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Habitat modification destabilizes spatial associations and persistence of Neotropical carnivores

Highlights

- Interspecific spatial associations are a key determinant of carnivore occurrence
- Forest loss and degradation erode the capacity for carnivores to coexist
- Jaguars play an irreplaceable role in spatially structuring mesocarnivore populations
- Carnivore conservation depends on maintaining both forest extent and quality

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In brief

Boron and Deere et al. analyze camera trap data from seven Neotropical carnivores across nine sites in Colombia to show that interspecific spatial associations are a key determinant of carnivore occurrence that can be destabilized by forest loss and degradation, with potentially cascading impacts on ecosystem stability and resilience.

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Habitat modification destabilizes spatial associations and persistence of Neotropical carnivores

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SUMMARY

Spatial relationships between sympatric species underpin biotic interactions, structure ecological communities, and maintain ecosystem health. However, the resilience of interspecific spatial associations to human habitat modification remains largely unknown, particularly in tropical regions where anthropogenic impacts are often greatest. We applied multi-state multi-species occurrence models to camera trap data across nine tropical landscapes in Colombia to understand how prominent threats to forest ecosystems influence Neotropical carnivore occurrence and interspecific spatial associations, with implications for biotic interactions. We show that carnivore occurrence represents a delicate balance between local environmental conditions and interspecific interactions that can be compromised in areas of extensive habitat modification. The stability of carnivore spatial associations depends on forest cover to mediate antagonistic encounters with apex predators and structurally intact forests to facilitate coexistence between competing mesocarnivores. Notably, we demonstrate that jaguars play an irreplaceable role in spatially structuring mesocarnivore communities, providing novel evidence on their role as keystone species. With increasing global change, conserving both the extent and quality of tropical forests is imperative to support carnivores and preserve the spatial associations that underpin ecosystem stability and resilience.

INTRODUCTION

Human modification of the natural environment through habitat loss and degradation is causing unprecedented disruption to the earth's terrestrial ecosystems. These impacts pose a significant threat to biodiversity, particularly in tropical regions,[1] with potentially catastrophic implications for ecosystem stability and resilience.[2] Understanding the mechanisms that underpin species distributions is central to mitigating human impacts on biodiversity. Species occurrence is predominantly described in relation to abiotic factors and/or local environmental characteristics.[3] Conversely, the role of biotic factors in shaping species distributions remains relatively understudied, most notably in the tropics.[4]

The extent to which individuals of different species co-occur within a shared habitat space, termed interspecific spatial associations, is crucial to understanding species distributions and has important consequences for ecosystem integrity.[5] Spatial associations can manifest as either positive, negative, or neutral, depending on whether species aggregate or segregate in space. Disruptions to the spatial arrangement of wildlife can upset the competitive balance between species, increasing the risk of displacement or even extinction.[6] This can alter the distribution of ecological functions that species provide, ultimately affecting ecosystem dynamics.[7] Although spatial associations are not a direct measure of biotic interactions,[8] species cannot interact if their spatiotemporal niche does not overlap.[9] Thus, co-occurrence conveys fundamental information about interactions between sympatric species. Taken as a whole, interspecific spatial associations play a central role in community assembly and are intricately linked to ecosystem productivity, functioning, and stability.[10] Thus, identifying how interspecific spatial associations are maintained across land-use gradients provides valuable insights into the long-term implications of anthropogenic impacts on ecosystem health and recovery.

Spatial dynamics between terrestrial carnivores are fundamental to maintaining ecological structure and trophic balance.[11,12] Through the act of predation, carnivores regulate the distribution, abundance, and behavior of prey populations, which mediates the impact of primary consumers on vegetation composition and successional dynamics.[13] Large carnivores, or apex predators, are often considered keystone species, assuming greater ecological importance by suppressing mesocarnivores through intraguild

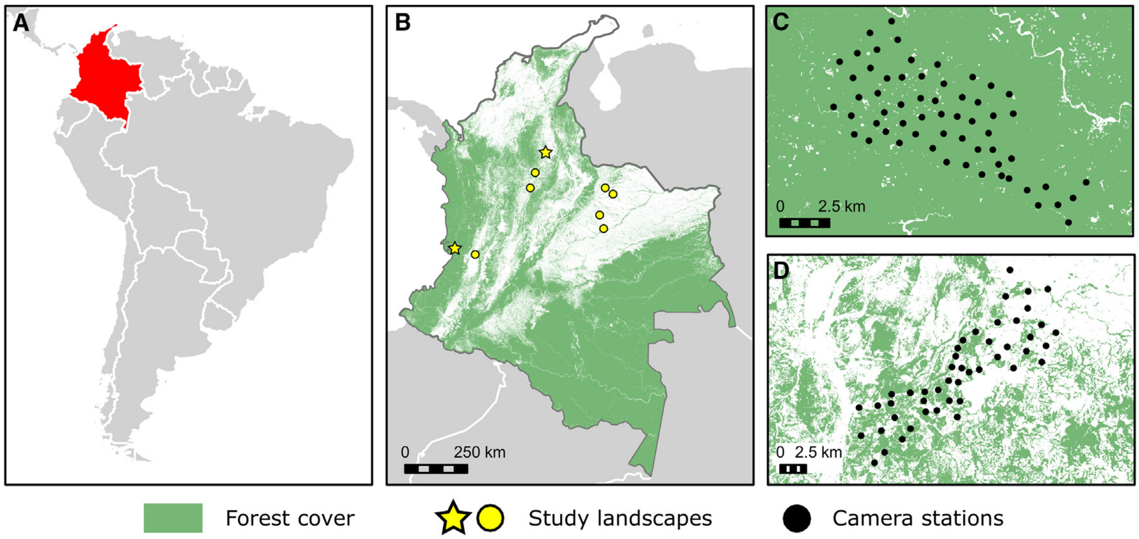

Figure 1. Geographic overview of the study system and survey design

(A) The location of Colombia within the wider Neotropical context; (B) the distribution of the nine study landscapes across Colombia; and landscape-specific examples of gridded camera trap deployments, denoted using star symbols, within (C) a pristine forested region (Bajo Calima, Valle del Cauca, northern Colombia) relative to (D) a human-modified landscape, where the proliferation of agriculture has resulted in habitat fragmentation (Puerto Wilches, Santander, western Colombia).

