- Temperature
- Precipitation (Source: WorldClim; Fick & Hijmans, 2017).

Study site

- Categorical variable

Dependent variable

Species detection

- Detection (1/0) for each species in each 7-day sampling occasion

Neighborhood effects

- Spatial autocorrelation occurs when observations are not independent across space.
- Autocovariate models address this by adding neighborhood effects as an additional covariates (Dormann, 2007; Bardos et al., 2015).
- Formula: Autocovariate, $A_i = \sum_{j \in N(i)} \frac{1}{d_{ij}} \cdot Y_j$

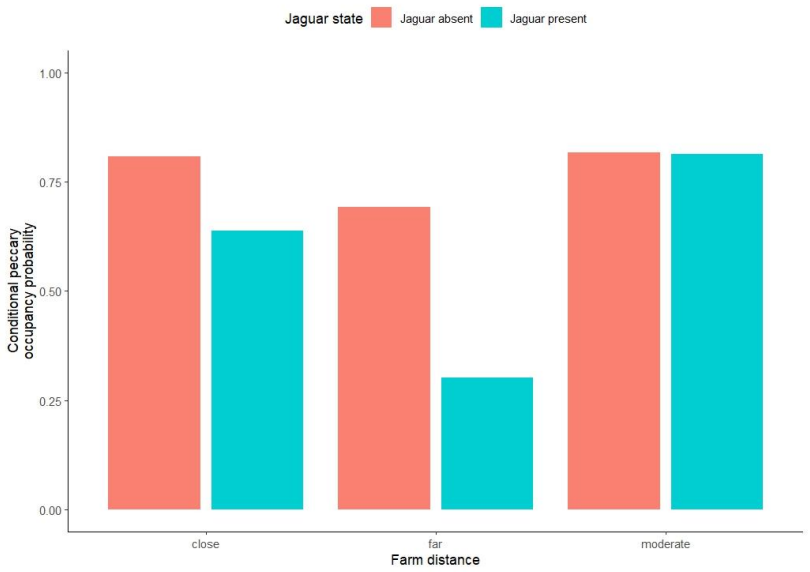
  Here, $N(i)$ is the set of neighboring sites around site i, d_{ij} is the Euclidean distance between site i and neighbor j, and Y_j is binary value representing species presence (1) or absence (0) at neighbor site j.
- Trial-and-error method (Augustin et al., 1996) was used to choose the neighborhood radius.
- A radius of 2 was selected because it best reduced spatial autocorrelation.

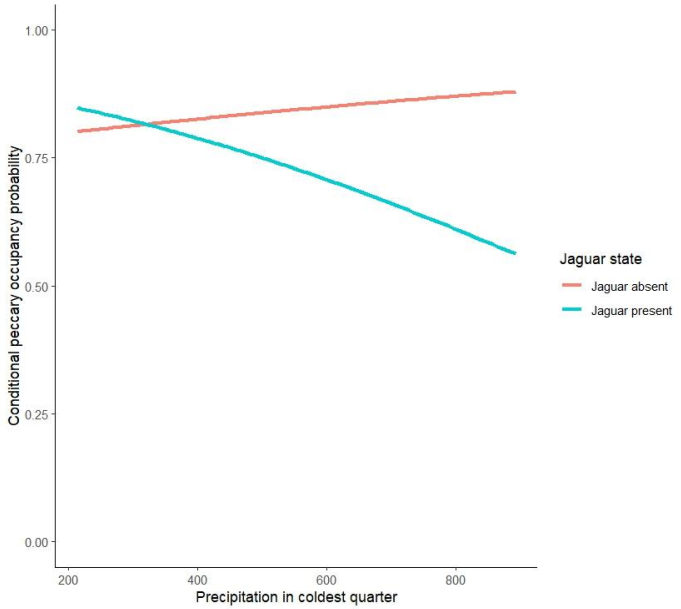
How are different factors influencing the presence of apex predators and their primary prey?

