Forest cover is more important than its integrity or configuration of the landscape in determining the habitat use of mammals in a modified landscape in Colombia

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Abstract

Human activities shape the structure of landscapes in different ways and hence modify animal communities depending on the type and intensity of these activities. Here, we used a multispecies occupancy model (MSOM) to understand mammalian habitat use patterns across a mosaic of tropical dry forest in Colombia and elucidate whether forest cover is more important than its integrity and other landscape configuration metrics. Surprisingly, our data suggest that none of the factors (including forest integrity) had a substantial effect on the mean community habitat use or species richness of mammals across the Montes de Maria, and there was no strong evidence to suggest any particular pattern in the distribution of functional groups in the landscapes. However, the percentage of forest cover was substantially important for herbivores, and consistently showed a moderate effect on the entire community, carnivores guild some individual species. There was high variability in the responses of each species to the examined variables that hinder us from broad generalizations, but in general, we also detected a moderate positive effect of forest cover in both diet specialists and generalists and species with small home ranges. Omnivores, on the other hand, tended to occupy more heterogeneous sites (moderate positive effects). The lack of substantial effects on most species and the absence of threatened species across this anthropogenic landscape suggests that the current community is composed of species tolerant to habitat modifications, but not only diet generalist species. This is most likely due to a long filtering process caused by land use transformation. However, our results highlight the relevance of conserving forest patches regardless of their level of modification or any other landscape attributes for maintaining assemblages of mammals.

Keywords: Fragmentation, multispecies occupancy model, Montes de María, forest integrity,

1. Introduction

Habitat loss and fragmentation (splitting of habitats, sensu (Fahrig, 2003) are well-known consequences of human activities that strongly affect biodiversity and ecosystem function in different ways (Crooks et al., 2017; Dirzo et al., 2014; Laurance et al., 2014). Human activities negatively affect most species by limiting their movements and creating ecological traps with an elevated risk of mortality of rare and specialized species (Battin, 2004) and reducing species richness and abundance (Deere et al., 2020; Fahrig, 2003). Mammals, for example, are among the most threatened groups by the above human-driven processes (Ceballos et al., 2017). However, other species have adapted to anthropogenic landscapes, with some even thriving in agroecosystems (Pardo, Campbell, et al., 2018) or urban environments (Hansen et al., 2020).

Therefore, understanding how and which animal species persist in disturbed landscapes is important not only for protecting rare populations or controlling potential problematic species but also because of their functional roles in the ecosystem.

Biodiversity analysis has primarily focused on either species richness or the abundance of specific species. Although these approaches provide important indications of the system's state, species richness alone is limited as an indicator of biodiversity change because the identities and specific species responses are not accounted for (Hillebrand et al., 2017; Pardo, Campbell, et al., 2018). On the other hand, diversity includes other important aspects, such as the trophic structure, functional traits or phylogenetic relationships of species, and the distribution of individuals within a community across the landscape (Noss, 1990). Functional diversity, in particular, is a recently popular metric that allows us to understand how the biological traits of species such as trophic level or guild and phylogenetic relationships, among others, influence the functioning of ecosystems (Tilman, 2001). This aspect has been extensively studied in birds and to a lesser extent in mammalian communities. Although there is increasing information about trait types for mammals (Jones et al., 2009; Wilman et al., 2014), the relationship between these traits and responses to environmental variables is still little explored, especially in anthropogenic landscapes with growing human pressures.

The effect of fragmentation processes or land use change affects not only taxonomic level parameters such as species richness but also other components such as the trophic structure of a community, functional traits, distribution of populations, or species interactions among other processes (Magioli et al., 2016; Morris, 2010). In consequence, anthropogenic pressures tend to homogenize vertebrate communities by a filtering mechanism which can result in communities mainly consisting of tolerant generalist species with wide niche breaths or reduced functional traits and networks (McKinney & Lockwood, 1999; Püttker et al., 2015). For example, some studies have found that the body mass of small mammals tends to be lower in disturbed/fragmented habitats than in undisturbed habitats (Lomolino & Perault, 2007). Similarly, infrastructure promotes smaller species with less carnivorous diets(Li et al., 2021; Suraci et al., 2021). Therefore, in human-dominated landscapes (HDLs), the responses of species to abiotic and biotic factors determine which species persist in the landscape, and responses of individual species can be very different, even within the same dietary group or similar traits (Burton et al., 2012).

Mammals play important roles as herbivores, predators, ecosystem engineers, and keystone species (Lacher et al., 2019). Therefore, understanding how communities in anthropogenic landscapes are structured and which traits are potentially disappearing will help us to anticipate potential ecological consequences on ecosystem functioning and evolutionary processes. Recently, important discussions have taken place regarding which factors are more important. In particular, whether quality or quantity is more important for species distribution or survival. Regolin et al., (2021), for example, suggest that quality is more important than forest cover for the habitat use of some neotropical mammals. On the other hand, Fahrig, (2003) suggests in her “habitat amount hypothesis” that the quantity of forest cover (not the number of patches or individual size) is more important regardless of the configuration of the system, while Zungu et al. (2020) found that both habitat amount and its spatial configuration were important for the occurrence of mammals. Since all responses can vary locally and depending on the intensity of habitat modification, it is important to assess these relationships in different contexts or biomes.

The Colombian Caribbean is a region that faces great conservation challenges, particularly in the current post-conflict (Negret et al., 2019), where deforestation, agriculture, livestock, illegal activities, and

unauthorized burning have increased considerably(Etter et al., 2008). These processes have had an important effect on the relationships between species and the functioning of the original ecosystems. In fact, Colombia has lost around 92% of the original dry forest (lowland forest with high strong rainfall pattern), and only fragmented areas remain (Garcia et al., 2014). The Caribbean region, in particular, has lost about 45% of the original dry forest. As such, the "Montes de Maria" region, is one of the most important regions for biodiversity in the Caribbean and Colombia since it is one of the last few places where some patches of Tropical Dry Forest still present, despite the heavy transformation of most areas and social conflicts (Garcia et al., 2014). Due to its social and ecological importance, current conservation efforts coincide in that one of the largest gaps of information for decision-making is understanding the relationship between fauna and its habitats and its repercussions on ecosystem services (Norden et al., 2020). Understanding which landscape factors are more important than others helps to inform conservation practice. For example, whether efforts in restoration should focus on quality or amount of habitat to promote conservation.

In this paper, we aim to understand how the structure of a human-modified landscape and forest integrity influence species richness and habitat use of mid and large-sized mammals in Montes de Maria. Specifically, we were interested in understanding how the entire community, three functional traits, and individual species respond to: **1)** forest integrity as an index of anthropogenic alteration of this ecosystem or quality, **2)** forest cover as a measure of habitat availability, **3)** conditional entropy as a measure of heterogeneity or complexity of the landscape and **4)** core area metric as a measure of configuration. Based on current evidence, we hypothesized that most species occurring in this disturbed region would not be drastically affected by fragmentation per se due to a long human selective pressure (filtering) which would have resulted in only tolerant species occupying this region. However, the probability of use of species would be mostly dependent on the percentage of the available forest as suggested by the habitat amount hypothesis (Fahrig, 2003). As such, we predicted that the percentage of forest cover will have stronger effects than metrics of configuration and integrity. However, these responses would vary among species and functional groups, with more sensitive species or specialized guilds being more dependent on the integrity of the forest.

2. Methods

2.1. Study Area

The study area corresponds to the Montes de María subregion in the Colombian Caribbean, encompassing the areas between the municipalities of San Juan Nepomuceno (Department of Bolivar) and Colosó in the Department of Sucre (Geographic coverage: minimum latitude and minimum longitude [9.5, -75.37], maximum latitude and maximum longitude [10.04, -75.05], Fig.1). The area is a heterogeneous anthropogenic landscape with Tropical Dry Forest fragments in a state of succession, shrubby vegetation, permanent and seasonal small holding agricultural crops (ñame, cacao, teak, oil palm, tobacco, other fruits), deforested areas for ranching activity, and associated ecosystems such as swamps, lagoons, pipes and groundwater. Montes de María was one of the regions of Colombia where the biodiversity has been significantly altered since the past century, as a result of habitat loss and fragmentation and illegal wildlife trade, Montes de María was one of the regions of Colombia where the armed conflict was experienced more severely due to the confluence of multiple armed actors who disputed control of the territory.

2.2. Data Collection

We surveyed 89 sites across the Magdalena Medio region using a single camera trap per site (Bushnell 24MP Aggressor Low Glow HD) from July to September 2018. Before deploying the cameras, we divided the study area into several 1200 ha hexagon-shaped polygons representing a gradient of forest cover (Fig. 1) using ArcGis (ESRI, 2011). Although we planned to survey the entire area, due to security concerns and access difficulties in certain areas, we selected 12 hexagons for analysis. These units were distributed in the two sectors, the North covering approximately 13,203 ha (outermost sites) and the South covering 6,434 ha. The north area is close to Los Colorados Fauna and Flora Sanctuary, while sites in the southern part are near a small regional protective forest (Serranía de Coraza Protective Forest Reserve). We used a systematic design with the selection of the initial point randomly and camera traps placed at least 1 km from each other and cameras were left in the field for 60 days. No bait was used, and cameras were placed facing evidence of animal activity (e.g. trails, footprints, faeces, among others) including in some circumstances human-made trails. We secured the cameras to trees at a height of 30-60 cm and were programmed in hybrid mode to take (photos and videos) with 2-second capture intervals, high sensor sensitivity, night vision, and 24-hour functionality.

