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

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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, we investigated potential unexpected change points (thresholds) in the response of terrestrial mammal's richness and community composition to increasing oil palm cover in the Llanos region of Colombia. We deployed camera traps to detect species across 56 sites (landscapes of ~220 ha each) and used segmented regression and Threshold Indicator Taxa Analysis (TITAN) for the identification of these thresholds. We found a negative linear relationship between the proportion of oil palm and species richness, but no evidence of a threshold. In contrast, we found strong signs of a community threshold when oil palm cover in the study area reached 45–75%, at which mammalian species composition (taxon-specific changes of abundance and occurrence frequency) drastically changed. When species were assessed individually, a significant threshold relationship to oil palm cover was found to occur in 10 of the 15 examined species, with four (squirrel, agouti, spiny rat, common opossum) having a negative drastic change at approximately 45% oil palm cover. Five species showed no evidence for any critical threshold (giant and lesser anteater, jaguarondi, white-tailed deer and raccoon). We used the community threshold identified above as a baseline to evaluate the conservation status of the four oil palm production zones in Colombia. We found that approximately 41% of the total area covered by oil palm in Colombia has crossed the identified threshold of 45–75%, suggesting urgent need for forest restoration to increase its extent if a collapse of their resident 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.

1. 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., 2017; 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; Laurance et al., 2014). Oil palm, in particular, is currently one of the major threatening processes for biodiversity retention in Southeast Asia (e.g. Danielsen et al., 2009). In this region, > 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 and 90% of species richness in birds and mammals (e.g. Maddox et al., 2007; Peh et al., 2006).

Oil palm production is rapidly expanding in Latin America (Furumo and Aide, 2017), where Colombia is the largest oil palm producer with approximately 500,000 ha currently under cultivation (Fedepalma, 2014). Oil palm production in Colombia is located in four zones (East, Pacific, Central and North region; Fedepalma, 2011), and the impact of this production varies across the zones (see Pardo et al., 2015). Contrary to Southeast Asia, most (~80%) of the oil palm expansion in Colombia, since the beginning of the 21st century, has taken place in previously transformed lands especially in areas historically used for cattle grazing (Furumo and Aide, 2017; Pardo et al., 2015). However, little is known about the likely impacts that the substantial increase in

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oil palm cover will have on Colombian biodiversity (Pardo et al., 2015). Few recent studies have suggested that oil palm plantations sustain significant lower levels of biodiversity than natural ecosystems (e.g. Gilroy et al., 2015; Pardo and Payán, 2015; Prescott et al., 2016). Nevertheless, 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, 1994; 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, 2001; Muylaert et al., 2016; Roque et al., 2018).

In this study, we 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. We 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), We predicted an abrupt decline (threshold) in species richness and composition in response to increasing oil palm cover within a landscape.

2. Material and methods

2.1. Study area

The study area is 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 and 394 m.a.s.l. (Fig. 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) and pastures (Pers. Obs. see also Romero-Ruiz et al., 2012). Other minor agricultural activities include rice and corn production. Oil palm production covers approximately 180,000 ha (Fedepalma, 2014), but it is predicted that the expanding oil palm cultivation in the region will occur at a faster rate than that of previous decades (Romero-Ruiz et al., 2012). The remnant natural ecosystem in the study area is secondary riparian forest (gallery forest) which varies in size and age, and some experience seasonal inundation.

2.2. Survey design

We sampled 56 sites (33 inside oil palm and 23 in riparian forest) located across an area of approximately 2000 km^2 (Fig. 1). Sites were selected strategically to examine a gradient of proportional area devoted to oil palm versus riparian forest cover (hereafter referred as forest). All 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.

We 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, as confirmed after a pilot study we conducted in the study area (data not published) (Pardo et al. unpublished data) 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.

2.3. Landscape variable selection

We 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 area or landscapes of ~220 ha (Fig. 1). We then calculated the percentage of the different land cover/use types (forest, oil palm and others) within these landscapes. To avoid potential effects of spatial autocorrelation in our predictor variables, we 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 type we 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). We updated the information from IDEAM (1:500,000) prior to the analysis using: i) Google Earth imagery and ii) Claslite classification–30 m resolution (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).