See also Table S1.

predation.[12] In the absence of apex predators, mesocarnivore populations may increase rapidly, a process termed "mesocarnivore release," which can have substantial impacts on the small prey that provide important ecosystem functions.[14] Despite their ecological importance, carnivores are declining globally due to habitat loss, persecution, and a diminishing prey base.[11] Large carnivores are particularly vulnerable to these threats due to their extensive area requirements and slow population growth rates,[15] resulting in cascading trophic effects.[13,16]

Within the carnivore guild, interference competition plays an important role in community assembly, particularly among sympatric species occupying similar ecological niches.[17] Competitive interactions are typically regulated by resource availability. When resources are abundant and widely distributed, species are more likely to co-occur, whereas degraded environments can exacerbate competitive interactions.[18] Intense competition can result in competitive exclusion (population decline or extirpation of a species at the expense of a competitor), which can disrupt ecosystems if the dominant competitor cannot fulfill the same ecological functions.[19] Carnivores minimize potentially fatal interactions through niche partitioning. For mesocarnivores, this may manifest as spatial avoidance of dominant apex predators or other competitors.[20] Accordingly, large carnivore distributions are predominantly governed by resource availability, while mesocarnivores must balance resource considerations against the risk of predation posed by large carnivore occurrence.[21] Human habitat modification hinders opportunities for niche diversification between sympatric carnivores by reducing the extent of suitable habitat and depleting or homogenizing the prey base.[22] Consequently, the loss and degradation of natural habitats has the potential to destabilize interspecific spatial associations, with broader consequences for biotic interactions and ecosystem health.

Here, we provide the most comprehensive study to date to understand how local environmental characteristics and interspecific spatial associations jointly shape Neotropical carnivore occurrence. The Neotropics harbor ca. 60% of the planet's biodiversity but are severely threatened by habitat loss and degradation. Since 2000, 78 Mha of forest have been converted to other land uses, while 72% of the remaining forest extent is considered degraded.[23,24] Drawing on an extensive camera trap dataset (28,522 camera trap nights) from nine tropical landscapes across Colombia (Figure 1; Table S1), we introduce the first application of multi-species, multi-state occurrence models to assess spatial associations between potentially interacting Neotropical carnivores. Using high-resolution satellite imagery to quantify the availability and quality of forest habitat, we sought to understand how pervasive human threats to forest ecosystems influence carnivore occurrence and interspecific spatial associations, with implications for biotic interactions.

We focused on seven prominent species within the Neotropical carnivore guild, comprising four felids (jaguar, *Panthera onca*; puma, *Puma concolor*; ocelot, *Leopardus pardalis*; jaguarundi, *Herpailurus yagouaroundi*) and three non-felid carnivores (crab-eating fox, *Cercodyon thous*; crab-eating racoon, *Procyon cancrivorus*; tayra, *Eira Barbara*). We partitioned the carnivore guild into three focal communities to assess different mechanisms dictating the spatial arrangement of species: (1) intraguild predation impacts on felids (jaguar, puma, ocelot, jaguarundi); (2) intraguild predation impacts on non-felids (crab-eating fox, crab-eating raccoon, tayra, jaguar, puma); and (3) competitive interactions between mesocarnivores (ocelot, jaguarundi, crab-eating fox, crab-eating raccoon, and tayra). Throughout, we consider jaguars and pumas to be apex predators in the featured communities and a potential source of intraguild predation. As with other large carnivores, jaguars are considered keystone species;

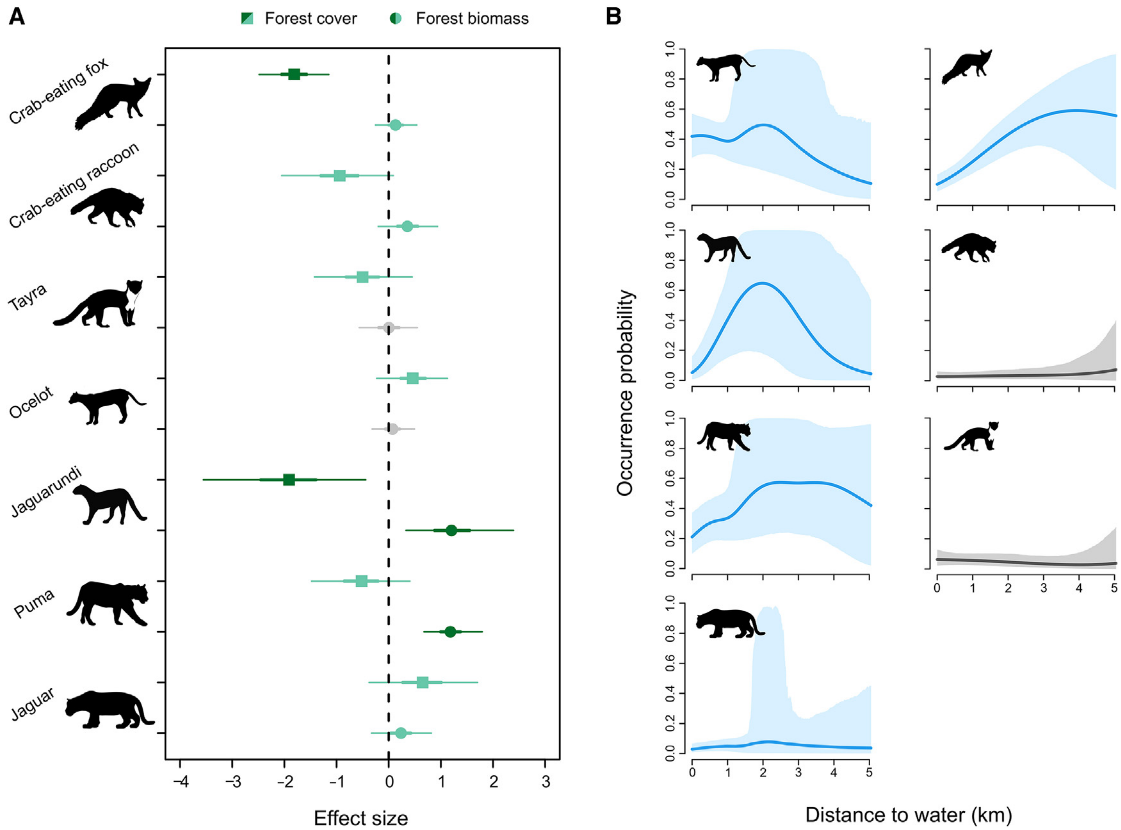

Figure 2. The influence of local environmental characteristics on Neotropical carnivore occurrence
The response of seven Neotropical carnivores to local environmental characteristics describing forest extent and condition and proximity to key resources. We present effect sizes for species responses to forest-related covariates (A) as the mean of the posterior distribution (points), with uncertainty expressed using 75% Bayesian credible intervals (BCIs, thick horizontal lines) and 95% BCI. Effects for species-specific associations were considered substantial if the 95% BCI did not overlap zero (vertical dashed line) and moderate if the 75% BCI did not overlap zero, color coded with dark and light shades, respectively. For proximity to water bodies (B), predicted occurrence probabilities were derived from posterior means (lines) and 95% BCI (shaded areas). Moderate or substantial responses based on linear or quadratic associations with proximity to water are presented in blue. Across all panels, non-influential responses, where statistical associations were neither substantial or moderate, are presented in gray.
See also Table S4.

