

The influence of landscape relative to site and patch variables on primate distributions in the Colombian Llanos

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Abstract

Context: Primates are an important component of biodiversity in tropical regions.

5 However, many studies on the effects of habitat change on primates ignore the relative influence of landscape composition and configuration.

Objectives: This study addresses the question: how important are landscape-scale forest area and composition relative to patch-scale (1 – 1080 ha) and site-scale (transect of 1 km) habitat variables for the occupancy and abundance of four primate species in the
10 Colombian Llanos.

Methods: Using a randomly stratified survey design, 81 fragments were surveyed for primate occupancy and abundance. We used zero-inflated models to test the relative influence of landscape-scale, patch-scale and site-scale variables on occupancy and abundance for each species. A 95% confidence set of models was constructed using the
15 cumulative Akaike weight for each model and the relative importance of each set of variables calculated for each primate species.

Results: Occupancy was determined by a combination of site-scale, patch-scale and landscape-scale variables but this varied substantially among the primate species.

Conclusion: Our study highlights the importance of managing primates at a range of
20 scales that considers the relative importance of site-, patch- and landscape-scale variables.

Key Words: primate conservation, forest cover, *Alouatta seniculus*, *Callicebus ornatus*, *Saimiri cassiquiarensis albigena*, *Sapajus apella fatuellus*, scale

25 Introduction

Deforestation and forest fragmentation continues at an alarming rate in the tropics (FAO 2011; Hansen et al 2013). Understanding how this drives the spatial distribution of wildlife populations is important for their conservation and management, especially in

tropical areas where the greatest losses are occurring (Fahrig 2001; McAlpine et al 2006;
30 Fisher and Lindenmayer 2007; Elith and Leathwick 2009; Guisan et al 2013; Arroyo-
Rodriguez and Fahrig 2014). Species' distributions are influenced not only by the
characteristics of individual habitat patches, but also by the composition and spatial
configuration of the surrounding landscape (McGarigal and McComb 1995; Guisan et al
2007; Elith and Leathwick 2009). Understanding the contribution of landscape-level
35 processes to species' distributions require a multi-scaled approach (Oja et al 2005;
McAlpine et al 2006; Wiens 2008), but this has often been ignored in studies of primate
species in the tropics (Arroyo-Rodriguez et al 2013b; Arroyo-Rodriguez and Fahrig
2014). Quantifying the response of primate species to landscape variables relative to the
more commonly studied site/patch level variables is therefore a key research priority.

40 Primates are an important component of biodiversity and ecosystem function in many
tropical regions. However, they are under threat from habitat loss and fragmentation
(Mittermeier and Oates 1985; Rylands et al 2008; Schipper et al 2008). Nonetheless,
most studies focus on the effects of site and patch-scale variables on primates and have
ignored the influence of landscape composition and configuration (Harcourt and Doherty
45 2005; Arroyo-Rodriguez et al 2013a; Benchimol and Peres 2013; Arroyo-Rodriguez and
Fahrig 2014; Carretero-Pinzón et al 2015). Only a few studies have included landscape-
scale (100 – 1000 ha) variables to predict the occurrence of primate species and
demographic change (Anzures-Dadda and Manson 2007; Escobedo-Morales and
Mandujano 2007; Arroyo-Rodriguez et al 2008; Pyritz et al 2010; Thornton et al 2011;
50 Arroyo-Rodriguez et al 2013b). This is a critical limitation because species' responses to
landscape change are influenced by the scale at which this occurs, that change processes
are ultimately multi-scaled in nature, and vary from species to species (Eigenbrod et al
2008; Smith et al 2013; Thorton et al 2011; Martin and Fahrig 2012; Arroyo-Rodriguez

et al 2013b). For example, Thornton et al (2011) and Arroyo-Rodriguez et al (2013b)
55 applied a multiscale approach to evaluate primate species' responses to habitat loss and
fragmentation. Thornton et al (2011) found that habitat fragmentation strongly affected
Geoffroy's spider monkey (*Ateles geoffroyi*) in Guatemala, within a 500 m buffer
distance from the forest fragment edge. On the other hand, Arroyo-Rodriguez et al
(2013b) found that populations of the black howler monkey (*Alouatta pigra*), in Mexico,
60 were primarily affected by changes in patch-scale attributes rather than landscape-scale
metrics in a 500 ha landscape. These conflicting results indicate the need for
comparisons across multiple species in the same landscape to disentangle the responses
of different species from variation among study sites (Carretero-Pinzon et al 2015).

