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Human disturbance and shifts in vertebrate community composition in a biodiversity hotspot

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Article impact statement: Human activities reduce the presence of large herbivores and predators, affecting ecosystem function, even in well-conserved forests.

Abstract

Understanding how human modification of the landscape shapes vertebrate community composition is vital to understanding the current status and future trajectory of wildlife. Using a participatory approach, we deployed the largest camera-trap network in Mesoamerica to date to investigate how anthropogenic disturbance shapes the occupancy and co-occurrence of terrestrial vertebrate species in a tropical biodiversity hotspot: the Osa Peninsula, Costa Rica. We estimated species richness in different categories of land protection with rarefaction analysis and estimated the expected occupancy with a joint species distribution model that included covariates for anthropogenic disturbance, land protection, habitat quality, and habitat availability. Areas with the most stringent land-use protections (e.g., Corcovado National Park, 24 species [95% CI 23–25]) harbored significantly more species than unprotected areas (20 species [19.7–20.3]), mainly due to a reduced presence of large-bodied species of conservation concern in unprotected areas (e.g., jaguar *Panthera onca* and white-lipped peccary *Tayassu pecari*). Small-bodied generalist species, such as opossums (Didelphidae) and armadillos (*Dasypus novemcinctus*), in contrast, were more common at disturbed sites, resulting in a significant difference in vertebrate community composition between sites with low and high disturbance. Co-occurrence of species was also mainly associated with response to disturbance. Similar responses to disturbance create two groups of species, those whose site-level occupancy usually increased as anthropogenic disturbance increased and those whose estimated occupancy decreased. The absence of large-bodied species entails an important loss of ecological function in disturbed areas and can hinder forest development and maintenance. Efforts to protect and restore forested landscapes are likely having a positive effect on the abundance of some threatened species. These efforts, however, must be sustained and expanded to increase connectivity and ensure the long-term viability of the wildlife community.

KEYWORDS
camera-trapping, collaborative network, community shift, endangered species, tropical forests

Perturbaciones Humanas y Cambios en la Composición de la Comunidad de Vertebrados en un Punto Caliente de Biodiversidad

Resumen: El entendimiento de cómo las modificaciones humanas del paisaje conforman la composición de las comunidades de vertebrados es vital para entender el estado actual y la trayectoria futura de la fauna. Mediante una estrategia participativa, desplegamos la mayor red de cámaras trampa en Mesoamérica hasta la fecha para investigar cómo la perturbación antropogénica determina la ocupación y coocurrencia de las especies terrestres de vertebrados en un punto caliente de biodiversidad tropical: la Península de Osa, Costa Rica. Estimamos la riqueza de especies en diferentes categorías de protección de suelo con un análisis de rarefacción y estimamos la ocupación esperada con un modelo de distribución conjunta de especies que incluyó covariables para la perturbación antropogénica, la protección del suelo, la calidad del hábitat y la disponibilidad del hábitat. Las áreas con la protección más estricta de uso de suelo (p. ej.: Parque Nacional Corcovado, 24 especies [95% CI 23-25]) albergaron significativamente a más especies que las áreas desprotegidas (20 especies [19.7-20.3]), principalmente debido a la presencia reducida de especies de talla grande de interés para la conservación en las áreas desprotegidas (p. ej.: el jaguar *Panthera onca*, el pecarí de labios blancos, *Tayassu pecari*). Al contrario, las especies generalistas de talla pequeña, como las zarigüeyas (Didelphidae) y el armadillo (*Dasypus novemcinctus*) fueron más comunes en los sitios perturbados, lo que resulta en una diferencia significativa en la composición de las comunidades de vertebrados entre los sitios con una perturbación baja y alta. La coocurrencia de especies también estuvo asociada principalmente con la respuesta a la perturbación. Las respuestas similares a la perturbación crean dos grupos de especies: aquellas cuya ocupación a nivel de sitio generalmente incrementó conforme incrementó la perturbación antropogénica y aquellas cuya ocupación estimada disminuyó. La ausencia de especies de talla grande conlleva una pérdida importante de la función ecológica en las áreas perturbadas y puede dificultar el desarrollo y mantenimiento del bosque. Los esfuerzos para proteger y restaurar los paisajes forestales probablemente estén teniendo un efecto positivo sobre la abundancia de algunas especies amenazadas. Estos esfuerzos, sin embargo, deben ser sostenidos y expandidos para incrementar la conectividad y asegurar la viabilidad a largo plazo de la comunidad faunística.

PALABRAS CLAVE:
bosques tropicales, cambios comunitarios, cámaras trampa, especie en peligro, red colaborativa

摘要

理解人类对景观的改变如何塑造脊椎动物群落组成对于了解野生动物的现状和未来轨迹至关重要。本研究使用参与式方法, 在中美洲部署了迄今为止最大的红外相机监测网络, 以调查人为干扰如何影响热带生物多样性热点地区——哥斯达黎加奥萨半岛的陆生脊椎动物分布和共存情况。我们通过稀疏性分析估算了不同保护类型的土地的物种丰富度, 并利用联合物种分布模型对物种分布区占有率进行了估计, 该模型的协变量包括人为干扰、土地保护、栖息地质量和栖息地可用性。土地利用保护最严格的区域(如科尔科瓦多国家公园, 有 24 个物种 [95%置信区间为23-25])的物种数量明显多于未保护区域 (20个物种 [19.7-20.3]), 这主要

是由于未保护区域内大型保护动物数量减少(如美洲豹 *Panthera onca* 、白唇西猯 *Tayassu pecari*)。相反, 体型较小的广生性物种, 如负鼠 (Didelphidae) 和犰狳(*Dasypus novemcinctus*), 则在受干扰地区更为常见, 这导致低干扰和高干扰位点之间脊椎动物群落组成产生显著差异。物种的共存也与其对干扰的响应有重要关系。根据对干扰的相似响应可以将物种分为两类, 一类物种的分布区占有率随人为干扰增加而增加, 另一类物种的占有率则下降。大型动物的缺失会导致受干扰地区生态功能严重丧失, 并可能阻碍森林的发展与维持。森林景观的保护和恢复可能会促进受威胁物种的丰度增加。然而, 我们还需要持续且更大范围的努力来增加连通性, 以保障野生动物群落的长期生存力。**【翻译: 胡怡思;审校: 聂永刚】**

