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# Human density modulates spatial associations among tropical forest terrestrial mammal species

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## Abstract

The spatial aggregation of species pairs often increases with the ecological similarity of the species involved. However, the way in which environmental conditions and anthropogenic activity affect the relationship between spatial aggregation and ecological similarity remains unknown despite the potential for spatial associations to affect species interactions, ecosystem function, and extinction risk. Given that human

disturbance has been shown to both increase and decrease spatial associations among species pairs, ecological similarity may have a role in mediating these patterns. Here, we test the influences of habitat diversity, primary productivity, human population density, and species' ecological similarity based on functional traits (i.e., functional trait similarity) on spatial associations among tropical forest mammals. Large mammals are highly sensitive to anthropogenic change and therefore susceptible to changes in interspecific spatial associations. Using two-species occupancy models and camera trap data, we quantified the spatial overlap of 1216 species pairs from 13 tropical forest protected areas around the world. We found that the association between ecological similarity and interspecific species associations depended on surrounding human density. Specifically, aggregation of ecologically similar species was more than an order of magnitude stronger in landscapes with the highest human density compared to those with the lowest human density, even though all populations occurred within protected areas. Human-induced changes in interspecific spatial associations have been shown to alter top-down control by predators, increase disease transmission and increase local extinction rates. Our results indicate that anthropogenic effects on the distribution of wildlife within protected areas are already occurring and that impacts on species interactions, ecosystem functions, and extinction risk warrant further investigation.

**KEYWORDS**
biodiversity, functional traits, global, interspecific spatial associations, occupancy model

# 1 | INTRODUCTION

As land use, hunting, and global climate change take a toll on biodiversity (Brodie et al., 2021), humans have restricted the activity of animal species in space (Gutzwiller & Anderson, 1999; Pelini et al., 2009; Tucker et al., 2018) and time (Gaynor et al., 2018). However, the influences of humans on spatio-temporal associations between animal species are less well understood. The aggregation or segregation of individuals from different species, known as interspecific spatial associations, provides unique spatial information that is not captured by other biodiversity metrics (Keil et al., 2021). Changes in spatial associations have the potential to affect a variety of ecological processes. First, as species change their spatial overlap with one another, the spatial distributions of the ecological functions they provide can change too (Keil et al., 2021). Community-wide changes in spatial associations can result in alterations to ecosystem functions, including seed dispersal (Brodie et al., 2009; Herrera & García, 2010), forest regeneration (Gardner et al., 2019), and nutrient cycling (Metcalfe et al., 2014). Second, changing spatial overlap can be indicative of higher extinction risk (Fidino et al., 2019), potentially due to increased competition or reduced resource availability. Finally, although interspecific spatial associations cannot be used to directly assess species interactions (Blanchet et al., 2020), changes in spatial associations can alter species interactions, such as competition, predation, and mutualisms (Carroll et al., 2019). Identifying the drivers of community-wide patterns of spatial association can

thereby provide insight about biodiversity and ecosystem functions in the Anthropocene.

In both plants and animals, interspecific spatial associations increase with functional trait similarity (hereafter ecological similarity) of species (in Carnivora- Davis et al., 2018; in plants- He & Biswas, 2019; Yin et al., 2021). This aggregation can occur because ecologically similar species require similar conditions and hence sort similarly among habitats best suited to their particular needs and traits (Leibold et al., 2004). However, if the ecological similarity of two species is limiting in terms of resource acquisition, competition can reduce the spatial overlap of ecologically similar species (Abrams, 1983).

How environmental and anthropogenic conditions affect the relationship between ecological similarity and interspecific spatial associations remains unknown. Yet, variation in interspecific spatial associations with ecological similarity across environmental and anthropogenic gradients could indicate protected area-level differences in species interactions, ecosystem functions, and the potential for local extinctions. Identification of relevant environmental gradients is important for predicting these broader ecological consequences.

Broad-scale environmental conditions which are relevant to species distributions and ecological interactions may be relevant factors in determining patterns of interspecific spatial associations. For example, if habitat type is important for structuring the spatial distributions of species within a community (Spasojevic et al., 2014),

then resource variability across space inherent to habitat diversity may affect interspecific spatial associations. Greater habitat diversity may result in spatial aggregation of ecologically similar species as they use habitats suited to their needs, or greater segregation of ecologically similar species if competition causes species to spatially partition. Ecologically similar species that use different resources may also segregate spatially. If energy availability is important for determining species distributions and interactions, then protected area-level productivity may affect interspecific spatial associations. High productivity is related to energy availability in an ecosystem and has been associated with higher animal biomass (McNaughton et al., 1989), species richness (Jetz & Fine, 2012) and functional diversity (Gorczynski et al., 2021), as well as more stochastic species distributions across space (e.g., in an experimental invertebrate pond system, Chase, 2010). Lower energy availability in lower productivity environments may alter patterns of biodiversity, including interspecific spatial associations. Reduced resource availability associated with low productivity may increase spatial aggregation by forcing species with similar resource requirements into contact with each other more frequently or increase spatial segregation if low productivity increases competition among similar species for the remaining resources. In these ways, variation in the level of habitat diversity and productivity among protected areas may affect the way species overlap with each other spatially based on their ecological similarity.

Human impacts on the environment may also affect the ecological processes underlying interspecific spatial associations. If humans reduce habitat suitability, deter movement of individuals (i.e., through a landscape of fear; Suraci et al., 2019), or increase competition among similar species for limited remaining resources, species may change their spatial association in response to human density. Human activity can also increase habitat suitability, such as through resource supplementation for some omnivores and carnivores (Manlick & Pauli, 2020), or through removal of predator species for some herbivores. Human presence and impacts have been linked to both increased (Farris et al., 2014; Murphy et al., 2021; Rota et al., 2016; Smith et al., 2018) and decreased (Cruz et al., 2018; Di Bitetti et al., 2010; Kafley et al., 2019; Ladle et al., 2018) spatial associations among species. Interspecific spatial associations are often species-pair-specific, with some species pairs aggregating and others segregating in the same system exposed to humans, but the extent to which ecological similarity among species or variation among study sites in anthropogenic pressure explains such variation has not previously been tested.

Understanding interspecific spatial associations among terrestrial mammals is particularly important because mammals play vital roles in maintaining biodiversity and ecosystem functions (Lacher et al., 2019). Mammals contribute to seed dispersal, forest regeneration, and nutrient cycling, among other functions. Indeed, functionality has declined in forests where mammals have been locally extirpated (Wright et al., 2007). Moreover, the large body sizes and resource requirements of mammals make them particularly vulnerable to human impacts (Dirzo et al., 2014) and many have experienced declines in abundance and diversity across the tropics (Pimm et al., 2014), making them a global conservation priority. Tropical forest mammals are diverse, with a wide variety of body sizes, dietary requirements, and habitat use, providing an excellent taxon for investigating the spatial associations of species spanning a large range in their level of ecological similarity.

Here, we test the extent to which protected-area level environmental and anthropogenic conditions predict tropical mammal interspecific spatial associations based on functional traits by assessing the spatial overlap of 1216 species pairs in 13 protected tropical forests around the world. We test the associations of habitat diversity, productivity, and human density with the relationship between mammal ecological similarity and interspecific spatial associations. We measure ecological similarity based on six functional traits (average body mass, diet composition, social group size, substrate use, activity period, and average litter size) that describe the quality and quantity of resources required for mammal species to persist in a location (Gorczynski et al., 2021; Gorczynski & Beaudrot, 2021). For example, body size, sociality, and litter size can capture the amount of resources a species requires, while diet, substrate use, and activity period can describe the type of resources a species requires. Differences in interspecific spatial associations of ecologically similar species based on environmental and anthropogenic conditions could indicate systematic changes in ecosystem functions, extinction risk, and species interactions.