2.3. Landscape Features

We used four covariates that we hypothesized could have an important effect on species response: Forest Landscape Integrity Index (FLII) which shows the conservation status of the forest by measuring the degree of forest modification for the beginning of 2019 (Grantham et al., 2020), and hence, here we used it as an index of forest quality. Forest cover (FOREST) as a measure o forest amount, Conditional Entropy (ENTROPY), and the Coefficient of variation of the core area (COREAREA), both as measures for configuration of the landscape (complexity and patch shape/area, respectively). We generated a mask, composed of a buffer of 500 m radius around each camera trap (i.e. landscapes of 78 ha), which was overlapped on each covariate to extract the average of the values inside the buffer. FLII works with observed pressures, inferred pressures and loss of forest connectivity, and the resulting layer has a spatial resolution of 300 m, ranging from 0 to 10, and the NA zones are non-forest zones defined. The higher values of FLII represent the forest with the greater integrity (i.e. the degree to which its structure, composition and function have been modified by anthropogenic actions; sensu Parrish et al., 2003). Two components of this index (observed human pressures and inferred human pressures) represent the human footprint that influences the integrity of forests, such as current land use, population density, intervention time, distance to roads, and a forest-adjusted biomass index (The value used corresponded to the average of these values inside the buffer).

Forest cover is simply the percentage of forest cover within the buffer. Entropy represents the complexity of the configuration of a spatial pattern. If the value of the conditional entropy is low, the cells of one category have adjacent cells predominantly of one category. However, if the value is high, it means that cells from one category have adjacent cells from many categories (Nowosad & Stepinski, 2019). Core area describes patch area and shape simultaneously (more core area when the patch is large and the shape is rather compact, i.e. a square) (Hesselbarth et al., 2019). To calculate the above variables, we used the Corine Land cover shapefiles for Colombia (IDEAM, 2018), which is available at a 30 m resolution. Landscape variables were calculated and extracted with ArcGIS® and the software R (R Core Team, 2020) using the package Landscape metrics (Hesselbarth et al., 2019). We also considered six other landscape variables (Mean edge density of forest classes, Simpson's Landscape Diversity Index, percentage of agriculture,

mesh size, Simpson evenness, and Shannon entropy but were omitted from the analysis due to multicollinearity issues (Spearman´s rank correlation coefficient >70%).

2.4. Traits Responses

We analyzed the responses to the above covariates at the community level, individual species level as well as three functional groups or traits (trophic guild, diet breadth, and home range) using a multi-species occupancy framework, (see section 2.5). To determine the trophic guild of mammals, we used the EltonTraits database (Wilman et al., 2014) to determine the percentage of food items consumed by each species (e.g, plant material, grass, vertebrates, etc.). Once these percentages were annotated, we classified the species into four guilds following (Oberosler et al., 2019) approach: (1) carnivore (>50% of diet based on vertebrates), (2) herbivorous (includes herbivores, browsers, granivores, and frugivores, with >50% plant material), (3) insectivorous (>50% invertebrates), (4) omnivorous (usually both plant and animal material).

To determine the diet breadth, we reclassified the PanTHERIA database (Jones et al., 2009) into wider categories for ease of analysis. Original values indicated a range of diet breadth from 1-7, so we redistributed this into only two categories: narrow diet (1-3), representing specialist species, and wide diet (4-7), representing more generalist diet species. Diet breadth is the number of dietary categories eaten by each species measured using any qualitative or quantitative dietary measure over any period of time, using any assessment method, for non-captive or non-provisioned populations; adult or age-unspecified individuals, male, female, or sex-unspecified individuals; primary, secondary, or extrapolated sources; all measures of central tendency; in all localities (Jones et al 2009). Categories were defined as vertebrate, invertebrate, fruit, flowers/nectar/pollen, leaves/branches/bark, seeds, grass, and roots/tubers.

For determining the home range categories, we also used the Elton Traits Database. It is defined as the size of the area (in Km^2) within which everyday activities of individuals or groups (of any type) are typically restricted, estimated by either direct observation, radio telemetry, trapping or unspecified methods over any duration of time, using non-captive populations; male, female, or sex unspecified individuals; primary, secondary, or extrapolated sources; all measures of central tendency; in all localities (Jones et al. 2009). When there was some doubt about the species' identity because some photos could not be identified to species level, we used the species closest relative or the genus (e.g. "*Mazama* sp" and "*Coendu* sp").

2.5. Modeling Framework

We analyzed the variation of species richness and occupancy (state variables) across the Montes de Maria region using the Bayesian hierarchical multi-species occupancy models (MSOM) as described by (R. Dorazio & Royle, 2005) with data augmentation to estimate species richness (see also Dorazio et al., 2006; Zipkin et al., 2010). This approach permits to assess the occurrence probabilities for multiple species within a community at the same time while accounting for detection probabilities. Since the parameters for each species are treated as random effects (i.e. species effects drawn from community-level distribution), using prior distributions and the hyperparameters of those priors to represent a community mean response, the approach is robust for reducing the bias in the inferences due to false-negative measurement errors. This helps to improve inferences for rare species with low detections due to the shrinkage or the borrowing of information by individuals across the community (Kéry & Royle, 2016). However, this also introduces a degree of bias to the estimates since species infrequently detected will be drawn more toward the

community average. We did not filter rare species from the community as we did not want to lose species from the different functional groups we were examining and therefore suggest caution in interpreting the individual species-specific occupancy associations of species with less than five detections or detected in less than 10% of the sites (i.e. Cougar– *Puma concolor*, Brown-eared woolly opossum– Caluromys lanatus, Brown four-eyed opossum– *Metachirus nudicaudatus*, Greater grison– *Galictis vittata*, Margay– *Leopardus wiedii*, Eastern cottontail–*Sylvilagus floridanus*, coendu–*Coendou* sp). The observed data (Y_{ij}) corresponds to the number of sampling occasions out of a total of k_j sampling occasions that species *i* was detected at camera station *j*. We grouped the detections per day into 10 sampling occasions. Only species detected at least on two sampling occasions were included (MacKenzie, 2006). Prior to modeling, we examined collinearity (Spearman´s rank correlation coefficient >70%) and standardized covariates (subtracting the mean and dividing by the standard deviation).

Model Formulation

In MSOM, the occurrence state (ψ) is modeled as a Bernoulli process, $z_{i,j} \sim \text{Bern}(\psi_{i,j})$, where z represents the detection not detection data and $\psi_{i,j}$ represent the latent occupancy state of species i at site j. The detection probability (observation process) is estimated within another hierarchical component as a function of k surveys or visits with a second Bernoulli process, $x_{i,j,k} \sim \text{Bern}(p_{i,j,k} * z_{i,j})$, where $x_{i,j,k}$ represents the observed detection histories, and $p_{i,j,k}$ is the detection probability of species i for temporal replicate k at site j, conditional on species presence ($z_{i,j} = 1$)" (Zipkin et al., 2010).The model assumes that variation in the abundance of a species across sampling sites does not affect species detection probabilities $p_{i,j,k}$. We used the four landscape variables described above for the occupancy parameter (ψ) and camera days (EFFORT) for the detection probabilities (i.e. the number of days the camera was active).

The occupancy model includes an intercept term, a species-specific random effect with varying intercepts and slopes as a function of the covariates. Since there was some clustering in the design, we used Random effects to account for potential lack of independence around nearby cameras within hexagons and zone (North and South). For the zone, we used Half-Cauchy prior used on zonal random effect to account for low number of factor levels (N=2). These two zones can represent different situations, with the north area being more conserved than the south area, and therefore could be used as a proxy for "conservation status". We used the posterior draws to estimate the effect of the variables on functional groups (trophic guild, diet breadth, and home range)

Occupancy model (ecological process):

$$Logit(\psi_{i,j}) = \mu_{i,j} + \alpha_{1,i} FLII_j + \alpha_{2,i} FOREST_j + \alpha_{3,i} ENTROPY_j + \alpha_{4,i} COREAREA_j$$

Observational model (Detection):

$$Logit(p_{i,j,k}) = \upsilon_{i,j} + \beta_{1,i} EFFORT_j$$

Where, μ and υ refer to the intercept terms for the occupancy and detection probability models respectively. αj denotes a logit-scale parameter for the mean probability of occurrence among all species at site j, and βj denotes a logit-scale parameter for the mean probability of detection among all species at site j (see Dorazio & Royle, 2005)). All models were constructed using informative priors and we considered variables to have a strong or substantial effect (significant) if parameter estimates (means) credible intervals (BCIs) at 95%

did not overlap zero, and considered a moderate effect if BCIs at 75% did not overlap zero. All analyses were performed in R (R Development Core Team, 2014) using JAGS via the 'jagsUI' package (Kellner, 2021), applying three parallel MCMC chains (nc), with 150,000 iterations (ni), removing the first 50,000 as a period of burn-in (nb), posterior chains were thinned by 100 (nt). We used the Gelman diagnostic plots to assess model convergence visually (Gelman et al., 1996). We further used two measures of model fit for the posterior predictive distribution using the lack of fit statistic (chat) and Bayesian P value (Bpv) with quantities close to 0.5 indicating adequate model fit, while $0.05 < P > 0.95$ indicative of poor model fit.