关键词: 视频, 群落转换, 热带森林, 合作网络, 红外相机技术, 濒危物种

INTRODUCTION

Tropical rainforests are among the most biodiverse ecosystems in the world (Myers et al., 2000) and are the most threatened by habitat loss and fragmentation (Corlett, 2012; Davies et al., 2006). Threats to wildlife arise from land-use change for food production, mineral extraction, urbanization, and expansion of transportation and energy infrastructure (Benítez-López et al., 2010; Brooks et al., 2002), as well as from poaching, wildlife trade, and retaliatory killings (Osuri et al., 2020). Mitigation of these threats is often limited by financial constraints that force countries with developing economies to prioritize resources among several pressing issues. This situation often leads to a lack of capacity to develop, oversee, and enforce conservation policies (Barrett et al., 2001). Preventing further biodiversity loss in the tropics thus requires creative, economically viable solutions for studying wildlife populations and understanding the factors that affect their abundance and distribution.

Variance in the nature and intensity of human activities, combined with the diversity of species and their life histories, creates a significant challenge to understanding the potential outcomes of anthropogenic disturbance. To fully understand these outcomes requires studying a diverse array of species, at a large spatial scale, across a gradient of disturbance levels (Gardner et al., 2009; Newbold et al., 2014). Too often, however, studies of tropical forest vertebrate communities have limited spatial and temporal scopes or focus on only a few species, due to insufficient equipment, funding, or training (Danielsen et al., 2005). Externally led and funded initiatives can occasionally achieve great spatial coverage and include several taxa, but resource irregularity and lack of training of local collaborators often prevents the continuation of such efforts (Sheil, 2001). Locally based approaches can help overcome such barriers by actively involving different stakeholders in monitoring efforts and reconciling the interests of managers and local communities (Danielsen et al., 2005; Danielsen et al., 2014). Collaboration between stakeholders also facilitates pooling existing resources and distributing the effort, thus greatly increasing the spatial and temporal scale and resolution that can be achieved in wildlife studies.

We used a large-scale, collaborative, participatory approach to study the terrestrial vertebrate community in a Neotropical biodiversity hotspot: the Osa-Golfito region in southern Costa Rica. The Osa is a key conservation target in Costa Rica because it sustains populations of emblematic species of concern often used as umbrella species, such as jaguar (*Panthera onca*), Baird's tapir (*Tapirus bairdii*), and white-lipped peccary (*Tayassu pecari*). Numerous programs have been implemented to protect species at risk, but many conservation challenges remain. Forests are interspersed between agricultural lands (pastures, rice, palm oil, and timber plantations), roads, towns, and villages, and logging and infrastructure development threaten to increase fragmentation further. Additionally, ongoing poaching and illegal gold mining continue to put several species at risk (Wong, 2014). Conservation approaches, however, are hindered by gaps in knowledge of how wildlife responds to different degrees of disturbance in the region because previous studies have mostly been limited to protected areas (Carrillo et al., 2000; Salom-Perez et al., 2007).

We sought to determine how human land management (e.g., land protection and development) affect the distribution and co-occurrence patterns of terrestrial mammals and ground birds in the Osa. We used an extensive array of camera traps and analyzed how species occupancy responds to anthropogenic disturbance, land protection status, and habitat quality. We explored the link between anthropogenic and environmental factors and key species traits, such as body size and trophic guild, and how species-specific responses determine community composition. Diet and habitat generalist species are generally more tolerant to disturbance because they can cope with high resource variability and exploit multiple resources both in the forest and near humans (Fisher & Burton, 2018). Similarly, species with small home ranges are generally more likely to tolerate habitat loss and degradation than species with large home ranges, such as large carnivores and herbivores (Morrison et al., 2007; Noonan et al., 2020). We, therefore, expected small generalist species, such as opossums (Didelphidae), raccoons and coatis (Procyonidae), to show no significant response to anthropogenic or environmental factors (Cantor et al., 2010). We expected small forest herbivores, such as agoutis and pacas (Dasyproctidae, Cuniculidae), to respond positively to availability of and good-quality habitat and to be unaffected by human disturbance (Jax et al., 2015). Meso-predators, such as small felines (Felidae) and weasels (Mustelidae), have relatively small territories and more potential prey items than large carnivores, but they are, nonetheless, sensitive to human presence, so we expected to see small

