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Richness, diversity, and factors influencing occupancy of mammal communities across human-modified landscapes in Colombia.

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Highlights

- Agriculture reduces community diversity and evenness, while increases dominance.
- Forests and vicinity to water increase species occupancy; pastures decrease it.
- Forest areas are crucial for pumas, ocelots, raccoons, pacas, and agoutis.
- Wetlands are important for jaguars, the apex predator.
- Key to maintain forests and wetlands and target future crop expansion on pastures.

Abstract

As human-modified landscapes are increasing in the tropics, it becomes critical to understand how they affect mammal communities to reconcile conservation and development. We combined land cover information and camera-trapping data to explore the effects of agricultural expansion on mammals in the Magdalena river valley of Colombia. We estimated species diversity, evenness, and dominance across two agricultural landscapes, modified by cattle ranching and oil palm cultivation. We further assessed which variables influence species- and community-level occupancy using multi-species occupancy models. Results highlight that modified landscapes display lower species richness, diversity and evenness, and higher dominance than more pristine sites. Residual forest cover and distance to water had significant effect on community occupancy (positive and negative respectively). Forests were particularly important for pumas, ocelots, lowland pacas, Central American agoutis, and crab-eating raccoons while wetlands had a positive effect on jaguars, the apex predator in the region. The influence of anthropogenic pressure was not clearly evident, though pastures were not valuable habitats for any mammal species, as they had a negative, yet not robust, effect on species and community occupancy. In light of rapidly expanding agriculture across the tropics, our findings highlight species-specific responses to disturbance that can inform land use planning and conservation policies. We stress the conservation value of forest and wetland habitat to mammal occupancy in heterogeneous ecosystems. Moreover, our results demonstrate that oil palm and crop expansion should target existing pastures, which displayed limited conservation value for Neotropical mammals but occupy vast swathes of land across Latin America.

Keywords: Panthera onca; camera trap; Bayesian statistics; land-use change; oil palm; pasture.

1. Introduction

Agricultural expansion is driving severe habitat loss and degradation, threatening biodiversity worldwide (Foley et al., 2005; Green et al., 2005; Tscharntke et al., 2012; Maxwell et al., 2016). This is particularly concerning across tropical countries, which are extremely rich in biodiversity but experiencing unprecedented land cover change (Gibbs et al., 2010; Laurance et al., 2014). Therefore, there is an urgent need to understand how species respond to different land cover types across modified landscapes to reconcile biodiversity conservation and agricultural expansion across the tropics (Crooks et al., 2011; Rondinini et al., 2011). Amongst agricultural sector, oil palm cultivation is of particular concern. These plantations have a negative effect on biodiversity, including mammals, and are expanding rapidly across the tropics (Fitzherbert et al., 2008; Yue et al., 2015; Wearn et al., 2017; Pardo et al., 2018a).

Tropical mammals are a conservation priority because they are declining due to land-use change and hunting (Schipper et al., 2008; Visconti et al., 2011; Barlow et al., 2016) with important consequences for ecosystem health and resilience. Mammals make significant contributions to ecosystem functioning including trophic regulation, nutrient cycling, carbon storage, seed dispersal and ultimately maintenance of forest structure (Brodie et al., 2009; Jansen et al., 2010; Estes et al., 2011; Sobral et al., 2017). Amongst mammals, large-bodied carnivores like jaguars *Panthera onca* are acutely threatened with extinction due to their slow population growth rates and extensive area and dietary requirements (Crooks, 2002; Cardillo et al., 2005; Carbone et al., 2011).

Conservation and management have largely moved away from single-species approaches to sustaining ecosystems and communities (Balmford et al. 2005; Santini et al., 2017). However, developing interventions to safeguard forest-dwelling mammals is hindered by their cryptic nature. Statistical approaches, like occupancy modelling, that account and correct for imperfect detection are, therefore, essential to provide a reliable evidence-base to support environmental policies (MacKenzie et al. 2002; Brodie et al. 2014; Guillera-Arroita 2017). Multi-species occupancy models (Dorazio & Royle 2005) go a step further as they enable us to simultaneously explore habitat and anthropogenic variables that influence both community and single species distribution, while providing robust inference for species infrequently detected during ecological surveys (Ahumada et al., 2011; Ahumada et al., 2013; Tobler et al., 2015; Rich et al. 2016; Wearn et al. 2017; Deere et al., 2017).

Colombia is the 4th largest palm oil producer (Ocampo-Penuela et al., 2018), but it is also a megadiverse country, covering 0.7% of the planet and hosting 10% of known biodiversity (Mittermeier et al., 1997). Yet the country's biodiversity is understudied due to a sustained period of conflict that rendered much of the region inaccessible. To our knowledge, this research is the first to study terrestrial mammals across agricultural landscapes in Colombia using multi-species occupancy models. We combine high-resolution land cover maps and camera trap data to achieve the following objectives: (1) assess how habitat availability and anthropogenic pressure (pastures, oil palm cultivation, and human settlements) influence community and species occupancy; (2) estimate Shannon diversity and evenness, and Berger-Parker dominance across two agricultural landscapes in the Magdalena river-valley of Colombia. We hypothesized that mammalian occupancy would respond positively to bottom-up resources (i.e. habitat availability) and negatively to top-down anthropogenic pressures, depending on species-specific habitat preferences and sensitivity to disturbance. The study sites comprised the dominant land use in Latin America, cattle ranching, (Grau & Aide, 2008) and oil palm cultivation. In face of a rapid land use change in the tropics, this study provides valuable information to inform management, land use planning and policies that reconcile agricultural expansion and mammal conservation.

2. Methods

2.1 Study sites

We conducted the study at two sites in the central region of the Magdalena River valley, Department of Santander, Colombia (Site-1 (7.3752N -73.8842E to 7.5404N -73.7118E; Site-2: 5.3450N -72.8471E to 5.4365N -72.7607E) (Fig. 1). Both sites are situated in the central part of the Magdalena river valley, in between the Central and Eastern Andes, in the Department of Santander, Colombia. The Euclidean distance between the two study sites is 93 km. The overall region is part of the tropical forest biome and is rich in wetlands with no altitudinal gradient (IDEAM et al., 2007). *Mean annual temperature is 27℃, and annual precipitation ranges between 2100-2600 mm (IDEAM et al., 2007). Land tenure is primarily private (different owners)* and there are no national protected areas.

The region is considered important for several species, including keystone mammals such as the jaguar (Payan-Garrido et al., 2013; Boron et al., 2016b) and endangered endemics like the brown spider monkey (*Ateles hybridus* ssp. *brunneus*) and white-footed tamarin (*Sanguinos leucopus*). However, most of the region's historical forest cover has been lost due to the expansion of cattle ranching and oil-palm agro-industries, while the remaining natural areas facing a high risk of conversion (Etter et al., 2006; Castiblanco et al., 2013; Link et al., 2013).

We chose these two sites because they are modified, to a large degree, by agriculture but still retained top predators like jaguars and pumas *Puma concolor* as well as other declining species of conservation importance. The dominant land cover classes across our study sites include:pastures (Site 1: 312 km^2/35%; Site 2: 244 km^2/36%), wetlands (Site-1: 182 km^2 Site-1/20% ; Site-2: 233 km^2/34% at Site-2), secondary forest (Site-1: 112 km^2/12%; Site-2: 129 km^2/19%), oil-palm plantations (Site-1:172 km^2/19% , Site-2: 17 km^2/2%) , water (Site-1:190km^2/10%;Site-2:Site-2: 43km^2/6%)), bare ground (Site-1: 24km^2/3%; Site-2: 13

km^2/2%), settlements <0.4%, and roads <0.6% (Fig. 1) (Boron et al., 2018). We identified these land cover types and their amounts across the study sites, which we defined by adding a buffer of 9.2 km around the camera stations. This reflects the maximum distance moved by the species with the largest home range in the study region, (jaguars; Nowell & Jackson, 1996).