2.4. Threshold and statistical analysis

The majority of studies using threshold analyses (i.e. identification of drastic change-points in the response of fauna; see introduction) focus on identifying the minimum amount of forested habitats in gradients of native vegetation loss, below which the population of species would likely go extinct (Andrén, 1994; Banks-Leite et al., 2014; Fahrig, 2001; Muylaert et al., 2016). Here, we focused on identifying the threshold for maximum percentage of oil palm plantation in a

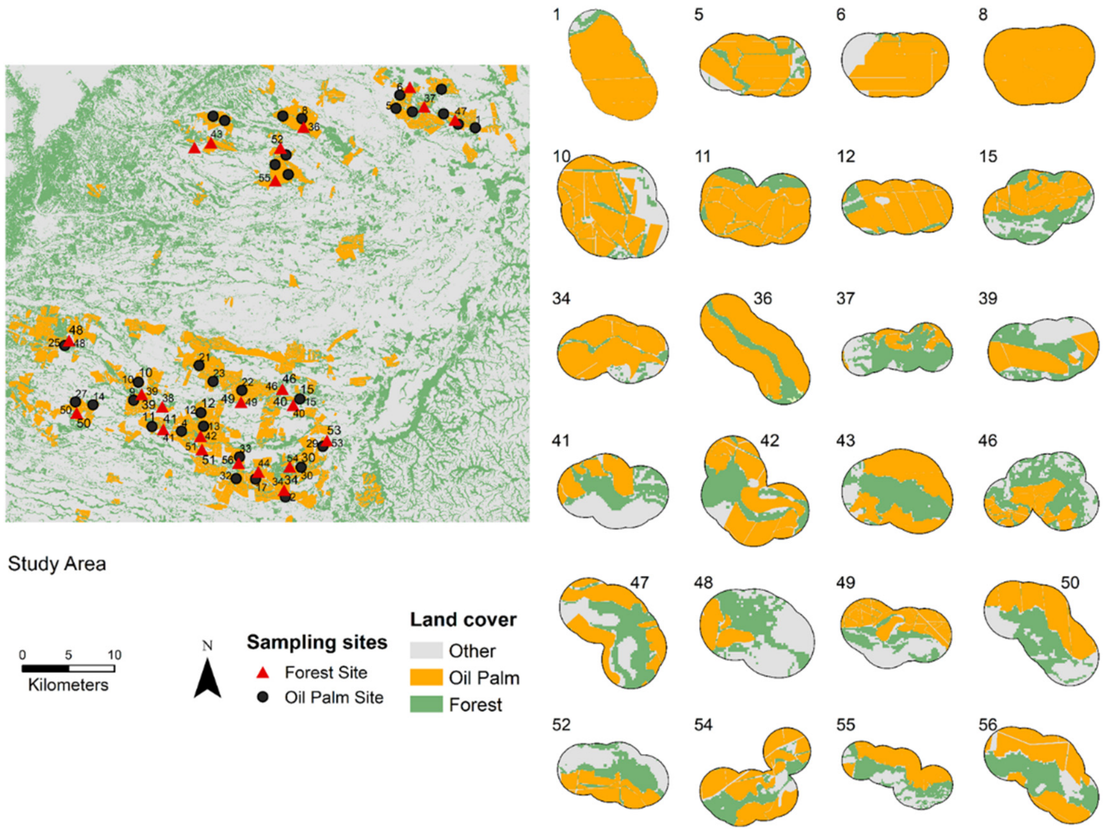

Fig. 1. Map of the study area and surveys sites locations across an oil palm dominated landscape in the Llanos Region, Meta Department, Colombia. Surveys sites in the right represent the landscapes constructed around each camera trap transect using a buffer of 500 m around each camera. Due to space limitation only the most relevant landscapes are shown to visualize the gradient of oil palm cover.

landscape above which mammalian species richness and composition (i.e. occurrences and abundances as an aggregate measure) would decline abruptly. We 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. Gilroy et al., 2015; Pardo et al., 2018); *iii*) past and predicted oil palm expansion has predominantly occurred in non-forested ecosystems (e.g. pastures and natural savannas; (Castiblanco et al., 2013; Furumo and Aide, 2017); 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 could trigger either a richness or a population decline in the local mammalian community.