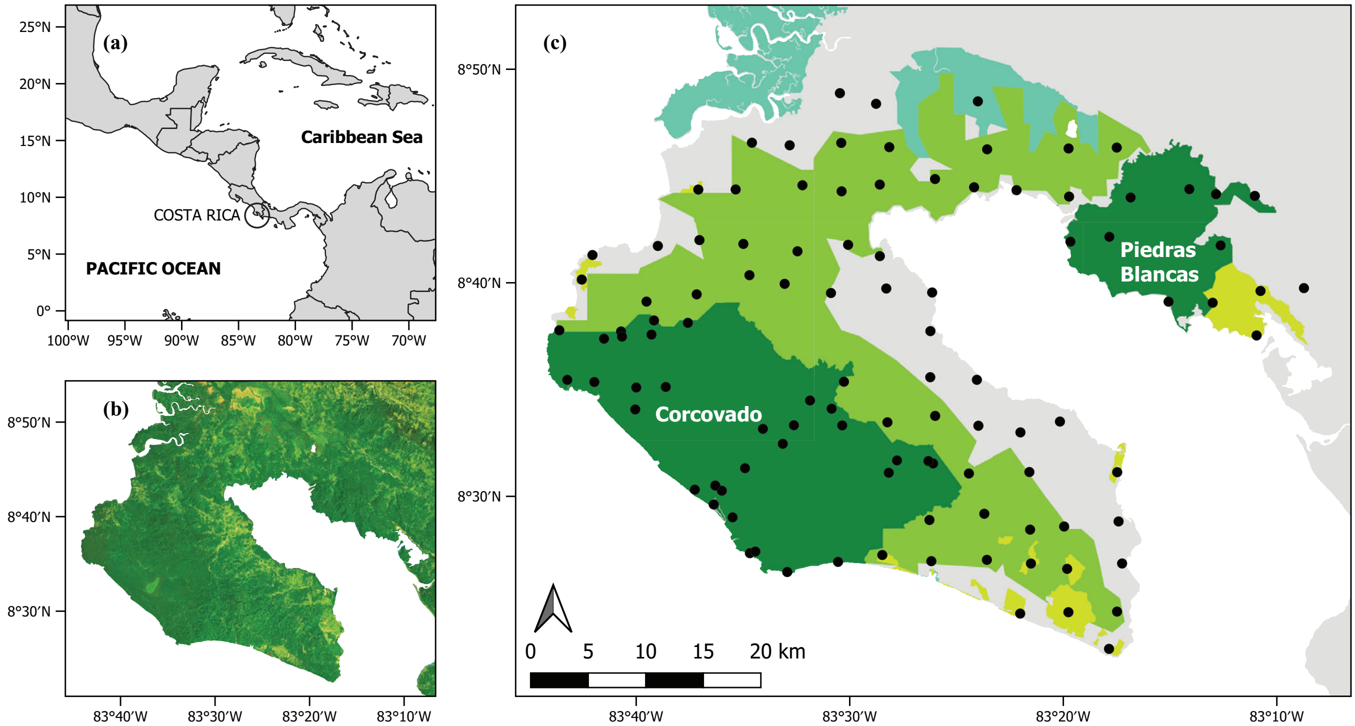

FIGURE 1 (a) Location of the study area on the Osa peninsula in southern Costa Rica (circle), (b) satellite image of the large proportion of forested area in the region, and (c) distribution of camera-trap stations throughout the study area and land management status (dark green, national parks; light green, Golfo Dulce Forest Reserve; turquoise, Térraba-Sierpe Wetlands; yellow-green, wildlife refuges; gray, unprotected areas)

to moderate effects of changes in habitat availability and some negative responses to human impact (Michalski & Peres, 2005). Finally, we expected large carnivores (e.g., jaguars and pumas) and herbivores (e.g., deer and tapirs) to be affected negatively by disturbance and positively by good-quality habitat.

METHODS

Study area

The Osa-Golfito region spans 1543 km^2 along the southern Pacific coast of Costa Rica (Figure 1). It has a tropical climate with high temperatures year-round (mean: 27 °C, range 23–32 °C) and heavy rainfall (mean 3700 mm, range 3000–6000 mm) concentrated in the rainy season from May to December (Solano & Villalobos 2005). Although human density has historically been low (<20/km^2), the region has seen significant land-use changes (Lewis, 1985). The original rainforest was largely replaced by pasture and later by banana and palm oil plantations, significantly limiting the distribution of wild species (Lewis, 1985). The region's biodiversity prompted the creation of several protected areas, allowing the forest to recover and animals to recolonize some areas over the last 50 years (Algeet-Abarquero et al., 2015). There is now a matrix of primary and secondary forests covering over 70% of the region, mostly inside protected areas (Figure 1). Two national parks, Corcovado (424 km^2), inside the Osa Peninsula, and Piedras Blancas (140 km^2), on the mainland, are structurally connected by the Golfo Dulce Forest Reserve (599 km^2), a mixture of public and private lands that also acts as a protection buffer between the parks and surrounding communities (Figure 1). Forest plantations (teak [*Tectona grandis*] and gmelina [*Gmelina arborea*]), small-scale agricultural activities, and human settlements are allowed inside the forest reserve, whereas hunting is prohibited throughout Costa Rica, regardless of land protection status. The rest of the region has small towns (<10,000 people) and villages and small- to medium-scale agricultural activities (cattle, palm oil, and rice).

Study species

We focused on medium and large-bodied mammal and ground bird species, which can be adequately studied with camera traps (Rovero et al., 2014). Many of these are of concern globally or locally. Jaguars and margays (*Leopardus wiedii*) are near threatened, white-lipped peccaries and great curassows (*Crax rubra*) are vulnerable, and Baird's tapirs are endangered, according to the International Union for Conservation of Nature Red List (Quigley et al., 2018; Garcia et al., 2016; de Olivera et al., 2015; Keuroghlian et al., 2013; BirdLife International, 2020). Pumas (*Puma concolor*), ocelots (*Leopardus pardalis*), jaguarundis (*Puma yagouarundi*), crab-eating raccoons (*Procyon cancrivorus*), collared peccaries (*Pecari tajacu*), red brocket deer (*Mazama temama*), pacas (*Cuniculus paca*), and grison (*Galictis vittata*) are threatened or endangered in Costa Rica (MINAE-SINAC-CONAGEBIO-FONAFIFO, 2019), despite being of least concern globally. The region is also home to common species like raccoons (*Procyon lotor*), white-nosed coatis (*Nasua narica*), three species of opossums (Didelphidae), tayra (*Eira barbara*), skunks (*Conepatus semistriatus*), armadillos (*Dasypus novemcinctus*), and agoutis (*Dasyprocta punctata*). Pacas, white-lipped peccaries, and tinamous (Aves, Tinamidae) are directly affected by poaching (Wong, 2014), and habitat loss due to illegal logging and gold mining threatens forest-dependent species (Dirzo et al., 2014; Wong, 2014).