## 2 | MATERIALS AND METHODS

### 2.1 | Study sites

We examined mammal co-occurrence (likelihood that two species occur in the same camera trap location over the course of a month) in 13 tropical forest protected areas spanning the Americas, Africa, Asia, and Madagascar using data from the Tropical Ecology Assessment and Monitoring Network (TEAM). The protected areas are located in landscapes with a range of habitat connectivity with some sites surrounded by intact forest (e.g., Nouabalé-Ndoki, Central Suriname Nature Reserve) and others largely isolated from other forests (e.g., Bwindi, Ranomafana, Udzungwa) (Table S1; Beaudrot et al., 2016).

### 2.2 | Camera trap sampling

Camera trap observations of mammals were collected during a single primary sampling period in 2015 using a standardized protocol (Jansen et al., 2014). At each site, a Reconyx RM45 or Hyperfire™ camera trap were deployed at 60 locations arranged in gridded arrays and positioned with 1–2 km between each other over 120–180 km² of forest. Standardized grids varied between sites in terms of dimensions and proximity to access trails but spacing remained constant among camera traps within a study site. Each camera trap was active in the field for at least 30 consecutive days in the dry

season (<100 mm rainfall/month) and used motion-activated photography to capture images of animals that triggered the motion sensor. Camera traps were affixed to trees between 40 and 60 cm off the ground. Camera trap photos were then processed and identified by local experts. Detections were grouped into 6-day sampling periods for modeling, with detections during different sampling periods considered independent detections. For each TEAM study site, the community consisted of ground-dwelling mammal species observed in more than three sampling periods and weighing more than 1 kg.

## 2.3 | Estimating species-pair co-occurrence

Occupancy models provide a robust method for estimating species occurrence (MacKenzie et al., 2002) and are more appropriate for comparing species occurrences than raw observational data, which can underestimate occurrence when animals are present but are not detected (i.e., due to imperfect detection). Using camera trap observations, we used a Bayesian two-species occupancy model that accounted for imperfect detection in R v4.1.2 (Davis et al., 2018; R Core Team, 2021; Richmond et al., 2010) to estimate the tendency for species-pairs to aggregate (co-occur more frequently than expected) or segregate (occur separately more frequently than expected). We applied the same model independently to each species pair observed to occur in the same protected area. The two-species occupancy model did not include covariates of occupancy or detection. In this way, we estimated pairwise species overlap across the range of environmental conditions within a protected area without directly measuring the effect of these conditions themselves on species occurrence. As a result, spatial associations of species estimated from this model could be a result of biological interactions, responses to environmental conditions, or a combination of both (Dormann et al., 2018). This resulted in a single, protected area-level estimate of spatial association for each species pair which we used to test for the effects of variation in protected area-level environmental conditions on interspecific spatial associations. All five parameters estimated in the models were given vague Uniform(0,1) priors. To estimate detection probability, camera trap observations were divided into six-day monitoring periods. The model produced a derived parameter known as the species interaction factor (SIF; Richmond et al., 2010), which we used to infer the degree of aggregation or segregation between two species. The SIF was calculated as follows:

$$SIF = \Psi_A \times \Psi_{BA} / (\Psi_A \times (\Psi_A \times \Psi_{BA} + (1 - \Psi_A) \times \Psi_{Ba}))$$

In this equation, $\Psi_A$ is the estimated occupancy of species A, $\Psi_{BA}$ is the estimated occupancy of species B in the presence of species A, and $\Psi_{Ba}$ is the estimated occupancy of species B in the absence of species A. In this model, species A is the dominant species, and its occupancy is independent of species B. Species B's occupancy is calculated such that it may be dependent on the presence or absence of species A and so is the subordinate species. In repeating this model

for all species pairs co-occurring at a site, species A was the species that came first alphabetically, meaning the dominance of the species pairs was not ecologically based and was effectively arbitrary. When SIF is equal to 1, the occurrences of the two species are unrelated to each other. When SIF and its 95% credible interval are greater than 1, we consider the two species more likely to co-occur than expected by random chance. When SIF and its 95% credible interval are less than 1, we consider the two species less likely to co-occur than expected by chance. We inspected the Gelman-Rubin ($\hat{R}$) convergence diagnostic (Brooks & Gelman, 1998) to assess convergence of all two-species occupancy models using a threshold of <1.05. We used 95% credible intervals of SIF estimates that did not include zero to identify species pairs that showed significant aggregation or segregation simply to highlight the species-pairs that showed relatively stronger patterns of spatial overlap or separation, while acknowledging that using camera trap data for one species in multiple co-occurrence models may cause an underestimation of the true variance of these estimates. The SIF estimates for all species pairs were used in the global model.

## 2.4 | Modeling variation in co-occurrence among species-pairs

Our goal was to test how habitat diversity, primary productivity, and human density measured at the protected area-level affected the relationship between ecological similarity and species co-occurrence within tropical forest protected areas. We used a generalized linear model with a Bayesian formulation to model SIF for each of the species pairs from the 13 study sites ($N = 1216$ species pairs) as a function of species-pair dissimilarity, three TEAM protected area-level predictors (habitat diversity, primary productivity, and human density), and the interaction between species-pair dissimilarity and each of these three site-level predictors. We included these interaction effects to test how environmental and anthropogenic factors may mediate associations between mammal species overlap and ecological similarity. We also included functional richness for each protected area as a fixed effect to control for diversity-based variation in co-occurrence among sites.

To measure species dissimilarity, we calculated the Gower's distance between each species pair in trait space using the 'cluster' package in R (Maechler et al., 2014). We used a suite of six ecological traits: average body mass, diet composition (graze, browse, fruits/seeds, invertebrates, vertebrates), social group size, substrate use, activity period, and average litter size. These traits have been previously published and used for the analysis of mammal functional diversity in TEAM-protected areas (Gorczynski et al., 2021; Gorczynski & Beaudrot, 2021).

We measured habitat diversity using the Shannon diversity index applied to landcover data for the camera trap sampling area. Habitat classifications were derived from 2015 MODIS land cover data at a resolution of 500 m (Friedl & Sulla-Menashe, 2019). All cells within the sampling area were classified based on the IGBP system (17 land-cover classes; classes identified in at least one TEAM site include the

following: evergreen broadleaf forests, woody savannas, savanna, grasslands, permanent wetlands, cropland/natural vegetation mosaic, water bodies), and the Shannon diversity of habitat types was calculated from the counts of each of these 17 unique cell classifications. Notably, evergreen broadleaf forests, which are the dominant habitat type in the study sites, encompass a variety of diverse forests including palm, bamboo, and hardwood, which cannot be differentiated.

To quantify an index of primary productivity, we used normalized difference vegetation index (NDVI) calculated as mean NDVI over the sampling area (minimum convex area within a 1 km buffer of the 60 camera traps). This information was extracted from 16-day MODIS Vegetation Indices at a resolution of 250m (Didan, 2015) and averaged across all cells in the sampling area during the year 2015.

Human density can be indicative of a variety of human activities that are damaging to wildlife, including land-use change, hunting, and human–wildlife conflicts (Newmark et al., 1994; Parks & Harcourt, 2002). For each TEAM study site, we extracted the mean human density in a 5-km buffer around the camera trap sampling areas from the Gridded Population of the World data set during the year 2015 (CIESIN, 2016).

Functional richness of each community was calculated using the "FD" package in R (Laliberté et al., 2015) and was included in the regression to control for variation in functional diversity at each site due to differences in biogeography and evolutionary history. All calculations were conducted in the same trait space including all species at all sites to preserve total inertia and distance between the same species occurring at different sites. None of the predictor variables were highly correlated ($r < 0.7$).