2.2 Camera trapping

We deployed 47 camera stations between April and August 2014 at Site-1 and 26 stations between September and December 2014 at Site-2 using a blocked design. This included dry and wet seasons at both sites (April, May, October, November, December: wet months; June, July, August, September: dry months). The minimum convex polygons connecting camera stations were 154.8 km^2 at Site-1 and 85.4 km^2 at Site-2. We set-up the cameras following standardized survey techniques for terrestrial mammals (Ahumada et al., 2011, 2013; Rovero et al., 2014), in a grid at intervals of 1.6±0.3 km, and across the main land cover types of the region: forests (N=35), wetlands (N=8), pastures (N=11), and oil palm plantations (N=13). The remaining cameras (N=6) were located in transitional habitat between wetland and oil palm "Edge" (Fig. 1). To optimize detection, we placed the cameras so that their field of view would be facing low resistance travel routes such as wildlife trails (Cusack et al., 2015). Twenty-eight (60%) and 19 (73%) stations were placed on roads/trails at Site-1 and Site-2 respectively and we took this into account in our modelling approach. Camera traps are consistently able to detect terrestrial mammals $\geq$ 0.5 kg, which are what we refer to in this manuscript (Rovero et al., 2010). We deployed Cuddeback Attack (model 1149) and Ambush (model 1170) camera traps and secured them to a tree at a height of 35 cm from the forest floor. Both camera models have an identical trigger speed (0.25 seconds) and a detection zone of 3-4 m due to the high temperatures characteristic of the region.

2.3 Species richness, diversity, and evenness

For each study site we produced species accumulation curves using EstimateS (Colwell, 2013).

Accumulation curves reach an asymptote once all detectable species have been recorded and were produced using the rarefaction method with 1000 randomizations (Magurran, 2004; Ahumada et al., 2011).We also calculated a) Shannon diversity index ($D_{Shannon}= -\Sigma p_i \ln p_i$ where p_i is the proportion of abundance for species i, N_i relative to the total abundance N); b) evenness index ($E_{Shannon} = D_{Shannon}/\ln (S)$, where S in the number of species observed)and c) the Berger–Parker dominance index ($D = N_i/N$ where N_i is the abundance of the most abundant species relative to the total abundance N) (Shannon, 1948; Berger & Parker, 1970; McCune et al., 2002).

We defined species abundances as integer capture rates, and calculated them using the total number of independent capture events of that species divided by the number of trap-nights (TN) and expressed as integer records per 100 trap nights (Carbone et al., 2001; O'Brien et al., 2003). Independent capture events were defined as consecutive photographs of individuals of the same species taken more than 30 min apart (O'Brien et al., 2003). Capture rates may not reflect real abundance, however they still provide more information than just incidence records (Carbone et al., 2001; Sollmann et al., 2013).

2.4 Multi-species occupancy modelling

We performed statistical analysis at the scale of the camera trap station (e.g. Rovero et al., 2014; Rich et al., 2016), and defined a sampling unit as the circular area with a radius of 800m around each camera station, corresponding to half the average distance between neighboring stations (Sollmann et al., 2012). Prior to analysis, we discarded species with fewer than five detections (i.e. eastern cottontail *Sylvilagus floridanus* and grison *Galictis victata*). To reduce zero inflation in the dataset, we constructed detection histories for each species grouping seven consecutive camera trap nights into one sampling occasion (Alexander et al., 2016; Everatt et al., 2014). This resulted in 12 sampling occasion at Site-1 and 14 at Site-2.

We implemented a hierarchical Bayesian multi-species model formulation (Dorazio & Royle, 2005) to estimate species and community occupancy while accounting for imperfect detection (MacKenzie et al., 2006) (see Appendix 1 for model code). This class of model is composed of two components: the state process, describing the ecological system, and the observation process, defining the sampling protocol. Relative to occupancy, this distinction differentiates between non-detection and true absence.

We modelled the occurrence (z) of species *i* at site *j* as a realization of a Bernoulli process, $z_{i,j} \sim \mathrm{Bern}(\psi_{i,j})$, where $\psi_{i,j}$ represents the latent occupancy state. To account for imperfect detection of true occupancy, detection probability was estimated as a function of temporal replicate *k* at site *j*. We denoted detection as a second Bernoulli process, $x_{i,j,k} \sim \mathrm{Bern}(p_{i,j,k} * z_{i,j})$, 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).

We connected occurrence and detection models of observed taxa through an additional hierarchical component that modeled coefficients from a community-level distribution governed by hyper-parameters. This protocol assumes similarity in community responses to covariates. Consequently, species-specific parameter estimates are a function of individual detection histories and average community-level responses, which provides more robust estimation precision for infrequently observed species (Pacifici et al. 2014). Hyper-parameters provide insights into community level responses to covariates of interest and among species variability (Kery and Royle, 2008). We defined the linear predictor for the state process (ψ) and observation process (p) models as:

$$\mathrm{logit}(\psi_{i,j}) = \mu_{(i)\ \mathrm{Site}(j)} + \alpha_{1i}\,\text{Distance Settlement}_j + \alpha_{2i}\,\text{Distance Water}_j + \alpha_{3i}\,\%\ \text{Forest Cover}_j + \alpha_{4i}\,\%\ \text{Pasture Cover}_j + \alpha_{5i}\,\%\ \text{Wetland Cover}_j + \alpha_{6i}\,\%\ \text{Oil Palm Cover}_j + \alpha_{7i}\,\text{Season}_j$$

$$\mathrm{logit}(p_{i,j,k}) = \upsilon_{(i)\ \mathrm{Habitat}(j)} + \beta_{1i}\,\text{Road}_j + \beta_{2i}\,\text{Season}_j$$

Occupancy and detection probabilities were defined on the logit scale, with site- and habitat-specific intercepts on the state and observation processes respectively. We specify intercepts and slopes as a function of individual taxa. Intercepts were specific to site (1 or 2) for occupancy and land cover class for detection (i.e. forest, pasture, oil palm, wetland, and edge between oil palm and wetland). We derived covariates from Landsat 8 satellite imagery using Object Oriented Image Analysis (Bock et al., 2005) and eCognition Developer 9 software (see Boron et al. 2018 for more details). Dominant land cover types (specified as % Forest/Pasture/Wetland/Oil Palm Cover) were extracted as proportions across each sampling unit with ArcMap 10.3. We measured the Euclidean distances of each camera station to water and settlements, which averaged 0.60 ± 0.07 km and 4.85 ± 0.29 km respectively. We tested for collinearity amongst covariates using a threshold value of $|r| = 0.7$ (Dormann et al., 2013) and no covariate was highly correlated to others. As mammals can use roads and trails to facilitate their movement (Cusack et al., 2015) we included a categorical covariate on detection probability (0/1 representing on/off roads/trails respectively). We grouped roads and trails together because the roads we refer to are not paved, ≤ 3 metres wide, not open to the public (inside private lands), not used regularly and thus not very different to trails. We also tested the effect of season (wet vs. dry) on both occupancy and probability of detection. To improve model convergence and place covariates on a comparable scale, we centered and standardized (by subtracting the mean and dividing by the standard deviation of all the sites) all continuous predictor covariates prior to analysis.

Parameter posterior distributions were estimated using Markov chain Monte Carlo (MCMC) simulation and conducted in WinBUGS version 1.4.3, called through R version 3.3.0 using the package “R2WinBUGS” (Sturtz *et al.* 2005). Hierarchical models were constructed using uninformative priors for all parameters. Unless stated otherwise, we present parameter estimates as mean values of the posterior distribution, accompanied by 95% Bayesian Credible

Intervals (BCI) to express uncertainty. Parameters were considered significantly influential if their 95% BCI did not overlap zero and weakly influential if their 90% BCI did not overlap zero. We ran three parallel MCMC chains for 75,000 iterations each, discarding the first 25,000 iterations during the burn-in process and thinning posterior samples by a value of 10. To assess convergence, trace plots were visually inspected for satisfactory mixing and the Gelman-Ruben statistic (Gelman and Hill, 2007) was observed to ensure a value of <1.1 for all parameters. We implemented a posterior predictive check to assess model fit compared to a simulated dataset, extracting Bayesian *P*-values as a numerical overview of the predictive distribution (~0.5 indicative of good model fit; $0.05<P>0.95$ indicative of poor model fit).