Camera-trap survey

To determine how anthropogenic factors and habitat quality determine the distribution of our study species, we set up camera-trap stations throughout the study area on lands with different protection categories and different degrees of anthropogenic disturbance (Figure 1). We deployed 120 camera-trap stations in a 4 × 4 km square grid, maintaining at least 1000 m between them. This cell size provided an optimum balance of coverage and resolution of the study area and maintained independence among stations for species with large home ranges (e.g., jaguars and peccaries). The data from 15 stations were lost due to camera malfunction or theft. Of the remaining stations, 70% ($n = 73$) were in secondary forest areas, followed by primary forests ($n = 29$; 28%), and only a few were in forest plantations ($n = 2$) or in pasture ($n = 1$). One fifth of our stations were outside protected areas (Table 1). Stations were deployed for 117 days on average (SD 38.9, range 32–241) from February to July 2018. This period is well beyond the 28 days required to accurately estimate local detection rates (Kays et al., 2020). The total effort was 12,276 trap nights (Table 1).

We placed cameras 30–50 cm off the ground, preferentially on game trails, and always without bait. This setup is appropriate for studying most terrestrial ground birds and mammals (except for small rodents) (Rovero et al., 2014). For every photograph, we identified the species captured and recorded the date and time. We collaborated with local government agencies, nongovernment organizations, ecolodges, and national and local and international universities. We also trained leaders from four local communities to set up and manage camera-trap surveys. More than 40 people participated in setting up and checking camera stations. Most stations had two paired cameras to potentially identify animals individually based on spot patterns. In total, we had 241 cameras, 173 Bushnell Trophy Cam (Overland Park, Kansas), 31 Reconyx Hyperfire HC500, PC800, Ultrafire XR6, or WP9 (Holmen, WI, USA), 30 Pantheracam V5 (Wappinger Falls, New York), and 7 Cuddeback 1224 (Green Bay, Wisconsin). To ensure setup consistency, a detailed protocol was distributed among participants with previous camera-trapping experience. A core team coordinated efforts and guided participants with less experience. This work was conducted under research permit INV-ACOSA-041-017 from the Costa Rican National System of Conservation Areas.

TABLE 1 Camera-trap survey effort and species richness for wild medium to large terrestrial mammal and bird species by land management category in the Osa Peninsula, Costa Rica

Management type	Stations (cameras)	Effort(trap days)	Detections	Observed richness	Estimatedrichness (95% CI)[a]	Mean disturbance (SD)[b]	Mean habitat integrity (SD)[c]	Mean habitat availability (SD)[d]
Wildlife refuge	11 (20)	1387	1420	22	24.7 (19.3–26.5)	0.23 (0.08)	0.60 (0.04)	0.35 (0.17)
Corcovado National Park	32 (79)	3702	4633	24	24.0 (23.0–25.0)	0.12 (0.03)	0.58 (0.03)	0.25 (24)
Golfo Dulce Forest Reserve	32 (62)	3564	4343	23	23.0 (22.6–23.4)	0.18 (0.03)	0.60 (0.04)	0.23(0.22)
Unprotected area	21 (42)	2582	2227	20	20.0 (19.7–20.3)	0.23 (0.08)	0.57 (0.07)	0.28 (0.23)
Piedras Blancas National Park	8 (15)	923	1033	19	19.9 (17.3–20.6)	0.21 (0.09)	0.57 (0.03)	0.27 (0.22)
Terraba-Sierpe National Wetland[e]	1 (1)	118	24	8	–	0.17	0.58	0

[a] Asymptotic richness estimate from the iNext R package.
[b] Global human modification index value.
[c] Proportion of primary forest within a 500-m radius around each station.
[d] Enhanced vegetation index within a 500-m radius around each station.
[e] Species accumulation curves not estimated for wetlands due to the low number of stations.

Species richness comparisons

We divided the data by land management category: unprotected land, wildlife refuge, forest reserve, and national park (Table 1). We confirmed adequate coverage and estimated species richness for each category with individual-based rarefaction curves in the iNEXT package (Hsieh et al., 2016) in R 3.6 (R Core Team, 2020). The two national parks were analyzed separately, considering the distance between them. We did not include the protected wetlands category in our analyses because we had only one station there.

Joint species distribution model

To determine the effect of human activities and habitat quality on the distribution of wild species, we used a joint species distribution model that accounts for imperfect detection and residual correlation among species (Tobler et al., 2019). Like previous multispecies occupancy models (Dorazio & Royle, 2005), this model estimates species-specific probabilities of detection and occupancy as a function of environmental covariates. We defined *site occupancy* as the probability that a species uses the area around a station. To estimate detection probability, we divided the total sampling period in distinct 6-day occasions and scored species detected during each occasion at a given station as 1 and undetected species as 0.

We included four predictors of occupancy: global human modification index (Kennedy et al., 2019), as an overall measure of anthropogenic disturbance; protected area status; percentage of primary forest, as a measure of availability of undisturbed habitat; and enhanced vegetation index, as a measure of habitat integrity. Mean human modification, proportion of primary forest, and mean vegetation index were calculated within 500 m around each station with QGIS 3.10 (QGIS Development Team, 2019). This scale should capture the environment that affects both resident species with small home ranges and transient species moving through the area. The human modification index includes transportation, human settlements, agriculture, extractive activities, and electric infrastructure and has values between 0 (no disturbance) and 1 (highest disturbance) (Kennedy et al., 2019). Values across our sites suggested low to intermediate impact in the region (mean [SD] = 0.22 [0.10], range: 0.01–0.55 [Appendix S1]). Land protection indicated whether stations were inside (1) or outside (0) protected areas. We used Landsat-7 satellite imagery to determine the proportion of primary forest and the mean enhanced vegetation index (Jiang et al., 2008) in the Google Earth Engine platform (Gorelick et al., 2017) to determine habitat quality and availability. We standardized and mean-centered covariates to facilitate comparisons of effect sizes. Because the placement of stations can influence detection probability greatly, we ran the model with different detection covariates, including placement on trail, land cover, and camera make.