Results: Coefficients from the multispecies model

Species pair Covariates	Model 1: Jaguar-Peccary	Model 2: Puma-Deer	Model 3: Jaguar-Deer	Model 4: Puma-Peccary
Intercept	-0.074 (0.13)	**0.62 (0.31)**	**-0.56 (0.26)**	**0.76 (0.27)**
Slope	-0.52 (0.34)	-0.29 (0.33)	-0.08 (0.35)	0.33 (0.40)
Hillshade	-0.47 (0.60)	**-1.38 (0.37)**	-0.10 (0.33)	-0.68 (0.53)
Temperature	-0.06 (0.41)	0.40 (0.40)	0.03 (0.33)	-0.54 (0.53)
Precipitation	**-0.47 (0.19)**	**0.97 (0.42)**	**-0.41 (0.17)**	0.39 (0.52)
Farm (far)	**-0.72 (0.34)**	-0.41 (0.32)	-0.15 (0.40)	-0.35 (0.35)
Farm (moderate)	0.84 (0.44)	0.27 (0.42)	0.29 (0.48)	-0.59 (0.56)
Village 2	**-0.35 (0.12)**	0.40 (0.38)	**-0.61 (0.14)**	0.04 (0.40)
Village 3	-0.03 (0.25)	-0.11 (0.14)	0.19 (0.14)	0.23 (0.27)
Predator autocovariate	-0.19 (0.11)	-0.03 (0.21)	**-0.26 (0.07)**	-0.06 (0.21)
Prey autocovariate	-0.11 (0.29)	0.35 (0.25)	0.43 (0.32)	**0.66 (0.30)**
Interaction of autocovariates	-0.65 (0.36)	**-1.47 (0.38)**	**-1.37 (0.43)**	**-1.34 (0.40)**

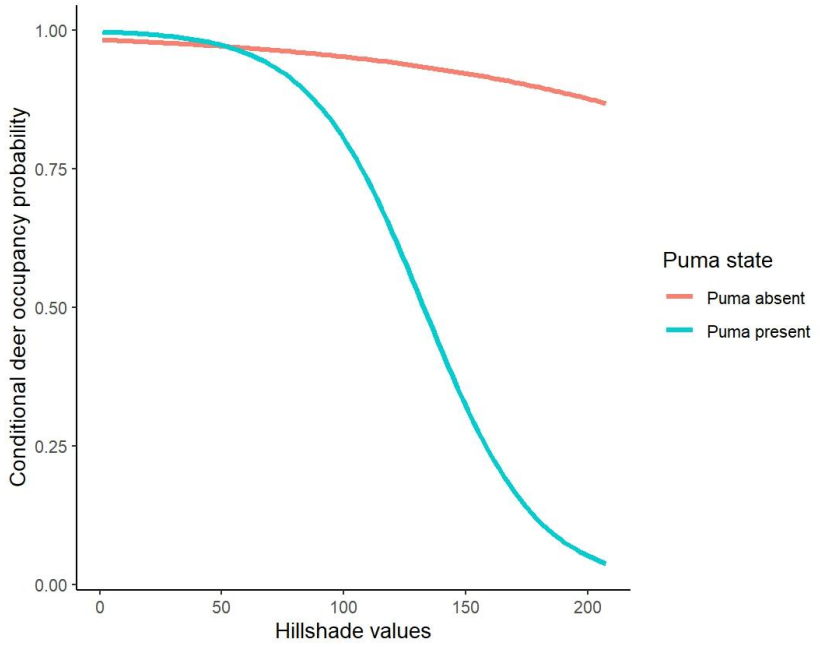
Predator	Prey	Covariate	Co-occurrence direction
Jaguar	Peccary	Farm (far)	↓
Jaguar	Peccary	Precipitation	↓
Jaguar	Deer	Precipitation	↓
Puma	Deer	Hillshade	↓
Puma	Deer	Precipitation	↑