however, empirical evidence of their ecological role is lacking. We hypothesized that the occurrence of apex predators would be primarily influenced by environmental characteristics, such as habitat availability (forest cover), habitat quality (forest biomass), and proximity to key resources (distance to water), while mesocarnivore distributions were expected to reflect a complex interplay between local habitat conditions and antagonistic interactions, manifested spatially as the presence of large carnivores.[12,14] Given that intact forest habitat is likely to be characterized by a diverse niche space and higher concentration of resources,[25] we predicted that pristine habitat conditions, comprising high forest cover and biomass, would favor coexistence between carnivores and that interspecific spatial associations would deteriorate as these properties declined along a gradient of human habitat modification.

RESULTS

We recorded 2,555 independent carnivore detections over the course of 6,828 sampling occasions, across 481 camera trap stations distributed within nine study landscapes. Of the carnivores retained for analysis, the ocelot was the most frequently detected species among felids (n = 471), while the jaguarundi was the least observed (n = 103). For non-felids, the crab-eating fox demonstrated the most detections (n = 812) and the tayra the fewest observations (n = 116). Species-specific detection summaries are provided in Table S2.

Model selection statistics found that interspecific spatial associations were an important determinant of occurrence for Neotropical carnivores (Table S3). Across all focal communities, models that explicitly accounted for spatial associations between species (M_2, M_3, and M_4) unanimously outperformed those that assumed carnivores occurred independently (ΔWAIC range: 69.9–106.2; Table S3). The best performing models suggested that carnivore spatial associations were mediated across gradients of human habitat modification.

Environmental determinants of carnivore occurrence

Species-specific associations with local environmental characteristics were found to be more prevalent for felids than non-felids

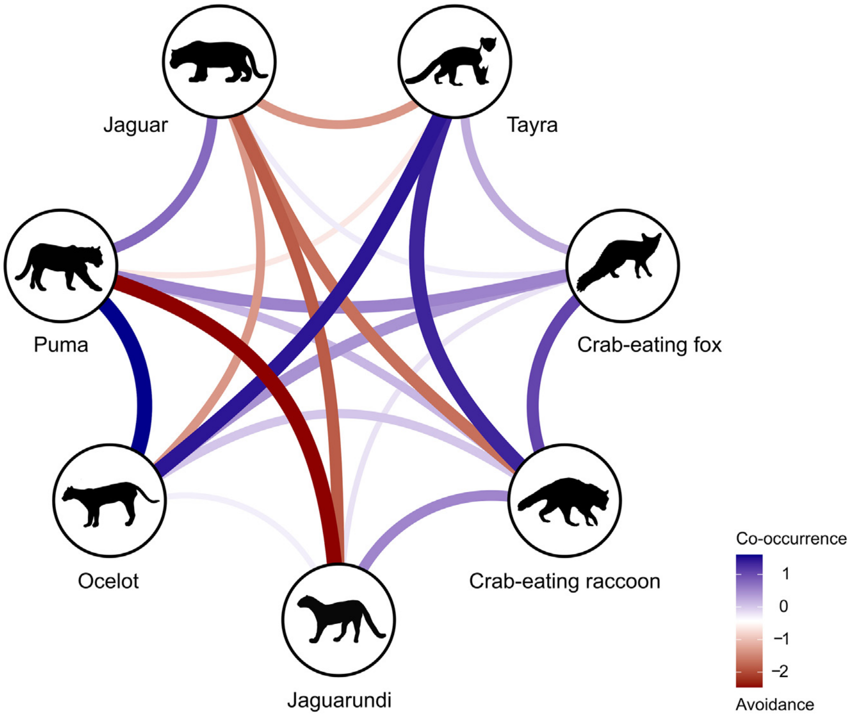

Figure 3. Spatial associations between Neotropical carnivores at constant environmental conditions

Connections reflect the degree of spatial overlap between competing carnivores, derived from intercept parameters associated with second-order occurrence in multi-species, multi-state models. Interactions are color coded to reflect a gradient of spatial habitat partitioning, ranging from co-occurrence (positive values, blue hues) to avoidance (negative values, red hues). A value of zero (white hues) indicates that occurrence patterns between two species are spatially independent. The magnitude of the interaction is expressed by the width of the connecting line.

See also Table S5.

(Figure 2; Table S4). Jaguar and ocelot occurrence demonstrated moderate (i.e., 75% credible interval does not overlap zero) increases in areas containing a greater proportion of forest cover, while puma, and particularly jaguarundi, occurrence was negatively affected by forest cover. Felid responses to forest quality were more consistent; all species except ocelots exhibited increases in occurrence probability in high biomass forests, which were found to be substantial (i.e., 95% credible interval does not overlap zero) for pumas and jaguarundi and moderate for jaguars. Across all felids, proximity to water demonstrated a quadratic association, with occurrence peaking at a distance of 2 km (Figure 2). However, the strength, nature, and extent of these trends around the threshold were variable, indicating complex, species-specific responses to water availability.

Comparatively, non-felid carnivores were more resilient to environmental conditions. Across species, occurrence was negatively associated with forest cover, indicating higher occurrence in areas characterized by low forest cover. However, the crab-eating raccoon exhibited a moderate preference for high biomass forest, suggesting some sensitivity to habitat degradation. Distance to water was only influential for the crab-eating fox, which demonstrated a substantial, predominantly linear association, highlighting that proximity to water is not an ecological constraint for this species.

Carnivore spatial associations across a gradient of human habitat modification

Pairwise spatial associations between species were found to be important determinants of occurrence among the Neotropical carnivores evaluated (Figure 3; Table S5). When environmental conditions were held constant, mesocarnivores were less likely to occupy sites where jaguars were found to be present; these effects were substantial for crab-eating raccoons and moderate for jaguarundi, ocelots, and tayras. Conversely, puma occurrence was moderately higher in areas inhabited by jaguars. The influence of pumas on mesocarnivores was found to be more variable. When pumas were present at a site, substantial impacts were noted on small felids, with jaguarundi demonstrating lower occurrence and ocelots exhibiting higher occurrence. Puma impacts on non-felids were only moderate, with crab-eating foxes more likely to occur and tayras less likely to occur when pumas were present.