To account for the influence of interspecific interactions on the distributions of species, we determined the strength of the correlation among species. The component of the correlation due to environmental factors was calculated as a function of the scaled regression coefficients and the covariance among predictors (details and R code in Pollock et al. [2014]). The residual correlations that were not explained by environmental covariates were captured by latent variables that describe the relationship among species (Tobler et al., 2019). We included 10 latent variables for 22 species, which can be interpreted as unmeasured site-level covariates that capture variance not explained by environmental factors (Tobler et al., 2019 suggest that $n/2$ latent variables may be necessary to capture unstructured residual correlations among n species).

Models were run in JAGS with the R2Jags package (Su & Yajima, 2020) in R (R Core Team, 2020). We used three chains of 100,000 iterations each, a burn-in of 50,000 iterations, and a thinning ratio of 50. Model convergence was assessed through inspection of the resultant Markov Chain Monte Carlo chains. We evaluated the importance of covariates based on their relative effect sizes. We also explored how species-specific traits, namely, body size and functional group (trophic guild extracted from the Elton Traits database [Wilman et al., 2014]), were related to the effect sizes.

RESULTS

We accumulated 13,680 independent detections of 26 wild terrestrial mammal and ground bird species (Appendix S2). Agouti (n = 5719 detections, 91% of stations), great curassow (n = 1090, 83%), tinamous (n = 1043, 68%), and coati (n = 1013, 88%) were the most common and widespread species. Jaguarundi, jaguars, and crested guan were detected fewer than 30 times each and at fewer than 20% of stations (Appendix S2). Grison, coyote (*Canis latrans*), and water opossum (*Chironectes minimus*) were detected only once and were, therefore, excluded from analyses (Appendix S2). We also excluded the Neotropical otter (*Lontra longicaudis*) (n = 7) because our camera placement was not suitable for aquatic species. We grouped records of northern (*Procyon lotor*) and crab-eating raccoons given the difficulty in distinguishing them in camera-trap images. There were 1337 detections related to anthropogenic activities: 1039 people, 238 dogs, 40 horses, and 15 cows (Appendix S2).

Species richness comparisons

The similarity between observed and estimated richness indicated good coverage of our survey (Table 1). In general, protected areas had more species than unprotected areas. An exception was Piedras Blancas National Park, which had similar species richness as unprotected areas (Table 1 & Appendix S1). Species composition in both national parks and the forest reserve was similar, except for four species that were absent from Piedras Blancas (jaguar, tapir, white-lipped peccary, and margay). Except for margays, these species were detected only in and around Corcovado National Park (Appendix S1).

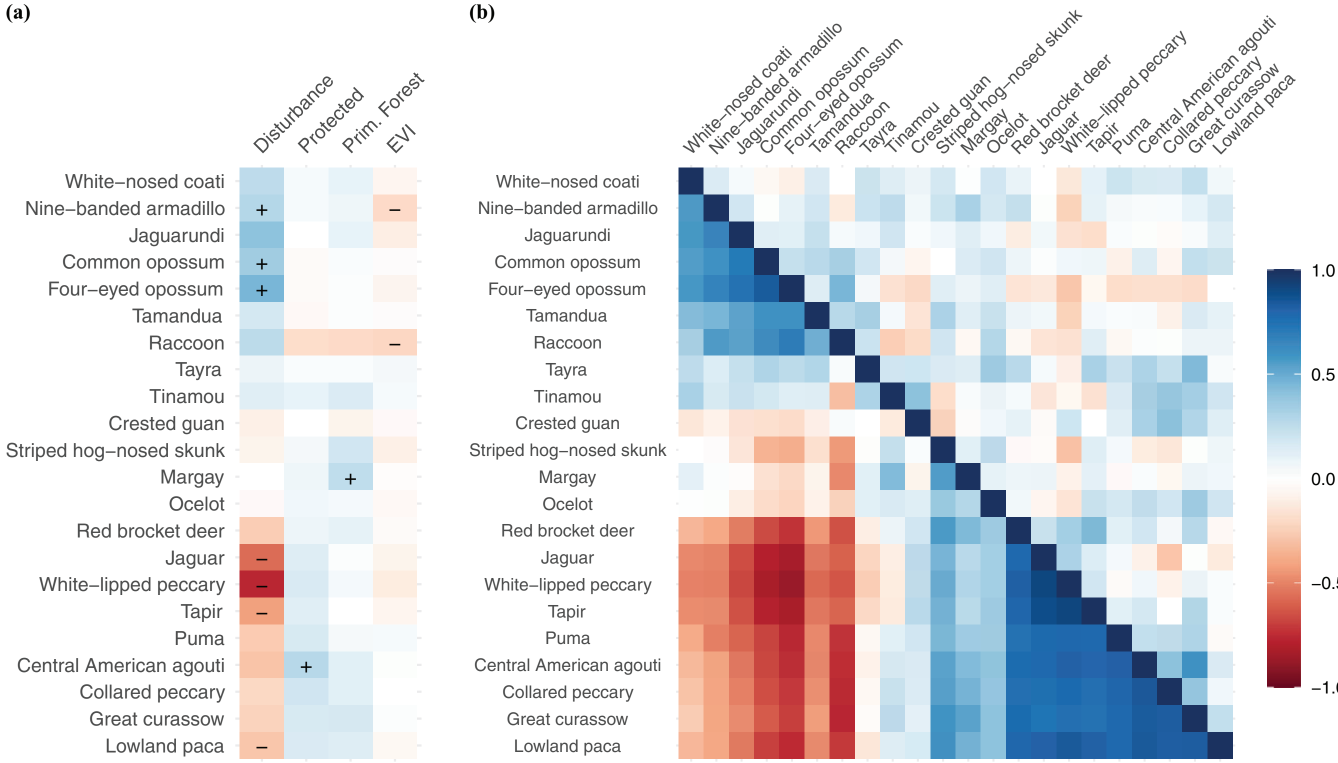

FIGURE 2 (a) Effects of covariates on the occupancy of wild species in the Osa peninsula, Costa Rica, based on mean posterior credibility estimate (blue, positive; red, negative; positive and negative symbols, clear effects based on 95% CIs reported [Appendix S2]) and (b) correlation between species occupancy (lower half of matrix, anthropogenic and environmental factors; upper half of matrix, interspecific interactions or unmeasured covariates [details in Methods])

