

Environmental and human-mediated factors influence vertebrate occupancy in two tropical ecosystems

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Abstract

A species presence within its geographic range can be influenced by environmental variables and disturbance history, resulting in particular occupancy patterns. Understanding the factors affecting occupancy is essential to evaluate the impact of human activities on species and design conservation or restoration measures. For tropical vertebrates, there is little understanding of how multiple factors influence occupancy and interactions with other species under different conditions and disturbance levels. In this study, we evaluated how natural and human-mediated factors determine the presence of mammals and terrestrial birds in two tropical landscapes that share some species but differ in the type of ecosystems and the degree of human disturbance. We adjusted single-season occupancy models for each species to assess the key variables (human-influenced and natural) determining its presence in each landscape, and co-occurrence models to evaluate potential inter-specific relationships. Although species richness was similar between landscapes, small, generalist species had a higher occupancy in the more disturbed landscape (ψ 0.58 Vs 0.40), while larger species had a higher occupancy in the less disturbed one (ψ 0.79 Vs 0.21). Species in the more fragmented and altered landscape were mainly affected by human-mediated variables, although the effect was not always negative, with smaller species being favored by such conditions. In contrast, in the less altered landscape, environmental variables were more determinant of vertebrate occupancy. Additionally, the number, magnitude, and direction of species interactions usually changed from one landscape to another. Results from this study contribute to the broader understanding of the mechanisms that determine vertebrate occupancy in tropical ecosystems. They confirm how human disturbance can have a direct effect on occupancy of larger species of mammals, and demonstrate how in more altered ecosystems factors associated with human presence may become more limiting or more beneficial than natural ones becoming the primary determinants of occupancy.

INTRODUCTION

A species geographic range is the result of complex interactions between its intrinsic characteristics and environmental factors (Brown et al., 1996). At such broad spatial scales, climate and other biophysical conditions play a major role (Lomolino et al., 2006). Additionally, recent studies have shown that anthropic factors can have an effect on species range size (Di Marco & Santini, 2015) and vulnerability to extinction (Di Marco & Santini, 2015). Such vulnerability may vary across biomes within the species range, reflecting the interaction between anthropic effects and environmental factors.

For most species, geographic ranges are composed of multiple local populations that interact with each other (Andrewartha & Birch, 1954) and are distributed across areas with high environmental heterogeneity. At the local scale (landscape, or local populations) the way in which environmental conditions and species interactions influence distribution (occupancy) is less known and continues to be debated (Araújo & Rozenfeld, 2014; Blanchet et al., 2020; Cazelles et al., 2016), especially with regards to the underlying processes that account for the observed patterns. However, there is increasing empirical evidence showing that at the local scale, species occupancy probabilities are often influenced by both environmental factors and the presence or absence of interacting species (Rota et al., 2016).

Some studies indicate that organisms can adapt differently to heterogeneous conditions in different parts of their ranges, showing plasticity (Sagarin et al., 2006), and in this sense the factors that affect their occupancy could vary across sites. In a similar fashion, the presence and magnitude of human impacts can modify positively or negatively occupancy. Human activities such as agricultural and urban expansion or hunting have been shown to affect negatively biodiversity through degradation and fragmentation of habitats, even causing local extinctions (Foley et al., 2005; Kinnaird et al., 2003; Tscharntke et al., 2012). On the other hand, human activities (voluntarily or involuntarily) can also provide food and refuge to some species, specially to those that are opportunistic (Fedriani et al., 2001; Oro et al., 2013), subsidizing their presence and abundance. These changes can, in turn, affect species interactions (trophic and competitive).

Understanding how habitat characteristics, species interactions and anthropic factors affect patterns of occupancy of species is crucial for making management and conservation decisions (Guisan & Thuiller, 2005; Williams et al., 2002). This can help to minimize the impact of human activities on biodiversity, and inform restoration processes, by focusing on factors that are more important for certain species.