We conducted a global Bayesian model using the package R2JAGS (Su & Yajima, 2015). The linear predictor of the model was as follows:

$$\mu_{ijk} = \alpha_0 + \alpha_1 x_{HaD_k} + \alpha_2 x_{PR_k} + \alpha_3 x_{HuD_k} + \alpha_4 x_{SppD_{ij}} + \alpha_5 x_{HaD_k} x_{SppD_{ij}}$$
$$+ \alpha_6 x_{PR_k} x_{SppD_{ij}} + \alpha_7 x_{HuD_k} x_{SppD_{ij}} + \alpha_8 x_{FR_k} + \epsilon_{ijk}$$

where $i$ and $j$ refer to species and $k$ refers to protected area; $\log(SIF)_{ijk}$ indicates the log transformed mean estimate of the SIF for each species pair, $SppD_{ij}$ indicates the ecological dissimilarity of each species pair, $HaD_k$ represents the protected area-level habitat diversity, $PR_k$ represents the protected area-level productivity, $HuD_k$ represents the protected area-level human density, $FR_k$ represents the protected area-level mammal community functional richness and $\epsilon$ is the lack of fit component to allow for uncertainty in our model fit, such that $\epsilon_{ijk} \sim Normal(0, \sigma)$ and $\sigma \sim Uniform(0, 10)$. All intercept and slope terms of the linear predictor were given vague Normal(0,100) priors. This linear predictor feeds into the following model, which accounts for the associated uncertainty in SIF estimates:

$$\log(SIF_{ijk}) \sim Normal(\mu_{ijk}, \sigma_{ijk})$$

where $\sigma_{ijk}$ is the variance associated to the SIF estimates of species $i$ and $j$ at study area $k$. Because SIF is bounded by 0, we log-transformed

SIF as the response variable and used a Gaussian distribution. We included two residual variation components in this model to propagate estimation uncertainty from the co-occurrence models following the approach described in Kéry & Royle (2015). This approach included incorporation of known uncertainty of the SIF estimate from the co-occurrence models, as well as the lack of fit component, which allowed the estimate to vary from the modeled relationship. The known uncertainty component used the posterior variance of SIF estimates from the two species occupancy models to inform the precision of these estimates in the model. This two-component approach to incorporating uncertainty was necessary given that the second stage analysis models outputs from the first stage, which each had their own variance in estimation (Kéry & Royle, 2015). We visually inspected trace plots from the model and checked that the Gelman-Rubin (Rhat) convergence diagnostic were <1.05 to ensure convergence. We also visually inspected posterior predictive checks to assess model fit. Finally, we checked the robustness of our model to the inclusion of SIF estimates with large variance by running the global model with the subset of the SIF estimates that had variance <0.04. Data and code for the methods and materials are available online (Gorczynski et al., 2022).

## 3 | RESULTS

We analyzed 1216 species pairs. The number of species pairs in each site ranged from six in Ranomafana, Madagascar, to 190 in Yasuní, Ecuador, with a median of 78 in Yanachaga, Peru (Figure 1; Table S1). The median SIF estimate of all 1216 species pairs was 1.03 (95% CI = 0.58, 1.88; Figure S1). The site-level median SIF ranged from 1.001 (Korup, Cameroon) to 1.208 (Volcán Barva, Costa Rica). We found 34 species pairs that showed significant aggregation (SIF 95% CI >1) and just 7 species pairs that showed significant segregation (SIF 95% CI <1; Table S2 and Figure S1).

Among all co-occurring species pairs, functional dissimilarity ranged from most similar at 0.011 (*Cercocebus torquatus* [collared mangabay] and *Mandrillus leucophaeus* [drill]) to most dissimilar at 0.794 (*Genetta servalina* [servaline genet] and *Loxodonta africana* [African elephant]) with a median of 0.375. Habitat diversity at the sampling points ranged from 0 (multiple sites) to 0.77 (Korup, Cameroon) with a median of 0.012 (Caxiuanã, Brazil; see Table S3 for full landcover classification). Primary productivity ranged from 0.412 (Korup, Cameroon) to 0.772 (Nouabalé-Ndoki, Republic of Congo) with a median of 0.685 (Yasuní, Ecuador). Human density in a 5 km buffer surrounding each sampling area ranged from 0.03 people per square kilometer (Central Suriname Nature Reserve, Central Suriname) to 175.45 (Bwindi Impenetrable Forest, Uganda) with a median of 22.30 (Korup, Cameroon). Functional richness ranged from 0.004 (Ranomafana, Madagascar) to 0.074 (Nouabalé-Ndoki, Republic of Congo) with a median of 0.057 (Volcán Barva).

Using these environmental and anthropogenic variables, we fitted a Bayesian regression to the 1216 SIF values obtained from the pairwise two-species occupancy models. This global regression included
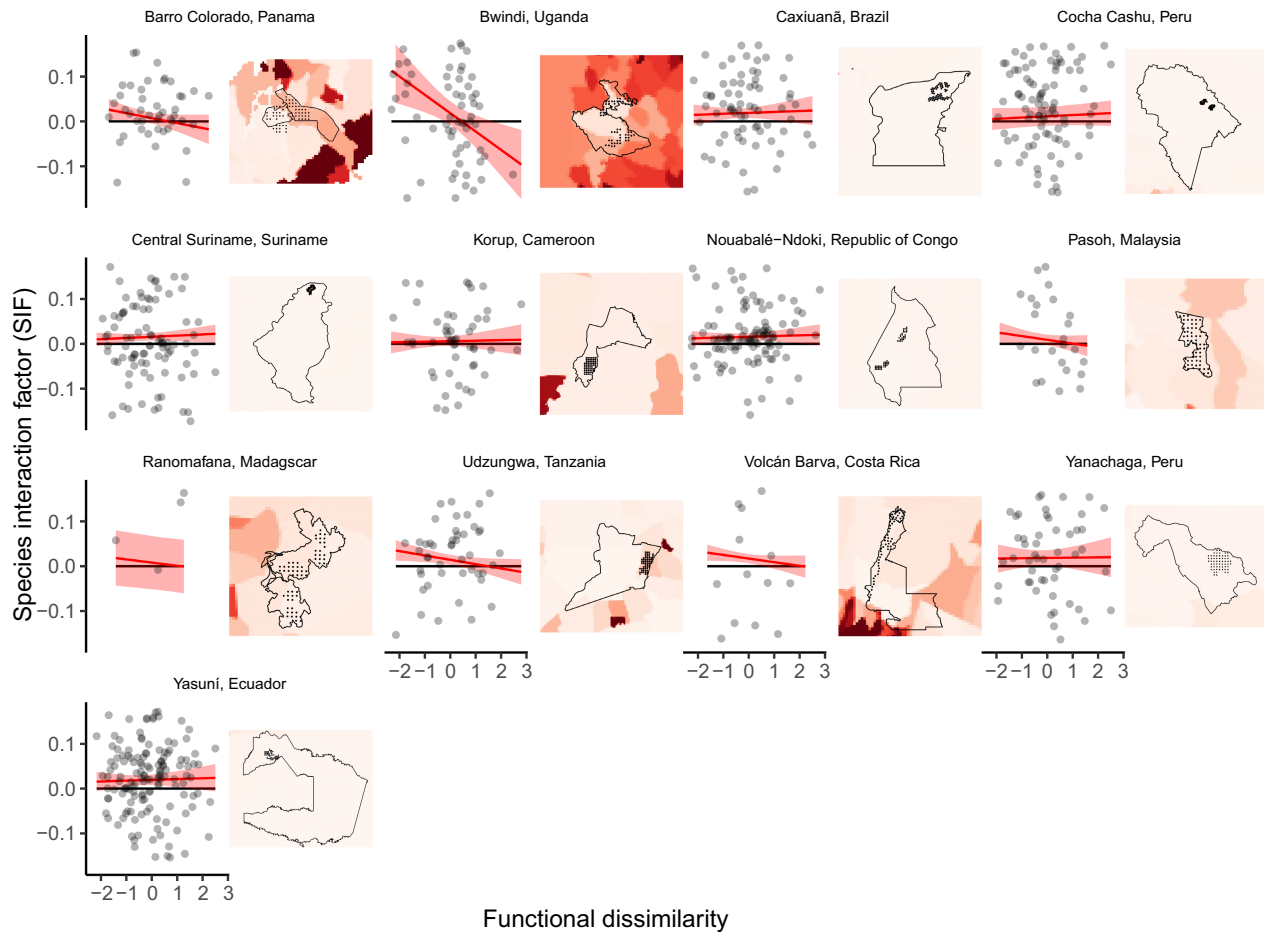
**FIGURE 1** Results showing predicted relationships between species ecological dissimilarity and pairwise interspecific spatial associations measured using the log-transformed SIF at each of the 13 protected area sites. Each point in the scatter plot represents a species pair. The black line represents zero, with all points above zero indicating species pair aggregation spatially, and below zero indicating species pair segregation spatially. Points for species pairs with SIF greater than 0.1 or less than −0.1 were not included in the scatter plots to better visualize the model fit. The red line represents model fit, with light red shading indicating the 95% credible interval. Within the map, the black line demarcates the protected area boundary. Black dots show camera trap sampling points. Red shading indicates human density with darker coloration indicating higher density. At sites with higher human density, ecologically similar species pairs showed more aggregation and ecologically dissimilar species showed more spatial separation. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