3. Results

The total sampling effort resulted in 3069 and 1903 trap nights at Site-1 and Site-2 respectively. Cameras were active for an average of 66 trap nights at Site-1 and 73 at Site-2. On average camera stations detected 5 species at both sites (Site 1: 5, range 0-12; Site 2: 5, range 0-10). We recorded a total of 17 terrestrial mammal species at each site consisting of different guilds and threat categories (Table 1) and three arboreal species (varied capuchins *Cebus versicolor*, howler monkey *Alouatta seniculus* and red-tailed squirrel *Sciurus granatensis*) that we excluded from analysis. Species accumulation curves indicate that we likely recorded most species at Site-1, whereas a larger sampling effort would have been required to characterise the mammal community at Site-2, as the curve does not reach an asymptote (Fig. 2). Overall sites displayed identical Shannon species diversity (Site 2: 2.01 vs. Site 1: 2.02) and species evenness (Site 2: 0.71 vs. Site 1: 0.71) and similar species dominance (Site 2: 0.32 vs. Site 1: 0.40).

Species occupancy varied from 0.54 (ocelot *Leopardus pardalis*) to 0.09 (Spiny rat *Proechymis* *chrysaeolus*) at Site-1 and from 0.31 (ocelot) to 0.12 (nine-banded armadillo *Dasypus novemcinctus*) at Site-2 (Table 1). Bayesian p values detailing model adequacy fit for single species (0.08-0.78) and the full model (0.51) indicated good to optimal fit (Table A2A1). Proportion of forest cover and distance to water were found to have significantly positive and negative influences respectively on community-level mammalian occupancy (Fig. 3 and Table 2). Pumas (0.985; 95% BCI: 0.185-1.876), ocelots (0.811; 95% BCI: 0.032 - 1.618), Central American agoutis *Dasyprocta punctuata (*1.008; 95% BCI: 0.222 - 1.884), lowland pacas *Cuniculus paca (*0.825; 95% BCI: 0.014 - 1.668), and crab-eating racoons *Procyon cancrivorus (*0.771; 95% BCI: 0.012 - 1.538) (Fig. 3 and Table A2) demonstrated a strong preference for areas dominated by forest cover. A further nine species were positively influenced by forest cover, though to a lesser extent (90% BCI non-overlapping zero) (Fig. 3 and Table A2). Consistent negative impacts of pasture cover on occupancy was documented for all species, though this trend was not significant at the community level t (Fig. 3 and Table 2). The negative effect of pasture was weakly influentialfor lowland pacas (-0.644; 90% BCI: -1.301 - -0.025), Central American agouti (-0.693; 90% BCI: -1.325 - -0.092), and jaguarundis (*Herpailurus yagouaroundi*) (-0.696; 90% BCI: -1.378 - -0.045) (Fig. 3 and Table A2). Wetlands increased jaguar occupancy (0.787; 90% BCI: 0.112 – 1.497); however, oil palm, distance to settlements, and season had unclear effects on community occupancy driven by high species variability (Tables 2 and A2, and Fig. 3).

Probability of detection across the community was not significantly affected by any of the covariates (land cover types, season, and camera placement on roads) (Table 2), although placing cameras on roads/trails significantly improved detection for jaguars (1.054; 95% BCI: 0.152-1.939), ocelots (0.869; 95% BCI: 0.171-1.612), crab-eating foxes *Cerdocyon thous (*1.024; 95% BCI: 0.297 - 1.753) and jaguarundi detection (0.723; 90%BCI: 0.148-1.296) (Table A3). We document species-specific covariate effects on occupancy and detection in

Tables A2-A4.

4. Discussion

As agricultural and human-modified landscapes are increasing across the tropics it becomes crucial to understand how they affect species and communities to inform evidence-based conservation interventions for species vulnerable to land-use change. Mammals are a key component of tropical forest ecosystems yet their populations continue to decline (Schipper et al., 2008; Visconti et al., 2011). We synthesized land cover information, and camera trapping data using multi-species occupancy models to produce an assessment of Neotropical mammal persistence in landscapes dominated by agriculture. Our results demonstrate that: a) modified landscapes display lower species diversity and evenness, and higher dominance compared to non-modified landscapes in the Neotropics in the literature; b) remaining forest areas and distance to water significantly influenced community level occupancy confirming our hypothesis; c) the effect of anthropogenic pressures was not clearly evident , although pastures were not valuable habitats for any mammal species and could therefore be targeted for future crop expansion.

4.1 Species richness and community structure

Species detection was commensurate with survey effort. At Site-2 the survey effort (26 stations) was not sufficient to detect all mammal species. At Site 1, where sampling effort was higher (47 stations), the number of terrestrial mammal species (17) was similar to what recorded with comparable survey efforts in an oil palm landscape in the Colombian Llanos (16 sp.) (Pardo & Payan, 2015) and in the Volcan Barva Transect in Costa Rica (15 sp.), which is situated in a highly fragmented landscape (Ahumada et al., 2011), while lower than in pristine areas such as the Peruvian Amazon (Tobler et al., 2008; Tobler et al., 2015), suggesting declining mammal richness with increasing habitat modification. However, richness may not be the most informative metric. The effect of habitat modification on species richness may not be immediately apparent because generalist species spread and/or colonise modified landscapes, as suitable niches become available (Ewers & Disham, 2006; Bogoni et al., 2016). Despite detecting different guilds (e.g. carnivores, herbivores, omnivores, insectivores) we recorded fewer species classified as threatened on the IUCN Red List (Vulnerable, Endangered and Critically Endangered) than other studies focussing on Neotropical mammals (e.g. Tobler et al. 2008; Payan, 2009; Ahumada et al. 2011), alluding to the sensitivity of vulnerable species to human modification. The complete absence of browsing herbivores like tapirs *Tapirus terrestris* and deer *Mazama* and *Odocoileus* sp. suggests that historical land transformation and overhunting could have been drivers of mammal decline and local extinction (Rodriguez-Mahecha et al., 2006). Deer and tapir have been the preferred quarry of hunters for centuries as their significant body size yields more bushmeat per unit of hunting effort (Redford & Robinson n.d.; Jerozolimski & Peres, 2003).

Both sites displayed lower diversity and evenness, and higher dominance than the equivalent values reported by Ahumada et al. (2011) for Neotropical mammal communities (Diversity: 2.5-3.0; Evenness: 0.91-0.93; Dominance: 0.09-0.14). Our results discussed so far confirm that while agricultural landscapes with remaining natural habitat cover still hold some potential for medium-large mammal conservation (Daily et al., 2003; Cassano et al., 2012; Magioli et al., 2016), habitat loss changes mammal communities, decreasing diversity and increasing dominance (Ahumada et al., 2011; Bogoni et al., 2016). Top predators like jaguars and pumas were still present in both study areas, however, their prey community seems impoverished as armadillos, pacas, peccaries (*Pecari tajacu*), capybaras, and deer were absent or rare across both sites. Therefore it is likely that puma survival depends on smaller prey such as widespread agoutis, while jaguars rely on aquatic prey like caimans *Caiman crocodilus* and turtles *Podocnemis* and *Trachemys* sp. (Da Silveira et al., 2010).

4.2 Factors influencing species and community occupancy and detection probability

In accordance with our hypotheses, the proportion of forest cover in each sampling unit had a robust effect on mammalian occupancy, confirming that maintaining connectivity and forest cover in agricultural regions is crucial to preserve functional assemblages (Magioli et al., 2016; Zimbres et al., 2017; Pardo et al., 2018a;b), and wider biodiversity (Prescott et al., 2016). The effect of forest cover was particularly strong for pumas, ocelots, lowland pacas, raccoons, and Central American agoutis. Pumas' and ocelots' preference for forest is well documented (e.g. Paviolo *et al.*, 2009; Davis *et al.*, 2011; Massara et al. 2015), reflecting higher prey occupancy (e.g. agoutis and pacas) coupled with lower human presence and disturbance. Proximity to water was also a strong determinant of community occupancy (distance to water had a significantly negative effect meaning community occupancy increases nearer to water). Water is a fundamental need of all species. Positive associations with water likely reflect the use of riparian forests for movement and dispersal as thanks to legislation these forests tend to be the only ones to remain in modified landscapes like our study sites (Nunez-Regueiro et al., 2015).