Mammals and terrestrial birds play important roles in the maintenance of ecosystem stability and biodiversity in tropical forests (Jansen et al., 2010; Sekercioglu, 2006; Terborgh, 1988). Many of these species are particularly vulnerable to local extirpations due to anthropic effects, such as hunting and habitat degradation, while others can be favored by anthropic subsidies (i.e. small and medium-sized mammals) (Fedriani et al., 2001; Oro et al., 2013; Porras et al., 2016). For this reason, they represent an ideal group for understanding the variation in factors that determine their presence in different landscapes. Colombia has a high diversity of mammals and terrestrial birds that occur in different habitats subject to varying degrees of human disturbance. The Middle Magdalena (MML) and Orinoquia landscape (OL), the two landscapes studied here, present differences in their predominant ecosystems as well as their level of human influence. The MML, while originally composed of vast humid tropical forests and wetlands, is now dominated by agricultural land uses, mainly cattle farming and palm oil, with high levels of fragmentation. Forest remnants are usually of less than 100 hectares. The OL is composed of different ecosystems, mainly savannas dissected by riparian forests, it has a much lower human density, and the predominant activity of extensive cattle farming has not resulted in drastic forest loss or degradation.

We use occupancy modeling to evaluate the factors that determine species presence within these two landscapes and assess how the importance of such factors (natural vs human-mediated) vary from one landscape to another. We also evaluate the prevalence of inter-specific interactions inferred through the effect of one species in the occupancy of another, and how these vary across landscapes. Discerning how occupancy is determined by environmental and anthropic factors in landscapes with different levels of disturbance can help to understand how species are affected by or are adjusting to human influence in tropical ecosystems.

MATERIAL AND METHODS

Study Area

We worked in two landscapes of Colombia, South America, as part of an ongoing biodiversity conservation and monitoring initiative. The first one (MML) is located within the Middle Magdalena River valley, and has temperatures averaging between 23 °C to 29 °C and an average precipitation of 2,900 mm/year. It overlaps the municipalities of Yondó (Antioquia), Puerto Parra and Cimitarra (Santander), and extends over an area of 253,600 has, from which 57% correspond to agriculture land use. This landscape presented a total forest loss of 29, 631 ha between years 200 and 2014 according to data from Hansen et al., (2013). The second landscape (OL), is situated within the Bita River basin, in the municipality of Puerto Carreño (Vichada), in the Orinoquia region, and has average temperatures between 23 °C and 36 °C and an average precipitation range of 2,000 – 3,000 mm/year. It spans an area of 407,400 ha, from which 64% are natural savannas (grasslands), 15% natural forests and 2.3% wetlands; while only 1% are agriculture land uses,

mainly pastures for livestock. This landscape lost around 74 ha of forest between 2000-2014 according to data from Hansen et al., (2013).

Sampling

We divided the landscape into a 1x1km grid, and located sampling stations within 11-27% of the cells, trying to cover as much habitat heterogeneity as possible while constrained by access and permits to enter private properties. Thus, the spatial sampling unit was a 1x1km cell, and each sampling station consisted of a camera trap with movement and infrared sensor (Reconix HC 500 Hiperfire) for detecting terrestrial birds and medium-size and large mammals. We installed 68 sampling stations in the MML between January-May of 2017 and 76 stations between January-April in the OL, both periods corresponding to the dry season in each landscape. Additionally, we conducted three independent 800 meter transects within sampled cells to look for signs and prints of ungulates and primates. Total sampling effort was 4,569 and 3,763 nights-camera in the MML and OL respectively. Cameras were active an average of 67 nights in the MML and 49 nights in the OL.

Covariables

One of our hypotheses is that factors that determine occupancy can vary across landscapes. We assessed this by evaluating the effect of multiple covariates on occupancy of studied species in each landscape. We included covariates from two categories, those corresponding to natural factors and those related directly or indirectly to anthropic factors. The first category included the area of total forest, the area of each type of forest according to a Corine Landcover classification (riparian forest and high-ground forest in MML and flooded forest in OL), area of natural grasslands (savanna), area of wetlands, and distance to water bodies. These areas were estimated for each 1 x1 Km cell and in a surrounding 1km buffer to explore different spatial scales of the effect. The second group of covariates included distance to closest human settlement, distance to roads, area of pastures (artificial land cover), and the area of open pastures and secondary vegetation. We also used land cover types to evaluate covariates affecting the probability of detection for each species. All variables were estimated using ArcGIS (ESRI 10.2.1).