Species Richness

We used data augmentation as described by (Kéry & Royle, 2016) to estimate species richness of the entire community as a derived parameter. We assume there could be around 46 terrestrial mammal species detectable by camera trapping in the study area. Since we analyzed 21 species, we use M ("true" species) = 46 minus n (observed species) as our data augmentation parameter (25 potential not detected species). Implementation of the model with a uniform prior is done by augmenting the data set with M-n all-zero encounter histories. Then the model for the augmented data set is a zero-inflated version of a model where the actual number of species in the community (N) is known (see also (Zipkin et al., 2010).

3. Results

With an effort of 5,429 camera days, we collected 49,417 photos from which 20,714 were terrestrial mammals totalizing 27 species. However, the number of species per camera site (landscape) was on average 7 (range: 1-12). Six of these species were omitted from the analysis as they did not meet the criteria or were seen only at one site (i.e. red howler monkey–*Alouatta seniculus*, pygmy squirrel–*Sciurillus pusillus pusillus*, Cotton-top tamarin–*Saguinus Oedipus*, capuchin monkey–*Cebus sp*, red-tailed squirrel–*Notosciurus granatensis*, domestic dog–*Canis lupus familiaris*). The carnivore guild was the most dominant guild, represented by eight species, followed by herbivores with six and omnivores with four species. The most common species (standardized capture frequencies >10) were, in descending order, central American agouti (*Dasyprocta punctata*), eastern cottontail (*Sylvilagus floridanus*), common opossum (*Didelphis marsupialis*), and paca (*Cuniculus paca*), while the less common species (standardized capture frequencies < 4) included 12 species such as cougar (*puma concolor*), greater grison (*Galictis vittata*), brown-eared woolly opossum (*Caluromys lanatus*), yagouaroundi (*Puma yagouaroundi*). Most species used in the analysis are categorized as Least Concern (LC) according to the IUCN red list (https://www.iucnredlist.org/) except for the margay (*Leopardus wiedii*), which is near threatened (NT). Importantly, the primate tamarin is a critically endangered species (CR).

Is forest integrity more important than other landscape attributes in explaining species occupancy and richness?

Surprisingly, none of the factors examined in this study appeared to exert a substantial effect (95% BCI overlap zero) on mammal community occupancy across the Montes de Maria area, including forest cover, which goes in contrast to our predictions and suggests a wide range of differential responses within the community (Fig 2). However, with a credibility level of 75%, we found a moderate positive effect of forest cover on the mean community occupancy, suggesting this is probably the only relatively important driver of species habitat use in the study area. This can be further supported by the greater slope found for this variable compared to the others (mean = 0.36, sd = 0.27, Fig. 3), which were close to zero. The effects of

landscape attributes on species richness were also very weak, as indicated by the slopes or magnitude of the effects (Fig. 4).

How does the landscape influence species according to their traits?

Similar to the results of the entire community, the effect of the variables within the guilds was not strong in general. Forest cover was only substantially important for herbivores, while only a moderate effect was found for carnivores. Similarly, the Conditional Entropy only had a moderate effect on omnivore species (Fig. 5); however, its credible intervals were wide, suggesting caution when generalizing this result. This suggests, once again, that the most important driver was forest cover and that only herbivores and carnivores are the groups where these effects are stronger in the community. When analyzing the effect of the type of dietary breath, our results showed that forest had a moderate effect on both groups (i.e. generalist—wide diets vs specialists—narrow diets), while no effect was found for the remaining variables. Although species with more specialist habits tended to increase habitat use as forest cover increased while generalist species had the opposite tendency (i.e. less likely to occupy landscapes with large forest cover), the magnitude of these responses was small as shown by their slopes (Fig. 6). On the other hand, only forest showed a moderate effect on the occupancy of species with small home ranges. However, the size of the effect (slope) was close to zero, suggesting there are no differences in the habitat use of species depending on their home ranges.

Species-specific responses

Species exhibit different responses to the same factor, varying from negative to positive. However, very few species showed a substantial response to some of the variables. In general, forest cover was the only factor showing a moderate effect in several species, while the association with the other factors was only substantial or moderately important for very few species. For example, FLII had a substantial negative effect only on the lowland paca and crab-eating fox, with two species showing moderate response, crab-eating raccoon (negative) and northern tamandua (positive). Forest was only important for the central agouti, but many species showed a moderate response (crab-eating fox–*Cerdocyon thous*, coendu–*Coendou sp*, lowland paca–*Cuniculus paca*, tayra–*Eira barbara*, greater grison–*Galictis vittata*, ocelot–*Leopardus pardalis*, collared pecari–*Pecari tajacu*, and northern tamandua–*Tamandua mexicana*. Conditional entropy was only important for the crab-eating fox and Core area for the tayra, with three species showing moderate response (naked-tailed armadillo–*Cabassous centralis*, tayra and eastern cotton tail–*Sylvilagus floridanus*) (Fig. 7).

4. Discussion

One of the main purposes of this study was to understand if forest integrity is more important than quantity in determining habitat use of terrestrial mammals across an anthropogenic landscape in Colombia. Surprisingly, our data suggest that none of the factors (including integrity) had a substantial effect (i.e. credible intervals overlapped zero with a confidence of 95%). However, the percentage of forest cover tended to be more important than its integrity in driving species habitat use. This attribute consistently showed a moderate effect on the entire community, some functional groups, and several individual species. As predicted, most species detected in this region were not drastically affected by the fragmentation metrics we used. This is most likely due to a long history of human selective pressure or filtering process which would have resulted in only tolerant species occupying this region at current times (Olden & Leroy Poff, 2004; Püttker et al., 2015). This is further supported by the lack of records of species of conservation concern, such as the jaguar (*Panthera onca*), tapir (*Tapirus terrestris*) or giant anteater (*Myrmecophaga tridactyla*), which have been reported in the region (Chacón-Pacheco et al., 2014; Montenegro et al., 2019),

and confirms the capacity of some species to use landscapes with different levels of alteration and human presence, supporting other studies in anthropogenic landscapes (Boron et al., 2019; Ceballos et al., 2019; Daily et al., 2003; Hansen et al., 2020; Loock et al., 2018; Pardo et al., 2019; Perfecto & Vandermeer, 2008)

Despite the apparent plasticity of species across the study area and the variability of responses, our results highlight the crucial role of forest cover for the presence of mammalian species regardless of its quality or the configuration of the landscape where patches are embedded, especially for herbivore species. The influence of forest size (at patch levels or the entire landscape) compared to forest quality and other aspects, such as configuration, has been an important debate in recent years (see Arroyo-Rodríguez et al., 2020; Villard & Metzger, 2014). Fahrig, (2017), for example, suggests that the amount of forest cover in a landscape is the most important factor for maintaining species richness regardless of the fragmentation process (e.g. geometry, number, area, and location of individual patches; see "habitat amount hypothesis"). Our results align with this hypothesis but in relation to habitat use of a mammalian community since our configuration proxy (e.g. core area, conditional entropy) did not show a substantial nor moderate effect. Interestingly, though, our results show that the effect of the forest was only moderate, except for herbivores.

Another potential reason why there was only a moderate response to forest cover might be related to the quality of the matrix. Although we did not measure the quality of the matrix per se, studies suggest that biodiversity extinction thresholds also depend on the matrix type (Boesing et al., 2018). According to this hypothesis, if the quality of the matrix is good, then the need for more forest cover is less important for maintaining species. Therefore, it is possible that the studied landscape does not have strong connectivity issues, and the matrix might be relatively permeable, allowing animals to move across the sites or patches. This could be partially supported by the effect of the conditional entropy, which was not important, and showed a strong correlation with the edge effect variable. Similarly, the agricultural cover was also correlated with forest, suggesting agriculture is neither an important driver in the landscape. Further, the study area is a mosaic of many different agricultural products such as cocoa, ñame, yuca, and different fruits and vegetables, most of them cultivated at small scales. Evidence suggests that some species are not strongly limited by some of these crops as animals can use them to move across the landscapes, particularly generalist carnivores and deer species (e.g. López-Ramírez et al., 2020; Nogeire et al., 2013). As a matter of fact, 62 interviews conducted in the area showed that people have conflicts with some mammal species such as the tayra, hog-nosed skunks (*conepatus semistratus*), jaguarundi and others (IAvH, 2018). However, a connectivity analysis conducted in the study area suggests that pastures are gaining momentum (IAvH, 2018), which could increase threats to species currently occupying the area.

Functional groups

Evidence suggests that filtering in anthropogenic landscapes leads not just to taxonomic homogenization but the process could also drive genetic and functional homogenization (Olden et al., 2004). In this study, we did not find strong correlates suggesting any differential response of functional groups (diet breath, home range, or trophic group), except for the herbivore guild, which responded strongly to forest cover. These results contradict Regolin et al.,(2021), who found that other proxies of habitat quality (distance to waterbodies and abundance of high shrubs) were more important than habitat amount in determining herbivores and frugivorous mammals' habitat use in the Brazilian Pantanal. It is worth noting that in their study, they also used some proxies for habitat quality at finer scales, such as the proportion of food resources (i.e. plants), while in our study, the proxy for habitat quality is a landscape measure that represents the structural integrity. Similarly, Suraci et al. (2021) found that life history traits were important in a North American landscape, suggesting that human presence and infrastructure promote smaller species with less carnivorous diets. Our study partially supports those findings since the first ten most common species were mainly represented by herbivores (5 of 6 detected), followed by omnivores (1/4), insectivores (2/3), and

finally carnivores (2/8). However, it is also known that carnivores' density is usually lower than those of other trophic levels. Therefore, disentangling whether this composition is caused directly and solely by the landscape structure in the study area requires further investigation.