2.4.1. 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, 2003, 2008). Segmented regression analysis splits explanatory variables into two or more linear regressions 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 mammalian community composition response to oil palm proportional landscape cover, we 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 each taxon 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 we 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, we 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 were 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 we used only those species that were independently detected > 10 times and at more than three sites.)

2.4.2. 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 oil palm production zones in Colombia (i.e. East, Pacific, Central and North region; Fedepalma, 2011), we 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). For this assessment, we first delimited the spatial extent of each of these zones using the farthest plantations as the limit, as there is no official delimitation for each zone. Then, we constructed a fishnet composed of 1 km^2 squares to cover the size of each production zone. This approach allowed us to quantify the proportion of oil palm plantations within each square.

3. Results

3.1. 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, we detected 24 terrestrial mammal species representing seven taxonomic orders and 16 families (see Pardo et al., 2018 for further details). We 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. 2), although the 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 on species richness until oil palm coverage reach approximately 35–40% in the landscapes, after which a downward trend in species richness is evident (Fig. 2).

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

A strong sign of community compositional change was identified when the oil palm cover in the landscape was between 45 and 75% (Fig. 3). Individually, 12 of the 15 species analyzed had a significant threshold response to oil palm land cover (Indicator Value –IndVal score $p < 0.05$) (Table S1). 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. 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 (Table S1).

A synchronous (similar) response to oil palm cover was identified in four species: squirrel (*sciurus* spp), agouti (*Dasyprocta fuliginosa*), spiny rat (*Proechimys* 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 (*Hydrochoerus 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 in the study area with a threshold between 55% and 75% (Fig. 4).

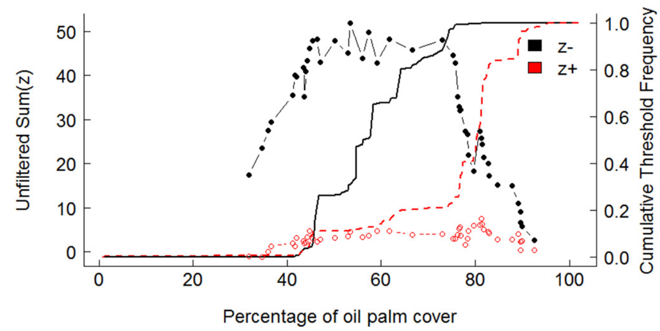

Fig. 3. Community threshold in response to increasing oil palm cover percentage in the Llanos region, Colombia. The cumulative probability curves indicate strong signs of community change between 45 and 75% of oil palm cover percentage. Solid (black) and dashed (red) lines represent the cumulative frequency 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). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

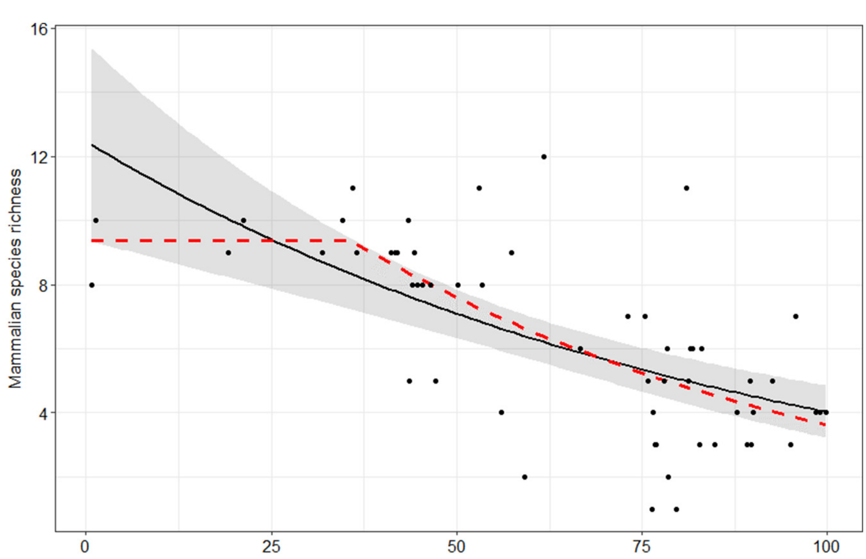

Fig. 2. Mammal species richness response to percentage of oil palm cover in the Llanos region of Colombia. Continuous black line is the prediction of the generalized linear model (GLM) fitted to the data and shaded gray area is its 95% confidence interval. The red dashed line shows the constrained segmented (GLM) regression to identify thresholds. Breakpoint is not significant for the segmented regression, but the effect of increasing oil palm cover is evident after it reaches approximately 35% in the landscapes with a negative trend. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

