Research Article

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Living in the edge: large terrestrial mammal and bird species traits and the ability to cope with extreme environmental conditions and human disturbance in a tropical dry forest in Colombia

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Abstract

Tropical drylands are characterized by extreme environmental conditions that, coupled with
anthropogenic habitat degradation, can limit the occurrence of native species. Species that are
most sensitive to these pressures may be prone to disappear in the context of climate change. In
this study, we evaluated the influence of environmental and anthropogenic variables on the
occurrence of large mammals and birds at the Tatacoa Desert, an arid region in central
Colombia. We tested the relationship between the magnitude of the species' responses to
environmental, human-related variables and to body mass, and percentage of carnivory.
Overall, we found a positive association between forest cover and the occupancy of the largest
mammals (> 8kg), negative associations between solar radiation and human footprint with
individual species occupancy, and a positive association of species occupancy with distance to
touristic sites. Our results suggest that the largest and/or more carnivore species may be affected
positively by forest cover and negatively by intense solar radiation highlighting the
consequences of the increasing process of desertification on large mammals and birds at the
upper Magdalena River basin of Colombia under the current scenario of global climate change.

Introduction

Tropical drylands are landscapes generally characterized by water scarcity, high temperatures,
high evapotranspiration, and highly variable and seasonal precipitation. The rough climatic and
environmental conditions of tropical drylands have been proposed to limit the abundance and
diversity of plants and partially influence their relatively low primary productivity (Hoover *et al.*
2020; Shachak *et al.* 2005). The combination of extreme abiotic conditions and low resource
availability at the primary producer level makes drylands a challenging habitat for many
organisms and restrict their use to a few animals and plants with the physiological or behavioral
adaptations to tolerate such environmental stress (Gyhrs *et al.* 2022; Peguero-Pina *et al.* 2020;
Shachak *et al.* 2005), generating high level of endemism in arid regions (Brito *et al.* 2014).

In addition to natural environmental and ecological stressors, animals living in tropical
drylands must nowadays deal with pervasive anthropogenic disturbances such as forest loss and
degradation, urbanization, and the presence of invasive species, among others human-induced
stressors (Hoover *et al.* 2020). There are also several conservation issues affecting drylands, such
as the lack of protected areas and the lack of studies describing the biodiversity of these
ecosystems (Brito *et al.* 2016, 2022). This poses additional challenges for the survival and
reproduction of native species living in these astringent ecosystems. Under this scenario, the
long-term permanence of animals such as ground-dwelling mammals and birds in drylands will
largely depend on their ability to tolerate extreme environments and anthropogenic
disturbances, or both.

Tolerance to extreme conditions can be associated to species traits (e.g., body size),
suggesting that, depending on a particular trait, a given species can be affected to a greater or
lesser extent by direct environmental pressures (Soto-Shoender *et al.* 2020; Verheyen *et al.* 2003;
Webb *et al.* 2002). For example, Cormont *et al.* (2011) found that insectivorous long-distance
migrant birds, can be affected negatively—in terms of population growth rates—under contexts
of increased weather variability, and, Suraci *et al.* (2021) found that mammals that can tolerate
disturbance on human-dominated landscapes were generally the smallest of the subset of species
studied, with short reproductive cycles, and with a lower extent of carnivorous diets. Thus, body
size and diet are traits that can respond to variable sources of selection, and under arid
conditions (e.g., water scarcity and high temperatures) may be limited by overheating and the
lack of energetic resources and water in the environment (Bastos *et al.* 2021; Degen 2012;
McNab 2010; Schiaffini 2016).

In the northern part of South America, there is a series of dry valleys isolated from each other by rainforest formations, and they are located at altitudes less than 1800 m along the Andes from Ecuador to Venezuela. These dry valleys are known as Andean arid and semi-arid enclaves. They are the result of the rain shadow effect created by the surrounding mountains, which promotes a predominantly arid climate (Sarmiento 1975, 1976; Soriano and Ruiz 2006). In Colombia, one of these arid enclaves is known as the *Tatacoa Desert,* located in the lowland ecosystems of the Upper Magdalena River Valley (ca. 400 m.a.s.l.), in between the Central and Eastern Andean Cordilleras. The vegetation is composed of a relatively low number of tree species (when compared to adjacent rainforests), xerophytic shrubs, and cacti and corresponds to the life zones of tropical dry forest and tropical very dry forest (Rojas-Marín *et al.* 2019). Little is known about the fauna of the *Tatacoa Desert*, but some studies with bats have shown that the diversity of species is usually lower than in the more humid surrounding areas, a pattern that is shared with the other arid enclaves of the Andes (Sarmiento 1976; Soriano and Ruiz 2006). Another study with amphibians, in which 29 species were recorded, highlights that the seasonality of the ecosystem is very important since the presence of some species can be conditioned by the rainy seasons (Acosta-Galvis 2012).

The Tatacoa Desert is a large area (covering approximately 300 km^2) characterized by an arid climate with downpours after long periods of drought, which causes intense surface erosion that is magnified by over a century of intense human activity, mainly associated to productive systems such as agriculture, cattle ranching, and more recently tourism (Hermelin 2016). This combination of extreme climatic conditions and intense human activity makes the Tatacoa Desert an ideal scenario to evaluate the response of ground-dwelling fauna (birds and mammals) and species traits to the pressures of a stringent environment using occupancy models. Furthermore, the Tatacoa Desert wildlife has been poorly studied, and knowledge on its ecological dynamics can provide valuable insights into the management of its heavily transformed ecosystems.