Data Analysis

We developed two types of occupancy models, single-species single-season and co-occurrence models. The first ones estimate the probability of occupancy for each site while considering the probability of detection and assessing the effect of covariates on both probabilities (Mackenzie et al., 2006). For each species we developed detection histories for each site, considering 15 consecutive camera trap days as a sampling occasion, thus having four sampling occasions for MML and three for OL. For ungulates we included six additional sampling occasions corresponding to the transects.

For each species, we first modelled detection probability using covariates within the cell and the type of sampling, and selected the best model using AIC and AICw (Burnham & Anderson, 2002). We then evaluated separately the influence of each individual covariable on the probability of occupancy and then generated additive models combining the variables with the best response and with $AIC < 2$. For those variables in the best models we estimated 80% confidence intervals to assess whether β coefficients, which describe the effect, overlapped with zero (Burnham & Anderson, 2002). All models were adjusted using the package “Unmarked” from R (Fiske & Chandler, 2011). In this way, we assessed the most important variables affecting occupancy in each landscape, both for shared species and for species unique to each landscape. For the agouties and anteaters, we compared species from the same genus between landscapes, and we did the same for the two species of curassow, which have similar habits and are both subject to hunting by humans. To evaluate the interacting effects of landscape and body size in occupancy levels we conducted a tow-way ANOVA, splitting the species in two groups, larger or smaller than 30kg.

To determine the effects of one species on the probability of detection or occupancy of another species, we

used co-occurrence occupancy models (Mackenzie et al., 2004). For each landscape we developed models for interactions between: *Panthera onca* (only MML), *Puma concolor*, *Cuniculus paca*, *Dasypsecta punctata* (MML) and *D. fuliginosa* (OL). We used the parameterization $\frac{\psi^{Ba}}{r^{Ba}}$ in the package RPresence for R (MacKenzie & Hines, 2020) and estimated the following probabilities: ψ^A probability of occupancy of the dominant species (A), ψ^{BA} probability of occupancy of the subordinate species when the dominant species is present, and ψ^{Ba} the probability of occupancy of the subordinate species when the dominant species is absent. We developed a set of models *a priori*, which assumed that the presence of the dominant species influenced the presence of the subordinate species ($\psi^{BA} \neq \psi^{Ba}$), and constrained models where the occupancy of the subordinate was independent of the presence of the dominant species ($\psi^{BA} = \psi^{Ba}$). We included those variables most important for each species derived from the single-species models and we run two models for each pair of species, switching the dominant species, as we assumed the effects were not symmetrical ($\psi^{BA} \neq \psi^{AB}$).

For the probabilities of detection, we estimated the following parameters: P^A probability of detecting the dominant species given the absence of the subordinate, P^B probability of detecting the subordinate given the absence of the dominant, r^A probability of detecting the dominant given that both are present, r^{BA} probability of detecting the subordinate given that both are present and the dominant is detected, r^{Ba} probability of detecting the subordinate given that both are present and the dominant is not detected. We built a set of models *a priori*, assuming that detection probabilities of each species were independent of the presence of the other species ($p^A = r^A$ and $p^B = r^{BA} = r^{Ba}$), others in which only the subordinate species was influenced by the presence of the dominant one ($p^A = r^A$ and $p^B \neq r^{BA} = r^{Ba}$) and models where each species was influenced by the presence and detection of the other species ($p^A \neq r^A$ and $p^B \neq r^{BA} \neq r^{Ba}$).

RESULTS

We detected 38 species of mammals in the camera trap surveys, 27 occurring in the Middle Magdalena, 23 in the Orinoquia landscape, and 12 in both (Table S1). The probability of detection ranged from 0.09 to 0.90 in the MML and from 0.01 to 0.68 in the OL. In general, for shared or similar species across landscapes, detection was higher in the MML, with the exception of the tapir and ocelot. Occupancy rates varied from 0.09 to 0.99 across landscapes, with larger species like the giant ant-eater, the puma and the tapir (> 30 Kg) having higher occupancy rates in the OL, while smaller species like the agouti, paca and armadillo had higher occupancy in the MML (Figure 1, $F_{1,16} = 9.5$, $P = 0.007$).