Contrary to expectation, anthropogenic pressures did not show a significant effect on community or species occupancy. The presence of oil palm, for example, did not have a significant effect on species, but this is likely because it only occupies a small percentage of the study sites. For example, Pardo et al. (2018b) report that Neotropical mammal communities drastically change when oil palm cover reaches 45–75%. Considering the documented negative effect of oil palm on mammals (Fitzherbert et al., 2008; Yue et al., 2015; Wearn et al., 2017; Pardo & Payan, 2015; Pardo et al., 2018a;b), the expansion of this crop in the Neotropics remains a concern. Recent estimates suggest that 21.1 million hectares of land is potentially suitable for oil palm expansion in Colombia (Pirker et al. 2016). Ensuring that this expansion is not met at the expense of tropical forest habitat should represent a regional conservation priority.

When unavoidable, new plantations should be established on already modified areas like pastures, which displayed limited conservation value for most mammal species. We found a negative (although not significant) effect of pasture on community occupancy. This was more evident for jaguarundis, lowland pacas, and agoutis. The negative effect of pasture on pacas and agouti could be due to lack of habitat cover and food resources. Our findings add to a growing body of literature demonstrating the low conservation value of pastures for a range of taxa (e.g. birds, beetles, and herpetofauna) (Gilroy et al., 2015; Prescott et al., 2016). Pastures account for a large proportion of agricultural land in Latin America and generally have low productivity (Grau & Aide, 2008). Thus directing oil palm expansion on pastures, albeit intensifying use of land, would additionally enable to maximise food security, carbon storage, and natural habitat cover (Garcia-Ulloa et al., 2012).

Finally, wetlands were important for jaguars, the apex predators, in agreement with previous evidence (Soisalo & Cavalcanti, 2006; Quigley et al. 2017). Jaguar conservation in the study region will ultimately depend on the preservation of wetlands and the aquatic prey they host (Da Silveira et al., 2010).

In interpreting these outputs, it is important to note that covariate influences on rare species occupancy may be underestimated due to the effects of shrinkage on parameter estimates. Given the prevalence of generalist species, community averages are driven by the response of these dominant species, thus, when statistical strength is borrowed for rare species, parameter estimates are drawn towards the community mean. At the same time shrinkage allows us to estimate occupancy for species that we would otherwise not be able to make reliable inferences for due to data limitations. In this respect, slight bias in parameter estimates is a fair trade-off (Pacifici et al., 2014).

Placing cameras on roads/established trails did not have an effect on community-level detection. However, it was important to improve detection of jaguars, ocelots, crab-eating foxes, and jaguarundis without affecting the detection of other species. Thus placing cameras on trails remains the preferred option to detect multiple mammal species including carnivores, which are known to use trails (Cusack et al., 2015).

4.3 Conclusions and management implications

Unprotected and increasingly human-modified areas can play a vital for species long-term survival and connectivity and thus it is important to further investigate how their composition and structure can affect species persistence and community composition. Furthermore, multi-species approaches are particularly valuable for informing conservation strategies as they enable us to move beyond single species to community impact assessments. Data on how mammal assemblages respond differentially to agricultural habitats represents key information to understand disturbance. Thus, similar studies to the one presented in this paper can add empirical evidence to environmental decision making. More specifically this study shows that species diversity tends to be low in human modified landscapes while species dominance increases. We can expect similar patterns in agricultural areas around the tropics. These effects may take time to unfold due to extinction debts owed to a legacy of human disturbance (Tilman et al., 1994). There is clear evidence that some species were more associated with natural habitats (e.g. pumas, ocelots, jaguars, pacas) than others. Therefore they are more likely to decline rapidly in modified landscapes with ramifications on their historical ranges and thus Red List categories (Ewers & Didham, 2006; Bogoni et al., 2016).

Overall, planning for agricultural activity needs to factor in displacement and absence of species vulnerable to land-use change in areas where they naturally occur. As oil palm expansion and agriculture continues across the tropics, including Colombia, it is critical to minimize its negative impact on biodiversity. This study helps refine conservation strategies and policy, having demonstrated that to reconcile agricultural expansion with mammal conservation, it is crucial to maintain natural forest cover, since it had a robust impact on community occupancy and is irreplaceable, as well as wetlands specifically for jaguars, the apex predators. Furthermore, it is important to conserve natural habitat cover across agricultural landscapes because no mammals displayed strong affiliation for oil palm and pasture. These findings can also inform land use planning and highlight that in order to avoid further negative impacts on biodiversity, future oil palm and crop expansion could be directed towards existing pastures, which have low productivity (Grau & Aide, 2008), and, as we attested, hold limited value for terrestrial mammals, and biodiversity in general (Gilroy et al., 2015; Prescott et al., 2016). Under these conditions, oil palm has the potential to expand without posing severe threat to vertebrate species in Colombia (Ocampo Penuela et al., 2018). However, this presuppose the existence of both, stronger regulatory approaches (e.g. land use planning that takes into account High Conservation Value forests and zero deforestation), as well as incentives that could help retain vital natural habitats and thus promote mixed landscapes (Lambin et al., 2014; Boron et al., 2016a).

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Figure captions

Fig. 1 Study map of the two agricultural study sites (Site-1 and Site-2) in the Magdalena river valley of Colombia, including land cover types and camera trap stations (Site-1: *N*=47; Site-2: *N*=26).

Fig. 2 Species accumulation curves across two study sites (Site-1 and Site-2) in the Magdalena river valley of Colombia.

Fig. 3 Caterpillar plots delineating effects of covariates on single species and community-level occupancy across two sites in the Magdalena river valley of Colombia. Mean hyper-parameter values and 95% Bayesian Credible Interval (BCI) values are presented in the grey background to each plot, providing an insight to community level responses to covariates. Species-specific mean posterior summaries are denoted with points, while horizontal lines represent the associated 95% BCI. Significant species-specific associations are in blue (95% BCIs do not overlap zero). Other relevant associations are in light blue (90% BCIs do not overlap zero).

Tables

Table 1. Terrestrial mammal species recorded across two study sites (Site-1 and Site-2) in the Magdalena river valley of Colombia, their IUCN (2015) and Regional Red List (Rodriguez-Mahecha et al. 2006) categories, occupancy (ψ) estimates and 95% Bayesian Credible Intervals (95% BCIs). Site-specific estimates assume covariates are held at their average values DD= Data Deficient, LC= Least Concern, NT= Near Threatened, VU= Vulnerable, EN= Endangered. The greater grison and eastern cotton tail were excluded from the occupancy modelling due to the low number of records.

Scientific name	**Common name**	**IUCN Red List**	**Regional Red List**	**Site-1 ψ (95% BCI)**	**Site-2 ψ (95% BCI)**
Apex carnivores					
Panthera onca	Jaguar	NT	VU	0.47 (0.24-0.77)	0.13 (0.03-0.33)
Puma concolor	Puma	LC	NT	0.32 (0.15-0.55)	0.16 (0.05-0.39)
Meso carnivores					
Cerdocyon thous	Crab-eating fox	LC	/	0.26 (0.08-0.61)	0.13 (0.02-0.36)
Galictis victata	Greater grison	LC	/	Not recorded	Recorded once
Herpailurus yagouaroundi	Jaguarundi	LC	/	0.37 (0.17-0.66)	0.13 (0.02-0.35)
Leopardus pardalis	Ocelot	LC	NT	0.54 (0.33-0.76)	0.31 (0.12-0.66)
Omnivores					
Didelphis marsupialis	Common opossum	LC	/	0.24 (0.09-0.53)	0.14 (0.03-0.38)
Eira barbara	Tayra	LC	/	0.28 (0.12-0.57)	0.28 (0.11-0.66)
Pecari tajacu	Collared peccary	LC	/	0.14 (0.03-0.38)	0.20 (0.05-0.55)
Proechymis chrysaeolus	Spiny rat	DD	/	0.09 (0.02-0.28)	0.16 (0.04-0.43)
Procyon cancrivorus	Crab-eating raccoon	LC	/	0.39 (0.20-0.63)	0.20 (0.08-0.45)
Grazing herbivores					
Sylvilagus floridanus	Eastern cottontail	LC	/	Recorded once	Not recorded
Hydrochoerus isthmius	Lesser capybara	DD	/	0.26 (0.08-0.61)	0.13 (0.02-0.36)
Frugivores					
Cuniculus paca	Lowland paca	LC	/	0.17 (0.05-0.40)	0.17 (0.05-0.41)
Dasyprocta punctata	Central American agouti	LC	/	0.20 (0.08-0.41)	0.19 (0.06-0.43)

Insectivores					
Dasypus novemcinctus	Nine-banded armadillo	LC	/	0.19 (0.07-0.45)	0.12 (0.02-0.32)
Myrmecophaga tridactyla	Giant anteater	VU	VU	0.21 (0.06-0.51)	0.14 (0.03-0.39)
Tamandua tetradactyla	Lesser anteater	LC	/	0.16 (0.05-0.38)	0.19 (0.06-0.47)
Total N. of species				**17**	**17**

Table 2. Hyper-parameter posterior summaries denoting community-level responses to covariates hypothesized to influence occupancy (ψ) and detection (*p*) of 16 mammal species at two study sites in the Magdalena river valley, Colombia. We present mean predicted posterior summary values and 95% Bayesian Credible Interval (95% BCI). Bold denotes covariates with significant effects on community occupancy.

