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Diversity and habitat use of medium-large sized mammals across oil palm landscapes in the Llanos region of Colombia

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James Cook University

To my parents and brothers,

and my beloved wife for their unconditional support

To nature which never stops to amaze

Declaration

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any University or other institution of tertiary education.

Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references given.

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(Signature) (Date)

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[1] Colombian Administrative Department of Science, Technology and Innovation

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Abstract

Rising demand for products derived from oil palm has resulted in accelerated expansion of its global cropping area. In Southeast Asia, where most of world´s oil palm is produced, forest loss due to oil palm cultivation has become one of the major threats to biodiversity. As reviewed in Chapter 1, oil palm is now rapidly expanding in Latin America, where Colombia is the largest oil palm producer with nearly 500,000 ha currently under cultivation. Although most oil palm expansion in Colombia has taken place on partially degraded lands or in areas previously used for crops or livestock, little is known about the biodiversity that currently exists in these landscapes and the effect that expanded oil palm agriculture will have. Because Colombia is one of the world's most biodiverse countries, understanding how oil palm production affects wildlife communities is vital to inform conservation planning and improve land-management practices.

In this thesis, I used mammal species as a focal group to evaluate how fauna have responded to expanding oil palm production in Colombia. Mammals are a diverse group and, as such, are good indicators of ecosystem degradation. This is because mammals occupy a wide range of ecological niches, have important and varied roles at a range of different trophic levels, and are often vulnerable to habitat fragmentation.

I conducted this study in the rural areas surrounding the towns of Restrepo, Cumaral, Cabuyaro, Acacias, Castilla la Nueva, and San Carlos de Guaroa, in the Department of Meta, in the eastern plains or Llanos Orientales region of Colombia. This region, which has become the largest oil palm-production zone in the country, is a seminatural savanna ecosystem interspersed by riparian forests of differing sizes and ages along rivers and streams and human land uses such as grazing and agriculture. Within this study area, I used unbaited, automatic camera traps at 56 sites located each at least 2 km apart (33 sites in oil palm plantations and 23 in riparian forest), spanning a total area of ~2,000 km^2 (194–394 m.a.s.l.) to detect terrestrial medium- and large-sized mammals (>0.5 kg). In the Llanos region, knowledge of the ecology and distribution of most terrestrial mammals is very limited. Therefore, I used multiple approaches (as described below) to address these gaps and understand the responses of mammals to oil palm plantations and other local- and landscape-level environmental factors in the Colombian Llanos.

First, in Chapter 2, I examined how species richness, abundance and composition of terrestrial mammal species differed between oil palm plantations and riparian forests. I also determined the influence of landscape- and habitat-level features on those metrics. Data from 12,403 camera-days revealed that species richness and the community-level composition of mammals differed significantly between oil palm and riparian forest, with site-level richness in oil palm plantations being 47% lower, on average, than in riparian forests. Within plantations, mammalian species richness was strongly and negatively correlated with the abundance of cattle, and positively correlated with the density of undergrowth vegetation.

Across the study area, the community composition of mammals at each camera-trap site was significantly influenced by cover type (oil palm versus riparian forest), the percentage of forest remaining, and the distance to the nearest town. Within oil palm sites, understory vegetation, cattle abundance, and canopy cover had significant effects on community composition. Species-specific responses varied between habitat types, with oil palm having positive effects on the abundance of medium-sized omnivore/carnivores, insectivores and grazers such as jaguarundi (*Puma yagouaroundi*), fox (*Cerdocyon thous*), giant anteater (*Myrmecophaga tridactyla*) and white-tailed deer (*Odocoileus cariacou*). My findings suggest that increasing habitat complexity and retaining native riparian forest – regardless of its physiognomic structure – in oil palm-dominated landscapes will help to support higher native mammal richness and abundance at both local and landscape scales.

Second, building on the above findings and in preparation for the imminent expansion of oil palm production in Colombia, I aimed to identify critical transition points (thresholds) in land cover change at which mammal communities drastically change. Identifying thresholds is especially crucial to anticipate sustainable oil palm-cover limits for conservation planning. Therefore, in Chapter 3, I investigated the possible existence of change points for terrestrial mammal richness and community composition along an increasing gradient of oil palm cover in the study area, which covered approximately 2,000 km^2. At each camera-trap site, I found a negative linear relationship between the proportion of oil palm and species richness, but no evidence for significant threshold effects on richness per se. In contrast, I found strong signs of a threshold change in mammal community composition when oil palm cover in the zone immediately surrounding the camera-trap reached 45-75%, beyond which mammalian species community composition drastically changed. Moreover, when species were assessed individually, a significant threshold response to oil palm land cover was found to occur in 10 of 15 species, with four [squirrel (*Sciurus spp*), agouti (*Dasyprocta fuliginosa*), spiny rat (*Proechimis spp*), common opossum (*Didelphis marsupialis*)] having a negative threshold at approximately 45% oil palm cover. The other five species showed no evidence of any critical transition point [giant anteater, lesser anteater (*Tamandua tetradactyla*), jaguarondi, white-tailed deer and crap-eating raccoon (*Procyon cancrivorus*)].

These findings contribute to the identification of the maximum oil palm cover allowable within production zones in Colombia to ensure the conservation of terrestrial mammals. I then used the 45-75% oil palm-cover threshold I identified to examine the conservation status of oil palm production zones across all of Colombia (North, South, West and East zones). For this assessment, I first delimited the spatial extend of each of these zones using the farthest plantations as the limit, as there is no official delimitation for each zone. Then, I used the community threshold identified above as a baseline and determined the percentage of oil palm at each production zone relative to that threshold in relation to the extent of these zones within a fishnet composed of 1 km^2 squares, constructed to cover the size of each production zone. I found that 41% of the ~340,000 ha total area covered by these four zones had already crossed the 45-75% threshold. This result suggests a need for urgent restoration of native forest to increase its extent in these zones if a potential collapse of mammal communities is to be avoided. The identified threshold for oil palm coverage can be used as a guideline to anticipate the minimum amount of remaining native forest needed to support resilient populations of mammals. As such, my results also suggest that maintaining a minimum forest cover of 25-55% in Llanos oil palm-dominated landscapes will help to promote mammal conservation—avoiding a ‘risk zone’ of drastic population declines.

Third, while the positive conservation role of remaining natural habitats in anthropogenic landscapes is relatively clear, quantifying the degree to which the agricultural matrix imposes limitations on animal use and movements is vital to understand species´ resilience to land-use change. In Chapter 4, I evaluated the habitat use and detection probabilities of 23 medium- and large-sized mammals in oil palm plantations and adjacent riparian forest in the Llanos region, using an occupancy framework. I also assessed the effect of undergrowth vegetation and proximity to forest on habitat-use probability within oil palm sites. Most species were detected only rarely, limiting the analysis to the 12 most common species found in both habitat types. This issue was particularly evident in oil palm, because seven species found in riparian forests were never detected there. Habitat use ($\hat{\Psi}$) was strongly influenced by habitat type for four species, showing a strong negative effect of oil palm, whereas the remaining eight species showed no effect of habitat type.

As expected, probabilities of oil palm and forest use varied somewhat among species. In general, omnivorous mesocarnivores, white-tailed deer, and the giant anteater were more likely to use oil palm whereas the remaining species, including ocelot (*Leopardus pardalis*) and lesser anteaters, showed a preference for forest habitats. In general, my findings suggest that retaining undergrowth vegetation inside plantations and maintaining nearby riparian corridors will reduce the negative impacts that a homogenous monoculture, such as an oil palm plantation, exerts on native mammal species. One caveat of this study is that historical land uses have varied across the Llanos region, potentially complicating the patterns I detected.

The ability of some animal species to adjust their behaviour in response to landscape changes and human presence may allow them to better adapt to new, human-altered conditions. However, behavioral responses to land-use change by mammal species are not well documented. In Chapter 5, I quantified the activity patterns of several terrestrial mammal species to investigate how this aspect of animal behaviour differs between oil palm plantations and riparian forests. I also evaluated the effect of human activity on the activity patterns of mammal species and examined temporal overlap of activity between species to investigate potential species interactions. I used 2,515 camera trap records of 23 mammal species from 12,403 camera days, and analyzed the data using Kernel density estimation and the coefficient of temporal overlap ($\hat{\Delta}$). Data were sufficient to assess the activity patterns of 10 species in riparian forest and seven species in oil palm plantations. Of these, four species [capybara (*Hydrochaerus hydrochaeris*), giant anteater, lesser anteater and common opossum] were represented by enough records ($n > 20$) in both oil palm and forest to allow for robust comparisons. Only capybaras showed a shift in activity patterns, changing from being crepuscular in the forest to predominantly nocturnal in oil palm plantations. Regarding the effect of humans on the activity patterns of mammals, capybaras, giant anteaters and white-tailed deer appeared to modify their activities to avoid human activities in oil palm plantations by becoming more crepuscular or nocturnal. This was not true of jaguarondi, which displayed activity levels that strongly overlapped temporally with human activities.

Pair-wise analyses suggested that temporal segregation occurred between some species occupying the same trophic position (e.g. fox and jaguarundi) within oil palm plantations, whereas conversely some predators and their prey (e.g. ocelot and armadillo [*Dasypus novemcinctus*]) had high overlaps in temporal activity patterns in riparian forest. My findings shed light on how the conversion of native forest to oil palm plantation can lead to behavioral changes of wildlife, a feature of the effect of anthropogenic land use change that is not frequently assessed.

This thesis is the most comprehensive analysis to date examining the effects of oil palm plantations on Colombian terrestrial mammals. Overall, my findings help document mammal diversity in oil palm-dominated landscapes in Colombia and improve understanding of the complex ecological relationships among mammal species in these landscapes. Importantly, oil palm plantations were unsuitable habitat for most native species. The environmental conditions and the history of oil palm development in the Colombian Llanos is dissimilar to that of Southeast Asia. Therefore, we cannot rely on information and recommendations from studies in that region to evaluate the South American context. We must consider the geographical and environmental particularities and land-use history of each geographic area when evaluating impacts of oil palm production on Colombia´s biodiversity. As such, the conclusions and recommendations contained in this thesis provide valuable information from which to develop more effective management practices to retain native mammals in Colombian oil palm landscapes.

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General Introduction

Agricultural expansion is the main driver of land-use change globally (Campbell et al., 2017). In the tropics, for instance, between 1980 and 2000 more than 55% of new agricultural land came at the expense of intact rain forests, while 28% came from disturbed rain forests (Gibbs et al., 2010). Savannas have also been heavily transformed for agriculture, and although concrete information on their rate of conversion is lacking it may be up to twice as fast as that of rain forests (Grace et al., 2006). Moreover, approximately half of the land clearing that has occurred in the last three centuries has taken place in savanna biomes (i.e. steppes/savanna/grasslands – (Goldewijk, 2001). In Brazil, for example, approximately half of all the natural savanna ecosystem was lost by the year 2000 (Brannstrom et al., 2008). In Colombia, conversion of savannas in the Llanos region alone has significantly increased from 1970 to 2011 with average annual rates of savanna conversion increasing to 100,000 ha for pastures and 10,000 ha for oil palm plantations (Etter et al., 2011).

The continued increase in the human population (Gerland et al., 2014) and their total food demand will result in an ongoing expansion of humanity's agriculture footprint (Laurance et al., 2014; Venter et al., 2016). Moreover, there is an ongoing steady rise in the global use of fats, oils, and biofuels derived from agricultural products (Laurance et al., 2014; Rands et al., 2010). Understanding the response of native fauna to land conversion and the subsequent agricultural landscapes is vital for conservation planning and management practices. This importance can be seen in the numerous attempts to quantify and develop practical recommendations aimed to make global agriculture more sustainable (e.g. Sayer et al., 2013).

The effectiveness of approaches aimed to reduce the negative effects of agriculture have been debated fiercely (e.g. Green et al., 2005). For instance, practices such as "land sparing" versus "wildlife friendly" production systems have been heavily scrutinized. Land sparing suggest intensification of agriculture while offsetting large natural ecosystems (e.g. Yue et al., 2015), whereas the wildlife friendly approach suggest alternatives where production and conservation can be managed in the same system (e.g. Bhagwat and Willis, 2008). However, the complexity of natural systems, markets, and society does not allow for silver bullet solutions (Ostrom, 2007). Further, the lack of regional information on the historical context that determine present-day patterns (Gardner et al., 2010) make the creation of immutable strategies impractical. Therefore, an assessment which takes into account different approaches to identifying biodiversity and its responses to land conversion, at different geographical scales and levels of organization (see Noss, 1990), is critical to the determination of suitable management approaches that balances human production systems and natural environments.

Oil palm in the Tropics

Global cultivation of oil palm (*Elaeis guineensis*) is centered in Southeast Asia where it is a major threat to biodiversity (Danielsen et al., 2009; Fitzherbert et al., 2008; Koh and Wilcove, 2008). Biodiversity studies in this region show oil palm has negative effects on a wide range of taxa such as birds, invertebrates, and mammals leading to reductions in richness, abundance and occurrence (Edwards et al., 2010b; Koh, 2008; Maddox et al., 2007; Peh et al., 2006)

Due to an increase in the global demand for energy products, oil palm production is rapidly growing in the Neotropics (i.e. Latin America) (Buttler and Laurance, 2009; Dammert, 2014; Furumo and Aide, 2017). Colombia, for example, is currently the largest oil palm producer in the Americas with nearly 500,000 ha under cultivation (Fedepalma, 2014). Although conversion of natural biomes to oil palm in Colombia has not been as dramatic as in Southeast Asia, and most recent cultivation areas has taken place in transformed ecosystem (pastures mainly), especially in the eastern region of the Llanos (reviewed by Pardo et al., 2015); if unplanned, this expansion could result in substantial modification of natural habitats (e.g. forests, savannas and wetlands), displacement of native wildlife, and disruption of ecosystem functioning (e.g. López-Ricaurte et al., 2017; Rodriguez-Becerra and van Hoof, 2003; Romero-Ruiz et al., 2012). Unfortunately, little is known about the level of biodiversity retention in oil palm dominated landscapes in Colombia (Reviewed by Pardo et al., 2015). Therefore, the identification of the possible threats that large-scale oil palm production pose to conservation are minimal and the development of effective management recommendations has been negligible and is urgently needed.

Mammalian species as a focal group for conservation

Geographic ranges of mammal species worldwide have been reduced by ~40% between ∼1900–2015, with major reductions occurring where human activities are most intensive (e.g. agriculture, settlements) (Ceballos et al., 2017). Although Colombia is ranked among the five most diverse countries in the world for mammals, supporting 518 species (Ramírez-Cháves et al., 2016), little is known of the distribution and natural history of most terrestrial mammals (Andrade-Ponce et al., 2016; Trujillo et al., 2010). This lack of information on Colombian mammals (especially that from camera trapping studies) is particularly evident for the Llanos and Amazon regions (Díaz-Pulido et al., 2017). This situation limits proper assessments on the conservation status of species through these regions. The western Llanos region, for example, has suffered a long history of disturbance by different agricultural process that have cleared savannas and reduced width of riparian forest (e.g. Etter et al., 2011; Madriñán et al., 2007), but the effect of these processes on mammals are unclear in the absence of this information.

Protected areas are vital for conservation (Bruner et al., 2001). However, the capacity of many protected areas to conserve biodiversity in the long-term is limited, given their increasing rate of destruction (Laurance et al., 2012; Sloan et al., 2014) along with that of the surrounding landscapes (Gardner et al., 2009). Therefore, improving biodiversity conservation in human dominated areas is essential. It has been suggested that in human dominated areas mammals are a good indicator of ecosystem quality, given their diversity, the wide array of ecological niches they occupy (Ceballos and Ehrlich, 2002), their important role in the food chain and vulnerability to fragmentation (Ritchie and Johnson, 2009). Further, this group displays a strong influence on ecosystem dynamics and forest structure given their role on seed dispersal, regulation of prey species populations among others (Estes et al., 2011; Terborgh, 1988). Therefore, systematically recording and analyzing the implications of ecosystem or land use change on mammal communities will help to identify appropriate management and mitigation measures for their conservation in human dominated landscapes.

This doctoral thesis aimed to fill the void in knowledge surrounding the potential impacts of oil palm plantations on Colombia's mammal diversity, by investigating how mammal communities and individual species responded to an oil palm dominated landscape in the western Llanos region of Colombia. While it would be ideal to have assessments of mammal communities before and after forest conversion to palm oil cultivation, these data are simply not available. However, in the absence of this information, I addressed this issue through multiple observational approaches.

To understand the diversity patterns and the structure of the mammalian community, I evaluated important community and population metrics, such as richness, abundance and occupancy. Further, I evaluated if oil palm had an effect on the behavioral responses of the assemblage detected in the study area. I was especially interested in understanding the patterns of mammal diversity inside oil palm plantations (the matrix), in comparison to the main natural ecosystem in the area (riparian or gallery forest) in an attempt to identify management alternatives that can improve biodiversity and connectivity in this human dominated landscape. This included an evaluation of the existence of thresholds for oil palm land cover and expansion that could trigger drastic decline in mammal communities. Altogether, these approaches allowed me to provide a comprehensive analysis of the mammal assemblage and individual species responses to oil palm in the Llanos regions. Below, I explain the main research questions (chapters), and the approaches followed to answer them.

Thesis overview

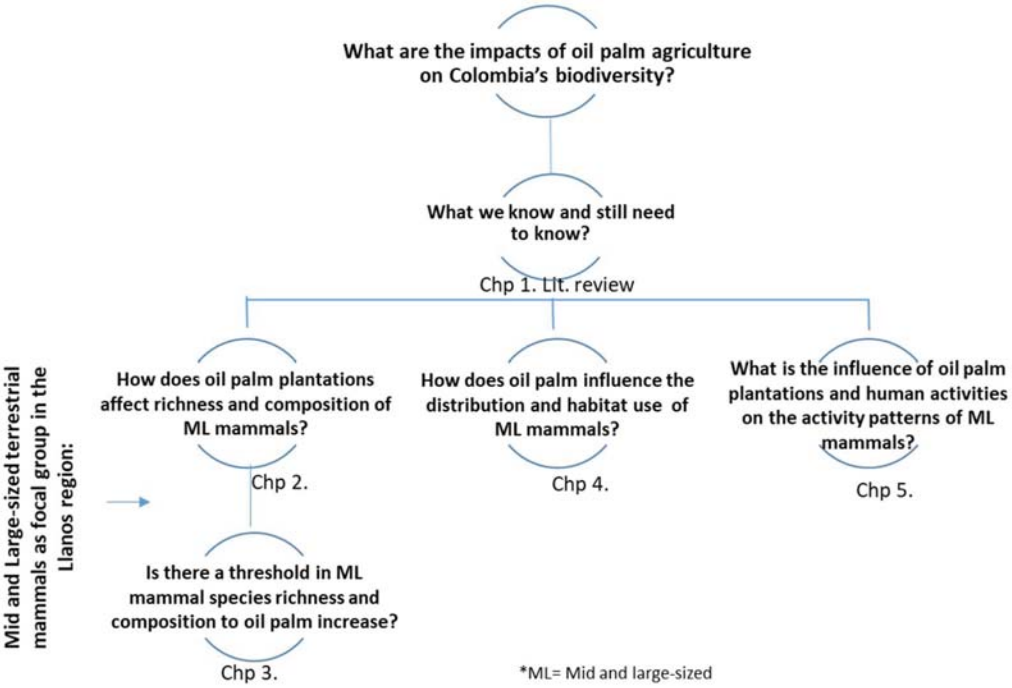

Figure 0.1. Schematic representation of the structure of the thesis starting from the broad general question that I addressed (top), followed by the main questions answered in the following chapters (Chp)

Chapter 1. The impacts of oil palm agriculture on Colombia's biodiversity: what we know and still need to know

This chapter is a literature review in which I examined the current state of knowledge and publications examining biodiversity in oil palm landscapes in Colombia. Here, I identified gaps in information and the current research priorities in the country to understand the potential impacts of palm oil cultivation on different taxonomic groups. I also briefly explored the history of oil palm production in Colombia and discuss the conservation strategies that have been implemented in the country. I propose research priorities to ensure the development of best management practices and identify areas of high priority in terms of assessments. This chapter has been published in the journal *Tropical Conservation Science*

Chapter 2. Terrestrial mammal response to oil palm dominated landscapes in Colombia

Given the limited information on biodiversity and its response to oil palm in Colombia (Chapter 1), in this chapter, I address the fundamental question: **how do oil palm plantations affect richness, abundance and composition of medium and large-sized mammals in the Llanos region, Colombia?** Several related questions are addressed in this chapter, but specifically: I compared terrestrial mammal species richness, abundance and composition in oil palm plantations with that of adjacent riparian forests. I then determined the influence of selected landscape and habitat variables on the aforementioned mammalian metrics within and between these land cover types.

Chapter 3. Identifying critical limits in oil palm cover for the conservation of terrestrial mammal in Colombia

Once I had determined that oil palm exerts an important negative influence on mammal richness and composition (chapter 2), the following fundamental question to address was: **what is the maximum cover of oil palm in a landscape that will still enable the persistence of mammal species?** To answer this question, I identified whether there was a threshold in mammalian species richness and abundance responses to oil palm increase in the Llanos region of Colombia (i.e. critical points in the gradient of oil palm cover that can trigger a drastic decline in mammal responses). Identifying threshold responses of mammalian species across a gradient of oil palm landscape cover is essential for guiding management actions in these transformed landscapes, both in terms of conserving remaining biodiversity, but also in informing future plantation design and planning.

Chapter 4. Assessing the probabilities of terrestrial mammals to occupy oil palm plantations in the eastern plains of Colombia

In chapter 2, I used species richness and abundance to understand the structure of mammal communities and populations. However, these metrics do not provide information on the distribution of species or the probability of habitat use and detectability across different habitats.

Therefore, in this chapter I answer two questions. First, to understand whether oil palm acts as a barrier or to what extent it is permeable to terrestrial mammals, I asked the question: **how does oil palm influence habitat use of terrestrial mammals in the Llanos region of Colombia?** In the second question, I used sites within oil palm only and responded to the question **how does undergrowth vegetation and proximity to forest influence the probability of habitat use by terrestrial mammals?** The second question researched only within oil palm plantations could serve to identify plausible management strategies that may improve the occupancy and connectivity of mammals inside these agroecosystems. To answer these questions, I used the occupancy framework which accounts for detection probabilities while concurrently estimating the probability of individual habitat use. I focus the discussion on the possible underlying mechanisms behind the patterns detected.

Chapter 5. Effects of oil palm and human activities on the activity patterns of terrestrial mammals in the Colombian Llanos

Behavioral responses can play an important role in determining the capacity of species to adapt to novel environments and human presence. In this chapter, I focused on mammals' activity patterns in oil palm compared to riparian habitats and aimed to answer the following: **what is the influence of oil palm plantations and human activities on the activity patterns of mammals in the Llanos region, Colombia?** Activity patterns are usually overlook in mammal research as it is assumed they are modulated only by evolutionary processes. However, changes in environment can alter species' behavioral responses including activity patterns. I used an overlap metric to answer this question and to understand potential temporal relationships within the assemblage (e.g. predator-prey relationships, temporal segregation). Given the paucity of information on the natural history of mammals in Colombia (especially in human dominated landscapes), in this chapter I contribute filling this knowledge gap and thereby provide a complementary approach to traditional mammal research focusing on richness or diversity metrics. This research approach is unique in Colombian mammal research.

Chapter 6. Short communications

In this section I present two brief communications. In one of the papers, I report new records of puma (*Puma concolor*), which has not been reported in the study area in decades. This work was published in the Colombian Journal “Biodiversidad Neotropical” in Spanish. In the second note, I suggest a protocol to improve camera trap surveying of mammals in riparian forests**.**

Chapter 7. Synthesis

Here, I summarize the most important results and conclusions of my research. I also discuss the outcomes and implications of my findings for conservation planning and management. I make specific suggestions for improving management practices across oil palm landscapes and suggest future research.

JCU-affiliated papers cited in this thesis

Here I highlight the list of papers I published during my PhD candidacy

Appendices

Here I include the supporting material for each chapter.

Photographic gallery

Here I have included some photographs from the camera trapping to identify the species mentioned in this thesis. I also included some photographs from outreach activities with farmers and interviews, both conducted during the PhD field work.

Chapter 1 The impacts of oil palm agriculture on Colombia's biodiversity: what we know and still need to know

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LEP conceived the idea, made the literature review, investigated and wrote the first draft of the chapter. GRC, WFL, WE edited the paper, supplied feedback and assistance.

Abstract

The inexorable expansion of oil palm plantations has been a major driver of biodiversity loss in the tropics. This has been particularly evident in Malaysia and Indonesia, where the majority of the world's oil palm is cultivated. In Latin America oil palm acreage has also been steadily increasing, especially in countries such as Colombia, the largest producer by far. However, information on the biological implications of rapid land conversion for oil palm in the region remains scarce. Here, I review the state of knowledge about the impacts of oil palm on biodiversity in Colombia. I also discuss the conservation strategies that have been implemented in the country and propose research that is needed to develop best management practices. The vast majority of research has focused on biotechnology, soils, biological pest control, carbon stock and reduction of greenhouse gases emission, but research on biodiversity is very scarce, or is not yet published. However, important investment and research into palm oil impacts on biodiversity in Colombia are being developed. Currently, the most threatened ecosystem is the savannas in the Orinoquia region, where most of future expansion is also predicted to occur. The demand for green markets and certification are slowly encouraging oil palm corporations to mitigate their 'biological footprint'. However, applied research on the possible impacts of oil palm on biodiversity are urgently needed to support conservation efforts in the oil palm dominated landscapes of Colombia, along with commitment by the government and companies to adopt the resulting recommendations.

Key words: African palm, deforestation, Llanos, palm oil, policy, RSPO

Introduction

Oil palm (*Elaeis guineensis*) is the world's fastest expanding agricultural crop in terms of production, with an annual rate of increase of approximately 9% (Fitzherbert et al., 2008). More than 13 million ha of land are under oil palm cultivation in the tropics (Rands et al., 2010). This expansion, has been a major driver of biodiversity loss, particularly in Malaysia and Indonesia, where the majority of the world's oil palm is cultivated. In both countries, at least 55% of oil palm expansion has occurred at the expense of natural forests making this crop one of the biggest threats to tropical biodiversity conservation (Koh and Wilcove, 2008).

The negative impacts of oil palm on tropical biodiversity have been well-documented for Southeast Asia (e.g. Campbell and Doswald, 2009; Danielsen et al., 2009; Edwards et al., 2010b; Fitzherbert et al., 2008; Koh and Wilcove, 2008) In Malaysia, mammals are particularly sensitive to the conversion of natural forests for oil palm. One study (Maddox et al., 2007) showed that only 10% of medium and large-sized mammalian species were found to use plantations to cross between primary forest patches, and that these were generally species of least conservation concern as per the International Union for Conservation of Nature (IUCN) categories of threatened species. Similar results have been observed in other taxa. For example, in Malaysia, forest conversion to oil palm has also reduced species richness of forest birds in some areas by as much as 80% (Peh et al., 2006).

Comparatively, there is a paucity of information on the biological implications of oil palm expansion in Latin America. This is despite the fact that land planted with oil palm in Colombia has more than doubled, from 181,724 ha in 2002 to 452,435 ha in 2012 (SISPA, 2012). By the end of 2013, around 476,781 ha of land (just under the size of Trinidad and Tobago) was being cultivated for oil palm, ranking the country as the 5th largest producer in the world and the largest producer in the Americas (Fedepalma, 2014; SISPA, 2012). Moreover, projections suggest there will be at least a two-fold increase from current levels by 2020, when just under a million hectares of land is expected to be allocated for palm oil production (MADR, 2006b).

Due to its rapid increase and projected expansion, there is growing concern over how oil palm agriculture could affect Colombia's biodiversity, especially given the negative impacts already documented in Southeast Asia. However, scientific research on the impacts of oil palm on Colombian biodiversity remain scarce. Studies on how the expansion of oil palm plantations has affected the diversity and relative abundance of different taxonomic groups are urgently needed. Such information will not only be useful for modelling species extinction risk under different land-use change scenarios but will help forecast whether the country can maintain its current trajectory of oil palm expansion without compromising national standards of biodiversity conservation.

Synthesizing oil palm-related information, particularly focused on Colombia, this review aims to: 1) determine the extent of oil palm research involving biodiversity and conservation; 2) summarize the impacts of oil palm on land use and biodiversity; 3) provide an outlook for oil palm expansion; 4) describe relevant biodiversity conservation strategies that are being followed to mitigate impacts from oil palm; and 4) propose future research directions to facilitate the development of best management practices for government and businesses to alleviate the impacts of oil palm on Colombia's biodiversity.

Background

Oil palm production in Colombia began in the 1960s and gradually expanded to its current extent of 106 towns in 16 Departments (States) dedicated to this agribusiness. At present, there are four main production zones in the country: 1) the Western Zone, in the southwestern region of Colombia on the Pacific coast; 2) the Northern Zone, in the northeastern region of the country near the Atlantic coast; 3) the Central Zone, an inter-Andean valley on the Magdalena River system; and 4) the Eastern Zone, at the foothills of the eastern chain of the Andes (MAVDT and Fedepalma, 2011) (Figure 1.1). The Eastern Zone has the greatest planted area, but the oldest plantations are located in the Northern and Central Zones. The Western zone is the least developed of the zones (MAVDT and Fedepalma, 2011).

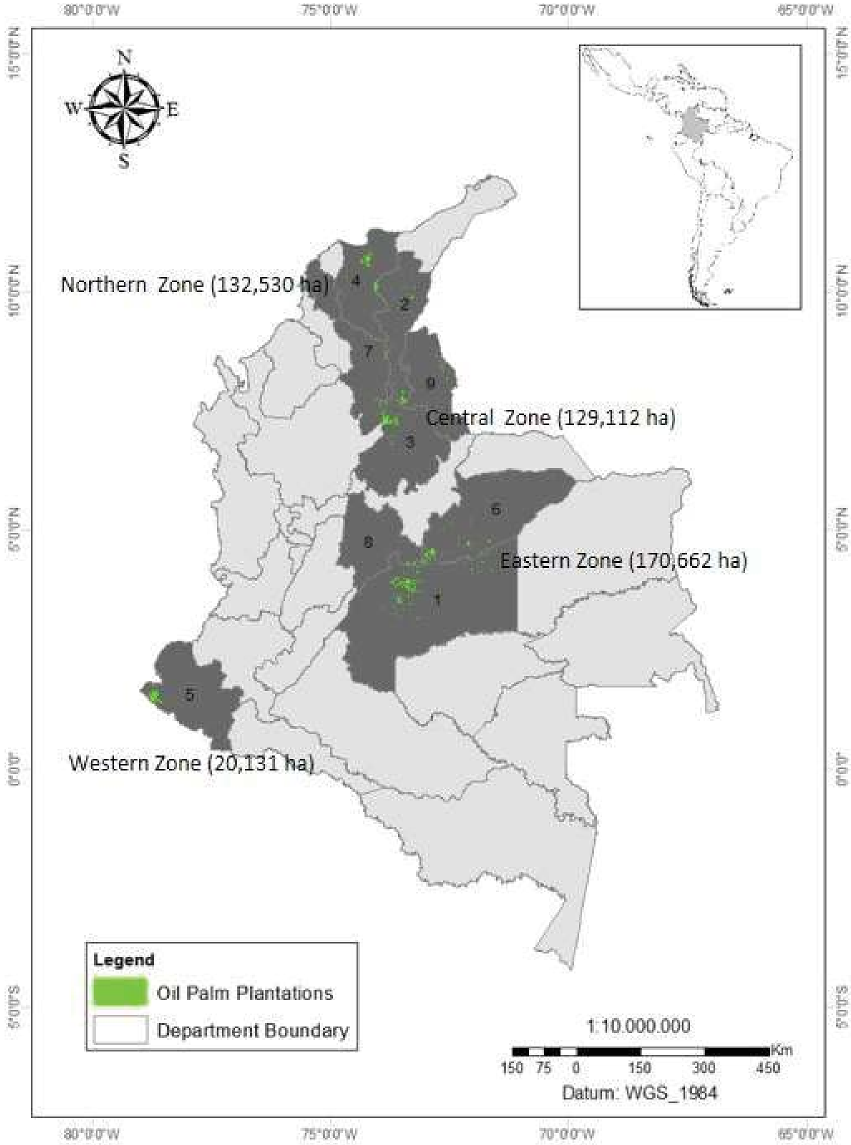

Figure 1.1. Location of oil palm plantations in Colombia. In parenthesis total cultivated area (ha) per zone by 2012. Numbers represent the ranking of the Departments by total production: Meta (1), Cesar (2), Santander (3), Magdalena (4), Nariño (5), Casanare (6), Bolivar (7), Cundinamarca (8), and Norte de Santander (9). Source: Statistical Yearbook 2013 (Fedepalma 2013, available at www.fedepalma.org) and GEF/BID PPB Project.

In 2001, the Colombian government identified oil palm as one of the country's most important economic sectors, which has stimulated its expansion as a major component of the country's biofuel program (MADR, 2006a). As part of this program, the government provided a range of economic incentives to promote palm oil production, including purchase price support, subsidies, tax exemptions, preferential taxes, research funding in biotechnology and production (Bochno, 2008; DNP, 2008, 2007). Even the use of palm oil has been endorsed by government policies, such as legislature implemented on 1 January 2010 requiring the mixing of biofuels with fossil fuels (i.e. a mixture of 10% biodiesel with 90% diesel) (DNP, 2008; MADR, 2006a).

While oil palm agriculture has undoubtedly provided benefits to Colombia's economy, it has also been associated with problems, especially in the Western Zone (Chocó) and Northern Zone (Caribe), such as social displacement, violence, illegal land appropriation, and paramilitary development (e.g. Avendaño, 2007; Biosintesis, 2000; Marin-Burgos et al., 2015; Mingorance, 2006; Mingorance et al., 2004; Montaño, 2008; Palacios, 2012; Perfetti et al., 2003; Salinas Abdala, 2008). Compared to these identified negative socioeconomic issues, however, the negative impacts of oil palm expansion on local biodiversity remains poorly documented.

Oil palm research involving biodiversity and conservation

Global context

Within the global oil palm research community, studies on the impacts of oil palm on biodiversity have been relatively scarce. Between 1970 and 2006, less than 1% (23) of all peer-reviewed publications relating to oil palm dealt with their possible impacts on biodiversity (Turner et al., 2008). To obtain a more up-to-date overview of oil-palm research globally, including those related to biodiversity and conservation, I first conducted a general search in the *Web of Science* database using the keywords "oil palm", and selected peer reviewed publications between the period 2006 and 2015. To help make my search more comprehensive, I also examined other search engines such as the Sustainable Palm oil Platform (SPP, http://www.sustainablepalmoil.org), and searched for oil-palm related documents from Colombia in national databases (e.g. from The Documentation Center of The National Federation of Oil Palm Growers: Fedepalma-http://cidpalmero.fedepalma.org/), university catalogues, and Google Scholar.

A total of 7975 publications were obtained for the period 2006-2015 using the keyword "oil palm". These publications were distributed across more than 60 subject categories, however I only examined papers from the following eight categories relevant to environmental research: *remote sensing*, *zoology*, *biology*, *biodiversity and conservation*, *planning development*, *forestry*, *environmental studies*, *environmental sciences*, and *ecology*. A total of 988 publications were obtained for these categories (12.4% of all records). However, after checking each publication, I discarded 493 papers because they were either unrelated to oil palm, or unrelated to any of the selected categories. For example, I omitted publications involving research on other palm or plant species (e.g. *Jatropha* spp.), socioeconomic issues, general concepts of sustainability with vague links to biofuels, and chemistry of oils, among others. As such, I was left with 502 oil palm publications belonging to those relevant categories and environmental research. Among these relevant publications, 141 were related to biodiversity and conservation globally (Table 1.1).

The vast majority of studies (230 papers, 45.8%) were conducted in Southeast Asia, and focused on the fields of *environment* and *biotechnology*. Only 59 (12%) and 82 (16.5%) publications were related to *biodiversity* and *conservation* respectively. Invertebrates were the most studied taxonomic group (24 papers), followed by mammals (18 papers), and birds (13 papers). Within the mammal's category the study interests focused on rodents (3), bats (3), carnivores (3), primates of the Neotropics (1), great apes (5 related to orangutan and one to great apes in Africa), and general forest communities (2). Notably, there was a scarcity of oil palm research related to the environment in Latin America; only 34 studies (6.8%) were conducted in this region and only 14 publications discussed biodiversity and conservation issues (Table 1.1).

Table 1.1. General type of publications and the studied country as reported in the *Web of Science* database across the period 2006-2015, using the search term "oil palm". The categories used were *remote sensing, zoology, biology, biodiversity and conservation, planning development, forestry, environmental studies, environmental sciences*, and *ecology*.

Country	**Mammals**	**Birds**	**Amphibians**	**Snakes**	**Arthropods**	**Conservation /Planning**	**Environmental**	**Biotechnology**	**Total**	**%**
Malaysia	8	10(a)	2		20	19 (b)	37	32	128	25,50
Indonesia	7	1				20	34 (c)	6	68	13,55
Malasia and Indonesia						8	12	6	26	5,18
Thailand							5	2	7	1,39
Cambodia							1		1	0,20
Papua New Guine						2	1	2	5	1,00
India					1			1	2	0,40
Ghana							2		2	0,40
Cameroon							2		2	0,40
Benin					1				1	0,20
Nigeria			1	1		1	1		4	0,80
Tanzania							1		1	0,20
Colombia		1(d)				2	4	2	9	1,79
Brazil					2	3	4	8	17	3,39
Peru						3			3	0,60
Costa Rica	1					1			2	0,40
Mexico						1	2		3	0,60
Woldwide/tropics	2	1				22	55 (e)	141	221	44,02
TOTAL	18	13	3	1	24	82	161	200	**502**	
%	3,59	2,59	0,60	0,20	4,78	16,33	32,07	39,84		

Category Conservation/Planning includes studies on the effect of fragmentation on animal communities, vegetation, logging, landscape and HCV; many of these documents are reviews. The category Environmental also includes studies concerned with ecosystem services, REED and Carbon Stock, policies and economic analysis for conservation. Biotechnology includes also topics related with phytopathology and biochemistry. a) two studies deal with birds and butterflies, other with birds, beetles and ants and other with arthropods, lizards, terrestrial mammals, birds and bats . b) one related to hunting in oil palm zones. c) one study includes also Singapur and Malaysia and two of them also explore consequences on mammals. d) includes dung beetles, ants and herpetofauna. e) generally reviews or laboratory research. A second filter using “Colombia” in the key words added one paper on snakes, one on ants and one on conservation for Colombia

Colombian context

Searching using the keywords “oil palm” and “Colombia” to retrieve oil palm related publications from the *Web of Science* database identified 75 publications related to the categories described above) for the period 1970-2014. The majority (54 papers) of these papers were related to biotechnology, soil studies (including one paper on soil macro-invertebrate communities and soil-based ecosystem services (Lavelle et al., 2014) and behavior or biology of insects (especially beetles and biological control). Seven publications were related to environmental issues such as carbon and greenhouse gases, whereas another eight papers focused on the socioeconomic aspects and history of oil palm development in Colombia. Only three papers were related to landscape planning or land-use change (Castiblanco et al., 2013; Garcia-Ulloa et al., 2012; Romero-Ruiz et al., 2012) and, notably, just three was related to biodiversity: one examined birds, dung beetles, ants and herpetofauna (Gilroy et al., 2015), another snakes (Lynch, 2015), and a third ants (Sanabria et al., 2014). It is worth noting that there are more papers about biotechnology and invertebrates related to agronomic fields (e.g. biological control), which were not the aim of this paper and therefore not included in this research as they fit within other categories in the *Web of Science* data base (e.g. Biochemistry, Biotechnology and applied microbiology etc.).

The only reference to Colombia in the publications within the Sustainable Palm Oil Platform was a short mention in the booklet “High Conservation Value Forests: The concept in theory and practice” (WWF, 2007). This paucity of oil palm research related to biodiversity and conservation in Colombia complicates efforts to mitigate the potential impacts of this crop on native species. Although research conducted in oil palm landscapes appears to have increased in the last five years, most findings have not yet been published, or have been published in local literature. Below, I summarize some findings from oil palm-related biodiversity research in Colombia.

Impacts of oil palm in Colombia

Land conversion

The construction of oil palm plantations has been associated in many cases with the clearing of primary forest, particularly in the Western Zone or Choco state (Avendaño, 2007; Biosintesis, 2000; Mingorance et al., 2004; WWF, 2009). However, reliable data on how much oil palm has expanded at the expense of natural ecosystems was unavailable until 2012-2013 (Castiblanco et al., 2013; Garcia-Ulloa et al., 2012; Romero-Ruiz et al., 2012). This can be attributed to the fact that oil palm development does not require an environmental license (except for the water concession and other issues related to industrial processes in the Mills), which has led to unregulated expansion (Biosintesis, 2000). In areas such as Guapi, Catatumbo, and Amazonia, environmental impact studies were not carried out prior to oil palm development (Salinas-Abdala, 2008).

The first attempt to assess the possible impacts of oil palm expansion on land use and biodiversity was made by the Institute Alexander von Humboldt (Biosintesis, 2000). They analyzed the economic incentives used to promote oil palm production in Colombia using a model to simulate its effects on the biodiversity in two oil palm zones (Northern and Western). Specifically, they constructed an index of biodiversity change using the diversity of mammals in different ecosystems as a proxy for the possible effect of land-use change if expansion took place. Their results showed that expanding the crop into the proposed areas (i.e. primary forest, secondary forest, pastures, and other crops) would produce a biodiversity reduction of 21.8% in those two zones. Further analysis at the municipality level suggests that, if the expansion took place only in current pasture lands and replaced other crops in Tumaco city, the effect on biodiversity would be positive, and would increase biodiversity by 80% (Biosintesis, 2000).

The degree of disturbance to natural ecosystems arising from oil palm plantations appears to vary, depending upon the growing region. In fact, the impacts of oil palm are not very clear for certain zones and time periods, particularly between the 1960s and 1970s. For example, anecdotal information on oil palm development by the first companies, indicated that in the San Alberto town (Northern Zone), almost 2,000 ha of oil palm between 1961 and 1964 was created at the expense of "…amazing primary forest." (Ospina and Ochoa, 1998). Conversely, Rodriguez-Becerra and van Hoof (2003) argued that only 17.5% of oil palm plantation expansion in Colombia has occurred in natural ecosystems (e.g. forest, savannas, or wetlands), while 82.5% has occurred in lands that were previously used for cattle ranching or crops. Similarly, Gómez et al. (2005)

stated that even though a high proportion of the area was originally forested, 87% of the areas planted for oil palm were previously used for annual crops and extensive cattle grazing with some degree of degradation.

Most worryingly, illegal clearance for oil palm (and related social problems) have been recorded in the Western Zone, which includes the region of Chocó, one of the most important biodiversity hotspots in the world (Myers et al., 2000). However, there are no exact calculations of the proportion of natural forest transformed to oil palm in this zone, since oil palm cultivation began in this region. Some people argue that forest loss was not a consequence of oil palm production, while others blame oil palm for producing a substantial loss of biodiversity. Corponariño (the environmental authority in this area), for example, argues that oil palm has caused the loss of 30% of the native natural vegetation in the area of "Alto Mira" in Tumaco city (Grupo Semillas, 2009).

The Ministry of Environment indicates that in the Orinoquia region (eastern Colombia), approximately 25% (3,626 ha) of the lands planted with oil palm between 2001 and 2005 occurred at the expense of gallery or riparian forest, wetlands, foothills, or natural savannas, while the other 75% were mainly transitional crops and pastures (MAVDT, 2008) (Table 1.2). However, the expansion of biofuels in Santander and the Magdalena Medio region between 2000 and 2005 may have had a low impact on natural ecosystems (MAVDT, 2008).

Modern techniques have improved the accuracy of estimating the amount of land converted to oil palm in Colombia. Romero-Ruiz et al. (2012) made a detailed description of land-use changes between 1987 and 2007 in the Orinoquia region. They identified oil palm cultivation as one of the main drivers for the alteration of savannas, reporting an increase of the land cultivated by oil palm from 31 km^2 in 1987 to 162 km^2 in 2007, with a greater rate of increment between 2000 and 2007 (Table 3). Castiblanco et al. (2013) using spatial regression analysis and econometric models, suggested that present (and possibly future) oil palm expansion will concentrate in areas dominated by pastures, and to a lesser extent, areas that are a mixture of agricultural land and natural forests. The authors examined historical trends of oil palm expansion between 2002 and 2008 and found that the majority (80%) of newly created oil palm plantations (155,100 ha) during this period, replaced non-natural ecosystems (Table 1.2).

Table 1.2. Main estimates of land conversion to oil palm in Colombia and in the eastern region of Colombia.

	Author	Period Analyzed	Land Cover	% Transformed to Oil Palm
Colombia	Castiblanco et al. (2013)	2002-2008	Pastures	51
			crop lands	29.1
			natural ecosystems (forest+savannas)	16
	Rodriguez-Becerra & van Hoff (2003)	Not explicitly stated, but is interpreted from the beginning of cultivation in Colombia to 2003	natural ecosystem (Forest+savannas +wetlands)	17.5
			crop lands and cattle pastures	82.5
Orinoco region	Romero-Ruiz et al. (2012)	1987-2000	Forest	0.03
			crops and exotic pastures	0.16
			High savannas	0.06
			Flooded savannas	0.04
		2000-2007	Forest	0.12
			crops and exotic pastures	0.36
			High savannas	0.03
			Flooded savannas	0.04
	MAVDT (2008)	2001-2005	Gallery forest, wetlands, foothills and savanna	25
			transitional crops and pastures	75

Transition from pastures to oil palm was more dominant in the Eastern and Central Zones, while the transitions from heterogeneous agricultural areas were highest in the Northern zone (Castiblanco et al., 2013). In the Western zone, there were no changes in the area of palm oil plantations during the period investigated. In the Eastern and Central zones, oil palm plantations exhibited the largest expansion, with 68,600 and 68,500 ha, respectively. In the Eastern Zone, 58% occurred at the expense of pastures, 11% of savannas, and 12% of irrigated rice crops. In the Central Zone, 51% originated from areas that were in pastures in 2002, and approximately 20% and 11% of the transformation occurred in heterogeneous agricultural areas and natural forests, respectively. In addition, 4% of the change took place in secondary vegetation. In the Northern Zone, 18,000 ha of new plantations were created between 2002 and 2008, mostly from pastures (26%), followed by heterogeneous agricultural areas (24%) (Castiblanco et al., 2013).

Biodiversity

Few published studies have compared species diversity between ecosystems within oil palm-dominated landscapes (Gilroy et al., 2015; Lynch, 2015; Pardo and Payán, 2015; Sanabria et al., 2014). However, some biodiversity surveys have been conducted in larger plantations, but most of their results have either not been published or need better methodological approaches. For example, Olarte and Carrillo (2007) conducted a survey in a plantation of Puerto Wilches (northern zone), and Rodríguez, (2010) undertook a rapid ecological assessment in Mapiripan (State of Meta). In Mapiripan, Olarte-González and Escovar-Fadul (2015) reported the presence of a mountain lion (*Puma concolor*) inside young oil palm plantation. Although such information provides an idea of possible species occurring around these plantations, more systematic sampling approaches are clearly needed.

Recent and ongoing oil palm related biodiversity research has been largely conducted by postgraduate students. For instance, two studies using jaguars (*Panthera onca*) as a focal species were conducted in the Northern Zone (i.e. J. Figel and V. Boron, pers. comm.). One study on mammalian diversity is currently being conducted in a plantation at the foothills of the Llanos Region (Z. Alvarez pers. comm.), and another is currently quantifying bird diversity (D. Tamaris pers. comm.). T. Angarita (pers. comm.) is currently studying the demography and the impacts of daily crop labor on snake populations in the Meta State, while the organization *Yoluka* (www.yoluka.org.co) has been researching the use of bats and snakes as biological controls. The authors of this review are also studying the diversity and habitat use of mid- and large-sized mammals in different plantations across the Eastern Zone.

Overall, the impacts of oil palm on species diversity appears to be variable, and I have yet to find any research documenting the extinction of animal species within them. Gilroy et al. (2015)

compared the diversity of ants, dung beetles, birds, and herpetofauna in oil palm plantations versus cattle pastures in the foothills of the Eastern Zone. They showed that oil palm plantations had similar or higher species richness across all four examined taxonomic groups when compared with improved pasture. For dung beetles, species richness in oil palm was equal to that of forest, whereas the other three taxa had highest species richness in forests.

Boron and Payán, (2013) compared the diversity of carnivores and their prey in a 640 ha oil palm plantation and the surrounding natural forest in the Northern Zone, concluding that oil palm plantations have a negative impact on the presence of these mammals. However, they also stated that the number of species was similar between the major types of ecosystems, but their composition and relative abundances varied. Large felids (pumas - *Puma concolor* and jaguar - *Panthera onca*) preferred secondary forests and the edge of oil palm plantations, whereas medium felids were recorded in higher frequencies in the plantations. Important prey for big felids, such as capybaras (*Hydrochoerus hydrochaeris*), spotted pacas (*Cuniculus paca*), and collared peccaries (*Pecari tajacu*), were also recorded only in forests.

Pardo and Payán (2015) studied the diversity and capture frequencies (a proxy for relative abundance) of medium- and large-sized mammals in three of the main ecosystems (i.e. gallery or riparian forest, oil palm plantation, and savanna) in a plantation of about 3,000 ha in the eastern Llanos (Casanare department, Eastern Zone). They found 16 medium- and large-sized mammals (including two mouse species), whose capture frequencies varied according to the type of land use. All 16 species were present in the riparian forest, eight of which were also associated with the oil palm plantation and six with savannas. Mammals found in the plantations were mainly mesopredators and generalist species, whose frequencies were higher in the plantation than in natural ecosystems. For example, jaguarondi (*Puma yagouaroundi*), fox (*Cerdocyon thous*), and white-tailed deer (*Odocoileus cariacou*) were more frequently detected inside plantations than in the surrounding natural ecosystems (Pardo and Payán, 2015).

I found only one publication on herpetofauna and ants inside oil palm plantations in Colombia. Lynch (2015) relates his explorations to different plantations across the country during 2006-2013 and estimated a total of 35 snake species in this monoculture. He also suggested that the rate of encounter for some species was greater in oil palm than in natural or transformed ecosystem, and reflects on the potential role of plantations in the conservation of snakes. Sanabria et al. (2014) studied the diversity of ants across different agricultural land uses in the Orinoco Basin (including oil palm), to identify species that could be used as indicator of soil ecosystem services. They found that improved pastures showed the highest species richness and semi-natural savanna the greatest abundance of ants. Pardo et al. (2013) also studied the diversity of birds and herpetofauna in the same ecosystems, recording 38 species of birds (detected only by camera trapping), 12 species of amphibians and 18 species of reptiles in the study area. The number of amphibians was very similar between the natural ecosystems and oil palm plantation, with seven and six species detected in these respective habitats. However, reptilian composition varied between the ecosystems, with eight species found in oil palm versus 13 species in natural ecosystems.

Outlook for oil palm expansion in Colombia

Estimates of the amount and types of land suitable for oil palm production have been variable and most have a degree of uncertainty, especially with regards to their compliance with conservation goals. Cenipalma and Corpoica (1999) suggested that Colombia has around 3.5 million ha suitable for oil palm cultivation without any restrictions, and another 6.1 million ha would have moderate restrictions. These areas are mainly located in the Eastern Zone, where around 1.9 million ha could be planted (Bochno, 2008). These calculations were made at a scale of 1:500,000 imagery, based only on soil quality and the climatic characteristics of the zones. The only restriction or criteria considering biodiversity was the exclusion of the natural forest of the Amazon and the Pacific regions. Even though this is an important restriction, it is still somewhat limited because it does not consider other ecosystems and important conservation areas in the country, such as wetlands, savannas and gallery (riparian) forest. The maps of Cenipalma and Corpoica (1999) were updated in 2009 with the inclusion of environmental, ecological, and socioeconomic factors to determine the suitability of soil to plant oil palm (MAVDT et al., 2009). The scale of this map was 1:500,000 and the aim was to identify zones that are suitable for oil palm cultivation, but several existing areas where productive plantations are already located were deemed non-suitable according to the map (Castiblanco et al., 2013).

Approximately 15 million ha was estimated as suitable for the eventual production of raw materials for biofuels in Colombia, including palm oil, sugar cane, and other biofuel materials in a study by Biofuels Consulting (2007), which was reviewed, analyzed and cited by the Ministry of Environment MAVDT (2008). However, an analysis comparing these suggested areas with the Continental, Coastal and Marine Ecosystems Map of Colombia (IDEAM et al., 2007) indicates that around 38% of these areas overlapped with natural ecosystems (MAVDT, 2008). Biofuel Consulting's report, using other indicators, estimated that Colombia has close to 1.1 million ha appropriate for oil palm cultivation without restriction, particularly in the Northern and Eastern regions. The analysis of MAVDT (2008) found that 15% of this area (164,331 ha) would overlap with natural ecosystems, with another expansion zone predicted in the south of the Eastern Zone, around the colonization front of the Northern Amazon region (Castiblanco et al., 2013).

Economic interest in the Orinoquia region, or Llanos, is increasing. The United States Department of Agriculture (USDA), for example, suggested that the "Altillanura" or highlands of the eastern region of Colombia have about 4.5 million ha that are suitable for agriculture, without the need for deforestation (USDA, 2009). The USDA has called this region the "new agricultural frontier of Colombia" and describes the important and recent interest of agro-industrial organizations in planting soybean, corn, and oil palm. Its low elevation, relatively flat terrain, and a mixture of pastures and savannah ecosystems make the region attractive for important investments in agribusiness. It is estimated that 70% of the Llanos region has been identified for conversion to plantations, or for petroleum and mining purposes (Romero-Ruiz et al., 2012). This is worrying as the Llanos region is rich in savannas and wetlands, shrubs, gallery forest, isolated groups of palms or native vegetation (e.g. "morichales", "matas de monte"), and other types of natural ecosystems that make it one of the most important regions for biodiversity in Colombia and South America (Lasso et al., 2010, Figure 1.2). Thus, research is urgently needed to better understand the threats in order to design best management practices for this unique region.

Figure 1.2. Aerial view of oil palm expansion in the Llanos region of Colombia. Meta state (left), Casanare state (right). Photo credit Lain E. Pardo

Developing oil palm plantations on degraded land is one way to mitigate biodiversity loss. Garcia-Ulloa et al. (2012) used spatially explicit modelling at the national level to compare the possible impacts of oil palm expansion under different scenarios. They suggested that Colombia would require 730,000 ha of land to meet the Government's proposed target of 3.5 million metric tons (Mt) of crude palm oil by 2020. The conversion of this area would imply the loss of approximately 4.4 Mt C of biomass carbon (production-oriented scenario). However, a carbon conservation scenario would substantially reduce biomass carbon losses relative to the production-oriented scenario (87% decrease to 0.55 Mt), but it would also require double the area of land than that required by the production-oriented scenario to reach the same production level. Garcia-Ulloa et al. (2012) suggest a hybrid scenario as the most environmental friendly approach. This scenario will minimize the impact of oil palm by using current cattle lands dominated by pastures, which have poor biodiversity values, low sustainability for long-term food production, and low biomass content. Geraldes et al. (2014) reached similar conclusions when analyzing 65 scenarios developed from a combination of alternative land use and fertilizer application.

Some Colombian ecosystems has been identified as potentially at risk. The ecosystems most threatened with the expansion of oil palm and other biofuel crops would mainly be located in the Eastern Zone and include the ecosystems in the following Departments (States): wetlands and grasslands of Meta and Vichada, and natural forest and gallery forest of Casanare, Meta, Santander and Vichada, including flooding savannas. There are also some concerns about the shrubs of La Guajira (Northern Zone) and especially about the dry forest of the Northern Zone, given its imperiled conservation status (MAVDT, 2008). Besides the aforementioned threats to forested habitats and disturbance to natural ecosystems, Pérez-Rincón (2003) also pointed out important negative repercussions in terms of water demand and possible alterations of hydrobiological regimes.