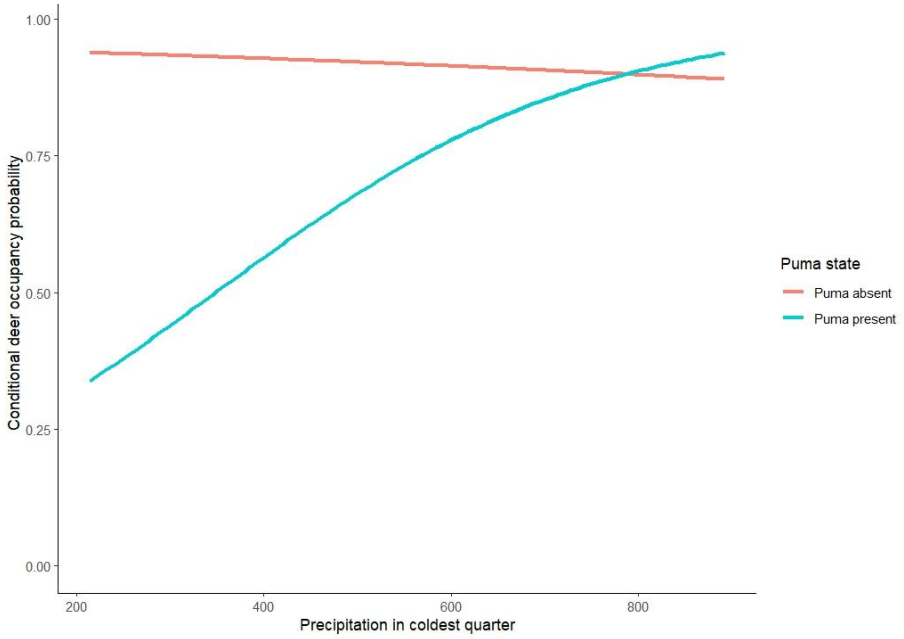




Jaguar-peccary interactions

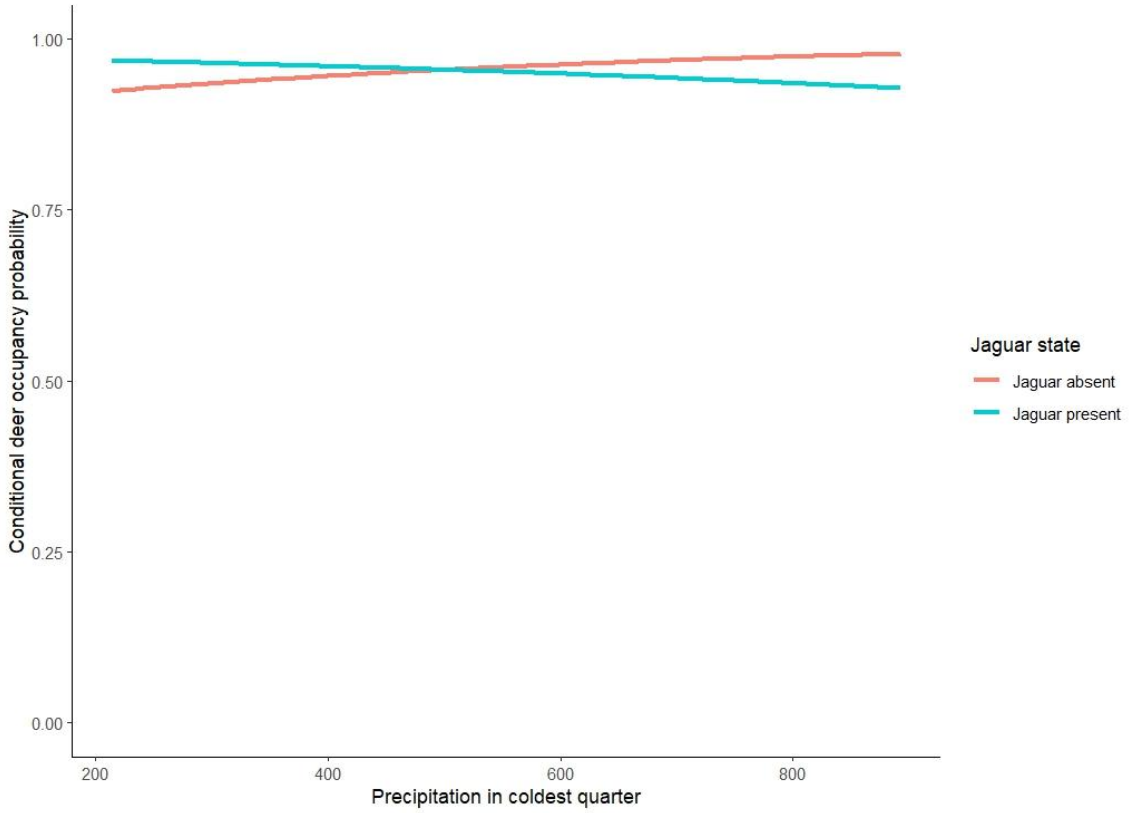
- **Distance from Farms:** Jaguars and peccaries are more likely to co-occur at moderate farm distances.
- **Precipitation:** Co-occurrence decreases with higher precipitation. This difference in peccary occupancy could possibly due to reduced escape ability in wet conditions.