	Mean	**Sigma**	**95% BCI**	
Intercept_ψ Site-1	-1.02	0.92	-1.71	-0.36
Intercept_ψ Site-2	-1.56	0.71	-2.40	-0.76
ψ_Distance settlements	-0.11	0.38	-0.43	0.22
ψ_Distance water *	**-0.39**	**0.32**	**-0.77**	**-0.03**
ψ_Forest *	**0.72**	**0.37**	**0.09**	**1.34**
ψ_Pasture	-0.42	0.42	-1.14	0.25
ψ_Wetland	0.18	0.45	-0.51	0.86
ψ_Oil Palm	0.36	0.44	-0.33	1.07
ψ_Season	0.23	0.50	-0.45	0.89
Intercept_P_Forest	-1.66	1.07	-2.42	-0.93
Intercept_P_Wetland	-1.36	0.68	-2.17	-0.65
Intercept_P_Edge	-1.19	0.56	-1.88	-0.54
Intercept_P_Pasture	-1.29	0.68	-2.08	-0.60
Intercept_P_Oil Palm	-1.64	1.68	-2.77	-0.59
P_Roads/Trails	0.15	0.75	-0.50	0.73
P_Season	0.09	0.42	-0.29	0.47

Supplementary information

Appendix 1. Model code used in the analysis.

```
### Hierarchical community occupancy model to assess response of neotropical mammals to
```

```
### habitat and anthropogenic covariates (written in BUGS language).
### Based on the Dorazio-Royle Community Model (2005; J. Am. Stat. Assoc., 100, 389-398).
### Implemented using code adapted from Zipkin et al. (2010; Biol. Conserv., 143, 479-484).
### Species-specific slopes and intercepts.
### Random intercepts on the process/occupancy model to account for sampling at
geographically
### distinct sites (N=2).
### Random intercepts on the observation model to account for variability in detectability
relative ### to habitat type (N=5).

sink("OM_Colombia_M1.txt")
cat("
  model{

  ### Hyperparameters for site-specific intercepts
  ###=========================================
  for (s in 1:2) {
      a1.mean[s] ~ dunif(0,1)
      mu.a1[s] <- log(a1.mean[s]) - log(1-a1.mean[s])
      tau.a1[s] ~ dgamma(0.1,0.1)
      sigma.a1[s] <- 1/sqrt(tau.a1[s])
      }
  ### Hyperparameters for habitat-specific intercepts
  ###=============================================
  for (h in 1:5) {
      a2.mean[h] ~ dunif(0,1)
      mu.a2[h] <- log(a2.mean[h]) - log(1-a2.mean[h])
      tau.a2[h] ~ dgamma(0.1,0.1)
      sigma.a2[h] <- 1/sqrt(tau.a2[h])
  }

  ### Hyperparameters for fixed effects on the process/occupancy model
  ###===============================================================
  mu.b1 ~ dnorm(0,0.001)
  mu.b2 ~ dnorm(0,0.001)
  mu.b3 ~ dnorm(0,0.001)
  mu.b4 ~ dnorm(0,0.001)
  mu.b5 ~ dnorm(0,0.001)
  mu.b6 ~ dnorm(0,0.001)
  mu.b7 ~ dnorm(0,0.001)
  tau.b1 ~ dgamma(0.1,0.1)
  tau.b2 ~ dgamma(0.1,0.1)
  tau.b3 ~ dgamma(0.1,0.1)
  tau.b4 ~ dgamma(0.1,0.1)
  tau.b5 ~ dgamma(0.1,0.1)
  tau.b6 ~ dgamma(0.1,0.1)
  tau.b7 ~ dgamma(0.1,0.1)
  sigma.b1 <- 1/sqrt(tau.b1)
  sigma.b2 <- 1/sqrt(tau.b2)
  sigma.b3 <- 1/sqrt(tau.b3)
```

```
sigma.b4 <- 1/sqrt(tau.b4)
sigma.b5 <- 1/sqrt(tau.b5)
sigma.b6 <- 1/sqrt(tau.b6)
sigma.b7 <- 1/sqrt(tau.b7)

### Hyperparameters for fixed effects on the observation/detection model
###=============================================================
mu.p1 ~ dnorm(0,0.001)
mu.p2 ~ dnorm(0,0.001)
tau.p1 ~ dgamma(0.1,0.1)
tau.p2 ~ dgamma(0.1,0.1)
sigma.p1 <- 1/sqrt(tau.p1)
sigma.p2 <- 1/sqrt(tau.p2)

### Create priors for species i from the hyperparameters
###==========================================
for (i in 1:(n+nzeroes)) {

### Species and site-specific intercepts for occupancy and detection
###========================================================
    for(s in 1:2) {
        a1[s,i] ~ dnorm(mu.a1[s], tau.a1[s])
        }

    for(h in 1:5) {
       a2[h,i] ~ dnorm(mu.a2[h], tau.a2[h])
       }

### Species-specific occupancy and detection fixed effects drawn from a normal distribution
### governed by community-level hyperparameters
###=======================================
    b1[i] ~ dnorm(mu.b1, tau.b1)
    b2[i] ~ dnorm(mu.b2, tau.b2)
    b3[i] ~ dnorm(mu.b3, tau.b3)
    b4[i] ~ dnorm(mu.b4, tau.b4)
    b5[i] ~ dnorm(mu.b5, tau.b5)
    b6[i] ~ dnorm(mu.b6, tau.b6)
    b7[i] ~ dnorm(mu.b7, tau.b7)

    p1[i] ~ dnorm(mu.p1, tau.p1)
    p2[i] ~ dnorm(mu.p2, tau.p2)

### Process model of true occurrence
###==========================
    for (j in 1:J) {
        logit(psi[j,i]) <- a1[Site[j],i] + b1[i]*dist.sett[j] + b2[i]*dist.water[j] +
                           b3[i]*forest[j] + b4[i]*pasture[j] + b5[i]*wetland[j] + b6[i]*OP[j] +
                           b7[i]*Season.psi[j]
        Z[j,i] ~ dbern(mu.psi[j,i])

```

```
  ### Observation model for replicated detections
###====================================
          for (k in 1:K[j]) {
                logit(p[j,k,i]) <-  a2[habitat[j],i] + p1[i]*road[j] + p2*season.det[j]
                  mu.p[j,k,i] <- p[j,k,i]*Z[j,i]
                  y[j,k,i] ~ dbern(mu.p[j,k,i])

# Calculate Pearson's chi-squared residuals to assess goodness of fit
# Based on Kery and Royle: Applied hierarchical modelling in ecology, pp. 235
# Calculate the observed and expected residuals
# Add small value to prevent division by zero
#==========================================
                 y.sim[j,k,i] ~ dbern(mu.p[j,k,i])
                chi2.actual[j,k,i] <- pow(y[j,k,i] - mu.p[j,k,i], 2)/ (mu.p[j,k,i] + 0.0001)
                chi2.sim[j,k,i] <- pow(y.sim[j,k,i] - mu.p[j,k,i], 2)/ (mu.p[j,k,i] + 0.0001)
                }

         chi2.actual.sum[j,i] <- sum(chi2.actual[j,1:n.reps[j],i])
        chi2.sim.sum[j,i] <- sum(chi2.sim[j,1:n.reps[j],i])
         }
# Calculate chi-squared discrepency for each species
#================================================
     fit.sp.actual[i] <- sum(chi2.actual.sum[,i])
     fit.sp.sim[i] <- sum(chi2.sim.sum[,i])
     c.hat.sp[i] <- fit.sp.actual[i]/fit.sp.sim[i]
     bpv.sp[i] <- step(fit.sp.sim[i] - fit.sp.actual[i])
    }

# Calculate overall chi-squared discrepency measure
#===============================================
fit.actual <- sum(chi2.actual.sum[1:n.sites, 1:n.sp])
fit.sim <- sum(chi2.sim.sum[1:n.sites, 1:n.sp])
c.hat <- fit.actual/fit.sim
bpv <- step(fit.sim - fit.actual)

# Derived quantities
# Difference in occupancy between Sites 1 and 2
#============
for(i in 1:n.sp){
   effect1[i] <- a1[2,i] - a1[1,i]
   }

# Number of occupied sites
#======================
for(i in 1:n.sp) {
   Nocc.fs[i] <- sum(Z[,i])
}

# Number of species occurring at each site
#====================================
```

```
    for(j in 1:n.sites) {
    Nsite[j] <- sum(Z[j,])
    }
    }
    ",fill=TRUE)
sink()
```

Table A1. Bayesian P values detailing model adequacy fit for single species and the full model. Values between 0.025 and 0.975 indicate good fit, 0.5 is deemed optimal fit.