Expected increase of the area planted with oil palm in Colombia varies according to different scenarios. Castiblanco et al. (2013), for example, suggest an expansion of oil palm coverage to approximately 647,687 ha by 2020 in Colombia, based on an econometric time intervention model that included the effect of subsidy policies that took effect in the country after 2002. However, when modelling a projection based on additional production requirements needed to meet the increasing biodiesel mixture targets established by the government, their predicted area increases up to approximately 930,000 ha. However, the Colombian National Federation of Oil Palm Growers (Fedepalma) expects to reach at least 1,600,000 ha by 2032 (Fedepalma, 2012).

Conservation strategies to mitigate impacts from oil palm

My literature search indicated that research in Colombia on oil palm has mostly focused on environmental and biotechnological issues. Thus, the approach and guidelines for environmental impact assessments (EIAs) have centered on production and carbon emissions reduction. Considerations of the effects on oil palm biodiversity and ecosystems have therefore become secondary. However, there has been greater interest in including these aspects in EIAs in recent times– this has been raised by different institutions such as research agencies (including NGOs), public entities, and oil palm growers.

Certification schemes along with national environmental regulations and international agreements have helped to increase awareness of biodiversity conservation issues. However, companies have a variable attitude toward environmental management, with some more committed than others(Rodríguez-Becerra, 2007; Rodriguez-Becerra and van Hoof, 2003). Nevertheless, the environmental performance of the oil palm industry in Colombia has improved substantively during the last few decades, along with the international and national trend (see

Rodríguez-Becerra, 2007). In 2002, for example, Fedepalma in conjunction with Ministry of Environment and the National Farmers Association (SAC), created the "Environmental Guide for the oil palm sector" (Fedepalma et al., 2002). This document briefly discusses the importance of protecting and conserving different types of forest and wetlands to maintain its fauna and flora species and allow connectivity between ecosystems. Colombia is now working to update this guide (MAVDT and Fedepalma, 2011), making ecosystems and biodiversity aspects more relevant, particularly through the identification of High Conservation Value Areas (HCV) and conservation planning.

Rodriguez-Becerra and van Hoof (2004, 2003) investigated the environmental perspectives of the oil palm sector. They suggested important advances in soil management, and highlight the progress in biological control, and organic fertilization (particularly in the Northern Zone). There have also been important advances in the reduction of water pollution, and some important investments have been made in water management in the Northern zone. Currently, more than 98% of the oil palm mills have water treatment systems before discharging effluent, compared to only 6% in 1992. Plantations now remove more than 95% of the organic load of the waste flow and, thus, companies in the sector generally adhere to current regulations(Rodriguez-Becerra and van Hoof, 2003). Most of these processes have been conducted under the coordination of Fedepalma and Cenipalma (Colombian Oil Palm Research Center). However, strong interest in biodiversity related research was only observed until recently.

In 2008, the Alexander Von Humboldt Institute conducted a strategic environmental assessment of the policies, plans and programs incorporating biofuels in Colombia, with emphasis on biodiversity(MAVDT, 2008). Positively, they assessed the situation and provided a number of valuable criteria for land use planning in biofuels. However, the study was short-lived and never integrated into ongoing monitoring plans.

The increasing role of the RSPO (Roundtable on Sustainable Palm Oil; www.rspo.org), albeit with some criticism (Laurance et al., 2010; Marin-Burgos et al., 2015), has apparently served to regulate international oil palm activity in recent years. In October 2008, Colombia hosted the first latin american meeting of the RSPO, in Cartagena, one year after the public commitment Conpes 3477 (DNP, 2007) or "Policy for the Competitive Development of the Colombian oil palm sector" was made. This policy focused mainly on production, and there were no guidelines regarding biodiversity considerations, except for a vague mention on the importance of considering the "social and environmental responsibility" into the business of oil palm. However, a subsequent policy in 2008 (DNP, 2008) resulted in the government paying more attention to environmental aspects, especially those related to carbon emissions reduction. This policy recommended updating the environmental guidelines for the sector, and encouraged the sector to work toward certification schemes, as a way to be more competitive in the international market. An analysis of the process of the national interpretation of RSPO is presented in Seeboldt and Salinas (2010) and Marin-Burgos et al. (2015).

Few regulations exist specifically to oil palm development in Colombia. Fedepalma, the Ministry of Environment and Regional Autonomous Corporations subscribed to an agreement in the context of the so-called scheme of Cleaner Production, but this was mostly concerned with carbon related issues. The only apparent policy designed to regulate agroindustry has been developed by the Regional Autonomous Corporation of Casanare, an environmental authority (Corporinoquia, 2011). This public organization developed specific regulations related to the use of water in some ecosystems that must be followed in selected parts of the Orinoquia region before an environmental license will be issued.

Few programs have started to focus on oil palm recently. WWF-Colombia, for example, identified High-Conservation Value (HCV) ecosystems in the Orinoco and Chocó ecoregions over the period 2012-2015 (WWF, 2007). Currently, the most important investment in biodiversity issues in Colombia (and Latin America) has been addressed through The Global Environment Facility of the United Nations (GEF). This initiative, called "Biodiversity Conservation in the areas of oil palm plantations" (GEF/BID PPB) is being developed jointly by Fedepalma, Cenipalma, IAvH, and WWF-Colombia. The GEF/BID PPB project, currently being developed over five years, is worth US$18.3 million and aims to strengthen biodiversity in agro-ecosystems through the processes of characterization of wildlife and ecosystems, maintenance of protected areas, identification of biological corridors, and environmental services (Fedepalma, 2012). This project is a significant investment that will aid in better understanding of biodiversity conservation in this agro-ecosystem in Colombia and provide important input into developing appropriate management guidelines for this sector.

Future research directions

The vast majority of research associated with oil palm plantations in Colombia has focused on biotechnology, soils, biological pest control, carbon stock research, and reduction of greenhouse gases. Landscape approaches such as land-use change modeling and the identification of HCV areas have only been recently reported, but knowledge about the retention of biodiversity within oil palm landscapes remains very scarce, meaning there is still large uncertainty about oil palm biodiversity impacts. The few wildlife studies have mostly focused on vertebrates, predominantly mammals and birds. Moreover, most research has been performed by independent academics, not as part of a governmental program, nor with a focus on the additional impacts of the biofuel incentives program. However, the GEF/BID PPB -project (described above) is the first national program for conservation planning in oil palm dominated landscapes and may generate important biodiversity information identifying the specific management needs for the country and for environmental sustainability.

My work identifies the need for greater investment in the following research themes:

- Diversity and population studies on all animal groups inside plantations and surrounding natural ecosystems (including fish and invertebrates). Research should include habitat use and dispersal of focal species.

- The definition of thresholds or maximum plantation size that could maintain natural movements and dispersal of species across production landscapes; including permeability, and landscape features that enhance the conservation value of these private lands.

- The examination of additional priorities includes complementary landscape and local scales studies. These analyses would include research on structural and functional connectivity, ecosystem services, and multi-temporal assessment of land use changes. For instance, it is important to monitor the advance of plantations in both forested and non-forested ecosystems using modern techniques of spatial analysis, especially natural savannas as in these biomes are where most expansion is predicted.

- The design of a multicriteria scheme to update the map of suitable zones for the expansion of oil palm, including not only soil and climatic characteristics, but also ecosystems and biodiversity aspects would be particularly useful to visualize the prospect of Colombia for sustainable oil palm developments.

- It is important to accurately delimit areas of natural savannas, seminatural savannas, low intensity pasture, and improved pasture to properly identify and assess areas suitable for oil palm cultivation. This accurate land cover delineation would be of particular use in the Llanos region where is does not yet exist and most of the current and projected oil palm expansion is taking place.

- Finally, it is necessary to understand how hydrobiological cycles and carrying capacity of water sources (e.g. rivers, “caños”) in savannas are altered by the expansion of oil palm in the Orinoquia region. This is because, savanna ecosystems have particular hydrobiological cycles which may be extremely sensitive to oil palm implementation.

Though several natural ecosystems have been transformed into oil palm plantations (especially in the Western Zone) in Colombia, the transformation of natural landscapes has not been as aggressive as in some Southeast Asian countries such as Indonesia or Malaysia. Unlike these countries, Colombia has large areas of land that has already been transformed to pastures or other types of agriculture prior to oil palm production, which to date has minimized the impact of expansion in forested ecosystems. This trend is clearly positive in terms of reducing the negative impacts of growing oil palm production and provides an opportunity to improve product competitiveness in a world that demands more environmentally-friendly products, though whether it will continue as such remains to be seen. Moreover, the future of native landcovers in the Orinoquia or Llanos Orientales region in Colombia is dire given the targeting of this region by agro-industrial development apart from oil palm (e.g. soybean, rice, forestry plantations). As such and given the pressure for mineral or fossil fuel extraction, and the explosion of agro-business in this complex and biodiversity-rich ecosystem the future of conservation is uncertain.

Conservation planning, at the nexus of economic environmental interests, is urgently needed. For instance, it is necessary to carefully analyze how the expansion of oil palm into Colombian landscapes is going to take place. At present, environmental and conservation assessments tend to focus on forested ecosystems, ignoring the importance of “non-forested” ecosystems such as savannas. As such, the fact that oil palm production in the Eastern zone does not generate considerable carbon debt (Valencia Botero et al., 2014) often overrides the other important conservation issues and concern in these Llanos´ ecosystems. Thus, I encourage analyzing conservation strategies to ensure they are being effectively applied in non-forested ecosystems such as savannas and associated ecosystems (e.g. wetlands) and attempting to ensure that “habitat loss” does not mean forest loss only. Emphasis on improving these assessments should be placed in particular of the rapidly expanding production regions for the Eastern and Northern zones of Colombia.

The availability of pastures and other converted lands in Colombia also offers an opportunity to minimize the impacts of future oil palm expansion. However, there is minimal evidence on the possible impacts, or even the potential benefits, of oil palm on local biodiversity. I recognize the importance of the oil palm sector for the economic development of the country and for the creation of jobs but finding a balance between the economical revenues and social and environmental (including biodiversity) aspects is critical. Heterogeneous landscapes or agro-ecosystems tend to be seen as having low importance for conservation of nature, but biodiversity within lands of complex land uses needs to be addressed. It is important that companies invest on identifying their territory in ecological terms and protect the natural capital of Colombia.

To conclude, Colombia has the potential to be a leader in sustainable oil palm development. Certification schemes such as the RSPO, and the growing demands of green markets have encouraged oil palm growers to improve their practices, hopefully leading to long-term alteration in production practices. National regulations and international commitments (e.g. Ramsar, Convention on Biological Diversity) can also help to positively influence the expansion of oil palm. However, official commitments and monitoring programs to evaluate the implementation, results, and recommendation of current efforts are also essential.

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Chapter 2 Terrestrial mammal responses to oil palm dominated landscapes in Colombia

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Statement of contribution of authors:

LEP conceived the main idea and research questions, suggested initial design, collected data, coordinated and carried out fieldwork, organized data, conducted all analysis, and wrote the first manuscript. MJC, WE, GRC helped with the design, analysis and the discussion, and supported the writing of the manuscript. WFL helped with research questions, design, funding, and final edition of the manuscript. For other contributions see acknowledgments.

Abstract

The rapid expansion of oil palm cultivation in the Neotropics has generated great debate around possible biodiversity impacts. Colombia, is the largest producer of oil palm in the Americas, but the effects of oil palm cultivation on native fauna are poorly understood. Here, I compared the richness, abundance and composition of terrestrial mammal species between oil palm plantations and riparian forest in the Llanos region of Colombia. Further, I determined the relationships and influence of landscape and habitat level variables on those metrics. I found that species richness and composition differed significantly between oil palm and riparian forest, with site level richness inside oil palm plantations being 47% lower, on average, than in riparian forest. Within plantations, mammalian species richness was strongly and negatively correlated with cattle abundance, and positively correlated with the density of undergrowth vegetation. Mammal composition at the landscape level was significantly influenced by cover type, percentage of remaining forest and the distance to the nearest town. Conversely, within oil palm sites, understory vegetation, cattle relative abundance, and canopy cover had significant effects on community composition. Species specific abundance responses varied between land cover types, with oil palm having positive effects on mesopredators, insectivores and grazers. My findings suggest that increasing habitat complexity, avoiding cattle and retaining native riparian forest– regardless of its structure– inside oil palm-dominated landscapes will help to support higher native mammal richness and abundance at both local and landscape scales.

Key words: agriculture, camera trap, gallery forest, human-dominated landscape, Llanos, riparian, savanna,

Introduction

Habitat loss caused by agricultural expansion is one of the main drivers of global biodiversity loss (Campbell et al., 2017; Laurance et al., 2014). Between 1980 and 2000, 55% of new arable land in the tropics came at the expense of intact forest (Gibbs et al., 2010). Within human dominated landscapes, the intensity of the agricultural effects on native fauna depends on the type of agriculture employed and landscape and local level factors (e.g. Cosentino et al., 2011; Franklin and Lindenmayer, 2009). Agriculture growth has been exacerbated by the rapid increase in food demand and the steady global in use of fats, oils, and biofuels (Rands et al., 2010). Oil palm (*Elaeis guineensis*) cultivation, for instance, has become a major threat to biodiversity in Southeast Asia, where global production is currently centered (Danielsen et al., 2009; Fitzherbert et al., 2008). Evidence from this region demonstrates that oil palm plantations have negative effects on the abundance and occurrence of a wide range of taxa, including birds, invertebrates, and mammals (Edwards et al., 2010b; Koh and Wilcove, 2008; Maddox et al., 2007; Yue et al., 2015).

In the Neotropics (Latin America), oil palm production is rapidly expanding (Buttler and Laurance, 2009; Dammert, 2014). This expansion is especially evident in Colombia, where the area under oil palm cultivation has increased to nearly 500,000 ha (Fedepalma, 2014), making the country the largest Neotropical oil palm producer. Initial government projections suggested oil palm cultivation in Colombia will increase to approximately one million hectares by the year 2020 (MADR, 2006b). Although this expansion by 2020 is unlikely (see Castiblanco et al 2013), if unplanned, this expansion could result in a substantial conversion of natural habitats (e.g., forests, savannas and wetlands), displacement of native wildlife, and disruption of ecosystem functioning (Rodriguez-Becerra and van Hoof, 2003; Romero-Ruiz et al., 2012). However, the likely effects of oil palm on Colombia's mammals are uncertain as systematic assessments of mammal response to oil palm conversion in Colombia are scarce (Pardo et al., 2015).

The Llanos Orientales region (eastern plains) of Colombia is renowned for its species and ecosystem diversity (Lasso et al., 2010). This region comprises large areas of savannas, grasslands, wetlands and riparian forest (known locally as gallery forest) (e.g. IDEAM et al., 2007; Lasso et al., 2010). However, conversion of savannas to agriculture in the Llanos region (especially in the western Llanos) has increased exponentially from 1970 to 2011, with annual conversion rates for pasture of approximately 100,000 ha and for oil palm plantations of 5-10,000 ha, especially in the western Llanos (Etter et al., 2011). Moreover, the "Altillanura" or high lands of the Llanos has been identified by the government and international agencies as the "new agricultural frontier of Colombia" (see Pardo et al., 2015), suggesting likely future large-scale conversion. The western Llanos is also the epicenter for Colombian oil palm production, with approximately 180,000 ha under production (Fedepalma, 2014), though most recent oil palm expansion has predominantly occurred on cropping and grazing lands (Castiblanco et al., 2013; Furumo and Aide, 2017; Garcia-Ulloa et al., 2012). There is, however, a paucity of biodiversity studies in the region (Díaz-Pulido et al., 2017), that can help to understand the biodiversity associated with the region, and the responses of wildlife to growing agriculture and land use change.

Mammals are a good indicator of ecosystem quality or change, given their diversity and the complexity of ecological niches they occupy (Ceballos et al., 2005). Mammals are also important for their role in ecosystem processes, benefits to humans (Bello et al., 2015; Camargo-Sanabria and Mendoza, 2016; Estes et al., 2011) and their intrinsic and cultural value (Castaño-Uribe, 2013). At the same time, mammals are one of the most globally threatened taxonomic groups due to habitat loss and fragmentation arising mostly as a byproduct of agricultural expansion (Dirzo et al., 2014). Colombia, for instance, contains the fifth highest level of mammal diversity globally, with 518 species recorded to date (Ramírez-Cháves et al., 2016). Of these species, 43 are presently threatened with extinction (Rodríguez-Mahecha et al., 2006). Therefore, it is important to identify the diversity patterns within and responses to oil palm production by Colombian mammal species to ensure the development of effective management strategies, to identify species of concern and to evaluate the capacity of the country to retain its mammal diversity in the face of rapid palm oil expansion.

In this study, I conducted an extensive camera trapping survey in the western Llanos Orientales-Colombia's leading oil palm production region, to compare species richness, abundance and composition of terrestrial mammals between oil palm plantations and riparian forests strips, the two most dominant land cover types in the region. Further, we determine the main landscape and habitat correlates driving mammalian species richness, abundance and composition within and between these land cover types in an attempt to identify management practices that may help minimize the impact of this expanding agricultural practice.

Methods

Study area

I conducted this study across a ~2,000 km^2 area in the rural areas surrounding the towns of Restrepo, Cumaral, Cabuyaro, Acacias, Castilla la Nueva, and San Carlos de Guaroa, in the Department of Meta, in the eastern plains or Llanos Orientales region of Colombia, (Fig 2.1).

This area ranges from 194–394 m.a.s.l. and contains a mosaic of different land cover types including natural ecosystems of differing successional status interspersed by human land uses such as grazing and agriculture. Oil palm production has steadily increased in extent across the area over the last two decades and is now the dominant land-use type (Romero-Ruiz et al., 2012). Secondary riparian forest strips (or gallery forest) of differing size and age are the predominant remnant native vegetation type and are delineated in this study as young (height < 5 m), intermediate (height ~8 m), and (rarely present) mature secondary forest (height >15 m) (Madriñán et al., 2007).

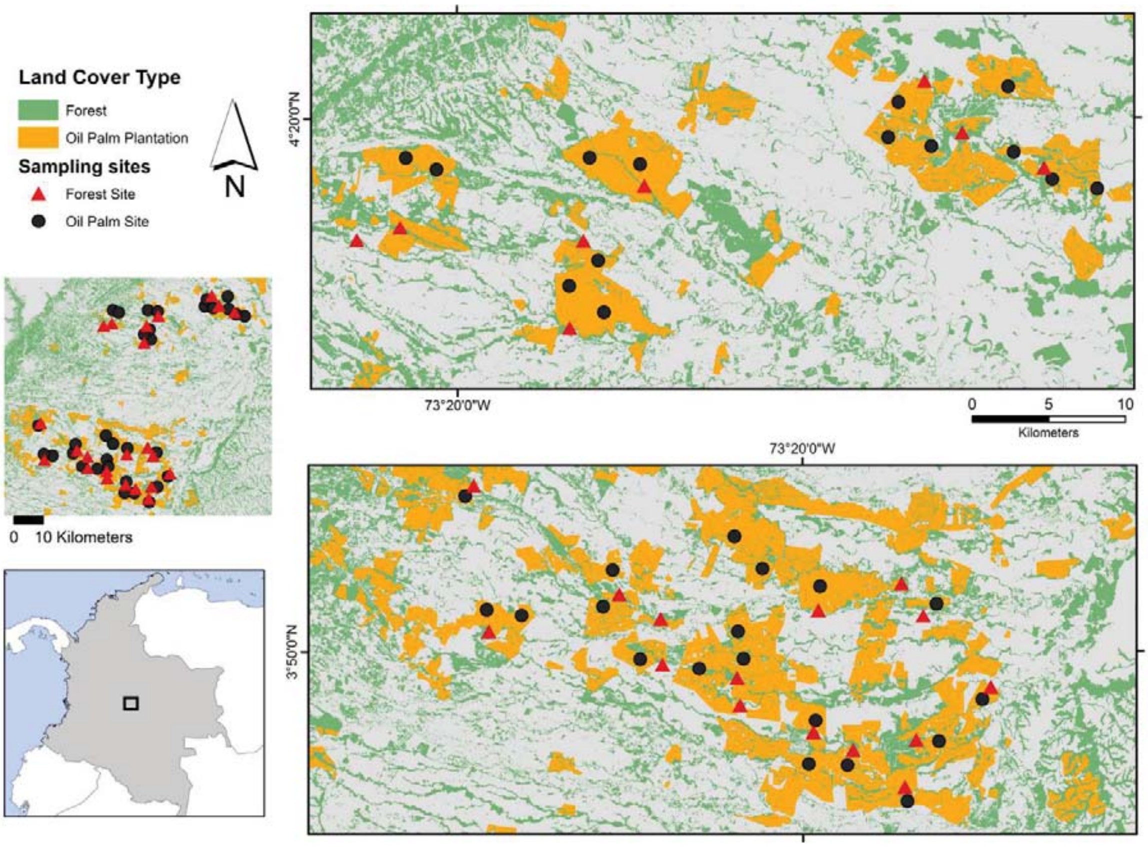

Figure 2.1. Study area and location of 56 sampling sites in the Department of Meta, Llanos, Colombia.

Sampling design

I sampled 33 sites in oil palm plantations (hereafter referred to as plantations) and 23 in riparian forests (hereafter referred to as forests) with sampling effort proportionate to the spatial extent of these land covers within the study area (Fig 2.1). Sampling in plantations was restricted to those planted before 2006 to avoid confounding responses due to plantation age. Sites within each cover type were a minimum of 2 km apart to ensure the spatial independence of samples (Team Network, 2008; Tobler et al., 2008b) and to encompass the average expected diameter of the common species' home ranges in the study area (Ferrer et al., 2009; Pardo and Payán, 2015).

I used camera traps to detect medium and large (> 1kg) terrestrial mammals in the dry/transition seasons across the September 2014 to January 2016. Since I had a limited number of cameras, the study area was not sampled simultaneously across all sites, and surveys were organized sequentially in different sessions. I used seven cameras to sample each site, as determined by a pilot study that I conducted in the study area (Pardo et al. not publ.). This sampling intensity was implemented to ensure greater sampling completeness compared with traditional practice of using a single camera per site (Burton et al., 2015). In riparian forests, camera traps were spaced ~250 m apart along transects to follow the linear nature of the vegetation type, and were set close to animal trails where possible. Due to the homogenous nature of oil palm plantations, cameras in this land cover were spaced similar distances to riparian forests, but were arranged in a zigzag pattern to maximize spatial coverage. I pooled the data derived from the seven cameras at each site into a single sample and used this as my sample unit for estimating species richness and relative abundance (see below). I identified mammal species using the most recent taxonomic classification of Colombian mammals (Ramírez-Cháves et al., 2016).

Cameras (Reconyx HC500 Hyperfire^{TM}, United States) were active for a minimum of 30 days at each site and were configured according to the following criteria: high sensitivity, one-second intervals between consecutive photographs (three per trigger), no delay or quiet period between triggers, a minimum distance of 1.5 m from an animal's potential path, and a height of 25–30 cm depending on the terrain. All cameras were fixed to trees or wooden poles (in the case of cameras inside plantations) with a steel security cable (Python^{TM}, US). Arboreal and other species not likely detected by camera trap were recorded opportunistically by direct observations, but were not use for analysis.

This research was conducted in compliance with the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes, 7th Edition, 2004 and the Qld Animal Care and Protection Act, 2001. This study received animal ethics approval from Animal Ethics Committee of James Cook University.

Species richness and abundance

To estimate species richness, I first computed species accumulation curves using the software EstimateS (Colwell, 2013). To eliminate the influence of the order in which each sample (days) was added, I randomized sample order (n=1,000). The number of mammalian species was estimated using the Chao 2 (S_{est}) estimator of richness(Colwell and Coddington, 1994) a non-parametric estimator that uses incidence data to avoid problems related to detection probabilities and abundance estimation. For each site, I calculated the estimated sampling completeness (ESC) by dividing the number of observed species (S_{obs}) over the estimated number of species (S_{est}) and then expressed the result as a percentage. A sample-based rarefaction curve was then used to evaluate the effectiveness of the sample effort in R package *vegan* (Oksanen et al., 2017; R Development Core Team, 2014), and to evaluate if species richness was significantly different between land covers (i.e. by examining the confidence intervals of the curve). I tested for potential spatial autocorrelation in the predictors to prevent an inflation of type two errors using Moran's I coefficient within the SAM software V4.0 (Rangel et al., 2010). In all instances (classes of the correlogram), Moran's I was not significant ($p > 0.05$).

I used capture frequencies of individual species as a proxy for a relative abundance index. This index was calculated as the number of independent photographs divided by the sampling effort x 100. Only detections of the same species taken at periods of greater than 30 minutes were considered as independent (O'Brien et al., 2003). Sample effort was defined as the sum of the number of days that the cameras were active within each transect (camera days). The relative abundance index offers a good alternative when the identification of individuals of species is impossible, and serves as a way to evaluate the structure of the assemblage in terms of commonness and rarity (Magurran and Henderson, 2011), or as a surrogate for "intensity of use”, but should not be used as a measure of abundance or density *sensu stricto* (see Wearn and Glover-Kapfer, 2017).

Landscape variables

I selected five landscape variables previously shown to influence mammal richness and composition: 1) percentage of forest (Laurance et al., 2002); 2) distance to roads (m); 3) distance to towns (m) (e.g. Clements et al., 2014) 4) land-cover/land-use types (hereafter refered to as land-cover type): oil palm plantation versus forest (Danielsen et al., 2009); and 5) the Normalized Difference Vegetation Index (NDVI) (Pettorelli et al., 2005).

To quantify the percentage of forest at each site, I created a 500 m-radius buffer around each camera within each individual transect and then merged the buffers into one single area for analysis. Distance to road and towns was calculated as the average Euclidean distance (m) to the nearest road or town (respectively) for all cameras within the site. These measurements were all obtained using Quantum GIS 2.0.1 (QGIS Development Team, 2016). Spatial information for the plantations was supplied by the National Federation of Oil Palm Growers (FEDEPALMA) and Land-cover maps acquired from the official ecosystems dataset for Colombia (IDEAM et al., 2007). To identify forested areas, I used data from a recent CLASlite classification (Asner et al., 2009) which provide improved accuracy and more recent assessment of forest cover.

To validate the geographic information available, I also used field notes, Google Earth imagery®, and aerial photographs taken from a flight over the study area (August 2014; S1 Fig). I calculated the NDVI of multispectral data using Landsat 8 images downloaded on January 2016 (https://landsat.usgs.gov/landsat-data-access). NDVI is widely used as a proxy for vegetation productivity and related parameters, such as net primary production, plant biomass, and vegetation density (Roldan and Poveda, 2006). Its influence on animal distribution and abundances has previously been confirmed, particularly in areas with land-uses gradients (Borowik et al., 2013; Pettorelli et al., 2005). NDVI values range between zero and one with higher values indicating dense green or unstressed vegetation that is relatively high in quality and productivity (Roldan and Poveda, 2006). This metric, however, may vary depending on weather conditions and seasonality (Borowik et al. 2013).

Habitat covariates

I used different sets of habitat covariates for assessing patterns within plantations and riparian forests. Within plantations habitat variables were related to crop management practices. These included: 1) the presence of undergrowth vegetation (a factor with two levels –see Appendix 1): clean (no)-to-low versus medium-to-high understory vegetation; 2) canopy cover (%); 3) distance (m) to the nearest forest patch; 4) palm height (m); and 5) relative abundance of cattle. To calculate relative abundance of cattle, I used the capture frequency (or catch per unit of effort), as I did for wild mammals described in previous section. In the forests, I considered four habitat covariates commonly used as a proxy of vegetation structure in natural vegetation systems: 1) canopy cover; 2) tree abundance; 3) diameter at breast height (DBH); and 4) tree height. Following the methods of Albesiano and Rangel (2006). I measured these covariates using a 10 x 10 m quadrat around each camera location within the transect, and then obtained a single value for the transect by averaging these measurements for each site.

Statistical analyses

Influence of landscape and habitat variables on species richness

I evaluated the influence of landscape and habitat variables on mean mammalian species richness using individual Poisson generalized linear mixed models (GLMMs) with habitat and landscape variables as fixed factors, and site as a random factor. Prior to model generation, I checked for correlated predictor variables following the protocol of Zuur (2010). To prevent undue influence of measurement unit on any explanatory variables, all explanatory variables were standardized (x–mean(x))/SD(x)). Standardizing in this manner has the additional benefit that the effect sizes of all variables can be directly compared via model coefficients. I used observed, rather than estimated species richness, as estimated richness had very high confidence intervals in some oil palm sites. Nevertheless, observed and estimated values were very similar and the correlation between the estimated richness and observed richness was high (Spearman's

$r = 0.91$). Primates were not used in any of the analysis because camera trapping is not a suitable technique for arboreal animals.

I generated models with all valid combinations of the covariates without interaction effects (32 models for landscape covariates, and 16 models for habitat covariates in the two land-cover types) and used an information-theoretic approach to determine the most parsimonious model based on Akaike's information criterion, corrected for small sample size (AICc) (Burnham et al., 2011). I used a model-averaging approach when more than one plausible model (i.e., Δ AICc <7) was identified, or when the evidence ratio in support of the "best" model was low. The relative importance of each variable was then assessed by summing the Akaike Weight (ω_i) of all plausible selected models containing that variable(Burnham et al., 2011). Analyses were conducted using the R packages *lme4* (Bates et al., 2015) and *MuMIn* (Barton, 2009).

Influence of landscape and habitat variables on abundance and composition

Analyses of abundance and composition were undertaken in two separate procedures. First, I used a Non-Metric Multidimensional Scaling (NMDS) ordination based on Bray Curtis dissimilarity matrix among sites to visualize overall differences in the structure and composition of the mammal assemblage between oil palm and forest (i.e. the distribution of capture records across species and sites). The NMDS is a flexible technique that uses rank orders to evaluate dissimilarities between different communities instead of absolute distances (Legendre and Legendre, 2012). This ordination was plotted a using the R package *vegan*.

Second, to test for the effect of landscape and habitat covariates on overall community composition and on individual species relative abundances, I used a multivariate version of generalized linear modeling (GLM) in *mvabund* R package (Wang et al., 2012). This package allows for quantification of factors affecting composition of the whole assemblage (multivariate) and individual species responses (univariate). For this analysis I rounded the capture frequencies and use it as the response variable, implementing a negative binomial distribution to account for mean/variance relationships. I used the traitglm function and GLM1path with L1 (LASSO) penalty to predict species abundance as a function of landscape and habitat covariates. This function automatically performs model selection, setting to zero any interaction coefficients that do not help reduce AIC (Wang et al., 2012; Warton et al., 2015). I included all covariates used for the species richness analyses and report the size and direction of the model coefficients as a measure of their importance. Only species recorded from more than 15 observations and at more than three sites were included because preliminary analysis returned very high standard errors of parameter estimates for species below these thresholds.

Results

General patterns of species richness and relative abundance.

I sampled a total of 12,403 camera days and identified 24 terrestrial mammal species (23 medium to large sized and one small mouse) and two arboreal monkeys, representing seven taxonomic orders and 16 families (Appendix 2). Of the 26 identified species, 24 were in the forest and 19 inside oil palm plantations. In the plantations, species richness per site ranged from 1–7, while in the forests, it ranged from 9–14. All species detected inside plantations were also detected in the forest, except for red-brocket deer (*Mazama spp*) and a small mouse (not identifiable by photographs), whereas seven species were detected only inside the forest. Another 17 species were recorded in both riparian forest and oil palm plantations (Appendix 2). In addition, three more primate species were recorded opportunistically by direct observations but only in the forests. These were the night monkey (*Aotus brumbacki*), the titi monkey (*Plecturocebus ornatus*), and the howler monkey (*Alouatta seniculus*). The first two are considered vulnerable (VU) by the Colombian national assessment of threatened species (MADS, 2014)

The sampling completeness for terrestrial mammals in the study area was relatively high, suggesting that the sampling intensity within sites as well as the number of sites examined captured most of the total species expected in the region (mean=84%; SD=15.97). Rarefaction curves showed a representative sample effort with clear asymptotes. Associated confidence intervals of these curves did not overlap, indicating that total richness between plantations and forest was significantly different (Fig 2.2).

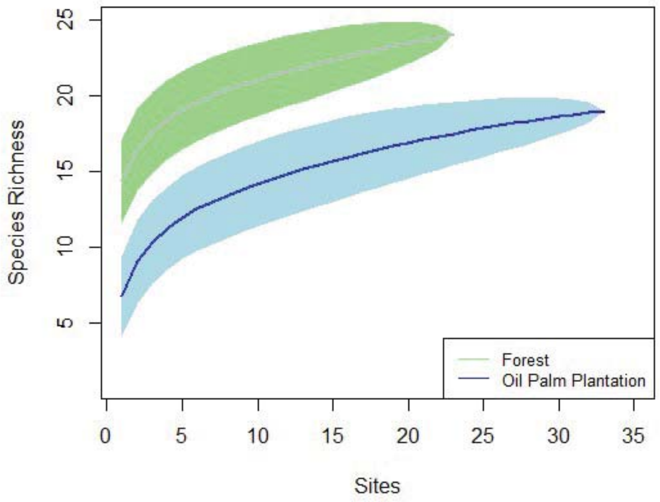

Figure 2.2. Sample-based rarefaction curves estimating medium and large terrestrial mammal species richness in Llanos, Colombia.

The detection frequency (i.e. relative abundance) of the majority of species was low across the study area (Fig 2.3). Indeed, eight species had fewer than three independent photographs in the entire survey (puma, grison, red-brocked deer, collared peccary, mouse, coendu, tayra, and four-eye opossum; for scientific names refer to Appendix 2). Of these species the last three were found exclusively inside riparian forests. Plantations had fewer total species detections than forests (582 and 2,085, respectively) (Appendix 2). For most other species, relative abundance varied greatly between the two land-cover types and between sites (Fig 2.3). One species, the fox, showed clearly higher abundances inside plantations than in riparian forest. Other species also showed higher abundances within plantations, but the magnitude of the difference between habitat types were smaller (i.e. jaguarondi, raccoon and white-tailed deer; Appendix 2, Fig 2.3). All remaining species were detected more frequently in riparian forest sites than in palm plantations. The giant anteater, however, was the only species widely distributed and with relatively high total detections across sites in both plantations and forests (Appendix 2, Fig 2.3).

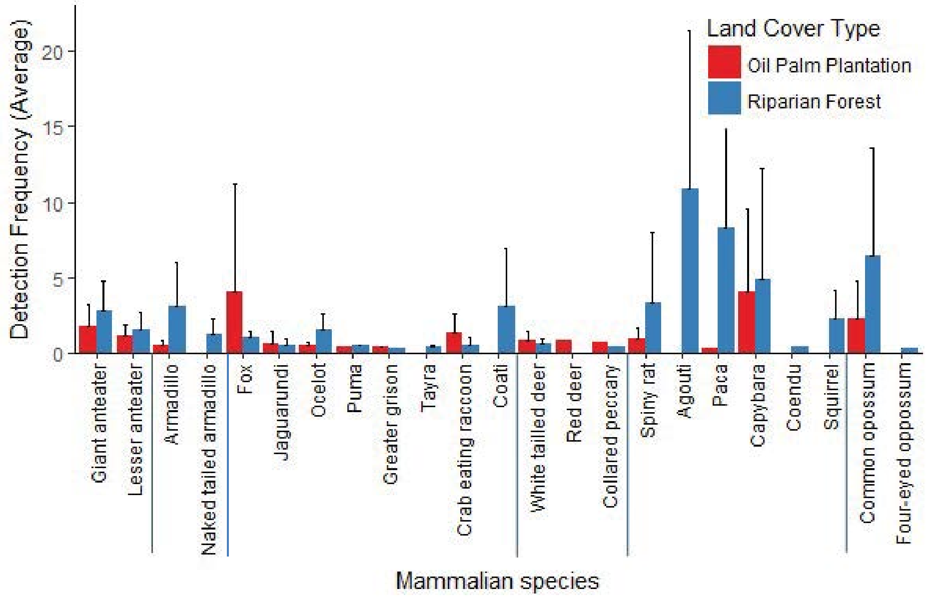

Figure 2.3. Mean detection/capture frequencies or relative abundances (number of independent photos/sample effort*100) of 23 terrestrial mammal species detected in oil palm plantations and riparian forests in Llanos, Colombia. Bars indicate the upper standard deviation range. Blue lines separate taxonomic orders (from left to right): Pilosa, Cingulata, Carnivora, Artiodactyla, Rodentia, Marsupialia.

Note: A mouse species and two species of primates were also detected, but they are not included in this figure because the first could not be identified by camera trap and the latter are not terrestrial mammals.

Drivers of mammal species richness

Landscape level effects

No single model offered the best explanation for species richness at the landscape level. Results from the averaged model (using 14 suitable candidate models of Δ AICc <7) revealed that land-cover type was clearly the main driver of differences in species richness ($\sum \omega_i$ = 100%; Table 2). Model averaged coefficients showed that plantations had a negative influence on mammal species richness with site level species richness in plantations 47% lower, on average [(β plantations = -0.74 (SE 0.13)] than that in forests, which showed a high positive influence in determining species richness [β forest = 2.21 (SE 0.08); Table 2.1)]. All remaining continuous variables exerted a weak influence on mammal species richness as indicated by the importance value (combined weight, $\sum\omega_i< 36\%$) of their averaged variable and effect sizes (Table 2.1). Percentage of forest, distance to towns, and NDVI all displayed slightly positive effects on species richness, while distance to roads had a slightly negative effect (Fig 2.4, Table 2.1; see Appendix 3 for model ranking).

Table 2.1. Relationship between landscape and habitat covariates and terrestrial mammalian richness in Llanos, Colombia as determined using a GLMM; estimates correspond to the conditional averaged parameter coefficient and relative importance is based on the *w*AIC - Akaike information criterion.

	Estimate	Adjusted SE	*w*AIC (Relative importance)
Landscape covariates			
Intercept	2.21	0.08	
Land-cover type (oil palm plantation)	–0.74	0.13	1.00
NDVI	0.07	0.07	0.36
Distance to nearest town (km)	0.03	0.06	0.24
Forest (%)	0.02	0.08	0.23
Dist. road (km)	–0.01	0.06	0.23
Habitat covariates for oil palm			
Intercept	1.27	0.20	
Cattle detection frequency	–0.27	0.15	0.69
Understory vegetation (medium-high)	0.41	0.24	0.55
Height (m)	–0.13	0.10	0.39
Distance to nearest patch (km)	–0.11	0.10	0.35
Canopy cover (%)	0.08	0.13	0.26
Habitat covariates for forest			
Intercept	2.22	0.07	
Number of trees	–0.05	0.08	0.22
DBH (cm)	0.05	0.08	0.22
Canopy cover (%)	–0.02	0.08	0.18
Height (m)	–0.01	0.09	0.18

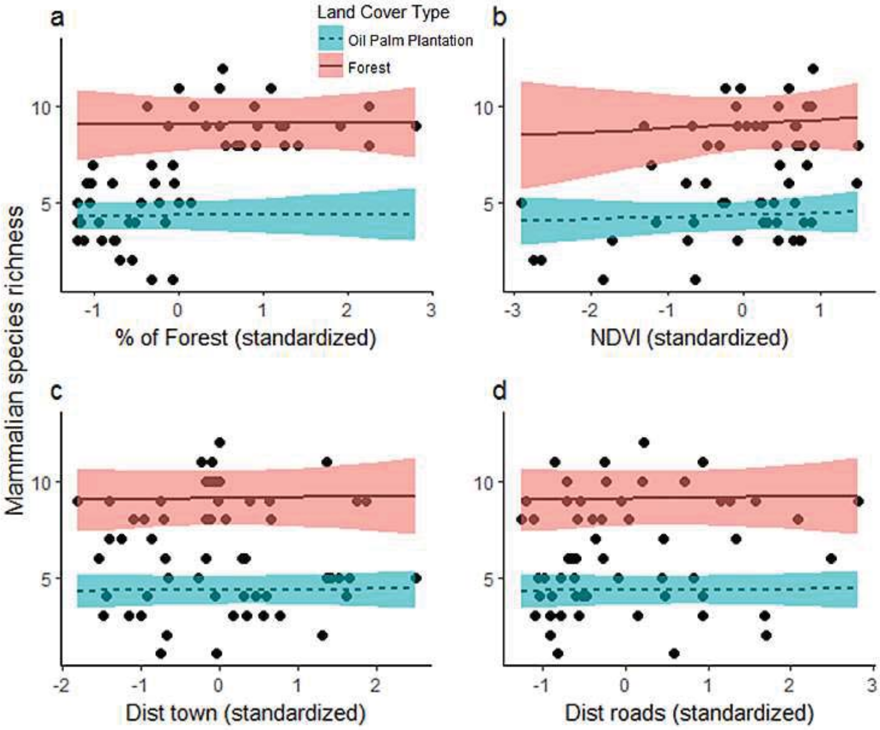

Figure 2.4. Relationship between mammalian species richness as a function of landscape covariates in Llanos, Colombia: a) percentage of forest, b) NDVI, c) distance to towns, and d) distance to roads, according to land-cover type (oil palm plantations vs forest). The trend lines are predicted values of the GLMM model averaged (holding other covariates constant) and shaded areas represent the 95% confidence intervals. Dotted points represent the actual values of the covariate. Effect of land-cover type is strong, while the slope of continues variables does not show an important effect on species richness

Habitat level effects in plantations

Similar to the landscape covariates, no single model was identified as being demonstrably better than any other and 15 candidate models were retained based on ΔAICc values (Appendix 4). Multimodel averaging indicated that the main predictors of mammalian species richness were relative abundance of cattle ($\sum \omega_i$ = 69%) and presence of understory vegetation ($\sum \omega_i$ = 55%). These variables exerted negative and positive effects on richness respectively. Importantly, sites with medium-to-high understory vegetation had 66% more species on average than plantations with no understory vegetation. All remaining variables had weaker effects on species richness [Palm tree height ($\sum\omega_i$ =39%), distance to forest patches ($\sum\omega_i$ 35%, and canopy cover ($\sum\omega_i$ 26%); Table 2.1]. Both palm height and distance to forest patches had a negative influence with species richness, while the relationship with canopy cover was positive.

Habitat level effects in forests

No single model emerged as a possible driver of mammalian richness inside forest (Appendix 5). Unlike plantations, the model averaged coefficients suggested no evidence of any particular covariate exerting a stronger influence on mammal species richness inside the forests, as shown by their similar contribution. As such, number of trees and DBH had combined effects among models of 22% each, while canopy cover and height had 18% (Table 2.1); only DBH exerted a positive influence on species richness.

Drivers of community composition and species abundance

Landscape level effects

Overall, ordination analysis indicated important dissimilarities in composition between plantations and forest, with plantation sites relatively more scattered and separated from each other (i.e. more different in composition) compared to forest sites (Fig 2.4). Multivariate GLM confirmed that mammal community composition differed significantly between forests and plantations (Deviance [Dev]=282.22, Pr (>Dev)=0.001) Similarly, the variables percentage of forest and distance to town also had a significant influence on assemblage composition (Deviance [Dev]=26.04, Pr (>Dev)= < 0.1; Deviance [Dev]=34.28, Pr (>Dev) < 0.05, respectively; Appendix 6, 7).

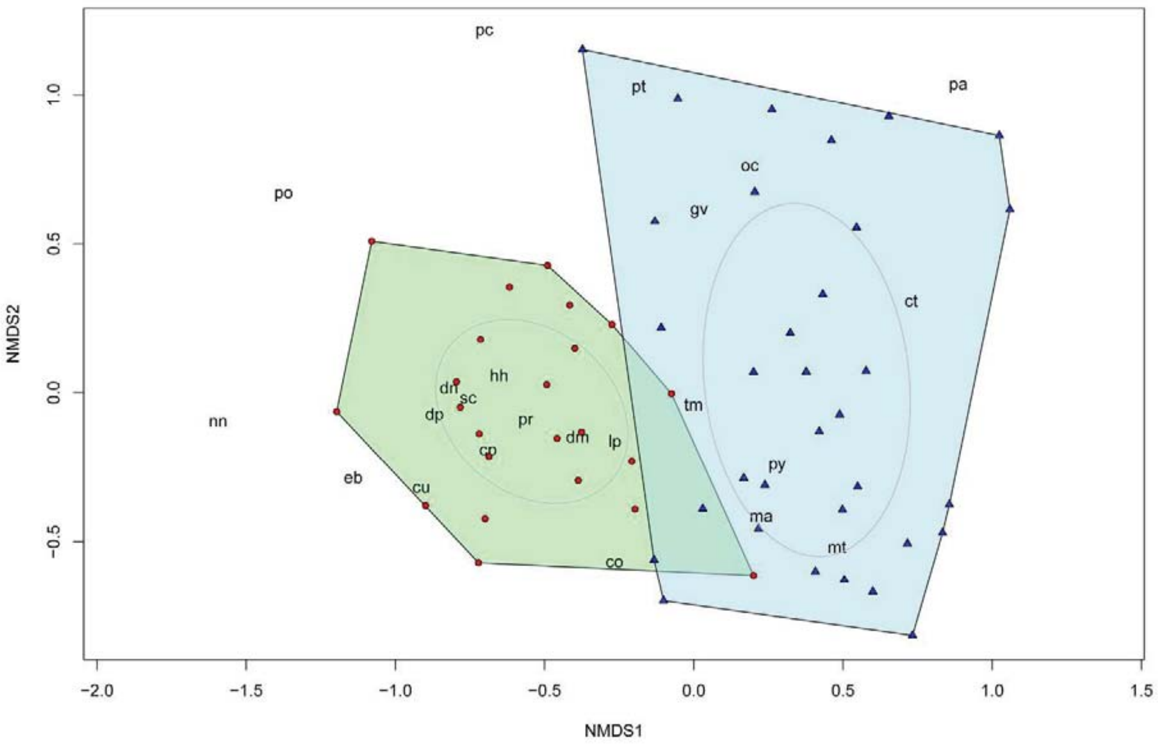

Figure 2.5. Overall mammal community composition across surveyed sites in oil palm plantations (triangles) and riparian forest (circles). Plot is based on capture frequencies of species using Bray-Curtis non-metric multidimentional analysis (NMDS) (stress = 0.22). Polygons connect the vertices of each cover type and ellipses emphasize the centroids of the community in each land cover. Species outside the boundaries were very rare in the landscape. Codes correspond to the initial letters of the scientific names of each species (refer to Appendix 2)

Individual species´ abundance response to oil palm cover varied between species. For example, the strongest negative effect of plantations on species abundances were shown by agouti and paca (Fig 2.6), while the strongest positive effect was found in foxes and jaguarundis (followed by white-tailed deer). Five species (giant and lesser anteaters, ocelots, raccoons, and common opossums) appeared to have neutral responses (i.e. not significant) to land-cover type showing a minimal (positively or negatively) influence (Fig 2.6). The effects of the remaining variables on species abundances were weak (not significant), except for the influence of percentage of forest in the landscape, which had negative and positive effects on capybara and raccoon, respectively (Fig 2.6).

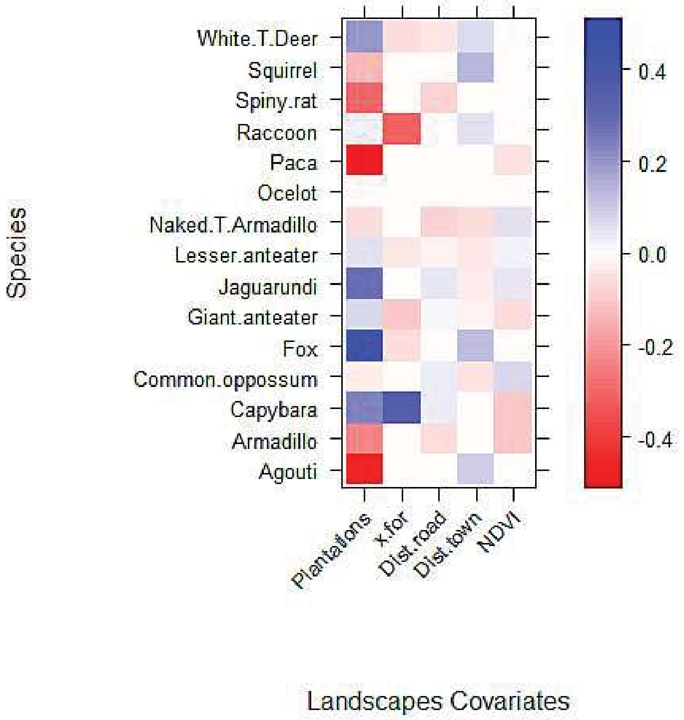

Figure 2.6 Mammalian relative abundance responses to selected landscape covariates in Llanos, Colombia. Values indicate GLM model coefficients and colors represent the effect sizes on the relative abundance of each species (univariate analysis). Abbreviations: Plantations=oil palm plantation, one of the 2 levels of the categorical variable "cover type" (i.e., riparian forest, and oil palm plantations); x.for=percentage of forests in the 500 m-radius buffer; Dist.road and Dist.town=the average nearest distance to roads and towns (respectively); NDVI: Normalized Difference Vegetation Index. Variables were standardized for direct comparison.

Habitat level effects inside plantations

Understory vegetation, relative abundance of cattle and canopy cover had a significant effect on the community composition (i.e. the overall combined effects of each factor, simultaneously assessed across all species) of mammals within plantations (Deviance [Dev]=20.88, Pr (>Dev)=0.045, Deviance [Dev]=29.57, Pr (>Dev)=0.002, Deviance [Dev]=19.87, Pr (>Dev)=0.043, respectively). Most of the individual species' coefficients were close to zero, with high standard errors, likely due to the low detections. Therefore, inferences for individual species responses inside oil palm should be taken cautiously. However, the detection of rare species, (i.e. those with less than 3 records) such as grison, puma, red-brocket deer, peccary, paca, (hence not suitable for statistical analysis) and capybara inside plantations were restricted to sites near to forest (i.e. mean distance among species of 430 m –SD 169 m).

Habitat covariates effects inside forests

There was no significant evidence of any habitat variable significantly influencing mammalian community composition inside the forests. DBH = [Dev]=12.33, Pr (>Dev) = 0.59; tree abundance = [Dev] = 0, Pr (>Dev) = 0.95; canopy cover = [Dev] =10.44, Pr (>Dev) = 0.75 and tree height = [Dev] = 22.43, Pr (>Dev) = 0.18.

Discussion

This study aimed to understand the structure and responses of mammal assemblages to an oil palm dominated landscape in Colombia. My results indicate that richness and composition are significantly lower in oil palm plantations compared to adjacent riparian forest. However, responses of individual species varied, with the relative abundances of most species responding negatively to oil palm, while other species appeared unaffected or even displayed positive responses to oil palm occurrence, such as mesopredators, insectivores and a grazer. This lower diversity of mammals in oil palm is similar to results previously reported for parts of Southeast Asia (Maddox et al., 2007; Wearn et al., 2017; Yue et al., 2015) and the Brazilian Amazon (Mendes-Oliveira et al., 2017). However, reductions in mammal diversity in this study occurred to a lesser degree than the previous findings from Southeast Asia. For example, at individual sites I detected an average of 47% fewer mammal species in plantations than in forests, whereas in some areas of Southeast Asia, fewer than 10% of total local native terrestrial mammals were found to occur in oil palm plantations (Maddox et al., 2007).

The relative minor differences in total mammal species richness (at the landscape level in particular) between plantations and forest, may be consequence of a long history of landscape transformation in the study area, especially for pasture creation (Etter et al., 2011; Madriñán et al., 2007). These effects can further be evident by the reduced abundance of species found. Historical land conversion practices and hunting may have already degraded the forest-dwelling mammals in the study area (i.e. more sensitive species such as giant armadillo–*Priodontes maximus*, danta–*Tapirus terrestris*, or jaguar–*Panthera onca*), decreasing the discernable difference in mammalian species richness between forests and plantations (see also Harding et al., 1998; Prugh et al., 2008). For instance, in the forests I detected only ~43% of the total medium- and large-sized mammal species that may exist in those areas and that are detectable by camera trap (~67 species) (Ferrer et al., 2009). Further, contrary to oil palm development in South East Asia, where 55% of expansion has occurred at the expense of forests (Koh and Wilcove, 2008), most recent expansion in Colombia has taken place in areas already modified for human land use (Castiblanco et al., 2013; Furumo and Aide, 2017). Therefore, I cannot unequivocally state that the decrease in present day species in the study area can be attributed solely to oil palm expansion. The lack of baseline data prior the implementation of oil palm limits further evaluations of population trends. Therefore, a monitoring program is recommended.

My study highlights the importance of secondary forest cover presence in human-dominated landscapes for biodiversity conservation. In this study, not only were forests important for retaining mammal species richness, but also for increasing the relative abundance of the majority of species. The lack of evidence found for any particular driver which significantly explained richness within riparian forest (see also Beca et al., 2017), suggests that regardless of the forests' structure, they are fundamental for maintaining mammal species in oil palm landscapes; which supports previous findings in secondary forests (Dent and Wright, 2009; Harvey et al., 2006). Nevertheless, the potential of secondary tropical forests to retain more biodiversity increase over time (Echeverría-Londoño et al., 2016). Similarly mammal diversity is improved in less disturbed and wide riparian forest (Lees and Peres, 2008; Yaap et al., 2016).

Therefore, facilitating the natural succession of vegetation from secondary to mature forest in oil palm-dominated landscapes may be an important conservation strategy for improving native mammal species. Despite not being shown to exert a strong influence as measured against standard statistical "significance', the fact that richness was positively correlated with NDVI could in part support this suggestion.

Contrary to my predictions, the percentage of forest cover in landscape failed to strongly explain species richness at the landscape level. Although as with NDVI, I found evidence of a positive relationship. This finding corresponds to previous studies (Mendes-Oliveira et al., 2017; Prugh et al., 2008). One possible explanation for this might be that the current mammal assemblage in this area is relatively resilient as long as a minimum forest cover persist. Perhaps as a consequence of the long history of agriculture in the region (see above). However, percentage of forest was important for the composition suggesting that changes in mammal populations (abundance) are more sensitive to percentage of forest than species richness, which has been supported in other studies (e.g. Hillebrand et al., 2008; Williams et al., 2017). Similarly, distance to towns was not a relevant factor explaining richness, but appered as significant for composition. This pattern may be related to the fact that hunting pressures tend to be higher in close proximities to settlements in tropical regions (Benítez-López et al., 2017).

Factors improving diversity inside plantations

I identified two factors explaining richness and composition inside plantations that may be useful for improving management practices which help to sustain local mammal diversity (in terms of both richness and composition): reducing cattle grazing pressure and maintaining a medium-to-high density of undergrowth vegetation. These factors are clearly linked, as cattle reduce undergrowth in plantations through grazing and soil compaction. Grazing has also previously been found to negatively affect the taxonomic and functional diversity of small mammals in Argentina (Chillo et al., 2016). Furthermore, it has been demonstrated that habitat heterogeneity and complexity helps sustain biodiversity in oil palm plantations (Azhar et al., 2014; Wearn et al., 2016) and other agroecosystems (Pereira et al., 2012; Tews et al., 2004; Tscharntke et al., 2012), by improving the complexity of trophic webs (Foster et al., 2011). In this sense, small patches of undergrowth vegetation throughout plantations can improve heterogeneity and provide habitats for numerous animal groups including arthropods, lizards, birds, and snakes (e.g. Lynch, 2015). Therefore, cattle grazing inside oil palm plantations should be minimized as it decreases mammal species diversity. Further, restricting cattle movement along riparian forest would foster forest regeneration (Lees and Peres, 2008).

Another potential management practice highlighted by my results was the level of canopy cover within plantation, which had a significant effect on the composition (but not in richness) of mammal species. This implies that plantations with higher levels of canopy cover may be used as a mechanism to increase species movement into and across oil palm plantations. Though, further study is required to fully examine the effects of canopy cover in mammal movement within plantations. One possibility would be to examine assemblage structure between oil palm varieties and/or hybrids that differ in leaf size.