Other studies have found that species with specialized niches are usually more vulnerable to habitat loss, fragmentation, and other disturbances (Purvis, 2000). Interestingly, in our study, species with wide or narrow diets (generalists and specialists, respectively) did not respond strongly to any of the variables and only showed a moderate response to forest loss, suggesting that species across this landscape are not filtered by their ecological niche. In some regions across the Tropics, insectivores and frugivores mammals exhibit high sensitivity to land-use change and other human disturbances (Rovero et al., 2019). However, in our study area, the effect of the remaining forest was only strong and positive for herbivores. Our results also go in accordance with the findings of (Bedoya-Durán et al., 2021) in the Andean region of Colombia. They examined the influence of some landscape attributes (i.e. land use type, fragmentation, connectivity, and human disturbance) on the occupancy of species within functional groups (i.e. guilds, size, and niche breadth) across privately protected areas and non-protected sites and found no clear effect, but suggest that the occupancy of forest-restricted species and large species tended to be positively related to the proportion of forest at a site. Boron et al., (2019) also found similar weak relationships in a community in the Magdalena Medio in Colombia, except for forest cover that strongly modulated habitat use of species. We did not include species size as we only detected one large species (puma–*Puma concolor*) and two small species (Brown-eared woolly opossum–*Caluromys lanatus*; Brown four-eyed opossum–*Metachirus nudicaudatus*), which were also very rare in the landscape. Forest cover showed a moderate negative influence on carnivores, while it was strong for herbivores. This confirms that carnivores are more tolerant to other land uses and occur in the landscape regardless of their characteristics. Other studies have also documented this tolerance and ecological plasticity of carnivore species, particularly mesocarnivores in anthropogenic landscapes, including foxes (*Cerdocyom thous*) and jaguarundis in industrialized agricultural lands (Pardo et al., 2018, Boron et al., 2019), other heterogeneous landscapes (Daily et al. 2003) and even cities (Hansen et al. 2020).

Although the effect of forest cover was only moderately important in species with small home ranges (CI at 75% did not overlap zero) and not relevant for species with large home ranges, the slopes suggest that species with small dispersion movements are distributed almost evenly in the landscape regardless of the size of the forest. In contrast, species with large home ranges tended to occur more likely in areas with little forest cover with decreasing habitat use when forest cover increased. This was an unexpected finding as species with large home ranges are expected to move across the landscape more easily and regularly. All species with large home ranges were carnivores (tayra, ocelot, margay, jaguarundi, cougar), probably this negative relationship with forest cover might suggest that good quality resources or prey are not restricted to large forest patches, and that small patches might be providing good resources. On the other hand, there could also be a detectability issue. Since carnivores are species with large home ranges, the chances of detecting these species in large forest patches could be lower. This is because there would be more space for them to move freely reducing the likelihood of crossing in front of the cameras, while in small patches the options are more restricted and therefore the chances of being detected by the camera when the animal is nearby are greater. This result on carnivores might suggest that the carnivore species are most likely moving across small patches, either because there are no connectivity issues or because of their capacity to move across different habitat types, including disturbed habitats which could provide food resources (see above paragraph). On the other hand, the fact that omnivore species were more likely to use more spatially heterogeneous landscapes might be related to their plasticity and opportunistic behaviors.

Species-specific responses

When trying to understand which species are mostly driving the occupancy patterns of the community, we found only a few species substantially affected by the landscape covariates, but some contradicted our predictions. For example, we expected that the quality of the forest should substantially drive the occupancy of paca since this is a forest specialist species. Our results confirmed this, but unexpectedly this relationship was found to be negative, while forest cover showed a moderate positive association, highlighting the importance of the quantity of habitat over forest integrity. Since Core Area also had a strong effect, it is apparent that the lowland paca distribution is not affected by edge effect issues, as opposed to the tayra that was strongly and positively affected by this variable and tended to increase habitat use in more homogeneous landscapes. Although tayra is a relatively common species in anthropogenic landscapes, our results highlight that they tend to occupy larger interior habitats inside the forest, which goes in accordance with Bianchi et al. (2021) findings in a heterogeneous landscape in Brazil. The crab-eating fox habitat use was greater in areas with low forest integrity and more heterogeneous composition, confirming its flexibility to move across anthropogenic landscapes (Boron et al., 2019; Pardo et al., 2019). The Central American agouti was clearly positively influenced by forest cover despite its quality which also goes in accordance with other studies, highlighting their dependency on habitat cover (Boron et al., 2019; Pardo, Campbell, et al., 2018). The presence of these forest-restricted species (including those not used in the analysis, see methods) suggests that some vital process such as seed dispersal is still occurring in the area helping to maintain the forest dynamic (see Camargo-Sanabria et al., 2014). However, the absence of large mammals limits the contribution of the present fauna as this group of species has important roles as, for example, the regulatory role of apex predators, and the dispersal of large-seeded plants which limits the growth of large wooded trees and in consequence limits carbon storage capacity of the forest (Bello et al 2015).

Conservation

Some scholars suggest that to design optimal human-modified landscapes for forest biodiversity conservation, forest patches should occupy at least 40% of the landscape and these patches should be embedded in a high-quality matrix or with less agriculture (Arroyo-Rodríguez et al., 2020). Our results support the claim to protect as much forest as possible but suggest that extant species are not restricted to high-quality forests. Therefore, we believe that conservation strategies in the study area should focus on conserving and restoring as much forest as possible without prioritizing its conservation status or quality, configuration of landscape or size/shape of individual patches; at least for non-threatened species, such as those currently found in these transformed landscapes. The strong association of herbivores with forest cover suggests their high vulnerability to the reduction of forest cover, which suggests further attention. This is supported by other studies that highlight the paramount importance of maintaining forest cover along gradients of human land use, given the evidence for stronger negative effects of forest loss on biodiversity in comparison to other factors such as forest configuration or other fragmentation processes per se (see (Fahrig, 2017). In this sense, private conservation could play an important role in anthropogenic landscapes, as evidence suggests that secondary forest or even small patches have important conservation implications (e.g. Fahrig, 2017). Even more, the presence of species of conservation concern such as the margay and the tamarin, confirms the importance of Montes de Maria landscape for the conservation of species.

As suggested by Hulme-Beaman et al. (2016), occupation does not denote dependency or that the species are not facing any threats. It is also possible that apparently stable populations are at their maximum tolerance and some could be experiencing a delayed response to threats (see Semper-pascual et al., 2017). Only a multitemporal analysis could provide insights into the potential conservation risks for the species currently occupying the study area. While some species might have shown tolerance to this landscape, this apparent tolerance might be limited to a certain level of alteration as there are thresholds for these responses, that once passed, the direction and magnitude of these effects could be dangerous ((Pardo, Roque, et al.,

2018; Suraci et al., 2021). Further, future studies should explore the possible impact of hunting and domestic animals in driving species distribution in this landscape, which could even be stronger than landscape measures (Deere et al., 2020). The lack of detection of species of conservation concern (jaguar, tapir, and giant anteater) suggests that they might have undergone local extinction or simply that they are so rare that they went under-detected. However, the area still supports potential prey for large predators (collared peccary, deer, lowland paca, etc.). Since we detected puma (another large predator), it could be speculated that the non-detection of jaguar could be mainly caused by poaching, which is considered one of the main factors threatening this species.

In conclusion, although we did not find strong evidence to suggest any particular pattern in the distribution of functional groups in the landscape, except for herbivores, our results reinforce the need to conserve any type of forested areas for the conservation of mammals regardless of the extend of human-driven modification (integrity) or the current configuration of the surrounding landscapes (fragmentation process). Our multispecies occupancy model allowed us to investigate the entire community, functional groups and species (some of them hard to study on their own due to low detectability) and allowed us to see the heterogeneous responses of mammals to fragmentation processes.