Species	**Bayesian P Value**
Central American agouti	0.60
Nine-banded armadillo	0.46
Capybara	0.62
Crab-eating fox	0.08
Giant anteater	0.52
Jaguar	0.53
Jaguarundi	0.59
Lesser anteater	0.46
Ocelot	0.39
Opossum	0.53
Lownland paca	0.33
Collared peccary	0.78
Puma	0.42
Crab-eating racoon	0.44
Spiny rat	0.49
Tayra	0.38
Full Model	0.51

Table A2. Posterior means and 95% Bayesian Credible Intervals (95% BCI) detailing the effect of habitat cover (Forest, Pasture, Wetland, Oil Palm), proximity covariates (Dist Settl., Dist Water) and seasonality (Season) on Neotropical mammal occupancy. Covariates are considered significant if their 95% BCIs do not overlap zero and presented here in bold with an asterisk. We additionally present in bold covariates with a weak influence (90% BCI do not overlap zero).

	Forest (95% BCI)	**Pasture (95% BCI)**	**Dist. settl. (95% BCI)**	**Dist. Water (95% BCI)**	**Wetland (95% BCI)**	**Oil palm (95% BCI)**	**Season (95% BCI)**
Capybara	0.469 (-0.580 - 1.372)	-0.347 (-1.360 - 0.629)	-0.354 (-1.211 - 0.33)	**-0.596** **(-1.427 - 0.071)**	0.483 (-0.464 - 1.581)	-0.004 (-1.281 - 1.054)	0.283 (-0.808 - 1.405)
Central American agouti	**1.008*** **(0.222 - 1.884)**	**-0.693** **(-1.735 - 0.177)**	0.259 (-0.263 - 0.862)	**-0.484** **(-1.114 - 0.083)**	-0.023 (-0.912 - 0.823)	0.626 (-0.269 - 1.614)	0.395 (-0.513 - 1.351)
Collared peccary	**0.820** **(-0.088 - 1.780)**	-0.523 (-1.627 - 0.435)	-0.068 (-0.816 - 0.702)	-0.354 (-1.049 - 0.366)	0.207 (-0.787 - 1.254)	0.366 (-0.612 - 1.37)	0.260 (-0.838 - 1.351)
Crab-eating fox	**0.656** **(-0.104 - 1.411)**	-0.276 (-1.104 - 0.517)	-0.141 (-0.643 - 0.351)	-0.213 (-0.721 - 0.335)	0.005 (-0.806 - 0.775)	0.355 (-0.466 - 1.188)	0.432 (-0.448 - 1.372)
Crab-eating racoon	**0.771*** **(0.012 - 1.538)**	-0.075 (-0.906 - 0.774)	-0.306 (-0.865 - 0.200)	**-0.355** **(-0.882 - 0.178)**	0.207 (-0.626 - 1.043)	0.040 (-0.951 - 0.934)	0.447 (-0.448 - 1.433)
Giant anteater	**0.638** **(-0.275 - 1.546)**	-0.335 (-1.339 - 0.641)	0.019 (-0.674 - 0.776)	-0.288 (-0.948 - 0.423)	0.338 (-0.623 - 1.440)	0.341 (-0.679 - 1.384)	-0.122 (-1.483 - 0.972)
Jaguar	0.522 (-0.364 - 1.360)	-0.599 (-1.682 - 0.332)	0.197 (-0.396 - 0.912)	**-0.529** **(-1.234 - 0.098)**	**0.787** **(-0.206 - 1.969)**	0.269 (-0.757 - 1.267)	-0.130 (-1.322 - 0.879)
Jaguarundi	**0.732** **(-0.116 - 1.591)**	**-0.696** **(-1.827 - 0.255)**	-0.245 (-0.958 - 0.397)	-0.341 (-0.984 - 0.316)	0.230 (-0.670 - 1.137)	0.768 (-0.241 - 2.071)	-0.196 (-1.458 - 0.83)
Lesser anteater	**0.681** **(-0.155 - 1.515)**	-0.186 (-1.087 - 0.749)	-0.278 (-0.952 - 0.336)	**-0.462** **(-1.123 - 0.157)**	-0.191 (-1.233 - 0.725)	0.532 (-0.374 - 1.545)	0.167 (-0.872 - 1.177)

Lowland paca	**0.825 *** **(0.014 - 1.668)**	**-0.644** **(-1.743 - 0.278)**	0.220 (-0.380 - 0.977)	-0.307 (-0.917 - 0.340)	0.279 (-0.635 - 1.237)	0.480 (-0.453 - 1.468)	0.284 (-0.695 - 1.268)
Nine-banded armadillo	**0.629** **(-0.238 - 1.467)**	-0.120 (-0.993 - 0.795)	-0.203 (-0.880 - 0.425)	**-0.405** **(-1.051 - 0.216)**	-0.270 (-1.361 - 0.657)	0.130 (-0.898 - 1.101)	0.101 (-0.982 - 1.109)
Ocelot	**0.811 *** **(0.032 - 1.618)**	-0.532 (-1.452 - 0.300)	-0.098 (-0.624 - 0.427)	-0.350 (-0.929 - 0.222)	0.135 (-0.693 - 0.949)	0.370 (-0.49 - 1.243)	0.504 (-0.452 - 1.581)
Opossum	**0.707** **(-0.149 - 1.555)**	-0.317 (-1.264 - 0.598)	-0.105 (-0.786 - 0.559)	**-0.457** **(-1.140 - 0.171)**	0.144 (-0.812 - 1.103)	0.412 (-0.521 - 1.395)	0.081 (-1.040 - 1.107)
Puma	**0.985 *** **(0.185 - 1.876)**	-0.512 (-1.450 - 0.349)	-0.182 (-0.745 - 0.340)	-0.300 (-0.842 - 0.252)	0.183 (-0.691 - 1.062)	0.143 (-0.759 - 0.983)	0.577 (-0.335 - 1.623)
Spiny rat	**0.615** **(-0.291 - 1.475)**	-0.344 (-1.354 - 0.620)	-0.319 (-1.094 - 0.329)	-0.399 (-1.079 - 0.263)	0.225 (-0.734 - 1.218)	0.376 (-0.580 - 1.351)	0.148 (-0.960 - 1.173)
Tayra	**0.712** **(-0.160 - 1.621)**	-0.498 (-1.505 - 0.415)	-0.100 (-0.711 - 0.556)	**-0.468** **(-1.139 - 0.142)**	0.092 (-0.848 - 1.027)	0.534 (-0.374 - 1.535)	0.430 (-0.565 - 1.517)