The variables influencing occupancy differed from one landscape to another. For species occurring only in the MML, the area of secondary vegetation in the cell, distance to human settlements, and area of forest were most determinant, while for those species occurring only in the OL, distance to water, area of natural savannah and distance to human settlements were the key predictors of occupancy (Figure 2). For species occurring in both landscapes, the most important variable influencing occupancy always changed from one landscape to another (Figure 2). For medium-sized herbivore mammals and birds, occupancy was influenced mainly by distance to human settlements and area of artificial pastures in the MML (anthropic factors), while in the OL the area of natural grassland, distance to water bodies, and area of riparian forest were the most determinant factors (Figure 2). Carnivore species were also influenced by distinct variables in each landscape. For this group in the MML, occupancy rates were high in areas with more forest, less artificial pasture, and away from human settlements. These factors switched to area of natural grassland, distance to water and distance to human settlements, respectively, in the OL (Figure 2).

Co-occurrence with another species was also important to determine occupancy in some cases, reflecting inter-specific interactions (Table 1). Such interactions changed between landscapes, with the MML presenting fewer interactions (zero values) and all of them positive (occupancy of species B increases in the presence of species A). In the MML the agouti increased its occupancy in the presence of the puma and jaguar; the puma had a higher occupancy in the presence of paca and jaguar, and the jaguar had a higher occupancy in the presence of paca and puma. The paca itself was not affected significantly by the presence of other species. In the OL, more combinations of species had significant interactions, and some of them were negative. In this

landscape, the paca had higher occupancy rates in the presence of agouti and puma, the agouti increased its occupancy in the presence of paca, but decreased it in the presence of puma (negative interaction), and the puma increased significantly in the presence of the paca but decreased in the presence of agouti (Table 1). In most cases, species interactions were mediated by another variable, which in the Middle Magdalena was distance to human settlements (except for Jaguar-paca interaction) (Figure 3). In the OL all interactions involving the agouti were mediated by the area of riparian forests and the puma-paca interactions by distance to water. Some of the relationships with the environmental variable in turn, changed in the presence and absence of the co-occurring species (Figure 3). The clearest example is for *Dasyprocta* in the MML, where results indicate that its occupancy is higher in the presence of *Puma concolor* and *Panthera onca*. The relationship to the other important factor, distance to human settlements, is positive in those cells with presence of these predators, but it becomes negative (higher occupancy at smaller distances to settlements) in their absence (Figure 3).

DISCUSSION

Occupancy values varied across species and landscapes, however a clear pattern emerged when comparing mammal species shared between the two landscapes, that larger species have a higher occupancy in the OL while smaller species have a higher one in the MML. The few previous studies in these regions agree with these results. Gómez et al., (2016) found high levels (>0.55) of occupancy for ungulates (tapirs and both species of peccaries) in the eastern highland savannas of El Tuparro National Park; while Boron et al., (2019) reported occupancy levels even lower than the ones reported here (<0.30) for smaller mammals (*Cuniculus*, *Dasyprocta*, *Eira*) in a human-modified landscape in the Middle Magdalena Valley. No studies however, had compared the same species across landscapes.

While differences in occupancy values between landscapes for a same species could be expected naturally (different ecosystems and context), the pattern of size-related occupancy suggests that human modification of the landscape is a determining factor. Populations of larger species like tapirs, pumas and giant ant-eaters have been reduced in the Middle Magdalena modified ecosystems. Larger mammals tend to be more affected by deforestation and human pressures like hunting, as they require larger areas of habitat and are more susceptible to hunting (Chichorro et al., 2019; Forero-Medina et al., 2009; Ripple et al., 2017). On the other hand, smaller, common species (not endemic, small-ranged), and especially rodents, habitat generalists with high reproductive rate, may become more abundant at sites with substantial human use (Dias et al., 2019; Gibb et al., 2020). Such is the case for *Cuniculus*, *Dasyprocta* and *Dasyprocta*, in the MML.