Joint species distribution model

The mean proportion of primary forest was 23%, but it varied widely (0–87%) among stations. The enhanced vegetation index was fairly uniform across the area (mean [SD] = 0.58 [0.04], range 0.33–0.66). Scaled covariates were not strongly correlated (Appendix S1). The best model of species occupancy was the one with no detection covariates, so we report the results of this model (based on the Watanabe-Akaike information criterion [Broms et al., 2016]: $\delta_{\mathrm{WAIC}} = 1.889$ with respect to the model that included camera make).

We found a clear negative effect—determined from the 95% credible intervals—of anthropogenic disturbance on the presence of white-lipped peccaries, jaguars, tapirs, and pacas (Figure 2). Conversely, common (*Didelphis marsupialis*) and four-eyed opossums (*Philander opossum*), and armadillos, responded positively to disturbance. Protection status had a clear influence only on agoutis, which were more likely to occur inside protected areas (Figure 2a). Habitat quality had practically no influence on occupancy probability. The proportion of primary forest had a clear positive effect only on margays (Figure 2a), and we only saw a clear effect of the enhanced vegetation index—our metric for habitat integrity—on raccoons and armadillos, with both more likely to be at lower-quality sites (Figure 2a).

The human modification index had the greatest mean absolute effect, roughly three times higher than the effect of the remaining covariates, although there was also greater variability around its estimates (Appendix S2). The effect of disturbance was related to body size. Large-bodied species typically showed negative responses to disturbance, whereas small-bodied species showed positive responses (Figure 3a). Species-specific responses were also related to functional group. Apex predators and herbivores responded negatively to human disturbance, whereas insectivores, mesopredators, and omnivores were relatively insensitive or responded positively (Figure 3b).

We saw large reductions in occupancy probability in response to increased disturbance for white-lipped peccaries (100% decline in occupancy probability), jaguars (100% decline), tapirs (86% decline), and red brocket deer (69% decline) (Figure 3c). Conversely, occupancy probability increased greatly for four-eyed opossums (665% increase in occupancy probability), jaguarundis (364% increase), armadillos (134% increase), raccoons (132% increase), and common opossums (108% increase) (Figure 3c). The occupancy probability of several species appeared insensitive to variation in anthropogenic disturbance (e.g., white-nosed coatis, tinamous, and tayras). As a result of these changes, rank occupancy differed significantly along the disturbance gradient. Species such as collared peccary and great curassow were highly likely to occur at sites with low disturbance, but they were much rarer at disturbed sites. Conversely, species such as the common opossum and tamandua (*Tamandua mexicana*) were much more common in areas with high disturbance (Figure 3c).