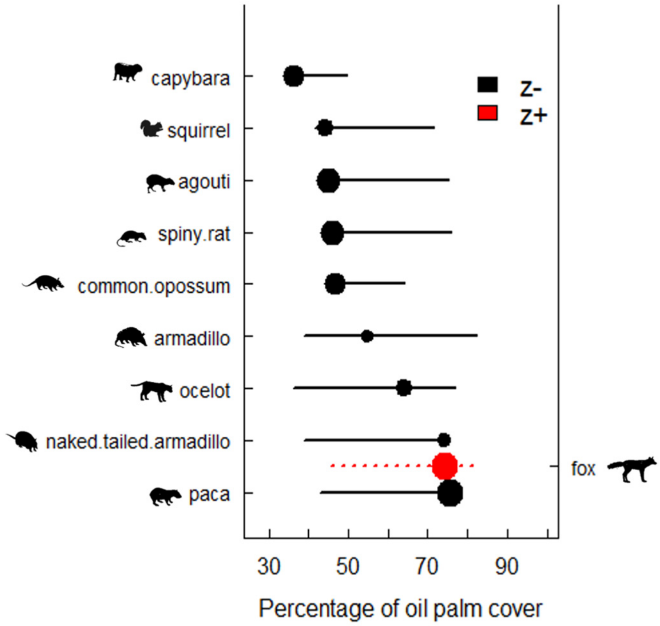

Fig. 4. Species specific thresholds of 10 mammalian species in response to the percentage of oil palm coverage in the Llanos region, Colombia. Only species that showed significant purity (> 0.90), reliability (> 0.90), and p (< 0.05) are shown. Z+/− = positive/negative effect on frequency of occurrence 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.

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

We 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 oil palm producing zones in Colombia. Our 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 1, Fig. 5).

4. 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 and a potential

Table 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[a] (ha)	Total below threshold (%)	Total at threshold (%)	Total beyond threshold (%)
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

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

hyper-abundance of foxes. The 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). However, to our 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" or threshold 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 Harding 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 unequivocally be attributed directly to oil palm plantations. 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 previously natural ecosystem.

4.1. Mammalian species composition thresholds in response to oil palm land cover

We found that the community composition of most mid-large sized mammals in the Llanos region of Colombia displayed a clear negative threshold between 45 and 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. Caution and a strict monitoring program should be implemented in landscapes where percentage of oil palm is situated at the range of the threshold, as within this interval is where most drastic changes and mammal declines are expected to occurred (i.e. "risk zone" see Roque et al., 2018). Further, our results showed that when oil palm cover increased to 75% or more, almost the entire 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, most of the community will certainly decline in landscapes composed of > 75% oil palm. Therefore, increasing forest cover by restoration processes and monitoring programs are urgently needed to reduce the probability of significant mammals decline in oil palm landscapes in the Llanos region with this level of coverage (see sections below).

We may use the identified threshold for oil palm coverage as a general guideline to anticipate the minimum amount of remaining forest needed to support resilient populations of mammals. As such, our results suggest that maintaining a forest cover between 55 and 25% in Llanos oil palm landscapes would help avoiding entering a "risk zone". We acknowledge, 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; Roque et al., 2018). 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% (Andrén,