In this study, we examine the relationship body size and level of carnivory of ground-dwelling large birds and mammals and response magnitudes to the environmental conditions and human disturbance on a lowland arid landscape in between the northern Andes mountains. We hypothesize that biggest taxa (those with body mass above the median of the studied species), and those with a higher degree of carnivorous diets will be negatively affected by both more arid environmental conditions and human disturbance. Conversely smaller, from the large species studied here, and those more herbivorous might not be affected or will be more abundant in arid and disturbed areas (Bergmann 1848; McNab 2010).

Methods

Study area

Our study was carried out in the Andean arid enclave known as *Tatacoa Desert*, a natural protected area located in the eastern bank of the Magdalena River in the municipalities of Villavieja and Baraya in the Department of Huila, in Colombia (N 3.278, W-75.156) (Hermelin 2016) (Figure 1).Tatacoa Desert is a large sub-desertic area that covers about 300 km^2 with an average

annual temperature of 28°C and an average annual precipitation of 1190mm distributed in two rainy periods (February–May/October–December) (Rojas-Marín *et al.* 2019; Sarmiento 1975, 1976). The geomorphology of Tatacoa Desert is characterized by a diverse array of landforms, such as alluvial fans, deep cliffs, and sand sheets, mainly shaped by erosion. The main erosional force are occasional heavy downpours that have dissected the landscape into intricate networks of gullies and ravines. Besides water, eolian processes and human activity are ongoing processes contributing to erode and modify the existing landscape (Hermelin 2016).

Camera-trap sampling

The camera-trap sampling was based on protocols developed by the Tropical Ecology Assessment and Monitoring Network (TEAM) (Jansen *et al.* 2014; TEAM Network 2011). The camera-trap stations array was planned in QGIS version 3.16 (QGIS Development Team 2020), randomly assigning the location of each camera-station on the forest cover map of the Tatacoa Desert. Afterward, in the field, cameras were set up as closely as possible to each one of the planned locations. Throughout the study area, we set up 34 camera-trap stations with one camera-trap per station. To ensure spatial independence between stations and given that there are no records of animals with large movements (e.g., jaguars) in the study area, the distance between camera trap stations varied between 500 and 1500 m. We performed a Moran's *I* test (Gittleman and Kot 1990) using the richness values of each camera to assess whether there was spatial autocorrelation between cameras. We used three camera trap models: (1) Bushnell TrophyCam HD, (2) Browning Strike Force, and (3) Moultrie D80. Cameras were placed on trees at an average height of 40 cm and were set up to take three photos on each activation event and with a 30 second delay between consecutive events. Cameras were continuously active during periods of 60–90 days between January and August of 2020. Overall, sampling effort accounted for 2883 trap nights, with an average of 84.8 days of activity per camera. The geographical coordinates of each camera-trap were recorded using a handheld GPS unit Garmin GPSMAP 64s. We organized and identified images using the open-access software Wild.ID (Fegraus *et al.* 2011), and then used the camtrapR package of the statistical software R (Niedballa *et al.* 2016; R Core Team 2022) to obtain independent records (independence interval of 1440 minutes) and presence–absence tables for statistical modeling. The species taxonomy was checked in three websites: (1) Integrated Taxonomic Information System (National Museum of Natural History and Smithsonian Institution 2023), (2) Mammal Diversity Database (Mammal Diversity Database 2024), and (3) Birdlife International (Birdlife International 2024).

Landscape covariates, body mass and carnivory

We estimated two groups of landscape covariates: (1) covariates related with environmental conditions and (2) covariates related to human activity. Environmental variables included forest cover and solar radiation. In order to estimate the percentage of forest cover, we generated a cover map using the Semi-Automatic Classification Plugin in the software QGIS version 3.16 (Congedo 2021; QGIS Development Team 2020) using three categories: forest, grassland, and bare ground. Then we quantified the percentage of forest using circular buffers at four spatial scales (radii of: 100 m, 300 m, 500 m, and 700 m) to choose the spatial scale at which the variable has a
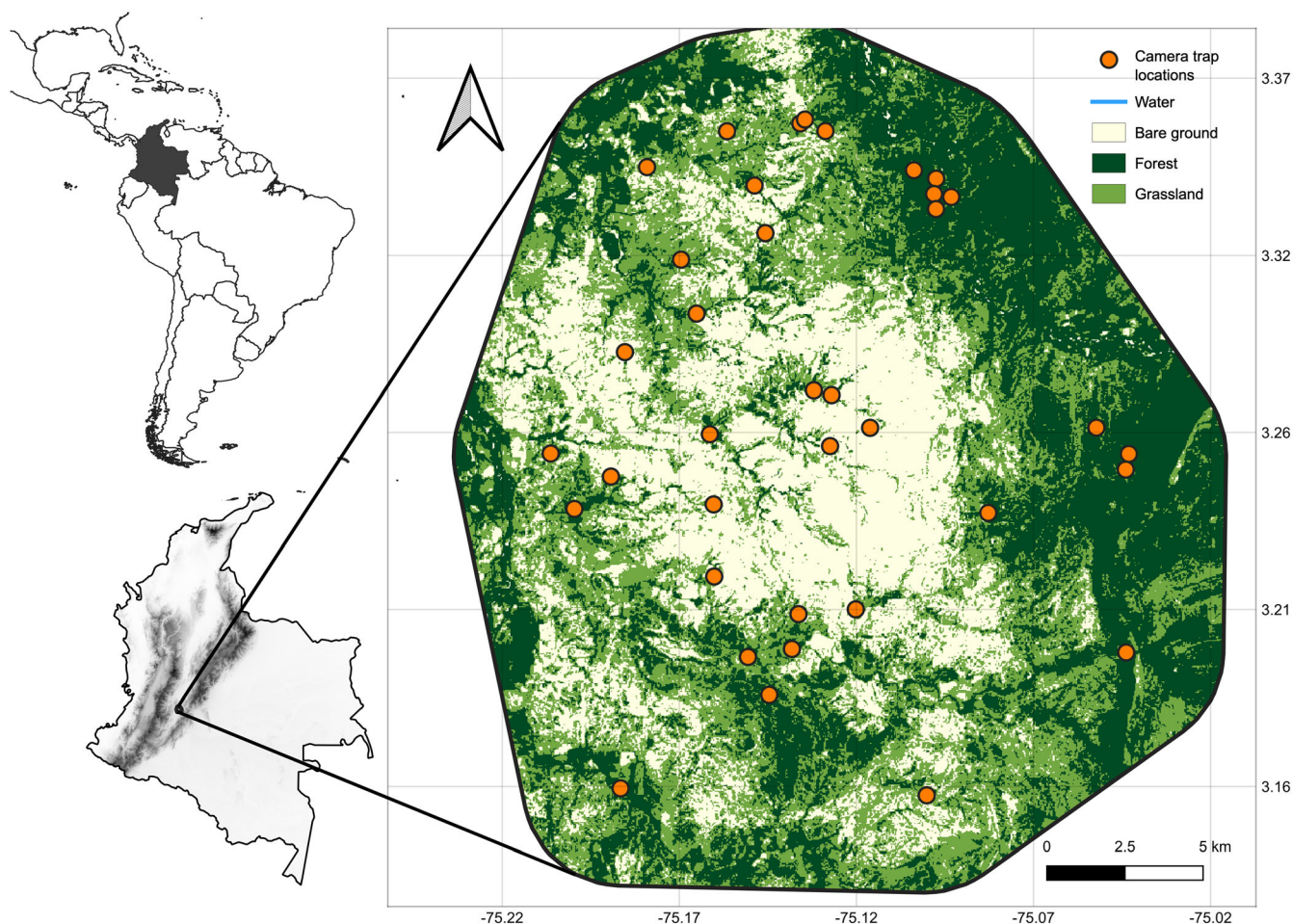
Figure 1. Camera trap locations in Tatacoa Desert, a protected area in Huila Department, Colombia, with land cover description.