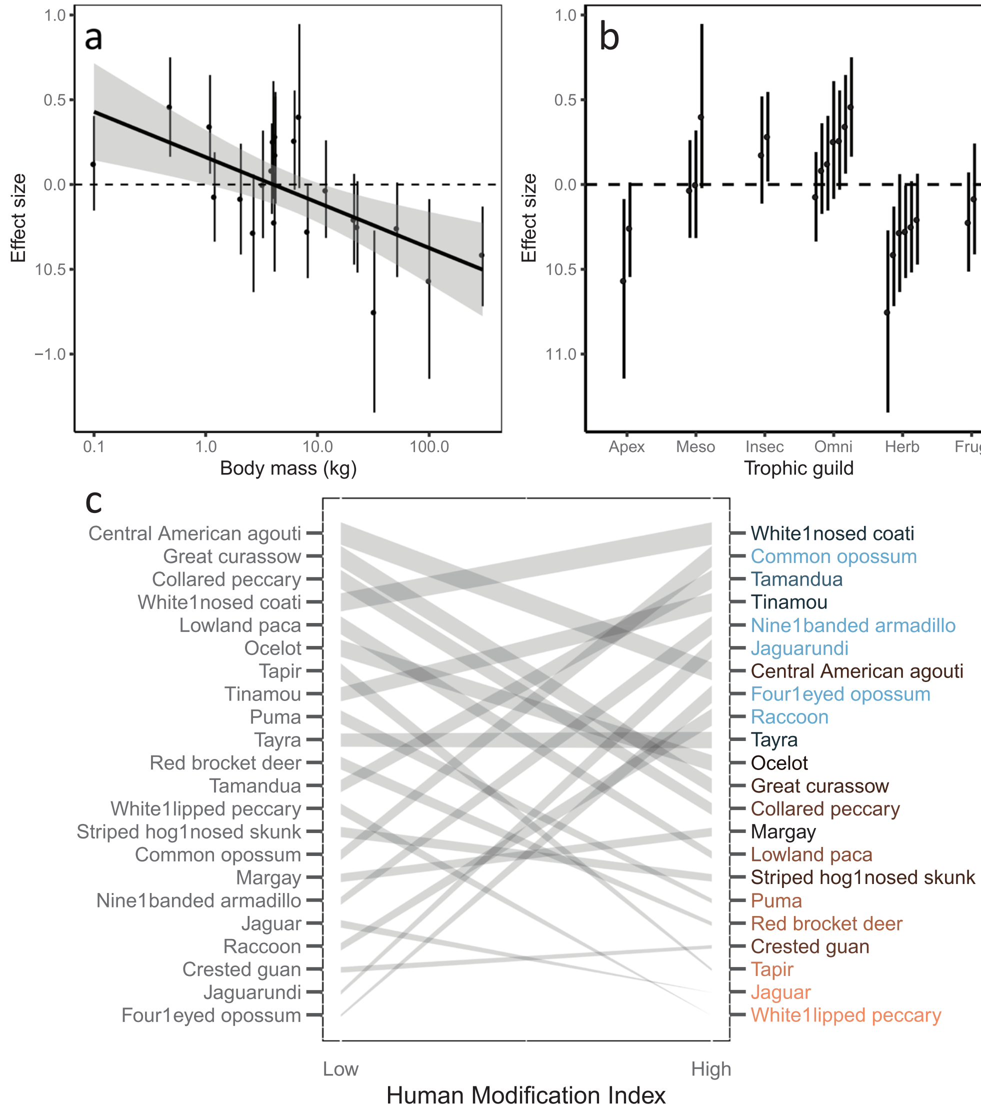

FIGURE 3 Mean effect size of the human disturbance index on occupancy relative to (a) body size (shading, 95% CI) and (b) functional group (Apex, apex predator; Frug, frugivore; Herb, herbivore; Insec, insectivore; Meso, mesocarnivore; Omni, omnivore) (points, mean effect size; vertical lines, 95% credible intervals). (c) Change in mean ranked occupancy estimates as human disturbance increases (left, lowest disturbance level; right, highest disturbance level; mean occupancy estimate at the lowest (left) and highest (right) levels of disturbance; colors, species that changed in occupancy relative to the occupancy estimate at low disturbance sites: blue, increase; black, neutral; orange, decrease); the darker the shade, the larger the percent change). For (b) specific body mass values and functional groups are in Appendix S1

Species correlations

Co-occurrence patterns were mostly explained by similar responses to environmental covariates and not by interspecific interactions (Figure 2b). Correlation due to environmental values largely corresponded to the response to anthropogenic disturbance. Shared responses to covariates grouped species into a disturbance-intolerant community or a disturbance-tolerant community. The first included apex predators (jaguar and puma) and herbivores (tapir, red brocket deer, white-lipped and collared peccary, paca, and agouti) (Figure 2b). This group had the strongest correlations and was negatively associated with anthropogenic disturbance. We also found strong, albeit lower, correlations among raccoons, opossums, coatis, tamanduas, armadillos, and jaguarundis, all of which showed positive responses to disturbance. Other species, including ocelots, margays, tayras, crested guans, skunks, and tinamous, only showed minor correlations with other species (Figure 2b).

DISCUSSION

The spatial scale and resolution of our study design allowed us to analyze how anthropogenic and environmental factors shape the wildlife community along a gradient of disturbance. The overall level of anthropogenic disturbance, as quantified by the global human modification index (Kennedy et al., 2019), had the greatest impact on individual species and the entire community. Species-specific responses to disturbance were seemingly associated with body mass and trophic guild, which created two distinct groups: species that did well under human development (i.e., small diet generalists) and species that do poorly (i.e., large specialists).

We found higher species richness in protected areas, similar to previous studies (Gray et al., 2016; Khazan et al., 2016). Protected areas favor population growth and expansion (Geldmann et al., 2013), but these effects can be context dependent, as evidenced by the lower richness observed in Piedras Blancas National Park. This park is connected to larger protected areas (Corcovado National Park and Golfo Dulce Forest Reserve) in a seemingly continuous forest (Figure 1) (Morales-Salazar et al., 2013). Nevertheless, Piedras Blancas is relatively isolated, bounded by a large river, a major road, and the Golfo Dulce. The apparent lack of functional connectivity could have greater implications because Piedras Blancas serves as a connection between populations on the peninsula and on the mainland. Maintaining the positive effects of these protected areas on wildlife will depend largely on ensuring connectivity at a regional scale (DeFries et al., 2005), for example, through the creation of wildlife corridors. The success of ongoing corridor initiatives in the Osa region, such as the Amistosa corridor between Osa and the Talamanca mountains (Desanti et al., 2009), requires understanding the anthropogenic and environmental factors that determine species distributions.

Anthropogenic disturbance had the greatest effects on occupancy and affected the most species, despite only low to moderate levels of modification in our study region (according to the categories established by Kennedy et al. [2019]). In contrast, indicators of habitat quality had almost no effect. Similar relationships between anthropogenic and environmental variables have been found for multiple taxa across the tropics (Newbold et al., 2014). We used a cumulative index that captures overall disturbance in our study region accurately (Appendix S1). Nevertheless, there could be different factors that affect each species. Some species may be avoiding human settlements or roads (Cavada et al., 2019; Benitez-Lopez et al., 2010), whereas others may be responding to the presence of domestic animals (Zapata-Ríos & Branch, 2018). Understanding these specific responses will be critical for managing species of conservation interest.

Large-bodied predators and herbivores were in general negatively affected by human modification. The absence of large-bodied species from highly disturbed areas is consistent with impacts seen from defaunation due to habitat conversion in other regions (Daily et al., 2003; Jorge et al., 2013; Whitworth et al., 2019). For species with large home ranges, the negative effects of disturbance may simply be explained by the lack of sufficient habitat. White-lipped peccary herds, for example, require up to 140 km^2 of forests (Moreira-Ramirez et al., 2019), which could only be found in and around the national parks. Other herbivores, such as tapirs and red brocket deer, have smaller home ranges (4.8 km^2 for Baird's tapir [Naranjo, 2019], 0.5 km^2 for red brocket deer [*Mazama americana*] [Gallina-Tessaro et al., 2019]) but depend on high-quality food found in minimally disturbed areas (Naranjo, 2019; Gallina-Tessaro et al., 2019). Additional anthropogenic pressures, such as the poaching of peccaries and pacas in the Osa region, further serve to limit these species to more undisturbed areas (Altrichter, 1999; Altrichter & Almeida, 2002)—along with the large-bodied predators that depend on them. Jaguars, for example, were largely limited to where white-lipped peccaries occur, their main prey in the Osa (Chinchilla, 1997) (Appendix S1). A decrease in mean community body mass along the disturbance gradient is the consequence of these processes and has been found in other tropical regions (Morrison et al., 2007; Vetter et al., 2011; Rovero et al., 2020).