Puma-deer

- **Hillshade:** A significant negative co-occurrence is observed with increasing hillshade (a measure of light and shadow from topography).
- **Precipitation:** Co-occurrence of the puma–deer exhibited an increasing trend under higher precipitation.
- Precipitation weakens deer health (Bender et al., 2011, 2012), making them easier prey, and pumas target deer in poor condition (Bender and Rosas-Rosas, 2016).



Jaguar-deer

- Jaguar–deer model showed that increased precipitation was associated with reduced co-occurrence.

Key takeaways

- Pumas are more ecologically flexible and can adjust their movement and hunting strategies in wetter conditions.
- Jaguars may experience reduced hunting efficiency in rainfall.
- Jaguar–peccary co-occurrence near farms can raise the risk of human–wildlife conflict.

Problem statement	Contributions of the study
How different external factors affects mammalian behaviors.	• Mammals are sensitive to forests' microclimate variation. • Prey availability are affecting their behavioral shifts.
How different factors are influencing apex predators' presence with their prey	Shows apex predators' vulnerability and resilience to climatic conditions.
How different human presence affect the mammalian behavior and distribution.	• Human presence are driving mammals towards nocturnality. • Agricultural landscape can increase predator prey co-occurrences.

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References

Alegre, V. B., de Faria Oshima, J. E., Kanda, C. Z., Jorge, M. L. S., Keuroghlian, A., Morato, R. G., ... & Börger, L. (2025). Predator–Prey Movement Interactions: Jaguars and Peccaries in the Spotlight. Biotropica, 57(1), e13423.

Altrichter, M., Taber, A., Beck, H., Reyna-Hurtado, R., Lizarraga, L., Keuroghlian, A., & Sanderson, E. W. (2012). Range-wide declines of a key Neotropical ecosystem architect, the Near Threatened white-lipped peccary Tayassu pecari. Oryx, 46(1), 87–98. https://doi.org/10.1017/S0030605311000421

Arwida, S., Dewayanti, R., Jaung, W., Boedhihartono, A. K., & Sayer, J. (2024). Will the Exodus of Young People Bring an End to Swidden Farming as a Major Forest Use in SE Asia? Sustainability, 16(13), 5302. https://doi.org/10.3390/su16135302

Aschoff, J. (1960). Exogenous and Endogenous Components in Circadian Rhythms. Cold Spring Harbor Symposia on Quantitative Biology, 25, 11–28. https://doi.org/10.1101/SQB.1960.025.01.004

Ávila-Nájera, D. M., Chávez, C., Lazcano-Barreto, M. A., Mendoza, G. D., & Pérez-Elizalde, S. (2016). Overlap in activity patterns between big cats and their main prey in northern Quintana Roo, Mexico. Therya, 7(3), 439-448.

Ávila–Nájera, D. M., Chávez, C., Pérez–Elizalde, S., Palacios–Pérez, J., & Tigar, B. (2020). Coexistence of jaguars (Panthera onca) and pumas (Puma concolor) in a tropical forest in south–eastern Mexico. Animal biodiversity and conservation, 43(1), 55-66.