greater influence on the large animals' assemblage occupancy. To achieve this, we conducted individual occupancy models for each spatial scale of the variable and selected the model with the highest estimated value. In order to estimate solar radiation (a measure of environmental astringency), we used the WorldClim 2 dataset (Fick and Hijmans 2017) extracting the values for each of the camera trap locations. Human activity variables included in this study were distance to touristic sites and the spatial human footprint. The former was calculated with QGIS version 3.16 (QGIS Development Team 2020), and the locations of the main touristic sites, such as stores and hotels, the latter was estimated using the legacy-adjusted Human Footprint Index for Colombia (Ayram et al. 2020). This index measures the level of human intervention on a scale of 0–100 based on information about land use type, rural population density, distance to roads, distance to settlements, the fragmentation index of natural vegetation, the biomass index relative to natural potential, and time of ecosystem intervention in years.

We used two species traits: average body mass and average percentage of carnivory of each species (S1). Both variables were extracted from the EltonTraits 1.0 dataset, a global species-level compilation of birds and mammals attributes (Wilman et al. 2014). For body mass, we extracted the value registered in the EltonTraits 1.0 dataset for each species, and the percentage of carnivory was calculated by adding the percentage of consumption of items

representing a carnivorous diet (endotherm vertebrates such as mammals and birds and ectotherm vertebrates such as reptiles and amphibians, fishes, and carrion) in the EltonTraits 1.0 dataset.

Occupancy modeling

To evaluate the response of the species recorded at Tatacoa Desert to environment and human activity while accounting for imperfect detection, we performed a hierarchical Bayesian multispecies occupancy model (Dorazio and Royle 2005; MacKenzie et al. 2002). This kind of model groups two components: (1) a state process, which is related to the ecological dynamic under study and (2) an observation process, related to the sampling method. In this model, the occurrence (z) of a species i at a site j was defined as a Bernoulli process, $z_{i,j} \sim \text{Bern}(\psi_{ij})$, where ψ_{ij} is the probability of occurrence of a species i at a camera site j. Then, to incorporate the imperfect detection, detection probability was calculated from temporally replicated data, in our study, we grouped seven consecutive camera-trap nights into one sampling occasion (to avoid zero inflation), resulting in camera-trap sites oscillating between 8 and 17 sampling occasions, known as the detection histories. From this temporal replicate, we estimated the probability of capturing a species i at camera station j on sampling occasion k. Thus, we defined a second Bernoulli process for detection as $x_{i,j,k} \sim \text{Bern}(p_{i,j,k} \times z_{i,j})$, where $x_{i,j,k}$ is the group of

Table 1. Species of large mammals and ground-dwelling birds registered in the Tatacoa Desert with occupancy (ψ) and detection (*p*) estimates and its 95% Bayesian credible intervals (BIC)