Both natural and human-mediated factors influenced occupancy of species in the two landscapes. However, in the less modified areas of the OL, mostly natural factors, such as area of flooded grassland, area of different types of forests and distance to water bodies were determinant, both for unique species and for species shared with the MML. Only two species in the OL were influenced by distance to human settlements, the puma and the tapir. On the other hand, in the more disturbed MML, ten out of the thirteen species were influenced by anthropic factors determining occupancy, such as distance to human settlements and the area of artificial land cover types. The area of forest was also an important factor in this landscape. Most notably, all shared species except the puma and tapir (same variable opposite effect), were influenced by a different factor in each landscape, usually moving from an anthropic factor in the MML to a natural factor in the OL.

These differences could highlight how in the more modified landscape, where forests are now represented by small, fragmented patches surrounded by crops and other agricultural land cover types, human-mediated factors have a stronger influence on the presence or absence of some terrestrial birds and mammals. This effect can be negative or positive, with some species apparently thriving in more disturbed conditions, while others avoiding them. Previous studies in tropical ecosystems have shown how many species of mammals and other game vertebrates are affected by human activities, like hunting, and therefore their abundance or occupancy increases away from human settlements or in no-hunting areas (Cavada et al., 2019; Nuñez-Iturri et al., 2008). On the other hand, some species of rodents and small mammals can benefit from such changes

in the landscape, being favored by human settlements, through the increase in open areas, water reservoirs and food availability from garbage or agriculture (Fedriani et al., 2001; Mendelssohn & Yom-Tov, 1999; Oro et al., 2013). Species of *Dasyprocta*, *Cuniculus* and *Pecari* have been reported as some of the main consumers of human-cultivated plants (crop raiders) in the Amazon (Abrahams et al., 2018), and armadillos have been reported to consume arthropods associated with cultivated lands (Gallo et al., 2019). In the MML, these rodent species and armadillos are increasing their occupancy closer to human settlements or in open, disturbed areas, perhaps as a consequence of the presence of crops; however, these same species in the OL, are more influenced by natural variables like distance to water, and area of riverine forests. In a less disturbed site (like the OL) natural factors become more important.

Understanding the effects of natural and anthropic variables in vertebrate occupancy in these two sites is further complicated by inter-specific interactions (Table 1). Species can interact directly or indirectly, through competition, mutualism and trophic relations, all of which can be mediated by other variables. In the MML, all interactions found were positive, and were influenced by the distance to human settlements, while in OL species interactions were mediated by natural factors.

We did not find evidence of exclusion between *Cuniculus* and *Dasyprocta*, two rodents of similar size. In the MML there were no interactions between them and in OL the occupancy of each species was higher in the presence of the other. However, in the MML *Dasyprocta* occupancy was positively correlated with the presence of Puma and Jaguar, which in turn were positively correlated with the presence of *Cuniculus*, one of their preferred prey (Ávila-Nájera et al., 2018; Gutiérrez-González & López-González, 2017; Novack et al., 2005), raising the question of a potential competition release between the rodents by these predators, who could be reducing the abundance of *Cuniculus* (not eliminating it), favoring the presence of *Dasyprocta* and explaining its higher occupancy in the presence of the predators. Curiously, the relationship between *Puma* and *Dasyprocta* is inverted in the OL, where the interaction becomes negative in both directions. This could be related to the fact that the occupancy of both *Dasyprocta* and *Cuniculus* is much lower in the OL, therefore there may not be competition release by the predators but instead *Dasyprocta* avoids sites occupied by *Puma* because without *Cuniculus* it also becomes a common prey. While specific experimental designs would be necessary to test these hypothesis, results clearly indicate how species interactions may vary from landscape to landscape as a result of interactions with other species and the influence of environmental or human-mediated variables.

Both Puma and jaguar occupancy was influenced by distance to human settlements, with both preferring higher distances away from humans in the MML, which has less remnant forest and more human-predator conflict, while the Puma was closer to humans in the OL, where there is less conflict with predators and less human density. There was no exclusive interaction between these two predators in the MML, on the contrary, the occupancy of each species was higher in the presence of the other. This is not rare and has been documented before (Scognamillo et al., 2003), and could be related to the fact that although their diets can be somehow different in a well-preserved ecosystem, in a disturbed site like the MML predators will necessarily have to occupy the few forest remnants, where habitat and preys are available.