References

Arroyo-Rodríguez, V., Fahrig, L., Tabarelli, M., Watling, J. I., Tischendorf, L., Benchimol, M., Cazetta, E., Faria, D., Leal, I. R., Melo, F. P. L., Morante-Filho, J. C., Santos, B. A., Arasa-Gisbert, R., Arce-Peña, N., Cervantes-López, M. J., Cudney-Valenzuela, S., Galán-Acedo, C., San-José, M., Vieira, I. C. G., … Tscharntke, T. (2020). Designing optimal human-modified landscapes for forest biodiversity conservation. *Ecology Letters*, *23*(9), 1404–1420. https://doi.org/10.1111/ELE.13535

Bedoya-Durán, M. J., Murillo-García, O. E., & Branch, L. C. (2021). Factors outside privately protected areas determine mammal assemblages in a global biodiversity hotspot in the Andes. *Global Ecology and Conservation*, *32*, e01921. https://doi.org/10.1016/J.GECCO.2021.E01921

Bianchi, R., Jenkins, J. M. A., Lesmeister, D. B., Gouvea, J. A., Cesário, C. S., Fornitano, L., de Oliveira, M. Y., de Morais, K. D. R., Ribeiro, R. L. A., & Gompper, M. E. (2021). Tayra (Eira barbara) landscape use as a function of cover types, forest protection, and the presence of puma and free-ranging dogs. *Biotropica*, *53*(6), 1569–1581. https://doi.org/10.1111/BTP.13005

Boesing, A. L., Nichols, E., & Metzger, J. P. (2018). Biodiversity extinction thresholds are modulated by matrix type. *Ecography*, *41*, 1–14. https://doi.org/10.1111/ecog.03365

Boron, V., Deere, N. J., Xofis, P., Link, A., Quiñones-Guerrero, A., Payan, E., & Tzanopoulos, J. (2019). Richness, diversity, and factors influencing occupancy of mammal communities across human-modified landscapes in Colombia. *Biological Conservation*, *232*, 108–116. https://doi.org/10.1016/J.BIOCON.2019.01.030

Burton, A. C., Sam, M. K., Balangtaa, C., & Brashares, J. S. (2012). Hierarchical Multi-Species Modeling of Carnivore Responses to Hunting, Habitat and Prey in a West African Protected Area. *PLoS ONE*, *7*(5), 38007. https://doi.org/10.1371/journal.pone.0038007

Camargo-Sanabria, A. A., Mendoza, E., Guevara, R., Martinez-Ramos, M., & Dirzo, R. (2014). Experimental defaunation of terrestrial mammalian herbivores alters tropical rainforest understorey diversity. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20142580–20142580. https://doi.org/10.1098/rspb.2014.2580

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, *114*(30), E6089–E6096. https://doi.org/10.1073/pnas.1704949114

Ceballos, G., Ehrlich, P. R., Pacheco, J., Valverde-Zúñiga, N., & Daily, G. C. (2019). Conservation in human-dominated landscapes: Lessons from the distribution of the Central American squirrel monkey. *Biological Conservation*, *237*, 41–49. https://doi.org/10.1016/J.BIOCON.2019.06.008

Chacón-Pacheco, J., González-Maya, J. F., & Jimenez, M. A. S. (2014). Reaparición del jaguar (Panthera onca) en el departamento de Sucre, Colombia. *Mammalogy Notes*, *1*(1), 8–9. https://doi.org/10.47603/manovol1n1.8-9

Crooks, K. R., Burdett, C. L., Theobald, D. M., King, S. R. B., di Marco, M., Rondinini, C., & Boitani, L. (2017). Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(29), 7635–7640. https://doi.org/10.1073/pnas.1705769114

Daily, G. C., Ceballos, G., Pacheco, J., Suzán, G., & Sánchez-Azofeifa, A. (2003). Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. *Conservation Biology*, *17*(6), 1814–1826. https://doi.org/10.1111/j.1523-1739.2003.00298.x

Deere, N. J., Guillera-Arroita, G., Platts, P. J., Mitchell, S. L., Baking, E. L., Bernard, H., Haysom, J. K., Reynolds, G., Seaman, D. J. I., Davies, Z. G., & Struebig, M. J. (2020). Implications of zero-deforestation commitments: Forest quality and hunting pressure limit mammal persistence in fragmented tropical landscapes. *Conservation Letters*, *13*(3). https://doi.org/10.1111/CONL.12701

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

Dorazio, R. M., Royle, J. A., Glimska¨r, A., Söderstrom, B., & Glimskär, A. (2006). Estimating species richness and accumulation by modeling species occurrence and detectability. In *Ecology* (Vol. 87, Issue 4).

Dorazio, R., & Royle, A. (2005). Estimating Size and Composition of Biological Communities by Modeling the Occurrence of Species . *Journal of American Statistical Association*, *100*(470), 389–398. https://www.jstor.org/stable/27590563

ESRI. (2011). *ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.*

Etter, A., McAlpine, C., & Possingham, H. (2008). Historical Patterns and Drivers of Landscape Change in Colombia Since 1500: A Regionalized Spatial Approach. *Annals of the Association of American Geographers*, *98*(1), 2–23. https://doi.org/10.1080/00045600701733911

Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Fahrig, L. (2017). Ecological Responses to Habitat Fragmentation Per Se. *Https://Doi.Org/10.1146/Annurev-Ecolsys-110316-022612*, *48*, 1–23. https://doi.org/10.1146/ANNUREV-ECOLSYS-110316-022612

Garcia, H., Corzo, G., Isaacs, P., & Etter, A. (2014). Distribución y estado actual de los remanentes del Bioma de Bosque Seco Tropical en Colombia: Insumos para su gestión. In C. Pizano & H. Garcia (Eds.), *El Bosque Seco Tropical en Colombia* (pp. 228–251). Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH).

Gelman, A., Meng, X.-L., & Stern, H. (1996). Posterior Predictive Assessment of Model Fitness Via Realized Discrepancies. *Statistica Sinica*, *6*, 733–807.

Grantham, H. S., Duncan, A., Evans, T. D., Jones, K. R., Beyer, H. L., Schuster, R., Walston, J., Ray, J. C., Robinson, J. G., Callow, M., Clements, T., Costa, H. M., Degemmis, A., Elsen, P. R., Ervin, J., Franco, P., Goldman, E., Goetz, S., Hansen, A., … Watson, J. E. M. (2020). Anthropogenic modification of forests means only 40% of remaining forests have high ecosystem integrity. *Nature Communications*, *11*, 5978. https://doi.org/10.1038/s41467-020-19493-3

Hansen, C. P., Parsons, A. W., Kays, R., & Millspaugh, J. J. (2020). Does Use of Backyard Resources Explain the Abundance of Urban Wildlife? *Frontiers in Ecology and Evolution*, *8*. https://doi.org/10.3389/FEVO.2020.570771

Hesselbarth, M. H. K., Sciaini, M., With, K. A., Wiegand, K., & Nowosad, J. (2019). landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography*, *42*(10), 1648–1657. https://doi.org/10.1111/ECOG.04617

Hillebrand, H., Blasius, B., Borer, E. T., Chase, J. M., Stanley, W., Downing, J. A., Klemens, B., Christopher, E., Seabloom, E. W., Hodapp, D., Larsen, S., Lewandowska, A. M., Waal, D. B. van de, & Ryabov, A. B. (2017). *Biodiversity change is uncoupled from species richness trends : consequences for conservation and monitoring*. *March*, 1–16. https://doi.org/10.1111/1365-2664.12959

Hulme-Beaman, A., Dobney, K., Cucchi, T., & Searle, J. B. (2016). An Ecological and Evolutionary Framework for Commensalism in Anthropogenic Environments. *Trends in Ecology & Evolution*, *31*(8), 633–645. https://doi.org/10.1016/J.TREE.2016.05.001

IAvH. (2018). *Evaluaciones regionales de biodiversidad para el paisaje montes de maría. STO2-FY18, producto 9.3b, contrato no. AID-514-h-17-00001*.

Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'dell, J., David, C., Orme, L., Safi, K., Sechrest, W., Boakes, E. H., Carbone, C., Connolly, C., Cutts, M. J., Foster, J. K., Grenyer, R., Habib, M., Plaster, C. A., Price, S. A., Rigby, E. A., … Purvis, A. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, *90*(9), 2648–2648. https://doi.org/10.1890/08-1494.1

Kellner, K. (2021). *jagsUI: A Wrapper Around "rjags" to Streamline "JAGS" Analyses*. R package version 1.5.2, <https://CRAN.R-project.org/package=jagsUI> .

Kéry, M., & Royle, J. A. (2016). *Applied Hierarchical Modeling in Ecology:Analysis of distribution, abundance and species richness in R and BUGS*. Academic Press.

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

Laurance, W. F., Sayer, J., & Cassman, K. G. (2014). Agricultural expansion and its impacts on tropical nature. *Trends in Ecology & Evolution*, *29*(2), 107–116. https://doi.org/10.1016/j.tree.2013.12.001

Li, W., Yang, P., Li, B., Liu, C., Sun, L., Li, J., & Jin-Hua Li, C. (2021). Habitat characteristics or protected area size: What is more important for the composition and diversity of mammals in nonprotected areas? *7250 | Ecology and Evolution*, *11*, 7250–7263. https://doi.org/10.1002/ece3.7540

Lomolino, M. v., & Perault, D. R. (2007). Body size variation of mammals in a fragmented, temperate rainforest. *Conservation Biology : The Journal of the Society for Conservation Biology*, *21*(4), 1059–1069. https://doi.org/10.1111/J.1523-1739.2007.00727.X

Loock, D. J. E., Williams, S. T., Emslie, K. W., Matthews, W. S., & Swanepoel, L. H. (2018). High carnivore population density highlights the conservation value of industrialised sites. *Scientific Reports 2018 8:1*, *8*(1), 1–9. https://doi.org/10.1038/s41598-018-34936-0

López-Ramírez, C., Restrepo-Quiroz, T., & Solari Torres, S. (2020). Diversity and ecology of non-volant mammals associated to a cacao agro-productive system, Granja Yariguíes, Santander, Colombia. *Actualidades Biológicas*, *42*(112), 13. https://doi.org/10.17533/UDEA.ACBI.V42N112A01

MacKenzie, D. (2006). Modeling the Probability of Resource Use: The Effect of, and Dealing with, Detecting a Species Imperfectly. *Journal of Wildlife Management*, *70*(2), 367–374. https://doi.org/10.2193/0022-541x(2006)70[367:mtporu]2.0.co;2

Magioli, M., Ferraz, K. M. P. M. de, Setz, E. Z. F., Percequillo, A. R., Rondon, M. V. de S. S., Kuhnen, V. V., Canhoto, M. C. da S., dos Santos, K. E. A., Kanda, C. Z., Fregonezi, G. de L., do Prado, H. A., Ferreira, M. K., Ribeiro, M. C., Villela, P. M. S., Coutinho, L. L., & Rodrigues, M. G. (2016). Connectivity maintain mammal assemblages functional diversity within agricultural and fragmented landscapes. *European Journal of Wildlife Research*, 431–446. https://doi.org/10.1007/s10344-016-1017-x

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, *14*(11), 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

Montenegro, O., López-Arévalo, H., Mora-Beltrán, C., Lizcano, Diego. J., Serrano, Hernán., Mesa, E., & Bonilla-Sánchez, A. (2019). Tropical ungulates of Colombia. In S. Tessaro-Gallina (Ed.), *Tropical ungulates of Colombia. Ecology and Conservation of Tropical Ungulates in Latin America* (pp. 157–195). Springer Nature Switzerland.