Scientific name	Common name	ψ (BCI 95%)	*p* (BCI 95%)
Mammals			
Cerdocyon thous	Crab-eating fox	0.48 (0.40–0.56)	0.19 (0.17–0.21)
Conepatus semistriatus	Skunk	0.04 (0.03–0.08)	0.13 (0.09–0.19)
Cuniculus paca	Lowland paca	0.07 (0.05–0.12)	0.14 (0.10–0.19)
Dasypus novemcinctus	Nine-banded armadillo	0.63 (0.49–0.72)	0.09 (0.07–0.11)
Didelphis marsupialis	Common opossum	0.19 (0.14–0.25)	0.19 (0.16–0.23)
Eira Barbara	Tayra	0.16 (0.10–0.23)	0.10 (0.07–0.13)
Galictis vittate	Greater grison	0.08 (0.05–0.14)	0.08 (0.06–0.12)
Leopardus pardalis	Ocelot	0.12 (0.08–0.17)	0.10 (0.07–0.14)
Mazama sp.	Deer	0.29 (0.22–0.38)	0.19 (0.16–0.24)
Pecari tajacu	Collared peccary	0.10 (0.06–0.15)	0.16 (0.12–0.20)
Procyon cancrivorus	Crab-eating raccoon	0.47 (0.39–0.55)	0.18 (0.15–0.21)
Puma yagouaroundi	Jaguarundi	0.43 (0.32–0.53)	0.09 (0.07–0.12)
Sylvilagus brasiliensis	Forest cottontail	0.23 (0.18–0.29)	0.32 (0.28–0.35)
Tamandua mexicana	Lesser anteater	0.49 (0.42–0.56)	0.21 (0.19–0.23)
Birds			
Aramides cajaneus	Grey-necked wood-rail	0.34 (0.29–0.41)	0.36 (0.33–0.39)
Colinus cristatus	Crested bobwhite	0.09 (0.06–0.13)	0.20 (0.16–0.26)
Ortalis columbiana	Colombian chachalaca	0.69 (0.59–0.76)	0.16 (0.14–0.18)

detection histories, and $p_{i,j,k}$ represent the detection probability of species i at a site j on a temporal replicate k, that being conditional to species presence ($z_{i,j} = 1$) (Boron *et al.* 2019; Rich *et al.* 2016).

We included (on a logit scale) the effect of environmental and anthropogenic covariates to the occurrence and detection probabilities. The occurrence was modeled as a function of the percentage of forest on a 300 m radii around each camera-trap site (the spatial scale that showed the greater influence on assemblage occupancy), the solar radiation, the distance to tourist sites, and the human footprint. The detection was modeled as a function of the solar radiation, and the percentage of forest on a 100 m radii around each camera-trap site under the assumption that the amount of forest around each camera influences the probability of detection on a smaller scale. The model includes the estimation of a hyperparameter for the assemblage response to covariates and species-specific responses; therefore, it is possible to compare the responses to covariates at the assemblage level against the species-specific response variations. The models for occurrence and detection are expressed as

$$\text{logit}(\psi_{ij}) = \mu_{(i)} + \alpha_{1i} \,\%\text{Forest Cover}_j + \alpha_{2i} \,\text{Distance Tourist}_j$$
$$+ \alpha_{3i} \,\text{Solar Radiation}_j + \alpha_{4i} \,\text{Human Footprint}_j$$

$$\text{logit}(p_{i,j,k}) = \upsilon_{(i)} + \beta_{1i} \,\%\text{Forest Cover}_j + \beta_{2i} \,\text{Solar Radiation}_j$$

Finally, we estimated parameter posterior distributions through Markov Chain Monte Carlo simulations (MCMC) implemented in JAGS (version 4.3.1) using the R packages rjags (Finley 2013) and jagsUI (Kellner *et al.* 2019). We obtained the posterior distributions of the model parameters with three chains of 500000 iterations and a burn-in sample of 200000. We thinned the chains by retaining every 100 sampled values (Drouilly *et al.* 2018). We used the Gelman-Rubin criteria to assess the model convergence, where values less than 1.1 indicate model convergence (Gelman *et al.* 2013).

Relationship between occupancy estimates and species traits

To evaluate if species traits might influence the magnitude of the species responses to the environmental and anthropogenic covariates, we implemented general linear models (GLMs). We used as predictors two traits: the body mass (on a logarithmic scale) and the percentage of carnivory of each species as a proxy of the diet. As response variables, we extracted the mean values of the species responses (estimates) to the covariates in the occupancy model. This analysis was performed in the statistical software R (version 4.2.0) (R Core Team 2022).