In the MML occupancy of predators and prey presented opposing relationships with distance to human settlements. Apparently prey species are favored by the heterogeneity created by human activities, while the felids like jaguar and puma tend to distance from these areas, perhaps as a consequence of conflict killings. This indicates a spatial segregation, mediated by human presence, between predators and preys in this study, a pattern that has been reported before in temperate systems (Dorresteijn et al., 2015; Muhly et al., 2011). In natural systems, prey species like *Cuniculus* and *Dasyprocta* prefer dense forests and are influenced by water bodies, to escape from predators (Goulart et al., 2009; Péres, 1992), just as it was observed for the OL, where these variables affected their occupancy and mediated their co-occurrence patterns with Puma.

Despite the limitations of extrapolating a local study to broader taxonomic and geographic categories and regions, our work presents a contribution to the understanding of the way in which human activities impact species and the way they interact with each other in these tropical landscapes. Considering the characteristics of the MML, it is hard to isolate the effects of the different human activities, habitat loss, fragmentation,

hunting, subsidies for certain species (food, garbage, etc). However, this work clearly shows that although the effects are not simple and in the same direction across all species, humans play a key role in the structuring of vertebrate communities. Although species richness is similar between the two studied areas, the probability of occupancy of species is very different, generalist species present higher occupancy values in the MML, but lower interactions with predators. These changes, coupled to the low occupancy of large seed dispersers like the tapir and active seed predators like the peccaries, can result in significant changes in the structure and composition of the vegetation and the ecosystems (Terborgh et al., 2008). In this sense, understanding such changes in vertebrate occupancy, both positive and negative, and the factors that cause them, should be a key question to inform conservation and restoration initiatives for vertebrate species and their habitat.

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AUTHORS' CONTRIBUTIONS

LV and GFM conceived the ideas and designed methodology; LV analyzed the data; LV, GFM, CAS and AMH interpreted the data; LV and GFM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data will be available at the Wildlife Insights Repository

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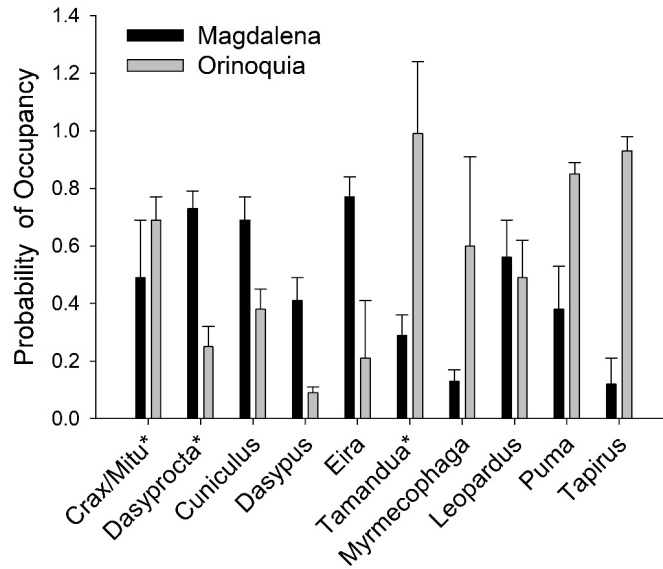


Figure 1. Probability of occupancy for shared species between the Middle Magdalena (MML) and Orinoquia Landscapes (OL). (Error bars = Standar Error). *Same genus - different species between landscapes.

Figure 2. Variables explaining the probability of occupancy of shared and unique species in the two landscapes. Values correspond to Beta coefficients; an asterisk indicates those coefficients that were not significant using 80% confidence intervals.