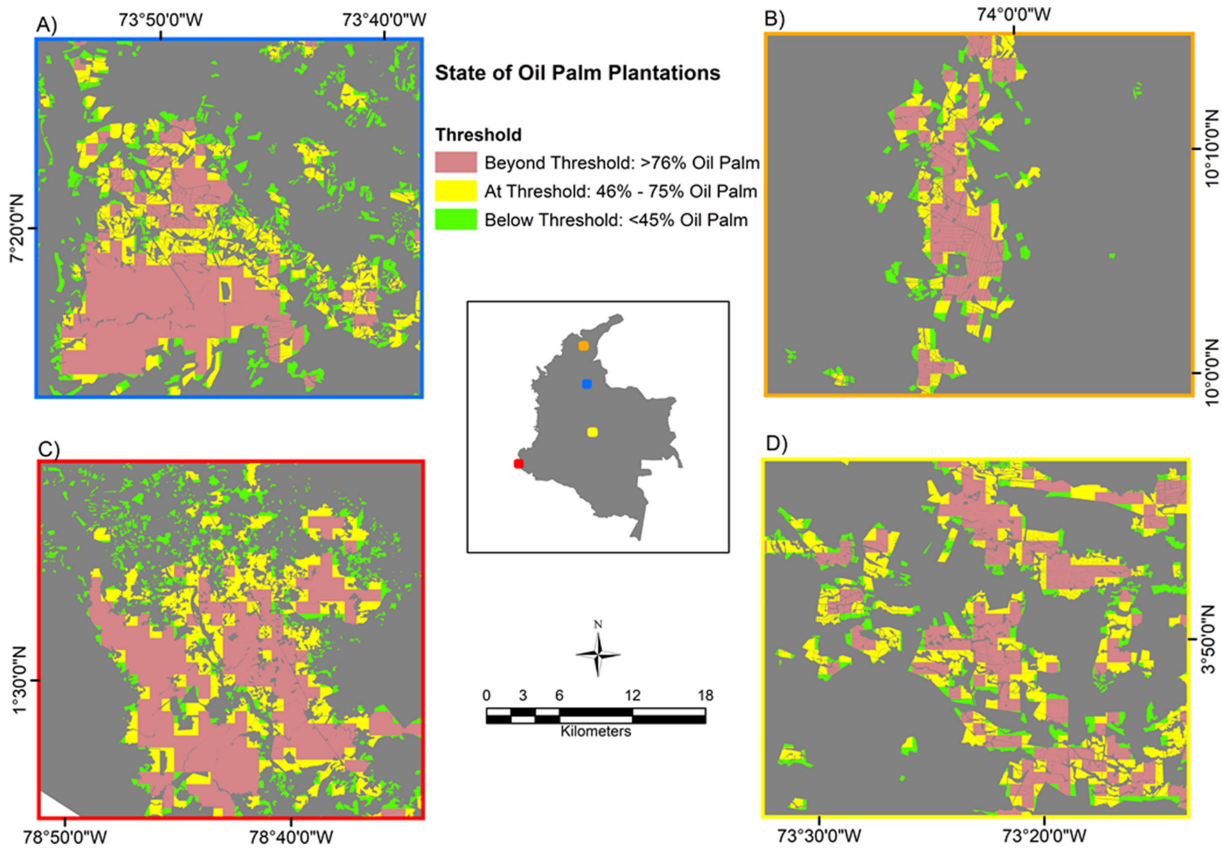

Fig. 5. Location and visual representation of the conservation status of the four major Colombian oil palm production zones (A: Central, B: North, C: West, D: East) according to the percentage of oil palm below, at, or above the oil palm coverage threshold (of 45–75%). Estimation based on a grid of 1 × 1 km.

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 previous natural habitats (see Pardo et al., 2018) by other types of production (especially cattle). Second, although riparian forests can vary in width, they constitute a small proportion of the Colombian Llanos landscape compared to the surrounding savanna ecosystems. These two factors further suggest that the identified threshold may be conservative if applied to other ecosystems or production zones. Therefore, for ecosystems with extensive and more conserved rainforest cover, such as the Amazon or Pacific region, a threshold analysis would most likely reveal higher values.

We did not find many species with synchonomous responses to oil palm cover, or strong evidence for common eco-morphological traits influencing their responses. However, the four species with responses at a similar level of oil palm cover were mostly rodents with similar body sizes; a group which tends to be common in forested ecosystems (Emmons, 1999). Our 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 capybaras appear to cross oil palm plantations, their relative abundances increases with percentage of forest cover (see also Camargo-Sanabria et al., 2014). Although capybara and paca are highly forest dependents, the paca appears 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 our study. Ocelot, for instance, displayed a negative threshold to oil palm until ~65% land cover, while jaguarondi displayed no clear threshold. Moreover, 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; Nogeire et al., 2013; Pardo et al., 2016), including oil palm (Jennings et al., 2015; Mendes-Oliveira et al., 2017; 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. 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).