The clear effect of understory vegetation for improving species richness and the potential of manipulating canopy cover inside plantation to promote abundance of species, would support approaches such as “wildlife friendly” production (e.g. Bhagwat and Willis, 2008) for the Llanos region. These results, differ from studies in Southeast Asia that found poor correlates between biophysical attributes of oil palm plantations or management alternatives and the diversity of mammal species (e.g. Yue et al., 2015). These alternatives would only be effective if the surrounding forest is maintained, as shown here.

Individual mammal species responses

I assessed individual mammal species responses to potential land-cover transformation (forests to oil palm plantations) as a proxy to evaluate their tolerance or sensitivity to oil palm. The giant anteater, for example, was widely detected in both land cover types across the landscape, and even showed a slightly positive response of abundance within plantations. This positive response confirms that the species can utilize other land cover types, such as forest, plantations or pastures (Rojano et al., 2015a, 2015b). Their relative high detection rate within oil palm is most likely due to the high prevalence of ants in plantations, as has previously been observed in the Llanos region (Gilroy et al., 2015; Sanabria et al., 2014). In this way, giant anteaters may persist in landscapes dominated by oil palm plantations, even though they are the only species categorized as Vulnerable by the IUCN (Miranda et al., 2014) and despite having a specific diet.

Nevertheless, conserving this species will also depend on maintaining areas of natural forest as suggested by the high rate of detections I found in forest and because of their dependency on this habitat for other activities such as resting (Mourao and Medri, 2007).

My results for giant anteater contrast those from Mendes-Oliveira et al., (2017) who found no evidence for giant anteaters inside oil palm plantations in the Amazon. One possibility for the difference between Mendes-Oliveira et al., (2017) results and those presented here could be related to predation pressure. Quiroga et al. (2016), for example, found that jaguar has very high preferences for hunting giant anteater, which capture frequencies can increase up to 70% at sites without jaguars. To what extent detection frequencies of giant anteaters in the plantations of our study area might be related to absence or presence of jaguars is uncertain. However, we did not find jaguar while Mendes-Oliveira et al., (2017) did.

Mesopredators in general were found to have a high tolerance to plantations. This result is similar to the study of Mendes-Oliveira et al., (2017) in an Amazon oil palm landscape; although they detected coati inside plantations. In my study area, fox and jaguarondi, in particular, were relatively abundant and positively associated with plantations. This finding confirms the ecological flexibility of these species (Emmons, 1999). Furthermore, the phenomenon of increased mesopredator abundance in agricultural landscapes, including oil palm, has been previously documented for numerous species throughout the tropics (Boron and Payán, 2013; Jennings et al., 2015; Nogeire et al., 2013; Pardo et al., 2016; Pardo and Payán, 2015; Rajaratnam et al., 2007; Wearn et al., 2017)

The most likely mechanism driving the aparent high relative abundance of mesopredators could be related to sufficient availability of resources through bottom-up effects (Muhly et al., 2013). I hypothesize that oil palm can facilitate an abundance increase of potential prey, such as lizards, frogs, small rodents, snakes, birds, and arthropods, a fact which has been reported in oil palm ecosystems (e.g. Akani et al., 2007; Gilroy et al., 2015; López-Ricaurte et al., 2017; Lynch, 2015; Prescott et al., 2016). In this way, these mesopredators could be acting as biological control agents for potential pest species (Foster et al., 2011) and thus potentially assisting plantation management. However, it is unknown whether an increase in mesopredator abundance (especially foxes) in oil palm plantations may result in other unintended outcomes, such as an increase in the predation of local fauna (see Crooks and Soulé, 1999; Hillebrand et al., 2008). Fox diet, though, can also include a wide variety of seed and fruits, including some Neotropical palm fruits (Gatti et al., 2006). Therefore, it will be important to understand the trophic relationships occurring in oil palm landscapes.

Overall, numerous terrestrial mammal species were found in both plantations and riparian forests, probably due to the historical context of land use in the study area (apart from likely hunting pressures), which could have limited the present-day community to generalist and more ecologically flexible species (Prugh et al., 2008). However, the highly uneven distribution of species-specific abundances within each land cover type, and the influence of some variables on composition but not in richness, suggest caution for the use of mammal species richness as the sole indicator of mammal response to land-use change. For example, in this study seven (29%) of the species detected inside the plantations were recorded from three or fewer individual photographs. Thus, I recommend a concurrent measurement of other metrics that complement richness (e.g. relative abundance) when assessing the effects of land-use change on mammals, (see Hillebrand et al., 2008; Williams et al., 2017). Moreover, it is also important to consider the historical context of land use transformation prior the implementation of oil palm. From a landscape perspective, this finding may suggest that the matrix (oil palm) is differentially permeable to mammal species, allowing some to move through oil palm on their way between preferred habitat sites, such as forest. However, it is important to note that rare (and hence more sensitive species such as the paca) detected inside the plantations were restricted to sites near forest (i.e. maximum ~430 m), as has also been noted in previous findings in oil palm landscapes (Mendes-Oliveira et al., 2017; Yue et al., 2015).

Conservation implications and future scenarios

Certification schemes for sustainable agriculture (e.g., the Roundtable on Sustainable Palm Oil—RSPO; https://www.rspo.org) have traditionally focused on identifying well-conserved areas (e.g. primary forests), or endangered species within production landscapes. However, within the study area in the Llanos region, none of these features are present, or are only present in places far from the study area. This may limit conservation strategies across the Llanos, as they would be considered of "low conservation value", likely discouraging initiatives from farmers. My findings suggest that maintaining secondary riparian forests, regardless of their structure, is a fundamental strategy for the conservation of mammal communities. However, the long history of land use transformation in the western Llanos has reduced riparian corridors to critical levels (e.g. Madriñán et al., 2007). Therefore, for this region (and perhaps regions with similar characteristics) an alternative way to encourage conservation is to focus on restoration of riparian forest strips and introduce elements of landscape design inside plantation, such as the maintenance of undergrowth vegetation along with the reduction of cattle as shown in this study. In this sense, enforcing stricter regulation of the minimum legal widths for vegetation buffer zones (see Corporinoquia, 2011) will be key for restoring mammal assemblage and facilitate the re-colonization or even re-introduction of forest-specialist species.

On the other hand, we only detected one species of conservation concern, the giant anteater, which was frequently detected in oil palm landscapes. Therefore, a question that remains is, which species should be prioritized? Most species were not categorized as conservation concern, which under present certification schemes may be considered irrelevant for conservation (see (Edwards et al. 2012). I therefore, suggest that certification schemes may need to be directed away from the identification of only high conservation remnant vegetation and/or listed endangered species, to include appreciation that all lands can provide some conservation value. As a matter of fact, usually people in the area (e.g. workers, owners) ignore the biodiversity surrounding their lands (Pardo not publ). Maximizing diversity, and their conservation at local scales plays an important role in maintaining regional diversity. In this sense, my results highlight the potential contribution of privately owned lands toward conserving regional mammal biodiversity. This is especially important in the context of the Llanos region, considering its lack of legislated protected areas.

If oil palm is mainly replacing pastures and other crops in Colombia (Furumo and Aide, 2017), a future important study would need to compare the diversity of mammals, and other groups, in different types of agriculture (e.g. pastures, rice, sugar cane) with those of oil palm cultivation to clearly understand the potential benefits and negative effects of each alternative. For example, the conversion of pastures to oil palm seems to have more positive than negative effect as diversity levels in pastures are usually lower (Dotta and Verdade, 2011; Gilroy et al., 2015)

In terms of the richness and composition of terrestrial mammal species, I found that the areas of San Carlos de Guaroa and Cabuyaro warrant special attention. In these zones, I detected rare and ecologically important species, such as the puma (see Pardo et al., 2017 for details), tayra, coati, and peccary, among others. Further, because of its proximity to relatively undisturbed savannas, San Carlos is an important area for habitat connectivity. Finally, the fact that this zone is relatively close to both “Corridor Meta-Casanare” and “Alto Rio Meta,” –two priority conservation areas suggested for the Orinoquia region (Lasso et al., 2010)– makes it an important area for regional mammal conservation.

Oil palm development provides social benefits in Colombia, and plays an important role as source of employment (MADR, 2006a). Therefore, engaging relevant stakeholders is vital to balancing socioeconomic and environmental goals. This is particularly challenging in the face of the likely future developments in isolated areas and natural savannas in Eastern Llanos (Pardo et al., 2015; Romero-Ruiz et al., 2012). Development in these areas is being partly driven by government incentives and corporate investments, but is also a response to the cessation of internal armed conflict which has allowed access to previously inaccessible areas (Baptiste et al., 2017). If well managed, oil palm can contribute to the sustainable development of Colombia (see Sayer et al., 2012). Recognizing the potential contribution of degraded lands and the implementation of better practices, such as those resulted from this study, would be a good incentive to promote conservation across oil palm landscapes, where highly threatened species or pristine lands are not always present. The future of tropical forest biodiversity in a human-modified world may depend on how well humans know and manage the matrix (Gardner et al., 2009), which, in Colombia’s western Llanos, predominantly comprise oil palm plantations.

Conclusions

This study provides the first comprehensive analysis of the landscape- and habitat-level effects of oil palm cultivation on terrestrial mammals in Colombia. I found that oil palm plantations supported significantly fewer mammal species and different composition than riparian forests. However, I identified that some species, particularly mesopredators, anteaters, and deer are relatively common in oil palm plantations than in remnant native riparian forests. I found that secondary riparian forests have a fundamental role in mammal conservation in this landscape, regardless of its structure or area. Therefore, if oil palm expansion occurs at the expense of remnant riparian vegetation there will be drastic deleterious consequence for mammal species in the Llanos region. Based on our results, I recommend that to maintain and increase native mammal diversity inside the plantations, oil palm growers should promote undergrowth vegetation and avoid cattle presence inside plantations. The present-day assemblage in the study area was limited to relative resilient species. In the absence of pristine or highly threatened species, I suggest the development of new ways of recognition for implementation of good practices that could promote the conservation value and awareness of degraded landscapes.

Supporting information

Photographs showing the characteristics of the study area in the Llanos region of Colombia (Appendix 1), Terrestrial mammal species detected by camera trapping surveys (Appendix 2), Model selection output comparing all possible combinations for the effect of variables on mammalian species richness at the landscape level (Appendix 3), Model selection output comparing all possible combinations for the effect of the variables on mammalian species richness within oil palm plantation level (Appendix 4), Model selection output comparing all possible combinations for the effect of variables on mammalian species richness within riparian forest level. (Appendix 5). Multispecies generalized linear models examining the relationship between the composition and individual abundance of medium and large terrestrial mammal species with selected landscape covariates (Appendix 6), The relationship between mammal species abundance and selected landscape variables (Appendix 7).

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Chapter 3 Identifying critical limits in oil palm cover for the conservation of terrestrial mammals in Colombia

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Statement of contribution of others:

LEP and FOR conceived the main idea and research questions. LEP collected data, coordinated and carried out fieldwork, organized data, conducted all analyses, and wrote the first manuscript. FOR supported the analysis and writing. MJC edited the manuscript and provided feedback in the writing process and the discussion, NY conducted the GIS analysis and provided feedback on drafts. WE helped determining the design, provided statistical assistance, and editorial input, WFL helped with research questions, design, funding, and the final editing of the manuscript. For other contributions, see acknowledgments.

Abstract

As oil palm plantations continue to expand in Neotropical regions, identifying critical transitions in land use, at which animal communities can be drastically altered, is crucial for conservation planning. Here, I investigated the existence of potential unexpected change points (thresholds) in the response of terrestrial mammal richness and community composition to increasing oil palm cover in the Llanos region of Colombia. For the identification of these points, I used segmented regression and Threshold Indicator Taxa Analysis (TITAN). The identified community threshold was then used to evaluate the conservation status of the four main oil palm production landscapes in Colombia. I found a negative linear relationship between the proportion of oil palm and species richness, but no evidence of a significant threshold effects on this metric. In contrast, I found strong signs of a community threshold in landscapes that had reached 45-75% oil palm cover, beyond which mammalian species community composition drastically changed. Moreover, a significant threshold relationship to oil palm land cover was found to occur in 10 of the 15 examined species, with four (squirrel, agouti, spiny rat, common opossum) having a synchronous response at approximately 45 % oil palm cover. However, five species showed no evidence for any critical threshold (giant and lesser ant eater, jaguarondi, white tailed deer and raccoon). I also found that approximately 41% of Colombian oil palm landscapes have crossed the identified community threshold of 45-75% oil palm cover, suggesting urgent need for restoration of these landscapes if a potential collapse of mammal communities is to be avoided. These findings provide guidance for the design of sustainable landscapes within production areas in Colombia to promote the conservation of terrestrial mammals.

Key words. carnivores, human dominated landscape, Llanos, Orinoquia, tipping point, TITAN analysis

Introduction

Human activities have drastically altered the structure of landscapes around the world, modifying biological communities, destroying habitats and causing species extinction (e.g. Ceballos et al., 2015, Newbold et al. 2015). In this sense, the conversion of native grasslands, forests, wetlands, and other forms of natural land cover to cultivated lands has become the major driver of biodiversity loss (e.g. Gibbs et al., 2010; Goldewijk, 2001; Laurance et al., 2014). Oil palm, in particular, is currently one of the major threatening processes for biodiversity retention in Southeast Asia (e.g. Edwards et al., 2010). In this region, more than 55% of oil palm expansion has occurred at the expense of native forest (Koh and Wilcove, 2008) and resulted in substantial biodiversity loss, including between 80- 90% of species richness in birds mammals (e.g. Maddox et al., 2007; Peh et al., 2006).

Oil palm production is rapidly expanding in Latin America (Furumo and Aide, 2017). Colombia, for instance, is the largest oil palm producer with approximately more than 480,000 ha currently under cultivation (Fedepalma, 2014). Initial production goals suggested a minimum of one million hectares to be planted by 2020 (MADR, 2006b). Although, at present this goal is most likely unachievable (see also Castiblanco et al., 2013), oil palm sector in Colombia is continuously growing. However, little is known about the likely impacts that a substantial increase in oil palm may have on Colombian biodiversity (reviewed by Pardo et al., 2015). Contrary to Southeast Asia, oil palm is not the main driver of deforestation in Colombia (Furumo and Aide, 2017), but few recent studies have confirmed that oil palm plantations sustain substantially lower levels of biodiversity than natural ecosystems (e.g. Gilroy et al., 2015; Pardo et al., 2018; Prescott et al., 2015). However, no assessment has yet been conducted to provide guidance on the proportions of land that should be allocated to cultivation and set aside for conservation if the impacts on local fauna are to be minimized.

Ecological communities and their functioning are substantially affected by the degree of human alteration. Elements such as the amount of natural cover or the configuration of a human created matrix (often-agricultural land) between remnant habitat, among others, can play a crucial role in the long-term viability of species in agricultural landscapes (Gardner et al., 2009; Perfecto and Vandermeer, 2008). Of particular importance, species responses to land use change are not always linear. For example, some species are known to show particular change-points, also known as thresholds, that describe critical points in environmental conditions (e.g. habitat amount or habitat proportion within a landscape) that once surpassed can trigger a drastic decline in their populations (or richness) (Andrén and Andren, 1994; Fahrig, 2002; Suding and Hobbs, 2009). Identifying threshold responses of mammalian species across a gradient of oil palm cultivation is key to assisting management actions in these transformed landscapes, both in terms of conserving remaining biodiversity, and importantly for informing future plantation design and conservation planning. This “threshold analysis” is a relative recent, yet reliable, approach by which to anticipate critical changes in biodiversity response to land use cover change across human dominated landscapes (HDL) (e.g. Fahrig, 2002; Muylaert et al., 2016; Roque et al., 2018)

In this study, I aimed to identify whether there was a threshold in mammalian species richness and composition responses to oil palm cover increase in the Llanos region of Colombia. I used this approach in an attempt to anticipate the maximum percentage of oil palm that could be planted to minimize potential decline in mammal communities. Given the negative effect of oil palm on native fauna, and the likely non-linear response of different taxonomic groups to gradients of different land uses (e.g. Boesing et al., 2018; Roque et al., 2018), I predicted an abrupt decline (threshold) in species richness and composition in response to increasing oil palm cover within a landscape. Moreover, I predicted that species response to this land cover change would reflect similarities in both shared evolutionary and morphological traits (e.g. feeding-guild, body size).

Methods

Study area

The study area was located in the Colombian Llanos Orientales region (hereafter Llanos), and included rural areas surrounding the towns of Restrepo, Cumaral, Cabuyaro, Acacias, Castilla la Nueva and San Carlos de Guaroa. All towns are situated in the Department of Meta and are located between 194-394 m.a.s.l. (Fig. 3.1). This area has a long history of landscape modification by human activity and is currently dominated by oil palm plantations (here after referred as oil palm). Other agricultural activities include cattle grazing and to a lesser extent rice production. Oil palm production is prevalent in the region and currently covers approximately 180,000 ha (Fedepalma, 2014). It is predicted that the expanding oil palm cultivation in the Llanos region will occur at a faster rate than that of previous decades (Romero-Ruiz et al., 2012), although this expansion is most likely to happen in lands used for pastures and in relative minor degree in natural/native savannas (e.g. Castiblanco et al., 2013). The remnant natural ecosystem in the region is secondary riparian forest (gallery forest) which varies in size and age, and at some locales experiences seasonal inundation.

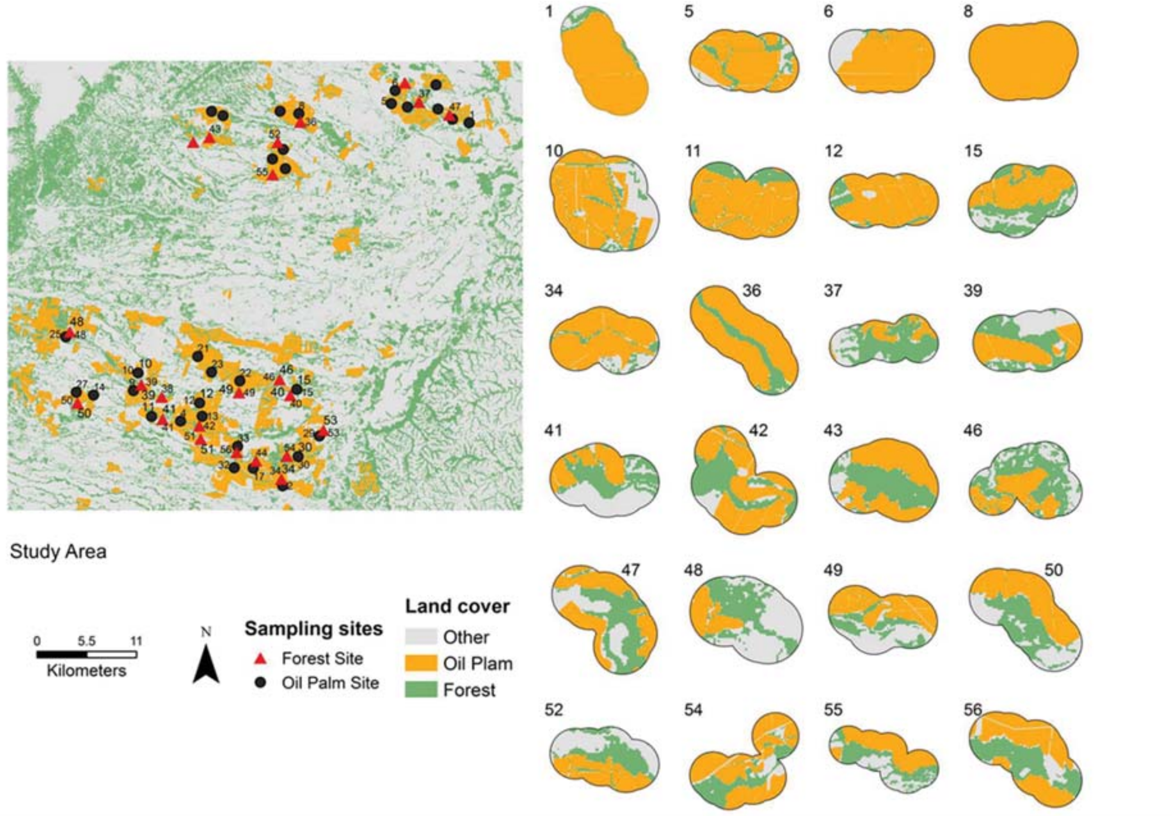

Figure 3.1. Map of the study area showing the distribution of the surveys sites locations (left) and the representative gradient of oil palm percentage (right) across the Llanos Region, Meta Department, Colombia.

Survey design

I sampled 56 sites (33 inside oil palm and 23 in riparian forest) located across an area of approximately 2,000 km^2 (Fig. 3.1). Sites were selected strategically to examine a gradient of proportional area devoted to oil palm versus riparian forest cover (hereafter referred as forest). Sites within each land cover were at least 2 km apart to maintain sample independence. This site placement exceeded the minimum criteria recommended for inter-site distance when examining inventories of terrestrial mammals in the Neotropics (e.g. Silveira et al., 2003; Team Network, 2008; Tobler et al., 2008). Furthermore, previous research in the area (i.e. Ferrer et al., 2009; Pardo and Payán, 2015) suggests that this inter-site distance corresponds to the average diameter of home ranges for most mammal species expected to occur in the study area. Surveys were conducted during the dry season between September 2014 and January 2016 and all sampled plantations had been established for a minimum of 10 years (i.e. planted no later than 2006) to account for any confounding effect of plantation age.

I used seven Reconyx HC500 HyperfireTM digital cameras at each site (sampling unit) to detect medium to large sized mammals (i.e. >0.5 kg) without baiting. Cameras were placed along a 1.5 km transect with the first camera randomly located and the remaining cameras set along a transect at 250 m intervals. This protocol was used to increase survey success per site (Pardo et al. Chapter 7) and is more effective than the traditional mammal research practice of using one camera per site (Burton et al., 2015). Where possible, cameras inside forests were placed along animal paths or facing small gaps in the vegetation to maximize capture success. Cameras were positioned in a zigzag arrangement within oil palm to increase coverage due to the regular pattern of tree planting. All cameras were fixed to trees or wooden poles with a steel cable and were configured to the following criteria: high sensibility sensor, one second interval between consecutive pictures (3 per trigger), no delay or quiet period between triggers, a minimum distance from the potential path of the animal of 1.0 m and at 25-30 cm height depending on the terrain. Cameras were active for 30 to 40 days.

Landscape variable selection

I quantified the different land cover/use at each site using ArcGIS (V10.2.1; Environmental Systems Research Institute, Inc. Redlands, CA). This quantification was done by creating a buffer with a 500 m radius around each camera within each transect (i.e. site) and merging the individual buffers into one single unit. I then calculated the percentage of the different land cover/use types (forest, oil palm and others) within this single unit per site. To avoid potential effects of spatial autocorrelation in my predictor variables, I assessed for autocorrelation using Moran's I in SAM software V4.0 (Rangel et al., 2010). In all instances Moran's I was not significant ($p > 0.05$).

To determine land cover I used official spatial data describing the extent and locations of plantations in Colombia supplied by the National Federation of Oil Palm Growers (FEDEPALMA), and land cover maps acquired from the National Institute for Environmental, Hydrological and Meteorological Studies (IDEAM) (IDEAM et al., 2007). I updated the information from IDEAM prior to the analysis using: i) Google Earth imagery and ii) Claslite classification (Asner et al., 2009) to identify and validate forested areas, as this provided more up-to-date and accurate data for this land cover, and iii) aerial photographs taken during a flight over the study area (August 2014).

Threshold and Statistical Analysis

The majority of studies using threshold analyses focus on identifying minimum thresholds for forested habitats or native vegetation loss (Andren, 1994; Banks-Leite et al., 2014; Fahrig, 2002; Muylaert et al., 2016). Here, I focused on identifying the threshold for maximum percentage of oil palm plantation in a landscape above which mammalian species richness and composition (i.e. occurrences and abundances as an aggregate measure) would decline abruptly. I used this inversed approach based on the following considerations: *i*) cultivation of oil palm is the dominant land use in the study area, and is continuously expanding; *ii*) previous studies in the region have highlighted strong negative effects of oil palm in local and landscape species richness and composition for numerous taxa (e.g. Pardo et al., 2018, Prescott et al., 2015); *iii*) past and predicted oil palm expansion has predominantly occurred in non-forested ecosystems (e.g. pastures and natural savannas (Furumo and Aide, 2017; Pardo et al., 2015); and *iv*) having a clear idea of the pattern of mammalian biodiversity in the agricultural matrix is fundamental for the identification of management alternatives (Gardner et al., 2009; Perfecto and Vandermeer, 2008). This approach enabled the identification of more direct management insights including a determination of the threshold at which oil palm coverage triggers either a richness or population decline in the local mammalian community.

Is there a threshold for mid-large sized mammalian species richness and composition in response to the proportion of oil palm cover in a landscape?

To identify thresholds in the observed mammalian species richness in response to the proportion of oil palm cover percentage, we built a segmented (piecewise) regression based on a generalized linear model (GLM) with Poisson distribution, in the R package (R Development Core Team, 2014) "Segmented" (Muggeo, 2008, 2003). Segmented regression analysis splits explanatory variables into two or more linear regressions in order to locate points where the linear relationship changes. To further test for any significant change in the initial relationship (non-segmented GLM), we used the pseudo score test (p.score) (Muggeo, 2016). We also tested for a null left slope by constraining the segmented regression as described by Muggeo (2008) and determined which of these models fitted better using Akaike Information Criteria (AIC) (Akaike, 1974) (i.e. GLM initial non-segmented model, GLM-segmented unconstrained model, and GLM-segmented constrained model) and graph the best curve for visual interpretation.

To identify mammal community composition response to oil palm proportional landscape cover, I used the R package Threshold Indicator Taxa Analysis–TITAN (Baker and King, 2010). TITAN determines signs of community compositional change for the entire assemblage across all detected species together (here after referred as community threshold), and a specific threshold for the individual species. For this threshold identification, the analysis uses the frequency of occurrence (i.e. number of sites where a species is detected) and abundance of the taxa as an indicator (Indicator Value of a Species–IndVal, see (Dufrêne and Legendre, 1997) to detect potential change points and strength of any response. Therefore, hereafter I refer to composition as the aggregate measure of these two parameters. The quality of each taxon response is evaluated with a measure of 'purity' and 'reliability' obtained by bootstrap resampling procedures set at n=500 (see Baker and King, 2010 for details).

Given the difficulty in identifying individuals within species for the composition analysis, I used frequency of detection (or catch per unit of effort) as a proxy for the relative abundance index (here after abundance). This index was calculated as the number of independent pictures/sampling effort*100. Measuring abundance this way allows for an evaluation of the structure of the assemblage in terms of commonness and rarity (Magurran and Henderson, 2011), but should not be confused as a measure of abundance or density *sensu stricto* (see discussion in (O'Brien, 2011). Independent pictures criteria was set to 30 minute intervals for consecutive photographs of the same species (O'Brien, 2011; O'Brien et al., 2003). Sample effort was calculated as the total number of days the cameras were active within each transect (Camera-days). To limit possible bias due to species rarity I used only those species that were independently detected more than 10 times and at more than three sites.)

What is the conservation status of mid-large sized mammals in the four major Colombian oil palm production zones?

To assess the conservation status of mid-large sized mammals within the four major oil palm production areas in Colombia (i.e. Eastern, Pacific, Central and Northern region; Fedepalma, 2011), I used the community threshold identified above as a baseline, and determined the percentage of each production zone relative to that threshold (below, at or above). Specifically, for each production area I quantified the proportion of oil palm plantations in relation to the surrounding landscape within a fishnet composed of 1 km^2 squares– an area similar (but lower) to the area of the buffers used in estimating the threshold value.

Results

Is there a threshold for mammalian species richness in response to the proportion of oil palm cover in a landscape?

Over a total survey effort of 12,403 camera trap days, I detected 24 terrestrial mammal species representing seven taxonomic orders and 16 families (see chapter 2 for further details). I found a significant decrease in total mammal species richness in response to increasing oil palm cover (initial GLM; Res.Dev = 47, 54 df, $\beta = -0.01$ (SE = 0.002), $p<0.001$; Fig. A1). Although, segmented regression analysis failed to reveal any significant break point in this relationship (adjusted Res.Dev = 43.20, 52 df, $\beta = 0.02$ (SE 0.01); $p = 0.86$). This was confirmed by the pseudo score test ($p = 0.12$). The constrained segmented regression curve (the best model) suggests the left slope had no apparent effect until oil palm coverage reach approximately 35-40% in the landscapes, after which a downward trend in species richness is evident (Fig. 3.2).

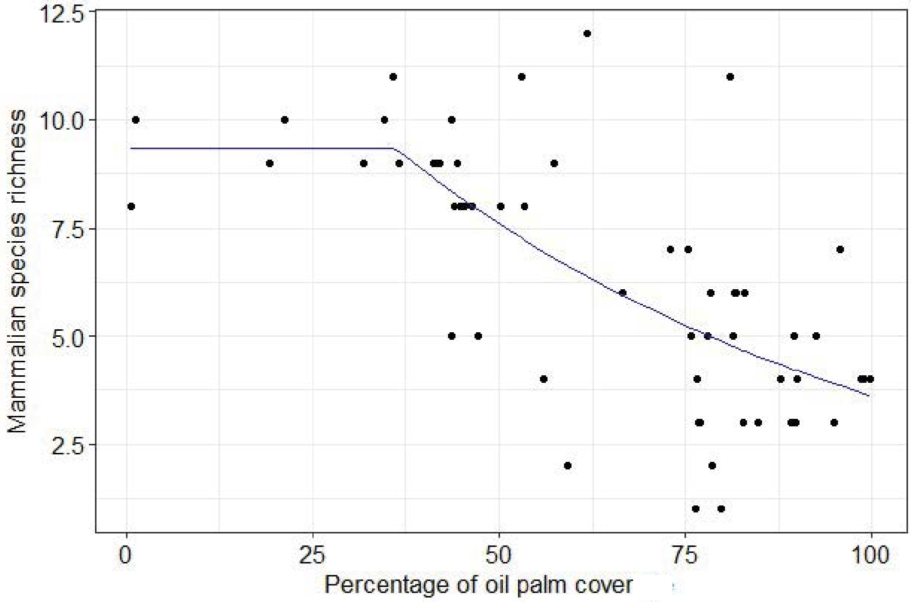

Figure 3.2. Mammal species richness response to percentage of oil palm cover in the Llanos region of Colombia. The blue trend line shows the constrained segmented (GLM) regression. Breakpoint was not significant, but the effect of increasing oil palm coverage is evident after approximately 35% oil palm coverage with a negative trend.

Is there a threshold for mammalian species composition in response to increasing oil palm land cover?

Most mammal species (except for the fox) decreased abruptly (in frequency of occurrence and relative abundance) as the proportion of oil palm reached this threshold. A strong sign of community compositional change was identified when the oil palm cover the landscape was between 45-75% (Fig. 3.3). Individually, 12 of the 15 species analyzed had a significant threshold response to oil palm land cover (Indicator Value –IndVal score $p < 0.05$) (Appendix 8). However, results for only 10 of these species were deemed to be reliable based on purity and reliability measures > 0.90. Of these species, nine responded negatively (Z^-) to an increase in oil palm cover, while only one species (fox–*Cerdocyon thous*) responded positively (Z^+) (Fig 3.4). On the other hand, five species displayed no obvious threshold in response to proportion of oil palm cover: the lesser anteater (*Tamandua tetradactyla*), giant anteaters (*Myrmecophaga tridactyla*), jaguarondi (*Puma yagouaroundi*), raccoon (*Procyon cancrivorus*), and white tailed deer (*Odocoileus cariacou*), with the first two species showing a negative relationship (Appendix 8).

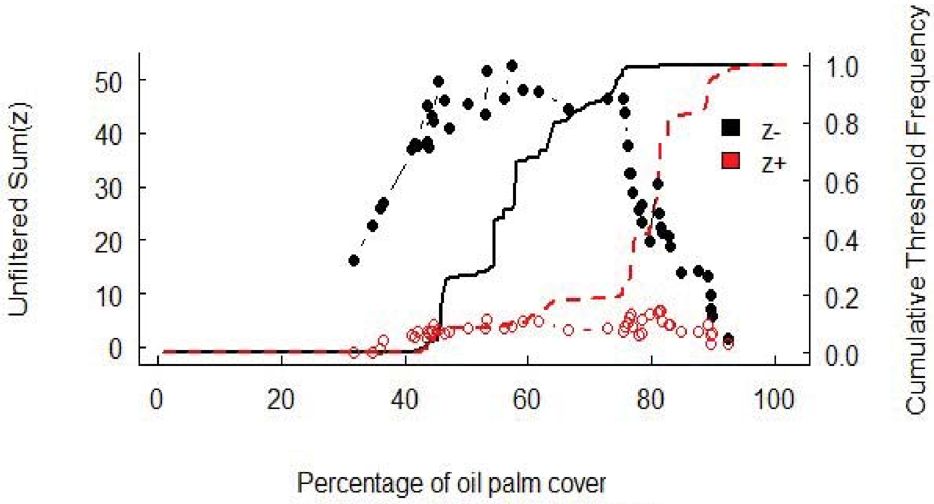

Figure 3.3. Community threshold in response to increasing oil palm cover percentage in the Llanos region, Colombia. The cumulative probability curves indicate strong signs of community change between 45-75% of oil palm cover percentage. Solid (black) and dashed (red) lines represent the cumulative frequency distribution of change points (filled and hollow circles) across 500 bootstrap replicates for sum (Z+) and sum (Z−), respectively. Z+/− = positive and negative effects across species frequency of occurrence and abundance (IndVal z score).

A synchronous (similar) response to oil palm cover was identified in four species: squirrel (*sciurus spp*), agouti (*Dasyprocta fuliginosa*), spiny rat (*Proechimis spp*) and common opossum (*Didelphis marsupialis*). These four species showed very similar threshold values where compositional declines occurred at approximately 45% oil palm cover. The species that was most sensitive to increasing oil palm was the capybara (*Hydrochaerus hydrochaeris*) with a threshold at ~40 % oil palm cover. The remaining four species (armadillo (*Dasypus novemcinctus*), naked armadillo (*Cabassous unicinctus*), ocelot (*Leopardus pardalis*) and paca (*Cuniculus paca*) showed higher tolerance to increasing oil palm with threshold between 55 % to 75% (Fig 3.4).

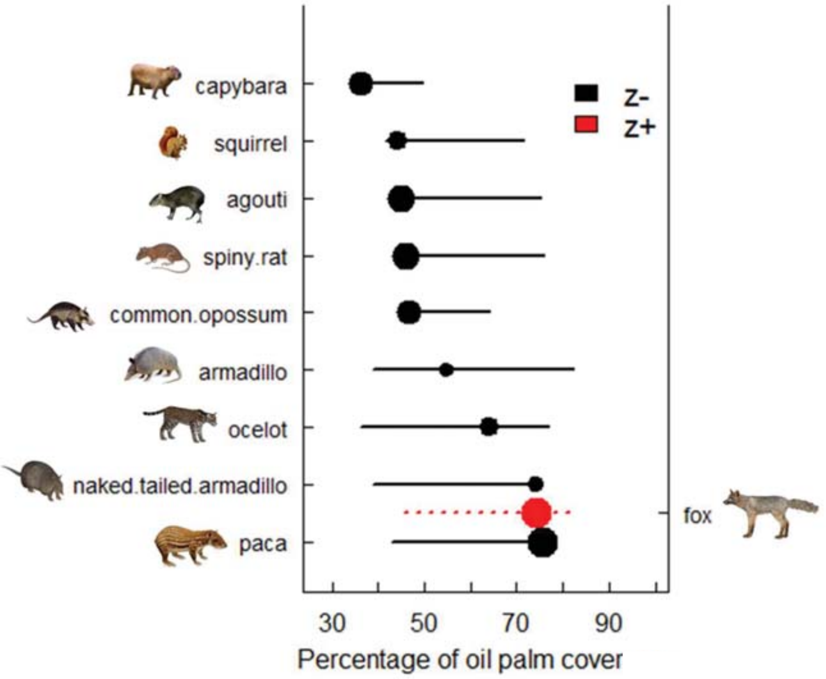

Figure 3.4. Species specific thresholds of 10 mammalian species in response to the percentage of oil palm cover in the Llanos region, Colombia. Only species that showed significant purity (>0.90), reliability (>0.90), and p (< 0.05) are shown. Z +/− = positive/negative effect on frequency of occurrence and abundance (IndVal z score). The sized of the circle (change point) is in proportion to the magnitude of the response (see Table S1). Horizontal lines represent 5-95% quantiles from the bootstrapped change point distribution. *Species with no evidence for threshold are not shown in the figure. These include the lesser and giant anteaters, jaguarundi, white tailed deer, and raccoon.

What is the conservation status of mammals in the major oil palm production zones of Colombia?

I used the community threshold for the mammalian community identified in the Llanos study area (i.e. 45-75% of oil palm cover) as a proxy to examine the status of the four major oil palm producing areas in Colombia. My estimates suggest that approximately 32% of the Colombian landscapes in which oil palm is cultivated are currently below the threshold limit while 41% exceed the threshold. The Western and Eastern production zones, in particular, presented high results with 50.75 % and 43.89 % (respectively) of their total available production area above the threshold (Table 3.1, Fig 3.5).

Table 3.1. Percentage of the land area in the four major Colombian oil palm production zones that are below, at, or beyond the oil palm coverage threshold (of 45-75%) at which mid-large sized mammal species landscape abundances significantly decline.

Zones	Total area* (ha)	Total Below Thresh (%)	Total At thresh (%)	Total Beyond thresh (%)
North	70,822	28.66	34.89	36.44
Center	93,577	32.55	29.42	38.02
East	136,894	23.02	33.01	43.89
West	38,147	21.05	28.19	50.75

*Areas for oil palm are based on official spatial data provided by the National Federation of Oil Palm Growers (FEDEPALMA) for year 2012.

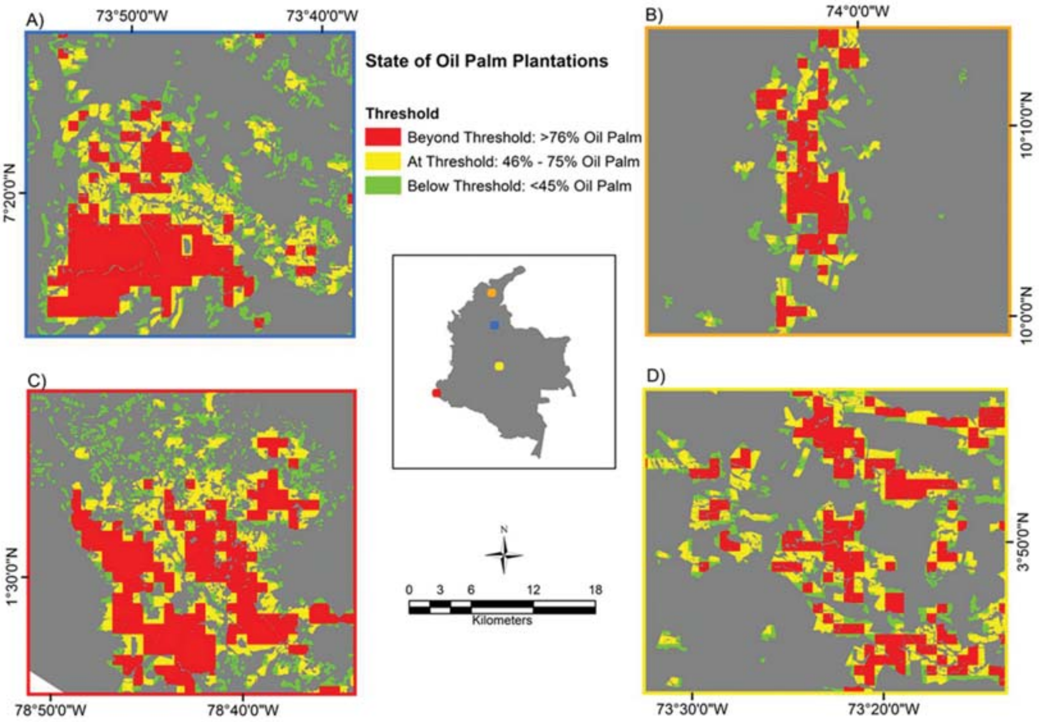

Figure 3.5. Location and visual representation of the conservation status of the four major Colombian oil palm production zones according to the percentage of oil palm below, at, or beyond the oil palm coverage threshold (of 45-75%). Estimation based on a grid of 1x1 km. Each letter corresponds to the four oil palm production zones: A = Center, B = North, C = West, D = East.

Discussion

We found that an increase in oil palm cover reduces mammal species richness and uncontrolled expansion may trigger a drastic decline (threshold) in mammalian assemblage's composition. This negative response to oil palm cover increase, corresponds with previous studies on mammal species in tropical landscapes dominated by oil palm (e.g. Azhar et al., 2014; Bernard et al., 2014; Pardo et al., 2018; Pardo and Payán, 2015). However, to my knowledge, there is no previous research attempting to evaluate a "safe-limit threshold" for mammal conservation in tropical oil palm landscapes. At an annual increase in oil palm cover of ~10,000 ha (Etter et al., 2011) in Colombia, effective conservation planning and management is vital and time-critical.

Recovery of landscapes which have surpassed their “change point” can be very costly, economically and in terms of ecosystem services (Oliver, 2016).

The inability to identify a significant threshold for mammalian species richness could be related to the historically high rate of natural land cover transformation which has occurred in the study area, previous and parallel to oil palm cultivation (Etter et al., 2006; Madriñán et al., 2007; Romero-Ruiz et al., 2012). This transformation likely reduced the original mammalian diversity, and therefore, minimized the overall present-day variation in species richness across the study area, resulting in a depauperate community of relatively common and resilient species (see Arding et al., 1998; Prugh et al., 2008). This suggestion of historical land transformation as a driver of mammal decline, may be further supported by the lack of detection of sensitive species expected to occur in the study area (Ferrer et al., 2009) such as tapir (*Tapirus terrestris*), jaguar (*Panthera onca*) and giant armadillo (*Priodontes maximus*); which cannot be attributed solely to oil palm plantations (see Pardo et al., 2018). It is important to note, for instance, that the level of transformation in the study area limited us from having more sites with 100 % forest. It is possible that future research in landscapes with bigger, and more mature forest (and therefore with more sites where percentage of oil palm is low) may find different trends, especially if oil palm expansion has taken place in previous natural ecosystem.

Mammalian species composition thresholds in response to oil palm land cover

I found that the community composition of mid-large sized mammals in the Llanos region of Colombia displayed a clear negative threshold between 45-75% in response to increasing oil palm cover. This finding suggests that plausibly a sustainable oil palm landscape in this region should contain a maximum of 45% of oil palm to prevent drastic mammalian community changes (i.e. signs of drastic change starts when oil palm reached this proportion). Further, this result also suggest that when oil palm coverage increased to 75% the whole terrestrial mammal community declined abruptly. This change point should be considered unsustainable (*sensu* Angelstam et al., 2003) for mammal conservation, as regardless of the specific threshold between species, once the proportion of oil palm reach this point (75%) the whole community will certainly decline. Therefore, restoration and monitoring programs are urgently needed to reduce the probability of significant mammals decline in oil palm landscapes in the Llanos region, especially in those landscapes that have between 45-75% of oil palm (see sections below).

We may use the identified threshold for oil palm coverage as a guideline to anticipate the minimum amount of remaining forest needed to support resilient populations of mammals. As such, my results suggest that maintaining a forest cover between 55-25% in Llanos oil palm landscapes would help to ensure mammal conservation (i.e. avoid entering a “risk zone” *sensu* Roque et al., 2016). I acknowledge, however, this suggestion must assume no effect of other landscape characteristics such as isolation or other land uses within our sampling sites, which can influence the estimation of thresholds (e.g. Boesing et al., 2018; de Oliveira Roque et al., 2018). Although I tried to minimize confounding factors by ensuring the buffer areas did not contain other land uses different than oil palm and forest, few sites inevitably included small proportion of other land uses. Future studies and other approaches may be able to take this situation into account to stablish, for example, whether the presence and proportion of proximate pastures or other crops influence the dynamic of species between oil palm and riparian forest (varying buffer sizes may be useful). However, oil palm dominance in the western Llanos is evident and the landscape is mostly a homogenous mosaic formed basically by oil palm, riparian forest, and pastures as confirmed by a flight over the study area and the satellite images used when selecting the sites. Despite these caveats, I am confident my approach gives insights into the design of more sustainable landscapes in the Llanos.

The minimum suggested forest cover (25%) is slightly lower than those suggested in other Neotropical areas for birds and mammals, which range between ~30-47 % (Andren, 1994; Banks-Leite et al., 2014; Estavillo et al., 2013; Muylaert et al., 2016; Ochoa-Quintero et al., 2015; Pardini et al., 2010). There could be two plausible reasons for this pattern. First, present day fauna occurring in the Llanos oil palm landscapes are relatively more resilient due to historical alteration of habitats, including other land uses before and parallel to oil palm cultivation. Second, although riparian forests can vary in width, they constitute a small proportion of the landscape compared to the surrounding savanna/pastures ecosystems of the Colombian Llanos. These two factors further suggest that the identified threshold may be conservative if applied to other ecosystems. Therefore, for ecosystems with extensive (and more conserved) rainforest cover, such as the Chocó region or the Amazon, a threshold analysis would most likely reveal higher values.

I did not find many species with synchronous responses to oil palm cover, or strong evidence for common ecomorphological traits influencing their responses. However, the four species with responses at a similar level of oil palm cover were mostly rodents (i.e. agouti, squirrel, common opossum, spiny rat) with similar body sizes; a group which tends to be common in forested ecosystems (Emmons, 1999). My results suggest that their resilience can be drastically affected when oil palm cover exceeds 45% of the landscape. The threshold values of the remaining examined species did not show any strong pattern between species or correlation between taxonomic group, trophic levels or body sizes. For example, the two biggest rodents in the Neotropics, the paca and capybara, differed in their response to oil palm increase, with the former being apparently more resilient (threshold values of 75% and 40% respectively). This finding, is in accordance with Pardo et al. (2018) who found that while capybara appear to cross oil palm plantations, their relative abundances increases with percentage of forest cover (see also Camargo-Sanabria et al., 2014b). Although capybara and paca are highly forest dependents, paca appear to possess a high tolerance to increasing oil palm cover due to their capability to exploit narrowed or fragmented riparian forest (Gallina et al., 2012). All together these findings confirm the fundamental role of maintaining riparian forests in oil palm landscapes.

Mesopredators (mid-sized omnivorous/carnivores mammals) showed greater tolerance to oil palm expansion than other mammal guilds in my study. Ocelot, for instance, displayed a negative threshold to oil palm until ~65% land cover, while jaguarondi displayed no clear threshold. Conversely, another generalist predator, the fox, exhibited a positive threshold response at ~75% of oil palm cover in the landscape. These species and other medium size carnivores have also previously been found to persist in agroecosystems in the tropical region (e.g. Daily et al., 2003; Jennings et al., 2015; Mendes-Oliveira et al., 2017; Nogeire et al., 2013; Pardo and Payán, 2015; Rajaratnam et al., 2007). One of the most likely reasons for this apparent tolerance to oil palm could be the increased availability of prey within plantations, such as lizards, invertebrates, and small mammals (see Pardo et al. 2018). Future work should be undertaken to definitively evaluate the mechanisms underlying the proliferation of mesopredators within oil palm production sites, as hyperabundance of mesopredators, especially for fox abundance, could have significant detrimental impacts on other prey species (e.g. Elmhagen and Rushton, 2007; Hillebrand et al., 2008; Prugh et al., 2009).

Conservation status of oil palm production zones

Large parts of Colombian oil palm landscapes are currently beyond the identified threshold of oil palm coverage (~41%) and thus their mammal communities are under threat. As such, the National Federation of Oil Palm growers (Fedepalma) should encourage restoration with native vegetation up to my suggested natural vegetation coverage levels if they wish to prioritize mammal conservation in these landscapes. I acknowledge that the threshold for oil palm cover in a landscape identified here may differ across the major production areas and a consideration of each local context is important. However, my results provide clear empirical evidence which may be useful for integrating into management regimes. It is worth mentioning that my estimation of the status of the oil palm production zones, is not equivalent to the total natural area converted to oil palm, which other studies have previously addressed (e.g. Furumo and Aide, 2017; Garcia-Ulloa et al., 2012).

Mammalian species play crucial roles in ecosystem dynamics. A reduction in the abundance or local extinction of these species would have consequences for forest dynamics and succession due to ecological roles such as seed dispersal capacity and roles in trophic cascades (Camargo-Sanabria and Mendoza, 2016; Dirzo and Miranda,1990; Estes et al 2011). Moreover, some species are common prey items for larger carnivores in the region such as puma or ocelots (e.g. armadillo, agouti, lapa, common opossum, etc. (e.g. Chinchilla, 1997; de Oliveira et al., 2010). Restoration of riparian forest strips is more important than solely maintaining current forest cover or even the identification of areas/species of high conservation value in these landscapes (see also Pardo et al., 2018); due to their limited extent in these human dominated areas such as the western Llanos region. Therefore, regulation and schemes such as the Roundtable on Sustainable Oil Palm (RSPO) could be highly improved by considering the particularities of the landscapes where oil palm production is taking place in Colombia such as those studied in this instance.

Regional context and implications for conservation and management

Despite the admittedly complex task of assessing the existence of thresholds in nature (Lindenmayer and Luck, 2005), the results of this study can aid landscape planning and design, particularly that within the studied Eastern oil palm zone of Colombia. Very few studies have evaluated the potential effect of the matrix in threshold analyses (e.g. Boesing et al. 2018). My results suggest limiting oil palm expansion to ~ 45% coverage in the landscape, and never exceeds 75% coverage. This information, further help lessening the reliance of landscape planning on the precautionary principle (Cooney, 2004) by guiding discussions on the extent of oil palm to be planted sustainably. This result is important, as balancing agriculture and biodiversity conservation is a key challenge in developing countries. Numerous schemes for sustainable oil palm production have previously been identified, including an important debate between land sparing and land sharing (wildlife friendly) approaches (e.g. Green et al., 2005; Koh et al., 2009; Laurance et al., 2010). My analysis is beyond this discussion but support the idea of designing landscapes where natural ecosystems (forest in this study) are an essential part in productive areas; which for Llanos may need to cover a minimum of 25%, minimum.

Current regulations for the Llanos region state that plantation projects of more than 1000 ha should retain or restore 10 ha of forest as set aside for conservation (Corporinoquia, 2013). Further, plantations should maintain a minimum distance of 100m between plantations and buffer zones of riparian forest (Corporinoquia, 2011a) –although, none of these measures have been empirically tested. My results, while highlighting the importance of those regulations, suggest increasing the minimum area of natural vegetation and reinforcing restoration programs to increase riparian forest coverage in the Eastern oil palm zone. In this sense, strengthening of the enforcement of the existing legislation is fundamental.

The majority of the expansion of oil palm in Colombia has occurred predominantly in lands previously covered by pastures (e.g. Castiblanco et al., 2013, Furumo and Aide, 2017). However, my results suggest that even under these circumstances, there is still a maximum tolerance of oil palm cover after which most species (even “common” and non-threatened species) are likely to decline. This finding is concordant with suggestions of Ceballos et al., (2017) who found that even population of vertebrate species deemed as non-threatened are at high risk of collapse worldwide, which highlight previous comments of the importance considering the biodiversity as a whole. Future studies will contribute to understand how the transformation of non-forested ecosystems, such as savannas, which are the most likely natural ecosystem to be converted to agriculture (e.g. Corporinoquia, 2013; Etter et al., 2011; Pardo et al., 2015), can affect native fauna. The full impact of agricultural afforestation (i.e. conversion on non-forested ecosystem such as wild grasslands and savannas to oil palm or other perennial crops) on biodiversity is still unclear. Although, López-Ricaurte et al. (2017) address this issue for birds communities in Colombia, suggesting difference in species richness and composition between savannas and oil palm.

The fact that I only found evidence for a threshold in mammal species composition but not in species richness, suggests abundance and occurrence are more sensitive to oil palm cover increase in the landscape. Therefore, conservation efforts should also consider the dynamics of the populations, rather than identifying species number alone. This observation is supported by those from other studies which suggest that the response of species richness to environmental factors is not as effective as other population metrics, such as abundances (e.g. Williams et al., 2017). A low correlation of species richness with different landscape attributes may be more apparent in human dominated landscapes, where the majority of species are usually more ecologically flexible and can be detected in different land cover types. Therefore, by examining species richness only, the responses or sensitivity of individual species to environmental changes can go unnoticed (Lindenmayer et al., 2005). If that were to occur it could be reinforced by the fact that species have different thresholds to land cover change as identified in my study area. Further, as suggested by Hillebrand et al. (2008) changes in species composition (e.g. evenness) response to human activities may be more rapid, and may alter community interactions and ecosystem functions that are not inferable from studies focused solely on extinction.

Conclusions

I found evidence of a potential drastic change point (threshold) in the response of terrestrial mammal species to increasing oil palm cover in landscapes composed of 45-75% oil palm cover; after which species composition declined precipitously. The identification of threshold allows to anticipate likely effects of land use change on biological communities. As such, landscapes that could support resilient mammal communities should contain ideally a maximum of 45% of oil palm, and certainly never exceeds 75% of the landscapes. On the other hand, most of the cultivation areas of the Llanos region of Colombia have already passed this sustainable limit for oil palm cover in relation to mammal conservation. Therefore, I recommend urgent restoration of these regions rather than measures focused solely on the identification current natural cover of high conservation value areas. Very few studies have evaluated potential non- linear effect of the human created matrices. Therefore, my analysis shed some light on current debates aimed to balance agriculture expansion and biodiversity conservation. Implementation of the practices identified here will offer Colombia the opportunity to become a role model for other Neotropical oil palm producing countries.

Supporting information

Taxa specific results from Threshold Indicator Taxa Analysis (TITAN) for 15 terrestrial mammal abundance and occurrence (IndVal) in response to oil palm percentage increment (Appendix 8),

Acknowledgments

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Chapter 4 Assessing the probabilities of terrestrial mammals to occupy oil palm plantations in the eastern plains of Colombia

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Statement of contribution of others:

LEP developed the main research question with input from WFL, GRC, and WE. LEP conducted all analysis with input from MVC. LEP collected the field data, coordinated surveys, data management, cleaning and processing. LEP wrote the first draft of the paper, with input from MVC. GRC, WE and MJC revised and edited the preliminary versions and WE provided feedback in the analysis with final revision from WFL

Abstract

Agriculture has created landscapes comprised of patchily distributed forests embedded within a matrix of human modified ecosystems. While the conservation role of remaining natural habitats in anthropogenic landscapes is relatively clear, quantifying the degree to which the agricultural matrix imposes limitation to animal use and movements is vital to understand species´ resilience to land use change. I evaluated the habitat use and detection probabilities of 23 medium- and large-sized mammals in oil palm plantations and adjacent riparian forest in the Llanos region, Colombia, using an occupancy framework. Further, I evaluated the effect of undergrowth vegetation and proximity to forest on habitat use probability within oil palm sites. Most species in the study area exhibited restricted distributions limiting the analysis to the 12 more common species. This issue was especially problematic within oil palm where I failed to detect seven species. Habitat use ($\hat{\Psi}$) was strongly influenced by habitat type in four species, showing a strong negative effect of oil palm, whereas the remaining eight species showed no effect of habitat type. However, probabilities of oil palm and forest use varied between species. In general, omnivorous mesocarnivores, white-tailed deer, and giant anteater were more likely to use oil palm while the remaining species, including ocelot and lesser anteaters, among others, showed preference for forest habitats. Historical land use changes in the Llanos region, previous and parallel to oil palm cultivation, might have influenced the pattern detected in this highly altered landscape. While resistance imposed by oil palm and the effect of the variables appeared to vary across species, my findings also suggest that allowing undergrowth vegetation inside plantations and maintaining nearby riparian corridors, will likely reduce the resistance imposed by oil palm for most of species in the assemblage.