Among mesocarnivores, there was little evidence of competitive exclusion, with most species displaying higher occurrence probability in sites inhabited by other mesocarnivores (Table S5). This was particularly prevalent within non-felids and, to a lesser extent, between non-felid and felid species. The only exception to this trend was documented between tayras and jaguarundi, which could not be incorporated into our modeling framework as the two species were never detected at the same camera trap station across the nine study landscapes.

Within the carnivore community, we found consistent evidence that pairwise spatial associations are mediated by habitat availability (Figure 4; Table S5). In areas characterized by a high proportion of forest cover, co-occurrence between carnivores generally increased, notably between mesocarnivores and apex predators. For mesocarnivores, we also highlight weak support for an influence of habitat quality on species co-occurrence (Figure S1; Tables S3 and S5), with species more likely to occur together in high biomass forests retaining their structural integrity.

DISCUSSION

Interspecific spatial associations are a fundamental component of ecological structure and resilience, yet they are frequently overlooked in biodiversity assessments used to support conservation decision-making. Based on a comprehensive dataset, we show that local environmental characteristics are an important determinant of habitat suitability for carnivores, but potentially fatal interactions with apex predators impose constraints on how species use the available habitat. We demonstrate that human impacts on forest ecosystems compromise habitat

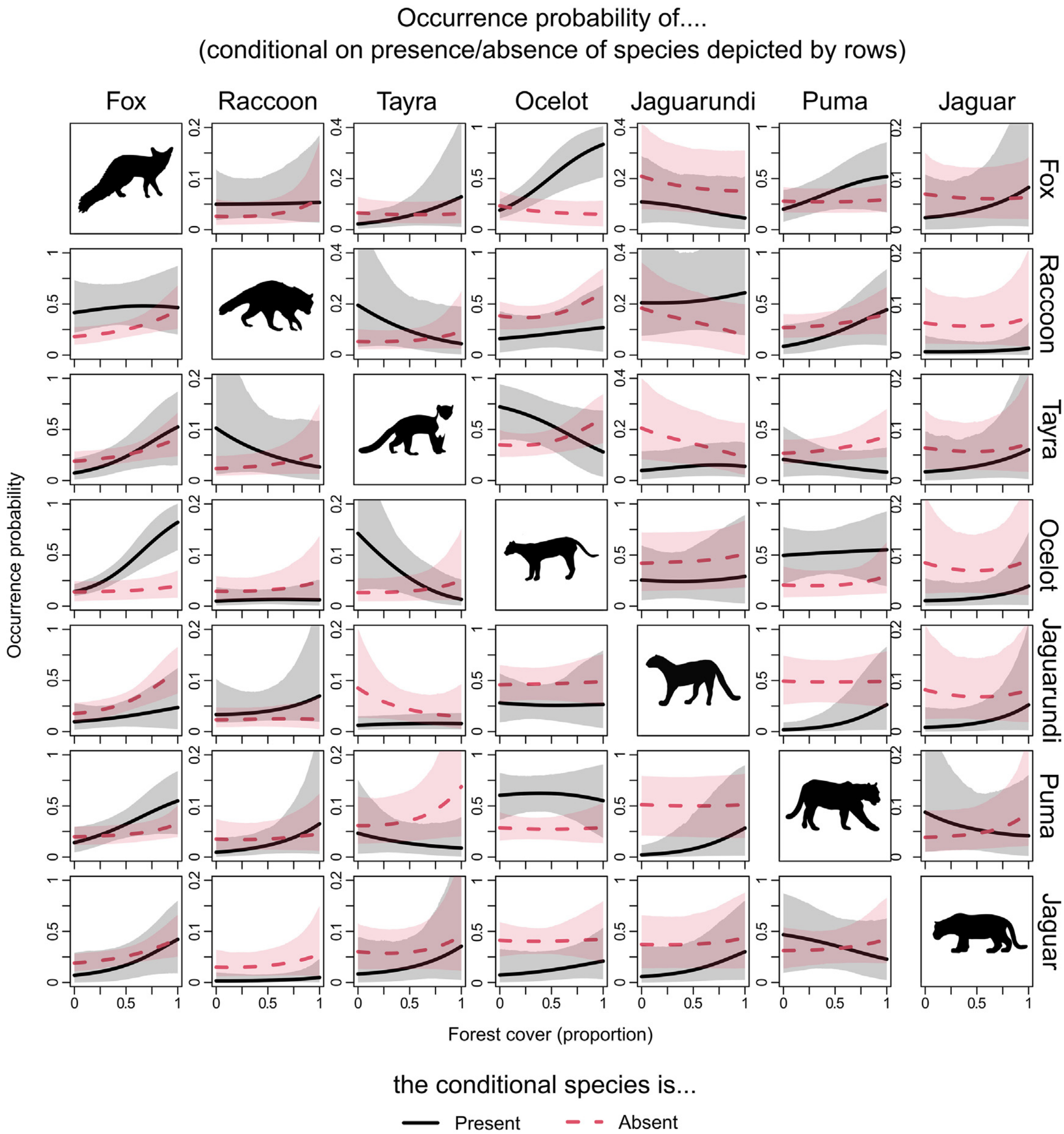

Figure 4. Spatial associations between Neotropical carnivores across a gradient of forest cover

Occurrence probabilities for seven Neotropical carnivore species conditional on the presence and absence of one another across a gradient of forest cover. Occurrence probabilities for species denoted by column are conditional on the presence/absence of the species denoted by row. Predicted responses are derived from posterior means (lines) and uncertainty is expressed using 95% Bayesian credible intervals (shaded areas). For species characterized by low probability of occurrence (raccoon, tayra, jaguarundi, and jaguar), the scale of the occurrence probability axis is magnified to provide a clearer interpretation of co-occurrence trends.

See also Figure S1 and Table S5.

suitability for carnivores and destabilize interspecific spatial associations, with important implications for biotic interactions and ecosystem functioning.