a significant interaction between species pair functional dissimilarity and human density ($\alpha_7 = -0.014$; 95% CI = −0.027, −0.0007; Figure 2) based on its 95% credible interval that did not overlap zero. Functionally similar species were more likely to co-occur in protected areas that had high human density in a five-kilometer buffer around the sampling area and functionally dissimilar species were less likely to co-occur as human density increased. Based on the model output, species pairs were most likely to overlap spatially if they were similar in terms of their functional traits and occurred in protected areas with high surrounding human density, while species pairs were most likely to spatially segregate if they were dissimilar in terms of their functional traits and occurred in protected areas with high surrounding human density (Figure 3). On the other hand, we failed to detect an interaction between species pair dissimilarity and habitat diversity or productivity that affected species spatial overlaps. Finally, we found non-significant main effects of habitat diversity ($\alpha_1 = -0.0097$; 95% CI = −0.025, 0.0062), human density ($\alpha_3 = 0.0076$; 95% CI = −0.0097,

0.025), and species dissimilarity ($\alpha_4 = -0.0037$; 95% CI = −0.010, 0.0027) on interspecific spatial overlap. Even though these effects were statistically non-significant based on 95% CI, much of their posterior distributions excluded zero, including 50% CIs, which suggests that these factors may be important for determining species co-occurrence independent of each other. A robustness check from the model using the subset of SIF estimates with variance <0.04 ($N = 485$ SIF estimates) produced qualitatively similar results as the model of all 1216 SIF estimates (Figure S2). A visual posterior predictive check indicated that the model fit the subset of the data well (Figure S3).

## 4 | DISCUSSION

Interspecific spatial associations are an important and understudied aspect of biodiversity that can affect species interactions, population dynamics, and ecosystem functions. The goal of this study was
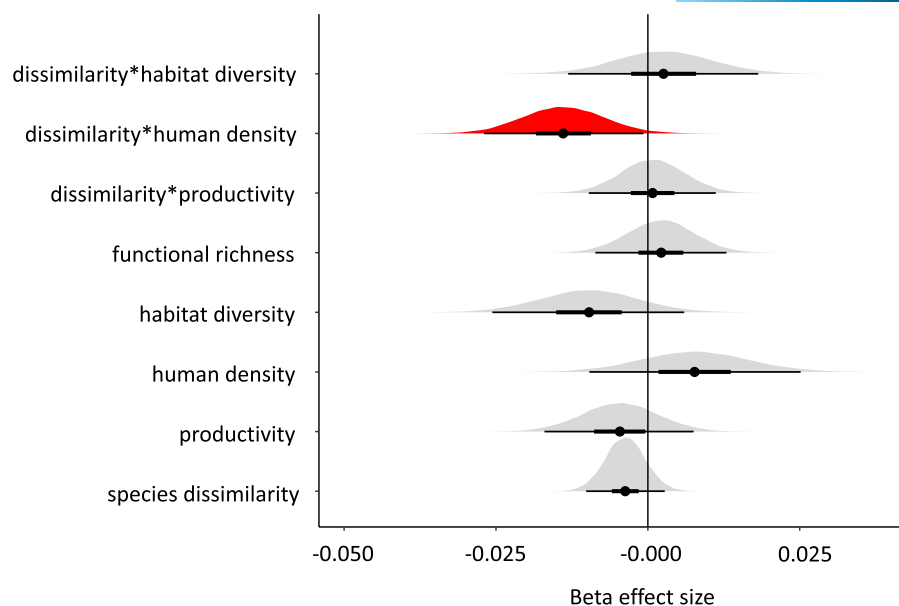
**FIGURE 2** Effect sizes of the predictor variables from the global model of species pair co-occurrence. Estimates were standardized with a mean of zero and variance of one for direct comparison. Black dots indicate median estimates, thick black bars indicate 50% credible intervals and thin black bars represent 95% credible intervals. Light gray distributions indicate that the 95% credible interval overlapped 0. The red distribution indicates the 95% credible interval did not include zero for the interaction between ecological dissimilarity and human density.
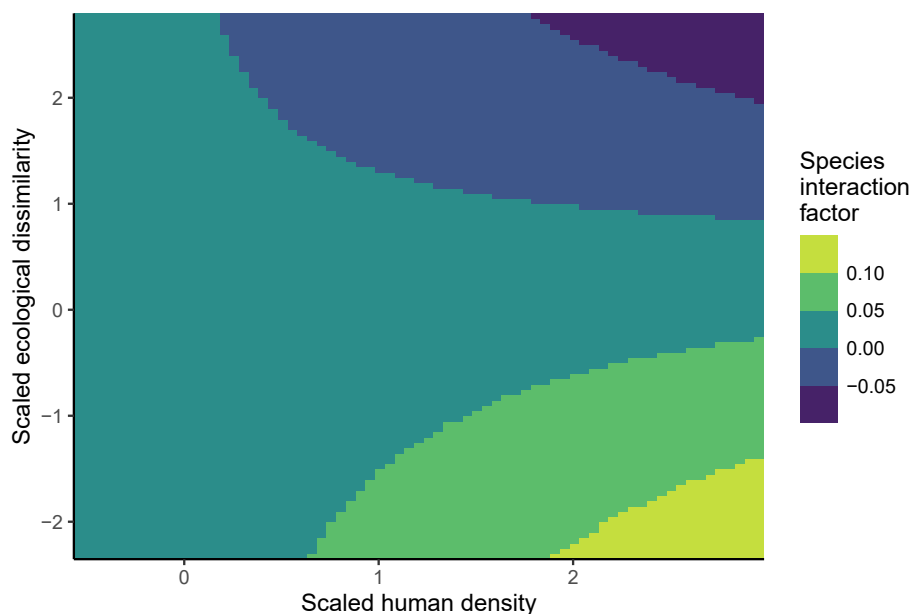