Key words. anteaters, land-use change, Llanos, matrix resistant, mesopredators, occupancy, permeability

Introduction

Agricultural expansion is one of the major drivers of global habitat fragmentation and habitat loss (e.g. Campbell et al., 2017; Laurance et al., 2014). This process has had clear negative effects on biodiversity worldwide (e.g. Gibbs et al., 2010; Laurance et al., 2014; Newbold et al., 2015). However, the intensity of the effects of land-use change on native fauna depend on the type of agriculture replacing natural ecosystems, as well as other landscape or local factors such as the type of crop, remaining vegetation and its spatial configuration and potential availability of new resources (Cosentino et al., 2011; Franklin and Lindenmayer, 2009; Prugh et al., 2008). Some agroecosystems, for example, can facilitate the occurrence of generalist species (e.g. (Daily et al., 2003; Muhly et al., 2013; Nogeire et al., 2013) while others may act as barriers or ecological traps with elevated risk of mortality for rare and specialized species (e.g. Battin, 2004; Maddox et al., 2007). Therefore, understanding how agroecosystems limit animal movement or occupancy is fundamental for determining species chances of survival under increasing agricultural expansion.

Oil palm has become one of the most important agricultural products in the world. However, the increased cultivation of oil palm has had negative effects on the biodiversity of many tropical regions such as Southeast Asia (e.g. Fitzherbert et al. 2008; Danielsen et al. 2009). Oil palm cultivation is increasing in Latin America (Neotropics) (Dammert, 2014; Furumo and Aide, 2017), where Colombia is the largest producer with ~500,000 ha currently under cultivation (Fedepalma 2014). To date most Latin-American and Colombian oil palm expansion has taken place in previously transformed lands (Furumo and Aide, 2017; Pardo et al., 2015), however there is concern that this practice may change and oil palm cultivation may expand into natural areas, especially in areas of the eastern Llanos region, or Orinoco Basin (Etter et al., 2011; López-Ricaurte et al., 2017).

Worldwide, geographic ranges of mammal species have reduced by ~30%, especially in locations of intensive human activities (e.g. agriculture and settlements) (Ceballos et al., 2017). While Colombia is globally ranked among the five most mammal diverse countries, with 518 species recorded to date (Ramírez-Chaves et al. 2016), little is known about the natural history and distribution of most of Colombia's terrestrial mammals (Andrade-Ponce et al., 2016; Trujillo et al., 2010). This dearth of mammal knowledge is especially apparent for human-dominated landscapes. The lack of mammal studies (especially camera trapping) is particularly evident in the Llanos, and Amazon regions ((Díaz-Pulido et al., 2017). The Llanos region, contains ~ 68% of the Colombian mammal diversity (Ferrer et al., 2009). However, this region has become the most attractive area for implementation of agribusiness development (such as oil palm) in Colombia (Pardo et al., 2015; Romero-Ruiz et al., 2012). The western Llanos, for example, is a large area composed of different ecosystems, including savanna, wetland, grassland and riparian forest (Lasso et al., 2010), which has suffered a long history of disturbance by several agricultural processes, particularly grazing, that have cleared savannas and reduced the width of riparian forests (e.g. Etter et al., 2011; Madriñán et al., 2007).

Investigations into the potential impacts of oil palm production on Colombian fauna have recently increased (e.g. Pardo et al. 2018, Gilroy et al., 2015; López-Ricaurte et al., 2017). Nevertheless, there is still a paucity of information evaluating mammal species responses to oil palm cover. This information is important, as the capacity of protected areas and hotspots to be the sole source of biodiversity conservation in the long-term is limited, given the increasing rate of destruction occurring in these areas (Laurance et al., 2012; Sloan et al., 2014), and the surrounding landscapes (Gardner et al., 2009). Evaluating the probability of a species to occupy areas of different land-uses, allows us to evaluate the degree of resistance (or permeability) imposed by the surrounding agricultural matrix and hence, the ability of these species to tolerate these ecosystems. In this sense, occupancy estimation— using camera trap data— has become an important analytical technique when formal estimation of abundance is not possible; increasingly being seen as a flexible approach for conservation planning (e.g. Schwenk and Donovan, 2011; Tan et al., 2017). Further, evaluating habitat use through occupancy modeling can explicitly account for imperfect detection during other survey techniques, making inferences more robust (MacKenzie et al., 2006)

Due to the rapid expansion of oil palm in Colombia, there is an urgent need to assess the ability of mammals to tolerate and traverse the new matrix of oil palm cover and to identify management practices that can reduce biodiversity impacts. Here, I compared the habitat use of terrestrial mammals between riparian forest and oil palm plantations in the eastern plains of Colombia in an attempt to evaluate whether the oil palm matrix acts as a movement barrier for these species and if so the degree to which this occurs. Further, I evaluated the local habitat variables of the distance to forest and the presence of undergrowth vegetation to determine whether they increase the likelihood of species occurrence within oil palm habitats.

Methods

Study area

The ~2,000 km^2 study area is located in the department of Meta, Colombian Llanos, in rural land surrounding the towns of Restrepo, Cumaral, Cabuyaro, Acacias, Castilla la Nueva and San Carlos de Guaroa. Elevations in the area range between 194– 394 m (Fig 2.1). This area has a long history of human activity and contains a heterogeneous pattern of land cover including natural ecosystems of differing successional status, interspersed by human land uses such as livestock grazing and crop production. The predominant land use is oil palm cultivation, followed by cattle grazing and then other cropping systems (see Romero-Ruiz et al., 2012). The remnant native vegetation in the region is predominantly secondary riparian forest strips (known locally as gallery forest) of differing sizes and ages, some of which experience seasonal inundation.

Survey design

I sampled 33 sites inside oil palm plantations (hereafter oil palm) and 23 sites within riparian forests (hereafter forest), with sampling effort proportionate to the spatial extent of these habitat types within the study area (Fig. 2.1). Sites within each habitat were a minimum of 2 km apart to ensure the spatial independence of samples. The criterion that sites be separated by >2km was imposed as it exceeds the minimum recommended inter-site distance for inventories of terrestrial mammals in the Neotropics (e.g. Silveira et al., 2003; Team Network, 2008; Tobler et al., 2008) and encompasses the average expected diameter of the home ranges of the most common species found in the study area (Ferrer et al., 2009; Pardo and Payán, 2015). Surveys in oil palm plantations were restricted to those planted before 2006 to avoid the confounding influence of plantation age. All surveys were conducted during the dry season, between September 2014 and January 2016.

Camera trapping

I deployed seven Reconyx HC500 HyperfireTM digital camera traps at each site (sampling unit) to detect terrestrial mammals (> 0.5 kg). This sampling design of seven camera traps was found in a pilot study conducted in the study area (Pardo et al. short. comm. 1) to improve estimates of the sampling completeness when compared with the traditional practice of using a single camera per site (Burton et al., 2015). In the forest, camera traps were spaced ~250 m apart along transects, and were set close to animal trails where possible. Due to the homogeneous nature of oil palm plantings cameras in this land cover type were arranged in a zigzag pattern in an attempt to maximize spatial coverage though at similar spacing as in the forests. I pooled the data derived from the seven cameras at each site into a single sample, and used this as the sample unit for estimating species occupancy (see below).

All cameras were fixed to trees or wooden poles with a steel cable (Python^{TM}, US) and were configured to the following criteria: high-sensitivity sensor, a 1-second interval between consecutive pictures (3 per trigger), no delay or quiet period between triggers. Cameras were installed a minimum distance from the potential path of the animal (e.g. trails) of 1 m and 25-30 cm height, depending on the terrain. Cameras were active for 30 to 40 days without baiting. Only terrestrial mammals were considered for analyses and were identified using the most recent taxonomic classification of Colombian mammals (Ramírez-Cháves et al., 2016).

Habitat use and detection probability

Oil palm effects on the habitat use and detection probabilities of terrestrial mammalian species at the landscape level were determined using a single season likelihood-based occupancy modelling protocol as developed by MacKenzie et al. (2006). This framework allows for the determination of factors that affect the distribution or habitat use of a particular species based on detection/non-detection data along temporal replicates (i.e. detection histories) at each site. Furthermore, occupancy analyses explicitly account for imperfect detection (p <1.0) and therefore facilitate evaluations of changes in detection probabilities and likelihood of species' use of particular habitats (e.g. MacKenzie et al., 2006; Nagy-reis et al., 2017). Since I was interested in the entire terrestrial mammal community, the criteria and assumptions about independence between sites within the occupancy framework were flexible (i.e. sites might not be closed to changes in occupancy). Thus, occupancy (Ψ) in this study is interpreted and referred to as habitat, or site, use probability (MacKenzie et al., 2006).

Detection histories were constructed using the compiled photographs from eight survey occasions, each formed by the combination of five camera survey days across all seven cameras per site. I first evaluated whether habitat type (oil palm versus forest) was a determinant driver for habitat use (Ψ) or detection probability (p) across the study area (n = 56 sites). Second, I selected sites within oil palm (n = 33) only to assess how two habitat characteristics of this monoculture influenced species habitat use: distance to nearest forest patches (m) ($\log_{10}$ transformed) and understory vegetation (high = 1 or low = 0).

To assess the influence of the explanatory variables in the two different analytical approaches, I used a model selection framework with Akaike's Information Criterion, corrected for small sample size (AICc) (Burnham and Anderson, 2002). I evaluated the models for goodness-of-fit against 1,000 simulated bootstrap datasets (MacKenzie and Bailey, 2004). All models that fit within Δ AICc < 2 were considered to have substantial support as the most likely factors influencing Ψ and/or p (Burnham and Anderson, 2002). I used the software program PRESENCE 3.1 (Hines, 2006) for all analyses of occupancy and model selection. Models that did not converge were not included in the model selection process. In cases where overdispersion was detected (which occurred only for the crab-eating fox), QAICc was used for model selection. The relative importance of the effect of each variable on species occupancy was assessed by summing the cumulative Akaike weight ($\Sigma\omega_i$) of those models containing the variable within the plausible models, using a cutoff of Δ AICc < 2. I also used a model-averaging approach to estimate an overall value of occupancy for the entire study area and for each habitat type.

For the first assessment, I constructed four models allowing habitat use (i.e. occupancy) (Ψ) and detection probabilities (p) to vary according to habitat type. If the null model [i.e. Ψ(constant), p(constant)]) appeared as the top model, then I concluded that habitat had no significant effect on the occupancy or detection probabilities of the species, and hence oil palm plantations had no apparent influence on habitat use probabilities. Further, to clearly understand how habitat use differed between the species detected inside oil palm and forest, I used the model Ψ(habitat), p(habitat) as a unifying criterion. This model was the most common model among top-ranking models across species (Appendix 9). Preliminary analyses showed that models constructed for species detected in less than three sites resulted in convergence issues. Therefore, estimation of

Ψ and p was not possible for these species, and naïve occupancy is reported instead (i.e. proportion of sites where species were detected without accounting for imperfect detection).

Since undergrowth vegetation could influence the detection probability (p) of animals inside oil palm, for the second assessment I first evaluated these effects on detection. To do this, I allowed p to be constant or vary according to undergrowth vegetation while maintaining the habitat use parameter– Ψ identified in the global model (all variables) [i.e. Ψ(undergrowth + distance to forest), p(constant)] vs Ψ(undergrowth + distance to forest), p(undergrowth)]. The best model for p was then used in the subsequent model selection of Ψ. Untransformed beta coefficients from these models were used to evaluate the direction and magnitude of the effect of the variables on Ψ estimates, which are presented for each of the top-ranking models. I predicted that the effects of undergrowth and distance to forest on habitat use would be positive and negative respectively, given the importance of heterogeneity and evidence for the strong effect of isolation from natural forests shown in other vertebrates (e.g. Tews et al., 2004; Tscharntke et al., 2012; Yue et al., 2015). I combined the detection history of species with similar direction in response to distance to forest (only those with strong evidence, Δ AICc <2) to improve the precision of the estimates inside oil palm, due to the low occurrences of species, and facilitate the visual interpretation of the results.

Results

Twenty-three terrestrial species of medium and large mammals and two species of arboreal primates were detected across the study area (Table 4.1). See Chapter two for a discussion regarding the composition and species richness.

Table 4.1. Naïve occupancy, model-averaged estimates of overall habitat use ($\hat{\Psi}$) and habitat preference of 24 terrestrial mammals detected in oil palm dominated landscapes in the Llanos region, Colombia. Positive Beta values suggest preference for oil palm and negative values suggest preference for forest for forest.

		Occupied sites		**Naive Occupancy**			**Overall estimated occupancy**			**Habitat preference**
Common name	**Scientific name**	**Forest**	**Oil Palm**	**Study area**	**Forest**	**Oil Palm**	**$\hat{\Psi}$ (Sd) study area**	**$\hat{\Psi}$ (Sd) forest**	**$\hat{\Psi}$ (Sd) oil palm**	**Beta oil palm (SE)**
Giant anteater	*Myrmecophaga tridactyla*	19	30	0.88	0.83	0.91	0.90 (0.04)	0.86 (0.07)	0.94 (0.06)	2.12 (2.60)
Lesser anteater	*Tamandua tetradactyla*	20	16	0.64	0.87	0.48	0.72 (0.16)	0.90 (0.13)	0.59 (0.17)	-1.64 (0.97)
Nine-banded Armadillo	*Dasypus novemcinctus*	16	3	0.34	0.70	0.09	0.57 (0.10)	0.69 (0.09)	0.49 (0.25)	-2.32 (1.15)
Naked-tailed armadillo	*Cabassous unicinctus*	9	0	0.16	0.39	0.00	0.19 (0.23)	0.47 (0.13)	0	--
Crab-eating fox	*Cerdocyon thous* *	6	26	0.57	0.26	0.79	0.60 (0.28)	0.27 (1.71)	0.82 (3.41)	2.57 (0.72)
Jaguarundi	*Puma yagouaroundi*	5	13	0.32	0.22	0.39	0.91 (0.10)	0.80 (0.21)	1 (#)	--
Ocelot	*Leopardus pardalis* *	16	12	0.50	0.70	0.36	0.72 (0.01)	0.72 (0.11)	0.71 (0.18)	-1.73 (0.85)
Puma	*Puma concolor*	2	1	0.05	0.09	0.03	--	--	--	--
Greater grison	*Galictis vittata*	1	2	0.05	0.04	0.06	--	--	--	--
Tayra	*Eira barbara*	2	0	0.04	0.09	0.00	--	--	--	--
Crab-eating raccoon	*Procyon cancrivorus* *	4	7	0.20	0.17	0.21	0.42 (0.20)	0.37 (0.22)	0.46 (0.23)	0.36 (0.95)
Coati	*Nasua nasua*	2	0	0.04	0.09	0.00	--	--	--	--
White-tailed deer	*Odocoileus cariacou* *	6	12	0.32	0.26	0.36	0.57 (0.17)	0.45 (0.19)	0.65 (0.21)	0.79 (0.95)
Red-brocket deer	*Mazama spp*	0	1	0.02	0.00	0.03	--	--	--	--
Collared peccary	*Pecari tajacu*	1	1	0.04	0.04	0.03	--	--	--	--
Spiny rat	*Proechimis spp*	21	2	0.41	0.91	0.06	0.40 (0.06)	0.88 (0.07)	0.06 (0.04)	-4.21 (1.21)
Agouti	*Dasyprocta fuliginosa*	18	0	0.32	0.78	0.00	0.69 (0)	0.67 (5.78)	0	-4.75 (1.13)
Lowland Paca	*Cuniculus paca*	23	1	0.43	1.00	0.03	0.43 (0.07)	1 (#)	0.03 (0.03)	--
Capybara	*Hydrochaerus hydrochaeris*	8	3	0.20	0.35	0.09	0.20 (0.05)	0.36 (0.10)	0.09 (0.05)	-1.62 (0.77)

Coendu	*Coendu spp*	1	0	0.02	0.04	0.00	--	--	--	--
Squirrel	*Sciurus spp*	9	0	0.16	0.39	0.00	--	--	--	--
Common opossum	*Didelphis marsupialis*	22	12	0.61	0.96	0.36	0.49 (0.27)	0.80 (3.32)	0.27 (1.69)	-3.62 (1.10)
Four-eyed opossum	*Philander opossum*	1	0	0.02	0.04	0.00	--	--	--	--

*Overall occupancy model did not converge, therefor $\widehat{\Psi}$ for study in these species is from null model [Ψ(.),p(.)], and for each habitat from Ψ(cov),p(.). Therefore, parentheses is SE and not SD

-- = Data deficient. Models using species with less than 4 detections resulted in convergence problems and high uncertainty.

= SD extremely high

General patterns of mammalian distribution in the study area

Most of the species in the study area were rare with only five species detected at more than 50% of the sites (naïve occupancy): giant anteater (*Myrmecophaga tridactyla*), lesser anteater (*Tamandua tetradactyla*), crab-eating fox–here after fox (*Cerdocyon thous*), ocelot (*Leopardus pardalis*), and common opossum (*Didelphis marsupialis*). Only two species occupied more than 70% of the oil palm sites with the giant anteater being the most widely distributed species (naïve occupancy 91%) followed by the fox (naïve occupancy = 79%; Table 4.1). Jaguarundi (*Puma yagouarondi*) was also detected at nearly 40% of the oil palm sites, but the remaining species detected in the oil palm plantations were rare usually only being detected on single occasions. Furthermore, nine out of 17 (53%) species detected within oil palm sites occupied less than 10% of the sites (Table 4.1). In forested sites, however, seven species occupied more than 70% of the sites: giant anteater, lesser anteater, nine-banded armadillo–here after armadillo (*Dasypus novemcinctus*), ocelot, spiny rat (*Proechimis spp*), agouti (*Dasyprocta fuliginosa*), lowland paca–here after paca (*Cuniculus paca*), and common opossum. At the other end of the occupancy spectrum within forested sites seven out of 23 species (30%) occupied less than 10% of the sites.

Effects of habitat type on species habitat use

Only 12 of the 23 identified species had sufficient detection records suitable for analyses. From these 12 species, strong evidence for an effect of habitat type on species habitat use (occupancy; Ψ) was observed for only four: naked-tailed armadillo (*Cabassous unicinctus)*, capybara (*Hydrochoerus hydrochaeris*), spiny rat and common opossum. For all of these four species there was a highly negative effect of oil palm (β coefficient) on the probability of habitat use (Table 4.1). No clear effect of habitat type was found for either species of anteaters, with the weight of evidence ($\Sigma\omega_i$) for the model that had constant habitat use [Ψ(.), *p*(hab)] receiving similar support as the model containing habitat type [Ψ(hab), *p*(hab)] (Appendix 9). However, the two anteater species showed different response directions for the effect of habitat type, with occupancy for giant anteater displaying a positive correlation with oil palm (β = 2.12; ± 2.60 SE), whereas occupancy for the lesser anteater had a negative correlation with oil palm (β = -1.64: ± 0.97 SE) (Table 4.1). I also observed no effect of habitat type (i.e. support for the model based on constant occupancy was higher) in the six remaining species: ocelot ($\Sigma\omega_i = 1$), fox ($\Sigma\omega_i = 1$), crab-eating raccoon (*Procyon cancrivorus*)–here after raccoon ($\Sigma\omega_i = 0.70$), white-tailed deer–*Odocoileus cariacou* ($\Sigma\omega_i = 0.71$), and to a lower extent armadillo ($\Sigma\omega_i = 0.61$), and jaguarundi ($\Sigma\omega_i = 0.55$). However, the models suggested that land cover had an important influence on the detection probabilities of all species (Appendix 10).

Habitat use probability between oil palm and riparian forest

Oil palm and forest shared 17 mammal species. However, only 10 species had adequate data (i.e. >3 occurrences) to compare their estimated habitat use probability between both habitats – Ψ (habitat), p(habitat). From these species, six had lower probability of oil palm use when compared to forest: capybara, spiny rat, armadillo, common opossum, ocelot and lesser anteater. Moreover, the first three of those species were the least likely species to use oil palm, according to the estimated probabilities of habitat use ($\widehat{\Psi}$) (Fig 4.1). Further, for these six species, habitat use was on average 2.2 (range 1.4-3.6) times higher for forest than oil palm. In contrast, fox, raccoon, white tailed deer and giant anteater were the most likely species to use or occupy oil palm plantations, with habitat use probabilities being on average ~2 times greater there than inside forest (range 1.4-3.0) (Fig. 4.1).

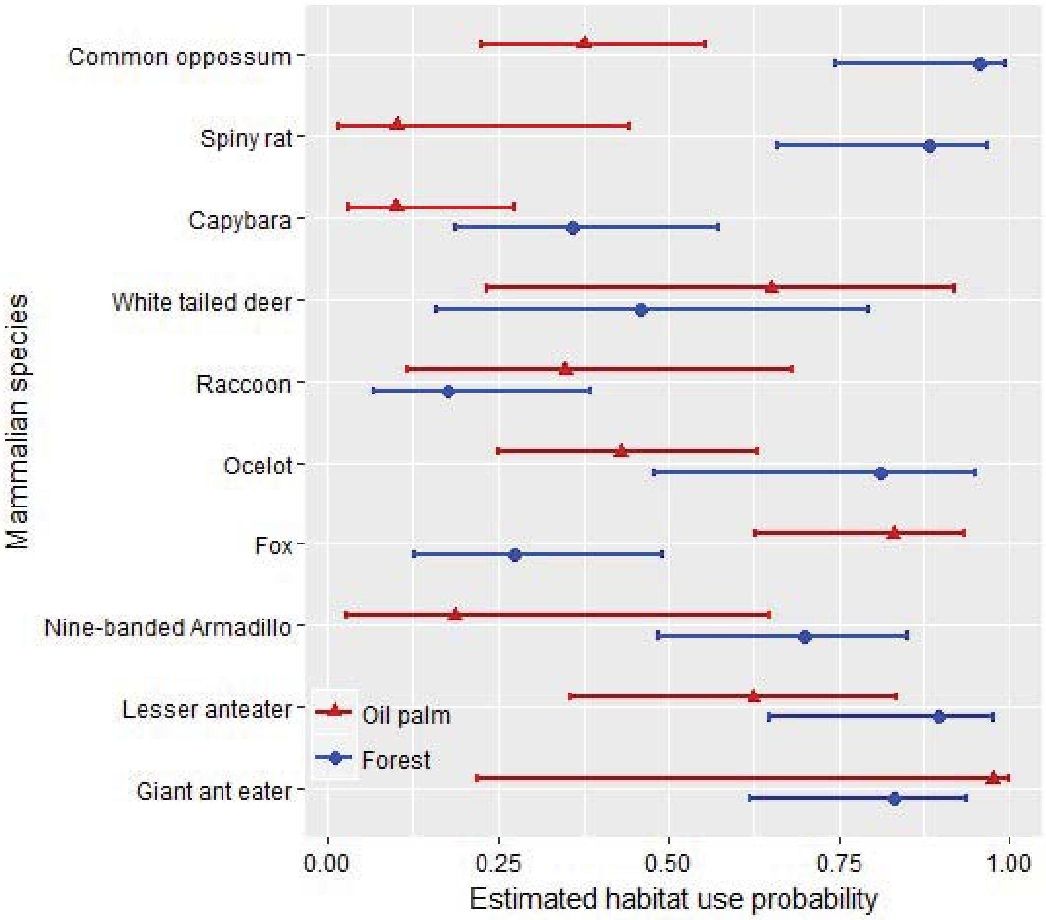

Figure 4.1. Estimated probability of habitat use ($\hat{\Psi}$) of selected species between oil palm and riparian forest in the Llanos region of Colombia. Model Ψ(cover), *p*(cover) was used to compare across species.

Note: only 10 of the 17 shared species were suitable for analysis (>3 detections per habitat). For rare species or those with converge issues see table 4.1. Some common names has been shortened to facilitated interpretation, see table 1 for scientific and common names. Confidence intervals are shown to assess the precision of the estimated occupancy, caution is advised if interpret as "significance" testing (i.e. overlap of confidence intervals do not necessary suggest no evidence of difference ("no significant"; see Helman and Stern 2006, and http://mikemeredith.net/blog/1303_Comparison_of_confidence_intervals.htmo)

Although the estimated habitat use of jaguarundi was the largest at four times greater in oil palm than in forest, these estimates were associated with high SEs (inside oil palm). For the eight species that were so infrequently detected that their models did not converge, naïve occupancy suggested larger differences between oil palm and forest. For example, the paca was only detected at one site inside oil palm but occupied all forested sites. Similarly, spiny rats occupied almost all forested sites and were detected only in two oil palm sites. However, other species were equally rare in both habitats (e.g. puma [*Puma concolor*], grison [*Galictis vittata*]). Estimated detection probabilities were below 0.2 for 11/13 species, particularly inside oil palm (7/11 species), while white-tailed deer, raccoon, fox and jaguarundi exhibited higher detection probabilities inside oil palm (Appendix 10).

Effects of variables on habitat use within oil palm sites

Ten species had sufficient frequency of detection to examine habitat use within oil palm. I found strong evidence of support for constant occupancy (i.e. no effect of understory vegetation or distance to nearest forest on habitat use) in giant anteater and fox (Fig. 4.2, Table 4.2). Undergrowth vegetation had a positive effect on the habitat use of the remaining eight species with particularly strong support ($\Sigma\omega\text{i} > 0.5$) for the lesser anteater, armadillo, and white-tailed deer (Fig. 4.2). Distance to nearest forest patch had the greatest influence on raccoon and capybara habitat use ($\Sigma\omega i > 0.66$), with positive and negative relationships respectively, closely followed by ocelot with a negative effect. However, modelling for habitat use of the ocelot also revealed similar level of support for models including constant occupancy (Fig. 4.2). Four species showed a negative relationship between distance to forest and habitat use probability (armadillo, ocelot, white tailed deer and capybara), whereas three species showed a positive relationship (jaguarundi, raccoon, common opossum) (Fig. 4.3). For jaguarundi and the common opossum both distance to forest and presence of undergrowth vegetation had the same level of support and direction of the effect, but their constant model had higher support, suggesting no influence of these variables on their habitat use (Fig. 4.2).

Table 4.2. Model selection results evaluating the effect of understory vegetation (veg) and distance to forest patch (dist) on estimated habitat use ($\hat{\Psi}$) and detection probabilities (*p*) for selected species within oil palm plantations in the eastern plains of Colombia (n = 33 sites). Only the top supported models are shown (Δ AICc < 2).

Species/Model	Δ AIC	AIC *w*	k	-2 log like	Intercept	SE	Beta$_1$	SE	Beta$_2$	SE
Giant anteater										
Ψ (.),*p*(.)	0.00	1.00	2	298.29						
Lesser anteater										
Ψ (veg),*p*(.)	0.00	0.53	3	165.42	-0.73	0.76	2.03	1.14		
Ψ (.),*p*(.)	1.62	0.23	2	169.47						
Nine-banded armadillo										
Ψ (veg),*p*(.)	0.00	0.42	3	36.02	-23.65	4.38	22.74	4.38		
Ψ (.),*p*(.)	0.79	0.28	2	38.81						
Ψ (veg+dist),*p*(.)	1.78	0.17	4	35.80	-26.10	4.77	28.33	4.57	-0.50	0.79
Fox										
Ψ (.),*p*(veg)	0.00	1.00	3	274.77						
Jaguarundi										
Ψ (.),*p*(.)	0.00	0.50	2	118.25						
Ψ (veg+dist),*p*(.)	0.71	0.35	4	113.93	-12.47	9.14	22.13	#	1.79	1.37
Ocelot										
Ψ (dist),*p*(.)	0.00	0.43	3	104.74	46.00	#	-6.44	#		
Ψ (.),p(.)	0.16	0.40	2	107.33						
Ψ (veg),*p*(.)	1.87	0.17	3	106.61	0.61	1.57	25.57	#		
Crab-eating Raccoon										
Ψ (dist),*p*(.)	0.00	0.45	3	76.94	-11.34	5.21	1.65	0.83		
Ψ (.),*p*(.)	1.23	0.24	2	80.17						
Ψ (veg+dist),*p*(.)	1.59	0.20	4	76.53	-12.72	5.41	0.83	1.29	1.77	0.82
White tailed deer										
Ψ (veg),*p*(.)	0.00	0.64	3	119.14	-1.88	1.13	3.28	1.73		
Ψ (veg+dist),*p*(.)	1.79	0.26	4	118.33	6.56	17.90	3.51	2.81	-1.31	2.76
Capybara										
Ψ (veg+dist),*p*(.)	0.00	0.45	4	39.58	-4.57	16.54	22.07	14.28	-3.20	1.68
Ψ (dist),*p*(.)	0.10	0.42	3	41.68	16.44	10.01	-3.10	1.74		
Common opossum										
Ψ (.),*p*(.)	0.00	0.43	2	162.84						
Ψ (dist),*p*(.)	1.24	0.23	3	161.65	-4.58	3.46	0.63	0.53		
Ψ (veg),*p*(.)	1.38	0.21	3	161.79	-1.05	0.68	0.81	0.81		

Notes: Δ AICc: difference in AIC values between each model with the lowest AIC model (best model); AICω: Akaike weight.; k: number of parameters in the model; SE: standard error. Understory vegetation is a binary covariate with 0= clean or low understory vegetation (the intercept), and 1= medium to high understory (beta), nearest distance to forest in log10, # = high standard errors, this does not affect the direction or effect of the untransformed beta estimate (Hines, 2006)

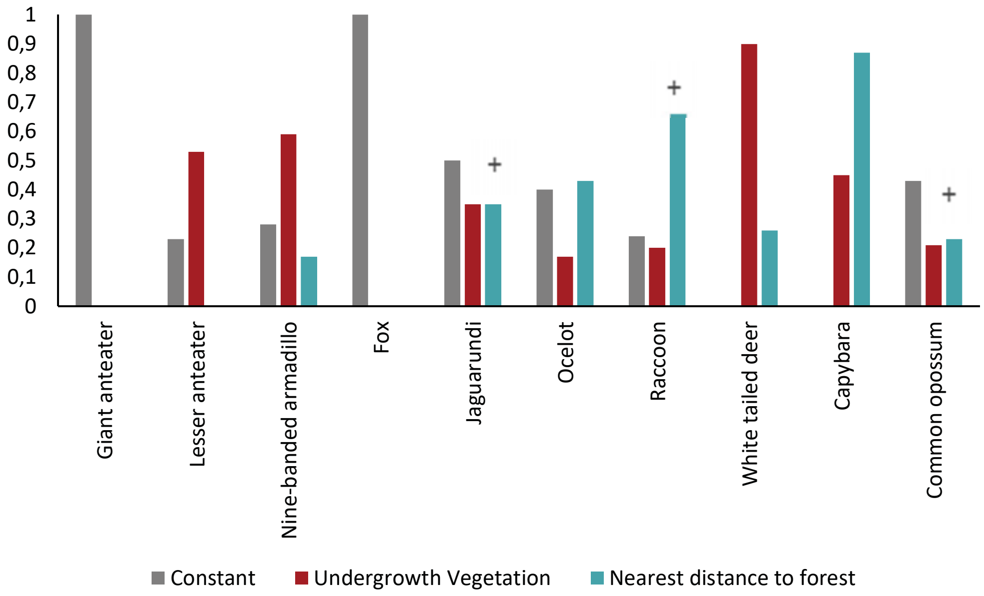

Figure 4.2. Cumulative Akaike weight, ($\Sigma\omega i$) for support of the influence of undergrowth vegetation and distance to nearest forest patch on the occupancy of selected medium and large mammals inside oil palm plantations in Colombia. Positive or negative signs indicate the direction of the effect for distance to nearest patch. Undergrowth vegetation had a positive effect in all species.

$^{*}\Sigma\omega_{i}$ calculated for top-ranked models Δ ACIc < 2

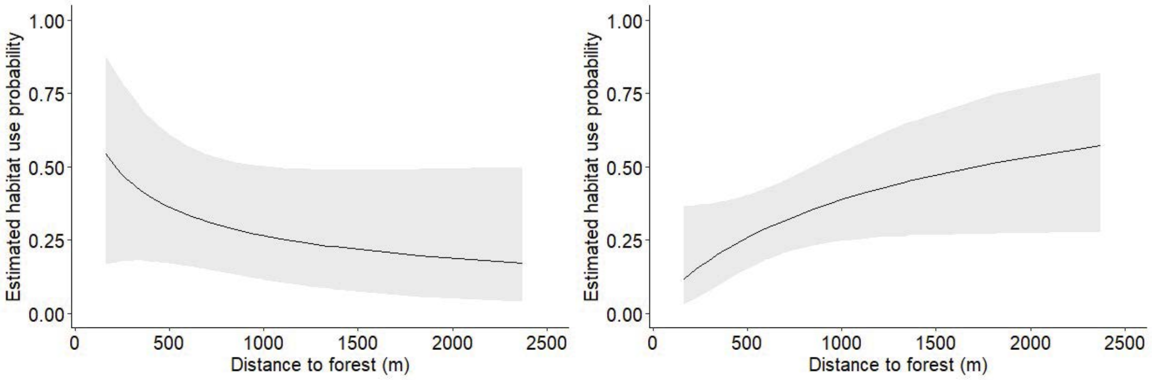

Figure 4.3. Estimated effect of distance to nearest forest on habitat use probability of selected species. Figure represent the effect on different species that showed strong evidence for the influence of distance to forest with left panel representing the cumulative effect on armadillo, ocelot, white-tailed deer, and capybara, whereas right panel represents the positive cumulative effects on jaguarondi, raccoon, and common opossum.

Note: species were grouped to make predictions more precise. Individual species develop wide confidence intervals due to sparse data inside oil palm, which limits interpretation of the effects of the variable. Selection on species were based on $\Sigma\omega_i$ from Fig.3.

Discussion

I found that the mammal community in the oil palm producing region of the Llanos in Colombia is composed mostly of generalist species, with restricted distributions and very low detection probabilities (especially for most species within oil palm). These results are supported by the findings of other research on different taxonomic groups in Colombia that have reported a negative relationship between oil palm and biodiversity metrics such as richness, occupancy, and abundance (e.g. Gilroy et al., 2015; López-Ricaurte et al., 2017; Pardo and Payán, 2015, Pardo et al. 2018). However, eight of 12 species were not significantly influenced by habitat type, which suggest that some species are able to use and move across the oil palm matrix.

Understanding the probability of species to use human altered environments or agroecosystems helps to evaluate the extent of impacts and prospects for wildlife-friendly agriculture. I found that oil palm is more likely use by generalist mesopredators, anteaters, and deer, while forest specialist such as seed dispersers (e.g. paca and other rodents), omnivores (e.g. armadillos) and marsupials were less likely to use oil palm, suggesting they are more sensitive to forest conversion to oil palm. As such, my findings highlight the importance of retaining secondary forest in agroindustrial landscapes for terrestrial mammal occurrence. The value of riparian forest has been emphasized by previous research (e.g. McShea et al., 2009; Yaap et al., 2016). In the following paragraphs, I briefly discuss the possible mechanisms behind the most conspicuous patterns detected in the study area.

Anteaters and omnivorous mammal species habitat use

The giant anteater displayed a preference for oil palm. This pattern clearly contrast the results of Mendes-Oliveira et al., (2017), who found negative associations for this species in the Brazilian Amazon. While the giant anteater is categorized as Vulnerable by the International Union for Conservation of Nature–IUCN (Miranda et al., 2014), I found they are widely distributed throughout both oil palm plantations and forest habitats. This habitat flexibility corresponds with other research suggesting that intermediate human disturbance and the associated habitat heterogeneity seem to favor the giant anteaters (Quiroga et al., 2016). This pattern suggests that food availability for giant anteaters is not a limiting factor inside oil palm plantations, which could be supported by the relatively high diversity and abundances of ant species (Gilroy et al., 2015; Sanabria et al., 2014) found in this crop. On the other hand, jaguars (*Panthera onca*) have a strong preference for giant anteaters in their diet (i.e. 75% of the biomass consumed) in central Brazil (Sollmann et al., 2013), and the capture frequencies of giant anteaters tend to increase when jaguar is absent (Quiroga et al., 2016). Therefore, it is possible that the absence (no detection) of jaguars in the current study area could in part facilitate the high occurrence of giant anteater sin the area.

Contrary to the giant anteater, the lesser anteater displayed a preference for forested habitats. This is despite the fact that the giant and lesser anteaters display similar dietary requirements (i.e. obligate insectivores –Emmons, 1999). Like the giant anteater, the lesser anteaters forage terrestrially, however, they also use trees for nesting and foraging (Brown et al., 2014; Gallo et al., 2017), which may in part explain their preference for forest. Further, lesser anteaters feed mainly on arboreal ants and termites, while giant anteaters mainly eat terrestrial ant species and tend to eat less termites (e.g. Sandoval-Gómez et al., 2012). Oil palm trees typically lack termite nests (LEP pers. obs.), so it is probable that the availability of food resources for the lesser anteater is reduced inside oil palm plantations and therefore their use of this habitat is reduced. Although the lesser anteater was able to cross oil palm plantations, this ability was reduced as distance to forest increases. Suggesting a scale-dependent effect of oil palm permeability for the species.

As with the lesser anteater, oil palm does not appear to offer enough resources for species such as armadillos or rodents as inferred by their low probability of oil palm use and detection. Naked-tailed armadillos, for example, prefer complex vegetation associated with gallery (riparian) forests running through savanna type habitats (Bonato et al., 2008). Similarly, although the nine-banded armadillo is commonly detected in sites associated with various land-use matrices (e.g. agricultural landscapes) in the Neotropics (e.g. Cove et al., 2013; Daily et al., 2003), reduced leaf litter and decomposing soil inside oil palm plantations most likely limits food resource availability for this species (e.g. soft-bodied invertebrates, fruits, seeds, and small vertebrates (da Silveira Anacleto, 2007; Sikes et al., 1990). High rates of disturbance associated with farming activity (e.g. harvesting, motor vehicles etc.) and vulnerability to mesopredators (e.g. fox, ocelots) could also play an important role in the identified reduced oil palm habitat use by nine-banded armadillos.

Herbivore, frugivore, and granivore mammal species habitat use

Paca and agouti are two medium-sized frugivores which are important seed dispersers in the study area. These species were detected exclusively within forested sites, most likely because oil palm does not provide the necessary fruit/seed resources for them. Additionally, their limited dispersal ability and small home ranges(Aliaga-Rossel et al., 2008; Beck-King et al., 1999) reduce their probability to cross the oil palm matrices in search for riparian forest patches. Considering the important role these species play in forest maintenance and regeneration (Camargo-Sanabria et al., 2014a; Dirzo and Miranda, 1990) their vulnerability to conversion of forested ecosystems to oil palm plantations in the region may alter ecosystem processes (see Pardo et al. 2018). This is despite the fact that these two species were common throughout the forested sites of the study area. Similar patterns were shown for other seed dispersers examined during this study such as spiny rats, which exhibited high habitat use of forested sites compared to oil palm plantations and squirrels for which only detections occurred in forest sites. As such, if oil palm expansion replaces native vegetation in the Llanos, it may threaten seed dispersing mammalian fauna, and as a consequence threaten the regenerative capacity of the local forested ecosystems.

Top and mesopredator mammal species habitat use

One top predator and eight mesopredators (seven carnivores and common opossum) were detected in the study with each exhibiting varying responses to the oil palm landscape. Pumas (*Puma concolor*) were rarely detected (see Pardo et al., 2017), which limit further inferences, but my findings are concordant with other research that found that some top predators such as puma are able to traverse oil palm plantations (e.g. pumas, jaguar and tiger— (Azhar et al., 2014; Mendes-Oliveira et al., 2017; Olarte-González and Escovar-Fadul, 2015). These findings however do not constitute evidence for oil palm being a permanent habitat or territories for apex predators. Moreover, in all of the above cases, oil palm sites were relatively close to forest habitats, suggesting a reliance on the retention of natural forest to maintain top predator occurrence in the landscape (see also Gonzalez-Maya et al., 2013; Polisar et al., 2003)

The higher habitat use probabilities for some mesopredators (e.g. fox, jaguarondi, raccoon) confirms their ecological flexibility and thus ability to occupy several types of land cover/use including agroecosystems (e.g. Emmons, 1999; Nogeire et al., 2013; Tófoli et al., 2009). Fox, in particular, clearly preferred oil palm habitat which is consistent with the previous findings of Mendes-Oliveira et al. (2017) and Pardo and Payán, (2015). Mechanisms underlying this ecological flexibility displayed by mesopredators may include their omnivorous diet and opportunistic behaviors conferring them the ability to eat a wide range of eating fruits, insects, amphibians, reptiles, crustaceans and rodents (e.g. De Arruda and Motta-Junior, 2004; Emmons, 1999; Giordano, 2016).

Although there is a lack of information on small rodents within oil palm plantations in Colombia, they have been reported as a pest in Southeast Asian plantations (Wood and Fee, 2003). Since the diet of mesopredators often includes a high proportion of small rodents (e.g. De Arruda and Motta-Junior, 2004; Tófoli et al., 2009), it is likely that the potential availability of rodents could increase oil palm use by this group of carnivores. Apart from rodents, the presence of other potential prey items (such as armadillos, reptiles and invertebrates) reported inside oil palm and in their diets (Emmons, 1999; Pardo and Payán, 2015; Tófoli et al., 2009), may also play a crucial role in their high oil palm use. Further studies are required to elucidate whether fox habitat use is also influenced by oil palm fruit, as previous research suggest foxes may consume this fruit as they have been recorded consuming similar palm fruits and seeds (De Arruda and Motta-Junior, 2004; Facure and Giaretta, 1996).

Similar to the jaguarundi, ocelots are obligate carnivores highly tolerant to anthropogenic systems (e.g. Cruz-Rodríguez et al., 2015; Daily et al., 2003; Liévano Latorre and López Arévalo, 2014; Mendes-Oliveira et al., 2017). However, ocelot had higher occupancy in forested sites, while jaguarundi showed a positive association with oil palm. This apparent difference in habitat selection between the species could be related to a spatial segregation between the two, which has been previously suggested as a way to minimize competition among mesocarnivores (e.g. Di Bitetti et al., 2010). On the other hand, given that the ocelot is mostly nocturnal, and jaguarundi is mostly diurnal (see Pardo et al. Chapter 5), it is probable that temporal resource partitioning may also play an important role (see Monterroso et al., 2014). Additionally, ocelots may be using oil palm for passage rather than as permanent territories for hunting. As such, dietary studies across these landscapes would help to elucidate whether the identified coexistence of these two species is achieved through resource partitioning.

Habitat use within oil palm plantations

Within oil palm plantations the existence of understory vegetation increased habitat use by the majority of species, and tended to have a stronger effect than the distance a site was from forest. This finding may occur as understory vegetation can increase habitat heterogeneity inside plantations thereby promoting diversity and trophic interactions at different scales (reviewed by Tews et al., 2004). Undergrowth vegetation in the oil palm plantations in this study was found to be especially important for deer, which suggests these resources could be important for foraging (Gallina et al., 2010) or hiding from predator or hunters.

The low contribution of distance to the forest in the habitat use of some species within oil palm reflects once again their habituation to oil palm. This finding corresponds with those of previous studies showing that attributes such as quality and cover type seemed to be more important than measures of isolation from forest patches (e.g. Daily et al., 2003; Prugh et al., 2008). This result, however, contrast to that of Yue et al. (2015) who found that distance to forest was the most important factor in determining occupancy of the whole mammalian assemblage in Southeast Asia. Although, they compared distance to forest patch with canopy cover, oil palm height and their interaction, not vegetation inside plantations. An important exception in the effect of distance to forest was the capybara whose habitat use was 3.6 times greater in riparian forest than in oil palm, and decreased with increasing distance to nearest forest patch, with detections never occurring further than 357 m from remnant forest. This finding supports the notion that capybaras are dependent on forested habitats, despite also being a common species in open natural savannas elsewhere in the country (Camargo-Sanabria et al., 2014b; Herrera and Macdonald, 1989).

The relationship between habitat use and proximity to forest varied among species. Four out of seven species showed a negative relationship between distance to nearest forest patch and habitat use (armadillo, ocelot, white tailed deer, and capybara). This relationship suggests that these species freely move inside oil palm but that they do not to occur far from the forest. Similarly, Mendes-Oliveira et al. (2017) identified that the median distance from the nearest forest edge for any mammal detected in their oil palm study was 960 m. In the present study, the average distance of rare species (those with insufficient data to model) from the nearest forest edge (< 3 sites; e.g. greater grison, puma, red brocket, peccary, paca) was 430 m (SD 169 m). This confirms that rare species that occurred in oil palm are restricted to locations close to forest. Further, species with a negative association with distance to the forest showed very low probabilities of habitat use beyond 1000 m. In other words, there are likely spillover effects from forests to oil palm plantations, though these are limited to relatively short distances from the forest. It is important to note that the maximum distance to the nearest forest in the study area was ~2400 m. Therefore, it is unknown whether these effects could be more accentuated when the closest forest patches are at greater distances.

Clearly, oil palm does not constitute suitable habitat for the majority of the mammals in the study area (see also Pardo et al. 2018). However, to assess the direct impacts of oil palm cultivation on Colombian biodiversity, it is important to consider the effects of previous land-use types as well as hunting history on the current patterns of diversity (see Gardner et al., 2010; Harding et al., 1998). Oil palm in Colombia has been implemented mostly in lands already modified by human uses (e.g. Castiblanco et al., 2013; Furumo and Aide, 2017). Therefore, the responses shown in this study could be influenced by the accumulation of historical processes of land-use changes (e.g. rice, cattle pastures), and not solely the effect of oil palm. It is likely that the species now occupying oil palm plantations are "survivors" (*sensu* Prugh et al., 2008) that are more readily adaptable to this agricultural ecosystem (see Pardo et al. 2018), or as shown, that are attracted to this new ecosystem. The inability to detect more sensitive species (e.g., tapirs [*Tapirus terrestis*], jaguars, giant armadillo [*Priodontes maximus*]) in the examined study area may support this hypothesis. A future question to investigate could be whether there are meta-population dynamics taking place in these agroecosystems.

The production of oil palm in already transformed lands may positively or negatively affect some of the relationships between resilient species across this relatively new anthropogenically transformed landscape. For instance, raccoons and foxes tend to prefer forest rather than pastures (Pineda-Guerrero et al., 2015), while in the study area they tended to prefer oil palm over forest. Therefore, future research is required to monitor the dynamics taking place among these assemblages and contrast the effects of other crops on mammalian communities compared with that of oil palm (e.g. pasture, rice, soy etc.). Future studies will also benefit from evaluating the influence of proximate land uses and configuration of the entire landscape mosaic, as well as using multiple approaches for assessing functional connectivity within oil palm landscapes, which are beyond the scope of the present investigation. However, oil palm dominance in the western Llanos is evident and the landscape is basically composed of oil palm, riparian forest, and pastures. Therefore, it is possible that the influence of other land uses or the configuration of the mosaic may have little effect on the patterns detected in this study.

Conclusions

I aimed to compare the habitat use and detection probabilities of terrestrial mammals between oil palm plantations and riparian forests in the Colombian Llanos. I found that the examined area exhibit a reduced diversity of terrestrial mammals, with oil palm showing low probabilities of use by most species. However, giant anteater, omnivorous mesopredators, and white-tailed deer seem to prefer to use this habitat, over riparian forest. Due to the varying species-specific responses of mammals to oil palm, caution must be exercised against a “one size fits all” solution and generalizations over the response of the entire mammal community. My results suggest that oil palm plantations in Colombia may be made more suitable for the majority of the resident mammal species with the provision of undergrowth vegetation and by ensuring remnant forests are retained in their proximity. The high habitat use found in forested habitats, even in those species positively associated by oil palm cover (e.g. giant anteater) implies that oil palm plantations alone would be insufficient for the persistence of wild mammals, and therefore at a minimum a heterogeneous landscape with interspersed native vegetation is required to maintain connectivity and habitat use by mammals across the oil palm matrix in Colombian landscapes

Supporting information

Model selection evaluating the effect of habitat type (hab) on occupancy and detection probabilities for selected mammal species (Appendix 9), Detection probability *p* for most common species across oil palm dominated landscapes in Colombian Llanos (Appendix 10)

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Chapter 5 Effects of oil palm and human activities on the activity patterns of terrestrial mammals in the Colombian Llanos

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LEP developed the main research question, statistical approaches and analysis with input from WE. GRC, WFL, WE helped with the design, LEP collected the field data and coordinate surveys, data management, cleaning and processing and analysis. LEP wrote the first draft of the paper. GRC, WE and MJC edited and supported the writing process with final revisions by WL

Abstract

The ability of animals to adjust their behaviour in response to landscape changes and human presence may allow them to better adapt to these conditions. However, behavioral responses to land use change by mammal species are not well documented. I quantified activity patterns of terrestrial mammals in oil palm plantations and riparian forest in Colombia to identify possible habitat specific behavioral changes of species. Further, I evaluated the effect of human presence on activity patterns and examined temporal overlap in activity between all possible species combinations to investigate interactions between species within each habitat. I used 2,515 camera trap records of 23 mammals from a survey comprising 12,403 camera days, and analyzed the data using Kernel density estimation and the coefficient of temporal overlap ($\hat{\Delta}$). Activity patterns of 10 species in riparian forest and seven species in palm plantations were determined with four (capybara, giant anteater, lesser anteater and common opossum) represented by enough records (i.e. n >20) in both oil palm and forest to allow robust analysis. Of these four species, only capybaras showed an evident shift in activity patterns between oil palm plantations and riparian forests, shifting from crepuscular in forest to predominantly nocturnal behavior inside oil palm. Further, capybaras, giant anteaters and white-tailed deer appeared to modify their activities inside oil palm plantations to avoid human presence ($\hat{\Delta}$ = 0.13 to 0.36), whereas jaguarundis had high overlap with human activities [$\hat{\Delta}$=0.85 (0.61-0.90)]. Species pair-wise analysis within oil palm plantations revealed temporal segregation between species occupying similar trophic position (e.g. foxes and jaguarundis), whereas some predators and their prey (e.g. ocelots and armadillos) had high overlaps in temporal activity patterns as might be expected. My findings shed light on how conversion of native forest to oil palm plantation can result in behavioral changes in species, a feature of the effect of anthropogenic land use change not captured in traditional studies that focus solely on measures such as species richness or abundance.

Key words: agroecosystem, anteaters, circadian rhythms, diel activity**,** mesopredators, temporal segregation

Introduction

The capacity of species to adapt to humans activities often determines their chance of survival in the face of anthropogenic habitat change (Sih et al., 2011; Wong and Candolin, 2015). Typically, responses to habitat alteration are analyzed through metrics (state variables) such as diversity and abundance (e.g. Gómez et al., 2016; Rovero et al., 2017; Wearn et al., 2017), and more recently estimates of occupancy (e.g. Pardo et al., 2016; Yue et al., 2015). These measures are based on sample counts, or proportional contributions of individual species to overall individual counts, which are then assessed against habitat variables such as area or type of land cover/use. However, behavioral modifications (e.g. foraging activities, food habits) also play an important role in the resilience of species in increasing human dominated landscapes (Sih et al., 2011; Wong and Candolin, 2015). Therefore, the study of activity patterns (i.e. sequences of daily routines) can also help to understand the influence of human presence on mammal assemblages and their flexibility to persist in human dominated landscapes.

Animal activity patterns are shaped by natural factors and physiological requirements of individual species, including thermoregulation requirements, seasonal changes in temperature and moisture as well as biotic interactions such as competition and predation pressure (Halle, 2006). Behavioral responses allow species to exist across a range of conditions and thus allow flexible response to the actual state of the environment or human driven processes (Halle, 2000). For example, evidence suggests that species may modify their behavior in response to hunting pressures (Bitetti et al., 2008). Further, some mammal species may modify their activity patterns depending on the habitat type, presence of human activity or size of forest patches. For example, in the Peruvian Amazon, the activity patterns of some bats change between land cover types such as agriculture and forest types (Presley et al., 2009). Similarly, in the Brazilian Amazon, nine banded armadillos (*Dasypus novemcinctus*) modify their activity patterns depending on the size of the forest fragments in which they occur, having strictly nocturnal activity in big fragments (>1000 ha), but a more cathemeral pattern in smaller ones (Norris et al., 2010). Similarly, (Wang et al., 2015a) found that pumas (*Puma concolor*), bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) reduced diurnal activities and increased nocturnal activity in locations associated with high human activity in California (USA).

Oil palm is one of the biggest threats to biodiversity in Southeast Asia (Fitzherbert et al., 2008; Koh and Wilcove, 2008). Although production of oil palm in Colombia is not the primary cause of deforestation in the country (Furumo and Aide, 2017), it is one of the most rapidly expanding crops in natural or seminatural ecosystems (Reviewed by Pardo et al., 2015), with ~500,000 ha planted at present (Fedepalma, 2014). Only recently have the effects of oil palm production on Neotropical fauna begun to be evaluated. For example, Gilroy et al. (2015) compared the diversity of selected animal groups in the Llanos region (eastern plains) and found that the diversity of ants, birds and herpetofauna was significantly higher in forests than in oil palm plantations. Similar results have been reported for other taxonomic groups including birds (e.g. López-Ricaurte et al., 2017; Prescott et al., 2015) and mammals (e.g. Pardo and Payán, 2015, Pardo et al. 2018). These studies used a tradition approach that links metrics of diversity to landscape variables and uses analyses which place species identities into broad functional groups (see above). However, no previous study has evaluated activity patterns of medium and large-sized mammalian assemblages in human dominated landscapes in Colombia.

In the Neotropics, the study of activity patterns has increased in recent years, especially in countries such as Perú, Bolivia and Brazil (e.g. Blake et al., 2012; Di Bitetti et al., 2010, 2006; Foster et al., 2013; Gómez et al., 2005; Lira-Torres and Briones-Salas, 2012; Maffei et al., 2005; Oliveira-Santos et al., 2008; Tobler et al., 2009, among others). However, very few of those studies quantify the temporal relationships between species in the community or between habitat types (e.g. Presley et al., 2009). This temporal approach is important as the study of activity patterns can be used as an indicator of resource use by species, potential predator-prey relationships, competition/coexistence between species, foraging effort (time and energy), and predation risk (e.g. Di Bitetti et al., 2010b; Foster et al., 2013; Houston et al., 2012; Weckel et al., 2006; Wong and Candolin, 2015). The effects of human landscape modification on behavior can be analyzed by comparing activity patterns overlaps between two or more ecosystems, or between pairs of species within a single habitat (i.e. between species interaction) (Ridout and Linkie, 2009). In human dominated landscapes, such as plantations, comparisons between human and animal species activity times can reveal potential coexistence or avoidance depending on an animal´s capacity to modify their daily routines. Therefore, studies of overlaps between activity patterns will help to determine whether the tolerance shown by some mammal's species to oil palm plantations is facilitated by changing periods of activity.

Colombia is ranked among the five most mammal diverse countries with 518 species recorded to date (Ramírez-Cháves et al., 2016). Nevertheless, very little is known of the natural history of terrestrial mammals, and much less is known about activity patterns (e.g. (Caceres-Martínez et al., 2016; González-Maya et al., 2015; Muñoz et al., 2002) with only two studies having previously assessed temporal overlap between species in Colombia (i.e. Caceres-Martínez et al., 2016; Ramírez-Mejía and Sánchez, 2016). The lack of mammal studies is particularly evident along riparian or gallery forest (Díaz-Pulido et al., 2017), which are forest strips bordering rivers or "caños", particularly in the Llanos region, located in the Orinoco Basin of Colombia. This type of forest is one of the most important remnant ecosystems in the Llanos due to its existence as a series of wildlife refuges and as corridors across natural savannas or mosaics of agricultural landscapes (Lasso et al., 2010, Pardo et al. 2018).