4.2. *Conservation status of oil palm production zones*

Large parts of Colombian oil palm landscapes are currently beyond the identified threshold and 41% of the total area covered by oil palm have crossed the identified threshold (> 75%). This result suggests that mammal communities are under threat. As such, the National Federation of Oil Palm growers (Fedepalma) should encourage restoration with native vegetation up to our suggested natural vegetation coverage levels if they wish to prioritize mammal conservation in these landscapes. We 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, our results provide clear empirical evidence which may be useful for integrating into management regimes. It is worth mentioning that our 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. Chinchilla, 1997; de Oliveira et al., 2010). Our results reinforce the importance of restoring and increasing the area of riparian forests. This strategy is more important than solely the maintaining of current forest cover or even the identification of areas of high conservation value in these landscapes; due to their limited extent in these human dominated landscapes such as the western Llanos region.

4.3. 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), and particularities of the study area (in terms of the type of land that is being converted to oil palm) the results of this study can aid landscape planning and design, particularly that within the studied Eastern oil palm production zone of Colombia. Very few studies have evaluated the potential effect of the matrix in threshold analyses (e.g. Boesing et al., 2018). Our results suggest limiting oil palm expansion to ~45% coverage in the landscape, and never exceed 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. The relatively broad values of the threshold identified here also reflect the different sensitivities of fauna coexisting in oil palm landscapes in the Llanos.

Numerous schemes for sustainable farming and 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). Land sparing supporters suggest that high yield agriculture system and offsetting of large areas of natural ecosystems will reduce impacts of agriculture, while wildlife friendly farming supports the need for low intensive agriculture interspersed with natural or native ecosystems (see Koh et al., 2009). Our analysis is beyond this discussion but support the idea of designing landscapes where natural ecosystems (riparian forests in this study) are an essential part in productive areas; which for Llanos may need to cover a minimum of 25%. Future studies should use supplementary analysis to evaluate the potential effect of other land use types surrounding oil palm landscapes as well as the effect of different scales on threshold responses. The effect of other land uses, though, might have been minimal in the study area as sites were only surrounded by oil palm and to a minor extend pastures. However, in other production zones such as the North and West, land use types and ecosystems adjacent to oil palm landscapes are more complex than in the Llanos region. Increasing heterogeneity of the matrix would reduce extinction thresholds in human dominated landscapes (Fahrig, 2001). Furthermore, as determined by Pardo et al. (2018) habitat enrichment, through the maintenance of understory vegetation, in oil palm plantations itself, would have important positive effects on species richness and composition.

Current regulations for the Llanos region state that plantation projects of > 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 100 m between plantations and buffer zones of riparian forest (Corporinoquia, 2011) – although, none of these measures have been empirically tested. Our 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 recent expansion of oil palm in Colombia has occurred predominantly in lands previously covered by pastures, especially in the study area in the Llanos, (e.g. Castiblanco et al., 2013; Furumo and Aide, 2017). Furthermore, it is suggested that future oil palm expansion will not overlap significantly with the distribution of threatened species (Ocampo-Peñuela et al., 2018). However, our results suggest that even under these circumstances, there is still a maximum tolerance to oil palm cover after which most species, even “common” and currently 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. 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) addressed this issue for birds communities in Colombia, suggesting a significant difference in species richness and composition between savannas and oil palm plantations. Therefore, environmental certification 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 (see Pardo et al., 2018).

The fact that we 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 the 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.

5. Conclusions

We found evidence of a drastic change point (threshold) in the response of 15 terrestrial mammals 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 anticipating 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, we recommend urgent restoration of these regions rather than measures focused solely on the identification of habitats or species of "high conservation value". Very few studies have evaluated potential non- linear effect of the human created matrices. Therefore, our 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.

Taxon-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 (Table S1).

Supplementary data to this article can be found online at doi:https://doi.org/10.1016/j.biocon.2018.08.026.

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