**FIGURE 3** The range of predicted log-transformed interspecific spatial associations based on human density and ecological dissimilarity as predicted from the global model. This plot includes all values of human density and ecological dissimilarity observed in this study. Each color represents a range of species interaction factor values including (1) < −0.05; (2) −0.05 to 0; (3) 0 to 0.05; (4) 0.05 to 0.1; and (5) >0.1. Predicted species interaction factors are highest (SIF >0.1; indicated in light green), indicating spatial aggregation, in protected areas with high human density and for species with low ecological dissimilarity (i.e., high ecological similarity).

to identify whether and how environmental and anthropogenic conditions at the protected-area level are associated with the relationship between mammal ecological similarity and interspecific spatial associations in tropical forest protected areas. Our results do not find support for variation in the co-occurrence of ecologically similar species depending on protected area-level habitat diversity or productivity. We did find, however, that the co-occurrence of ecologically similar species differed depending on human density surrounding the camera trap sampling area. The ways in which spatial associations between mammal species shift in response

to humans have been reported as variable (Cruz et al., 2018; Di Bitetti et al., 2010; Farris et al., 2014; Kafley et al., 2019; Ladle et al., 2018; Rota et al., 2016; Smith et al., 2018). Our comparison of the environmental and anthropogenic predictors of interspecific spatial associations based on more than 1200 species pairs suggest that humans are associated with increasing spatial aggregation of ecologically similar species within tropical protected areas. Human density could limit suitable habitat availability, create a landscape of fear (Suraci et al., 2019), or provide novel resources (Manlick & Pauli, 2020). Changes in spatial associations in human-dominated landscapes have been shown to have ecological consequences including alteration of top-down control by predators (Ramesh et al., 2017), increased disease transmission (Hassell et al., 2017), and increased local extinction rate (Fidino et al., 2019). Similar disruption to ecological processes could be occurring in protected areas exposed to high human density, and long-term study is necessary to assess the ecological effects of differences in spatial overlap.

Mechanisms driving spatial overlap are difficult to disentangle because different mechanisms can produce identical patterns (Blanchet et al., 2020). In our model, both biotic interactions and response to environmental conditions could be driving species spatial associations. Extensive prior knowledge about ecological interactions between species pairs is necessary to infer the mechanisms driving interspecific spatial associations. For example, anthropogenic linear features such as seismic lines, pipelines, and roads (Dickie et al., 2017) have been shown to facilitate increased predation of carnivores on ungulates, resulting in increased overlap of predator and prey species near these features (Fisher & Ladle, 2022). In our case, it is uncertain whether higher human density allows ecologically similar mammals to co-occur more often because of increased species sorting (i.e., similar species use the same habitats because of similar resource requirements; Weiher & Keddy, 1995), decreased competition (i.e., relaxed competition for resources permits greater sharing of space; Abrams, 1983) or another mechanism. Human density could affect either species sorting or competition in multiple ways. For example, habitat loss and landscapes of fear frequently result in increased clustering of species as the space available to species declines (Suraci et al., 2019). This pattern would be particularly strong for ecologically similar species that use similar resources. Alternatively, human settlements can provide novel food sources and habitats (Manlick & Pauli, 2020) such as waste piles and agricultural landscapes. Additional resource availability could reduce competition between ecologically similar species and allow them to co-occur spatially. Furthermore, the relevant but non-significant effects of species dissimilarity and human density (negative and positive, respectively) indicate that these factors may be influencing species spatial overlap independent of each other as well. That is, ecological similar species may be more likely to overlap regardless of anthropogenic conditions, providing support for results from previous studies on interspecific spatial associations (Davis et al., 2018). Species may also be more likely to overlap in protected areas with high human density regardless of their traits. The mechanisms behind human-associated increases in overlap of ecologically similar

species in tropical forests require further investigation, which could be accomplished by more in-depth study of pairwise species interactions. Given that these patterns were identified for wildlife within protected area boundaries, the effects of human density may be more pronounced in non-protected areas, and the extent of this association warrants further investigation.

Human density is associated with a variety of detrimental ecological consequences. Such consequences include reduced local mammal species richness (McKee et al., 2013) and increased species extinction risk, particularly for organisms with more ecologically sensitive traits such as low reproductive rates and large body sizes (Cardillo et al., 2004, 2005). Moreover, increasing human density has been linked to variation in mammal population size and population dynamics, with some species increasing in abundance and others decreasing (i.e., winners and losers- Tucker et al., 2021). Our result that ecologically similar species were more strongly aggregated with higher surrounding human density suggests that humans may also modulate spatial associations among species on a broad scale. It is important to note, however, that it is likely not human density per se that increases interspecific spatial associations. Higher human density is associated generally with a wide variety of disruptive human activities such as hunting, changes in type and intensity of land use, habitat degradation and loss, and conflict between humans and wildlife that arise from shared space use (Newmark et al., 1994; Parks & Harcourt, 2002). These activities can have direct effects on wildlife and be detrimental to mammal diversity (Brodie et al., 2021). It is likely that a combination of human impacts affects mammal interspecific spatial associations in these systems, but causal mechanisms require further investigation. In addition, we quantified human density outside of the protected areas, whereas we quantified habitat diversity and productivity for the camera trap sampling areas within protected forests; thus, our results suggest that processes outside the protected area, as well as inside, may affect mammal communities (Laurance et al., 2012).

Patterns of significant aggregation and segregation among individual species pairs also reflect the relationship between co-occurrence, ecological similarity, and human density. For example, agoutis (*Dasyprocta spp.*) and pacas (*Cuniculus paca*), which are functionally similar small-bodied, ground-dwelling frugivores that partition temporally, exhibited spatial aggregation in all seven neotropical sites (SIF >1, Table S2). Of these seven sites, significant aggregation of this species pair based on 95% CIs was observed at three sites including the two neotropical sites with the highest surrounding human density, Volcán Barva in Costa Rica and Barro Colorado in Panama. In the protected area with the highest surrounding human density, Bwindi Impenetrable Forest in Uganda, the yellow-backed duiker (*Cephalophus silvicultor*) and the black-fronted duiker (*Cephalophus nigrifrons*) aggregated significantly; both species avoid human activities such as hunting and farming (Diarrassouba et al., 2020; Sylvie Fonkwo et al., 2011). Interestingly, both duiker species showed significant segregation from the olive baboon (*Papio anubis)*, which raids crops and often thrives near human habitation (Warren, 2009).

Despite the fact that spatial partitioning based on habitat preferences for land cover, elevation, and hydrological conditions have been extensively documented for mammals (IUCN, 2021; Marshall et al., 2014; Rondinini et al., 2011), we did not find that mosaics of broad-scale vegetation types, such as broad-leaf evergreen forest and mixed forest, resulted in greater aggregation or segregation among species than exclusively broad-leaf evergreen systems. As protected tropical forests, many of these sites are largely broad-leaf evergreen landcover, which may reduce the power of this variable to predict co-occurrence. The non-significant negative effect of habitat diversity on species spatial overlap may be indicative of increased habitat partitioning in sites with greater diversity of landcover types, although this was not related to species ecological dissimilarity. Nevertheless, finer-scale, unmeasured habitat variation, such as microclimate, understory vegetation structure, and specific resource availability may be more important for determining spatial overlap than the landcover classifications used in this study. Similarly, increases in productivity can increase mammal biomass (McNaughton et al., 1989) and functional diversity (Gorczynski et al., 2021), but we did not find evidence that the relationship between ecological similarity and interspecific spatial associations depended on productivity. Tropical forests tend to be highly productive, and even though there was substantial variation among sites in NDVI, the effect of primary productivity would likely become more pronounced when compared to lower productivity systems.