Since the study of animal behaviour in human dominated landscapes is limited to date, the understanding of the ability of animals to adjust their behaviour in response to human activities is also poorly known. The objective of this study was, therefore, to elucidate whether oil palm and human activities influence the activity patterns of mammalian species in oil palm dominated landscapes in Colombia. For this, I quantified the overlap between periods of animal activity using the records from a large-scale camera trapping project in the Colombian Llanos. Specifically, I addressed the following questions: 1) Do species modify their activity patterns between habitats? 2) Do mammal species inside oil palm plantations avoid times of high human activity? 3) Does species-specific temporal interactions differ between these two habitats?

Methods

Study area

The study area was located in the Colombian Llanos Orientales region (here after Llanos), and included rural areas surrounding the towns of Restrepo, Cumaral, Cabuyaro, Acacias, Castilla la Nueva and San Carlos de Guaroa. All towns are situated in the department of Meta, between 194-394 m a.s.l. This area has a long history of landscape modification through human activity with the current dominant practice being oil palm plantations. Other activities include cattle grazing and to a lesser extent, rice cultivation. The remnant natural ecosystem in the region is predominantly secondary riparian forest strips (gallery forest) varying in size and age, some of which experience seasonal innundation.

Survey design

I sampled 56 sites, 33 inside oil palm plantations and 23 within riparian forest, covering an area of approximately 2000 km^2. Sites were separated by at least 2 km to maintain sample independence. This site placement criteria exceeded the minimum recommended inter-site distance for inventorying terrestrial mammals in the Neotropics (e.g. Silveira et al., 2003; Team Network, 2008; Tobler et al., 2008). Furthermore, this inter-site distance corresponds to the average diameter of home ranges for the common mammal species occurring in the study area (Ferrer et al., 2009; Pardo and Payán, 2015). Surveys were conducted during the dry season between September 2014 and January 2016 and only plantations of at least 10 years of age (i.e. planted no later than 2006) were surveyed.

Camera trapping

To detect terrestrial mammals, I used seven Reconyx HC500 HyperfireTM digital cameras at each site (sampling unit). Cameras were placed along a 1.5 km transect with the first camera randomly located and the remaining cameras set every 250 meters. This protocol was used to increase survey success per site, having been found superior (Pardo et al., in prep) to the traditional mammal research approach of 1 camera per site (Burton et al., 2015). Where feasible, to maximize capture success cameras inside riparian forests (here after referred to as forest) were placed along animal paths or facing small gaps in the vegetation. Cameras were positioned in a zigzag arrangement to increase coverage and capture probabilities within the oil palm plantations (here after referred to as oil palm) due to the uniform planting of oil palm trees.

All cameras were fixed to trees or wooden poles with a steel cable and were configured to the following criteria: high sensibility sensor, one second interval between consecutive pictures (three per trigger), no delay or quiet period between triggers, located at approximately one-two meters from the potential path of animals and at 25-30 cm height depending on the terrain. Cameras were active for 30 to 40 days without baiting. Only terrestrial mammals were considered for analysis. Detections (i.e. records) of individuals from the same species were considered as independent when consecutive photographs of the species occurred across periods of greater than 30 minutes (O'Brien et al., 2003).

Activity patterns

To estimate daily activity patterns of terrestrial mammals and determine how they differ between oil palm and riparian forest, I followed the approach developed by Ridout and Linkie (2009). In this approach, periods of species activity are estimated using a circular Kernel probability density function, and similarities between two activity patterns (e.g. between different habitats, or between species) are quantified by the coefficient of overlapping ($\hat{\Delta}$). This coefficient ranges from zero (i.e. no overlap) when two activities patterns are totally segregated from each other to one if they completely overlap.

Since coefficient of overlapping can be influenced by sample size, I used a smoothing parameter of $\hat{\Delta}_4$ for species with more than 75 records and $\hat{\Delta}_1$ for those with less than 50 (Ridout and Linkie, 2009). I included only those species with more than 20 records (independent detections), to ensure the analysis was robust and to avoid making inferences about species where limited data were available. Therefore, in cases where the same species had more than 20 records in either of the two habitats, but less than this in the other, the estimated activity pattern is shown for the habitat with more than the minimum records and no overlap was estimated, due to potential imprecision. I used the same framework to evaluate the influence of human activity on the activity patterns of species inside oil palm plantations (for species with high detections during diurnal hours) and to evaluate interspecific temporal relationships across all possible pair-wise species comparisons within each land use type. All analysis were conducted in the R package "overlap" (Meredith and Ridout, 2017; R Development Core Team, 2014).

I classified the activity of all species into four broad time categories modified from van Schaik and Griffiths, (1996) as per visual examination of the estimated kernel probability density plots. Species were considered diurnal when the maximum activity density (area under the curve) occurred between 6:00 –18:00 h, nocturnal when between 18:00 – 6:00 h, and crepuscular when the peak of density plots was between 5: 00 – 6:00 h (dawn) and/or 17:00–18:00 h (dusk). The final category, cathemeral (see Halle, 2006), was used when a species showed no clear preference for any or the three previous categories, as demonstrated by irregular activity over the 24-hour period.

Results

I recorded 2,515 independent photographs from 23 medium and large-sized terrestrial mammals across the study area, of which 1947 were from the forest and 568 in oil palm plantations (Table 5.1). Further, I recorded 2,344 instances of human activity in palm plantations, and 78 inside forest. The majority of mammal species in the study area were nocturnal. Agouti and jaguarondi were exceptions in that they were clearly diurnal, and white-tailed deer and capybara that tended to be crepuscular (in oil palm and forest respectively). Giant anteater had a cathemeral pattern, although activities were higher at crepuscular and nocturnal times. Overall capture records of individual species (sample size) were low, especially for species inside oil palm (see Pardo et al. Chapter 2). Consequently, there was limited scope for comparison between habitat types (oil palm and forests) for most of the 17 shared species (e.g. Table 5.1).

Table 5.1. Independent detection (photographs) of the 24 mammalian species detected across the study area in the Llanos region, Colombia. Independency criteria =30 minutes between consecutive photographs of the same species.

Common name	**Scientific name**	**Riparian forest**	**Oil palm plantation**
Giant anteater	*Myrmecophaga tridactyla*	116	123
Lesser anteater	*Tamandua tetradactyla*	65	39
Nine-banded armadillo	*Dasypus novemcinctus*	119	4
Naked tailed armadillo	*Cabassous unicinctus*	25	0
Fox	*Cerdocyon thous*	14	226
Jaguarundi	*Puma yagouaroundi*	6	20
Ocelot	*Leopardus pardalis*	57	15
Puma	*Puma concolor*	2	1
Greater grison	*Galictis vittata*	2	1
Tayra	*Eira barbara*	2	0
Crab eating raccoon	*Procyon cancrivorus*	6	16
Coati	*Nasua nasua*	15	0
White tailled deer	*Odocoileus cariacou*	8	22
Red deer	*Mazama*	0	2
Collared peccary	*Pecari tajacu*	1	1
Spiny rat	*Proechimis spp*	182	3
Mice	nn	0	2
Agouti	*Dasyprocta fuliginosa*	425	0
Paca	*Cuniculus paca*	469	1
Capybara	*Hydrochaerus hydrochaeris*	99	29
Coendu	*Coendu spp*	1	0
Squirrel	*Ssciurus spp*	44	0
Common opossum	*Didelphis marsupialis*	288	63
Four eyed oppossum	*Philander opossum*	1	0
Total records		1947	568

* nn = species not identifiable by camera trap

Activity patterns within habitats

Riparian forest

In riparian forest, 10 out of 23 species had sufficient records (n > 20) to reliably estimate their activity patterns (Table 5.1), two of which were found exclusively in forest (naked tailed armadillo–*Cabassous unicinctus* and agouti– *Dasyprocta fuliginosa*). Ocelots (*Leopardus pardalis*), lesser anteaters (*Tamandua tetradactyla*), capybaras (*Hydrochaerus hydrochaeris*), and common opossums (*Didelphis marsupialis*) showed greater activity during night times, compare to day time. However, capybaras were predominantly active around crepuscular times (particularly at dusk). Giant anteaters (*Myrmecophaga tridactyla*) were relatively cathemeral in their behavioral patterns though they displayed a concentration of activity during crepuscular times, and a tendency to be inactive at midday (Fig. 5.1, 5.2). Nine-banded armadillos (*Dasypus novemcinctus*; here after referred to as armadillo), naked armadillos, pacas (*Cuniculus paca*) and spiny rats (*Proechimis spp*), were all strictly nocturnal. Armadillos showed a peak in activities around 20:00 h and naked armadillos around 5:00 h (similar to the spiny rats, lesser anteaters and ocelots). Only one species in forest was strictly diurnal (agouti; though inactive around mid-day) (Table 5.2, Fig. 5.2)

Oil Palm Plantations

In oil palm, seven out of 17 species recorded were detected enough times to allow for analysis. Only capybaras were strictly nocturnal in this habitat type, contrary to forest where they were also active in the late afternoon displaying crepuscular activity patterns. The remaining species showed a nocturnal habit with few detections recorded during daylight hours (e.g. fox– *Cerdocyon thous*, white tailed deer– *Odocoileus cariacou*). White-tailed deer and jaguarondis (*Puma yaguaroundi*) had more records in oil palm plantations than inside forests, with white-tailed deer showing a tendency towards cathemerality, but with a clear narrow peak of activity around 18:00 h (i.e. partially crepuscular), while jaguarundis were strictly diurnal. However, jaguarundi showed a preference for the morning reaching a peak of activity around mid-day, after which activities decline notably (Fig. 5.2). Inside oil palm, the cathemerality displayed by giant anteaters was less evident than that in forest, though in both habitats this species was inactive during the midday hours.

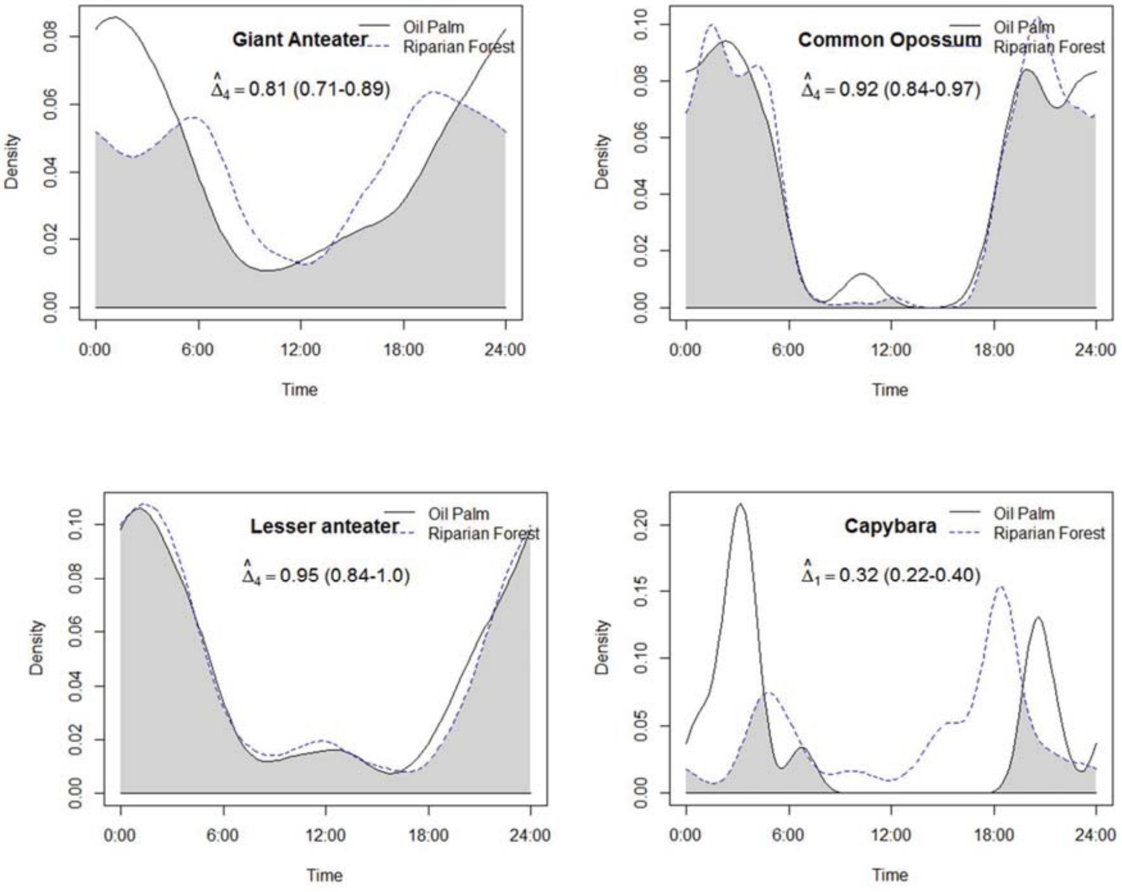


Figure 5.1. Activity patterns and overlap coefficient estimate ($\hat{\Delta}$) for most common shared species between riparian forest and oil palm plantations in the Llanos region of Colombia. The shaded region denotes the activity overlap of each species between the two land cover types, based on Kernel density. $\hat{\Delta}$ ranges from 0-1, being 1 complete overlapping, parenthesis indicates the 95% confidence intervals. Only species with minimum 20 records in both habitats were analyzed (for sample sizes refer to Table 1).

Table 5.2. Overlapping coefficient estimate ($\hat{\Delta}$) based on Kernel density function estimates between selected species pairs inside riparian forest and corresponding activity period categories across oil palm dominated landscapes in the Llanos region, Colombia.

-	-	Lesser anteater *	Armadillo	Naked tailed armadillo *	Ocelot	Spiny rat	Agouti	Paca	Capybara	Common opossum	Activity Period Category
- 	**Giant anteater**	0.68 (0.57 - 0.79)	0.63 (0.54 - 0.72)	0.60 (0.45-0.73)	0.86 (0.49-0.69)	0.67 (0.56-0.73)	0.42 (0.34-0.51)	0.62 (0.53-0.70)	0.70 (0.62-0.78)	0.64 (0.61-0.77)	Cathemeral: with two peaks of activity at dawn and dusk
-	- 	**Lesser anteater**	0.73 (0.62-0.84)	0.72 (0.56-0.87)	0.75 (0.62-0.87)	0.82 (0.71-0.89)	0.23 (0.11-0.30)	0.75 (0.66-0.84)	0.46 (0.33-0.57)	0.77 (0.67-0.85)	Mostly nocturnal with important activity around 3:00h
-	-	- 	**Armadillo**	0.70 (0.52-0.87)	0.73 (0.61-0.84)	0.80 (0.70-0.89)	0.05 (0.01-0.1)	0.92 (0.86-0.97)	0.41 (0.32-0.50)	0.87 (0.79-0.94)	Nocturnal estrictly: peak of activity around 21:00h
-	-	-	- 	**Naked tailed armadillo**	0.70 (0.54-0.86)	0.86 (0.71-0.98)	0.09 (-0.01-0.15)	0.70 (0.54-0.87)	0.43 (0.28-0.54)	0.79 (0.63-0.93)	Nocturnal estrictly: peak of activity around 3:00h
-	-	-	-	- 	**Ocelot**	0.77 (0.63-0.93)	0.30 (0.19-0.40)	0.70 (0.54-0.87)	0.63 (0.50-0.74)	0.80 (0.70-0.90)	Mostly nocturnal with a slightly peak around 5:00h
-	-	-	-	-	- 	**Spiny rat**	0.10 (0.06-0.14)	0.81 (0.74-0.87)	0.46 (0.35-0.54)	0.86 (0.79-0.93)	Nocturnal strictly: peak of activity around 5:00h
-	-	-	-	-	-	- 	**Agouti**	0.04 (0.02-0.06)	0.47 (0.37-0.55)	0.11 (0.08-0.15)	Diurnal strictly: low density of activity around 12:00h
-	-	-	-	-	-	-	- 	**Paca**	0.41 (0.33-0.50)	0.88 (0.85-0.93)	Nocturnal strictly: no evident concentration of activity
-	-	-	-	-	-	-	-	- 	**Capybara**	0.49 (0.40-0.58)	Mostly crepuscular with peak of activity around 18:00h
-	-	-	-	-	-	-	-	-	- 	**Common opossum**	Mostly nocturnal, no evident concentration of activity

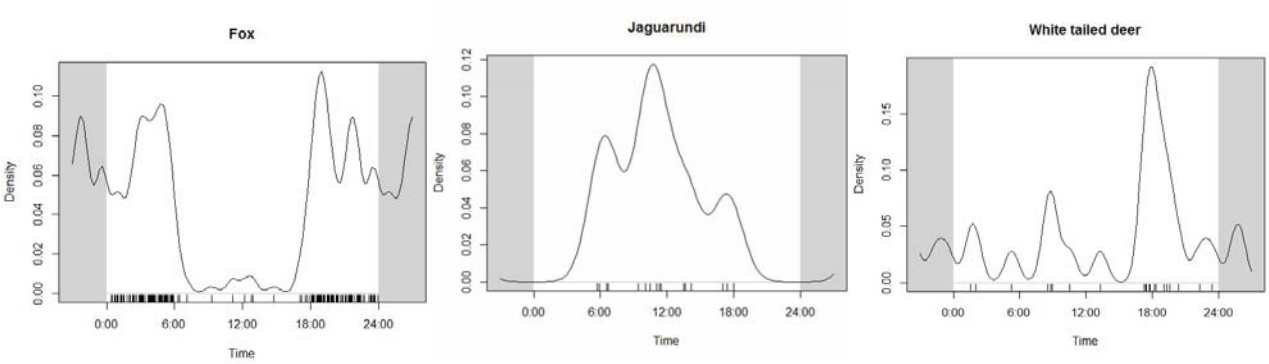
Activity period categories: a) diurnal (6:00 –18:00 h), b) nocturnal (18:00 – 6:00 h) and c) crepuscular when most of the records were between 5: 00 – 6:00 h (dawn) and 17:00–18:00 h (for dusk) (modified from Schaik and Grifiths 1996) $^*\hat{\Delta}_1$ less than 50 records.

Do species modify their activity patterns between habitats?

Given the low capture rates in the majority of species, it was only possible to analyze changes in activity patterns between habitat types for four species (n > 20): capybara, giant anteaters, lesser anteaters and common opossums (Table 5.1), of which only capybara displayed a shift in activity patterns between habitats. Some species such as the white tailed deer, jaguarondi or ocelot despite being present in both habitat, records were minimal in either of the habitats. For these species, though, activity patterns densities are shown for the habitat with more reliable data in Figure 5.2.

Capybaras displayed quite distinct periods of peak activity which differed between habitats ($\hat{\Delta} =$ 0.32 (C.I. 0.22-0.40) and showed clear and distinct peaks of activity for each land cover. In the riparian forest, for instance, Capybara activity peaked at approximately 5:00 h and again around 18:00 h, indicating crepuscular behaviour. However, in oil palm, while capybaras again displayed two peaks of activity, these were centered round 3:00 h and 21:00 h, indicating more nocturnal behavior (Fig. 5.1). Capybara activity was never detected after ~7:00 h in oil palm plantations. In contrast, giant anteaters, lesser anteaters and common opossums displayed no major changes or modification of activity patterns between land cover types (overlap of activities > 0.80; Fig. 5.2). Giant anteater activity declined appreciably after 6:00 h inside oil palm whereas their activity in forests tended to increase at a similar time period. Subsequently, giant anteater activities in oil palm remained low until ~17:00h and peaked around 1:00 h, whilst in forest, the giant anteaters had two evident peaks of activities at crepuscular times (dawn and dusk)

a) Oil palm plantation



b) Riparian Forest

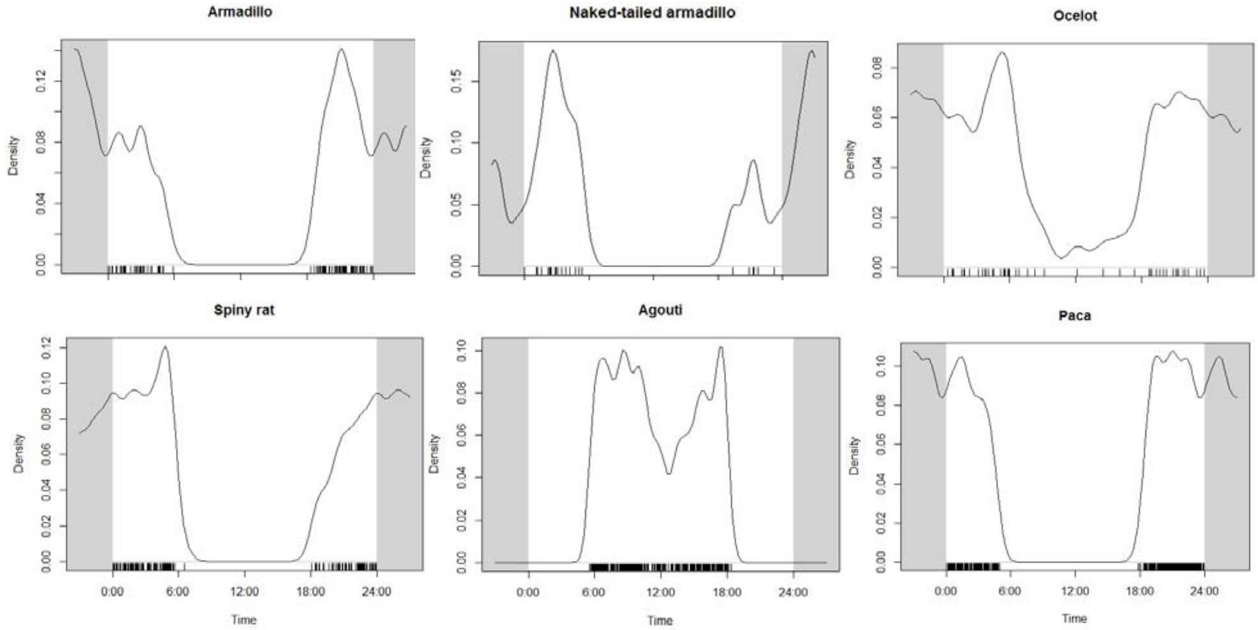


Figure 5.2. Activity patterns estimates for selected species in oil palm plantations (a) and riparian forest (b) in the Llanos region of Colombia. The graphs were constructed using Kernel density functions for species with more than 20 records in any of the habitats. For species with robust data for both habitats refer to Fig. 5.1.

Do species inside oil palm avoid times of high human activity?

Only four species were detected frequently enough in oil palm plantations to enable analysis of their response to human activities. Of these four species, the giant anteater appeared to avoid human activities inside oil palm plantations ($\hat{\Delta}$= 0.27; CI = 0.19-0.33). Similarly, white tailed deer appear to avoid humans ($\hat{\Delta}$= 0.36; CI = 0.17-0.53), with a clear peak after human activities ceases at 18:00 h (Fig. 5.3). Capybaras had the lowest behavioral overlap with humans due to their markedly nocturnal behavior inside oil palm ($\hat{\Delta}$ =0.13; CI = 0.02-0.19). In total contrast, jaguarondis displayed activity concurrent with human activities ($\hat{\Delta}$ =0.86; CI = 0.80-0.96; Fig. 5.3), with a peak of activities around mid-day.

How do species-specific interactions differ between habitats?

Interspecific interactions within forest

The most similar activity pattern cycles was identified between pacas and armadillos ($\hat{\Delta}$= 0.92; CI= 0.86-0.97), whereas the species with the most dissimilar patterns were agoutis and armadillos ($\hat{\Delta}$= 0.05; CI = 0.01-0.1). Capybaras and giant anteaters were the only species with relatively similar activity periods with the strictly diurnal agoutis ($\hat{\Delta}$ = 0.47; CI = 0.37-0.55 and $\hat{\Delta}$ = 0.42; CI = 0.34-0.51, respectively], followed by ocelots with a low overlap ($\hat{\Delta}$=0.30; CI = 0.19-0.40) (Table 5.2), reflecting their capacity to be active during the day or night times. Potential prey-predator relationships showed that ocelots and common opossum were active during a similar time period $\hat{\Delta}$ = 0.80; CI = 0.70-0.90), followed by ocelots and spiny rats ($\hat{\Delta}$ = 0.77; CI = 0.63-0.93), and armadillo ($\hat{\Delta}$ = 0.73; CI = 0.61-0.84). Interestingly, both armadillos showed different peaks of activities with nine banded armadillo being more active around 21:00 h while naked-tailed armadillo activity peaked around 3:00 h.

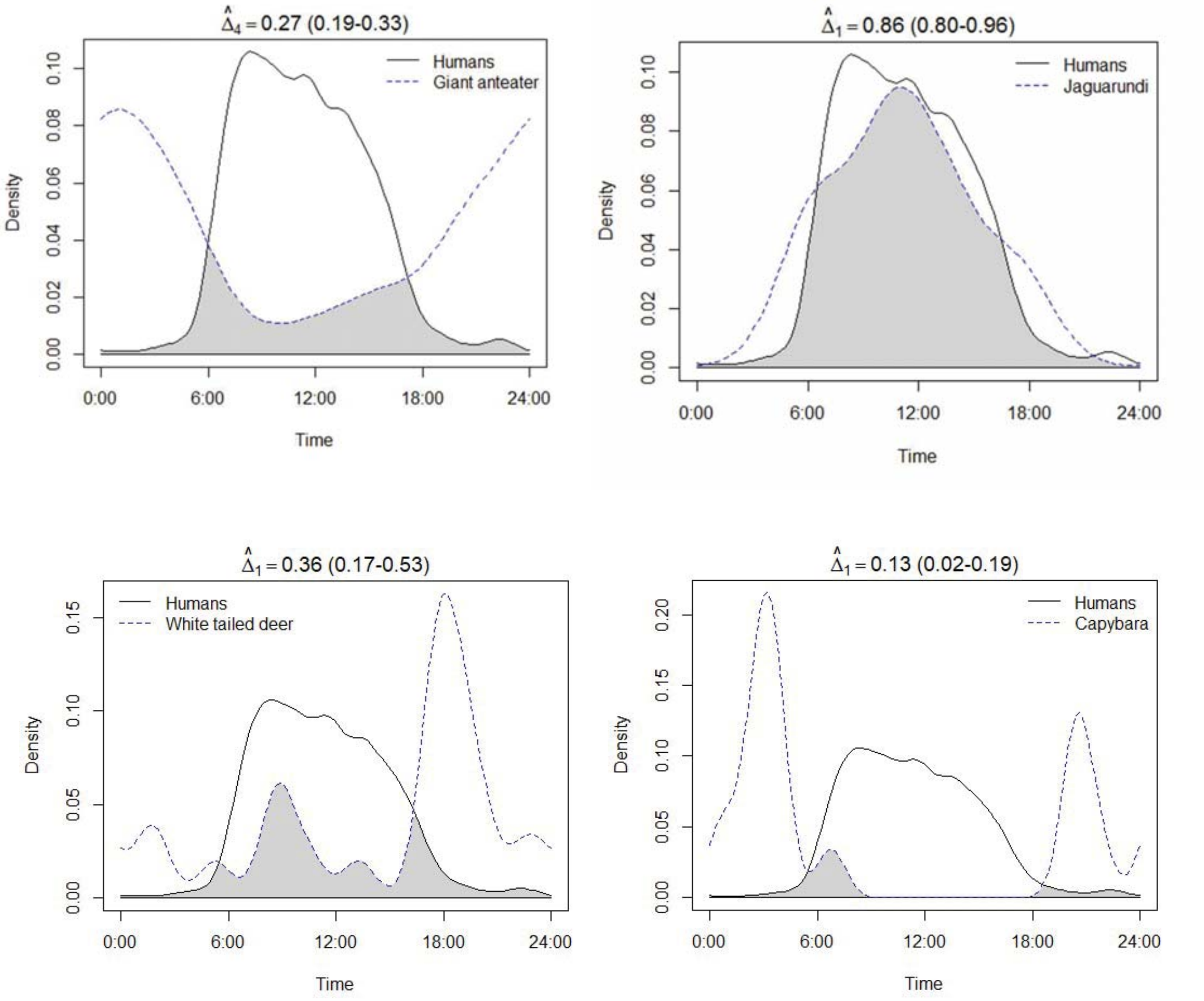


Figure 5.3. Activity patterns and overlap coefficient estimate ($\hat{\Delta}$) based on Kernel density function estimates between humans and giant anteater, and humans and jaguarondi inside oil palm plantations in the Llanos region of Colombia. Humans (n= 2344), giant anteater (n =123), jaguarondi (n= 20), white tailed deer (n=22) and capybara (n = 29). Category humans include any independent photograph of workmen and/or machinery (e.g. tractor, trucks).

Table 5.3. Overlapping coefficient estimate ($\hat{\Delta}$) based on Kernel density function estimates between selected species pairs inside oil palm and corresponding activity period categories across oil palm dominated landscapes in the Llanos region, Colombia.

-	-	**Lesser anteater ***	**Fox**	**Jaguarundi ***	**White tailed deer ***	**Capybara ***	**Common opossum ***	**Activity Period Category**
	**Giant anteater**	0.90 (0.79-0.99)	0.77 (0.69-0.84)	0.38 (0.22-0.52)	0.53 (0.33-0.70)	0.60 (0.43-0.73)	0.85 (0.76-0.94)	Cathemeral: lower activity at midday, one peak of activity around 2:00h.
-	- 	**Lesser anteater**	0.75 (0.62-0.84)	0.31 (0.12-0.45)	0.47 (0.24-0.65)	0.62 (0.42-0.75)	0.86 (0.72-0.97)	Mostly nocturnal with one peak of activity around 2:00h
-	-	- 	**Fox**	0.27 (0.14-0.44)	0.56 (0.37-0.72)	0.61 (0.45-0.71)	0.84 (0.74-0.92)	Mostly nocturnal with no evident peck of activity
-	-	-	- 	**Jaguarundi**	0.43 (0.19-0.60)	0.16 (0.01-0.30)	0.24 (0.07-0.39)	Strict diurnal with a slightly peak around midday
-	-	-	-	- 	**White tailed deer**	0.34 (0.11-0.47)	0.50 (0.29-0.69)	Cathemeral: with a peak of activity around 18:00 h
-	-	-	-	-	- 	**Capybara**	0.66 (0.47-0.77)	Nocturnal: peak of activity around 3:00h and 21:00h
-	-	-	-	-	-	- 	**Common opossum**	Mostly nocturnal with no evident peck of activity

* Activity period categories: a) diurnal (6:00 –18:00 h), b) nocturnal (18:00 – 6:00 h) and c) crepuscular when most of the records were between 5: 00 – 6:00 h (dawn) and 17:00–18:00 h (for dusk) (modified from Schaik and Grifiths 1996). *$\hat{\Delta}$1 less than 50 records.

Interspecific interaction within oil palm

The lesser anteaters and giant anteaters had very similar activity patterns showing an interspecific overlap ($\hat{\Delta}$) of 0.90 (CI. 0.79-0.99). However, overlapping between the giant anteaters and lesser anteaters activity patterns inside oil palm were greater than inside forests (i.e. $\hat{\Delta}$ = 0.90; CI = 0.79-0.99 and $\hat{\Delta}$ = 0.68; CI = 0.57-0.79, respectively) (Table 5.2, 5.3). Whereas the most different activity patterns was identified between jaguarondi and capybara ($\hat{\Delta}$=0.16; CI = 0.01-0.30) (Table 3), followed by the jaguarondi and common opossum; due to jaguarundi´s marked diurnality ($\hat{\Delta}$=0.24; CI = 0.07-0.39). Overall, most of the species had relatively similar activity patterns inside oil palm with overlapping values ranging from 0.4-0.5.

The two most frequently detected mesopredators (foxes and jaguarundis) had clear temporal segregation in their activity patterns ($\hat{\Delta}$=0.27; CI = 0.14-0.44).

Discussion

Overall the activity patterns identified for the study area are not unexpected based on the biology and evolutionary history of Neotropical mammals (e.g. Blake et al., 2012; Eisenberg and Redford, 1999; Emmons, 1999; Gómez et al., 2005; Ramírez-Mejía and Sánchez, 2016). Further, the majority of mammal species in the Llanos region in Colombia did not modify their activity patterns as a response to oil palm plantation except for Capybara. However, most of the species inside plantation showed to avoid human activity.

Effect habitat and human activities

Capybaras modified their behavioral patterns inside plantations to avoid human activities by becoming more nocturnal. Capybaras are the biggest grazing rodent in the Neotropics (Emmons, 1999). In the Amazonia they are suggested to be cathemeral (Gómez et al., 2005), while in natural savannas, they usually spend considerable time grazing in the evening (Camargo-Sanabria et al., 2014b; Herrera and Macdonald, 1989). However, most natural savannas in the study area have been cleared for agriculture or cattle ranching (e.g. Etter et al., 2011). Probably, as a consequence, I only detected capybaras in 20% of the study area (see Pardo et al. Chapter 4). The conversion of native grasslands to other land uses may have forced remaining populations of capybaras to use the grass that grows inside oil palm plantations (LEP pers. obs). Therefore, capybaras could have shifted their feeding times to avoid humans and be able to use the new available resources inside oil palm, as shown in this study. A mechanism previously described for other species (e.g. Wang et al., 2015)

My findings confirm that one way the giant anteater adapt to oil palm habitats is through the modification of their activity patterns to avoid human activities inside this crop. Interestingly in more conserved landscapes such as the Ecuadorian Amazonia giant ant eater seem to be entirely diurnal (Blake et al. 2012), while in the study area tend to be active day and night. This aspect of its biology confirms the plasticity of this species to adapt to anthropomorphic landscapes (Quiroga et al., 2016; Rojano et al., 2015; Pardo Chapter 2,4).

Some species had a limited number of detections that did not allow for overlap analysis, although some patterns were identified. Ocelots, for example, also tended to become more nocturnal in oil palm. This behavioral plasticity supports previous findings suggesting that activity patterns could be modified in response to the environmental and human disturbances (e.g. Norris et al., 2010; Presley et al., 2009; Wang et al., 2015a; Wong and Candolin, 2015). White tailed deer, on the other hand were found to be most active around dusk inside oil palm plantations. Previous studies suggest that this species display a clearly crepuscular pattern of activity peaking in both the morning and evening (e.g. Gallina and Bello-Gutierrez, 2014). Moreover, in another oil palm plantation in the Llanos region, (Pardo et al., 2013) found two activity peaks for this species supporting crepuscular behaviors. However, the fact that only one peak of activity was found for deer inside plantations in this study supports the view that this species prefers to be active when humans are not present. This is suggested as dusk coincides with the end of daily working/harvesting activities inside the analysed plantations.

The habituation of jaguarondi towards people inside oil palm has been registered to occur in other wild animals that take advantage of human-dominated environments and resources (e.g. organic waste, food, protection (Lowry et al., 2013; Samia et al., 2015). Apparently, the jaguarondi is not hunted in the Llanos, contrary to giant anteaters, ocelots or deer which are persecuted or hunted in some areas (e.g. Usma and Trujillo, 2011, Pardo et al. not.publ.). Likely, the jaguarondi has learnt that people are not a threat, and therefore this species does not show any change in behavior due to people, as oppose to the remaining mentioned species that avoided people when using oil palm plantations. The behavior of jaguarundi may be different towards people in areas where this species is occasionally hunted (e.g. Chacón-Pacheco and González-Maya, 2007). The no detection of ocelot during day times inside oil palm is concordant with other studies of ecologically similar species such as the servals (*Leptailurus serval).* As such, Ramesh and Downs (2013), found no significant differences of this African felid densities in a mosaic of land uses in South Africa, but found that they avoided activity during the day time in intensively farmed areas.

Jaguarondis were found to display a strictly diurnal activity pattern, a behavioral pattern supported by the findings of previous studies (Di Bitetti et al., 2010; Giordano, 2016). Moreover, the six records of jaguarondis inside forests suggest no substantial shifts in activity patterns between oil palm and forests (i.e. all detections were also during the day time). Conversely, ocelots were found to be strictly nocturnal inside oil palm plantations. These clear differences in the activity patterns of jaguarondis and ocelots support the idea of temporal and spatial segregation thereby minimizing the competition between these two mesocarnivores (Di Bitetti et al., 2010; Monterroso et al., 2014). It is likely that ocelots and jaguarundis exhibit avoidance in space (depending on habitats) and time in the study area, with ocelots more active in forests and at night time whilst jaguarondi activity is higher in oil palm plantations during diurnal hours (see Pardo et al. Chapter 2, 4). This behavioral avoidance is likely due to similarities in diet, which has been reported to be approximately 60% for both jaguarundis and ocelots– in the Mata Atlantica (Rocha-Mendes et al., 2010). This dual avoidance (in space and time) has been described for other carnivores such as the interactions between lions (*Panthera leo*) and hyenas (*Crocuta crocuta*) with cheetahs (*Acinonyx jubatus*) (Durant, 1998). As such, these behavioral adaptations have important positive effects in terms of improving each species relative fitness through a reduction in competition (Ashby, 1972; de Oliveira et al., 2010; Di Bitetti et al., 2010).

Temporal interactions in the assemblage within each land cover type

Giant and lesser anteaters, were active at different time periods in forests likely due to differences in niche preferences. Although both species have similar diets, lesser anteaters can exploit food resources in both the terrestrial and canopy insect communities, whereas giant anteaters specialize in terrestrial communities (Gallo et al., 2017). Since oil palm plantations predominanlty support terrestrial insect communities (i.e. soil ants and termites LEP Pers. obs.), and both ant-eating species prefer nocturnal activities, it is expected that they may be required to be active at similar hours. Inversely, the possibility of having another insect community to forage inside forests could help reduce temporal overlapping of these species by allowing for niche specialization through spatial segregation.

Differences in activity patterns analyzed through overlap coefficients estimation has been used as a proxy to assess species avoidance or segregation in predator-prey relationships (e.g. Halle, 2006; Ridout and Linkie, 2009; Weckel et al., 2006). Overall, oil palm was dominated by two mesopredators (fox and jaguarondi), whereas forest was dominated only by ocelots. The broad niche and the evident differences found in the activity patterns between jaguarundis and ocelots, may indicate that these species specialize in different prey (see de Oliveira et al., 2010). In this sense, jaguarundis could have specialized in preying on reptiles and birds that are also active during the day (e.g. Tófoli et al., 2009), whereas ocelots may have specialized in preying small nocturnal mammals such as rodents, opossums, or armadillos (de Oliveira et al., 2010); as can be inferred from the overlapping value for these species within riparian forest ($\hat{\Delta}>0.70$). Jaguarundi is known to be a highly generalist species within the carnivore guild (e.g. Rocha et al. 2016) with their diet including even snakes, and tegu lizards (*Tupinambis spp*) (Tófoli et al., 2009), two common reptiles species found within oil palm plantations (LEP pers. obs., Lynch, 2015). Further investigation on the diet of these mesopredators would be important to confirm this hypothesis.

My findings give insights, on likely predator-prey relationships, and on the general ecology of terrestrial mammals in human dominated landscapes in Colombia, a field that has been poorly documented. Few studies in the Neotropics have assessed possible temporal interactions among species, being only Brazil, Ecuador and Bolivia, the countries that have carried out most of the research (Blake et al., 2012; de Oliveira et al., 2010; H. Gómez et al., 2005; Maffei et al., 2005). While predator-prey relationships can demonstrate synchronization between activity periods (e.g. de Oliveira et al., 2010; Halle, 2006; Lima, 2002; Linkie and Ridout, 2011; Weckel et al., 2006), conclusions about potential interactions between predators and prey should be drawn carefully in the absence of spatial or dietary assessments (Meredith and Ridout, 2017; Weckel et al., 2006).

Conclusions

This is the first study evaluating the influence of industrial-scale oil palm-agriculture and human activities on activity patterns of mammal species in Colombia. Overall, I found no substantial differences in activity patterns between oil palm plantations and riparian forest (i.e. no modification given presence of oil palm) in the majority of species, except for the capybara. This species as well as giant anteater, deer and ocelots tended to avoid humans inside oil palm. Interestingly jaguarondis, a relative common diurnal species did not show evidence of human avoidance inside oil palm. Further, my results provide evidence of mammalian temporal segregation as a mechanism to avoid interspecific competition in some relatively common species, such as jaguarundi and fox, and high overlap of activity periods in potential predator-prey relationships (e.g. ocelots and armadillos). This study contributes to the understanding of mammalian resilience to anthropogenic landscapes and the natural history of poorly known species. This behavioral modification is a feature of the effect of anthropogenic land use change not captured in traditional mammal studies that focus on measures such as species richness or abundance. Further, this complements the growing documentation aimed to understand biodiversity in oil palm landscapes in Colombia.

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Chapter 6 Short communications

The following two papers are short communications. The first was published in Spanish and the second is ready for submission.

I) Records of cougar (*Puma concolor*, Linnaeus, 1771) in the countryside of San Carlos de Guaroa, Meta, Colombia

Published as:

Pardo, L.E., G.R. Clements W. Edwards, A. Rojas-Rojas, and W.F. Laurance.2017. Registros de puma (*Puma concolor,* linnaeus, 1771) en zona rural de San Carlos de Guaroa, Meta, Colombia. Revista Biodiversidad Neotropical. 7(1): 56-61

II) A camera trap protocol to efficiently sample mammals in Neotropical riparian forests

Lain E. Pardo, Gopalasamy Reuben Clements, William F. Laurance

Ready for submission to Mammal research

Records of cougar *(Puma concolor*, Linnaeus, 1771) in the countryside of San Carlos de Guaroa, Meta, Colombia

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Abstract

The Knowledge of carnivores distribution in Colombia is limited, especially in human dominated landscapes. Using camera trapping to detect mammals in 56 sites across an oil palm (*Elaeis guineensis*) dominated landscape in the eastern plains of Colombia, we confirmed the presence of puma (*Puma concolor*) only in the outskirts of San Carlos de Guaroa. My results bring to attention the scarcity of puma in the region and highlights the role of riparian forests for the conservation of this species in agricultural landscapes.

Keywords: camera trap, carnivores, Llanos Orientales, oil palm, riparian forest.

Introducción

El puma (*Puma concolor*) es un depredador tope de gran distribución en el Neotrópico, asociado con diferentes ecosistemas desde el nivel del mar hasta la alta montaña (Emmons, 1999). Suele observarse en ecosistemas conservados, sin embargo, se ha reportado su presencia en plantaciones forestales, en matrices agrícolas con ecosistemas naturales e incluso en bosques de zonas periurbanas (Arias-Alzate et al., 2015; Pardo et al., 2016; Pardo and Payán, 2015) A pesar de su flexibilidad ecológica, la conservación del puma en Colombia se ve amenazada por la pérdida de hábitat debido a la ampliación de la frontera agrícola y la cacería (Castaño-

Uribe et al., 2013). Los grandes carnívoros como el puma son organismos claves en las cadenas tróficas influyendo directa e indirectamente en el funcionamiento de los ecosistemas a través de la regulación de cascadas tróficas (Estes et al., 2011; Paine, 1980). Sin embargo, es poco lo que se conoce sobre su distribución en paisajes transformados en Colombia.

Colombia es el quinto productor de palma de aceite o africana (*Elaeis guineensis*) en el mundo, con un total de 476.781 hectáreas sembradas hasta el año 2013 (Fedepalma, 2014), del millón de hectáreas proyectado inicialmente para el año 2020 (MADR, 2006b). El rápido desarrollo de la palma de aceite ha generado un gran debate en torno a sus posibles impactos sobre la biodiversidad de Colombia. Sin embargo, la mayoría de estudios en cultivos de palma de aceite se han realizado en Asia (Pardo et al., 2015), por lo que se conoce muy poco sobre el verdadero impacto de estos cultivos sobre la biodiversidad, los suelos o los sistemas hidrobiológicos en el Neotrópico.

En este trabajo se reporta la presencia del puma en la zona rural aledaña al municipio de San Carlos de Guaroa, en el departamento del Meta, Colombia, así como algunas características de los sitios donde se detectaron con el ánimo de aportar al conocimiento sobre la distribución de esta especie. La evidencia obtenida para este trabajo hace parte de los primeros resultados de una investigación más amplia que adelanta el autor principal con miras a entender la diversidad y uso de hábitat de mamíferos asociados con paisajes dominados por palma de aceite en los Llanos Orientales de Colombia, un área clave para la futura expansión de este cultivo (Romero-Ruiz et al., 2012).

Metodología

Entre septiembre del 2014 y enero del 2016 se realizó un muestreo sistemático e intensivo con cámaras trampa Reconyx Hyperfire H550^{TM}, en gran parte de la zona palmera del departamento del Meta, cubriendo los municipios de Restrepo, Cumaral, Cabuyaro, Acacias, Castilla la Nueva y San Carlos de Guaroa. El paisaje es heterogéneo con predominio de plantaciones de palma de aceite, pasturas para el ganado, cultivos menores como arroz y presencia de bosques galería a lo largo de varios caños o ríos. La altura sobre el nivel del mar del área de estudio oscila entre los 200 y 400 m aproximadamente.

Se muestrearon 56 sitios en proporción al área de los dos tipos de uso de tierra dominante (plantación de palma y bosques de galería), de los cuales 33 sitios estaban dentro de plantaciones de palma de aceite y 23 en bosques de galería de distintos caños. Los sitios se ubicaron a más de 2 km de distancia entre ellos para asegurar independencia de las muestras, instalando en cada sitio transectos de 7 cámaras separadas 250 m entre sí. Las cámaras se dejaron activas durante 30 y 35 días, sin uso de cebo y se instalaron a una altura de 25-30 cm del suelo configurando la cámara en sensibilidad alta. Para describir la estructura de la vegetación en cada sitio dentro del bosque de galería, se construyeron parcelas de vegetación de 10 x 10 m en cada una de las cámaras del transecto, siguiendo la metodología sugerida (Albesiano and Rangel-Ch, 2006).

Resultados

A pesar de tratarse de uno de los muestreos más extensos realizados en esta zona de los Llanos (~12400 días/cámara en total y seis municipios), solo se confirmó la presencia de puma en 3 sitios independientes en jurisdicción de San Carlos de Guaroa: un individuo joven en el caño/canal Ibabá, a ~6 km del casco urbano (3°46’1.47”N, 73°14’56.10”W) (Figura 6.1 y 6.2A); un individuo adulto en el caño Guaroa (3°46’4.08”N, 73°19’18.67”W) (Figura 1 y 2B) y un individuo adulto atravesando una plantación de palma de aceite (3°49’39.63”N, 73°22’55.76”W) (Figura 6.1 y 6.2C), a ~530 m del bosque de galería más cercano; esta plantación tiene aproximadamente 25 años y presenta vegetación o rastrojo en medio de los lotes. Dadas las características físicas de los individuos adultos antes señalados, es muy probable que se trate de individuos distintos. No hubo registros o rastros de jaguar (*Panthera onca)* en ninguno de los 56 sitios muestreados, pero sí de carnívoros mesodepredadores como yaguarundi (*Puma yagouaroundi*), zorro (*Cerdocyon thous*) y ocelote (*Leopardus pardalis*).

La estructura del bosque donde se detectaron los individuos es principalmente secundaria y de baja altura, especialmente el canal Ibabá que a su vez es una franja boscosa estrecha (Figura 6.3). Un poco más del 70% de los arboles tiene alturas hasta los 8 m, por lo que el estrato dominante en estos bosques de galería se puede clasificar como subarbóreo o de arbolitos (5-12 m) según (Rangel-Ch y Lozano-C., 1986). Por otro lado, 70% de la vegetación tiene DAP (diámetro a la altura del pecho) menor de 10 cm y con pocas excepciones de árboles de gran porte, sugiriendo ciertos procesos de extracción de madera en años anteriores. Sin embargo, es muy variable la estructura a lo largo de los bosques. Así, en algunos puntos se encontraron áreas más abiertas y más conservadas, por lo general con predominio de palmas como ya- gua (*Attalea spp.*), seje (*Oenocarpus spp.*), moriche (*Mauritia spp.*) y palma que camina (*Sacrotea spp.*), indicando al mismo tiempo un patrón de anegamiento o semiestacionalidad (Figura 6.3).

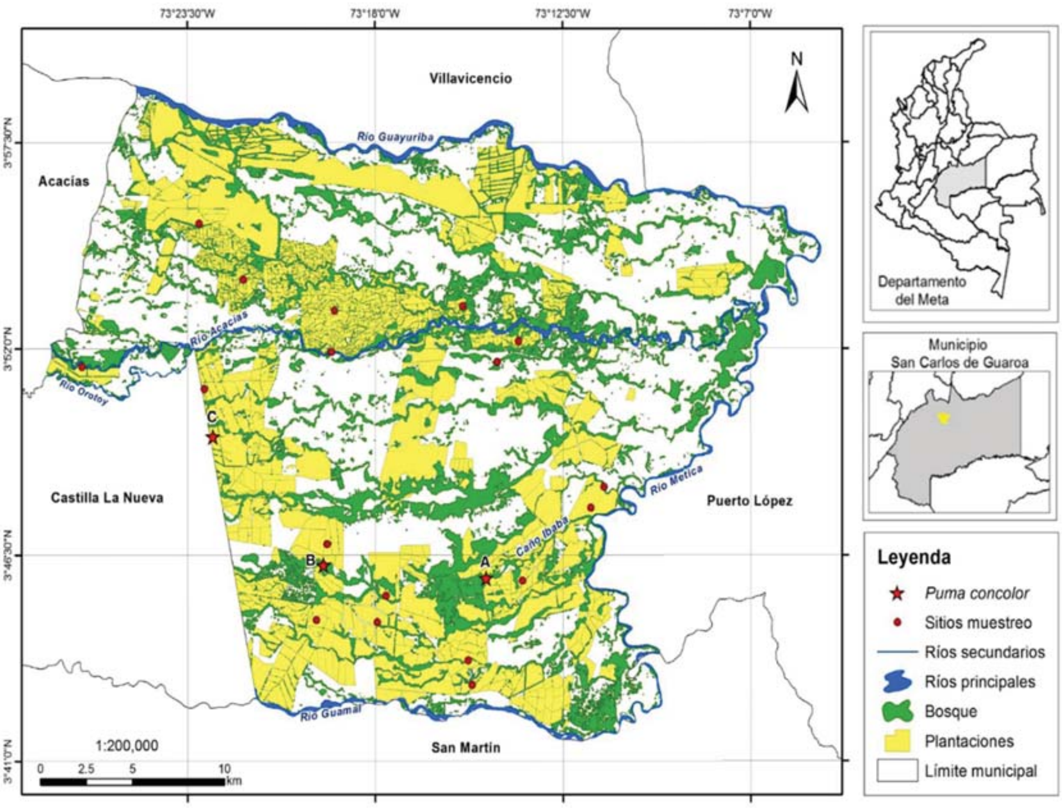

Figure 6.1. Registros de *Puma concolor* en paisajes dominados por plantaciones de palma de aceite en zona rural del municipio de San Carlos de Guaroa entre noviembre y diciembre 2015. (Las letras corresponden a las imágenes de los individuos en la Figura 2).

Figure 6.2. Fotos de individuos de puma (*Puma concolor*) detectados mediante fototrampeo (A, B, C). Vista general del bosque donde se detectó el individuo de la imagen B. Zona rural del municipio de San Carlos de Guaroa.

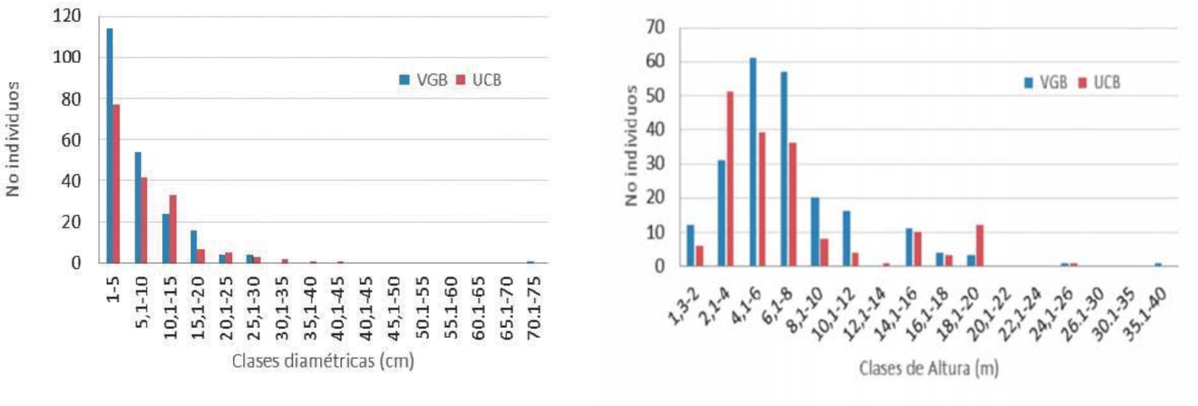

Figure 6.3. Estructura general de las clases de DAP (diámetro a la altura del pecho) y de altura de los bosques de galería donde se registró puma. Descriptores estimados a partir del conjunto de parcelas de 10 x 10 m ubicados en cada cámara trampa. VGB= código transecto en caño Guaroa, UCB= código transecto caño Ibabá. San Carlos de Guaroa.

Discusión

Los escasos registros de estos depredadores sugieren que sus poblaciones están restringidas a pocas zonas dentro de este gran paisaje agropecuario. Estos resultados eran de esperarse teniendo en cuenta que gran parte de los bosques y las sabanas naturales del área de estudio han sido degradadas por actividades antrópicas como la agricultura y ganadería décadas atrás (Madriñán et al., 2007; Romero-Ruiz et al., 2012), lo cual puede afectar a especies de gran movilidad como el puma. En este sentido, la zona aledaña al municipio de San Carlos constituye un importante punto de conectividad para la presencia de puma. Para los Llanos Orientales de Colombia solo se conoce un reporte de puma dentro de plantaciones de palma en zona rural del municipio de Mapiripán, departamento del Meta (Olarte-González and Escovar-Fadul, 2015) y otro en bosques de galería adyacentes a una plantación en el municipio de Paz de Ariporo, departamento del Casanare (Pardo and Payán, 2015). Sin embargo, el contexto paisajístico y urbano de estas áreas es muy distinto al descrito en la zona de estudio, la cual ha experimentado décadas atrás, mayores procesos de cambio de uso del suelo y urbanismo.

Aunque el municipio de San Carlos hace parte del área de distribución del puma (Ferrer et al., 2009), hasta donde se pudo establecer este es el único registro publicado para la zona. Consultando las bases de datos del Sistema de Información sobre Biodiversidad (SiB Colombia) del Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, de Biovirtual del Instituto de Ciencias Naturales de la Universidad Nacional de Colombia y de Global Biodiversity Information Facility (GBIF), existe un único registro para el departamento del Meta del año1957 por Idrobo JM y no se pudo encontrar reportes publicados en otras investigaciones, tesis o informes técnicos por parte de otras entidades o de la autoridad ambiental del municipio.

Los muestreos también confirmaron la presencia de algunas presas potenciales como lapas (*Cuniculus paca*), ñeques (*Dasyprocta fuliginosa*), armadillos (*Dasypus novemcinctus*), osos palmeros (*Myrme- cophaga tridactyla*), venado cola blanca (*Odocoileus cariacou*) entre otros, en los bosques de galería. La existencia de estas especies podría favorecer la presencia de pumas en la zona como sugiere (Scognamillo et al., 2003) e incluso, al mismo tiempo, podría prevenir la depredación de ganado (Burgas et al., 2014). El venado y chiguiro en particular fueron detectados con más frecuencia en la zona de San Carlos que en los demás municipios, por lo que puede ser una posible explicación al hecho de haber detectado puma solo en este municipio. Sin embargo, deben ponerse a prueba esta y otras hipótesis con una investigación más puntual.

Las observaciones de este estudio indican que el puma puede estar presente en áreas con cierta perturbación antrópica y/o cerca de asentamientos humanos, como se ha observado en otros estudios (Arias-Alzate et al., 2015). Asimismo, reflejan la importancia de los bosques de galería (incluso secundarios) para la conservación del puma (y otras especies asociadas) resaltando el valor potencial de conservación de la heterogeneidad en paisajes dominados por actividades humanas. Sin embargo, estos registros no son evidencia de poblaciones estables, para lo cual se necesitan otros estudios y un monitoreo sistemático. Al estar conectados los caños Ibabá y Guaroa con el río Metica, es importante evaluar el estado de conservación de estos sitios y su potencial como puntos de conectividad con la zona de sabana ondulada o serranía al costado oriental del río Metica, la cual presenta menos alteración.