Results

In total, we recorded 17 species, 14 large mammals, and 3 ground-dwelling birds. We did not find spatial autocorrelation in richness values between the camera traps from Moran's I test ($p = 0.175$). The correlation values between the covariates used in the occupancy model were forest cover and solar radiation = –0.11; forest cover and distance to touristic sites = 0.45; forest cover and spatial human footprint = 0.35; solar radiation and distance to touristic sites = 0.24; solar radiation and spatial human footprint = 0.27; and distance to touristic sites and spatial human footprint = 0.33. Values of species occupancy probability varied from 0.04
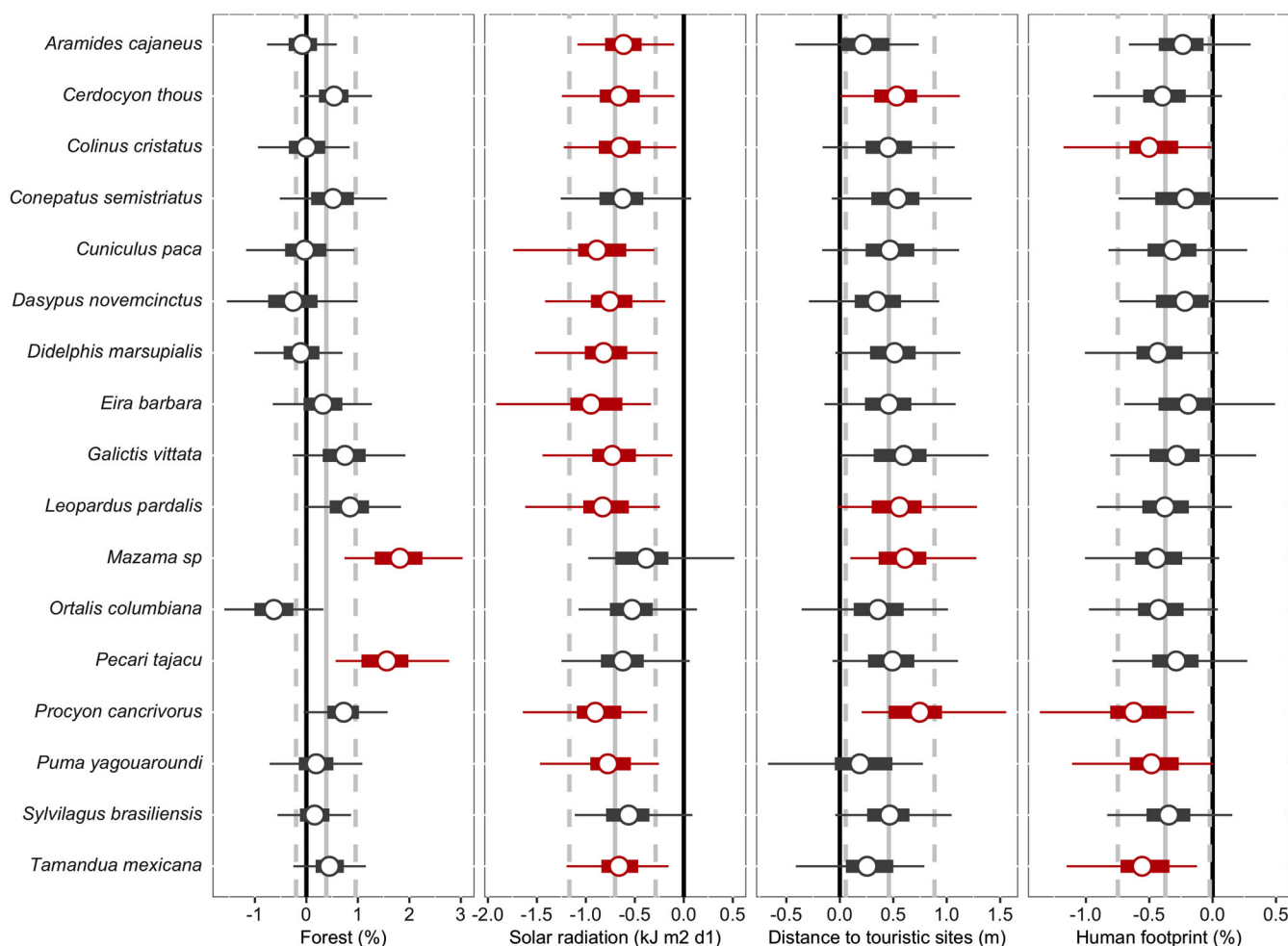
Figure 2. Assemblage- and species-level responses of occupancy (standardize beta coefficients) to (from right to left) forest cover, solar radiation, distance to touristic sites, and spatial human footprint. Lines represent posterior mean and 95% Bayesian credible intervals (BCIs) of the assemblage mean hyperparameter, white dots show the posterior mean for each species, lines, and bars show the 95% and 50% BCIs, respectively. The species 95% BCIs that do not overlap zero colored indicated in red.

(*Conepatus semistriatus*) to 0.69 (*Ortalis columbiana*), and the values of species detection probability varied from 0.08 (*Galictis vittata*) to 0.36 (*Aramides cajaneus*) (Table 1). At the assemblage-level occupancy, the percentage of forest had a positive but not significant effect (0.39; 95% BCI: −0.17 to 0.98), the solar radiation had a negative and significant effect (−0.71; 95% BCI: −1.17 to −0.29), the distance to touristic sites had positive and significant effect (0.46; 95% BCI: 0.05 to 0.89), and the spatial human footprint had a negative and significant effect (−0.36; 95% BIC: −0.73 to −0.01) (Figure 2). In terms of the detection probability, neither the percentage of forest nor the solar radiation had a significant effect on the assemblage (Figure 3). At the species-specific level, the percentage of forest showed a significantly positive effect on two species, the solar radiation showed a significantly negative effect over 12 species, the distance to tourist sites showed a significantly positive effect over 4 species, and the spatial human footprint showed a significantly negative effect over 4 species (Figures 2, S2).

Regarding the correlation between the responses of the species to each covariate in the occupancy model and the species traits, the body mass showed a positive correlation (Estimate = 0.31, $R^2 = 0.49$, $p = 0.001$) with the forest (Figure 4A), but did not have a significant correlation with the other variables: solar radiation (estimate = −0.019, $R^2 = 0.03$, $p = 0.484$), distance to touristic sites

(estimate = 0.034, $R^2 = 0.10$, $p = 0.20$), and human footprint (estimate = −0.00004, $R^2 = 0$, $p = 0.99$). The percentage of carnivory showed a negative correlation (estimate = −0.0024, $R^2 = 0.31$, $p = 0.019$) with solar radiation (Figure 5A) but did not have a significant correlation with the other variables: forest (estimate = 0.002, $R^2 = 0.02$, $p = 0.542$), distance to touristic sites (estimate = 0.0003, $R^2 = 0.005$, $p = 0.768$), and human footprint (estimate = 0.0004, $R^2 = 0.015$, $p = 0.634$).

Discussion

The combination of extreme environmental conditions and human activities can strongly and differentially affect biological communities as well as individual species within ecosystems (Degen 2012; Suraci *et al.* 2021). This study provides evidence of how mammals and terrestrial birds in drylands are affected by the stringent environment of Tatacoa Desert drylands in Colombia and how particular life-history traits can modulate the way species respond to environmental and anthropological pressures.