There are multiple ways in which future investigations of interspecific spatial associations can expand on our results here. First, we used species-level trait values based to data availability but recognize that incorporating data on differences in traits between individuals or sites may increase the ability to detect variation. Analysis of multiple years of data could reveal greater variation in co-occurrence patterns. For example, the local colonization and extinction dynamics of many mammal species at these study sites respond to mammal community composition (Beaudrot et al., 2019). Increasing spatial overlap of ecologically similar species in anthropogenic landscapes implies that species may need to find new ways to differentiate resource use, such as through temporal differentiation. In fact, species have been found to alter their activity period in response to human presence (Gaynor et al., 2018). The use of two-species occupancy models that incorporate temporal overlap (e.g. Ait Kaci Azzou et al., 2021; Kellner et al., 2022) could allow us to further understand how ecologically similar species aggregate or segregate temporally across an ecological community in response to global change. Finally, understanding interspecific spatial associations among terrestrial mammals and other vertebrates could reveal important insight about whether the patterns of co-occurrence shown in this study are taxon-specific or found more widely in tropical forest systems.

Anthropogenic activity is causing substantial changes in global biodiversity. Protected areas aim to conserve biodiversity but vary in their effectiveness (Laurance et al., 2012). Some TEAM study sites have recently lost mammal diversity, both taxonomic and functional, from human-induced local extinctions (Gorczynski et al., 2021;

Rovero et al., 2020), particularly in sites with high surrounding human density (e.g., Bwindi, Pasoh, Barro Colorado). Our findings that humans may affect the spatial associations of species within and among protected areas provides additional context for tropical biodiversity loss. Increase in spatial aggregation among ecologically similar species may be indicative of extinction debt (Kuussaari et al., 2009) if it results in population declines and extinctions in the future. This could occur due to reduced resource availability or increased competition associated with greater spatial overlap, leading to an inability for species to coexist over time. If we are to preserve diverse mammal communities in tropical forest protected areas, we must work to mitigate the negative effects associated with high human density including hunting, land use change and human-wildlife conflicts (Newmark et al., 1994; Parks & Harcourt, 2002).

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## REFERENCES

Abrams, P. (1983). The theory of limiting similarity. *Annual Review of Ecology and Systematics*, 14, 359–376. https://doi.org/10.1146/annurev.es.14.110183.002043

Ait Kaci Azzou, S., Singer, L., Aebischer, T., Caduff, M., Wolf, B., & Wegmann, D. (2021). A sparse observation model to quantify species distributions and their overlap in space and time. *Ecography*, *44*(6), 928–940.

Beaudrot, L., Acevedo, M. A., Lessard, J. P., Zvoleff, A., Jansen, P. A., Sheil, D., Rovero, F., O'Brien, T., Larney, E., Fletcher, C., Andelman, S., & Ahumada, J. (2019). Local temperature and ecological similarity drive distributional dynamics of tropical mammals worldwide. *Global Ecology and Biogeography*, *28*(7), 976–991. https://doi.org/10.1111/GEB.12908

Beaudrot, L., Ahumada, J. A., O'Brien, T., Alvarez-Loayza, P., Boekee, K., Campos-Arceiz, A., Eichberg, D., Espinosa, S., Fegraus, E., Fletcher, C., Gajapersad, K., Hallam, C., Hurtado, J., Jansen, P. A., Kumar, A., Larney, E., Lima, M. G. M., Mahony, C., Martin, E. H., … Andelman, S. J. (2016). Standardized assessment of biodiversity trends in tropical forest protected areas: The end is not in sight. *PLoS Biology*, *14*(1), 1002357. https://doi.org/10.1371/journal.pbio.1002357

Blanchet, F. G., Cazelles, K., & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions. *Ecology Letters*, *23*(7), 1050–1063. https://doi.org/10.1111/ele.13525

Brodie, J. F., Helmy, O. E., Brockelman, W. Y., & Maron, J. L. (2009). Bushmeat poaching reduces the seed dispersal and population growth rate of a mammal-dispersed tree. *Ecological Applications*, *19*(4), 854–863.

Brodie, J. F., Williams, S., & Garner, B. (2021). The decline of mammal functional and evolutionary diversity worldwide. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(3), e1921849118. https://doi.org/10.1073/pnas.1921849118

Brooks, S. P., & Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, *7*(4), 434–455. https://doi.org/10.1080/10618600.1998.10474787

Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., Orme, C. D. L., & Purvis, A. (2005). Evolution: Multiple causes of high extinction risk in large mammal species. *Science*, *309*(5738), 1239–1241. https://doi.org/10.1126/science.1116030

Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J., & Mace, G. M. (2004). Human population density and extinction risk in the world's carnivores. *PLoS Biology*, *2*(7), e197. https://doi.org/10.1371/journal.pbio.0020197, E197

Carroll, G., Holsman, K. K., Brodie, S., Thorson, J. T., Hazen, E. L., Bograd, S. J., Haltuch, M. A., Kotwicki, S., Samhouri, J., Spencer, P., Willis-Norton, E., & Selden, R. L. (2019). A review of methods for quantifying spatial predator–prey overlap. *Global Ecology and Biogeography*, *28*(11), 1561–1577. https://doi.org/10.1111/geb.12984

Center for International Earth Science Information Network - CIESIN - Columbia University (2016). Gridded Population of the World, Version 4 (GPWv4): Population Density [Data set]. NASA Socioeconomic Data and Applications Center (SEDAC). https://doi.org/10.7927/H4NP22DQ

Chase, J. M. (2010). Stochastic community assembly causes higher biodiversity in more productive environments. *Science*, *328*(5984), 1388–1391. https://doi.org/10.1126/science.1187820

Cruz, P., Iezzi, M. E., De Angelo, C., Varela, D., Di Bitetti, M. S., & Paviolo, A. (2018). Effects of human impacts on habitat use, activity patterns and ecological relationships among medium and small felids of the Atlantic Forest. *PLoS One*, *13*(8), e0200806. https://doi.org/10.1371/journal.pone.0200806

Davis, C. L., Rich, L. N., Farris, Z. J., Kelly, M. J., Di Bitetti, M. S., Di Blanco, Y., Albanesi, S., Farhadinia, M. S., Gholikhani, N., Hamel, S., Harmsen, B. J., Wultsch, C., Kane, M. D., Martins, Q., Murphy, A. J., Steenweg, R., Sunarto, S., Taktehrani, A., Thapa, K., … Miller, D. A. W. (2018). Ecological correlates of the spatial co-occurrence of sympatric mammalian carnivores worldwide. *Ecology Letters*, *21*(9), 1401–1412. https://doi.org/10.1111/ele.13124

Di Bitetti, M. S., De Angelo, C. D., Di Blanco, Y. E., & Paviolo, A. (2010). Niche partitioning and species coexistence in a Neotropical felid assemblage. *Acta Oecologica*, *36*(4), 403–412. https://doi.org/10.1016/j.actao.2010.04.001

Diarrassouba, A., Gnagbo, A., Kouakou, Y. C., Campbell, G., Tiedoué, M. R., Tondossama, A., Kühl, H. S., & Koné, I. (2020). Differential response of seven duiker species to human activities in Taï National Park, Côte D'ivoire. *African Journal of Ecology*, *58*(1), 58–68. https://doi.org/10.1111/AJE.12680

Dickie, M., Serrouya, R., McNay, R. S., & Boutin, S. (2017). Faster and farther: wolf movement on linear features and implications for hunting behaviour. *Journal of Applied Ecology*, *54*(1), 253–263. https://doi.org/10.1111/1365-2664.12732