La conservación de la biodiversidad no debe recaer solo en el mantenimiento de reservas o áreas protegidas, ya que estas no garantizan por si mismos la conservación a largo plazo de especies de gran movilidad como el puma (Noss et al., 1996) y se encuentran bajo presión constante debido a los procesos de degradación que ocurren a sus alrededores (Laurance et al., 2012). Por el contrario, la conservación de la biodiversidad también debe ser evaluada en tierras dominadas por actividades humanas (Daily et al., 2003). Por esta razón, es importante la cooperación con los dueños de tierra (palmeros y ganaderos) de la zona para permitir y facilitar el flujo de especies silvestres a través de la conservación y restauración de los bosques de galería y otros ecosistemas naturales que se encuentren en sus tierras. Es importante, de igual forma, fortalecer el control de la cacería ilegal y la educación ambiental para lograr un cambio en la percepción de los pobladores sobre estas especies de carnívoros.

Conclusiones

Los grandes depredadores pueden servir como especies focales en programas de conservación regionales, por su papel en la dinámica de los ecosistemas, sus amplios rangos de acción, su susceptibilidad a los cambios del paisaje, entre otros (Castaño-Uribe et al., 2013; Noss et al., 1996), de manera que el registro de puma en este paisaje antropogénico debe ser un incentivo para mejorar el manejo de estas áreas, no solo con el fin de mantener sus funciones ecosistémicas, sino para resaltar el valor intrínseco de esta especie y la convivencia con la naturaleza. Estos reportes deben ser manejados adecuadamente con el fin de evitar la persecución hacia esta especie por parte de los habitantes locales, quienes suelen temer a estos grandes carnívoros debido a algunos eventos de depredación sobre especies domésticas (Garrote, 2012; González-Maya et al., 2013), situación que parece no presentarse aún en San Carlos. Hasta donde se conoce, nunca antes en el área de estudio se había realizado un muestreo tan intensivo, por lo que estos resultados son importantes para el conocimiento de la fauna en sistemas antropomórficos. Sin embargo, es importante continuar las investigaciones y establecer un plan de monitoreo para evaluar si estos registros sugieren el retorno de este felino a esta zona o por el contrario sean estos los últimos individuos que se movilizan en este paisaje. Otras investigaciones deberán confirmar también los factores que influyen en la presencia de esta y otras especies en el área.

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A camera trap protocol to efficiently sample mammals in Neotropical riparian forests

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Abstract

Camera trapping is arguably the most widely used non-invasive method to survey wild mammals. Various camera trap study designs have been proposed depending on study objectives, species sampled and ecosystem type. However, camera trap protocols to efficiently sample ground-dwelling mammals in riparian forests have yet to be developed. I conducted a pilot project in the Llanos region of Colombia to determine the optimal number and spacings of camera traps to obtain high sampling completeness of mammals in riparian (gallery) forests. To achieve better completeness in species richness estimation, I recommend transect surveys using at least five cameras with an inter-camera distance of around 250 m. My protocol serves as a reference to improve sampling efficiency of mammals in Neotropical riparian forests.

Keywords: gallery forest, Llanos, Neotropics, richness, transect, survey design

Introduction

Camera traps have become the method of choice when it comes to studying ground-dwelling and arboreal mammals in forests. This non-invasive technique has been used to answer a broad range of scientific questions, including the determination of species richness, occupancy, and abundance (O'Connell et al., 2011). More importantly, camera trap data can be used to assist in the conservation of endangered species that are cryptic in nature (e.g. Linkie et al. 2013).

Camera traps have been widely used to answer different questions involving numerous species in diverse ecosystems making it almost impossible to standardize camera trap sampling designs (Kelly, 2008). For instance, Burton et al. (2015) found that between 2008 and 2013, only half of the 266 studies they examined reported spacings between adjacent camera stations (between 20 m and 8 km; mean = 1.3 km, SD = 1.3 km) with sampling independence typically assumed, but rarely tested. In fact, detailed aspects of sampling methodologies are often omitted from camera trapping studies (Si et al. 2014). Burton et al. (2015) also found that the scale of spatial and temporal sampling effort varied considerably across studies; the number of camera stations in a study varied from one up to 1174 (median = 31, n = 229), with camera density ranging from 10 per hectare to <1 per 1000 km^2 (median = 1 per 2.9km^2, n = 104).

Camera trap surveys have been mainly conducted in large tracts of forests, or forest fragments within a matrix of different land uses (e.g. Wallace et al. 2003; Tobler et al. 2008b). However, riparian or gallery forests are arguably one of the least studied forest types, particularly in the Neotropics (Trujillo et al. 2010). Riparian forests differ from other forest types in terms of their shape and functionality being usually linear due to their association with river courses and varying in terms of height and structure particularly of understory vegetation (Vincelli, 1981). As such, grid-based camera trap arrays to assess mammal diversity may not be suitable due to their elongated shapes and variable width. In Colombia, riparian forest is commonly found in the Llanos region, a flat region dominated by grasslands and wetlands with natural flooding cycles (Trujillo et al., 2010). In this study, I determined the optimal number and spacing of camera traps to efficiently sample mammals in riparian forests in the Llanos region of Eastern Colombia, and compared the effect of seasonality to determine the best time for sampling.

Materials and methods

Camera trap sampling protocol

I evaluated a camera-trapping protocol for sampling mammals in riparian forests across three phases at four spatially independent sites in an oil palm dominated landscape in Cumaral, Department of Meta, Colombian Llanos. I employed a transect-based camera trapping design, with each of the first two phases having a different transect lengths and inter-trap spacing to determine ideal camera trap configurations. Further a third phase was implemented to test the effect of season in surveying terrestrial mammals, using the optimal arrangement of cameras identified in the previous phases.

In the first phase (short transect, short inter-trap distance, dry season), I placed one reference camera randomly along a 1000-m transect, with the remaining ones deployed at ~50 m intervals from this reference camera. At two sites (site 1 and 2), 21 cameras were simultaneously deployed over a 30-day period along animal trails. If the camera deployment location was found to be unsuitable (e.g. too close to a river edge, unsuitable vegetation, etc.), it would be redeployed within a 15-m radius. Based on the results from the first experiment, the inter-camera distance was increase and a longer transect was used with this alteration being deemed the second phase. For this second phase (long transect, long inter-trap distance, dry season), I used a 2250-m transect at two sites (site 3 and 4) following the same procedure in phase one, but with cameras deployed at least ~250 m apart. For the third phase (long transect, long inter-trap distance, wet season), I extended the camera-trapping period over a rainy season to investigate the effects of seasonality using the same sites and best configuration of camera placements configuration found to work better the second phase.

For all phases, I used Reconyx HC500 camera traps (Hyperfire^{TM}, USA) configured at the following settings: high sensitivity, 1-sec interval between consecutive pictures (3 pictures taken per trigger), no delay or quiet period between triggers, ≥ 1 m from the potential path of the animal, and 0.25-0.30 m from the ground depending on the terrain. All cameras were secured with steel security cables (Python^{TM} USA) and no bait was used to attract animals.

Protocol evaluation

To assess the mammalian sampling efficiency or completeness of the camera-trapping protocol for all three phases I computed species accumulation curves using Program EstimateS (Colwell, 2013). I conducted sample order randomization (n=1000) to eliminate the influence of the order in which each sample (days) was added. I then estimated the number of mammal species using the Chao 2 (S_{est}) estimator of richness (Colwell and Coddington, 1994), a non-parametric estimator that uses incidence data to avoid problems related to detection probabilities and abundance estimation.

For each camera trap configuration used during the three phases, I calculated the estimated sampling completeness (ESC) by dividing the number of observed species (S_{obs}) over its estimated number of species (S_{est}) and expressed the result as a percentage. For each configuration, I also calculated the 'true' sampling completeness (TSC) by dividing the number of observed species (S_{obs}) over the *total* number of species detected by all cameras at each site (S_{tot}) and again expressed the result as a percentage. This allowed me to assess sampling efficiency that is 'closer to reality' by accounting for the additional species that were actually present, but not detected, in the different configurations tested. I compared the average richness between the two seasons with a t test (Quinn and Keough 2002).

Results

Sampling efficiency generally decreased when fewer cameras were deployed for both transect lengths (1000 m and 2250 m transect). However, estimated sampling completeness (ESC) was higher than 'true' sampling completeness (TSC) for several configurations of cameras (Figs. 7.1 and 7.2). For example, the ESC for the last three transect configurations (with less cameras analyzed) was 100% for site 1 and 83-100% for site 2 (Fig. 7.1). However, cameras detected much fewer species at those sites than were actually present (i.e. TSC= <20% for site 1 and between 44-56% for site 2). The same pattern can be seen in the results from the transects in the second phase, but the differences were not as striking as in the first phase (Fig. 7.2). This finding suggests caution should be used when relying on assessments of effectiveness of the surveys solely derived from completeness calculated over estimated values of richness (ESC).

None of the different trials within the 2250 m transect detected less than 60% of the species present in the survey area, suggesting that this increase camera coverage was more effective. In regard to the effect of the season in the surveys, I detected more species in the dry season in both sites. However, the confidence intervals for these estimates were quite large and those for each season overlapped each other, suggesting that the differences were not significant (Fig. 7.3).

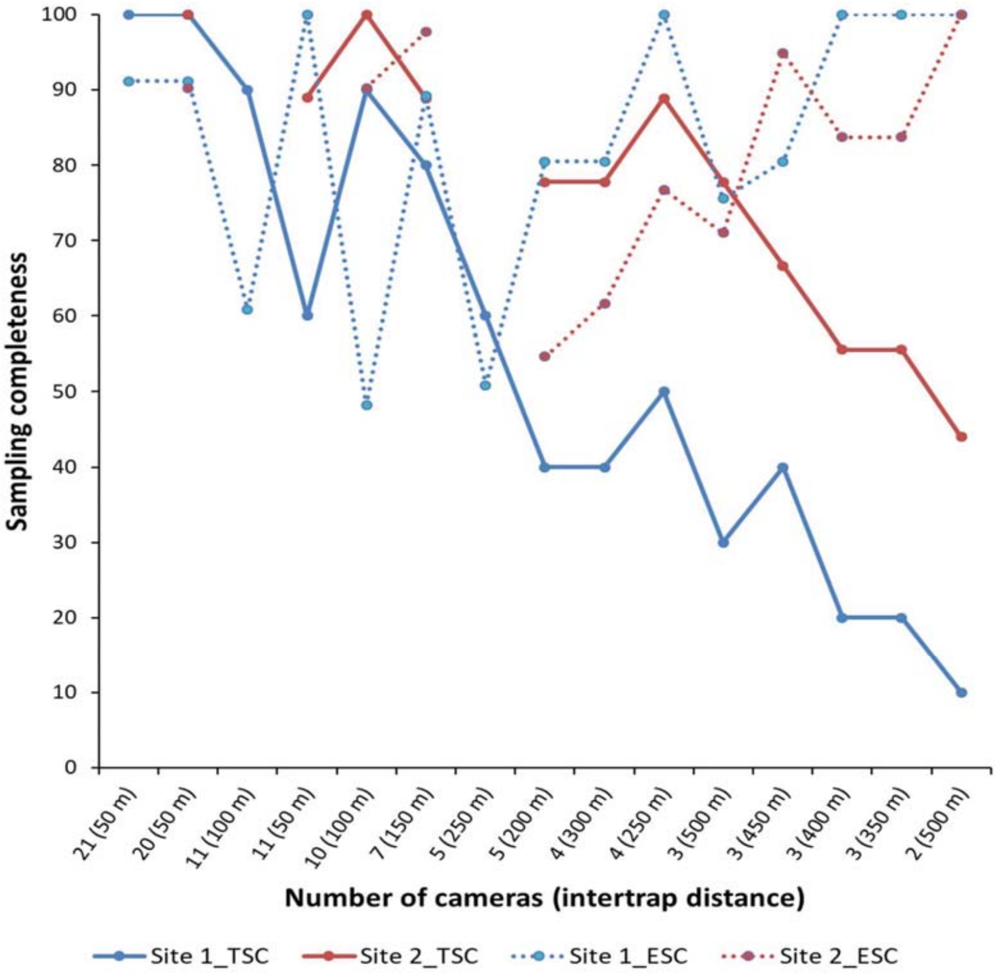

Figure 6.4. Estimates of sampling efficiencies of medium and large sizes mammals in the Llanos region of Colombia. Estimates are given for the different configurations of cameras

within a 1000-m transect (minimum inter-camera distance 50 m) at two survey sites. Estimated Sampling Completeness (ESC) is calculated using the estimated number of species by Chao 2 (observed species/estimated species*100), and True Sampling Completeness (TSC) is calculated using the total number of species detected at each site (observed species/total species in site*100). ESC tended to overestimate completeness or effectiveness of the survey when using less cameras.

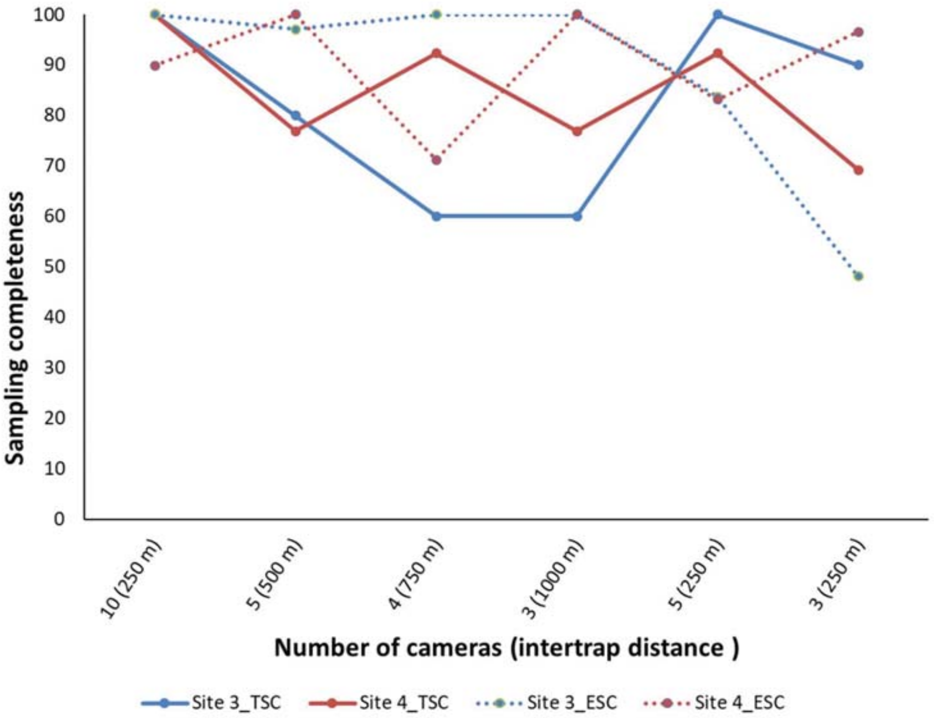

Figure 6.5. Estimates of sampling efficiencies of medium and large sizes mammals in the Llanos region of Colombia. Estimates are given for the different configurations of cameras within a 2250-m transect (minimum intertrap distance 250 m) at two survey sites. Estimated Sampling Completeness (ESC) is calculated using the estimated number of species by Chao 2 (observed species/estimated species*100), and True Sampling Completeness (TSC) is calculated using the total number of species detected at each site (observed species/total species in site*100). ESC tended to overestimate completeness or effectiveness of the survey when using less cameras.

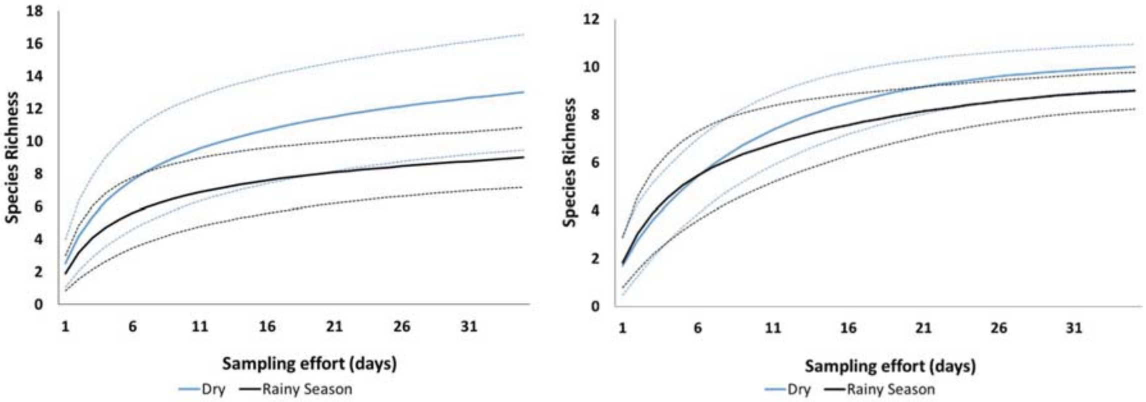

Figure 6.6. Estimated mammalian species richness accumulation curves assessing across the dry and rainy season at two sites in the Llanos region, Colombia. Dashed lines represent confidence intervals (95%). These curves were constructed with a configuration of 7 cameras every 250 m along a 2250 m transect at site 3 (left) and site 4 (right).

Discussion

I found that the number of cameras and the area they cover were important in accurately determining the number of species along riparian forest. Previous research, however, have suggested that the spatial arrangement of camera traps for inventory purposes can be flexible (Rovero et al. 2013) and that the area covered (or camera spacing) may have little impact on the number of species detected (Kelly, 2008; Tobler et al., 2008a). The majority of camera trap studies undertaken in the Tropics to date suggest that the use of one camera every 1km or 2km (e.g. Team Network 2008; Tobler et al. 2008) is sufficient to accurately assess the diversity of mammals. However, this study confirms that using only one or even three cameras every 1 or 2 km may be insufficient to infer patterns of richness in riparian forest, as it may underestimate the true species richness at the site level. Moreover, this bias in the results is not always apparent when calculating the sampling completeness using the estimated number of species (ESC), which is a common practice when assessing the quality of the survey.

Depending on the scale of the survey, the use of minimal cameras during a survey might leave areas insufficiently surveyed which could bias mammal community estimates, whilst on the other hand, placing numerous cameras with minimal inter-camera distances would be unnecessary for surveying mid-large sized mammals as shown in my results; apart from being an expensive and time-consuming task. While there are no rules of thumbs which could be applied for every field design, my results suggest that using at least 5-7 cameras along a transect, separated by 250 m, across a sampling duration of 20-30 days at each sample unit would be sufficient to effectively survey the mammal community in a Neotropical riparian forest. The general repeatability of this survey for the greater Neotropics would need to be validated, although, this general recommendation would obviously need to be altered depending upon the area requiring survey, research question and on resource availability (i.e. available cameras).

My finding correspond to previous studies which found a positive influence of the number of cameras on detection probabilities (e.g. Gompper et al. 2006; Pardo et al. 2016). It has been found that even the placement of four cameras on the same tree, facing each cardinal points, could have an important impact on occupancy studies in temperate forests (Pease et al., 2016). In this study, I recorded a greater crab-eating raccoon (*Procyon cancrivorous)* in only one of the 10 cameras placed on a transect. Therefore, relying on one or three cameras would have probably resulted in a false absence for this site. On the other hand, the duration of any survey and the number of cameras used are also tradeoffs researchers much contend with (Long and Zielinski, 2012), especially as the number of cameras available is often limiting given their current price. My results concur with general recommendations in other studies suggesting that an increase in the number of days or camera-days a study covers would increase the likelihood of detecting rare species, especially in areas with low densities of animals (e.g. Gompper et al. 2006; Team Network 2008; Si et al. 2014)

Contrary to studies on single species, experimental design for the estimation of richness may be challenging due to the different biology of the species within an assemblage. For instance, protocols for estimating parameters such as occupancy or animal abundance usually consider the home range of species to determine the configuration of the cameras and sampling design (Karanth and Nichols, 1998; O'Brien, 2011; Rovero et al., 2013; Silver et al., 2004). In general, they suggest that there should be at least one sampling site per the smallest home range of the target species in the sampled area. On the other hand, estimation of local richness/diversity would include a variety of species with different behaviors, home ranges and habitat requirements, making it difficult to determine a rule of thumb in terms of sampling protocols. I consider, therefore, that the protocol proposed here would help to alleviate these limitations by increasing the likelihood of detecting different species which may have different home ranges.

The exact location of cameras may also represent some constraints. As such, the selection of trails is generally recommended for terrestrial mammals in camera trapping studies designs (e.g. Tobler et al. 2008; O'Brien 2011). However, other researchers suggest caution when using only such landmarks, especially for occupancy, richness or a particular guild of mammals, and rather encourage the use of random sampling (e.g. Kays et al. 2009; Harmsen et al. 2010; Wearn et al. 2013). Having this debate in mind, the sampling approach identified in this research enables a systematic approach to locate cameras across different habitat features within an area of interest, a design also previously suggested for optimizing sampling of some mammal guilds (Mann et al., 2015).

One of the most challenging issues in sampling wildlife mammals relates to imperfect detection, this is a species may be present but not detected (MacKenzie, et al. 2006). Detectability of animals can be affected by many different factors depending on the scale of analysis. These factors can vary from the type of camera used (e.g. detection zones, sensibility, trigger speed etc.), location of the camera (e.g. trails or not, attractants or not, temperature, etc.), habitat or landscapes characteristics (e.g. mesoscales or macroscales variables), to body mass and abundance of the animal (for a complete discussion of some of these issues refer to Wellington et al. 2014, Meek et al. 2014, Du Preez et al. 2014, Burton et al. 2015, O'Connell et al. 2011, Rovero et al. 2013, Balme et al. 2014, Gomper et al. 2006). Therefore, no single design can be used for every scientific question, and approaches may vary due to different aspects of the research objectives.

Although my results derived from a pilot project in a small spatial area they are amongst the first to be conducted in Colombian riparian forest to assess issues related to sampling design. This is pertinent as riparian forests are important habitats for mammals in the Llanos region (Trujillo et al., 2010) of Colombia especially in human dominated landscapes (e.g. Pardo and Payán, 2015). However, as mentioned, very few studies have been conducted in this ecosystem in either the Llanos or Orinoquia region (Trujillo et al., 2010), especially using camera-trapping (Díaz-Pulido et al., 2017). Thus, the protocol identified here may serve as a base for designing future camera trapping surveys in this region or other Neotropical riparian forests, particularly for studies occurring at the landscape scale. I do not claim to have solved issues related to sampling design or confront theoretical frameworks (e.g. detectability, relative abundance, estimators approaches) that are well analyzed in the literature (P D Meek et al., 2014; O'Connell et al., 2011; Scotson et al., 2017; Si et al., 2014; Srbek-Araujo and Chiarello, 2013; Wearn and Glover-Kapfer, 2017; Williams et al., 2002). However, the approach suggested here enriches the discussion on mammalian population survey techniques to assess richness/diversity estimation in Neotropical riparian forest.

Conclusion

In this paper, I bring attention on the importance of avoiding the use of a single camera to reach conclusions on mammal species richness at a particular site. Moreover, the placement of one or three cameras (as is most current practice) at a site to estimate mammal species richness would have resulted in erroneous outcomes. I showed that the use of transects containing 5-7 cameras separated by 250 m, improve estimation of richness of terrestrial mammals in riparian forest. However, my proposed sampling design is by no means a 'one-size-fits-all' protocol but should serve as an empirically supported reference for future assessments of mammalian community richness in riparian forests.

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JCU affiliated publications produced during my PhD candidacy

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, e0197539.

Díaz-Pulido, Abud M, Alviz A, Arias A, Aya C, Benítez A, Bonilla A, Botero S, Bravo…**Pardo LE**, et. al. 2017. Fototrampeo: Una herramienta para el muestreo de mamíferos medianos y grandes. In Moreno LA, Andrade GI, Ruíz-Contreras LF (Eds.). Biodiversidad 2016. Estado y tendencias de la biodiversidad continental de Colombia.

Pardo, L.E., L. Lafleur, M. Spinola, J. Saenz, and M.V. Cove. 2017. Camera Traps Provide Valuable Data to Assess the Occurrence of the Great Currasow (*Crax rubra*) in Northeastern Costa Rica. Neotropical Biodiversity. 3(1):182-188**.**

Pardo, L.E., G.R. Clements W. Edwards, A. Rojas-Rojas, and W.F. Laurance.2017. Registros de puma (*Puma concolor,* linnaeus, 1771) en zona rural de San Carlos de Guaroa, Meta, Colombia. Revista Biodiversidad Neotropical. 7(1): 56-61.

Pardo, L.E, Cove, M. Spinola, J.C. de la Cruz, and J. Saenz. 2016. Assessing Species Traits and Landscape Relationships of the Mammalian Carnivore Community in a Neotropical Biological Corridor. Biodiversity and Conservation. Biodiversity and Conservation. 25:739–752

Pardo, L.E and E. Payán. 2015. Mamíferos de un agropaisaje de palma de aceite en las sabanas inundables de Orocué, Casanare, Colombia. Biota Colombiana 16 (1): 54-66.

Pardo L.**E**, W.F. Laurance, G.R. Clements and W. Edwards. 2015. The impacts of oil palm agriculture on Colombia's biodiversity: what we know and still need to know. Tropical Conservation Science Vol.8 (3): 828-845.

Chapter 7 Synthesis

Background

Colombia is a megadiverse country (Mittermeier et al., 1997), currently experiencing a rapid expansion of oil palm plantations (Dammert, 2014). Due to the known negative biodiversity impacts of oil palm cultivation in Southeast Asia (Koh and Wilcove, 2008; Peh et al., 2006; Yue et al., 2015), there is a concern about the potential threats of this cultivation on Colombia´s biodiversity. Although, most of the recent expansion of oil palm in Colombia has replaced already transformed lands (Furumo and Aide, 2017), there is a paucity of studies examining biodiversity surrounding oil palm landscapes and its potential negative effects on biodiversity, especially its impacts on mammal species (Pardo et al., 2015). Therefore, identification of potential mitigation measures and management actions are still unclear.

Mammals are important for their role in ecosystem processes and their intrinsic and cultural values (Castaño-Uribe, 2013; Estes et al., 2011). They provide benefits to humans through pollination, prey control and seed dispersal among others (Camargo-Sanabria and Mendoza, 2016; Estes et al., 2011). Colombia contains one of the most diverse mammal communities of any country in the world (Ramírez-Cháves et al., 2016), though 43 mammal species are currently threatened with extinction (Rodríguez-Mahecha et al., 2006). Therefore, there is an important need to identify the response of Colombian mammals to human activities and land use change to ensure the identification of effective management strategies, identify species of concern and evaluate the actual capacity of the country to retain its mammal diversity in the face of rapid oil palm expansion. This information is especially important in production landscapes as the capacity of protected areas and hotspots to conserve biodiversity in the long-term is limited. This limitation is in part due to the increasing rate of destruction occurring in these areas (Laurance et al., 2012; Sloan et al., 2014), and human-driven processes occurring in the surrounding landscapes (Gardner et al., 2009).

This doctoral thesis explored multiple themes coalesced around a central core topic of the diversity patterns and responses of terrestrial mammal species (> 0.5 kg) to oil palm plantations and associated factors in Colombia. This study is the most comprehensive analysis of mammal diversity across oil palm-dominated landscapes in Colombia conducted to date and the largest systematic camera trap survey in Llanos region. The more than 12,000 camera-days of data collected across 56 sites allow us to have a clear knowledge of medium-large sized mammal diversity patterns in the western Llanos region. Most importantly, my results provide unequivocal evidence showing how these species respond to land use change and habitat features at both the habitat and landscape level. As such, my thesis has not only filled an important gap in the knowledge for these landscapes, but also informs conservation planning and the development of better management practices for sustainable oil palm cultivation in Colombia. Therefore, this thesis will be of interest and a source of science based practical information for oil palm managers, conservation practitioners and policy makers in the region, and at the national level. The aim of this final chapter is to synthesize the central findings of my doctoral research (chapters 2-5), its general implications and to suggest future research directions.

Chapter 2. Terrestrial mammal response to oil palm dominated landscapes in Colombia

Oil palm plantations exerted a strong negative effect on species richness and community composition with species richness 47% lower (on average) than in riparian forests. While 17/24 species were shared between oil palm plantations and forests, the capture frequencies (relative abundances) differ significantly in some species, with few species appearing to tolerate, and take advantage of oil palm plantations (fox, jaguarondi, giant anteater, white tailed deer, and crab eating raccoon). My results reinforce the importance of retaining riparian vegetation across the landscape for biodiversity conservation, independently from their structural characteristics, as shown by the weak influence of these features to predict species richness. This finding is supported by that of previous research into mammal diversity in human dominated landscapes (e.g. Azhar et al., 2014; Harvey et al., 2006b; Mendes-Oliveira et al., 2017; Pardini et al., 2005; Yaap et al., 2016).

Inside oil palm plantations, I found evidence suggesting that intensification of cattle grazing reduces the number of mammal species. Conversely, maintaining undergrowth vegetation can increase mammal species richness by up to 66% (on average). This finding is likely due to the increase in habitat heterogeneity and complexity that undergrowth vegetation provides in the plantations. Positive effects of habitat enrichment, as in this instance with undergrowth vegetation, on biodiversity conservation has been demonstrated in other systems and human dominated landscapes (e.g. Azhar et al., 2014; Pereira et al., 2012; Tews et al., 2004; Tscharntke et al., 2012; Wearn et al., 2016), but not inside Neotropical oil palm plantations. In fact, some previous studies have suggested poor prospects of habitat improvement inside Asian oil palm plantations (e.g. Yue et al., 2015). Finally, my work clearly identifies areas of high mammal diversity and species of conservation concern, which could enable land managers to prioritize conservation efforts. However, due to the lack of IUCN listed critical conservation species and high conservation value areas (e.g. pristine forest) within the study area, I recommend modifying conservation approaches (in human dominated landscapes) such as the oil palm certification schemes, to focus on restoration processes instead. Recognizing the potential value of human modified landscapes for conservation may encourage farmers to promote biodiversity concern, regardless of the existence of iconic species or available intact habitats to set aside.

Chapter 3. Identifying critical limits in oil palm cover for the conservation of terrestrial mammals in Colombia

Balancing agriculture and biodiversity conservation is a key challenge in developing countries (Gardner et al., 2009). Therefore, identifying maximum tolerance of species to increasing agricultural expansion enables the determination of sustainable limits or thresholds before a population collapse will occur. I identified a clear negative linear relationship between increasing oil palm cover (%) in a landscape and mammal species richness. These results are supported by previous research on oil palm expansion and other animal taxa in Colombia (Gilroy et al., 2015; López-Ricaurte et al., 2017; Prescott et al., 2016). However, species richness response to increase of oil palm revealed no obvious threshold. In contrast, I identified strong signs of a community threshold in species' frequency of occurrence and relative abundance to oil palm coverage of a landscape of between 45-75% in 10 out of 15 of the examined species. Moreover, a landscape with more than 75% of oil palm coverage was identified as unsustainable for ongoing mammalian community survival (*sensu* Angelstam et al., 2003). If we use the identified threshold of 45-75% as a surrogate for the minimum amount of remaining forest needed to support resilient populations of mammals, my results suggest that a landscape compose of less than 55% of forest would likely enter a risk zone. Further a minimum of 25% of natural vegetation (i.e. riparian forest) should be maintained within the Llanos oil palm landscapes to maintain mammal populations.

I used the community threshold (45-75%) as a proxy to evaluate the current conservation status of the four major oil palm production zones in Colombia (North, South, West and East). Using this metric, I found that approximately 41% of Colombian oil palm landscapes have crossed this threshold (75% oil palm). This suggests that in addition to measures to preserve the current natural cover (i.e. forest) in these regions, restoration measures should be implemented. There is no previous research which has identified a "safe-limit threshold" for mammal conservation in tropical oil palm landscapes. At an annual increase in oil palm cover in Colombia of ~10,000 ha (Etter et al., 2011), effective conservation planning and management is vital and time-critical.

Chapter 4. Assessing the probabilities of terrestrial mammals to occupy oil palm plantations in the eastern plains of Colombia

While the positive conservation significance of remnant natural habitats in human modified landscapes is well known (e.g. Gibson et al., 2011), understanding the ability of animals to use and move across the surrounding agricultural matrices is vital for conservation planning (e.g. Daily et al., 2003). Here, I evaluated habitat use and detection probabilities of 23 medium and large sized mammals in oil palm plantations and adjacent riparian forest in the Llanos region, Colombia, using an occupancy framework (MacKenzie et al., 2006). Further, I evaluated the effect of undergrowth vegetation and proximity to forest on habitat use probability within oil palm sites.

I found that most species exhibited limited distributions across the study area and only five species occurred at more than 50% of the 56 sites evaluated. Moreover, only two species occupied more than 70% of the examined oil palm plantations sites, whereas seven species occupied greater than 70% of the riparian forest sites. Habitat use probability ($\hat{\Psi}$) was strongly influenced by habitat type in four species, showing a high negative effect of oil palm, whereas the remaining eight species showed constant habitat use across the study area with varying probabilities of oil palm and forest use. In general omnivores, mesocarnivores, deer, and giant anteater had higher probabilities to use oil palm while the remaining species, including ocelot and lesser anteater, showed a clear preference for forest habitats. These results correspond in part with similar research in Colombia that has reported a negative relationship between oil palm and other biodiversity metrics such as richness, occupancy, and abundance in different taxonomic groups (e.g. López-Ricaurte et al., 2017; Pardo and Payán, 2015). However, they also show that oil palm could be permeable to some degree to several common species in the Llanos.

While habitat use and the effect of the variables appeared to vary according to the species, my findings also suggest that allowing undergrowth vegetation inside plantations and maintaining nearby riparian corridors, will likely reduce the resistance imposed by oil palm for most species in the resident assemblage. Historical land use changes in the Llanos region (Etter et al., 2011), previous and parallel to oil palm cultivation, might have influenced the strength (weak) of the pattern detected in this highly human dominated landscape. No previous study has identified species-specific habitat use probabilities of mammals across oil palm landscapes. This information will therefore help practitioners to understand the dynamics occurring in this ecosystem and identify management practices that could promote the connectivity between oil palm and riparian forest in the Llanos region, as not all species responded similarly.

Chapter 5. Effects of oil palm and human activities on the activity patterns of terrestrial mammals in the Colombian Llanos

Behavioral responses can play an important role in determining the capacity of species to adapt to novel environments and human presence. I found that only capybaras showed a clear shift in their activity patterns between oil palm plantations and riparian forests; shifting from crepuscular in forest to predominantly nocturnal behavior inside oil palm. Conversely, giant and lesser anteaters, and common opossums used both land cover types equivalently, suggesting no significant effect of oil palm plantations on their activity patterns. Capybaras, giant anteaters, white-tailed deer, and ocelots appeared to modify their activities inside oil palm to avoid human presence, whereas jaguarundis had a high overlap with human activities. Altogether, the behavioral flexibility of the above species is in concordance with previous finding on some terrestrial mammals including deer, mesopredators, and omnivorous species (e.g. Gallina and Bello-Gutierrez, 2014; Norris et al., 2010; Wang et al., 2015b) which shows their capacity to occupy human dominated areas. However, no previous reports of these behavioral responses had been documented for Colombia.

Pair-wise analysis of several mammal species revealed a temporal segregation between some species, such as fox and jaguarundis inside oil palm plantations, and high overlap in activity patterns between potential predator-prey relationships (e.g. ocelots and armadillos). This study contributes to the understanding of mammalian resilience to anthropogenic landscapes and the natural history of poorly known species in the Neotropics. Moreover, this study identified behavioral effect of anthropogenic land use change on mammal species which is not captured in traditional studies that focus on measures such as species richness or abundance. Further, these findings complement the growing documentation examining biodiversity and natural history of species found in oil palm landscapes in Colombia.

Colombian context

Although oil palm development in Colombia has been associated with social conflict and displacement in the past (Mingorance, 2006), it is important to recognize the current social benefits of oil palm cultivation in Colombia, and its important role as source of employment (MADR, 2006a). Therefore, engaging with relevant stakeholders is vital to balancing socioeconomic and environmental goals. This is particularly challenging in the face of likely future developments in isolated areas and natural savannas in Eastern Llanos (Pardo et al., 2015; Romero-Ruiz et al., 2012). This likely development is being partly driven by government incentives and corporate investments, but it is also a response to the cessation of internal armed conflict, which is allowing access to previously inaccessible areas (Baptiste et al., 2017). My findings represent an important contribution identifying oil palm plantation biodiversity and management regimes that can assist the continued survival of Colombia's native mammals in these rapidly expanding landscapes. The future of tropical forest biodiversity in a human-modified world may depend on how well humans know and manage the matrix (Gardner et al., 2009), which, in Colombia's western Llanos, is predominantly comprised by oil palm plantations.

Oil palm development in Colombia has been unique to that of other tropical regions in that most of the expansion has taken place in already transformed lands (e.g. Furumo and Aide, 2017). Therefore, it is important to take into account the historical land use processes in the past when attempting the identification of impacts and better practices. However, as shown by my results (see box 1, 2) setting limits to oil palm development even in already transformed landscapes is important for conservation outcomes. Overall, restoration of riparian forest across oil palm dominated landscapes is clearly the most important goal for conservation practitioners, along with the implementation of some management practices inside oil palm; such as those shown in this thesis (e.g. undergrowth retention). Further, identification of critical species for conservation (as per IUCN categories) or high conservation value (HCV) habitats alone in these landscapes would result in poor conservation outcomes as my results clearly show that most of the oil palm dominated landscapes in the Llanos lack these elements. Therefore, appreciation of current fauna and identifying their role in transformed lands would encourage oil palm growers to better engage in conservation processes.

Research priorities

Although research on fauna associate with oil palm landscapes has increased within the last three years, especially on birds (e.g. Gilroy et al., 2015; López-Ricaurte et al., 2017; Prescott et al., 2016), further studies are required in the areas of small and flying mammals, reptiles and invertebrates. Further, it is important to understand the trophic interactions emerging in these “novel” ecosystems. My findings suggest that understory vegetation is positively correlated with richness, composition and occupancy of species within oil palm plantations, however, the mechanisms behind this pattern is yet to be empirically tested (i.e. food web interactions). Therefore, study the biodiversity of different groups (invertebrates and small vertebrates) within these potential “new habitats” is important in the elucidation of this mechanism. This information will be useful not only to understanding the community and the dynamics promoting biodiversity across these landscapes, but also in evaluating potential ecosystem services provided by species (see Foster et al., 2011). This assessments could also potentially help to evaluate plausible reintroduction programs or “rewilding”; along with restoration processes (see Hobbs and Harris, 2001).

Studies in hydro-biological cycles are urgently needed to address the capacity of the country to sustain oil palm, given climate change scenarios and the climatic particularities of the Llanos and other Colombian oil palm production regions. Finally, further questions that await research could include: if plantations are primarily replacing cattle pastures and other crops, could there be positive benefits for biodiversity in this context? How effective are current strategies for sustainability (i.e. certification programs)? Are the conservation impacts of oil palm equivalent to other potential biofuel crops? Since oil palm is an exotic crop in Latin America, does this novel ecosystem increases the appearance of invertebrate pest that can be harmful for native ecosystems? Many hectares of oil palm plantations has been loss in the western zone due to different diseases, could this be spread to native palms?

Although, it is highly unlikely that the government target of 1-3 million ha planted by 2020 will be achieved (Castiblanco et al 2013), oil palm is still an important growing economic sector. Therefore, investment in environmental monitoring and better management practices, which take into account the considerations identified in this thesis, within the oil palm industry can make Colombia a leader in sustainable oil palm production and play an important role in social and rural development (see Sayer et al., 2012), particularly in the face of the current post-conflict scenario (see Baptiste et al., 2017).

Conclusions

The main goal of this study was to identify the diversity patterns and responses of terrestrial mammals to oil palm landscapes to aid conservation planning in the Llanos region. My findings clearly demonstrate that oil palm is not a suitable habitat for the majority of species of the Llanos region and show the negative impacts of large-scale oil palm plantations if land conversion occurs at the expenses of forest; though, few species were highly tolerant to this ecosystem. For existing plantations, I identified some management practices, which can occur inside oil palm plantations or at the landscape scale, that can significantly improve the conservation value of oil palm production lands for mammalian species and improve connectivity in the area. The specific responses identified in this study also provide valuable information to assist in the identification of vulnerable or more sensitive species, as well as important locations for conservation programs and monitoring.

In box 1 and 2 I have summarized my findings and their practical implication for both conservation and general knowledge. These findings are unique in that they are the first to provide information on the mammal assemblage and the community dynamics that take place in Colombian oil palm dominated landscapes. Thus, this information fills an important knowledge gap in this area both for Colombia and the greater Neotropical region. In the face of rapid extinction rates and population declines (Ceballos et al., 2017), finding a balance between production development and wildlife is without doubt urgent. I'm confident that my findings, articulated with other recent (and future) investigations in Colombia, in conjunction with a willingness by the industry to incorporate these findings into management practices will help to minimize the impact of oil palm development on wildlife while contributing to social development.

Box 1. Management recommendations derived from this study

Recommendation	Evidence from this thesis
Conserve forest strips (gallery or riparian forest)	Forest cover was clearly the fundamental factor for the presence of mammal species in the study area, including the diversity found inside oil palm plantations. More than 16 species showed a preference for forest and seven of them were only detected in the forest. Further, species thriving in oil palm also occasionally require adjacent forest. Moreover, I found that regardless of the structure or age of riparian forest these forests are an important refuge and can act as corridors for most species in oil palm landscapes in the Llanos region. They also show to provide a spillover process towards oil palm plantations, which increased number of species within this crop. However, oil palm sustained ~47% less species on average than that found in riparian forest.
Restore riparian forest width	Along with the conservation of extant forests. It is imperative to establish a restoration program that results in an increase in the width of riparian forest strips. Moreover, simply respecting the legal minimum width of these corridors is a clear determinant for species survival. My results showed that approximately 32% and 41% of the Colombian landscapes in which oil palm is cultivated are currently within the threshold limits for oil palm coverage in relation to riparian forest and beyond (respectively), which means restoration is fundamental.

Avoid removing understory vegetation inside plantations	It is important to promote habitat heterogeneity inside the plantation. Allowing understory vegetation (i.e. no mowing) can improve the species richness by up to 66% and the probability of habitat use of species. Other forms of enrichment should also be evaluated such as artificial nest, water holes, etc.
Avoid cattle inside plantations	Cattle inside plantations had a negative impact on species richness and also limits the growth of understory vegetation. Therefore, it would be beneficial to exclude cattle from plantations. Finding other techniques to control livestock movement, such as the use of fences or enclosures should be evaluated as well.
Maintain close proximity to forest	Occupancy varied according to the species, however the majority of mammals had higher probability of occupancy when close to riparian forest. Potential spillover effects from forest fauna to oil palm seemed to be limited to a short distance from the forest. Results from rare species found in oil palm suggest that maximum travel distance of these species from forest into oil palm was approximately 500 m.
Target species for conservation based on my results	Given the different responses of individual species, a sole focal species approach might not be the best option. Instead, a multiple species or an ecosystem focus would better fit conservation practices according to the pattern observed in the landscape (see box 2). Fox populations, however, should be monitored as their apparent hyperabundance in plantations could have negative effects on surrounding biodiversity.

Evaluate the high conservation value paradigm for promoting conservation in oil palm landscapes	No species of conservation concern were found in the study area, and the only species categorized as Vulnerable (IUCN), appeared to be widely distributed and oil palm tolerant (giant anteater). Does this mean oil palm landscapes lack conservation value? I propose an evaluation of the high conservation value paradigm to include the importance of valuing present-day communities (i.e. biodiversity as a whole regardless of conservation categories) and altered landscapes for regional conservation; which may better encourage oil palm growers. This is further supported by the fact that populations of even common species may collapse at different amount of oil palm in the landscapes, as per threshold analysis results.
Important areas for conservation	In terms of the composition and richness of terrestrial mammal species, The areas of San Carlos de Guaroa and Cabuyaro warrant special attention. Rare and ecologically important species, such as the puma, tayra, coati, and peccary, occurred in these zones. Further, because of its proximity to relatively undisturbed savannas, San Carlos is an important area for habitat connectivity. This zone is also highly important for conservation given its relatively close proximity to both "Corridor Meta-Casanare" and "Alto Rio Meta," two priority conservation areas suggested for the Orinoquia region (Lasso et al. 2010).

Sustainable landscape: ideally landscapes should contain maximum 75% oil palm coverage, and minimum 25% of forest to aid conservation of terrestrial mammals	According to my threshold analysis, landscapes beyond 45% oil palm coverage put at risk the resilience of the majority of species. This is a warning point at which monitoring and specific assessment of biodiversity should be conducted. Landscapes with a ratio of more than 75% of oil palm to native cover were found to be unsustainable for mammal communities. Using this point as a base, allowed me to suggest that a minimum 25% of forest is need to aid conservation of mammal populations in the Llanos region of Colombia. However, ideally protecting 55% of natural ecosystems would help to avoid entering a risk zone.

Box 2. Species category of sensitivity if land use changes produces from forest to oil palm according to the different approaches used in this research.

Category	Description	Species
Non sensitive ("Winners")	These species showed to be relatively common and some possible thrive within oil palm plantations. Analysis resulted in positive relationships or non-evident effects. Fox in particular showed to be unexpectedly dominant and with high probabilities of using oil palm. However remaining species also needed presence of forest across the landscape as complementary habitat.	fox, giant anteater, jaguarundi, white tailed deer, raccoon
Tolerants	These species are not as common as species in the "non sensitive" category. They also use oil palm and riparian forest, but preferred forest, especially the capybara which showed high dependency for proximate forest.	ocelot, lesser anteater, common opossum, capybara (titi, capuchin)
Sensitive ("Losers")	These species showed high dependency of forest and they were not observed inside plantations (except for armadillo which was observed occasionally)	agouti, paca, armadillo, naked tailed armadillo, spiny rat, squirrel (howler monkey, zocay, night monkey)
Rare species, need data	These species had narrow distribution and very low detections, limiting analysis through any of the methods used. Therefore, is difficult to be certain about their trends and preference. However, these species were fundamentally forest specialist, and therefore may be considered potentially in the "sensitive" group. Although, species such as puma and grison, were able to move across oil palm in their way to forested habitats.	puma, grison, tayra, four-eyed opossum, coendu, coati

*This is an overall description based on the parameters studied in this thesis, some particularities may apply per species as discussed in the thesis

-- END --

Appendices

Chapter 2

Appendix 1. Images of the study area in the Llanos region of Colombia (Meta department). a) Aerial photographs (August 2014) of the landscape highlighting riparian forest and oil palm plantations structure. b) Differences in management schemes of undergrowth vegetation in oil palm plantations in Llanos, Colombia. Photo credit: L.E. Pardo.

No undergrowth-low

Medium-high undergrowth

Appendix 2. Terrestrial mammal species detected by camera trapping surveys (Aug. 2014 – Dec. 2015) in oil palm plantations and riparian forests in Llanos, Colombia

				FORESTS			**PLANTATIONS**		
Order/family	**Common name**	**Scientific name**	**TC**	**Total ind. photos**	**Proportion in survey**	**Total occupied sites**	**Total ind. photos**	**Proportion in survey**	**Total occupied sites**
Pilosa									
Myrmecophagidae	giant anteater	*Myrmecophaga tridactyla* ^{mt}	I	116	5.56	19	123	21.03	30
Myrmecophagidae	lesser anteater	*Tamandua tetradactyla* ^{tt}	I	65	3.21	20	39	6.67	16
Cingulata									
Dasypodidae	Nine-banded armadillo	*Dasypus novemcinctus* ^{dn}	I*	119	5.71	16	4	0.68	3
Dasypodidae	naked tailed armadillo	*Cabassous unicinctus* ^{cu}	I	25	1.20	9	ND		
Carnivora									
Canidae	fox	*Cerdocyon thous* ^{ct}	MO	14	0.67	6	226	38.63	26
Felidae	jaguarundi	*Puma yagouaroundi* ^{py}	MC	6	0.29	5	20	3.42	13
Felidae	ocelot	*Leopardus pardalis* ^{lp}	MC	57	2.73	16	15	2.56	12
Felidae	puma	*Puma concolor* ^{pc}	T	2	0.10	2	1	0.17	1
Mustelidae	greater grison	*Galictis vittata* ^{gv}	MC	1	0.05	1	2	0.34	2
Mustelidae	tayra	*Eira Barbara* ^{eb}	MO	2	0.10	2	ND		
Procyonidae	crab eating raccoon	*Procyon cancrivorus* ^{pa}	MO	6	0.29	4	16	2.74	7
Procyonidae	coati	*Nasua nasua* ^{pn}	MO	15	0.72	2	ND		

				FORESTS			PLANTATIONS		
Order/family	**Common name**	**Scientific name**	**TC**	**Total ind. photos**	**Proportion in survey**	**Total occupied sites**	**Total ind. photos**	**Proportion in survey**	**Total occupied sites**
Artiodactyla									
Cervidae	white-tailed deer	*Odocoileus cariacou* ^{oc}	HG	8	0.38	6	22	3.76	12
Cervidae	red brocket deer	*Mazama spp* ^{ma}	HG	ND			2	0.34	1
Tayassuidae	collared peccary	*Pecari tajacu* ^{pt}	HO	1	0.05	1	1	0.17	1
Rodentia									
Echimyidae	spiny rat	*Proechimys spp* ^{pr}	HR	182	8.73	21	3	0.52	2
NN	mouse	*not identified* ^{nn}	HR				2	0.34	1
Dasyproctidae	agouti	*Dasyprocta fuliginosa* ^{df}	HR	425	20.38	18	ND		
Cuniculidae	paca	*Cuniculus paca* ^{cp}	HR	469	22.49	23	1	0.17	1
Caviidae	capybara	*Hydrochoerus hydrochaeris* ^{hh}	HG	99	4.75	8	29	4.96	3
Erethizontidae	coendu	*coendu spp* ^{co}	HF	1	0.05	1	ND		
Sciuridae	squirrel	*sciurus spp* ^{sc}	HR	44	2.11	9	ND		
Didelphiomorpha									
Didelphidae	common opossum	*Didelphis marsupialis* ^{dm}	O	288	13.81	22	63	10.77	12
Didelphidae	four-eyed opossum	*Philander opossum* ^{po}	O	1	0.05	1	ND		
Primates									
Cebidae	tufted capuchin	*Sapajus apella*	O	86	4.12	19	3	0.51	2
Cebidae	squirrel monkey	*Saimiri sciureus*	O	61	2.93	15	11	1.89	2

All species are LC (least concern) according to the International Union for the Conservation of Nature Red List Categories (IUCN), except for the giant anteater, which is VU (vulnerable). TC=Trophic Category: I=insectivorous, MO=mesopredator/omnivore, MC=mesopredator/obligate carnivore, HG=herbivorous/grazer, HR=herbivorous/granivorous, HO=herbivorous/omnivorous, O=omnivorous, T=top predator/obligate carnivorous, HF=herbivorous/folivorous. Total ind. Photos = sum of independent photos; independence between consecutive pictures was defined as 30 minutes. ND=not detected. Superscript corresponds to the code for Fig 5.2. A tapir was found in semi-captivity in one farm.

Appendix 3. Model selection output comparing all possible combinations for the effect of variables on mammalian species richness at the landscape level.

Inter	cover	dis.road	dis.town	NDVI	% for	R^2	df	logLik	AICc	Δ AICc	AICω
2.22	-0.76	NA	NA	NA	NA	0.60	3.00	-113.62	233.71	0.00	0.28
2.20	-0.72	NA	NA	0.07	NA	0.60	4.00	-113.05	234.88	1.17	0.15
2.22	-0.77	NA	0.02	NA	NA	0.60	4.00	-113.55	235.89	2.18	0.09
2.20	-0.73	NA	NA	NA	0.02	0.60	4.00	-113.59	235.97	2.26	0.09
2.22	-0.77	-0.01	NA	NA	NA	0.60	4.00	-113.60	235.98	2.27	0.09
2.20	-0.73	NA	0.03	0.08	NA	0.61	5.00	-112.87	236.94	3.23	0.06
2.18	-0.69	NA	NA	0.07	0.02	0.60	5.00	-113.01	237.22	3.51	0.05
2.20	-0.73	-0.01	NA	0.07	NA	0.60	5.00	-113.03	237.25	3.54	0.05
2.21	-0.74	NA	0.02	NA	0.02	0.60	5.00	-113.52	238.25	4.54	0.03
2.22	-0.77	-0.01	0.02	NA	NA	0.60	5.00	-113.54	238.28	4.57	0.03
2.21	-0.74	-0.01	NA	NA	0.02	0.60	5.00	-113.57	238.33	4.63	0.03
2.18	-0.69	NA	0.03	0.08	0.02	0.61	6.00	-112.83	239.38	5.67	0.02
2.20	-0.73	-0.01	0.03	0.08	NA	0.61	6.00	-112.86	239.44	5.73	0.02
2.18	-0.70	-0.01	NA	0.07	0.02	0.60	6.00	-112.99	239.69	5.98	0.01
2.21	-0.74	-0.01	0.02	NA	0.02	0.60	6.00	-113.51	240.73	7.02	0.01
2.18	-0.70	-0.01	0.03	0.08	0.02	0.61	7.00	-112.82	241.98	8.27	0.00
1.80	NA	NA	NA	0.12	0.25	0.46	4.00	-121.86	252.51	18.80	0.00
1.80	NA	NA	NA	NA	0.27	0.41	3.00	-124.03	254.51	20.81	0.00
1.80	NA	NA	0.03	0.13	0.25	0.46	5.00	-121.74	254.69	20.98	0.00
1.80	NA	0.01	NA	0.12	0.25	0.46	5.00	-121.83	254.85	21.14	0.00
1.80	NA	0.02	NA	NA	0.27	0.41	4.00	-123.97	256.72	23.02	0.00
1.80	NA	NA	0.00	NA	0.27	0.41	4.00	-124.02	256.83	23.13	0.00
1.80	NA	0.02	0.03	0.13	0.25	0.46	6.00	-121.68	257.08	23.37	0.00
1.80	NA	0.02	0.01	NA	0.27	0.41	5.00	-123.96	259.13	25.42	0.00
1.83	NA	NA	NA	0.18	NA	0.15	3.00	-134.27	275.00	41.30	0.00
1.83	NA	0.04	NA	0.17	NA	0.16	4.00	-133.92	276.63	42.92	0.00

1.83	NA	NA			0.02	0.18	NA	0.16	4.00	-134.23	277.25	43.54	0.00
1.83	NA		0.05		0.02	0.18	NA	0.17	5.00	-133.83	278.87	45.16	0.00
1.84	NA	NA		NA		NA	NA	0.00	2.00	-138.96	282.15	48.44	0.00
1.84	NA		0.05	NA		NA	NA	0.02	3.00	-138.51	283.48	49.78	0.00
1.84	NA	NA			-0.01	NA	NA	0.00	3.00	-138.93	284.33	50.62	0.00
1.84	NA		0.05		0.00	NA	NA	0.02	4.00	-138.51	285.80	52.10	0.00

Abbreviations: inter= intercept, cover = cover type oil palm and riparian forest (the intercept), Dist.road (km) and Dist.town (km) = the average nearest distance to roads and towns (respectively), % for = percentage of forest in the 500 m radius buffer, NDVI: Normalized Difference Vegetation Index. Variables were standardized for direct omparison. R^2 = variance explained df =degrees of freedom, , logLik = maximum likelihood function, AICc = Akaike Information Critiria corrected for small samples, Δ AICc: difference in AIC values between each model with the lowest AIC model (best model); AICω: Akaike weight.

Appendix 4. Model selection output comparing all possible combinations for the effect of variables on mammalian species richness within oil palm plantation level.