Morris, R. J. (2010). Anthropogenic impacts on tropical forest biodiversity: A network structure and ecosystem functioning perspective. In *Philosophical Transactions of the Royal Society B: Biological Sciences* (Vol. 365, Issue 1558, pp. 3709–3718). Royal Society. https://doi.org/10.1098/rstb.2010.0273

Negret, P. J., Sonter, L., Watson, J. E. M., Possingham, H. P., Jones, K. R., Suarez, C., Ochoa-Quintero, J. M., & Maron, M. (2019). Emerging evidence that armed conflict and coca cultivation influence deforestation patterns. *Biological Conservation*, *239*, 108176. https://doi.org/10.1016/J.BIOCON.2019.07.021

Nogeire, T. M., Davis, F. W., Duggan, J. M., Crooks, K. R., & Boydston, E. E. (2013). Carnivore Use of Avocado Orchards across an Agricultural-Wildland Gradient. *PLoS ONE*, *8*(7), 1–6. https://doi.org/10.1371/journal.pone.0068025

Norden, N., González-M., R., Avella-M., A., Salgado-Negret, B., Alcázar, C., Rodríguez-Buriticá, S., Aguilar-Cano, J., Castellanos-Castro, C., Calderón, J. J., Caycedo-Rosales, P., Cuadros, H., Díaz-Pulido, A., Fajardo, Z., Franke-Ante, R., García, D. H., González, M. A., Hernández-Jaramillo, A., Idárraga-Piedrahita, Á., López-Camacho, R., … García, H. (2020). Building a socio-ecological monitoring platform for the comprehensive management of tropical dry forests. *Plants, People, Planet*, *0*, ppp3.10113. https://doi.org/10.1002/ppp3.10113

Noss, R. F. (1990). Indicators for Monitoring Biodiversity: A Hierarchical Approach. *Conservation Biology*, *4*(4), 355–364. https://doi.org/10.1111/j.1523-1739.1990.tb00309.x

Nowosad, J., & Stepinski, T. F. (2019). Information theory as a consistent framework for quantification and classification of landscape patterns. *Landscape Ecology*, *34*(9), 2091–2101. https://doi.org/10.1007/S10980-019-00830-X/FIGURES/2

Oberosler, V., Tenan, S., Zipkin, E. F., & Rovero, F. (2019). Poor management in protected areas is associated with lowered tropical mammal diversity. *Animal Conservation*, acv.12525. https://doi.org/10.1111/acv.12525

Olden, J. D., & Leroy Poff, N. (2004). Clarifying biotic homogenization. *Trends in Ecology & Evolution*, *19*(6), 282–283; author reply 283-4. https://doi.org/10.1016/j.tree.2004.03.024

Olden, J. D., Poff, N. L. R., Douglas, M. R., Douglas, M. E., & Fausch, K. D. (2004). Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology & Evolution*, *19*(1), 18–24. https://doi.org/10.1016/J.TREE.2003.09.010

Pardo, L. E., Campbell, M. J., Cove, M. v., Edwards, W., Clements, G. R., & Laurance, W. F. (2019). Land management strategies can increase oil palm plantation use by some terrestrial mammals in Colombia. *Scientific Reports*, *9*(1), 7812. https://doi.org/10.1038/s41598-019-44288-y

Pardo, L. E., Campbell, M. J., Edwards, W., Clements, G. R., & Laurance, W. F. (2018). Terrestrial mammal responses to oil palm dominated landscapes in Colombia. *PLOS ONE*, *13*(5), e0197539. https://doi.org/10.1371/journal.pone.0197539

Pardo, L. E., Roque, F. de O., Campbell, M. J., Younes, N., Edwards, W., & Laurance, W. F. (2018). Identifying critical limits in oil palm cover for the conservation of terrestrial mammals in Colombia. *Biological Conservation*, *227*, 65–73. https://doi.org/10.1016/J.BIOCON.2018.08.026

Parrish, J. D., Braun, D. P., & Unnasch, R. S. (2003). Are We Conserving What We Say We Are? Measuring Ecological Integrity within Protected Areas. *BioScience*, *53*(9), 851. https://doi.org/10.1641/0006-3568(2003)053[0851:AWCWWS]2.0.CO;2

Perfecto, I., & Vandermeer, J. (2008). Biodiversity Conservation in Tropical Agroecosystems. *Annals of the New York Academy of Sciences*, *1134*(1), 173–200. https://doi.org/10.1196/annals.1439.011

Purvis, A. (2000). Nonrandom Extinction and the Loss of Evolutionary History. *Science*, *288*(5464), 328–330. https://doi.org/10.1126/science.288.5464.328

Püttker, T., de Arruda Bueno, A., Prado, P. I., & Pardini, R. (2015). Ecological filtering or random extinction? Beta-diversity patterns and the importance of niche-based and neutral processes following habitat loss. *Oikos*, *124*(2), 206–215. https://doi.org/10.1111/OIK.01018

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Regolin, L., Oliveira-Santos, G., Ribeiro, M. C., & Bailey, L. L. (2021). Habitat quality, not habitat amount, drives mammalian habitat use in the Brazilian Pantanal. *Landscape Ecology*, *36*, 2519–2533. https://doi.org/10.1007/s10980-021-01280-0

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. (2019). 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

Semper-pascual, A., Macchi, L., Sabatini, F. M., Decarre, J., Baumann, M., Blendinger, P. G., Mastrangelo, M. E., & Kuemmerle, T. (2017). *Mapping extinction debt highlights conservation opportunities for birds and mammals in the South American Chaco*. *December*, 1–12. https://doi.org/10.1111/1365-2664.13074

Suraci, J. P., Gaynor, K. M., Allen, M. L., Alexander, | Peter, Brashares, J. S., Schuttler, S., Çağan, |, Şekercioğlu, H., Shepherd, B., Whipple, L., Whittington, J., Wittemyer, G., Christopher, |, & Wilmers, C. (2021). Disturbance type and species life history predict mammal responses to humans. *Glob Change Biol*, *00*. https://doi.org/10.1111/gcb.15650

Tilman, D. (2001). Functional diversity. In Academic (Ed.), *Encyclopedia of biodiversity* (pp. 109–120).

Villard, M. A., & Metzger, J. P. (2014). Beyond the fragmentation debate: A conceptual model to predict when habitat configuration really matters. *Journal of Applied Ecology*, *51*(2), 309–318. https://doi.org/10.1111/1365-2664.12190

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, *95*(7), 2027–2027. https://doi.org/10.1890/13-1917.1

Zipkin, E. F., Andrew Royle, J., Dawson, D. K., & Bates, S. (2010). Multi-species occurrence models to evaluate the effects of conservation and management actions. *Biological Conservation*, *143*(2), 479–484. https://doi.org/10.1016/J.BIOCON.2009.11.016

Zungu, M. M., Maseko, M. S. T., Kalle, R., Ramesh, T., & Downs, C. T. (2020). Effects of landscape context on mammal richness in the urban forest mosaic of EThekwini Municipality, Durban, South Africa. *Global Ecology and Conservation*, *21*, e00878. https://doi.org/10.1016/J.GECCO.2019.E00878