Small insectivores and omnivores responded positively on average to disturbance. The effect on insectivores, however, needs to be interpreted with caution given the contrast with previous studies that showed negative effects of disturbance (Rovero et al., 2020). We had only two species classified as insectivores (armadillos and tamanduas), both of which are small (<5 kg). It is, therefore, possible that the observed effect of guild may be confounded by the effect of body size in our data set. The species that showed a clear positive response to human modification (opossums and armadillos) are small generalists that can exploit small, low-quality forest patches and edges close to humans. In addition, these species may also benefit from reduced predation in more disturbed areas (da Fonseca & Robinson, 1990), thus allowing them to thrive further.

By combining two types of joint species distribution models, we were able to parse the correlation in occupancy among species. We distinguished the effect of interspecific interactions, captured by the residual correlation (Tobler et al., 2019), from the effect of similar responses to environmental covariates (Pollock et al., 2014). This analysis allowed us to infer how informative the selected covariates were and provided more information about how they shape the community. In the Osa, the low residual correlation, relative to the correlation due to covariates, indicated that anthropogenic and environmental factors largely explained the distribution of most of our study species. Although interspecific interactions, such as competition and predation, may still explain some of the variation in the distribution, habitat use, or daily activity patterns of these species (Silva-Pereira et al., 2011), these processes would not be captured by our analyses or at our selected spatial scale. Disentangling the spatial and temporal dynamics of habitat use specifically for each species remains a key avenue for future studies that are specifically designed to capture habitat use and population dynamics of species of concern.

The different species' responses generated a significant shift in community composition between areas with low and high disturbance. This shift in community composition implies an important loss of ecological functions—and overall functional diversity—outside protected areas. Jaguars, for example, are apex predators in Neotropical forests and important regulators of large herbivores (Weckel et al., 2006; Jorge et al., 2013). Their absence could have cascading effects that modify the composition of the vertebrate community and the services it provides. Furthermore, large herbivores, such as tapirs and peccaries, are critical dispersers and predators of seeds and ecosystem engineers that can determine future forest composition (e.g., Keuroghlian & Eaton, 2009; Paine et al., 2016; Culot et al., 2017). The fate of forest ecosystems in the region is, therefore, intrinsically linked to the functioning of these species' populations.

Numerous conservation efforts have been made in the Osa to protect species at risk. National parks have been complemented by smaller private and mixed protected areas; logging regulations have become more stringent; and the establishment of payment for ecosystem services has engaged private landowners in forest protection (DeClerck et al., 2010), resulting in an 11% increase in forest cover between 1987 and 2017 (Shrestha et al., 2018). Additionally, an increase in ecotourism, driven mainly by Corcovado National Park, has likely changed people's attitudes toward natural habitats, and many now attribute a high value to intact ecosystems (Almeyda Zambrano et al., 2010; Hunt et al., 2015). These efforts may be promoting the recovery of at-risk populations. Tapirs and pumas, for example, were previously only found inside Corcovado National Park (Carrillo et al., 2000), but we detected them well beyond the park's boundaries. Other species of conservation concern, however, seem to be restricted to Corcovado National Park and immediately adjacent lands, notably jaguars and white-lipped peccaries (Olson et al., 2019, 2020). Although we could be underestimating the area that these species occupy due to their large home ranges and low densities (Neilson et al., 2018), their distribution is, nevertheless, severely limited by disturbance, reinforcing the need for continued protection of large proportions of natural habitat. Given the conservation and ecological importance of jaguars and their prey as umbrella species (Thornton et al., 2016), special efforts should be made to better understand their distribution and increase connectivity with other subpopulations. A more accurate estimate may require further monitoring with stations closer together. Our results also highlight the need to analyze community-level responses to determine the success of conservation efforts (Burgar et al., 2019).

Understanding the distribution and co-occurrence patterns of mammals at a large spatial scale requires significant effort, in terms of time, financial, and technical resources, as well as expertise and knowledge about the study area. Because of these challenges, large-scale studies remain few and far between. Ours is only the third study in 30 years to analyze the terrestrial mammal community outside protected areas in the Osa region (Carrillo et al., 2000; Bustamante, 2008). Using a coordinated, multistakeholder network of camera traps allowed us to optimally use the resources available while taking advantage of local knowledge. This approach can be much more efficient than individual efforts, particularly when studying species with extensive home ranges, the most threatened by human activities. This collaborative strategy can be replicated in other countries to make the best use of limited resources, but requires strong organizational and leadership skills, clear objectives and expectations, and constant commitment from all stakeholders. Once collaboration is established, however, regular large-scale monitoring can become more feasible. Importantly, these networks can also serve as a key link to involve local communities in conservation planning (Kainer et al., 2009).

Despite the relatively low human development of the Osa region and some apparent successes of ongoing conservation efforts, human disturbance had a clear effect on the distribution of wild animals. The absence of some key species from corridor areas between Corcovado and Piedras Blancas National Parks should be a cause for concern because it might prevent connectivity among populations, even with increasing forest cover. Conservation efforts focused on large charismatic species like jaguars and tapirs could have great success in addressing these issues, provided they give special emphasis to their ecological functions as predators, seed dispersers, and seed predators. Restoration and wildlife corridor initiatives need to ensure functional connectivity for all terrestrial species, but in particular for forest-dependent species with large habitat requirements. Locally based efforts can be an essential tool for these projects because they facilitate constant monitoring and engage human communities in conservation. We encourage conservation organizations and agencies to collaboratively manage the Greater Osa Ecosystem, focusing on maintaining strategic wild-land buffers and enhancing connectivity between protected areas. Finally, we recommend the continued engagement of government agencies, different nongovernmental organizations, and local communities for large-scale monitoring to ensure the success of conservation plans and the long-term viability of Neotropical wildlife communities.

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