Banks-Leite, C., Ewers, R. M., Folkard-Tapp, H., & Fraser, A. (2020). Countering the effects of habitat loss, fragmentation, and degradation through habitat restoration. One Earth, 3(6), 672–676. https://doi.org/10.1016/j.oneear.2020.11.016

Bardos, D. C., Guillera-Arroita, G., & Wintle, B. A. (2015). Valid auto-models for spatially autocorrelated occupancy and abundance data. Methods in Ecology and Evolution, 6(10), 1137–1149. https://doi.org/10.1111/2041-210x.12402

Bender, L. C., Boren, J. C., Halbritter, H., & Cox, S. (2011). Condition, survival, and productivity of mule deer in semiarid grassland-woodland in east-central New Mexico. Human-Wildlife Interactions, 5(2), 276-286.

Bender, L. C., Hoenes, B. D., & Rodden, C. L. (2012). Factors influencing survival of desert mule deer in the greater San Andres Mountains, New Mexico. Human-Wildlife Interactions, 6(2), 245-260.

Bender, L. C., & Rosas-Rosas, O. C. (2016). Compensatory puma predation on adult female mule deer in New Mexico. Journal of Mammalogy, 97(5), 1399–1405. https://doi.org/10.1093/jmammal/gyw094

Brook, L. A., Johnson, C. N., & Ritchie, E. G. (2012). Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. Journal of applied ecology, 49(6), 1278-1286.

Burgos, T., Escribano-Ávila, G., Fedriani, J. M., González-Varo, J. P., Illera, J. C., Cancio, I., ... & Virgós, E. (2024). Apex predators can structure ecosystems through trophic cascades: Linking the frugivorous behaviour and seed dispersal patterns of mesocarnivores. Functional Ecology, 38(6), 1407-1419.

Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J., Griffiths, M., Holden, J., Kawanishi, K., Kinnaird, M., Laidlaw, R., Lynam, A., Martyr, D., O'Brien, T., Seidensticker, J., Sunquist, M., Tilson, R., & Shahruddin, W. (2001). The use of photographic rates to estimate densities of tigers and other cryptic mammals. Animal Conservation, 4, 75–79. https://doi.org/10.1017/S1367943001001081

Carbone, C., & Gittleman, J. L. (2002). A Common Rule for the Scaling of Carnivore Density. Science, 295(5563), 2273–2276. https://doi.org/10.1126/science.1067994

Cummings, A. R., Karale, Y., Cummings, G. R., Hamer, E., Moses, P., Norman, Z., & Captain, V. (2017). UAV-derived data for mapping change on a swidden agriculture plot: Preliminary results from a pilot study. International Journal of Remote Sensing, 38(8–10), 2066–2082. https://doi.org/10.1080/01431161.2017.1295487

Chad, D., Adhikari, G., Rawat, Y. B., Dhami, B., Miya, M. S., & Neupane, B. (2025). Who's active when and where? Unraveling the habitat use and temporal strategies of prey in a predator-human shared landscape. Global Ecology and Conservation, e03682.

References

De Azevedo, F. C. C. (2008). Food habits and livestock depredation of sympatric jaguars and pumas in the Iguacu National Park area, south Brazil. Biotropica, 40(4), 494-500.

De Oliveira, T. D. (2002). Ecología comparativa de la alimentación del jaguar y del puma en el neotrópico. El jaguar en el nuevo milenio, 265-288.