At the assemblage level, forest cover did not have a significant effect on occupancy. Solar radiation was negatively associated suggesting a strong influence of environmental stress (heat) and affecting the spatial configuration of species occurrence
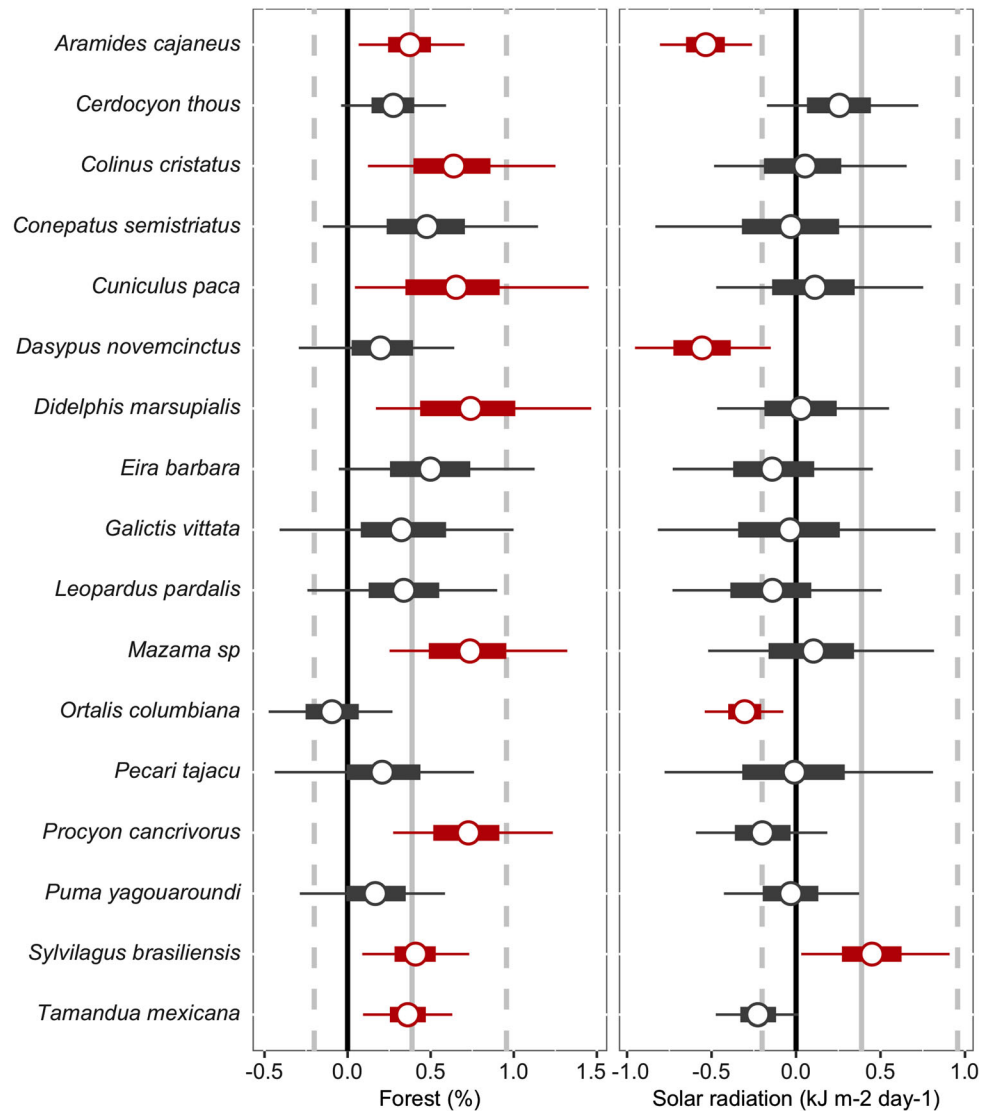
Figure 3. Assemblage and species-level responses of detection (standardize beta coefficients) to (from right to left) forest cover and solar radiation. Lines represent posterior mean and 95% Bayesian credible intervals (BCI) of the assemblage mean hyperparameter, white dots show the posterior mean for each species, lines and bars show the 95% and 50% BCIs, respectively. The species 95% BCIs that do not overlap zero are colored in red.

throughout the landscape (Allen *et al.* 2015; de Gabriel Hernando *et al.* 2021; Gibson *et al.* 2004). The assemblage responded positively to the distance to touristic sites, possibly as a general pattern in which the species avoid contact with humans due to negative interactions. This behavior has been reported in several studies, where mammals tend to avoid touristic roads or even change their occurrence pattern after touristic activities (Barcelos *et al.* 2022; LI *et al.* 2015). Regarding the human footprint, the association with assemblage occupancy was negative, a pattern that has been widely documented for mammals in different ecosystems around the world (Hill *et al.* 2020; Nickel *et al.* 2020; Thatte *et al.* 2020; Toews 2016; Toews *et al.* 2018). Overall, these results highlight the vulnerability of terrestrial vertebrate communities living in extreme ecosystems, areas with intense human activity, or both.

At the species level, the percentage of forest cover had a differential effect. The occupancy of several species such as the lowland paca (*Cuniculus paca*), the common opossum (*Didelphis marsupialis*), and the forest cottontail (*Sylvilagus brasiliensis*) was not influenced by forest cover. The Colombian chachalaca (*O. columbiana*) had a negative association with forest cover, and we found a strong and positive association between forest