Environmental determinants of carnivore occurrence

Conservation efforts to protect vulnerable carnivores are hindered by a limited understanding of how species respond to environmental characteristics at scales appropriate to management. Our results demonstrate that carnivore dependence on forest availability is mediated by ecological specialization. We found that jaguar and ocelot occurrence moderately increased with forest cover, which has been particularly well-documented for jaguars throughout the Neotropics.[21,26] Forested areas provide greater availability of preferred prey and cover structures that increase hunting efficiency for ambush predators like jaguars.[25,27] In contrast, many observed carnivores (puma, jaguarundi, crab-eating fox, crab-eating raccoon, tayra), tended toward less-forested habitats, as indicated by a negative association with forest cover. This further evidences the ecological plasticity of these species, characterized by a wider dietary niche breadth and opportunistic hunting strategies, which allow the exploitation of resources across a range of habitats.[26] Collectively, these results highlight that carnivore communities become increasingly dominated by highly adaptable, disturbance-tolerant generalists as deforestation increases. Biotic homogenization represents a significant conservation concern, as intact wildlife communities are imperative to maintain ecological resilience.[28]

Across the tropics, high biomass forests have been associated with diverse species assemblages for a range of taxa.[29,30] However, to date, few studies have assessed the importance of forest quality on Neotropical carnivore persistence. We found consistent positive associations between carnivore occurrence and biomass, suggesting that structurally intact forests convey ecological benefits to carnivores. Complex forest structures, both vertically and horizontally, provide a greater wealth of resources to primary consumers, resulting in a diverse and abundant prey base.[31] Moreover, the structural environment provides important areas of refugia for carnivores, particularly for individuals engaged in vulnerable behaviors such as denning or prey processing.[32] Dense vegetation also provides security from anthropogenic pressure, as human hunters tend to target more open areas.[33] Our results suggest that carnivores avoid impoverished habitats characterized by low biomass, alluding to the potential for negative feedback loops in degraded systems. Active avoidance of degraded areas by carnivores could release primary consumers from predatory control, hindering natural forest regeneration and leaving disturbed habitats in a state of arrested succession.

Water is a fundamental resource for all species, including Neotropical carnivores;[26] however, we demonstrate that carnivore associations with water may be more complex than previously described. We found consistent non-linear associations between felid occurrence and proximity to water, peaking at a distance of 2 km, which may reflect their movement patterns relative to home range size. For example, ocelots have an average daily travel distance of 1.90 (± 0.25) km/day,[34] thus ensuring their home ranges accommodate access to water within a days travel time. Alternatively, our results could be an artifact of the remote-sensing data available for water bodies, which is likely biased toward large, navigable rivers that can act as conduits for human access and a source of anthropogenic intrusion. Therefore, felids must optimize habitat selection to balance proximity to a key resource against sensitivity to human pressure.

Reconciling idiosyncratic carnivore responses to local environmental characteristics poses challenges to conservation. Although our findings are in general agreement with previous studies, carnivores are highly adaptive and associations with environmental characteristics are geographically variable.[35] Overall, felids seem more sensitive to human habitat modification than other carnivores. Given that felids are obligate carnivores, it is unlikely that their functional roles can be compensated by canids or mustelids that have a much greater dietary niche breadth. Although avoided deforestation is paramount to protect the most vulnerable felids, forest quality was a more consistent and influential determinant of carnivore habitat selection. Consequently, we support growing calls for environmental legislation to place greater emphasis on preserving forest quality as well as extent.[1,25]

Habitat gradients mediate carnivore spatial associations

Antagonistic interactions regulate the distribution and composition of carnivore communities.[14] We demonstrate that interspecific spatial associations are strong determinants of Neotropical carnivore occurrence, with models explicitly accounting for species interactions consistently outperforming those that assume species occur independently. Failure to accommodate interspecific spatial associations into conservation planning therefore overlooks important ecological constraints on how carnivores interact with available habitat.

Sympatric carnivores minimize antagonistic interactions through niche partitioning,[18] especially because the stakes are unusually high within the guild due to their behavioral and morphological adaptations for killing.[36] The realized niche of a species therefore represents a compromise between habitat suitability and the competitive landscape. At constant environmental conditions, we demonstrate that carnivore communities are spatially structured by intraguild predation mediated by body size, as has been demonstrated elsewhere.[37,38] We found that sites occupied by jaguars were generally avoided by mesocarnivores, introducing novel insights into the role of jaguars as keystone species in Neotropical ecosystems. Antagonistic interactions are disproportionately costly for smaller-bodied species; therefore, areas frequented by dominant apex predators are avoided to minimize the threat of potentially lethal interactions.[39] Although our results do not provide direct empirical support for the mesocarnivore release hypothesis, we evidence the capacity for top predators, especially jaguars, to spatially structure mesocarnivore populations,[40] thus fulfilling an important ecological role in tropical ecosystems.

Notably, the influence of pumas on mesocarnivore occurrence was less pronounced, suggesting that they may not be a functional substitute for jaguars. Contrary to the assumption that carnivore interactions are exclusively negative, our results revealed a degree of spatial overlap between pumas and subordinate carnivores. This finding could indicate that mesocarnivores derive ecological benefits from puma presence in certain conditions through resource provisioning. When the relative body size between apex predator and subordinate carnivore is reduced, the energetic reward of facultative scavenging may outweigh the risks associated with intraguild predation.[41] Alternatively, the selection pressure to avoid jaguars may be stronger than the pressure to avoid pumas or there may be temporal or spatial avoidance on a scale finer than that used in the analysis.

The principle of limiting similarity posits that interspecific interactions are most pronounced between closely related species sharing common traits, necessitating niche diversification to alleviate competition.[42] Spatially, this is expected to manifest as avoidance within functional groups, such as apex predators or mesocarnivores. Functionally similar species tend to be of equivalent body size; therefore, engaging in aggressive interactions incurs a greater risk of injury.[38] In contrast, we found that species within functional groups tended to occupy the same sites. This is perhaps to be expected for species with analogous ecological requirements.[43] Previous studies have reported no evidence of spatial segregation between jaguars and pumas or within the mesocarnivore community.[26] These species may adopt alternative mechanisms to facilitate coexistence, such as temporal avoidance or dietary partitioning. For example, within the mesocarnivore community, jaguarundi and tayras are typically diurnal, whereas ocelots, foxes, and racoons are mostly crepuscular and nocturnal.[44] Moreover, ocelots and jaguarundis are obligate carnivores and mostly prey on terrestrial species,[45,46] whereas crab-eating foxes, racoons, and tayras have a wider dietary spectrum, including fruits and aquatic and semiaquatic prey.[47]

Understanding the extent to which human habitat modification disrupts interspecific spatial associations provides valuable insights into the consequences of land-use change on ecosystem stability. Our results suggest that forest availability is central to carnivore coexistence, particularly between apex predators and mesocarnivores. Generally, abundant resources distributed across large tracts of favorable habitat will promote species coexistence.[48] Conversely, reductions in habitat extent force carnivores to coexist in smaller habitat patches and compete for a depleted prey base, thus exacerbating antagonistic interactions.[18] Under these circumstances, conventional mechanisms of coexistence may not be possible, resulting in competitive exclusion, displacement, and, eventually, extirpation. For mesocarnivore communities, we demonstrate that the impacts of forest loss may be offset to some degree by habitat quality. Heterogeneous environments, such as high biomass forests, facilitate coexistence by providing supplementary axes for niche diversification.[49,50] For example, varied physical structures can provide fine-scale refuges for competing mesocarnivores,[49] while structurally complex forests allow species to partition space across vertical strata.[51]