Debata, S., & Swain, K. (2018). Estimating Mammalian Diversity and Relative Abundance Using Camera Traps in a Tropical Deciduous Forest of Kuldiha Wildlife Sanctuary, Eastern India. Mammal Study, 43, 1–9. https://doi.org/10.3106/ms2017-0078

Desbiez, A. L. J., & Kluyber, D. (2013). The Role of Giant Armadillos (Priodontes maximus) as Physical Ecosystem Engineers. Biotropica, 45(5), 537–540. https://doi.org/10.1111/btp.12052

F. Dormann, C., M. McPherson, J., B. Araújo, M., Bivand, R., Bolliger, J., Carl, G., G. Davies, R., Hirzel, A., Jetz, W., Daniel Kissling, W., Kühn, I., Ohlemüller, R., R. Peres-Neto, P., Reineking, B., Schröder, B., M. Schurr, F., & Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. Ecography, 30(5), 609–628. https://doi.org/10.1111/j.2007.0906-7590.05171.x

Ewing, T., & Gangloff, M. (2016). Using changes in naïve occupancy to detect population declines in aquatic species; case study: Stability of Greenhead Shiner in North Carolina. Journal of the Southeastern Association of Fish and Wildlife Agencies, 3, 1-5.

Faurby, S., Davis, M., Pedersen, R. Ø., Schowanek, S. D., Antonelli, A., & Svenning, J. C. (2018). PHYLACINE 1.2: the phylogenetic atlas of mammal macroecology. Ecology, 99(11), 2626.

Finch, E. A., Rajoelison, E. T., Hamer, M. T., Caruso, T., Farnsworth, K. D., Fisher, B. L., & Cameron, A. (2022). The effect of swidden agriculture on ant communities in Madagascar. Biological Conservation, 265, 109400. https://doi.org/10.1016/j.biocon.2021.109400

Fontes, B., Desbiez, A., Massocato, G., Srbek-Araujo, A. C., Sanaiotti, T., Bergallo, H. de, Ferreguetti, A., Noia, C., Schettino, V., Pagotto, R., Moreira, D., Gatti, A., & Banhos, A. (2020). The local extinction of one of the greatest terrestrial ecosystem engineers, the giant armadillo (Priodontes maximus), in one of its last refuges in the Atlantic Forest, will be felt by a large vertebrate community. Global Ecology and Conservation, 24.

Fragoso, J. M. V., Silvius, K. M., & Correa, J. A. (2003). LONG-DISTANCE SEED DISPERSAL BY TAPIRS INCREASES SEED SURVIVAL AND AGGREGATES TROPICAL TREES. Ecology, 84(8), 1998–2006. https://doi.org/10.1890/01-0621

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. Science, 360(6394), 1232–1235. https://doi.org/10.1126/science.aar7121

González, C. A. L., & Miller, B. J. (2002). Do Jaguars (Panthera onca) Depend on Large Prey? Western North American Naturalist, 62(2), 218–222.

Guyana Lands and Surveys Commission. (2013). Guyana national land use plan. Georgetown, Guyana: Guyana Lands and Surveys Commission.

Halle, S. (2000). Ecological Relevance of Daily Activity Patterns. In Activity Patterns in Small Mammals (pp. 67–90). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-18264-8_5

Harris, A. E., Hallett, M. T., Davis, M., Carter, M., Singh, D., Roopsind, A., Maharaj, G., & Bicknell, J. E. (2023). Use of logging roads by terrestrial mammals in a responsibly managed neotropical rainforest in Guyana. Forest Ecology and Management, 548, 121401. https://doi.org/10.1016/j.foreco.2023.121401

Henley, D. (2011). Swidden Farming as an Agent of Environmental Change: Ecological Myth and Historical Reality in Indonesia. Environment and History, 17(4), 525–554. https://doi.org/10.3197/096734011x13150366551535

Iriarte, J. A., Franklin, W. L., Johnson, W. E., & Redford, K. H. (1990). Biogeographic variation of food habits and body size of the America puma. Oecologia, 85, 185-190.