cover and the occupancy of large species in the assemblage, the deer (*Mazama* sp.) and the collared peccary (*Pecari tajacu*) (Figure 2). This result evidence the importance of forest as refugia for these large and herbivores/omnivores animals (Gálvez *et al.* 2013; Keuroghlian *et al.* 2015; Rios *et al.* 2021; Torres *et al.* 2014). Solar radiation had a negative effect on all species and a significant effect on 12 out of 17 species sample in this study being the most influential variable in the model. Distance to touristic sites had a significant effect for four species: crab-eating fox (*Cerdocyon thous*), ocelot (*Leopardus pardalis*), deer (*Mazama* sp.), and crab-eating raccoon (*Procyon cancrivorus*), probably because they are highly affected by activities in these areas, such as hunting, vehicle movement, and the presence of domestic species (Bogoni *et al.* 2022; Ménard *et al.* 2014; Salvatori *et al.* 2023). Human footprint, an index that summarizes several human activities (Ayram *et al.* 2020), had a negative influence over all of species, being significant for four of them: Crested bobwhite (*Colinus cristatus*), crab-eating raccoon (*Procyon cancrivorus*), jaguarundi (*Puma yagouaroundi*), and lesser anteater (*Tamandua mexicana*). This pattern may reflect the direct impact of human activities on the presence of these species in the landscape, possibly due to increased mortality of individuals interacting in spaces with greater human activity
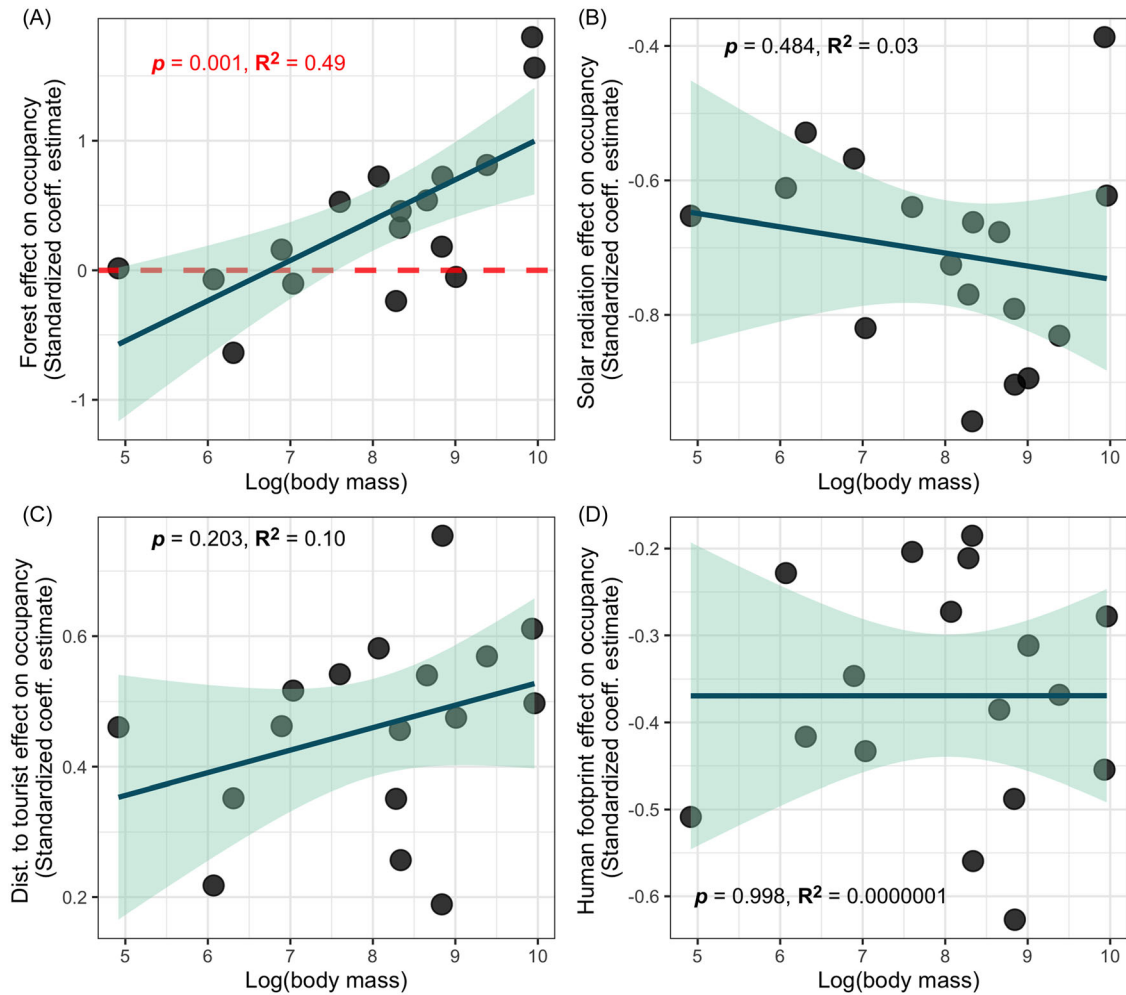
Figure 4. Relationship between body mass and the occupancy responses of the species to landscape covariates. (A) Forest effect on occupancy (the red dashed line represents the zero value), (B) solar radiation effect on occupancy, (C) distance to tourist sites effect on occupancy, (D) human footprint effect on occupancy.

(higher values of the human footprint index). Hill *et al.* (2020) found that mammal mortality caused by human activities, such as hunting or roadkill, is positively correlated with higher values of a human footprint index, and that mortality increases in animals with greater longevity. Presumably, our results reflect higher mortality rates in areas with greater human impact.

We found a positive relationship between the body mass and the forest effect on occupancy (Figure 4A), evidencing that animals rely more strongly on forest cover at the Tatacoa drylands. We also found a negative relationship between the percentage of carnivory and solar radiation effect on occupancy (Figure 5B), suggesting that in hot and arid ecosystems, it is difficult for predators to prevail, due to limitations in prey in open areas with higher solar exposition. These patterns partially support our hypothesis, in which more carnivorous species are negatively affected by extreme environmental conditions; however, our hypothesis posits that more carnivorous animals would be negatively affected in areas with intense human activity, but we did not find support.