Species occurrence, spatial associations, and resulting interspecific interactions are central to ecosystem integrity and health.[10] Our results emphasize the sensitivity of spatial mechanisms of coexistence to human habitat modification. As ecosystems become more impacted by human activities, carnivore communities become increasingly depleted due to competitive exclusion. Diverse and functional communities are fundamental to maintain ecosystem processes.[52] Therefore, depauperate carnivore assemblages may not possess the regulatory capacity to maintain trophic balance, resulting in cascading impacts on terrestrial ecosystems.[13,16]

Conclusions

Across the tropics, human habitat modification is a pervasive threat to biodiversity.[1] Here, we provide valuable insights as to how keystone species like carnivores persist in human-modified areas, practically demonstrating that a combination of habitat quality and availability are fundamental to balance resource demands and competitive constraints. We show that carnivores favor high biomass areas to meet their ecological requirements, but interspecific spatial associations dictate how species interact with available habitat. The stability of carnivore communities depends on declining forested habitat to mediate antagonistic interactions with apex predators and structurally intact forests to promote coexistence among mesocarnivores. Our findings illustrate that jaguars play a unique and irreplaceable role in the spatial structuring of Neotropical carnivore communities. However, recent estimates suggest that jaguars have been extirpated across large parts of the Neotropical realm,[53] and forest loss continues unabated in areas important for jaguar conservation,[54] mirroring pressures facing apex predators elsewhere in the tropics.[55] Although securing the long-term viability of large carnivore populations should be central to conservation efforts across the tropics, we caution that prioritizing apex predator recovery could have unintended consequences for subordinate carnivores when human impacts on natural ecosystems are extensive.

Given the fundamental importance of carnivores to natural forest regeneration, restoring intact and functional carnivore communities should be a conservation priority across deforested and degraded tropical landscapes. We encourage carnivore conservation programs to capitalize on ambitious multilateral agreements (i.e., Bonn Challenge or New York Forest Declaration) and incentive schemes (i.e., Reducing Emissions from Deforestation and forest Degradation; REDD+) to provide the economic impetus needed to support landscape-scale strategies and stronger regulatory approaches (e.g., zoning and land-use planning that take into account large areas of intact forests and limit edge effects),[1,56] though integrated initiatives may require more robust monitoring protocols to ensure compatibility with carnivore conservation objectives.[57] With alarming rates of forest loss and continued anthropogenic impacts across the tropical biome, the fate of carnivores will be intricately linked to our capacity to exploit conservation opportunities that prevent further erosion of tropical forest habitat.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2023.07.064.

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AUTHOR CONTRIBUTIONS

Conceptualization, V.B., N.J.D., and E.P.; methodology, V.B., N.J.D., and E.P.; formal analysis, N.J.D. and M.H.; investigation, V.B., M.H., E.P., D.S., and R.B.; data curation, V.B., N.J.D., M.H., R.B., and D.S.; writing – original draft, V.B., N.J.D., M.H., E.P., D.S., and R.B.; writing – review and editing, V.B., N.J.D., M.H., and E.P.; visualization, N.J.D.; project administration, V.B., M.H., and E.P.; funding acquisition, V.B., M.H., and E.P. Both V.B. and N.J.D contributed equally and have the right to list their name first in their CV. All authors contributed to the article and approved the submitted version.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw and analyzed data	This paper	Zenodo: https://doi.org/10.5281/zenodo.8255666
Software and algorithms		
R version 4.1.1	R Core Team[58]	https://cran.r-project.org/bin/windows/base/
JAGS version 4.2.0	Plummer[59]	https://sourceforge.net/projects/mcmc-jags/
Other		
Global forest cover derived from remote-sensing data products	Hansen et al.[60]; Global Forest Watch	https://glad.umd.edu/projects/global-forest-watch
Global forest biomass derived from remote-sensing data products	Harris et al.[61]; Global Forest Watch	https://www.globalforestwatch.org
Colombian water bodies derived from remote-sensing data products	Institute of Hydrology, Meteorology and Environmental Studies	http://www.ideam.gov.co/en/capas-geo

RESOURCE AVAILABILITY

Lead contact

Further information and requests should be directed to and will be fulfilled by the lead contact, Dr Valeria Boron (valeria.boron@gmail.com).

Materials availability

This study did not generate unique reagents.

Data and code availability

Neotropical carnivore detection histories and site-level covariates implemented in the analysis are deposited in Zenodo: https://doi.org/10.5281/zenodo.8255666. Accession numbers are listed in the key resources table. This study does not report original code. Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Only non-invasive camera traps were used to collect species occurrence information. Non-invasive survey methods do not require a permit according to Colombian legislation.

METHOD DETAILS

Study sites

The study was conducted across nine tropical landscapes in Colombia (Figure 1). Study landscapes comprised natural vegetation cover, subjected to varying levels of human habitat modification, ranging from near pristine (97% forest cover) to severely degraded (5% forest cover; Table S1). Collectively, these landscapes provided a distinct disturbance gradient to assess human impacts on carnivore persistence and co-occurrence. Land-use change in and around study landscapes was consistent with trends elsewhere in Colombia, where deforestation has risen dramatically since 2010, largely due to the expansion of cattle ranching and the proliferation of monoculture plantations such as oil palm, sugarcane and, more recently, rice. Further descriptions of study landscapes are provided below and in Table S1.

Study landscape descriptions

Bajo Calima, Valle del Cauca: Bajo Calima is located in the department of Valle del Cauca along the Pacific coast of Colombia. These study areas receive an average rainfall of 7000 to 9000 mm and have a mean annual temperature of 26-28° C.[57] Natural land cover is tropical rainforest with small areas of pastures and subsistence agriculture.[62] In Bajo Calima, land tenure is communal and there are no protected areas. Jaguars are present in both areas.

Cauca River Valley, Valle del Cauca: this study site is located in the department of Valle del Cauca. The area received annual precipitation of 1000-1500 mm and has a mean annual temperature of 24-26° C.[57,62] The natural land cover of tropical dry forest has been replaced by sugarcane monocultures in this region, with some fragments of secondary forest and *Guadua spp.* remaining near riparian areas.[62] Neither pumas or jaguars are present in the area, and jaguaroundis (*Herpailarus yagouaroundi*) and crab-eating foxes (*Cerdocyon thous*) are the only carnivores present. The study area mostly consists of private property with one small departmental protected area within called Laguna del Sonso.