References

Joseph, L. N., Field, S. A., Wilcox, C., & Possingham, H. P. (2006). Presence–Absence versus Abundance Data for Monitoring Threatened Species. Conservation Biology, 20(6), 1679–1687. https://doi.org/10.1111/j.1523-1739.2006.00529.x

Kelly, M. J., & Holub, E. L. (2008). Camera Trapping of Carnivores: Trap Success Among Camera Types and Across Species, and Habitat Selection by Species, on Salt Pond Mountain, Giles County, Virginia. Northeastern Naturalist, 15(2), 249–262. https://doi.org/10.1656/1092-6194(2008)15[249:ctocts]2.0.co;2

Kronfeld-schor, N., & Dayan, T. (2003). Partitioning of Time as an Ecological Resource. Annu. Rev. Ecol. Evol. Syst, 34, 153–181. https://doi.org/10.1146/annurev.ecolsys.34.011802.132435

Lee, S. X. T., Amir, Z., Moore, J. H., Gaynor, K. M., & Luskin, M. S. (2024). Effects of human disturbances on wildlife behaviour and consequences for predator-prey overlap in Southeast Asia. Nature Communications, 15, 1521. https://doi.org/10.1038/s41467-024-45905-9

Levi, T., & Peres, C. A. (2013). Dispersal vacuum in the seedling recruitment of a primate-dispersed Amazonian tree. Biological Conservation, 163, 99–106. https://doi.org/10.1016/j.biocon.2013.03.016

Li, P., Feng, Z., Jiang, L., Liao, C., & Zhang, J. (2014). A Review of Swidden Agriculture in Southeast Asia. Remote Sensing, 6(2), 1654–1683. https://doi.org/10.3390/rs6021654

Link, A., & Di Fiore, A. (2006). Seed dispersal by spider monkeys and its importance in the maintenance of neotropical rain-forest diversity. Journal of Tropical Ecology, 22, 235–246. https://doi.org/10.1017/S0266467405003081

Manlick, P. J., & Pauli, J. N. (2020). Human disturbance increases trophic niche overlap in terrestrial carnivore communities. Proceedings of the National Academy of Sciences, 117(43), 26842–26848. https://doi.org/10.1073/pnas.2012774117

Oberosler, V., Groff, C., Iemma, A., Pedrini, P., & Rovero, F. (2017). The influence of human disturbance on occupancy and activity patterns of mammals in the Italian Alps from systematic camera trapping. Mammalian Biology, 87, 50–61. https://doi.org/10.1016/j.mambio.2017.05.005

O'Brien, T. G., Kinnaird, M. F., & Wibisono, H. T. (2003). Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Animal Conservation Forum, 6(2), 131–139. https://doi.org/10.1017/S1367943003003172

Paemelaere, E. A. D., Hallett, M. T., de Freitas, K., Balvadore, S., Ignace, M., Mandook, A., Mandook, N., Lewis, M., Igancio, L., Joaquim, M., O'Shea, B., & van Vliet, N. (2025). Medium and large mammal responses to fire in a neotropical savanna system in Guyana. Biotropica, 57(1), e13397. https://doi.org/10.1111/btp.13397

Pickles, R., McCann, N., & Holland, A. (2011). Mammalian and avian diversity of the Rewa Head, Rupununi, Southern Guyana. Biota Neotropica, 11, 237–251. https://doi.org/10.1590/S1676-06032011000300021

Pierre, M. A., Ignacio, L., & Paemelaere, E. A. (2020). Large-and medium-bodied terrestrial mammals of the Upper Berbice region of Guyana. Check List, 16(5), 1229-1237.

Pollock, J. E. (2006). Detecting population declines over large areas with presence-absence, time-to-encounter, and count survey methods. Conservation Biology: The Journal of the Society for Conservation Biology, 20(3), 882–892. https://doi.org/10.1111/j.1523-1739.2006.00342.x

Smith, F., Lyons, S., Ernest, S. K. M., Jones, K., University, K., Dayan, T., Marquet, P., Brown, J., & Haskell, J. (2003). Body Mass of Late Quaternary Mammals (Data Set).

Sollmann, R. (2018). A gentle introduction to camera-trap data analysis. African Journal of Ecology, 56(4), 740–749. https://doi.org/10.1111/aje.12557

Wilcove, D. S. (1986). Habitat fragmentation in the temperatezone. Conservation biology, 237-256.

Wong, M. K., & Didham, R. K. (2024). Global meta-analysis reveals overall higher nocturnal than diurnal activity in insect communities. Nature Communications, 15(1), 3236.