Didan, K. (2015). MOD13Q1 MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SIN Grid V006 [Data set]. NASA EOSDIS Land Processes DAAC; https://doi.org/10.5067/MODIS/MOD13Q1.006

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the anthropocene. *Science*, *345*(6195), 401–406. https://doi.org/10.1126/science.1251817

Dormann, C. F., Bobrowski, M., Dehling, D. M., Harris, D. J., Hartig, F., Lischke, H., Moretti, M. D., Pagel, J., Pinkert, S., Schleuning, M., Schmidt, S. I., Sheppard, C. S., Steinbauer, M. J., Zeuss, D., & Kraan, C. (2018). Biotic interactions in species distribution modelling: 10 questions to guide interpretation and avoid false conclusions. *Global Ecology and Biogeography*, *27*(9), 1004–1016. https://doi.org/10.1111/geb.12759

Farris, Z. J., Karpanty, S. M., Ratelolahy, F., & Kelly, M. J. (2014). Predator–primate distribution, activity, and co-occurrence in relation to habitat and human activity across fragmented and contiguous forests in Northeastern Madagascar. *International Journal of Primatology*, *35*(5), 859–880. https://doi.org/10.1007/s10764-014-9786-0

Fidino, M., Simonis, J. L., & Magle, S. B. (2019). A multistate dynamic occupancy model to estimate local colonization-extinction rates and patterns of co-occurrence between two or more interacting species. *Methods in Ecology and Evolution*, *10*(2), 233–244. https://doi.org/10.1111/2041-210X.13117

Fisher, J. T., & Ladle, A. (2022). Syntopic species interact with large boreal mammals' response to anthropogenic landscape change. *Science of the Total Environment*, *822*, 153432. https://doi.org/10.1016/J.SCITOTENV.2022.153432

Friedl, M., & Sulla-Menashe, D. (2019). MCD12Q1 MODIS/Terra+Aqua Land Cover Type Yearly L3 Global 500m SIN Grid V006 [Data set]. NASA EOSDIS Land Processes DAAC. https://doi.org/10.5067/MODIS/MCD12Q1.006

Gardner, C. J., Bicknell, J. E., Baldwin-Cantello, W., Struebig, M. J., & Davies, Z. G. (2019). Quantifying the impacts of defaunation on natural forest regeneration in a global meta-analysis. *Nature Communications*, *10*(1), 1–7. https://doi.org/10.1038/s41467-019-12539-1

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

Gorczynski, D., & Beaudrot, L. (2021). Functional diversity and redundancy of tropical forest mammals over time. *Biotropica*, *53*(1), 51–62. https://doi.org/10.1111/btp.12844

Gorczynski, D., Hsieh, C., Ahumada, J., Akampurila, E., Andrianarisoa, M. H., Espinosa, S., Johnson, S., Kayijamahe, C., Lima, M. G. M., Mugerwa, B., Rovero, F., Salvador, J., Santos, F., Sheil, D., Uzabaho, E., & Beaudrot, L. (2022). Data and code for human density modulates spatial associations among tropical forest terrestrial mammal species. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.573n5tbb5

Gorczynski, D., Hsieh, C., Luciano, J. T., Ahumada, J., Espinosa, S., Johnson, S., Rovero, F., Santos, F., Andrianarisoa, M. H., Astaiza,

J. H., Jansen, P. A., Kayijamahe, C., Moreira Lima, M. G., Salvador, J., & Beaudrot, L. (2021). Tropical mammal functional diversity increases with productivity but decreases with anthropogenic disturbance. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1945), 20202098. https://doi.org/10.1098/rspb.2020.2098

Gutzwiller, K. J., & Anderson, S. H. (1999). Spatial extent of human-intrusion effects on subalpine bird distributions. *Condor*, *101*(2), 378–389. https://doi.org/10.2307/1370001

Hassell, J. M., Begon, M., Ward, M. J., & Fèvre, E. M. (2017). Urbanization and disease emergence: Dynamics at the wildlife–livestock–human interface. *Trends in Ecology and Evolution*, *32*(1), 55–67. https://doi.org/10.1016/j.tree.2016.09.012

He, D., & Biswas, S. R. (2019). Negative relationship between interspecies spatial association and trait dissimilarity. *Oikos*, *128*(5), 659–667. https://doi.org/10.1111/oik.05876

Herrera, J. M., & García, D. (2010). Effects of forest fragmentation on seed dispersal and seedling establishment in ornithochorous trees. *Conservation Biology*, *24*(4), 1089–1098. https://doi.org/10.1111/j.1523-1739.2010.01459.x

IUCN. (2021). The IUCN red list of threatened species. Version 2021-1

Jansen, P. A., Ahumada, J. A., Fegraus, E., & O'Brien, T. G. (2014). TEAM: A standardized camera trap survey to monitor terrestrial vertebrate communities in tropical forests. In P. Fleming, P. Meek, G. Ballard, P. Banks, A. Claridge, J. Sanderson, & D. Swann (Eds.), *Camera Trapping: Wildlife Management and Research* (1st ed., pp. 263–270). Csiro Publishing.

Jetz, W., & Fine, P. V. A. (2012). Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. *PLoS Biology*, *10*(3), e1001292. https://doi.org/10.1371/JOURNAL.PBIO.1001292

Kafley, H., Lamichhane, B. R., Maharjan, R., Khadka, M., Bhattarai, N., & Gompper, M. E. (2019). Tiger and leopard co-occurrence: Intraguild interactions in response to human and livestock disturbance. *Basic and Applied Ecology*, *40*, 78–89. https://doi.org/10.1016/j.baae.2019.07.007

Keil, P., Wiegand, T., Tóth, A. B., McGlinn, D. J., & Chase, J. M. (2021). Measurement and analysis of interspecific spatial associations as a facet of biodiversity. *Ecological Monographs*, *91*(3), e01452. https://doi.org/10.1002/ECM.1452

Kellner, K. F., Parson, A. W., Kays, R., Millspaugh, J. J., & Rota, C. T. (2022). A two-species occupancy model with a continuous-time detection process reveals spatial and temporal interactions. *Journal of Agricultural, Biological, and Environmental Statistics*, *27*(2), 321–338.

Kéry, M., & Royle, J. A. (2015). *Applied hierarchical modeling in ecology: Analysis of distribution, abundance and species richness in R and BUGS* (Vol. *1*). Academic Press. https://doi.org/10.1016/c2015-0-04070-9

Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M., & Steffan-Dewenter, I. (2009). Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution*, *24*(10), 564–571. https://doi.org/10.1016/j.tree.2009.04.011

Lacher, T. E., Davidson, A. D., Fleming, T. H., Gómez-Ruiz, E. P., McCracken, G. F., Owen-Smith, N., Peres, C. A., & Vander Wall, S. B. (2019). The functional roles of mammals in ecosystems. *Journal of Mammalogy*, *100*(3), 942–964. https://doi.org/10.1093/JMAMMAL/GYY183

Ladle, A., Steenweg, R., Shepherd, B., & Boyce, M. S. (2018). The role of human outdoor recreation in shaping patterns of grizzly bear-black bear co-occurrence. *PLoS One*, *13*(2), e0191730. https://doi.org/10.1371/journal.pone.0191730

Laliberté, E., Legendre, P., & Shipley, B. (2015). FD: measuring functional diversity from multiple traits, and other tools for functional ecology. *R Package (p. Version 1.0-12)*. http://www.elaliberte.info

Laurance, W. F., Carolina Useche, D., Rendeiro, J., Kalka, M., Bradshaw, C. J. A., Sloan, S. P., Laurance, S. G., Campbell, M., Abernethy, K., Alvarez, P., Arroyo-Rodriguez, V., Ashton, P., Benítez-Malvido, J., Blom, A., Bobo, K. S., Cannon, C. H., Cao, M., Carroll, R., Chapman, C., … Zamzani, F. (2012). Averting biodiversity collapse in tropical forest protected areas. *Nature*, *489*(7415), 290–294. https://doi.org/10.1038/nature11318

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, *7*(7), 601–613. https://doi.org/10.1111/J.1461-0248.2004.00608.X

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, A. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, *83*(8), 2248–2255. https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., & Studer, M. (2014). Package "cluster" (p. 79).