Inter	can.cov	dis.patch	freq.cattle	height	und.veg	R^2	df	logLik	AICc	Δ AICc	AICω
1.17	NA	NA	-0.23	NA	0.37	0.31	4.00	-58.89	127.21	0.00	0.11
1.42	NA	NA	-0.32	NA	NA	0.24	3.00	-60.45	127.73	0.51	0.09
1.07	NA	NA	NA	NA	0.56	0.24	3.00	-60.54	127.92	0.70	0.08
1.41	NA	NA	-0.29	-0.13	NA	0.29	4.00	-59.32	128.07	0.86	0.07
1.40	NA	-0.14	-0.32	-0.15	NA	0.34	5.00	-58.05	128.32	1.10	0.07
1.41	NA	-0.13	-0.35	NA	NA	0.29	4.00	-59.45	128.33	1.12	0.07
1.21	NA	NA	-0.22	-0.10	0.31	0.33	5.00	-58.30	128.81	1.60	0.05
1.20	NA	-0.10	-0.26	NA	0.32	0.33	5.00	-58.31	128.84	1.62	0.05
1.12	NA	NA	NA	-0.12	0.47	0.27	4.00	-59.76	128.95	1.74	0.05
1.13	0.11	NA	NA	NA	0.45	0.26	4.00	-59.97	129.38	2.16	0.04
1.42	0.07	NA	-0.27	NA	NA	0.25	4.00	-60.22	129.87	2.65	0.03
1.18	0.03	NA	-0.21	NA	0.36	0.31	5.00	-58.87	129.96	2.74	0.03
1.07	NA	-0.06	NA	NA	0.55	0.25	4.00	-60.33	130.08	2.87	0.03
1.24	NA	-0.12	-0.25	-0.12	0.25	0.37	6.00	-57.44	130.10	2.89	0.03
1.41	0.08	-0.13	-0.29	NA	NA	0.30	5.00	-59.16	130.55	3.34	0.02
1.41	0.02	NA	-0.28	-0.13	NA	0.29	5.00	-59.31	130.84	3.63	0.02
1.13	NA	-0.08	NA	-0.13	0.45	0.29	5.00	-59.33	130.88	3.67	0.02
1.43	0.20	NA	NA	NA	NA	0.16	3.00	-62.14	131.10	3.89	0.02
1.15	0.07	NA	NA	-0.09	0.41	0.28	5.00	-59.51	131.23	4.02	0.02
1.40	0.02	-0.14	-0.31	-0.14	NA	0.34	6.00	-58.04	131.31	4.09	0.01
1.15	0.12	-0.08	NA	NA	0.42	0.28	5.00	-59.59	131.40	4.18	0.01
1.21	0.04	-0.10	-0.24	NA	0.30	0.34	6.00	-58.25	131.74	4.53	0.01
1.44	NA	NA	NA	-0.18	NA	0.14	3.00	-62.49	131.80	4.59	0.01
1.20	-0.02	NA	-0.23	-0.10	0.32	0.33	6.00	-58.29	131.80	4.59	0.01
1.43	0.15	NA	NA	-0.13	NA	0.20	4.00	-61.29	132.00	4.79	0.01
1.43	0.22	-0.12	NA	NA	NA	0.19	4.00	-61.44	132.32	5.10	0.01

1.43	0.16	-0.12	NA	-0.14	NA	0.24	5.00	-60.38	132.98	5.77	0.01
1.44	NA	-0.10	NA	-0.20	NA	0.18	4.00	-61.82	133.07	5.85	0.01
1.18	0.09	-0.09	NA	-0.11	0.37	0.31	6.00	-58.98	133.18	5.97	0.01
1.24	-0.01	-0.12	-0.26	-0.13	0.25	0.37	7.00	-57.43	133.34	6.12	0.01
1.45	NA	NA	NA	NA	NA	0.02	2.00	-64.66	133.71	6.50	0.00
1.45	NA	-0.06	NA	NA	NA	0.03	3.00	-64.48	135.78	8.57	0.00

Abbreviations: inter= intercept, can.cov =canopy cover, dis.patch =distance to nearest patch of forest, freq.cattle =frequency of cattle, height = height of palm tree, und.veg = understory vegetation with two categories “clear to low” represented by the intercept and “medium high”.Variables were standardized for direct comparison. R^2 = variance explained df =degrees of freedom, , logLik = maximum likelihood function, AICc = Akaike Information Critiria corrected for small samples, Δ AICc: difference in AIC values between each model with the lowest AIC model (best model); AICω: Akaike weight.

Appendix 5. Model selection output comparing all possible combinations for the effect of variables on mammalian species richness within riparian forest level.

Inter	can.cov	DB	height	trees	R^2	df	logLik	AICc	Δ AICc	AIC
2.22	NA	NA	NA	NA	0.00	2.00	-48.61	101.82	0.00	0.37
2.22	NA	0.05	NA	NA	0.02	3.00	-48.34	103.95	2.13	0.13
2.22	NA	NA	NA	-0.03	0.01	3.00	-48.49	104.25	2.44	0.11
2.27	-0.04	NA	NA	NA	0.00	3.00	-48.57	104.40	2.58	0.10
2.22	NA	NA	0.01	NA	0.00	3.00	-48.61	104.47	2.66	0.10
2.25	NA	0.09	-0.09	NA	0.04	4.00	-48.17	106.56	4.74	0.03
2.28	-0.06	0.05	NA	NA	0.03	4.00	-48.27	106.77	4.96	0.03
2.22	NA	0.05	NA	0.00	0.02	4.00	-48.34	106.91	5.09	0.03
2.25	-0.03	NA	NA	-0.03	0.01	4.00	-48.47	107.17	5.36	0.03
2.22	NA	NA	0.00	-0.03	0.01	4.00	-48.49	107.21	5.39	0.02
2.27	-0.05	NA	0.02	NA	0.00	4.00	-48.55	107.32	5.51	0.02
2.27	-0.03	0.09	-0.08	NA	0.04	5.00	-48.15	109.84	8.02	0.01
2.25	NA	0.10	-0.10	0.01	0.04	5.00	-48.16	109.85	8.03	0.01
2.28	-0.06	0.06	NA	0.01	0.03	5.00	-48.27	110.07	8.25	0.01
2.25	-0.03	NA	0.00	-0.03	0.01	5.00	-48.47	110.48	8.66	0.00
2.28	-0.04	0.10	-0.09	0.02	0.04	6.00	-48.13	113.52	11.70	0.00

Abbreviations: inter= intercept, can.cov =canopy cover, DBH =Diameter at Breast Height, height = tree height, trees = tree abundance. Variables were standardized for direct comparison. R2 = variance explained df =degrees of freedom, logLik = maximum likelihood function, AICc = Akaike Information Critiria corrected for small samples, Δ AICc: difference in AIC values between each model with the lowest AIC model (best model); AICω: Akaike weight.

Appendix 6. Multispecies generalized linear models examining the relationship between composition and individual abundance of medium and large-sized terrestrial mammal species with selected landscape covariates in the Llanos region, Colombia.

	Cover		**Forest (%)**		**Dist.road**		**Dist.town**		**NDVI**	
	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)	Dev	Pr(>Dev)
Multivaraite	282.22	0.001	26.04	0.089	25.27	0.137	34.28	0.021	26.34	0.12
Univariate										
giant ant eater	1.924	0.535	3.279	0.669	0.95	0.968	1.208	0.919	2.028	0.883
lesser ant eater	8.277	0.03	0.278	1	1.566	0.906	3.89	0.58	5.688	0.342
armadillo	31.647	0.001	0.119	1	4.088	0.572	3.293	0.637	2.499	0.846
naked armadillo	11.886	0.012	0.954	0.992	5.626	0.354	1.242	0.919	1.138	0.946
fox	14.752	0.002	0.071	1	0.003	0.995	3.486	0.637	0.774	0.967
jaguarundi	0.278	0.822	0	1	3.326	0.644	0.997	0.919	4.668	0.517
ocelot	24.82	0.001	0.165	1	0.043	0.995	1.708	0.869	0.152	0.982
crab eating raccoon	1.981	0.535	6.835	0.159	0.154	0.994	0.633	0.919	0.284	0.982
white tailed deer	0.38	0.822	0.034	1	2.374	0.8	0.596	0.919	2.125	0.883
spiny rat	34.525	0.001	0.031	1	3.964	0.572	0.561	0.919	1.691	0.897
agouti	46.103	0.001	0.283	1	0.049	0.995	4.284	0.554	0.195	0.982
paca	69.129	0.001	0.171	1	0.309	0.994	2.188	0.825	0.289	0.982
capybara	2.757	0.483	13.518	0.005	0.398	0.994	0.159	0.919	1.835	0.897
squirrel	18.945	0.001	0	1	0.252	0.994	6.018	0.316	0.398	0.979
common oppossum	14.817	0.002	0.298	1	2.171	0.813	4.015	0.576	2.574	0.846

Abbreviations: Land cover type refers to riparian forest and oil palm plantations, forest (%) = percentage of forest in the 500 m radius buffer, Dist.road and Dist.town = the average nearest distance (m) to roads and towns (respectively), NDVI: Normalized Difference Vegetation Index. Variables were standardized for direct comparison. *Dev = Deviance, analysis conducted in R package mvabund– Wang et al. 201

Appendix 7. The relationship between mammal species abundance and selected landscape variables in the Llanos region Colombia. Coefficients are from the saturated model using the multispespecies generalized linear modelling prior to shrinkage with Lasso penalty (R package *mvabund*– Wang et al. 2012). SE is the standard error of the coefficient. For scientific names and details of the species, refer to Table 1 of the manuscript.

	Giant.anteater		**Lesser.anteater**		**Armadillo**		**Naked.T.Armadillo**	
	Coefficient	*SE*	*Coefficient*	*SE*	*Coefficient*	*SE*	*Coefficient*	*SE*
(Intercept)	1.15	0.23	0.19	0.27	0.71	0.35	-1.93	0.69
Land Cover Type (oil palm plantation)	-0.97	0.37	-0.95	0.43	-4.89	1.24	-12.69	156.02
Forest (%)	-0.36	0.19	-0.13	0.21	0.18	0.27	0.37	0.40
Dist. Road (km)	0.08	0.12	-0.23	0.16	-0.60	0.27	-1.26	0.65
Dist. Town (km)	-0.16	0.12	-0.25	0.17	0.25	0.26	-0.32	0.55
NDVI	-0.18	0.12	0.49	0.22	-0.57	0.36	0.79	0.73

	Fox		**Jaguarundi**		**Ocelot**		**Raccoon**	
	Coefficient	*SE*	*Coefficient*	*SE*	*Coefficient*	*SE*	*Coefficient*	*SE*
(Intercept)	-1.33	0.64	-3.19	0.95	0.16	0.31	-1.71	0.90
Land Cover Type (oil palm plantation)	2.29	0.89	0.35	1.45	-3.10	0.85	-1.46	1.51
Forest (%)	-0.11	0.43	-0.30	0.82	-0.11	0.25	-2.33	1.06
Dist. Road (km)	-0.08	0.26	0.52	0.34	-0.06	0.20	-0.04	0.44
Dist. Town (km)	0.45	0.25	-0.37	0.50	-0.32	0.23	0.33	0.38
NDVI	0.24	0.24	1.19	0.72	-0.12	0.30	0.28	0.48

	White.T.Deer		**Spiny.rat**		**Agouti**		**Paca**	
	Coefficient	*SE*	*Coefficient*	*SE*	*Coefficient*	*SE*	*Coefficient*	*SE*
(Intercept)	-1.65	0.58	0.92	0.38	1.88	0.43	2.13	0.30
Land Cover Type (oil palm plantation)	0.21	0.81	-3.95	0.91	-16.66	169.27	-16.98	174.08
Forest (%)	-0.06	0.40	0.03	0.29	0.08	0.33	0.02	0.24
Dist. Road (km)	-0.43	0.34	-0.50	0.25	0.05	0.26	0.19	0.18
Dist. Town (km)	0.29	0.27	-0.04	0.28	0.74	0.32	0.27	0.22
NDVI	0.46	0.34	0.51	0.41	0.22	0.48	-0.23	0.34

	Capybara		**Squirrel**		**Common.oppossum**	
	Coefficient	*SE*	*Coefficient*	*SE*	*Coefficient*	*SE*
(Intercept)	-2.33	0.91	-0.60	0.57	1.45	0.43
Land Cover Type (oil palm plantation)	1.00	1.30	-14.19	159.49	-1.80	0.68
Forest (%)	2.11	0.58	0.14	0.39	0.22	0.32
Dist. Road (km)	0.25	0.38	-0.01	0.28	0.14	0.22
Dist. Town (km)	-0.38	0.42	1.01	0.40	-0.35	0.24

NDVI	-0.60	0.42		0.41	0.63		0.46	0.28	

Abbreviations: Land cover type refers to riparian forest and oil palm plantations, forest (%) = percentage of forest in the 500 m radius buffer, Dist.road (km) and Dist.town (km) = the average nearest distance to roads and towns (respectively), NDVI: Normalized Difference Vegetation Index. Variables were standardized for direct comparison.

Chapter 3

Appendix 8. Taxa specific results from Threshold Indicator Taxa Analysis (TITAN) for 15 terrestrial mammal abundance and occurrence (IndVal) in response to oil palm percentage increment in 56 sites in the llanos region, Colombia. Filter (1 or 2) correspond to those species with purity and reliability above 90% (1 for negative indicators and 2 for positive indicators), value of cero corresponds with species that do not meet these criteria, and hence no evidence for threshold.

	ienv.cp	**zenv.cp**	**freq**	**maxgrp**	**IndVal**	**obsiv.**	**zscore**	**5%**	**10%**	**50%**	**90%**	**95%**	**pur**	**rel**	**z.med**	**filter**
Giant anteater	33.23	41.45	49	1	63.68	0.02	2.31	26.5	39.12	44.95	83.88	89.79	0.80	0.82	2.81	0
Lesser anteater	76.02	76.02	36	1	54.01	0.01	3.16	41.4	43.59	75.54	82.26	83.88	0.97	0.92	3.82	0
Armadillo	54.69	54.69	19	1	49.80	0.00	4.24	38.7	41.94	55.37	81.21	82.26	1.00	0.99	5.50	1
Naked-tailed armadillo	45.04	74.16	9	1	32.14	0.00	4.37	38.8	43.40	58.25	74.64	75.54	1.00	1.00	5.38	1
Fox	45.88	74.16	32	2	62.69	0.01	3.36	45.5	45.88	75.10	81.48	82.84	1.00	0.99	4.40	2
Jaguarundi	91.24	43.59	18	2	34.59	0.05	1.90	43.5	44.17	60.43	92.47	95.37	0.91	0.86	3.08	0
Ocelot	33.23	64.18	28	1	60.11	0.00	5.70	36.2	45.04	62.00	75.56	76.75	1.00	0.99	5.61	1
Crab eating raccoon	89.79	80.29	11	2	35.73	0.00	3.87	38.8	41.69	80.29	89.79	89.79	0.89	0.94	4.55	0

White-tailed deer	81.38	81.38	18	2	27.49	0.18	0.91	36.2	42.61	80.56	89.36	89.79	0.70	0.56	2.17	0
Spiny rat	45.88	45.88	23	1	79.65	0.00	7.78	44.0	45.55	49.78	71.18	75.92	1.00	1.00	8.37	1
Agouti	43.59	45.04	18	1	65.08	0.00	7.83	42.6	42.76	45.04	74.38	75.34	1.00	1.00	8.23	1
Paca	41.85	75.54	24	1	70.56	0.00	8.79	42.8	43.59	58.25	74.16	75.33	1.00	1.00	9.55	1
Capybara	36.24	36.24	11	1	64.98	0.00	7.08	35.6	36.24	43.65	48.28	49.69	1.00	1.00	7.62	1
Squirrel	41.85	44.17	9	1	39.59	0.00	5.72	41.6	41.85	45.88	68.54	71.63	1.00	1.00	6.64	1
Common opossum	45.88	46.75	34	1	82.08	0.00	6.84	44.3	45.55	53.09	59.57	64.18	1.00	1.00	7.15	1

* ienv.cp = environmental change point for each taxon based on IndVal maximum (used if imax = TRUE)
* zenv.cp = environmental change point for each taxon based on z maximum (default, imax = FALSE)
* freq = number of non-zero abundance values per taxon (sites where species is detected max value = 56 sites).
* maxgrp = 1 = z- (negative response); 2= z+ (positive response).
* IndVal = Dufrene & Legendre (1997) IndVal statistic, scaled 0-100%.
* obsiv.prob =pval = (number of random IndVals >= observed IndVal)/ numprm.
* zscore = IndVal z score.
* 5%, 10%, 50%, 90%, 95% = change point quantiles among bootstraps.
* pur=purity = proportion of bootreps matching observed maxgrp assignment.
* rel=reliability = proportion of bootrep pvals <= 0.05.
*z.median—median score magnitude across all bootstrap replicates
* filter—logical (if >0) indicating whether each taxa met purity and reliability criteria, value indicates

For details on how to interpret the parameters refer to Baker and King 2010.

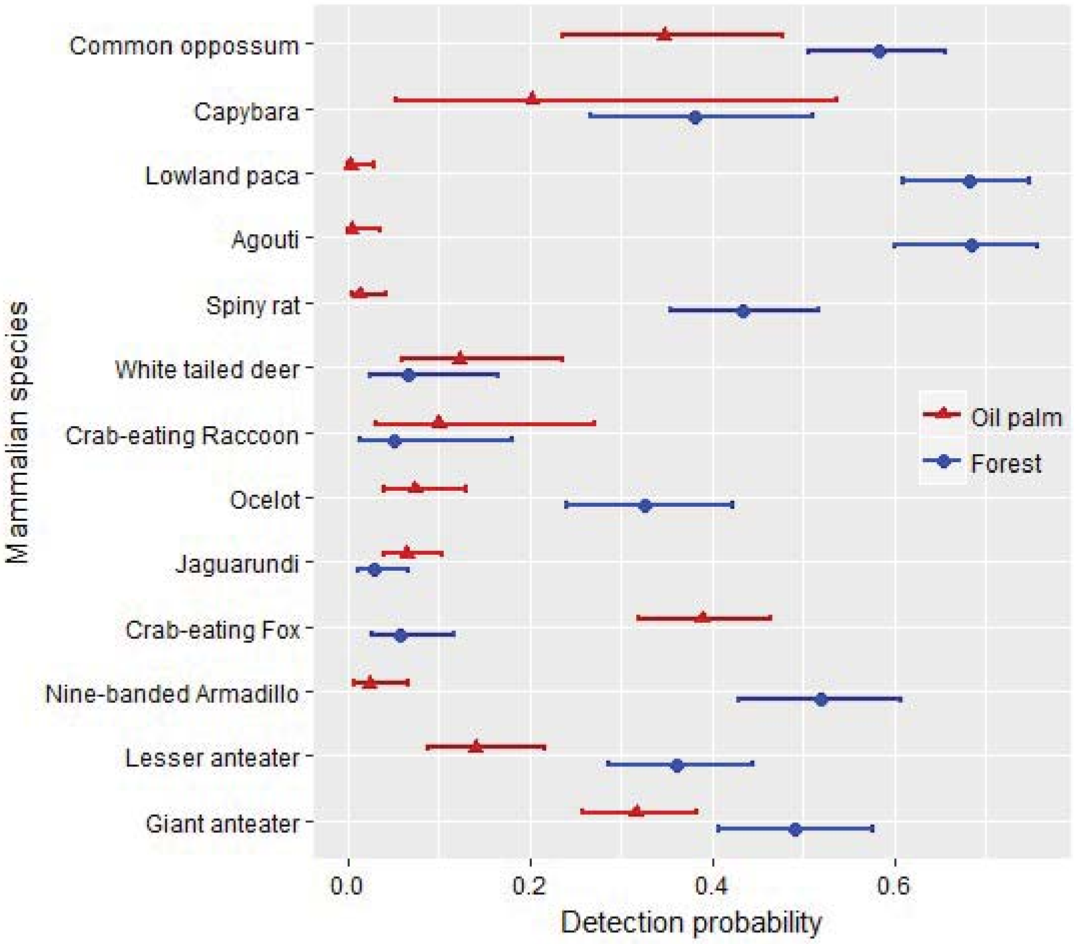
Chapter 4

Appendix 9. Model selection evaluating the effect of habitat type (hab) on habitat use and detection probabilities for selected mammal species*. Habitat type is a binary variable where 0=forest (intercept) and 1= oil palm plantation (β), a negative value of the corresponding β coefficient suggest preference for forest, and vice versa.

Model	AIC	Δ AICc	AIC *w*	*k*	β (SE) Oil palm
Giant anteater					
Ψ (.),p(hab)	526.26	0	0.501	3	
Ψ (hab),p(hab)	526.32	0.06	0.4862	4	2.12 (2.60)
Lesser anteater					
Ψ (hab),p(hab)	391.21	0	0.4979	4	-1.64 (0.97)
Ψ (.),p(hab)	391.32	0.11	0.4713	3	
Armadillo					
Ψ (.),p(hab)	242.34	0	0.6103	3	
Ψ (hab),p(hab)	243.25	0.91	0.3872	4	-2.31 (1.15)
Naked-tailed armadillo					
Ψ (hab),p(.)	110.55	0	0.7612	3	-26.48 (#)
Fox					
Ψ (.),p(hab)	365.87	0	0.9965	3	
Jaguarundi					
Ψ (.),p(.)	170.78	0	0.5548	2	
Ψ (hab),p(.)	171.22	0.44	0.4452	3	27.03 (#)
Ocelot					
Ψ (.),p(.hab)	294.61	0	0.9998	3	
Raccoon					
Ψ (.),p(.)	124.6	0	0.4516	2	
Ψ (.),p(hab)	125.76	1.16	0.2529	3	
White-tailed deer					
Ψ (.),p(.)	190.76	0	0.3984	2	
Ψ (.),p(hab)	191.27	0.51	0.3087	3	
Ψ (hab),p(.)	192.25	1.49	0.1891	3	0.79 (0.95)
Capybara					
Ψ (hab),p(.)	166.95	0	0.5784	3	-1.69 (0.95)
Ψ (hab),p(hab)	168.66	1.71	0.246	4	-1.61 (0.96)
Spiny rat					
Ψ (hab),p(hab)	260.92	0	0.5125	4	-4.20 (1.22)
Ψ (.),p(hab)	261.59	0.67	0.3666	3	
Common opossum					
Ψ (hab),p(hab)	404.11	0	0.969	4	-3.62 (1.10)

Notes: Δ AICc: difference in AIC values between each model with the lowest AIC model (best model); AICω*:* Akaike weight.; k: number of parameters in the model; SE: standard error. Only species with = land cover type, a binary covariate with 0= forest (intercept) and 1= oil palm (beta). # = high standard error, so species-specific occupancy estimates are imprecise. However, direction of the effect is not affected (Hines et al 2006). *Only species with sufficient data to conduct modeling are shown (i.e. at least 4 detections per habitat). For rare species refer to naïve occupancy table 1.

Appendix 10. Detection probability($\hat{p}$)for most common species across oil palm dominated landscapes in Colombian Llanos. Error bars indicate confidence intervals.



Photographic gallery

Species identified by camera trapping or direct observations

Giant anteater (*Myrmecophaga tridactyla*)

Lesser anteater *(Tamandu tetradactyla)*

Nine-banded armadillo *(Dasypus novemcinctus)*

Naked tailed armadillo *(Cabassous unicinctus)*

Crab-eating Fox *(Cerdocyon thous)*

Jaguarundi *(Puma yagouaroundi)*

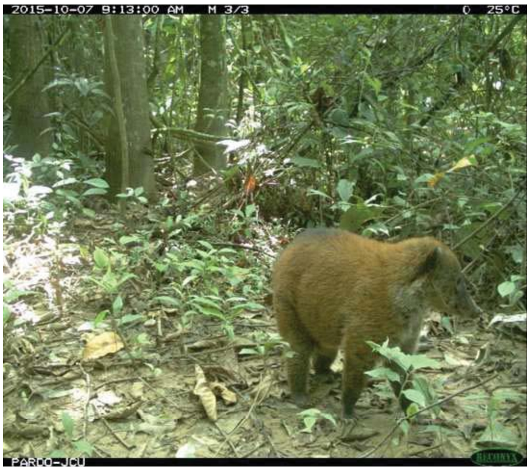
Ocelot *(Leopardus pardalis)*

Puma *(Puma concolor)*

Greater grison *(Galictis vittata)*

Tayra *(Eira Barbara)*

Crab-eating raccoon *(Procyon cancrivorus)*



Coati *(Nasua nasua)*

White tailled deer (*Odocoileus cariacou*)

Red deer (*Mazama* spp)

Collared peccary (*Pecari tajacu*)

Spiny rat (*Proechimis* spp)

Mouse

Agouti (*Dasyprocta fuliginosa*)

Paca *(Cuniculus paca)*

Capybara *(Hydrochaerus hydrochaeris)*

Coendu *(Coendu spp)*

Squirrel *(Sciurus spp)*

Common opossum *(Didelphis marsupialis)*

Four eyed oppossum *(Philander opossum)*

Tufted capuchin *(Sapajus apella)*

Squirrel Monkey *(Saimiri sciureus)*

Night Monkey *(Aotus brumbacki)*

Ornate titi *(Pleturocebus ornatus)*

Tapir *(Tapirus terrestris)**semidomestic

Howler monkey *(Alouatta seniculus)*

Additional information


Installation of camera traps inside the forest


Installation of camera traps inside oil palm


Anaconda accidentally killed after cutting the understory vegetation.


Semi-domestic tapirs found in farm near to an oil palm plantation


Outreach activities showing partial results to some workers in an oil palm plantation


Surveys conducted to workers (Photo Credit Sandra Salamanca)

References

Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans. Automat. Contr. 19, 716–723. https://doi.org/10.1109/TAC.1974.1100705

Akani, G.C., Ebere, N., Luiselli, L., Eniang, E.A., 2007. Community structure and ecology of snakes in fields of oil palm trees (Elaeis guineensis) in the Niger Delta , southern Nigeria 500–506.

Albesiano, S., Rangel-Ch, J.O., 2006. Estructura De La Vegetación Del Canón Del Río Chicamocha, 500-1200 M; Santander- Colombia: Una Herramienta Para La Conservación. Caldasia 28, 307–325.

Aliaga-Rossel, E., Kays, R.W., Fragoso, J.M. V., 2008. Home-range use by the Central American agouti (Dasyprocta punctata) on Barro Colorado Island, Panama. J. Trop. Ecol. 24, 367–374. https://doi.org/10.1017/S0266467408005129

Andrade-Ponce, G.P., Montaño-Salazar, S.M., Riveros-Loaiza, L.M., Ramírez-Cháves, H.E., Suárez-Castro, A.F., 2016. Estado del conocimiento y prioridades de investigación sobre las familias Canidae , Mephitidae y Procyonidae (Mammalia: Carnivora) en Colombia. Rev. Acad. Colomb. Cienc. Ex. Fis. Nat. 40, 500–513.

Andren, H., 1994. Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat : A Review. Oikos 71, 355–366.

Andrén, H., Andren, H., 1994. Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat: A Review. Oikos 71, 355. https://doi.org/10.2307/3545823

Angelstam, P.K., Bütler, R., Lazdinis, M., Mikusinski, G., Roberge, J., 2003. Habitat thresholds for focal species at multiple scales and forest biodiversity conservation — dead wood as an example. Ann. Zool. Fenn. 40, 473–482.

Arias-Alzate, A., Delgado-V, C., Navarro, F., González-Maya, J.F., 2015. Presencia de Puma (Puma concolor) en un paisaje periurbano al sur del Valle de Aburrá, Antioquia, Colombia. Mammal. Notes 2, 24–28.

Ashby, K.R., 1972. Patterns of daily activity in mammals. Mamm. Rev. 1, 171–185. https://doi.org/10.1111/j.1365-2907.1972.tb00088.x

Asner, G.P., Knapp, D.E., Balaji, A., Paez-Acosta, G., 2009. Automated mapping of tropical deforestation and forest degradation: CLASlite. J. Appl. Remote Sens. 3, 33543. https://doi.org/10.1117/1.3223675

Avendaño, T., 2007. El biodiesel de la palma aceitera en Colombia, El Programa de las Américas del IRC. Silver City, New Mexico, USA.

Azhar, B., Lindenmayer, D.B., Wood, J., Fischer, J., Zakaria, M., 2014. Ecological impacts of oil palm agriculture on forest mammals in plantation estates and smallholdings. Biodivers. Conserv. 23, 1175–1191. https://doi.org/10.1007/s10531-014-0656-z

Baker, M.E., King, R.S., 2010. A new method for detecting and interpreting biodiversity and ecological community thresholds. Methods Ecol. Evol. 1, 25–37. https://doi.org/10.1111/j.2041-210X.2009.00007.x

Balme, G., Hunter, L., Robinson, H., 2014. Baited camera-trap surveys - Marginally more precise but at what cost? A response to du Preez et al. (2014). Biol. Conserv. 179, 144–145. https://doi.org/10.1016/j.biocon.2014.09.021

Banks-Leite, C., Pardini, R., Tambosi, L.R., Pearse, W.D., Bueno, A.A., Bruscagin, R.T., Condez, T.H., Dixo, M., Igari, A.T., Martensen, A.C., Metzger, J.P., 2014. Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. Science (80-.). 345, 1041–1045.

Baptiste, B., Pinedo-Vasquez, M., Gutierrez-Velez, V.H., Andrade, G.I., Vieira, P., Estupiñán-Suárez, L.M., Londoño, M.C., Laurance, W., Lee, T.M., 2017. Greening peace in Colombia. Nat. Ecol. Evol. 1, 102. https://doi.org/10.1038/s41559-017-0102

Barton, K., 2009. MuMIn: Multi-Model Inference. R package version 0.12.2/r18.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Softw. 67, 1–48.

Battin, J., 2004. When Good Animals Love Bad Habitats: Ecological Traps and the Conservation of Animal Populations. Conserv. Biol. 18, 1482–1491. https://doi.org/10.1111/j.1523-1739.2004.00417.x

Beca, G., Vancine, M.H., Carvalho, C.S., Pedrosa, F., Alves, R.S.C., Buscariol, D., Peres, C.A., Ribeiro, M.C., Galetti, M., 2017. High mammal species turnover in forest patches immersed in biofuel plantations. Biol. Conserv. 210, 352–359. https://doi.org/10.1016/j.biocon.2017.02.033

Beck-King, H., Helversen, O. von, Beck-King, R., 1999. Home Range, Population Density, and Food

Resources of Agouti paca (Rodentia: Agoutidae) in Costa Rica: A Study Using Alternative Methods1. Biotropica 31, 675–685. https://doi.org/10.1111/j.1744-7429.1999.tb00417.x

Bello, C., Galetti, M., Pizo, M.A., Magnago, L.F.S., Rocha, M.F., Lima, R.A.F., Peres, C.A., Ovaskainen, O., Jordano, P., 2015. Defaunation affects carbon storage in tropical forests. Sci. Adv. 1, 1–11. https://doi.org/10.1126/sciadv.1501105

Benítez-López, A., Alkemade, R., Schipper, A.M., Ingram, D.J., Verweij, P.A., Eikelboom, J.A.J., Huijbregts, M.A.J., 2017. The impact of hunting on tropical mammal and bird populations. Science 356, 180–183. https://doi.org/10.1126/science.aaj1891

Bernard, H., Baking, E.L., Giordano, A.J., Wearn, O.R., Ahmad, A.H., 2014. Terrestrial Mammal Species Richness and Composition in Three Small Forest Patches within an Oil Palm Landscape in Sabah, Malaysian Borneo. Mammal Study 39, 141–154. https://doi.org/10.3106/041.039.0303

Bhagwat, S.A., Willis, K.J., 2008. Agroforestry as a solution to the oil-palm debate. Conserv. Biol. 22, 1368–9. https://doi.org/10.1111/j.1523-1739.2008.01026.x

Biosintesis, 2000. Incentivos económicos perversos para la conservación de la biodiversidad: el caso de la palma africana. Bol. Inf. Inst. Humboldt 21.

Bitetti, M.S. Di, Ferrari, C.A., Angelo, C. De, Blanco, Y. Di, 2008. Differential Responses to Hunting in Two Sympatric Species of Brocket Deer (Mazama americana and M . nana) 40, 636–645.

Blake, J.G., Mosquera, D., Loiselle, B.A., Swing, K., Guerra, J., Romo, D., 2012. Temporal activity patterns of terrestrial mammals in lowland rainforest of Eastern Ecuador. Ecotropica 18, 137–146.

Bochno, E., 2008. Estrategia de desarrollo de Biocombustibles: implicaciones para el sector. Ministerio de Agricultura y Desarrollo Rural (MADR), Bogotá D,C.

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

Bonato, V., Martins, E.G., Machado, G., da-Silva, C.Q., dos Reis, S.F., 2008. Ecology of the Armadillos Cabassous unicinctus and Euphractus sexcinctus (Cingulata: Dasypodidae) in a Brazilian Cerrado. J. Mammal. 89, 168–174. https://doi.org/10.1644/06-MAMM-A-187.1

Boron, V., Payán, E., 2013. Abundancia de carnívoros en el agropaisaje de las plantaciones de palma de aceite del valle medio del río Magdalena, Colombia., in: Castaño-Uribe, C., Gonzalez-Maya, J.F., Zarrate-Charry, D., Ange-Jaramillo, C., Vela-vargas, I.M. (Eds.), Plan de Conservación de Felinos Del Caribe Colombiano: Los Felinos Y Su Papel En La Planificación Regional Integral Basada En Especies Clave. Fundación Herencia Ambiental Caribe, ProCAT Colombia, The Sierra to Sea Institute, Santa Marta, Colombia, p. 233.

Borowik, T., Pettorelli, N., Sönnichsen, L., Jedrzejewska, B., 2013. Normalized difference vegetation index (NDVI) as a predictor of forage availability for ungulates in forest and field habitats. Eur. J. Wildl. Res. 59, 675–682. https://doi.org/10.1007/s10344-013-0720-0

Brannstrom, C., Jepson, W., Filippi, A.M., Redo, D., Xu, Z., Ganesh, S., 2008. Land change in the Brazilian Savanna (Cerrado), 1986-2002: Comparative analysis and implications for land-use policy. Land use policy 25, 579–595. https://doi.org/10.1016/j.landusepol.2007.11.008

Brown, D.D., Montgomery, R.A., Millspaugh, J.J., Jansen, P.A., Garzon-Lopez, C.X., Kays, R., 2014. Selection and spatial arrangement of rest sites within northern tamandua home ranges. J. Zool. 293, 160–170. https://doi.org/10.1111/jzo.12131

Bruner, a G., Gullison, R.E., Rice, R.E., da Fonseca, G. a, 2001. Effectiveness of parks in protecting tropical biodiversity. Science 291, 125–8. https://doi.org/10.1126/science.291.5501.125

Burgas, A., Amit, R., Lopez, B.C., 2014. Do attacks by jaguars Panthera onca and pumas Puma concolor (Carnivora: Felidae) on livestock correlate with species richness and relative abundance of wild prey? Rev. Biol. Trop. 62, 1459–67.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second. ed. Springer, New York.

Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. Behav. Ecol. Sociobiol. 65, 23–35. https://doi.org/10.1007/s00265-010-1029-6

Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E., Boutin, S., 2015. Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. J. Appl. Ecol. https://doi.org/10.1111/1365-2664.12432

Buttler, R.A., Laurance, W.F., 2009. Is oil palm the next emerging threat to the Amazon ? Trop. Conserv. Sci. 2, 1–10.

Caceres-Martínez, C.H., Acevedo Rincón, A.A., González-Maya, J.F., 2016. Terrestrial medium and large-sized mammal’s diversity and activity patterns from Tamá National Natural Park and buffer zone, Colombia. Therya 7, 285–298. https://doi.org/10.12933/therya-16-397

Camargo-Sanabria, A.A., Mendoza, E., 2016. Interactions between terrestrial mammals and the fruits of two neotropical rainforest tree species. Acta Oecologica 73, 45–52. https://doi.org/10.1016/j.actao.2016.02.005

Camargo-Sanabria, A.A., Mendoza, E., Guevara, R., Martinez-Ramos, M., Dirzo, R., 2014a. Experimental defaunation of terrestrial mammalian herbivores alters tropical rainforest understorey diversity. Proc. R. Soc. B Biol. Sci. 282, 20142580–20142580. https://doi.org/10.1098/rspb.2014.2580

Camargo-Sanabria, A.A., Pardo, L.E., López-Arévalo, H., Sanchez-Palomino, P., Caro, C.I., 2014b. Área de acción y movimientos del chigüiro (Hydrochoerus hydrochaeris) en el municipio de Paz de Ariporo, Casanare, Colombia: Algunas consideraciones para su manejo, in: López-Arévalo, H.F., Sánchez-Palomino, P., Montenégro, O. (Eds.), El Chigüiro Hydrochoerus Hydrochaeris En La Orinoquía Colombiana: Ecología, Manejo Sostenible Y Conservación. Biblioteca José Jerónimo Triana No. 25. Instituto de Ciencias Naturales. Universidad Nacional de Colombia, Bogotá D.C., p. 436.

Campbell, A.&, Doswald, N., 2009. The impacts of biofuel production on biodiversity: A review of the current literature.

Campbell, B.M., Beare, D.J., Bennett, E.M., Hall-Spencer, J.M., Ingram, J.S.I., Jaramillo, F., Ortiz, R., Ramankutty, N., Sayer, J.A., Shindell, D., 2017. Agriculture production as a major driver of the earth system exceeding planetary boundaries. Ecol. Soc. 22, 8. https://doi.org/10.5751/ES-09595-220408

Castaño-Uribe, C., 2013. Algunos contextos culturales de la jaguaridad en el Caribe colombiano, in: Castaño-Uribe, C., González-Maya, J.F., Zárrate-Charry, D., Ange-jaramillo, C., Vela-Vargas, M. (Eds.), Plan de Conservación de Felinos Del Caribe Colombiano: Los Felinos Y Su Papel En La Planificación Regional Integral Basada En Especies Clave. Fundación Herencia Ambiental Caribe, ProCAT Colombia, The Sierra to Sea Institute, Santa Marta, Colombia, pp. 107–130.

Castaño-Uribe, C., González-Maya, J.F., Zárrate-Charry, D., Ange-Jaramillo, C., Vela-Vargas, I.M., 2013. Plan de Conservación de Felinos del Caribe colombiano: Los felinos y su papel en la planificación regional integral basada en especies clave., Fundación Herencia Abiental Caribe, ProCAT Colombia, The Sierra to Sea Institute. Fundación Herencia Ambiental Caribe, ProCAT Colombia, The Sierra to Sea Institute, Santa Marta, Colombia.

Castiblanco, C., Etter, A., Aide, T.M., 2013. Oil palm plantations in Colombia: a model of future expansion. Environ. Sci. Policy 27, 172–183. https://doi.org/10.1016/j.envsci.2013.01.003

Ceballos, G., Ehrlich, P.R., 2002. Mammal Population Losses and the Extinction Crisis. Science (80- .). 296, 904–907. https://doi.org/10.1126/science.1069349

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human – induced species losses: entering the sixth mass extinction. Sci. Adv. 1, 1–5. https://doi.org/10.1126/sciadv.1400253

Ceballos, G., Ehrlich, P.R., Dirzo, R., 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines 6089–6096. https://doi.org/10.1073/pnas.1704949114

Ceballos, G., Ehrlich, P.R., Soberón, J., Salazar, I., Fay, J.P., 2005. Global mammal conservation: what must we manage? Science 309, 603–7. https://doi.org/10.1126/science.1114015

Cenipalma, Corpoica, 1999. Evaluación edafoclimática de las tierras del trópico bajo colombiano para el cultivo de la palma de aceite. Centro de Investigación en Palma de Aceite (Cenipalma) and Corporación Colombiana de Investigación Agropecuaria (Corpoica), Bogotá D.C.

Chacón-Pacheco, J., González-Maya, J.F., 2007. Noteworthy record of subsistence hunting and meat consumption of jaguarundi (Puma yagouaroundi) in Colombia. Rev. Mex. Mastozoología Nueva época 3, 10–13.

Chillo, V., Ojeda, R.A., Capmourteres, V., Anand, M., 2016. Functional diversity loss with increasing livestock grazing intensity in drylands: the mechanisms and their consequences depend on the taxa. J. Appl. Ecol. https://doi.org/10.1111/1365-2664.12775

Chinchilla, F.A., 1997. La dieta del jaguar (Panthera onca), el puma (Felis concolor) y el manigordo (Felis pardalis) (Carnivora: Felidae) en el Parque Nacional Corcovado, Costa Rica. Rev. Biol. Trop. 45, 1223–1229.

Clements, G.R., Lynam, A.J., Gaveau, D., Yap, W.L., Lhota, S., Goosem, M., Laurance, S., Laurance, W.F., 2014. Where and how are roads endangering mammals in Southeast Asia's forests? PLoS One 9, 1–25. https://doi.org/10.1371/journal.pone.0115376

Colwell, R.K., 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application published at: http://purl.oclc.org/estimates.

Colwell, R.K., Coddington, J., 1994. Estimating terrestrial biodiversity through extrapolation. Philos.

Trans. R. Soc. London. Ser. B Biol. Sci. 345, 101–118. https://doi.org/10.1098/rstb.1994.0091

Cooney, R., 2004. The Precautionary Principle in Biodiversity Conservation and Natural Resource Management: An issues paper for policy-makers, researchers and practitioners. Gland, Switzerland and Cambridge.

Corporinoquia, 2013. Resolución 500.41-13-1571: Por medio de la cual se modifica la resolución 200.41.11-1130 de Junio 22 de 2011, que define los criterios generales para el desarrollo de proyectos forestales, agricolas y agroindustriales en la jurisdicción de CORPORINOQUI [WWW Document]. URL http://www.corporinoquia.gov.co/index.php/home/normatividad.html (accessed 10.5.14).

Corporinoquia, 2011a. Resolución 200.41-11.1130 Por medio del cual se definen los criterios regionales para el desarrollo de proyectos forestales, agrícolas y agroindustriales en la jurisdicción de CORPORINOQUIA [WWW Document]. URL http://www.corporinoquia.gov.co/index.php/home/normatividad.html (accessed 10.15.16).

Corporinoquia, 2011b. Resolución No 200.41-11-1130.

Cosentino, B.J., Schooley, R.L., Phillips, C.A., 2011. Connectivity of agroecosystems: Dispersal costs can vary among crops. Landsc. Ecol. 26, 371–379. https://doi.org/10.1007/s10980-010-9563-1

Cove, M. V, Spínola, R.M., Jackson, V.L., Sáenz, J.C., Chassot, O., 2013. Integrating occupancy modeling and camera-trap data to estimate medium and large mammal detection and richness in a Central American biological corridor. Trop. Conserv. Sci. 66, 781–795.

Crooks, K.R., Soulé, M., 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400, 563–566. https://doi.org/10.1038/23028

Cruz-Rodríguez, C., González-Maya, J., Rodríguez-Bolaños, A., Cepeda-Mercado, A., Belant, J.L., 2015. Ocelot Leopardus pardalis (Carnivora: Felidae) Spatial Ecology In A Fragmented Landscape Of Columbia. Rev. Mex. Mastozoología Nueva época 5, 17–24.

da Silveira Anacleto, T.C., 2007. Food Habits of Four Armadillo Species in the Cerrado Area, Mato Grosso, Brazil. Zool. Stud. 46, 529–537.

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. Conserv. Biol. 17, 1814–1826. https://doi.org/10.1111/j.1523-

1739.2003.00298.x

Dammert, J.L., 2014. Cambio De Uso De Suelos Por Agricultura a Gran Escala En La Amazonía Andina: El Caso De La Palma Aceitera. USAID-ICAA, Lima.

Danielsen, F., Beukema, H., Burgess, N.D., Parish, F., BrÜhl, C.A., Donald, P.F., Murdiyarso, D., Phalan, B., Reijnders, L., Struebig, M., Fitzherbert, E.B., 2009. Biofuel Plantations on Forested Lands: Double Jeopardy for Biodiversity and Climate. Conserv. Biol. 23, 348–358. https://doi.org/10.1111/j.1523-1739.2008.01096.x

De Arruda, A., Motta-Junior, J.C., 2004. Food habits of two syntopic canids, the maned wolf (Chrysocyon brachyurus) and the crab-eating fox (Cerdocyon thous), in southeastern Brazil. Rev. Chil. Hist. Nat. 77, 5–14.

de Oliveira, T.G., Tortato, M.A., Silveira, L., Kasper, C.B., Mazim, F.D., Lucherini, M., Jácobo, A.T., Soares, J.B.G., Marquez, R. V., Sunquist, M.E., 2010. Ocelot ecology and its effect on the small-felid guild in the lowland Neotropics, in: Macdonald, D.W., Loveridge, A.J. (Eds.), Biology and Conservation of Wild Felids. Oxford University Press, New York, pp. 559–580.

Dent, D.H., Wright, J., 2009. The future of tropical species in secondary forests: A quantitative review. Biol. Conserv. 142, 2833–2843. https://doi.org/10.1016/j.biocon.2009.05.035

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

Di Bitetti, M.S., Paviolo, A., De Angelo, C., 2006. Density, habitat use and activity patterns of ocelots (Leopardus pardalis) in the Atlantic Forest of Misiones, Argentina. J. Zool. 270, 153–163. https://doi.org/10.1111/j.1469-7998.2006.00102.x

Díaz-Pulido, A., Abud, M., Alviz, Á., Arias, A., Aya, C., Benítez, A., Bonilla, A., Botero, S., Bravo, E., Calero, H., Acevedo, M., Duque, J.S., Fernández, C., Forero-Medina, G., Galeano, A., Garcia, S., Goméz, D., Jose, F.G.-M., Hernández, V., Cabrera, A., López-Arévalo, H., López, J.P., Marín, D., Mazabe, E., Monsalve, S., Olarte, G., Pardo, L.E., Payan, E., Pérez, K., Quintana, R., Reyes, A., Rodriguez-Posada, M., Rojano, C., Salazar, E., Solari, S., Soto, C., Stasiukynas, D., Suárez, G., Valderrama, C., Valderrama, S., Valencia-Mazo, D., Valenzuela, L., Vela, M., Zarrate-Charry, D., 2017. Fototrampeo, in: Moreno, L.A., Andrade, G.I., Ruíz-Contreras, L.F. (Eds.), Biodiversidad 2016. Estado Y Tendencias de La Biodiversidad Continental de Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá D.C., Colombia.

Dirzo, R., Miranda, A., 1990. Contemporary neotropical defaunation and forest structure, function, and diversity. A sequel to John Terborgh. Conservation Biology 4: 444-447F1450 4.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. Science 345, 401–6. https://doi.org/10.1126/science.1251817

DNP, 2008. Lineamientos de política para promover la producción sostenible de biocombustibles en Colombia. Conpes 3510.

DNP, 2007. Estrategia para el desarrollo competitivo del sector palmero colombiano. Conpes 3477. Departamento Nacional de Planeación (DNP), Bogotá D.C.

Dotta, G., Verdade, L.M., 2011. Medium to large-sized mammals in agricultural landscapes of south-eastern Brazil. Mammalia 75, 345–352. https://doi.org/10.1515/MAMM.2011.049

Du Preez, B.D., Loveridge, A.J., Macdonald, D.W., 2014. To bait or not to bait: A comparison of camera-trapping methods for estimating leopard Panthera pardus density. Biol. Conserv. 176, 153–161. https://doi.org/10.1016/j.biocon.2014.05.021

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366. https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2

Durant, S.M., 1998. Competition refuges and coexistence: an example from Serengeti carnivores. J. Anim. Ecol. 67, 370–386. https://doi.org/10.1046/j.1365-2656.1998.00202.x

Echeverría-Londoño, S., Newbold, T., Hudson, L.N., Contu, S., Hill, S.L.L., Lysenko, I., Arbeláez-Cortés, E., Armbrecht, I., Boekhout, T., Cabra-García, J., Dominguez-Haydar, Y., Nates-Parra, G., Gutiérrez-Lamus, D.L., Higuera, D., Isaacs-Cubides, P.J., López-Quintero, C.A., Martinez, E., Miranda-Esquivel, D.R., Navarro-Iriarte, L.E., Noriega, J.A., Otavo, S.E., Parra-H, A., Poveda, K., Ramirez-Pinilla, M.P., Rey-Velasco, J.C., Rosselli, L., Smith-Pardo, A.H., Urbina-Cardona, J.N., Purvis, A., 2016. Modelling and projecting the response of local assemblage composition to land use change across Colombia. Divers. Distrib. 1–13. https://doi.org/10.1111/ddi.12478

Edwards, D.P., Hodgson, J.A., Hamer, K.C., Mitchell, S.L., Ahmad, A.H., Cornell, S.J., Wilcove, D.S., 2010a. Wildlife-friendly oil palm plantations fail to protect biodiversity effectively. Conserv. Lett. 3, 236–242. https://doi.org/10.1111/j.1755-263X.2010.00107.x

Edwards, D.P., Hodgson, J. a., Hamer, K.C., Mitchell, S.L., Ahmad, A.H., Cornell, S.J., Wilcove, D.S., 2010b. Wildlife-friendly oil palm plantations fail to protect biodiversity effectively. Conserv. Lett. 3, 236–242. https://doi.org/10.1111/j.1755-263X.2010.00107.x

Eisenberg, J.F., Redford, K.H., 1999. Mammals of the Neotropics: the Central Neotropics. Vol 3. The University of Chicago Press, Chicago.

Elmhagen, B., Rushton, S.P., 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? Ecol. Lett. 10, 197–206. https://doi.org/10.1111/j.1461-0248.2006.01010.x

Emmons, L.H., 1999. Mamíferos de los bosques húmedos de América Tropical. Una guia de campo, 2nd ed. FAN, Santa Cruz, Bolivia.

Estavillo, C., Pardini, R., Da Rocha, P.L.B., 2013. Forest loss and the biodiversity threshold: An evaluation considering species habitat requirements and the use of matrix habitats. PLoS One 8, 1–10. https://doi.org/10.1371/journal.pone.0082369

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet Earth. Science (80-.). 333, 301–306. https://doi.org/10.1126/science.1205106

Etter, A., McAlpine, C., Pullar, D., Possingham, H., 2006. Modelling the conversion of Colombian lowland ecosystems since 1940: drivers, patterns and rates. J. Environ. Manage. 79, 74–87. https://doi.org/10.1016/j.jenvman.2005.05.017

Etter, A., Sarmiento, A., Romero,Milton H., 2011. Land Use Changes(1970-2020) and Carbon Emissions in the Colombian Llanos, in: Hill, M.J., Hanan, N.P. (Eds.), Ecosystem Function in Savannas. Measurements and Modeling at Landscape to Global Scales. New York, pp. 383–402.

Facure, K., Giaretta, A., 1996. Food habits of carnivores in a coastal Atlantic Forest of southeastern Brazil. Mammalia 3, 499–502. https://doi.org/10.1515/mamm-1996-0319

Fahrig, L., 2002. Effect of Habitat Fragmentation on the Extinction Threshold. Ecol. Appl. 12, 346–353. https://doi.org/10.2307/3060946

Fedepalma, 2014. Anuario Estadístico 2014. La agroindustria de la palma de aceite en Colombia y en el mundo: 2009-2013. Fedepalma, Bogotá D.C.

Fedepalma, 2012. Síntesis del Proyecto GEF Conservación de la Biodiversidad en las Zonas de Cultivos de Palma. Fedepalma, Bogotá D.C.

Fedepalma, MMA, SAC, 2002. Guía Ambiental para el subsector de la Agroindustria de la Palma de Aceite. Fedepalma, Ministerio del Medio Ambiente, Sociedad de Agricultores de Colombia, Bogotá D.C.

Ferrer, A., Beltrán, M., Díaz-Pulido, A., Trujillo, F., Mantilla-Meluk, H., Herrera, O., Alfonso, A., Payan, E., 2009. Lista de los mamíferos de la cuenca del río Orinoco. Biota Colomb. 10, 179–207.

Fitzherbert, E.B., Struebig, M.J., Morel, A., Danielsen, F., Brühl, C.A., Donald, P.F., Phalan, B., 2008. How will oil palm expansion affect biodiversity? Trends Ecol. Evol. 23, 538–545. https://doi.org/10.1016/j.tree.2008.06.012

Foster, V.C., Sarmento, P., Sollmann, R., Tôrres, N., Jácomo, A.T.A., Negrões, N., Fonseca, C., Silveira, L., 2013. Jaguar and Puma activity patterns and predator-prey interactions in four brazilian biomes. Biotropica 45, 373–379. https://doi.org/10.1111/btp.12021

Foster, W.A., Snaddon, J.L., Turner, E.C., Fayle, T.M., Cockerill, T.D., Ellwood, M.D.F., Broad, G.R., Chung, A.Y.C., Eggleton, P., Khen, C.V., Yusah, K.M., 2011. Establishing the evidence base for maintaining biodiversity and ecosystem function in the oil palm landscapes of South East Asia. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 366, 3277–91. https://doi.org/10.1098/rstb.2011.0041

Franklin, J.F., Lindenmayer, D.B., 2009. Importance of matrix habitats in maintaining biological diversity. Proc. Natl. Acad. Sci. U. S. A. 106, 349–50. https://doi.org/10.1073/pnas.0812016105

Furumo, P.R., Aide, T.M., 2017. Characterizing commercial oil palm expansion in Latin America: land use change and trade. Environ. Res. Lett. 12, 24008. https://doi.org/10.1088/1748-9326/aa5892

Gallina, S., Bello-Gutierrez, J., 2014. Patrones de actividad del venado cola blanca en el noreste de México. Therya 5, 423–436. https://doi.org/10.12933/therya-14-200

Gallina, S., Mandujano, S., Bello, J., López-Arévalo, H., Weber, M., 2010. White-tailed deer Odocoileus virginianus (Zimmeermann 1780), in: Barbanti, J.M., González, S. (Eds.), Neotropical Cervidology: Biology and Medicine of Latin Amarican Deer. Jaboticabal, Brazil: Funep and Gland, Switzerland: IUCN, Jaboticabal, Brazil, p. 393.

Gallina, S., Pérez-Torres, J., Guzmán-Aguirre, C.C., 2012. Use of the paca, Cuniculus paca (Rodentia: Agoutidae) in the Sierra de Tabasco State Park, Mexico. Rev. Biol. Trop. (Int. J. Trop. Biol 60, 1345–1355.

Gallo, J.A., Abba, A.M., Elizalde, L., Di Nucci, D., Ríos, T.A., Ezquiaga, M.C., 2017. First study on food habits of anteaters, Myrmecophaga tridactyla and Tamandua tetradactyla, at the southern limit of their distribution. Mammalia 81, 601–604. https://doi.org/10.1515/mammalia-2016-0117

Garcia-Ulloa, J., Sloan, S., Pacheco, P., Ghazoul, J., Koh, L.P., 2012. Lowering environmental costs of oil-palm expansion in Colombia. Conserv. Lett. 5, 366–375. https://doi.org/10.1111/j.1755-263X.2012.00254.x

Gardner, T.A., Barlow, J., Chazdon, R., Ewers, R.M., Harvey, C.A., Peres, C.A., Sodhi, N.S., 2009. Prospects for tropical forest biodiversity in a human-modified world. Ecol. Lett. 12, 561–582. https://doi.org/10.1111/j.1461-0248.2009.01294.x

Gardner, T.A., Barlow, J., Sodhi, N.S., Peres, C.A., 2010. A multi-region assessment of tropical forest biodiversity in a human-modified world. Biol. Conserv. 143, 2293–2300. https://doi.org/10.1016/j.biocon.2010.05.017

Garrote, G., 2012. Depredación del jaguar (Panthera onca) sobre el ganado en los Llanos Orientales de Colombia. Mastozoología Neotrop. 19, 139–145.