Figures main text

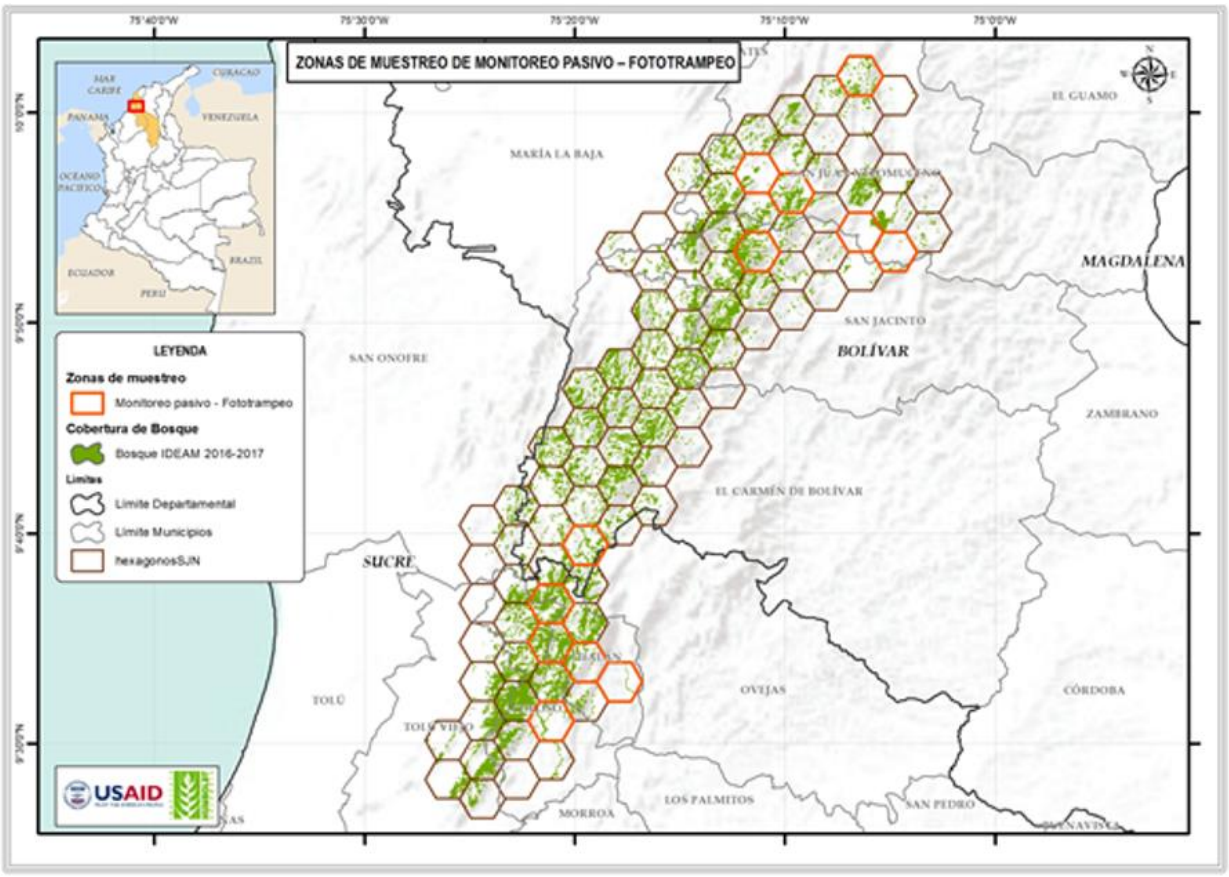

Figure 1. Selected units (in red) where camera traps were deployed in the Montes de María along a gradient of forest cover.

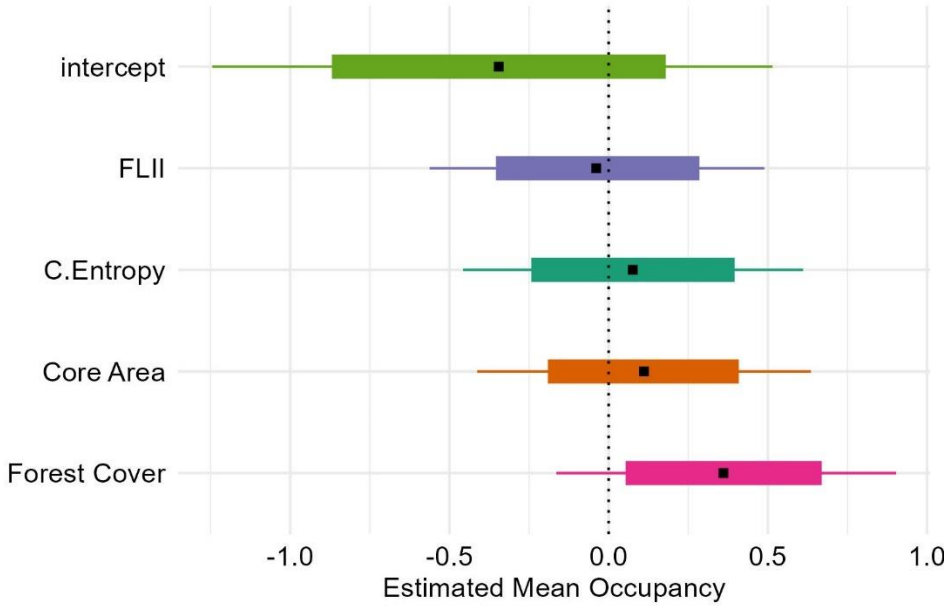

Figure 2. Estimated effect (slopes in logit scale) of the different variables on the mean mammal community occupancy in the Montes de Maria region, Colombia. Small black squares represent the mean, lines the 95% Bayesian Credible Intervals (BCI) and boxes the 75% BCI. Effects were considered substantial if the 95% BCI did not overlap zero and moderate if 75% BCI did not overlap zero.

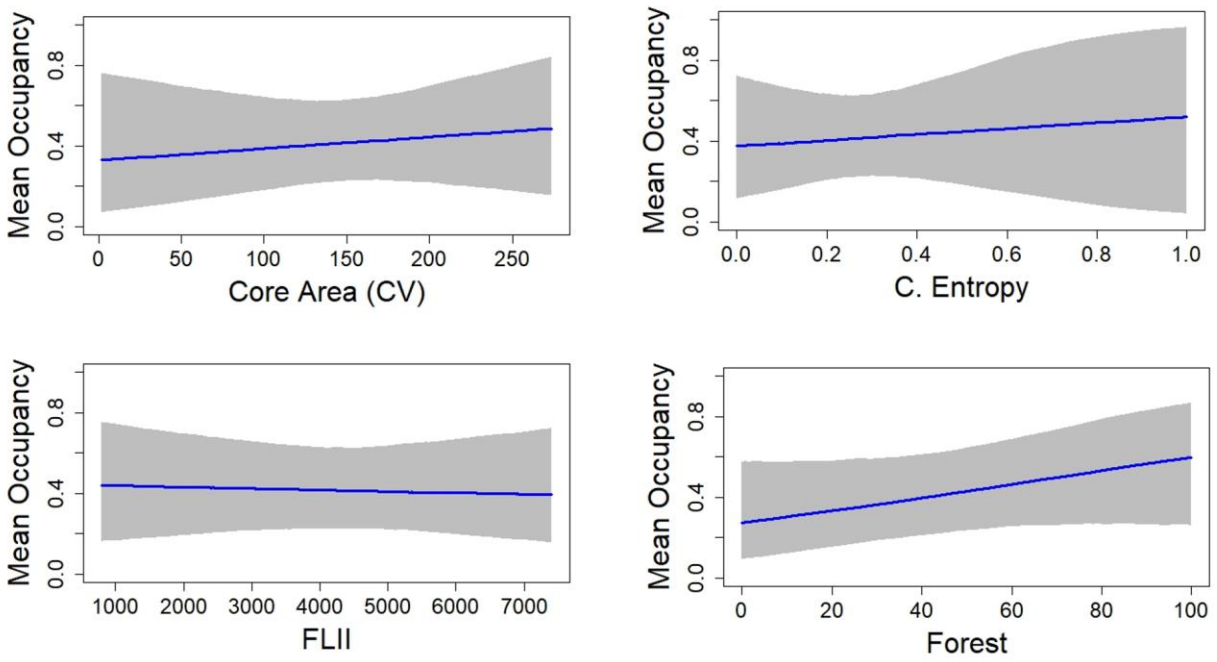

Figure 3. Estimated mean occupancy response of the entire mammal community in relation to four landscape variables in the Montes de Maria region, Colombia. Only forest cover showed a moderate effect.

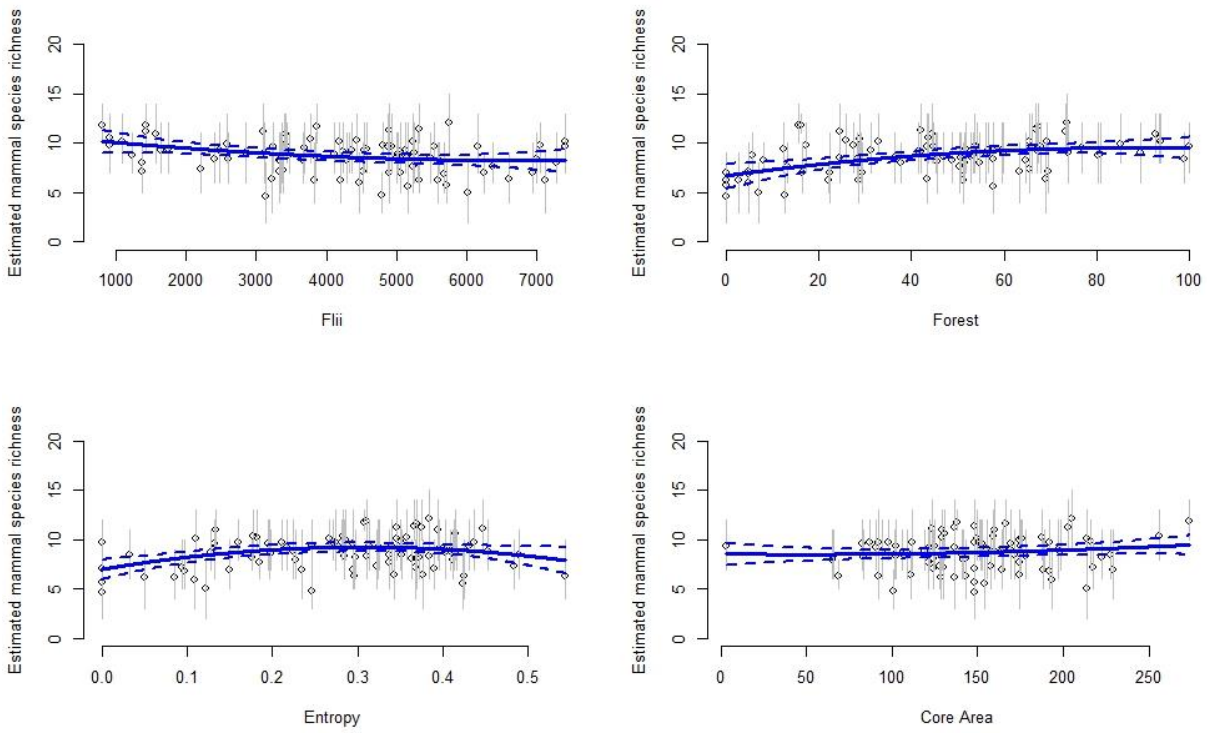

Figure 4. The effect of each landscape variable on estimated site-specific species richness in Montes de Maria, Colombia.