Santander study sites: the Cimitarra, Carare, and Puerto Wilches study sites are located in the department of Santander in the inter-Andean valley of the Magdalena River. This area is naturally humid tropical forest, with a mean annual temperature of 27° C and 2500-3000 mm of rainfall annually.[57,62] Principal land use is cattle pastures and oil palm plantations in the case of Carare and Puerto Wilches with some forest fragments. The Cimitarra study site is principally cacao and oil palm plantations with secondary forest fragments. All study sites were done on private property and no protected areas existed within the three. Jaguars are the apex predator in Carare and Wilches and pumas in Cimitarra.

Casanare study sites: the four studies (Encanto de Guanapalo, La Aurora, Northern Casanare, and Southeastern Casanare) were carried out in the department of Casanare in the Llanos (plains) ecosystem. Casanare is located in the Orinoquia region of eastern Colombia. The department is composed primarily of seasonally flooded tropical savannahs bordered by Andean mountains and foothills in the western portion of the department. The Llanos of Casanare have a mean annual temperature of 27° C and average rainfall between 2000 to 2500 mm.[57] Wet and dry seasons are very distinct, with a rainy season from April to November. The dominant land cover is natural and introduced grasslands which are principally used for extensive cattle ranching,[62] along with riparian forests and increasing monocultures such as oil palm and rice. El Encanto de Guanapalo and La Aurora are private protected areas that maintain natural land cover and have extensive cattle ranching operations. Northern Casanare is composed of private land with extensive cattle ranches. Southeastern Casanare is an oil palm plantation with riparian forest fragments, comprised of 3004 hectares of oil palm and 753 hectares of natural vegetation.[63] Jaguars are the apex predator in La Aurora and Northern Casanare, pumas are the apex predator in El Encanto de Guanapalo and Southeastern Casanare.

Mammal surveys

To survey the carnivore community, we deployed 481 camera traps across the nine study landscapes between 2012 and 2020. Within each landscape, camera traps were installed using a gridded system, predominantly imposed on forested habitat following standardized survey techniques for terrestrial mammals[26] (Table S1). Deployments comprised up to 83 camera stations per grid (mean: 53.44, range 25-83) separated by an average inter-trap distance of 1.2 km (range: 0.8-1.5 km). On average, study landscapes were surveyed for 3,169 camera trap nights (CTNs; range: 1,137-5,738 CTNs). Camera stations were deployed for a single season during the 11-year study period, comprising up to 90 CTNs (mean: 60 range: 10-90 CTNs). Cameras provided continuous monitoring at each station (24-hour operation) with a 30-second interval between photographic captures. While some variation in survey design and sampling effort was evident across study landscapes, all fall within optimal recommendations for multi-species applications of camera trap methods in the tropics.[62,63]

Ecological covariates

We collated ecological data on the extent and quality of forest habitat, and proximity to water, based on their reported influence on carnivore habitat selection.[25,26] Forest cover was defined using satellite-based approximations (30-m resolution) as areas with a minimum of 70% canopy cover, time-calibrated to account for regional forest loss between 2009 and 2020.[60] Forest quality was expressed as aboveground biomass (t ha^{-1}), which is a composite measure of forest structure reflecting the extent of habitat degradation due to logging.[64] Biomass data were derived from random forest models trained using ground-based forest inventory data collocated to Geoscience Laser Altimeter System (GLAS) LiDAR waveform metrics across 148,898 Neotropical locations, and spatially extrapolated based on statistical associations with Landsat surface reflectance values, biophysical variables and high-resolution canopy cover data (data obtained from: https://www.globalforestwatch.org, based on methods developed by Harris et al.[61]). Spatial predictions of biomass were constrained to forest habitat post-hoc using time-calibrated estimates of forest extent. Forest cover and biomass were extracted as mean values across 500-m radius buffers surrounding each camera station. We calculated proximity to water (km) as the Euclidean distance from freshwater sources (i.e., rivers, lakes) derived from the most recent publicly available dataset (http://www.ideam.gov.co/en/capas-geo).

QUANTIFICATION AND STATISTICAL ANALYSIS

Prior to modelling, we constructed detection histories for all carnivore species encountered across the network of camera trap stations, whereby detection/non-detection data were partitioned into sampling occasions consisting of five camera trap nights. To ensure sufficient temporal replication, only camera trap stations registering two or more sampling occasions were retained for analysis, resulting in 468 stations comprising up to 18 occasions. We excluded four species that were detected infrequently during sampling (greater grison *Galictis vittata*, margay *Leopardus wiedii*, oncilla *Leopardus tigrinus*, South American coati *Nasua*; < 10 total detections; Table S2) as changes in occurrence and detection cannot be reliably uncoupled when observation data are sparse. Moreover, we recognise that semi-aquatic species (i.e., giant otter *Pteronura brasiliensis*) cannot be reliably detected using our survey methods, and therefore restrict inferences to predominantly terrestrial taxa.

We implemented a multi-state multi-species occurrence model to explore carnivore occurrence and interspecific spatial associations across a national-scale disturbance gradient. Throughout, we follow the standard convention of interpreting occurrence-related parameters as probability-of-use when the home range estimates of focal species exceed camera spacing.[65] Probability-of-use reflects episodic use of home range elements to meet ecological demands, indicative of fine-scale habitat selection. Traditional single-season, single-species occurrence models capitalise on spatially or temporally replicated surveys to explicitly account for imperfect detection by separating the latent ecological state of interest from the observation process underpinning the data. Here, we extend this framework to accommodate pairwise interactions between multiple co-occurring carnivores, following analytical protocols established by Rota et al.[4]

For the multi-state specification, detection data were collapsed into discrete community states, which denote the observed presence/absence of all species at each station and sampling occasion. Communities encompass 2^N distinct states, where N corresponds to the number of species observed during sampling. For example, in the simplest model comprising two species, S_1 and S_2, four distinct community states are observable (2^2): the site is unoccupied (0,0), the site is occupied by either S_1/S_2 only (1,0 and 0,1 respectively), or by both species simultaneously (1,1). In the context of the three focal carnivore communities, this resulted in the following compositional characteristics: 1) felids (N=4; 16 community states); 2) non-felids (N=5; 32 community states), and; 3) mesocarnivores (N=5; 32 community states). Due to carnivore representation occurring across more than one focal community, we draw inferences about felids, non-felids and apex predator impacts from the felid and non-felid focal communities and restrict the mesocarnivore grouping to explore interactions between subordinate carnivores only.