Magdalena

SpA/SpB	<i>Cuniculus</i>	<i>Dasyprocta</i>	<i>Puma</i>	<i>Jaguar</i>
<i>Cuniculus</i>		0	0.88	0.55

<i>Dasyprocta</i>	0		0	0
<i>Puma</i>	0	0.72		1.00
<i>Jaguar</i>	0	0.65	0.88	
Orinoquía	Orinoquía	Orinoquía	Orinoquía	Orinoquía
	<i>Cuniculus</i>	<i>Dasyprocta</i>	<i>Puma</i>	<i>Jaguar</i>
<i>Cuniculus</i>		0.21	0.99	NA
<i>Dasyprocta</i>	0.59		-0.63	NA
<i>Puma</i>	0.06	-0.94		NA
<i>Jaguar</i>	NA	NA	NA	

Table 1. Difference in the probability of occupancy of species B (columns) in the presence and absence of species A (rows), for each pair of species ($\psi^{BA} - \psi^{Ba}$). Zero values indicate that occupancy of B is the same in the presence or absence of A, suggesting no interaction. Values different from zero, indicate an effect of species A over species B, with positive and green values indicating a higher occupancy in the presence of A and negative and orange values a higher occupancy in the absence of A.

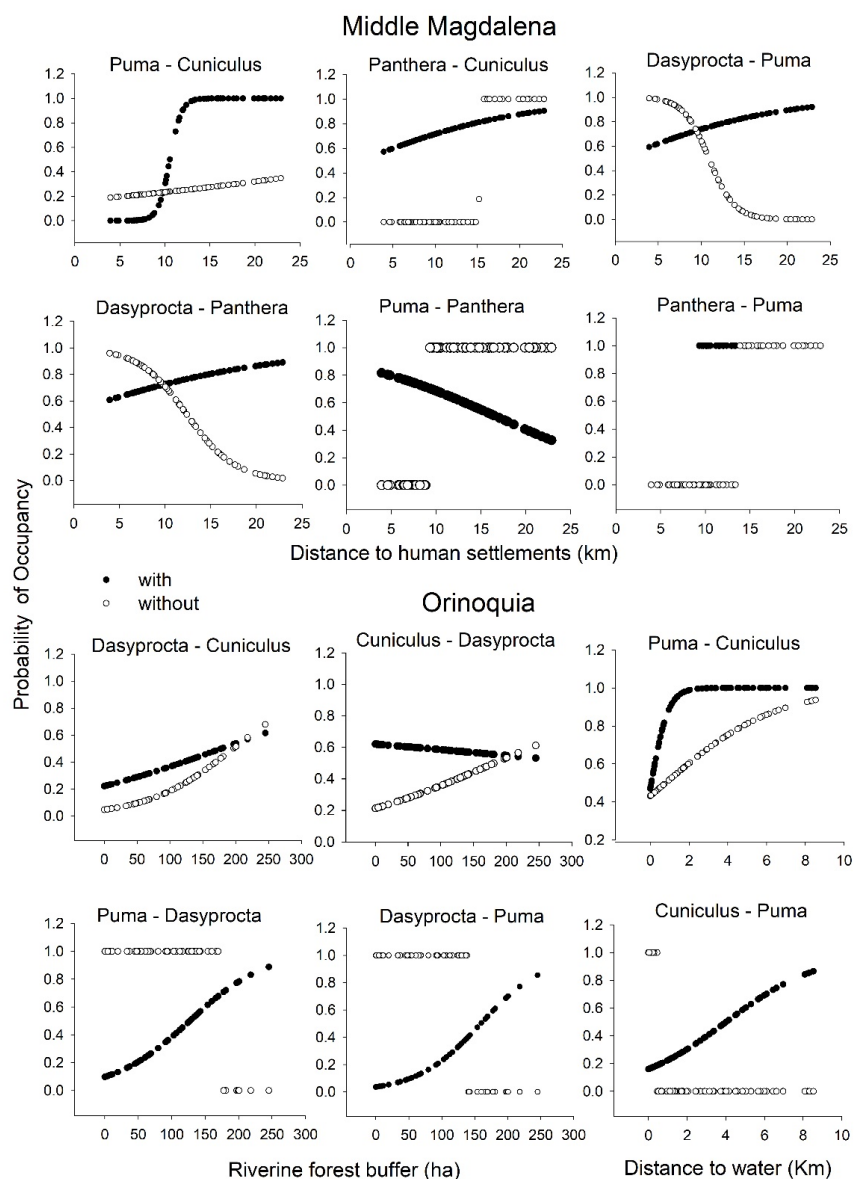


Figure 3. Changes in the probability of occupancy of species B (left in each title) in the presence (black dots) and absence (circles) of species A (right in each title) as a function of the covariable that affects the interaction.