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

Marshall, A. J., Beaudrot, L., & Wittmer, H. U. (2014). Responses of primates and other frugivorous vertebrates to plant resource variability over space and time at Gunung Palung National Park. *International Journal of Primatology*, *35*(6), 1178–1201. https://doi.org/10.1007/S10764-014-9774-4/FIGURES/5

McKee, J., Chambers, E., & Guseman, J. (2013). Human population density and growth validated as extinction threats to mammal and bird species. *Human Ecology*, *41*(5), 773–778. https://doi.org/10.1007/s10745-013-9586-8

McNaughton, S. J., Oesterheld, M., Frank, D. A., & Williams, K. J. (1989). Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature*, *341*(6238), 142–144. https://doi.org/10.1038/341142a0

Metcalfe, D. B., Asner, G. P., Martin, R. E., Silva Espejo, J. E., Huasco, W. H., Farfán Amézquita, F. F., Carranza-Jimenez, L., Galiano Cabrera, D. F., Baca, L. D., Sinca, F., Huaraca Quispe, L. P., Taype, I. A., Mora, L. E., Dávila, A. R., Solórzano, M. M., Puma Vilca, B. L., Laupa Román, J. M., Guerra Bustios, P. C., Revilla, N. S., … Malhi, Y. (2014). Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. *Ecology Letters*, *17*(3), 324–332. https://doi.org/10.1111/ele.12233

Murphy, A., Diefenbach, D. R., Ternent, M., Lovallo, M., & Miller, D. (2021). Threading the needle: How humans influence predator–prey spatiotemporal interactions in a multiple-predator system. *Journal of Animal Ecology*, *90*(10), 2377–2390. https://doi.org/10.1111/1365-2656.13548

Newmark, W. D., Manyanza, D. N., Gamassa, D.-G. M., & Sariko, H. I. (1994). The conflict between wildlife and local people living adjacent to protected areas in Tanzania: Human density as a predictor. *Biology*, *8*(1), 249–255.

Parks, S. A., & Harcourt, A. H. (2002). Reserve size, local human density, and mammalian extinctions in U.S. protected areas. *Conservation Biology*, *16*(3), 800–808.

Pelini, S. L., Prior, K. M., Parker, D. J., Dzurisin, J. D. K., Lindroth, R. L., & Hellmann, J. J. (2009). Chapter 11-Climate change and temporal and spatial mismatches in insect communities. In T. M. Letcher (Ed.), *Climate change* (pp. 215–231). Elsevier. https://doi.org/10.1016/B978-0-444-53301-2.00011-7

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M., & Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, *344*(6187), 1246752. https://doi.org/10.1126/science.1246752

R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Ramesh, T., Kalle, R., & Downs, C. T. (2017). Staying safe from top predators: patterns of co-occurrence and inter-predator interactions. *Behavioral Ecology and Sociobiology*, 71(2), 1–14. https://doi.org/10.1007/s00265-017-2271-y

Richmond, O. M. W., Hines, J. E., & Beissinger, S. R. (2010). Two-species occupancy models: A new parameterization applied to co-occurrence of secretive rails. *Ecological Applications*, 20(7), 2036–2046.

Rondinini, C., Di Marco, M., Chiozza, F., Santulli, G., Baisero, D., Visconti, P., Hoffmann, M., Schipper, J., Stuart, S. N., Tognelli, M. F., Amori, G., Falcucci, A., Maiorano, L., & Boitani, L. (2011). Global habitat suitability models of terrestrial mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1578), 2633–2641. https://doi.org/10.1098/RSTB.2011.0113

Rota, C. T., Ferreira, M. A. R., Kays, R. W., Forrester, T. D., Kalies, E. L., Mcshea, W. J., Parsons, A. W., & Millspaugh, J. J. (2016). A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution*, 7(10), 1164–1173. https://doi.org/10.1111/2041-210X.12587

Rovero, F., Ahumada, J., Jansen, P. A., Sheil, D., Alvarez, P., Boekee, K., Espinosa, S., Lima, M. G. M., Martin, E. H., O'Brien, T. G., Salvador, J., Santos, F., Rosa, M., Zvoleff, A., Sutherland, C., & Tenan, S. (2020). A standardized assessment of forest mammal communities reveals consistent functional composition and vulnerability across the tropics. *Ecography*, 43(1), 75–84. https://doi.org/10.1111/ecog.04773

Smith, J. A., Thomas, A. C., Levi, T., Wang, Y., & Wilmers, C. C. (2018). Human activity reduces niche partitioning among three widespread mesocarnivores. *Oikos*, 127(6), 890–901. https://doi.org/10.1111/oik.04592

Spasojevic, M. J., Copeland, S., & Suding, K. N. (2014). Using functional diversity patterns to explore metacommunity dynamics: A framework for understanding local and regional influences on community structure. *Ecography*, 37(10), 939–949. https://doi.org/10.1111/ecog.00711

Su, U., & Yajima, M. (2015). R2jags: Using R to run "JAGS." R Packages, 12. https://cran.r-project.org/web/packages/R2jags/R2jags.pdf

Suraci, J. P., Clinchy, M., Zanette, L. Y., & Wilmers, C. C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters*, 22(10), 1578–1586. https://doi.org/10.1111/ELE.13344

Sylvie Fonkwo, N., Evaristus Angwafo, T., & Mbida, M. (2011). Abundance and distribution of large mammals in the Bakossi landscape area, Cameroon. *Journal of Soil Science and Environmental Management*, 2(2), 43–48. http://www.academicjournals.org/JSSEM

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J. L., Bertassoni, A., Beyer, D., Bidner, L., Van Beest, F. M., Blake, S., Blaum, N., ... Mueller, T. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, 359(6374), 466–469. https://doi.org/10.1126/science.aam9712

Tucker, M. A., Santini, L., Carbone, C., & Mueller, T. (2021). Mammal population densities at a global scale are higher in human-modified areas. *Ecography*, 44(1), 1–13. https://doi.org/10.1111/ecog.05126

Warren, Y. (2009). Crop-raiding baboons (*Papio anubis*) and defensive farmers: A west african perspective. *West African Journal of Applied Ecology*, 14(1), 1–11. https://doi.org/10.4314/wajae.v14i1.44705

Weiher, E., & Keddy, P. A. (1995). Assembly rules, null models, and trait dispersion: New questions from old patterns. *Oikos*, 74(1), 164. https://doi.org/10.2307/3545686

Wright, S. J., Stoner, K. E., Beckman, N., Corlett, R. T., Dirzo, R., Muller-Landau, H. C., Nuñez-Lturri, G., Peres, C. A., & Wang, B. C. (2007). The plight of large animals in tropical forests and the consequences for plant regeneration. *Biotropica*, 39(3), 289–291. https://doi.org/10.1111/j.1744-7429.2007.00293.x

Yin, D., Liu, Y., Ye, Q., Cadotte, M. W., & He, F. (2021). Trait hierarchies are stronger than trait dissimilarities in structuring spatial co-occurrence patterns of common tree species in a subtropical forest. *Ecology and Evolution*, 11(12), 7366–7377. https://doi.org/10.1002/ECE3.7567

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.