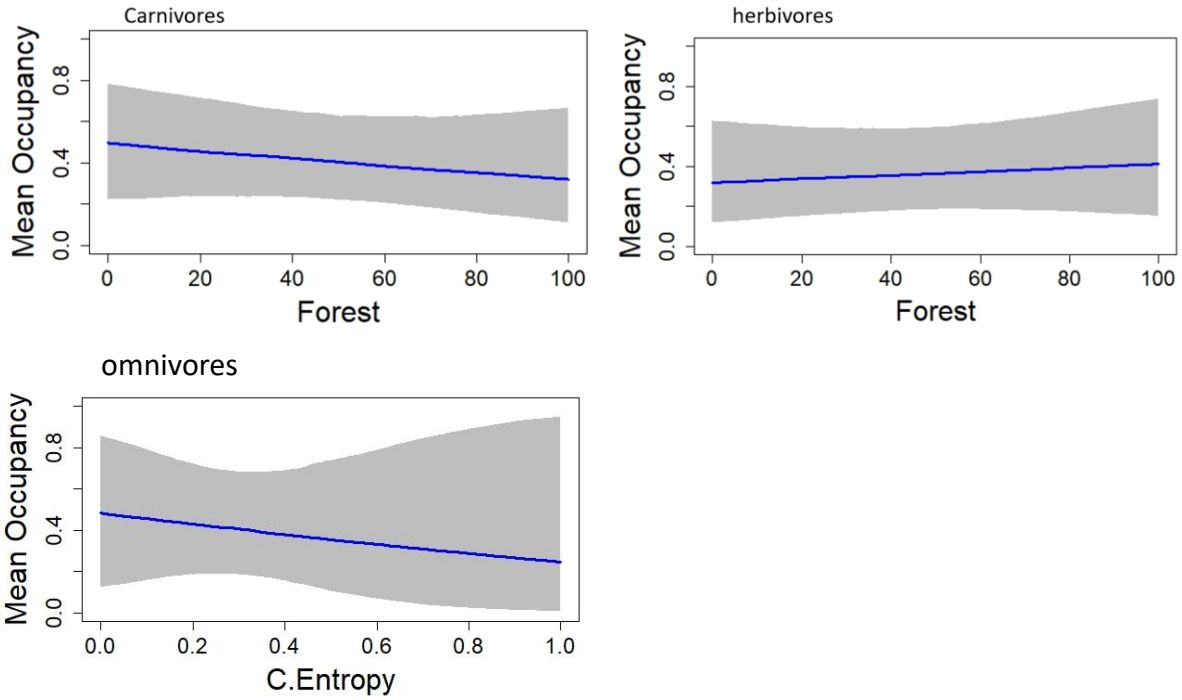

Figure 5. Estimated mean occupancy response of the most important variables on different guilds. Only variables and guilds with substantial and moderate responses are shown. The effect of the forest was only substantial for herbivores, while only a moderate effect was found for carnivores. The Conditional entropy also had a moderate effect on omnivore species.

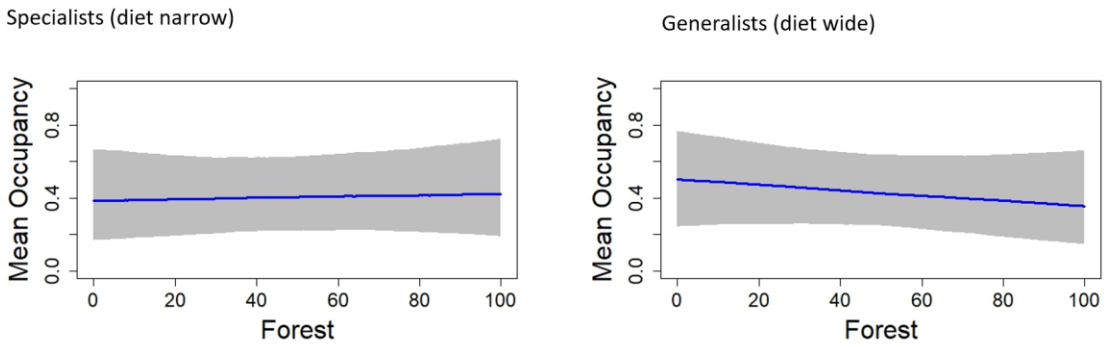

Figure 6. Estimated mean occupancy response of specialist (left) and generalists (right) species to forest cover in the Montes de Maria region, Colombia.

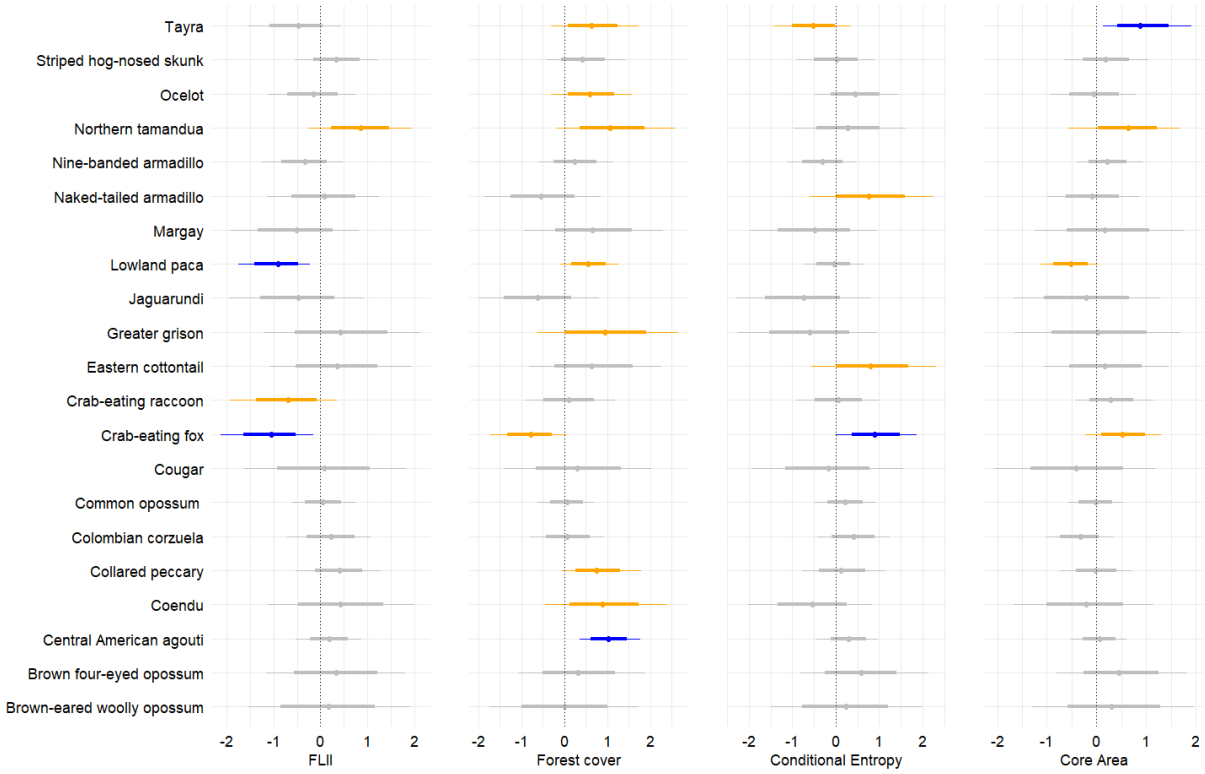

Figure 7. Estimated effect (slopes in logit scale) of the different variables on each species occupancy probability Montes de Maria, Colombia. The plot represents the posterior summaries (mean, 95% and 75% Bayesian Credible Intervals) of the estimated slopes on the logit-linear model for the four covariates in the occupancy (ψ) model. Points represent the mean, lines the 95% Bayesian Credible Intervals (BCI) and boxes the 75% BCI. Effects were considered substantial if the 95% BCI did not overlap zero (blue) and moderate if 75% BCI did not overlap zero (orange).