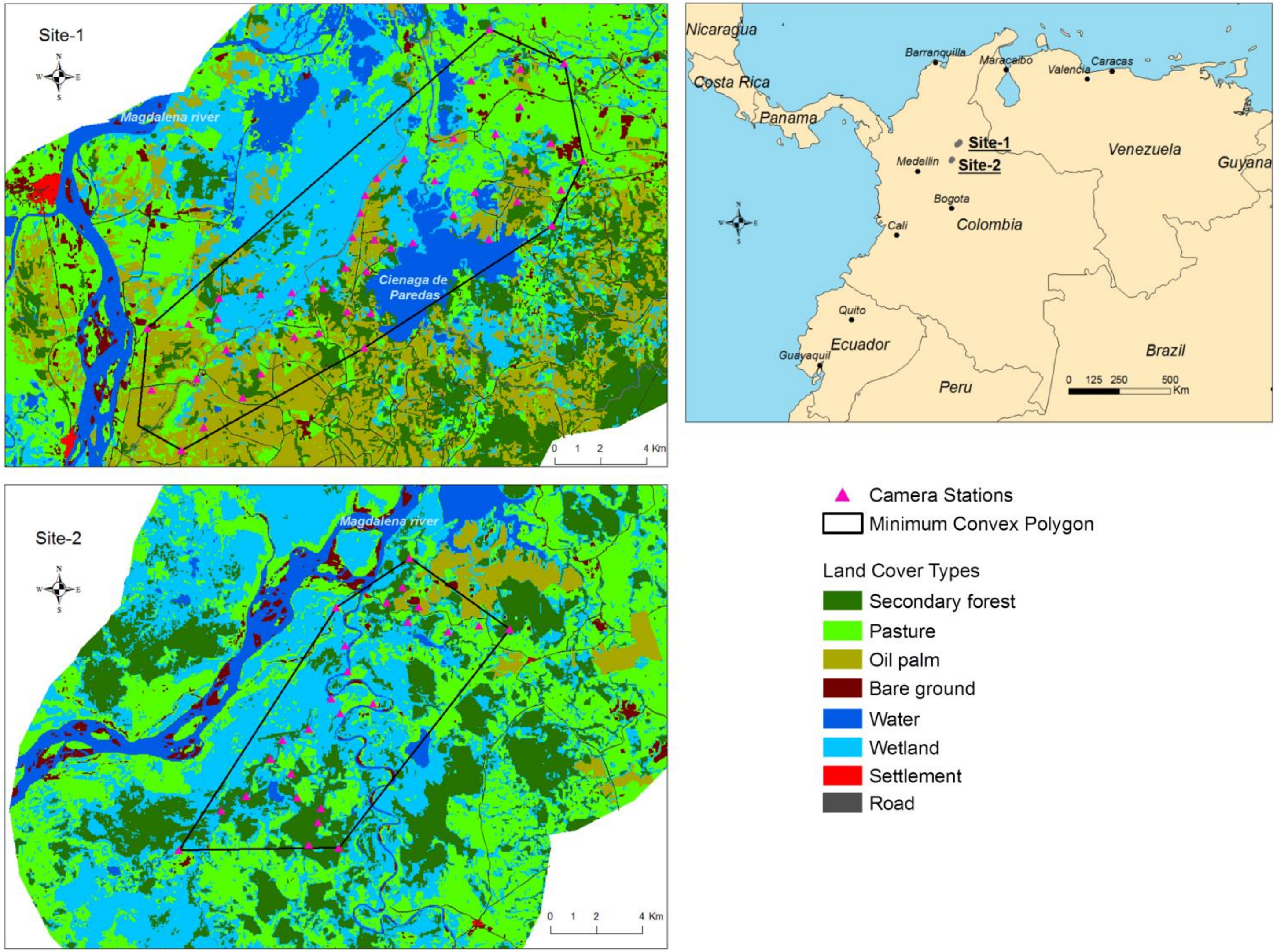
Table A3. Posterior means and 95% Bayesian Credible Intervals (95% BCI) detailing the effect of camera trap placement (Roads) and seasonality (Season) on Neotropical mammal detection probability. Covariates are considered significant if their 95% BCIs do not overlap zero and presented here in bold with an asterisk. We additionally present in bold covariates with a weak influence (90% BCIs do not overlap zero).

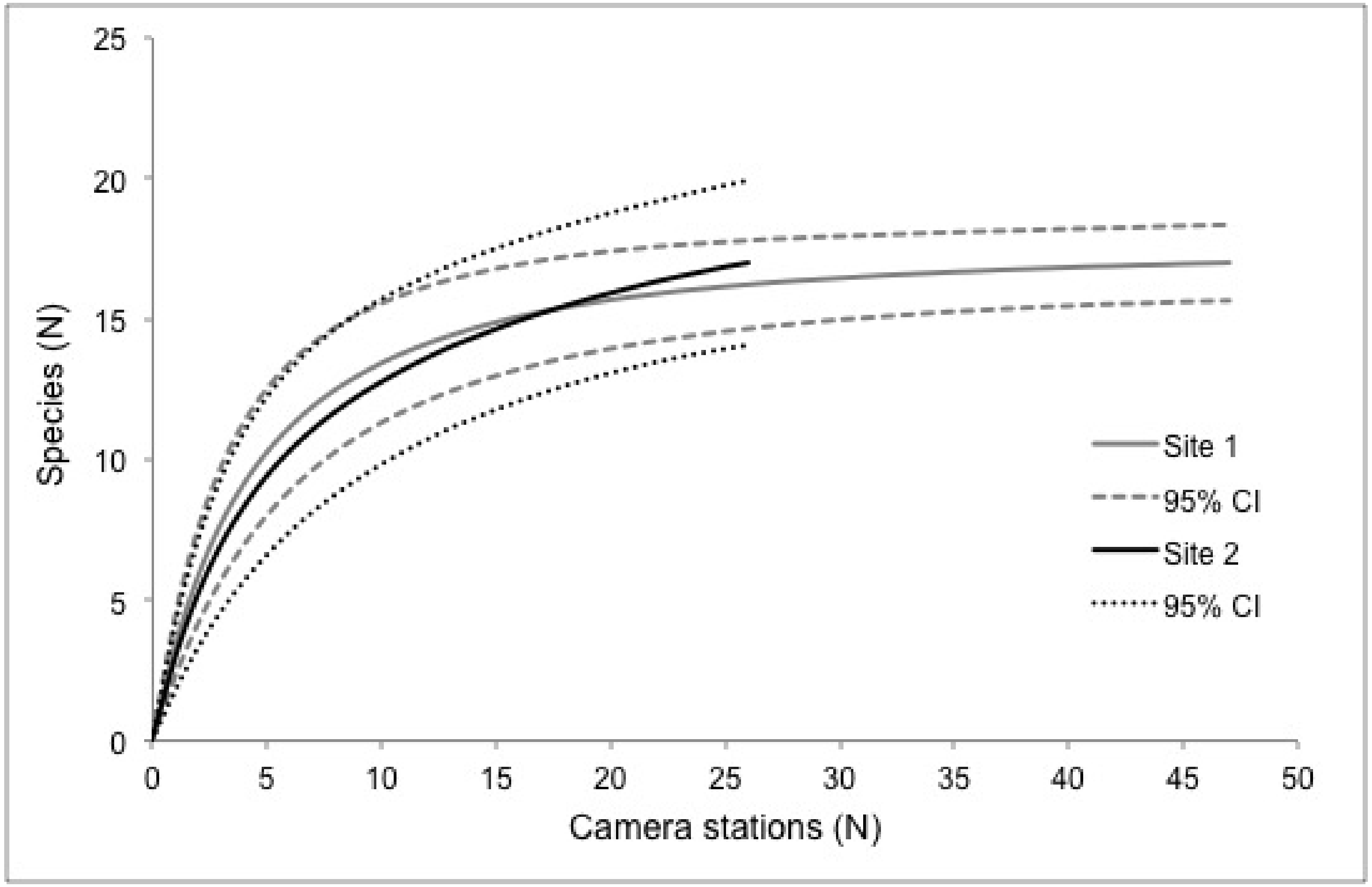
	Roads (95% BCI)	**Season (95% BCI)**
Capybara	-0.369 (-1.486 – 0.649)	0.022 (-0.784 - 0.778)
Central American agouti	0.177 (-0.741-1.070)	**0.637 (-0.008 - 1.374)**
Collared peccary	-0.562 (-2.039 - 0.708)	0.017 (-0.853 - 0.810)
Crab-eating fox	**1.024* (0.297 - 1.753)**	0.266 (-0.244 - 0.795)
Crab-eating racoon	0.286 (-0.518 - 1.083)	**0.465 (-0.081 - 1.065)**
Giant anteater	-0.195 (-1.578 - 1.096)	-0.114 (-1.020 - 0.677)
Jaguar	**1.054 * (0.152 - 1.939)**	-0.086 (-0.789 - 0.563)
Jaguarundi	**0.723 (-0.159 - 1.634)**	-0.031 (-0.811 - 0.698)
Lesser anteater	0.030 (-1.386 -1.346)	0.023 (-0.754 - 0.733)
Lowland paca	-0.042 (-1.117 - 0.942)	0.194 (-0.498 - 0.912)
Nine-banded armadillo	-0.071 (-1.450 - 1.185)	0.082 (-0.700 - 0.844)
Ocelot	**0.869 * (0.171 - 1.612)**	-0.053 (-0.599 - 0.468)
Opossum	-0.427 (-1.550 - 0.592)	0.080 (-0.711 - 0.858)
Puma	0.350 (-0.468 - 1.181)	-0.018 (-0.664 - 0.608)
Spiny rat	-0.439 (-2.034 - 0.853)	0.085 (-0.744 - 0.891)
Tayra	-0.047 (-1.044 - 0.912)	-0.203 (-0.953 - 0.445)