Gatti, A., Bianchi, R., Rosa, C.R.X., Mendes, S.L., 2006. Diet of two sympatric carnivores, Cerdocyon thous and Procyon cancrivorus, in a restinga area of Espirito Santo State, Brazil. J. Trop. Ecol. 22, 227–230. https://doi.org/10.1017/S0266467405002956

Geraldes, É., Acevedo, H., Freire, F., 2014. Greenhouse gas intensity of palm oil produced in Colombia addressing alternative land use change and fertilization scenarios. Appl. Energy 114, 958–967. https://doi.org/10.1016/j.apenergy.2013.09.010

Gerland, P., Raftery, A.E., Sevčíková, H., Li, N., Gu, D., Spoorenberg, T., Alkema, L., Fosdick, B.K., Chunn, J., Lalic, N., Bay, G., Buettner, T., Heilig, G.K., Wilmoth, J., 2014. World population stabilization unlikely this century. Science 346, 234–7. https://doi.org/10.1126/science.1257469

Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N., Foley, J.A., 2010. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. Proc. Natl. Acad. Sci. 107, 16732–16737. https://doi.org/10.1073/pnas.0910275107

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T. a., Barlow, J., Peres, C. a., Bradshaw, C.J. a., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478, 378–381. https://doi.org/10.1038/nature10425

Gilroy, J.J., Prescott, G.W., Cardenas, J.S., Castañeda, P.G.D.P., Sánchez, A., Rojas-Murcia, L.E., Medina-Uribe, C.A., Haugaasen, T., Edwards, D.P., 2015. Minimizing the biodiversity impact of Neotropical oil palm development. Glob. Chang. Biol. 21, 1531–1540. https://doi.org/10.1111/gcb.12696

Giordano, A.J., 2016. Ecology and status of the jaguarundi Puma yagouaroundi: a synthesis of existing knowledge. Mamm. Rev. 46, 30–43. https://doi.org/10.1111/mam.12051

Goldewijk, K.K., 2001. Estimating global land use change over the past 300 years. Global Biogeochem. Cycles 15, 417–433. https://doi.org/10.1029/1999GB001232

Gómez, B., Montenegro, O., Sánchez-Palomino, P., 2016. Abundance variation of ungulates in two protected areas of the Colombian Guayana estimated with occupancy models. Therya 7, 89–106. https://doi.org/10.12933/therya-16-342

Gómez, H., Wallace, R.B., Ayala, G., Tejada, R., 2005. Dry season activity periods of some Amazonian mammals. Stud. Neotrop. Fauna Environ. 40, 91–95. https://doi.org/10.1080/01650520500129638

Gómez, P., Mosquera, M., Castilla, C., 2005. Oil palm : a sustainable agro-industry in Colombia. OCL 12, 121–124.

Gompper, M.E., Kays, R.W., Ray, J.C., Lapoint, S.D., Bogan, D.A., Cryan, J.R., 2006. A Comparison of Noninvasive Techniques to Survey Carnivore Communities in Northeastern North America. Wildl. Soc. Bull. 34, 1142–1151. https://doi.org/10.2193/0091-7648(2006)34[1142:ACONTT]2.0.CO;2

González-Maya, J.F., Cepeda-Mercado, A., Zárrate-Charry, D., Granados-Peña, R., Pérez-Ascaino, W., González, M., 2013. Conflictos felinos-vida silvestre en el Caribe Colombiano: un estudio de caso en los departamentos del Cesar y La Guajira, in: Castaño-Uribe, C., González-Maya, J.F., Zárrate-Charry, D., Ange-Jaramillo, C., Vela-vargas, I.M. (Eds.), Plan de Conservación de Felinos Del Caribe Colombiano: Los Felinos Y Su Papel En La Planificación Regional Integral Basada En Especies Clave. Fundación Herencia Ambiental Caribe, ProCAT Colombia, The Sierra to Sea Institute, Santa Marta, Colombia, pp. 51–59.

Gonzalez-Maya, J.F., Romero-Rendón, J.F., Zárrate-Charry, D.A., Castaño-Uribe, C., González, M., Víquez-R, L.R., Arias-alzate, A., 2013. Evaluación geográfica y prioridades de conservación de hábitat para felinos en el Caribe colombiano, in: Castaño-Uribe, C., González-Maya, J.F., Zárrate-Charry, D., Ange-Jaramillo, C., Vela-vargas, I.M. (Eds.), Plan de Conservación de Felinos Del Caribe Colombiano: Los Felinos Y Su Papel En La Planificación Regional Integral Basada En Especies Clave. Fundación Herencia Ambiental Caribe, ProCAT Colombia, The Sierra to Sea Institute, Santa Marta, Colombia, p. 232.

González-Maya, J.F., Zárrate-Charry, D., Vela-Vargas, I.. M., Jiménez-Alvarado, J.S., Gómez-Hoyos, D., 2015. Activity patterns of Tayra Eira barbara populations from Costa Rica and Colombia: evidence of seasonal effects Patrones de actividad de poblaciones de la Tayra Eira barbara en Costa Rica y Colombia: evidencia de efectos estacionales. Rev. Biodiverisidad Neotrop. 5, 96–104. https://doi.org/10.18636/REBIONEO2JD20152

Grace, J., José, S.J., Meir, P., Miranda, H.S., Montes, R.A., 2006. Productivity and carbon fluxes of tropical savannas. J. Biogeogr. 33, 387–400. https://doi.org/10.1111/j.1365-2699.2005.01448.x

Green, R.E., Cornell, S.J., Scharlemann, J.P.W., Balmford, A., 2005. Farming and the fate of wild nature. Science 307, 550–5. https://doi.org/10.1126/science.1106049

Grupo Semillas, 2009. Problemática ambiental y rural Misión internacional de verificación sobre la situación ocasionada por los agrocombustibles en Colombia: Palma aceitera y caña de azúcar. Rev. Semillas 40, 75–80.

Halle, S., 2006. Polyphasic Activity Patterns in Small Mammals. Folia Primatol 77, 15–26. https://doi.org/10.1159/000089693

Halle, S., 2000. Ecological relevance of daily activity patterns, in: Halle, S., Stenseth, N.C. (Eds.), Activity Patterns in Small Mammals: An Ecological Approach: Springer, New York, pp. 67–90.

Harding, J.S., Bnfield, E.F., Bolstad, P. V., Helfman, G.S.., Jones III, E.B.D., 1998. Stream biodiversity : The ghost of land use past. Proc. Natl. Acad. Sci. 95, 14843–14847.

Harmsen, B.J., Foster, R.J., Silver, S., Ostro, L., Doncaster, C.P., 2010. Differential use of trails by forest mammals and the implications for camera-trap studies: A case study from Belize. Biotropica 42, 126–133. https://doi.org/10.1111/j.1744-7429.2009.00544.x

Harvey, C.A., Medina, A., Sánchez, D.M., Vílchez, S., Hernández, B., Saenz, J.C., Maes, J.M., Casanoves, F., Sinclair, F.L., 2006. Patterns of animal diversity in different forms of tree cover in agricultural landscapes. Ecol. Appl. 16, 1986–1999.

Herrera, E.A., Macdonald, D.W., 1989. Resource Utilization and Territoriality in Group-Living Capybaras (Hydrochoerus hydrochaeris). J. Anim. Ecol. 58, 667. https://doi.org/10.2307/4855

Hillebrand, H., Bennett, D., Cadotte, Mark, W., 2008. Consequences of Dominance: A Review of Evenness Effects on Local and Regional Ecosystem Processes. Ecology 89, 1510–1520. https://doi.org/10.1890/07-1861.1

Hines, J.E., 2006. Presence-Software to estimate patch occupancy and related parameters.

Hobbs, R.J., Harris, J.A., 2001. Restoration Ecology : Repairing the Earth ' s Ecosystems in the New Millennium. Restor. Ecol. 9, 239–246.

Houston, A.I., Prosser, E., Sans, E., 2012. The cost of disturbance : a waste of time and energy ? Oikos 121, 597–604. https://doi.org/10.1111/j.1600-0706.2011.19594.x

IDEAM, IGAC, IAvH, Invemar, Sinchi, I., IIAP, 2007. Ecosistemas continentales, costeros y marinos de Colombia. ed. Instituto Geográfico Agustín Codazzi (IGAC), Bogotá D.C., Colombia.

Jennings, A.P., Naim, M., Advento, A.D., Aryawan, A.A.K., Ps, S., Caliman, J.P., Verwilghen, A., Veron, G., 2015. Diversity and occupancy of small carnivores within oil palm plantations in central Sumatra, Indonesia. Mammal Res. 60, 181–188. https://doi.org/10.1007/s13364-015-0217-1

Karanth, K.U., Nichols, J.D., 1998. Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79, 2852–2862. https://doi.org/10.1890/0012-9658(1998)079[2852:EOTDII]2.0.CO;2

Kays, R., Kranstauber, B., Jansen, P., Carbone, C., Rowcliffe, M., Fountain, T., Tilak, S., 2009. Camera traps as sensor networks for monitoring animal communities, in: The 34th IEEE Conference on Local Computer Networks, LCN. pp. 811–818. https://doi.org/10.1109/LCN.2009.5355046

Kelly, M.J., 2008. Design, evaluate, refine: camera trap studies for elusive species. Anim. Conserv. 11, 182–184. https://doi.org/10.1111/j.1469-1795.2008.00179.x

Koh, L.P., 2008. Can oil palm plantations be made more hospitable for forest butterflies and birds ? J. Appl. Ecol. 45, 1002–1009. https://doi.org/10.1111/j.1365-2664.2007.0

Koh, L.P., Levang, P., Ghazoul, J., 2009. Designer landscapes for sustainable biofuels. Trends Ecol. Evol. 24, 431–8. https://doi.org/10.1016/j.tree.2009.03.012

Koh, L.P., Wilcove, D.S., 2008. Is oil palm agriculture really destroying tropical biodiversity? Conserv. Lett. 1, 60–64. https://doi.org/10.1111/j.1755-263X.2008.00011.x

Lasso, C.A., B, A.R., Matallana, C.L., Ramírez, W., Señaris, J.C., Díaz-pulido, A., Corzo, G., Giraldo, A., Degwitz, A., Navas, A., Castro, A., Barbarino, A., Machado-alli-, A., Busto, B., Montaña, C., Marrero, C., Brewer-carías, C., Cons-, E., Mijares, F., Che-, F., Romero, G., Hernández, J., Señaris, J.C., Del-, J., Fariñas, J., Pérez, K.E., Pérez, L., Mesa, L., Bernal, M., Merchán, M., Lasso-al-, O.M., Hoogesteijn, R., Antelo, R., Winter, S., Croceta, T., Trujillo, F., 2010. Biodiversidad de la cuenca del Orinoco: bases científicas para la identificación de áreas prioritarias para la conservación y uso sostenible de la biodiversidad. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, WWF Colombia, Fundación Omacha, Fundación La Salle e Instituto de Estudios de la Orinoquia (Universidad Nacional de Colombia), Bogotá.

Laurance, W.F., Carolina Useche, D., Rendeiro, J., Kalka, M., Bradshaw, C.J. a., Sloan, S.P., Laurance, S.G., Campbell, M., Abernethy, K., Alvarez, P., Arroyo-Rodriguez, V., Ashton, P., Benítez-Malvido, J., Blom, A., Bobo, K.S., Cannon, C.H., Cao, M., Carroll, R., Chapman, C., Coates, R., Cords, M., Danielsen, F., De Dijn, B., Dinerstein, E., Donnelly, M. a., Edwards, D., Edwards, F., Farwig, N., Fashing, P., Forget, P.-M., Foster, M., Gale, G., Harris, D., Harrison, R., Hart, J., Karpanty, S., John Kress, W., Krishnaswamy, J., Logsdon, W., Lovett, J., Magnusson, W., Maisels, F., Marshall, A.R., McClearn, D., Mudappa, D., Nielsen, M.R., Pearson, R., Pitman, N., van der Ploeg, J., Plumptre, A., Poulsen, J., Quesada, M., Rainey, H., Robinson, D., Roetgers, C., Rovero, F., Scatena, F., Schulze, C., Sheil, D., Struhsaker, T., Terborgh, J., Thomas, D., Timm, R., Nicolas Urbina-Cardona, J., Vasudevan, K., Joseph Wright, S., Carlos Arias-G., J., Arroyo, L., Ashton, M., Auzel, P., Babaasa, D., Babweteera, F., Baker, P., Banki, O., Bass, M., Bila-Isia, I., Blake, S., Brockelman, W., Brokaw, N., Brühl, C. a., Bunyavejchewin, S., Chao, J.-T., Chave, J., Chellam, R., Clark, C.J., Clavijo, J., Congdon, R., Corlett, R., Dattaraja, H.S., Dave, C., Davies, G., de Mello Beisiegel, B., de Nazaré Paes da Silva, R., Di Fiore, A., Diesmos, A., Dirzo, R., Doran-Sheehy, D., Eaton, M., Emmons, L., Estrada, A., Ewango, C., Fedigan, L., Feer, F., Fruth, B., Giacalone Willis, J., Goodale, U., Goodman, S., Guix, J.C., Guthiga, P., Haber, W., Hamer, K., Herbinger, I., Hill, J., Huang, Z., Fang Sun, I., Ickes, K., Itoh, A., Ivanauskas, N., Jackes, B., Janovec, J., Janzen, D., Jiangming, M., Jin, C., Jones, T., Justiniano, H., Kalko, E., Kasangaki, A., Killeen, T., King, H., Klop, E., Knott, C., Koné, I., Kudavidanage, E., Lahoz da Silva Ribeiro, J., Lattke, J., Laval, R., Lawton, R., Leal, M., Leighton, M., Lentino, M., Leonel, C., Lindsell, J., Ling-Ling, L., Eduard Linsenmair, K., Losos, E., Lugo, A., Lwanga, J., Mack, A.L., Martins, M., Scott McGraw, W., McNab, R., Montag, L., Myers Thompson, J., Nabe-Nielsen, J., Nakagawa, M., Nepal, S., Norconk, M., Novotny, V., O'Donnell, S., Opiang, M., Ouboter, P., Parker, K., Parthasarathy, N., Pisciotta, K., Prawiradilaga, D., Pringle, C., Rajathurai, S., Reichard, U., Reinartz, G., Renton, K., Reynolds, G., Reynolds, V., Riley, E., Rödel, M.-O., Rothman, J., Round, P., Sakai, S., Sanaiotti, T., Savini, T., Schaab, G., Seidensticker, J., Siaka, A., Silman, M.R., Smith, T.B., de Almeida, S.S., Sodhi, N., Stanford, C., Stewart, K., Stokes, E., Stoner, K.E., Sukumar, R., Surbeck, M., Tobler, M., Tscharntke, T., Turkalo, A., Umapathy, G., van Weerd, M., Vega Rivera, J., Venkataraman, M., Venn, L., Verea, C., Volkmer de Castilho, C., Waltert, M., Wang, B., Watts, D., Weber, W., West, P., Whitacre, D., Whitney, K., Wilkie, D., Williams, S., Wright, D.D., Wright, P., Xiankai, L., Yonzon, P., Zamzani, F., 2012. Averting biodiversity collapse in tropical forest protected areas. Nature 489, 290–294. https://doi.org/10.1038/nature11318

Laurance, W.F., Koh, L.P., Butler, R., Sodhi, N.S., Bradshaw, C.J. a, Neidel, J.D., Consunji, H., Mateo Vega, J., 2010. Improving the performance of the Roundtable on Sustainable Palm Oil for nature conservation. Conserv. Biol. 24, 377–81. https://doi.org/10.1111/j.1523-1739.2010.01448.x

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G., Sampaio, E., 2002. Ecosystem Decay of Amazonian Forest Fragments: a 22-Year Investigation. Conserv. Biol. 16, 605–618. https://doi.org/10.1046/j.1523-1739.2002.01025.x

Laurance, W.F., Sayer, J., Cassman, K.G., 2014. Agricultural expansion and its impacts on tropical nature. Trends Ecol. Evol. 29, 107–16. https://doi.org/10.1016/j.tree.2013.12.001

Lavelle, P., Rodríguez, N., Arguello, O., Bernal, J., Botero, C., Chaparro, P., Gómez, Y., Gutiérrez, A., Hurtado, M. del P., Loaiza, S., Pullido, S.X., Rodríguez, E., Sanabria, C., Velásquez, E., Fonte, S.J., 2014. Soil ecosystem services and land use in the rapidly changing orinoco river basin of colombia. Agric. Ecosyst. Environ. 185, 106–117. https://doi.org/10.1016/j.agee.2013.12.020

Lees, A.C., Peres, C.A., 2008. Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. Conserv. Biol. 22, 439–449. https://doi.org/10.1111/j.1523-1739.2007.00870.x

Legendre, P., Legendre, L.F., 2012. Numerical Ecology, third edition. ed. Elsevier, Amssterdam.

Liévano Latorre, L.F., López Arévalo, H.F., 2014. Comunidad De Mamíferos No Voladores En Un Área Periurbana Andina, Cundinamarca, Colombia. Acta Biológica Colomb. 20, 193–202.

https://doi.org/10.15446/abc.v20n2.43477

Lima, S.L., 2002. Putting predators back into behavioral predator–prey interactions. Trends Ecol. Evol. 17, 70–75. https://doi.org/10.1016/S0169-5347(01)02393-X

Lindenmayer, D.B., Fischer, J., Cunningham, R.B., 2005. Native vegetation cover thresholds associated with species responses. Biol. Conserv. 124, 311–316. https://doi.org/10.1016/j.biocon.2005.01.038

Lindenmayer, D.B., Luck, G., 2005. Synthesis: Thresholds in conservation and management. Biol. Conserv. 124, 351–354. https://doi.org/10.1016/j.biocon.2005.01.041

Linkie, M., Guillera-Arroita, G., Smith, J., Ario, A., Bertagnolio, G., Cheong, F., Clements, G.R., Dinata, Y., Duangchantrasiri, S., Fredriksson, G., Gumal, M.T., Horng, L.S., Kawanishi, K., Khakim, F.R., Kinnaird, M.F., Kiswayadi, D., Lubis, A.H., Lynam, A.J., Maryati, Maung, M., Ngoprasert, D., Novarino, W., O'Brien, T.G., Parakkasi, K., Peters, H., Priatna, D., Rayan, D.M., Seuaturien, N., Shwe, N.M., Steinmetz, R., Sugesti, A.M., Sunarto, Sunquist, M.E., Umponjan, M., Wibisono, H.T., Wong, C.C.T., Zulfahmi, 2013. Cryptic mammals caught on camera: Assessing the utility of range wide camera trap data for conserving the endangered Asian tapir. Biol. Conserv. 162, 107–115. https://doi.org/10.1016/j.biocon.2013.03.028

Linkie, M., Ridout, M.S., 2011. Assessing tiger – prey interactions in Sumatran rainforests. J. Zoo 284, 224–229. https://doi.org/10.1111/j.1469-7998.2011.00801.x

Lira-Torres, I., Briones-Salas, M., 2012. Abundancia relativa y patrones de actividad de los mamíferos de los Chimalapas, Oaxaca, Mexico. Acta Zool. Mex. 28, 566–585.

Long, R., Zielinski, W., 2012. Designing Effective Noninvasive Carnivores Surveys, in: Long, R., MacKay, P., Zielinski, W., Ray, J. (Eds.), Noninvasive Survey Methods for Carnivores. Island Press, Washington, pp. 8–44.

López-Ricaurte, L., Edwards, D.P., Romero-Rodríguez, N., Gilroy, J., 2017. Impacts of oil palm expansion on avian biodiversity in a Neotropical natural savanna. Biol. Conserv. 213, 225–233. https://doi.org/10.1016/j.biocon.2017.07.009

Lowry, H., Lill, A., Wong, B.B.M., 2013. Behavioural responses of wildlife to urban environments. Biol. Rev. 88, 537–549. https://doi.org/10.1111/brv.12012

Lynch, J.D., 2015. The role of plantations of the african palm (Elaeis guineensis JacQ.) in the conservation of snakes in Colombia. Caldasia 37, 169–182.

MacKenzie, D., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2006. Occupancy Estimation and Modeling: Inferring patterns and dynamics of species occurrence. Elsevier Academic Press, United States of America. https://doi.org/10.2981/0909-6396(2006)12[450:OEAMIP]2.0.CO;2

MacKenzie, D.I., Bailey, L.L., 2004. Assessing the fit of site-occupancy models. J. Agric. Biol. Environ. Stat. 9, 300–318. https://doi.org/10.1198/108571104X3361

Maddox, T., Priatna, D., Gemita, E., Salampessy, A., 2007. The conservation of tigers and other wildlife in oil palm plantations. ZSL Conservation Report No . 7. The Zoological Society of London, London.

MADR, 2006a. Estrategia de Desarrollo de Biocombustibes: Implicaciones para el sector. Ministerio de Agricultura y Desarrollo Rural (MADR), Bogotá D.C.

MADR, 2006b. Apuesta exportadora agropecuaria 2006-2020. Ministerio de Agricultura y Desarrollo Rural (MADR), Bogotá D.C., Colombia.

Madriñán, L.F., Etter, A., Boxall, G.D., Ortega-Rubio, A., 2007. Tropical alluvial forest fragmentation in the eastern lowlands of Colombia (1939-1997). L. Degrad. Dev. 18, 199–208. https://doi.org/10.1002/ldr.767

MADS, 2014. Resolución 0192 de 2014. Ministerio de Ambiente y Desarrollo Sostenible (MADS), Bogotá D.C., Colombia.

Maffei, L., Noss, A.J., Cuéllar, E., Rumiz, D.I., 2005. Ocelot (Felis pardalis) population densities, activity, and ranging behaviour in the dry forests of eastern Bolivia: data from camera trapping. J. Trop. Ecol. 21, 349–353. https://doi.org/10.1017/S0266467405002397

Magurran, A.E., Henderson, P.A., 2011. Commonnes and rarity, in: Magurran, A.E., McGill, B.J. (Eds.), Biological Diversity: Frontiers in Measurement and Assesment. Oxford University Press, Oxford, pp. 97–105.

Mann, G.K.H., O'Riain, M.J., Parker, D.M., 2015. The road less travelled: assessing variation in mammal detection probabilities with camera traps in a semi-arid biodiversity hotspot. Biodivers. Conserv. 24, 531–545. https://doi.org/10.1007/s10531-014-0834-z

Marin-Burgos, V., Clancy, J.S., Lovett, J.C., 2015. Contesting legitimacy of voluntary sustainability certification schemes: Valuation languages and power asymmetries in the Roundtable on Sustainable Palm Oil in Colombia. Ecol. Econ. 117, 303–313.

https://doi.org/10.1016/j.ecolecon.2014.04.011

MAVDT, 2008. Evaluación ambiental estratégica de políticas, planes y programas de biocombustibles en Colombia con énfasis en biodiversidad. Ministerio de Ambiente, Vivienda y Desarrollo Territorial, Bogotá D.C.

MAVDT, Fedepalma, 2011. Guía ambiental de la agroindustria de la palma de aceite en Colombia. Versión para consulta. Colombia.

MAVDT, IDEAM, MADR, IGAC, Fedepalma, Cenipalma, WWF, IAvH, 2009. Zonas aptas ambientalmente para el cultivo de palma de aceite en Colombia, escala 1:500.000. Instituto Geográfico Agustín Codazzi, Bogotá D.C.

McShea, W.J., Stewart, C., Peterson, L., Erb, P., Stuebing, R., Giman, B., 2009. The importance of secondary forest blocks for terrestrial mammals within an Acacia/secondary forest matrix in Sarawak, Malaysia. Biol. Conserv. 142, 3108–3119. https://doi.org/10.1016/j.biocon.2009.08.009

Meek, P.D., Ballard, G., Claridge, A., Kays, R., Moseby, K., Brien, T.O., Connell, A.O., Sanderson, J., Swann, D.E., Tobler, M., Townsend, S., 2014. Recommended guiding principles for reporting on camera trapping research 23, 2321–2343. https://doi.org/10.1007/s10531-014-0712-8

Meek, P.D., Ballard, G., Claridge, A., Kays, R., Moseby, K., O'Brien, T., O'Connell, A., Sanderson, J., Swann, D.E., Tobler, M., Townsend, S., 2014. Recommended guiding principles for reporting on camera trapping research. Biodivers. Conserv. 23, 2321–2343. https://doi.org/10.1007/s10531-014-0712-8

Mendes-Oliveira, A.C., Peres, C.A., Maués, P.C.R. de A., Oliveira, G.L., Mineiro, I.G.B., de Maria, S.L.S., Lima, R.C.S., 2017. Oil palm monoculture induces drastic erosion of an Amazonian forest mammal fauna. PLoS One 12, e0187650. https://doi.org/10.1371/journal.pone.0187650

Meredith, M., Ridout, M., 2017. Overview of the overlap package 1–9.

Mingorance, F., 2006. " The flow of palm oil Colombia- Belgium / Europe A study from a human rights perspective ."

Mingorance, F., Minelli, F., Le Du, H., 2004. El cultivo de la palma africana en el chocó: legalidad ambiental, territorial y derechos humanos. Human Rights everywhere, Diócesis de Quibdó, Quibdó, Colombia.

Miranda, F., Bertassoni, A., Abba, A.., 2014. Myrmecophaga tridactyla. IUCN Red List Threat. Species e.T14224A4.

Mittermeier, R., Robles, P., Gorttsch, M.., 1997. Megadiversidad: Los paises biológicamente más ricos del mundo. CEMEX, México.

Montaño, N.A., 2008. La palma africana en el pacífico colombiano: su ilegalidad, consecuencias y violación de derechos territoriales. Rev. Luna Azul 113–126.

Monterroso, P., Alves, P.C., Ferreras, P., 2014. Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe : implications for species coexistence. Behav. Ecol. Sociobiol. 68, 1403–1417. https://doi.org/10.1007/s00265-014-1748-1

Mourao, G., Medri, M., 2007. Activity of a specialized insectivorous mammal (Myrmecophaga tridactyla) in the Pantanal of Brazil. J. Zool. 271, 187–192. https://doi.org/10.1111/j.1469-7998.2006.00198.x

Muggeo, V.M.R., 2016. Testing with a nuisance parameter present only under the alternative: a score-based approach with application to segmented modelling. J. Stat. Comput. Simul. 86, 3059–3067. https://doi.org/10.1080/00949655.2016.1149855

Muggeo, V.M.R., 2008. segmented: An R package to Fit Regression Models with Broken-Line Relationships. R News 8, 20–25. https://doi.org/10.1159/000323281

Muggeo, V.M.R., 2003. Estimating regression models with unknown break-points. Stat. Med. 22, 3055–3071. https://doi.org/10.1002/sim.1545

Muhly, T.B., Hebblewhite, M., Paton, D., Pitt, J.A., Boyce, M.S., Musiani, M., 2013. Humans Strengthen Bottom-Up Effects and Weaken Trophic Cascades in a Terrestrial Food Web. PLoS One 8, e64311. https://doi.org/10.1371/journal.pone.0064311

Muñoz, J., Betancur, O., Duque, M., 2002. Patrones de hábitat y de actividad nocturna de Agouti paca en el Parque Nacional Natural Utría (Chocó, Colombia). Actual. Biológicas 24, 75–85.

Muylaert, R.L., Stevens, R.D., Ribeiro, M.C., 2016. Threshold effect of habitat loss on bat richness in cerrado-forest landscapes. Ecol. Appl. 26, 1854–1867. https://doi.org/10.1890/15-1757.1

Myers, N., Mittermeier, R. a, Mittermeier, C.G., da Fonseca, G. a, Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–8. https://doi.org/10.1038/35002501

Nagy-reis, M.B., Estevo, A., Nagy-reis, M.B., Nichols, J.D., 2017. When habitat matters : Habitat preferences can modulate co-occurrence patterns of similar sympatric species When habitat matters : Habitat preferences can modulate co-occurrence patterns of similar sympatric species. https://doi.org/10.1371/journal.pone.0179489

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50. https://doi.org/10.1038/nature14324

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, 1–6. https://doi.org/10.1371/journal.pone.0068025

Norris, D., Michalski, F., Peres, C.A., 2010. Habitat patch size modulates terrestrial mammal activity patterns in Amazonian forest fragments. J. Mammal. 91, 551–560. https://doi.org/10.1644/09-MAMM-A-199.1

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

Noss, R.F., Quigley, H.B., Hornocker, M.G., Merrill, T., Paquet, P.C., 1996. Conservation Biology and Carnivore Conservation in the Rocky Mountains. Conserv. Biol. 10, 949–963. https://doi.org/10.1046/j.1523-1739.1996.10040949.x

O'Brien, T.G., 2011. Abundance, density and relative abundance: A conceptual framework, in: O'Connell, A.., Nichols, J.D., Karanth, K.U. (Eds.), Camera Traps in Animal Ecology: Methods and Analyses. Springer, New York, pp. 71–96. https://doi.org/10.1007/978-4-431-99495-4_6

O'Brien, T.G., Kinnaird, M.F., Wibisono, H.T., 2003. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Anim. Conserv. 6, 131–139. https://doi.org/10.1017/S1367943003003172

O'Connell, A.F., Nichols, J.D., Ullas, K. (Eds.), 2011. Camera Traps in Animal Ecology: Methods and Analyses. Springer, New York.

Ochoa-Quintero, J.M., Gardner, T.A., Rosa, I., de Barros Ferraz, S.F., Sutherland, W.J., 2015. Thresholds of species loss in Amazonian deforestation frontier landscapes. Conserv. Biol. 29, 440–451. https://doi.org/10.1111/cobi.12446

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, H., Szoecs, E., Wagner, H., 2017. Vegan: Community Ecology Package. R package version 2.4-3.

Olarte-González, G., Escovar-Fadul, T., 2015. First record of Puma concolor Linneus , 1771 (Carnivora : Felidae) preying Odocoileus virginianus (Zimmermann , 1780) on a palm-oil plantation in the Meta department , Colombia. Mammal. Notes 2, 8–10.

Olarte, J., Carrillo, M., 2007. Inventario de Flora y Fauna Asociada a cultivos de palma aceitera (Elaeis guineensis) en la plantación de Indupalma, San Alberto-Cesar. Bogotá D.C.

Oliveira-Santos, L.G.R., Tortato, M.A., Graipel, M.E., 2008. Activity pattern of Atlantic Forest small arboreal mammals as revealed by camera traps. J. Trop. Ecol. 24, 563–567. https://doi.org/10.1017/S0266467408005324

Oliver, T.H., 2016. How much biodiversity loss is too much? Science (80-.). 353, 220–221. https://doi.org/10.1126/science.aag1712

Ospina, M., Ochoa, D., 1998. La palma africana en Colombia: apuntes y memorias, Vol 2. ed. Fedepalma, Bogotá D.C., Colombia.

Ostrom, E., 2007. A diagnostic approach for going beyond panaceas. Proc. Natl. Acad. Sci. U. S. A. 104, 15181–7. https://doi.org/10.1073/pnas.0702288104

Paine, R.T., 1980. Food Webs: Linkage, Interaction Strength and Community Infrastructure. J. Anim. Ecol. 49, 667–685.

Palacios, P., 2012. Forced Displacement: Legal Versus Illegal Crops. Def. Peace Econ. 23, 133–160. https://doi.org/10.1080/10242694.2011.597238

Pardini, R., de Bueno, A.A., Gardner, T.A., Prado, P.I., Metzger, J.P., 2010. Beyond the fragmentation threshold hypothesis: Regime shifts in biodiversity across fragmented landscapes. PLoS One 5. https://doi.org/10.1371/journal.pone.0013666

Pardini, R., de Souza, S.M., Braga-Neto, R., Metzger, J.P., 2005. The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. Biol. Conserv. 124, 253–266.

https://doi.org/10.1016/j.biocon.2005.01.033

Pardo, L.E., Antelo, R., Amezquita, A., Soto, C., Payán, E., 2013. Vertebrados de Altamira. Un informe para lograr la coexistencia de grandes vertebrados en el agropaisaje llanero. Fundación Panthera, Fundación Palmarito, Bogotá D.C.

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, e0197539. https://doi.org/10.1371/journal.pone.0197539

Pardo, L.E., Clements, G.R., Edwards, W., Rojas-Rojas, A. V., Laurance, W.F., 2017. Registros de puma (Puma concolor Linnaeus, 1771) en zona rural de San Carlos de Guaroa, Meta, Colombia. Rev. Biodivers. Neotrop. 7, 108–113. https://doi.org/10.18636/BIONEOTROPICAL.V7I2.490.G625

Pardo, L.E., Cove, M. V., Spinola, R.M., de la Cruz, J.C., Saenz, J.C., 2016. Assessing species traits and landscape relationships of the mammalian carnivore community in a neotropical biological corridor. Biodivers. Conserv. 25, 739–752. https://doi.org/10.1007/s10531-016-1089-7

Pardo, L.E., Laurance, W.F., Clements, G.R., Edwards, W., 2015. The impacts of oil palm agriculture on Colombia's biodiversity: what we know and still need to know. Trop. Conserv. Sci. 88, 828–845.

Pardo, L.E., Payán, E., 2015. Mamíferos de un agropaisaje de palma de aceite en las sabanas inundables de Orocué, Casanare, Colombia. Biota Colomb. 16, 54–66.

Pease, B.S., Nielsen, C.K., Holzmueller, E.J., 2016. Single-camera trap survey designs miss detections: Impacts on estimates of occupancy and community metrics. PLoS One 11, 1–14. https://doi.org/10.1371/journal.pone.0166689

Peh, K.S.-H., Sodhi, N.S., de Jong, J., Sekercioglu, C.H., Yap, C. a.-M., Lim, S.L.-H., 2006. Conservation value of degraded habitats for forest birds in southern Peninsular Malaysia. Divers. Distrib. 12, 572–581. https://doi.org/10.1111/j.1366-9516.2006.00257.x

Pereira, P., Alves da Silva, A., Alves, J., Matos, M., Fonseca, C., 2012. Coexistence of carnivores in a heterogeneous landscape: Habitat selection and ecological niches. Ecol. Res. 27, 745–753. https://doi.org/10.1007/s11284-012-0949-1

Pérez-Rincón, A., 2003. Los agrocombustibles: ¿Solo canto de sirenas? Análisis de los impactos ambientales y sociales para el caso colombiano, in: Agrocombustibles: Llenando Tanques Y

Vaciando Territorios. CENSAT-Agua Viva. Editorial Bochica, Bogotá D.C., pp. 81–116.

Perfecto, I., Vandermeer, J., 2008. Biodiversity Conservation in Tropical Agroecosystems. Ann. N. Y. Acad. Sci. 1134, 173–200. https://doi.org/10.1196/annals.1439.011

Perfetti, M., Ricardo, H., Ortiz, O., Zárate, C., Muñoz, J., Arango, P., 2003. Impactos socioeconómicos de la agroindustria de la palma de aceite en Colombia., in: Informe CRECE. pp. 1–120.

Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.M., Tucker, C.J., Stenseth, N.C., 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends Ecol. Evol. 20, 503–510. https://doi.org/10.1016/j.tree.2005.05.011

Pineda-Guerrero, A., González-Maya, J.F., Pérez-Torres, J., 2015. Conservation value of forest fragments for medium-sized carnivores in a silvopastoral system in Colombia. Mammalia 79, 115–119. https://doi.org/10.1515/mammalia-2013-0050

Polisar, J., Maxit, I., Scognamillo, D., Farrell, L., Sunquist, M.E., Eisenberg, J.F., 2003. Jaguars, pumas, their prey base, and cattle ranching: Ecological interpretations of a management problem. Biol. Conserv. 109, 297–310. https://doi.org/10.1016/S0006-3207(02)00157-X

Prescott, G.W., Edwards, D.P., Foster, W.A., 2015. Retaining biodiversity in intensive farmland: Epiphyte removal in oil palm plantations does not affect yield. Ecol. Evol. 5, 1944–1954. https://doi.org/10.1002/ece3.1462

Prescott, G.W., Gilroy, J.J., Haugaasen, T., Medina-Uribe, C.A., Foster, W.A., Edwards, D.P., 2016. Reducing the impacts of Neotropical oil palm development on functional diversity. Biol. Conserv. 197, 139–145. https://doi.org/10.1016/j.biocon.2016.02.013

Presley, S.J., Willig, M.R., Castro-Arellano, I., Weaver, S.C., 2009. Effects of Habitat Conversion on Temporal Activity Patterns of Phyllostomid Bats in Lowland Amazonian Rain Forest. J. Mammal. 90, 210–221. https://doi.org/10.1644/08-MAMM-A-089.1

Prugh, L.R., Hodges, K.E., Sinclair, A.R.E., Brashares, J.S., 2008. Effect of habitat area and isolation on fragmented animal populations. Proc. Natl. Acad. Sci. U. S. A. 105, 20770–5. https://doi.org/10.1073/pnas.0806080105

Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S., Brashares, J.S., 2009. The Rise of the Mesopredator. Bioscience 59, 779–791. https://doi.org/10.1525/bio.2009.59.9.9

QGIS Development Team, 2016. QGIS Geographic Information System. Open Source Geospatial Foundation.

Quinn, G.P., J.Keough, M., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, New York.

Quiroga, V.A., Noss, A.J., Boaglio, G.I., Di Bitetti, M.S., 2016. Local and continental determinants of giant anteater (Myrmecophaga tridactyla) abundance: biome, human and jaguar roles in population regulation. Mamm. Biol. 81, 274–280. https://doi.org/10.1016/j.mambio.2016.03.002

R Development Core Team, 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Viena, Austria.

Rajaratnam, R., Sunquist, M., Rajaratnam, L., Ambu, L., 2007. Diet and habitat selection of the leopard cat (Prionailurus bengalensis borneoensis) in an agricultural landscape in Sabah, Malaysian Borneo. J. Trop. Ecol. 23, 209. https://doi.org/10.1017/S0266467406003841

Ramírez-Cháves, H., Suárez-Castro, A., González-Maya, J.F., 2016. Cambios recientes a la lista de los mamíferos de Colombia. Notas Mastozoológicas 3, 1–20.

Ramírez-Mejía, A.F., Sánchez, F., 2016. Activity patterns and habitat use of mammals in an Andean forest and a Eucalyptus reforestation in Colombia. Hystrix, Ital. J. Mammal. 27. https://doi.org/10.4404/hystrix-27.2-11319

Rands, M.R.W., Adams, W.M., Bennun, L., Butchart, S.H.M., Clements, A., Coomes, D., Entwistle, A., Hodge, I., Kapos, V., Scharlemann, J.P.W., Sutherland, W.J., Vira, B., 2010. Biodiversity conservation: challenges beyond 2010. Science 329, 1298–303. https://doi.org/10.1126/science.1189138

Rangel-Ch, J.O., Lozano-C., 1986. Un perfil de vegetación entre la plata (Huila) y el volcan Puracé. Caldasia 14, 503–547.

Rangel, T.F., Diniz-Filho, J.A.F., Bini, L.M., 2010. SAM: A comprehensive application for Spatial Analysis in Macroecology. Ecography (Cop.). 33, 46–50. https://doi.org/10.1111/j.1600-0587.2009.06299.x

Ridout, M.S., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. J. Agric. Biol. Environ. Stat. 14, 322–337. https://doi.org/10.1198/jabes.2009.08038

Ritchie, E.G., Johnson, C.N., 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecol. Lett. 12, 982–998. https://doi.org/10.1111/j.1461-0248.2009.01347.x

Rocha-Mendes, F., Mikich, S.B., Quadros, J., Pedro, W.A., 2010. Feeding ecology of carnivores (Mammalia, Carnivora) in Atlantic Forest remnants, Southern Brazil. Biota Neotrop. 10, 21–30. https://doi.org/10.1590/S1676-06032010000400001

Rodríguez-Becerra, M., 2007. Desempeño ambiental del sector palmero en Colombia. Palmas 28, 208–213.

Rodriguez-Becerra, M., van Hoof, B., 2004. El desempeño ambiental del sector palmero colombiano: Evaluación y perspectivas. Fedepalma, Bogotá D.C.

Rodriguez-Becerra, M., van Hoof, B., 2003. El desempeño ambiental del sector palmicultor colombiano: una década de avances y un futuro promisorio. Palmas 24, 69–86.

Rodríguez-Mahecha, J.V., Landazábal Mendoza, C., Nash, S.D., Conservación Internacional Colombia., Colombia. Ministerio de Ambiente, V. y D.T., 2006. Libro rojo de los mamíferos de Colombia. Conservación Internacional Colombia, Bogotá :

Rodríguez, D., 2010. Caracterizaciones biológicas en la Hacienda Macondo (Mapiripán, Meta). Rev. Orinoquia 14, 18–27.

Rojano, C., López, M.E., Miranda-Cortés, L., Ávila, R., 2015a. Área de vida y uso de hábitats de dos individuos de oso palmero (Myrmecophaga tridactyla) en Pore , Casanare , Colombia. Edentata 16, 37–45.

Rojano, C., Padilla, H., Giraldo, A., Álvarez, G., Ramos, E., 2015b. Registro de presencia del oso palmero (Myrmecophaga tridactyla) en plantaciones forestales comerciales en Colombia. Edentata 16, 1–6.

Roldan, P.A., Poveda, G., 2006. Variedad espacio-temporal de los indices NDVI y EVI. Aplicación a cinco regiones colombianas. Meteorol. Colomb. 10, 47–59.

Romero-Ruiz, M.H., Flantua, S.G., Tansey, K., Berrio, J.C., 2012. Landscape transformations in savannas of northern South America: Land use/cover changes since 1987 in the Llanos Orientales of Colombia. Appl. Geogr. 32, 766–776. https://doi.org/10.1016/j.apgeog.2011.08.010

Roque, F. de O., Menezes, J.F.S., Northfield, T., Ochoa-Quintero, J.M., Campbell, M.J., Laurance, W.F., 2018. Warning signals of biodiversity collapse across gradients of tropical forest loss. Sci. Rep. 8, 1622. https://doi.org/10.1038/s41598-018-19985-9

Roque, F. de O., Ochoa-Quintero, J., Ribeiro, D.B., Sugai, L.S.M., Costa-Pereira, R., Lourival, R., Bino, G., 2016. Upland habitat loss as a threat to Pantanal wetlands. Conserv. Biol. 30, 1131–1134. https://doi.org/10.1111/cobi.12713

Rovero, F., Owen, N., Jones, T., Canteri, E., Iemma, A., Tattoni, C., 2017. Camera trapping surveys of forest mammal communities in the Eastern Arc Mountains reveal generalized habitat and human disturbance responses. Biodivers. Conserv. 26, 1103–1119. https://doi.org/10.1007/s10531-016-1288-2

Rovero, F., Zimmermann, F., Berzi, D., Meek, P., 2013. "Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. Hystrix 24. https://doi.org/10.4404/hystrix-24.2-6316

Salinas-Abdala, Y., 2008. Expansión de la Palma. KAS Pap. 1–21.

Samia, D.S.M., Nakagawa, S., Nomura, F., Rangel, T.F., Blumstein, D.T., 2015. Increased tolerance to humans among disturbed wildlife. Nat. Commun. 6, 8877. https://doi.org/10.1038/ncomms9877

Sanabria, C., Lavelle, P., Fonte, S.J., 2014. Ants as indicators of soil-based ecosystem services in agroecosystems of the Colombian Llanos. Appl. Soil Ecol. 84, 24–30. https://doi.org/10.1016/j.apsoil.2014.07.001

Sandoval-Gómez, V.E., Ramírez-Cháves, H.E., Marin, D., 2012. Registros de hormigas y termitas presentes en la dieta de osos hormigueros (Mammalia : Myrmecophagidae) en tres localidades de Colombia. Edentata 13, 1–9.

Sayer, J., Ghazoul, J., Nelson, P., Klintuni Boedhihartono, A., 2012. Oil palm expansion transforms tropical landscapes and livelihoods. Glob. Food Sec. 1, 114–119. https://doi.org/10.1016/j.gfs.2012.10.003

Sayer, J., Sunderland, T., Ghazoul, J., Pfund, J.-L., Sheil, D., Meijaard, E., Venter, M., Boedhihartono, A.K., Day, M., Garcia, C., van Oosten, C., Buck, L.E., 2013. Ten principles for a landscape approach to reconciling agriculture, conservation, and other competing land uses. Proc. Natl. Acad. Sci. U. S. A. 110, 8349–56. https://doi.org/10.1073/pnas.1210595110

Schwenk, W.S., Donovan, T.M., 2011. A Multispecies Framework for Landscape Conservation Planning. Conserv. Biol. 25, 1010–1021. https://doi.org/10.1111/j.1523-1739.2011.01723.x

Scognamillo, D., Maxit, I.E., Sunquist, M., Polisar, J., 2003. Coexistence of jaguar and puma in a mosaic landscape in the Venezuelan Ilanos. J.Zool., Lond. 259, 269–279.

Scotson, L., Johnston, L.R., Iannarilli, F., Wearn, O.R., Mohd-azlan, J., Wong, W.M., Gray, T.N.E., Dinata, Y., Suzuki, A., Willard, C.E., Frechette, J., Loken, B., Steinmetz, R., Moßbrucker, A.M., 2017. Best practices and software for the management and sharing of camera trap data for small and large scales studies 1–15. https://doi.org/10.1002/rse2.54

Seeboldt, S., Salinas, Y., 2010. Responsabilidad y sostenibilidad de la industria de la palma: Son factibles los principios y criterios de la RSPO en Colombia? Oxfam Novib, INDEPAZ, Bogotá D.C.

Si, X., Kays, R., Ding, P., 2014. How long is enough to detect terrestrial animals? Estimating the minimum trapping effort on camera traps. PeerJ 2, e374. https://doi.org/10.7717/peerj.374

Sih, A., Ferrari, M.C.O., Harris, D.J., 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evol. Appl. 4, 367–387. https://doi.org/10.1111/j.1752-4571.2010.00166.x

Sikes, R.S., Heidt, G.A., Elrod, D.A., 1990. Seasonal Diets of the Nine-banded Armadillo (Dasypus novemcinctus) in a Northern Part of Its Range. Am. Midl. Nat. 123, 383–389. https://doi.org/10.2307/2426566

Silveira, L., Jácomo, A.T.A., Diniz-Filho, J.A.F., 2003. Camera trap, line transect census and track surveys: A comparative evaluation. Biol. Conserv. 114, 351–355. https://doi.org/10.1016/S0006-3207(03)00063-6

Silver, S.C., Ostro, L.E.T., Marsh, L.K., Maffei, L., Noss, A.J., Kelly, M.J., Wallace, R.B., Gómez, H., Ayala, G., 2004. The use of camera traps for estimating jaguar Panthera onca abundance and density using capture/recapture analysis. Oryx 38, 148–154. https://doi.org/10.1017/S0030605304000286

SISPA, 2012. Sistema de Información Estadística del Sector PalmeroTitle. http://sispa.fedepalma.org/.

Sloan, S., Jenkins, C.N., Joppa, L.N., Gaveau, D.L.A., Laurance, W.F., 2014. Remaining natural vegetation in the global biodiversity hotspots. Biol. Conserv. 177, 12–24. https://doi.org/10.1016/j.biocon.2014.05.027

Smythe, N., 1991. Dasyprocta punctata and Agouti paca (Guatusa, Cherenga, Agouti, Tepezcuintle, Paca), in: Janzen, D. (Ed.), Historia Natural de Costa Rica. Editorial de la Universidad de Costa

Rica. San José, Costa Rica, San Jose, Costa Rica, pp. 463–465.

Sollmann, R., Betsch, J., Furtado, M.M., Hofer, H., Jácomo, A.T.A., Palomares, F., Roques, S., Tôrres, N.M., Vynne, C., Silveira, L., 2013. Note on the diet of the jaguar in central Brazil. Eur. J. Wildl. Res. 59, 445–448. https://doi.org/10.1007/s10344-013-0708-9

Srbek-Araujo, A.C., Chiarello, A.G., 2013. Influence of camera-trap sampling design on mammal species capture rates and community structures in southeastern Brazil. Biota Neotrop. 13, 51–62. https://doi.org/10.1590/S1676-06032013000200005

Suding, K.N., Hobbs, R.J., 2009. Threshold models in restoration and conservation: a developing framework. Trends Ecol. Evol. 24, 271–279. https://doi.org/10.1016/j.tree.2008.11.012

Tan, C.K.W., Rocha, D.G., Clements, G.R., Brenes-Mora, E., Hedges, L., Kawanishi, K., Mohamad, S.W., Mark Rayan, D., Bolongon, G., Moore, J., Wadey, J., Campos-Arceiz, A., Macdonald, D.W., 2017. Habitat use and predicted range for the mainland clouded leopard Neofelis nebulosa in Peninsular Malaysia. Biol. Conserv. 206, 65–74. https://doi.org/10.1016/J.BIOCON.2016.12.012

Team Network, 2008. Terrestrial Vertebrate Protocol Implementation Manual, v. 3.0. Tropical Ecology, Assessment and Monitoring Network, Center for Applied Biodiversity Science, Conservation International, Arlington, USA.

Terborgh, J., 1988. The Big Things that Run The World-A Sequel to E. O. Wilson. Conserv. Biol. 2, 402–403.

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. 31, 79–92. https://doi.org/10.1046/j.0305-0270.2003.00994.x

Tobler, M., Carrillo-percastegui, S.E., Powell, G., 2009. Habitat use , activity patterns and use of mineral licks by five species of ungulate in south-eastern Peru. J. Trop. Ecol. 25, 261–260. https://doi.org/10.1017/S0266467409005896

Tobler, M.W., Carrillo-Percastegui, S.E., Leite Pitman, R., Mares, R., Powell, G., 2008a. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. Anim. Conserv. 11, 169–178. https://doi.org/10.1111/j.1469-1795.2008.00169.x

Tobler, M.W., Carrillo-Percastegui, S.E., Pitman, R.L., Mares, R., Powell, G., 2008b. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals.

Anim. Conserv. 11, 169–178.

Tófoli, C., Rohe, F., Setz, E., 2009. Jaguarundi (Puma yagouaroundi) (Geoffroy, 1803) (Carnivora, Felidae) food habits in a mosaic of Atlantic Rainforest and eucalypt plantations of southeastern Brazil. Braz. J. Biol 69, 871–877.

Trujillo, F., Beltrán, M., Diaz-Pulido, A., Ferrer, A., Payan, E., 2010. Mamiferos, in: Lasso, C.A., Usma, J., Trujillo, F. (Eds.), Biodiversidad de La Cuenca Del Orinoco: Bases Científicas Para La Identificación de Áreas Prioritarias Para La Conservación Y Uso Sostenible de La Biodiversidad. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, WWF Colombia, Fundación Omacha, Fundación La Salle e Instituto de Estudios de la Orinoquia (Universidad Nacional de Colombia)., Bogotá D.C., pp. 311–336.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol. Rev. 87, 661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x

Turner, E.C., Snaddon, J.L., Fayle, T.M., Foster, W. a, 2008. Oil palm research in context: identifying the need for biodiversity assessment. PLoS One 3, e1572. https://doi.org/10.1371/journal.pone.0001572

USDA, 2009. The Altillanura- Colombia's Next Agricultural Frontier.GAIN report. United States Department of Agriculture (USDA), USA.

Usma, J., Trujillo, F., 2011. Biodiversidad del Departamento del Casanare: identificación de ecosistemas estratégicos. Gobernación del Casanare-WWF Colombia, Bogotá D.C., Colombia.

Valencia Botero, M.J., Rincón Pérez, L.E., Cardona Alzate, C.A., 2014. Efecto del cambio en el uso de la tierra en la obtención de palma aceitera para la producción de biodiesel en Colombia. Ing. y Univ. 18, 91–102. https://doi.org/10.11144/Javeriana.IYU18-1.ecut

van Schaik, C.P., Griffiths, M., 1996. Activity Periods of Indonesian Rain Forest Mammals. Biotropica 28, 105–112. https://doi.org/10.2307/2388775

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A., Watson, J.E.M., 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation.

Nat. Commun. 7, 12558. https://doi.org/10.1038/ncomms12558

Vincelli, P., 1981. Estudio de la vegetacion del Territorio Faunistico del Tuparro. Cespedecia 10, 5–54.

Wallace, R.B., Gomez, H., Ayala, G., Espinoza, F., 2003. Camera Trapping for Jaguar (P Anthera Onca) in the Tuichi Valley , Bolivia 10, 133–139.

Wang, Y., Allen, M.L., Wilmers, C.C., 2015a. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. Biol. Conserv. 190, 23–33. https://doi.org/10.1016/j.biocon.2015.05.007

Wang, Y., Allen, M.L., Wilmers, C.C., 2015b. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. Biol. Conserv. 190, 23–33. https://doi.org/10.1016/j.biocon.2015.05.007

Wang, Y., Naumann, U., Wright, S.T., Warton, D.I., 2012. mvabund – an R package for model-based analysis of multivariate abundance data. Methods Ecol. Evol. 3, 471–474. https://doi.org/10.1111/j.2041-210X.2012.00190.x

Warton, D.I., Shipley, B., Hastie, T., 2015. CATS regression – a model-based approach to studying trait-based community assembly 6, 389–398. https://doi.org/10.1111/2041-210X.12280

Wearn, O., Glover-Kapfer, P., 2017. Camera-trapping for conservation: a guide to best-practices, WWF Conservation Technology Series.

Wearn, O.R., Carbone, C., Rowcliffe, J.M., Bernard, H., Ewers, R.M., 2016. Grain-dependent responses of mammalian diversity to land-use and the implications for conservation set-aside. Ecol. Appl. 26, 1409–1420. https://doi.org/10.1890/15-1363

Wearn, O.R., Rowcliffe, J.M., Carbone, C., Bernard, H., Ewers, R.M., 2013. Assessing the status of wild felids in a highly-disturbed commercial forest reserve in Borneo and the implications for camera trap survey design. PLoS One 8 (11), e77598. doi:10.1371/journal.pone.0077598. https://doi.org/10.1371/journal.pone.0077598

Wearn, O.R., Rowcliffe, J.M., Carbone, C., Pfeifer, M., Bernard, H., Ewers, R.M., 2017. Mammalian species abundance across a gradient of tropical land-use intensity: a hierarchical multi-species modelling approach. J. Appl. Ecol. 212, 162–171. https://doi.org/10.1016/j.biocon.2017.05.007

Weckel, M., Giuliano, W., Silver, S., 2006. Jaguar (Panthera onca) feeding ecology: Distribution of predator and prey through time and space. J. Zool. 270, 25–30. https://doi.org/10.1111/j.1469-

7998.2006.00106.x

Wellington, K., Bottom, C., Merrill, C., Litvaitis, J.A., 2014. Identifying performance differences among trail cameras used to monitor forest mammals. Wildl. Soc. Bull. 38, 634–638. https://doi.org/10.1002/wsb.425

Wilcken, S., Kalko, E.K. V., 2004. Die Vielfalt neotropischer Fledermäuse: Fliegende Alleskönner. Biol. unserer Zeit 34, 230–239. https://doi.org/10.1002/biuz.200410255

Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. Analysis and Management of Animal Populations. Academic Press, San Diego.

Williams, D.R., Alvarado, F., Green, R.E., Manica, A., Phalan, B., Balmford, A., 2017. Land-use strategies to balance livestock production, biodiversity conservation and carbon storage in Yucatán, Mexico. Glob. Chang. Biol. https://doi.org/10.1111/gcb.13791

Wong, B.B.M., Candolin, U., 2015. Behavioral responses to changing environments. Behav. Ecol. 26, 665–673. https://doi.org/10.1093/beheco/aru183

Wood, B.J., Fee, C.G., 2003. A critical review of the development of rat control in Malaysian agriculture since the 1960s. Crop Prot. 22, 445–461. https://doi.org/10.1016/S0261-2194(02)00207-7

WWF, 2009. Documento de Posición de WWF Colombia. Bogotá D.C.

WWF, 2007. High Conservation Value Forests: The concept in theory and practice. WWF International, Switzerland.

Yaap, B., Magrach, A., Clements, G.R., Mcclure, C.J.W., Paoli, G.D., Laurance, W.F., 2016. Large Mammal Use of Linear Remnant Forests in an Industrial Pulpwood Plantation in Sumatra , Indonesia. Trop. Conserv. Sci. 9, 1–13. https://doi.org/10.1177/1940082916683523

Yue, S., Brodie, J.F., Zipkin, E.F., Bernard, H., 2015. Oil palm plantations fail to support mammal diversity. Ecol. Appl. 25, 2285–2292. https://doi.org/10.1890/14-1928.1

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x