We modelled the latent community state, Z, at site j as a realisation of a categorical random process, which extends the Bernoulli distribution beyond a single dimension:

$$Z_j \sim \text{Categorical}(\psi_j)$$

where ψ_j is a vector describing the site-specific probability of observing each community state, such that the sum of probabilities across states is equal to one. Due to this, 2^i-1 probabilities, termed "natural parameters", are estimated independently, while the remaining probability can be derived from subtraction, i.e., $\psi = (\psi_1, \psi_2, \psi_3, (1- \psi_1 - \psi_2 - \psi_3))$. As the true community state is only partially observed, the collapsed detection data (y_{jk}) is linked to the vector of state probabilities (Z_j) using a second categorical distribution:

$$y_{jk} \mid Z_j \sim \text{Categorical}(\lambda_{Zj})$$

where y_{jk} denotes the observed presence/absence of all species at site j during sampling occasion k, λ_{Zj} represents column Z_j of community detection matrix (λ), within which, all dimensions equal the number of community states, columns sum to one and the values reflect the probability of detecting a state (p) conditional on the true community state.

We modelled natural parameters as linear combinations of covariates using the multinomial logit link function to explore how local environmental characteristics influenced the probability that a site is occupied by a single carnivore species (first order occurrence), or multiple carnivores concurrently (i.e., second or higher order occurrence involving two to i species). Throughout, we restrict inference on spatial associations to second-order occurrence only, fixing all higher order interactions, involving more than two species, to zero.

For each carnivore community, we constructed four candidate models (M_1-M_4) varying in the degree to which pairwise spatial associations were described:

$M_{1\text{-}4}$: $\psi^{1st\ order}{}_j$	$\mu_{\alpha\ landscape(j)} + \alpha_1 X_{1\alpha(j)} + \alpha_2 X_{2\alpha(j)} + \alpha_3 X_{3\alpha(j)} + \alpha_4 X_{3\alpha}{}^2{}_{(j)}$
M_1: $\psi^{2nd\ order}{}_j$	Fixed at zero
M_2: $\psi^{2nd\ order}{}_j$	μ_γ
M_3: $\psi^{2nd\ order}{}_j$	$\mu_\gamma + \gamma_1 X_{1\gamma(j)}$
M_4: $\psi^{2nd\ order}{}_j$	$\mu_\gamma + \gamma_1 X_{2\gamma(j)}$
$M_{1\text{-}4}$: p_{jk}	$\mu_{\beta\ Habitat(j)} + \beta_1 X_{1\beta(j)}$

where $\psi^{1st\ order}$ and $\psi^{2nd\ order}$ denote single-species occurrence (first-order occurrence) and pairwise associations between species (second-order occurrence) respectively; p represents detection probability, and; $\mu_\alpha/\mu_\gamma/\mu_\beta$ and $\alpha/\gamma/\beta$ are vectors of intercept and slope parameters associated with first-order occurrence, second-order occurrence and detection probability respectively. Slope parameters associated with first order occurrence were interpreted directly as the log-odds of occurrence relative to a one-unit change in a covariate ($X_{N\alpha}$). While slope parameters relative to second order occurrence were interpreted as the difference in the log-odds per unit change in the covariate ($X_{N\gamma}$) when the other species is either present or absent. When second order occurrence parameters equal zero species occurrence was assumed to be independent. Throughout, subscript j represents a site-specific index.

Across all models, first-order occurrence was described as a function of habitat extent and quality (forest cover, $X_{1\alpha}$; forest biomass, $X_{2\alpha}$) and proximity to key environmental resources (distance to water, $X_{3\alpha}$). Distance to water was modelled using a quadratic term to account for non-linear responses. We also implemented landscape-specific fixed intercepts to address spatially-structured variation in survey design and unobserved ecological factors ($\mu_{\alpha\ landscape}$) and provide geographically coarse estimates of baseline occurrence at constant environmental conditions (i.e., covariates held at their average values). Similarly, detection was modelled consistently across the candidate set using covariates presumed to influence the observation process. These included habitat-specific fixed intercepts ($\mu_{\beta\ habitat}$), to account for fine-scale differences in animal movement characteristics according to land-use,[66] and a categorical covariate documenting whether the camera trap was deployed on an established trail ($X_{1\beta}$).

For second-order occurrence, linear predictors were altered to explore the importance, nature and extent of interspecific spatial associations. M_1 was broadly equivalent to a traditional multi-species occurrence model, assuming that the presence or absence of one carnivore species does not influence that of another. M_2 represents an intercept only formulation which assumes that species do influence the occurrence patterns of other carnivores irrespective of local environmental conditions. The intercept term thus reflects the degree of spatial overlap between competing carnivores, where positive values indicate co-occurrence and negative values indicate spatial avoidance. Both M_3 and M_4 also assume a dependence between carnivore occurrence patterns, but that spatial associations vary relative to human impacts on habitat conditions. We infer impacts of habitat loss from forest cover ($X_{1\gamma}$) and habitat degradation from forest biomass ($X_{2\gamma}$). Intercept terms for M_3 and M_4 are interpreted as in M_2, but at constant environmental conditions.

To determine whether interspecific spatial associations represent an important consideration in assessments of carnivore habitat use and identify the prominent human impacts underpinning spatial associations, we ranked competing models using Watanabe-Akaike Information Criterion (WAIC[67]; Table S3). WAIC is a within-sample model selection statistic analogous to AIC but robust to latent parameters. We consider substantial support for models with ΔWAIC < 4 and weak support for models with $4 \leq \Delta\text{WAIC} \leq 10$.

All models were implemented in a Bayesian framework using JAGS v. 4.2.0[59] called through R v. 4.1.1[58] with the jagsUI package.[68] We specified three Markov chains per parameter, comprising 150,000 samples, using a 10,000-step adaptation and a 75,000-iteration burn-in period. Samples were thinned by a rate of 75, resulting in 1,000 posterior samples per chain, totalling 3,000 per parameter. We assessed model convergence visually, by inspecting traceplots to verify adequate mixing, and statistically, using the Gelman-Rubin statistic, where values of Rhat <1.1 indicate parameter convergence.[69] Across all models/parameters, we found no evidence to indicate that samplers failed to converge (Rhat range: 1.000 – 1.004). Throughout, we report parameters as the mean of the posterior distribution, and express dispersion using a combination of 75% (12.5^{th} and 87.5^{th} percentile of the posterior distribution) and 95% (2.5^{th} and 97.5^{th} percentiles of the posterior distribution) Bayesian credible intervals (BCIs). We regard parameters to have substantial statistical support if the 95% BCI did not overlap zero overlap and moderate support if the 75% BCI did not overlap zero. Unless stated otherwise, reported credible intervals correspond to the 95% threshold.