Some studies in arid ecosystem have also highlighted how animal body size and diet are affected by the landscape conditions. For example, Rich *et al.* (2016) found that the influence of protected areas over mammals and ground-dwelling birds occupancy was particularly strong for large herbivore species, and also, that the presence of grasslands and floodplains had a

positive influence on the occupancy of large carnivore species. Another study in South Africa compared the occupancy of mammals and ground-dwelling birds in protected areas compared to private agricultural land and found that the occupancy of herbivores and large species was higher within the protected area, while in agricultural land there was a predominant occurrence of insectivores and smaller species (Drouilly *et al.* 2018).

In terms of human activity, our model evidenced, at the assemblage and species level, the variables negatively affected the occupancy probabilities. However, neither body mass nor the percentage of carnivory was associated with the magnitude of the effect on occupancy from human activity variables. Contrarily, Suraci *et al.* (2021) found that in places with the presence of humans and higher values of human footprint, there is a higher probability of finding smaller, less carnivorous, and fast-reproducing species, thus highlighting the importance of these traits to predict the response of communities to human activity.

Our study evidence that in arid ecosystems, a combination of extreme environmental conditions and human activity influences the assemblage's composition and that some life-history traits can be useful to predict the potential response of ground-dwelling birds and mammals to the global scenario of habitat transformation and climate change. Particularly, at the Tatacoa drylands, the larger and the more carnivore species may find it more difficult to persist due
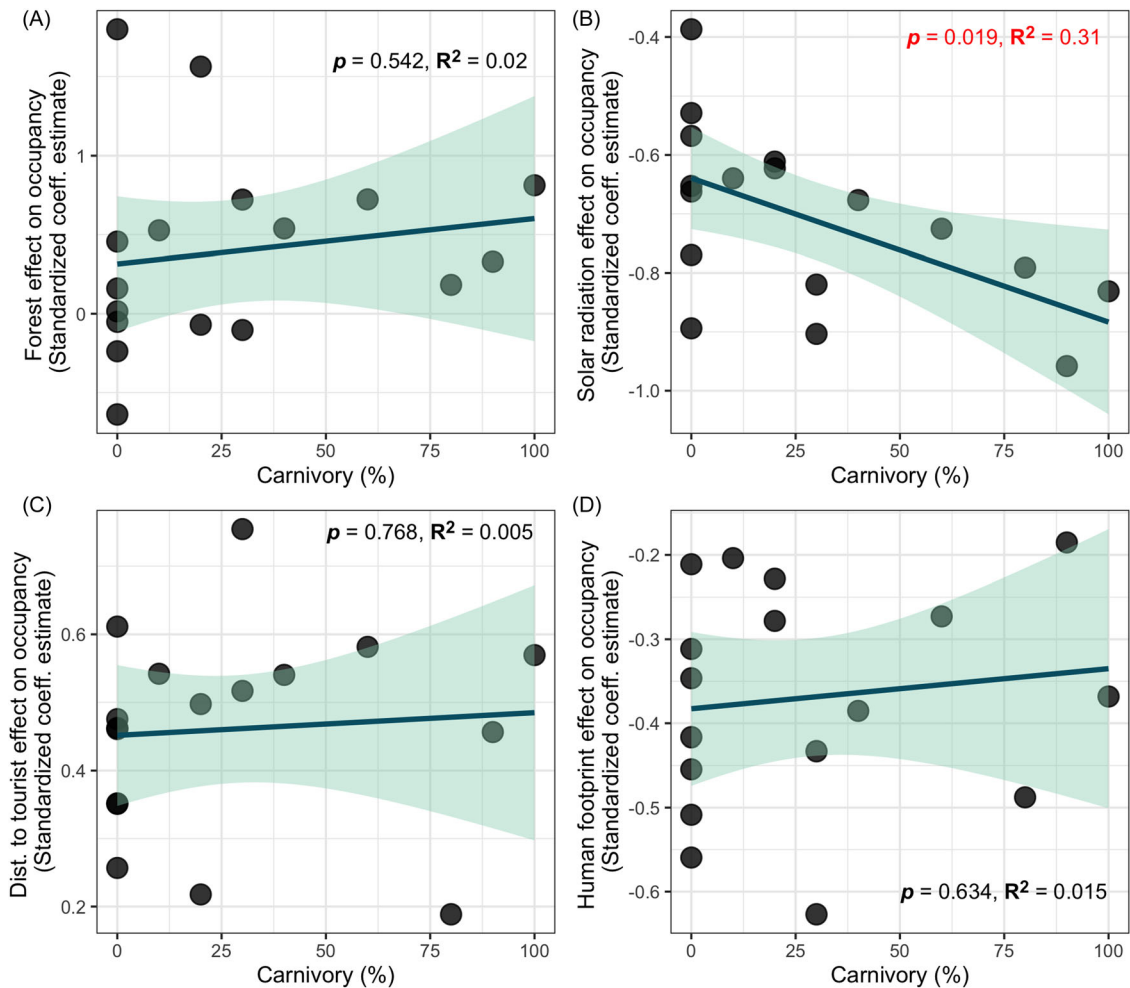
Figure 5. Relationship between percentage of carnivory and the occupancy responses of the species to landscape covariates. (A) Forest effect on occupancy, (B) solar radiation effect on occupancy, (C) distance to tourist sites effect on occupancy, (D) human footprint effect on occupancy.

to sparse forest cover and intense solar radiation. Finally, these results can be used to plan the conservation management of other forested areas within the Magdalena River Valley that are being transformed into fragmented and arid landscapes due to intense human-made disturbances (de Luna Uribe 2017; Marín Valencia *et al.* 2018; Meza-Joya *et al.* 2019).

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