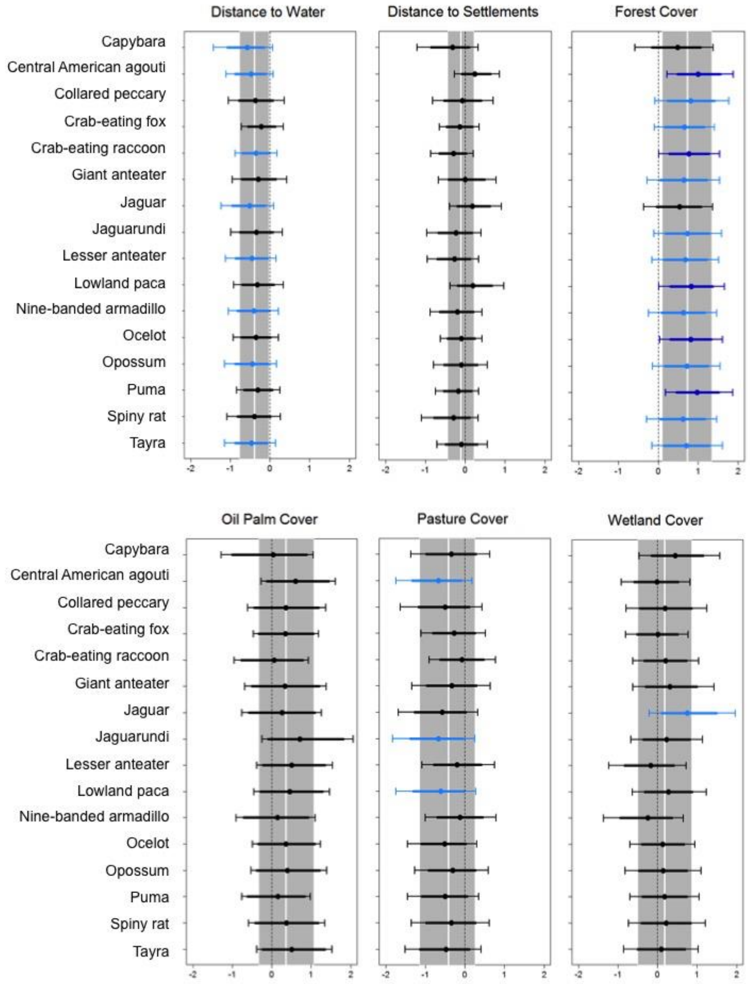
Table A4. Average detection probability, including 95% Bayesian Credible Interval, for Neotropical mammals in five reference habitat classes.

	Forest (95% BCI)	**Pasture (95% BCI)**	**Edge (95% BCI)**	**Wetland (95% BCI)**	**Oil palm (95% BCI)**
Capybara	0.053 (0.009 - 0.218)	0.214 (0.052 - 0.535)	0.175 (0.041 - 0.402)	0.252 (0.109 - 0.487)	0.045 (0.001 - 0.582)
Central American agouti	0.555 (0.313 - 0.779)	0.192 (0.030 - 0.540)	0.287 (0.141 - 0.516)	0.156 (0.020 - 0.490)	0.154 (0.043 -0.435)
Collared peccary	0.038 (0.004 - 0.199)	0.171 (0.042 - 0.392)	0.197 (0.040 - 0.482)	0.178 (0.043 - 0.436)	0.388 (0.108 - 0.778)
Crab-eating fox	0.308 (0.162 - 0.514)	0.349 (0.206 - 0.537)	0.324 (0.165 - 0.572)	0.300 (0.136 - 0.567)	0.281 (0.127 - 0.499)
Crab-eating racoon	0.302 (0.144 - 0.530)	0.265 (0.134 - 0.458)	0.224 (0.100 - 0.409)	0.157 (0.047 - 0.348)	0.075 (0.012 - 0.362)
Giant anteater	0.105 (0.024 -0.358)	0.227 (0.075 - 0.489)	0.199 (0.055 - 0.433)	0.214 (0.064 - 0.506)	0.048 (0.001 - 0.591)
Jaguar	0.086 (0.030 - 0.212)	0.239 (0.072 - 0.571)	0.285 (0.136 - 0.527)	0.334 (0.160 - 0.598)	0.026 (0.001 - 0.400)
Jaguarundi	0.077 (0.025 - 0.210)	0.194 (0.032 - 0.549)	0.263 (0.120 - 0.488)	0.210 (0.074 - 0.449)	0.057 (0.010 - 0.224)
Lesser anteater	0.174 (0.050 - 0.491)	0.170 (0.052 - 0.365)	0.204 (0.044 - 0.503)	0.177 (0.027 - 0.514)	0.099 (0.019 - 0.343)

Lowland paca	0.180 (0.066 - 0.400)	0.320 (0.134 - 0.635)	0.215 (0.077 - 0.430)	0.159 (0.035 - 0.401)	0.152 (0.023 - 0.612)
Nine-banded armadillo	0.137 (0.041 - 0.366)	0.186 (0.054 - 0.407)	0.207 (0.043 - 0.503)	0.172 (0.025 - 0.505)	0.318 (0.046 - 0.864)
Ocelot	0.179 (0.094 - 0.313)	0.166 (0.048 - 0.363)	0.305 (0.146 - 0.566)	0.190 (0.085 - 0.358)	0.285 (0.156 - 0.456)
Opossum	0.190 (0.072 - 0.413)	0.187 (0.031 - 0.525)	0.194 (0.051 - 0.431)	0.265 (0.103 - 0.561)	0.035 (0.001 - 0.397)
Puma	0.192 (0.091 - 0.357)	0.174 (0.027 - 0.496)	0.197 (0.079 - 0.381)	0.188 (0.054 - 0.438)	0.488 (0.193 - 0.790)
Spiny rat	0.105 (0.020 - 0.392)	0.191 (0.032 - 0.545)	0.240 (0.092 - 0.471)	0.176 (0.029 - 0.506)	0.688 (0.273 - 0.950)
Tayra	0.181 (0.072 - 0.398)	0.205 (0.077 - 0.406)	0.226 (0.085 - 0.450)	0.148 (0.031 - 0.375)	0.133 (0.032 - 0.409)


Site-1
N
W
E
S
Magdalena river
Cienaga de Paredas
0 1 2 4 Km
Nicaragua
Costa Rica
Panama
Barranquilla
Maracaibo
Valencia
Caracas
Site-1
Site-2
Medellin
Venezuela
Guyana
Bogota
Cali
Colombia
Quito
Ecuador
Guayaquil
Peru
Brazil
0 125 250 500 Km
Site-2
Magdalena river
0 1 2 4 Km
▲ Camera Stations
☐ Minimum Convex Polygon
Land Cover Types
Secondary forest
Pasture
Oil palm
Bare ground
Water
Wetland
Settlement
Road


25
20
15
10
5
0
Species (N)
0
5
10
15
20
25
30
35
40
45
50
Camera stations (N)
Site 1
95% CI
Site 2
95% CI


Distance to Water
Distance to Settlements
Forest Cover
Oil Palm Cover
Pasture Cover
Wetland Cover
Capybara
Central American agouti
Collared peccary
Crab-eating fox
Crab-eating raccoon
Giant anteater
Jaguar
Jaguarundi
Lesser anteater
Lowland paca
Nine-banded armadillo
Ocelot
Opossum
Puma
Spiny rat
Tayra
-2
-1
0
1
2