In Colombia, the main drivers of deforestation are human population growth and
65 migration, infrastructure projects, palm oil plantations, agriculture and cattle ranching
(Etter et al 2006, 2008; Fedepalma 2014; Ecopetrol 2015). Orinoquia (an area of
388,101 km² in size) is a region of Colombia with high rates of conversion of natural
savannas and the degradation of gallery forest and lowland rain forest (Etter et al 2008).
This region is part of the Orinoco River catchment (Dominguez 1998), and is an
70 important area for primate biodiversity. In Orinoquia, the main drivers of habitat loss
and fragmentation are similar to those in the rest of Colombia and includes the
cultivation of illegal crops (Armenteras et al 2009, 2013; Castiblanco et al 2013). The
region supports from 2 - 10 primate species depending on the vegetation composition
and structure, including the endemic dusky titi monkey (*Callicebus ornatus*),
75 Brumback's night monkey (*Aotus brumbacki*) and the Colombian squirrel monkey
(*Saimiri cassiquiarensis albigena*) (Defler 2010). Therefore, this region provides an
excellent opportunity to simultaneously understand the responses of multiple primate
species to landscape and site/patch variables. Further, studies evaluating the effects of

habitat loss and fragmentation on primates in Orinoquia are scarce and limited to density
80 estimates of populations in forest fragments (Wagner et al 2009; Carretero-Pinzon
2013a) and behavioral studies of species living in forest fragments (Zarate and
Stevenson 2014). Better understanding of the influence of landscape change on the
region's diverse primate community is therefore critical for their conservation.

This study addressed the question: how important is landscape-scale forest area and
85 configuration relative to patch-scale and site-scale habitat variables for the occupancy
and abundance of four primate species in the Colombian Llanos. This question was
addressed by using count data from four diurnal primate species in 81 fragments and
zero-inflated generalised linear models. We found that the abundance and occupancy of
the primate species studied are influenced by a combination of site, patch and landscape
90 variables, with their relative importance varying with the species.

Methods

Study Area

The study was conducted in the Los Llanos bioregion (sensu Lasso et al 2010), near the
town of San Martin in the Colombian Orinoquia (Figure 1a). The Llanos is characterized
95 by lowland alluvial terraces and plains, dissected by rivers originating in the Andes or in
the upland savannahs and draining into the Orinoco River (Lasso et al 2010). The
vegetation is dominated by flooded and dryland savannas, gallery forest associated with
drainage lines and lowland rainforest (Lasso et al 2010). There are five primate species
living sympatrically in the region: red howler monkey (*Alouatta seniculus*), dusky titi
100 monkey (*Callicebus ornatus*), black-capped capuchin (*Sapajus apella fatuellus*),
Colombian squirrel monkey (*Saimiri cassiquiarensis albigena*) and Brumback's night
monkey (*Aotus brumbacki*) (Carretero-Pinzon 2013a). We focus on the first four species

because logistic and time constraints available did not make it possible to survey the nocturnal species (*A. brumbackii*) present in the study area.

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Figure 1 approximately here#

Survey Design

Site selection: A randomly stratified survey design (Rogerson 2010) based on forest
110 fragment size and the proportion of forest surrounding each patch at a 1000 m buffer distance were used to select potential sites for primate and vegetation surveys (Figure 1b). The design was based on a land cover map derived from a mosaic of Landsat 7 ETM images from 2000 (www.earthexplorer.usgs.gov) at a 30 m spatial resolution using a supervised classification with ArcMap 10.1 (ESRI ArcGIS 10).

115 Four classes of land cover were identified (crops, forest, pastures and water). The classified map was then used to stratify each forest patch by size (3 classes: 1 – 50 ha, 51 – 100 ha and 101 – 1000 ha) and the percentage of forest cover surrounding the fragments at a 1000 m buffer radius (3 classes: 0 – 33 %, 34 – 66 % and > 0.67 %). The selection of the largest fragment size category (101 – 1000 ha) was chosen to be
120 consistent with Marsh (2003). The minimum fragment size considered (1 ha) was based on the smallest fragment in which any of the primate species had been observed previously in the study area (Carretero-Pinzón Pers. Obs.). The buffer distance was based on an intermediate value within the range of the dispersal distances of the target primate species (200 m – 3000 m; Crockett 1996; Arroyo-Rodriguez and Dias 2010;
125 Defler 2010; Carretero-Pinzon unpublished data). A combination of forest fragment size and the percentage of forest cover surrounding the fragments (9 classes, Table 1) were then used to randomly select 10 sites per class with sites widely distributed across the

study region. Spatial autocorrelation among fragments was minimised by selecting fragments at least 1 km apart.

130 Landowners were contacted to obtain permission for data collection in the selected survey sites. Selected sites more than 60 km from the focal area of San Martin and which were near areas of conflict (i.e. guerrillas) were eliminated for logistical and security reasons. The final set of selected fragments was then evaluated in the field for minimum canopy height. Fragments with canopies less than 10 m in height were
135 considered regenerating or regrowth forest and were not included in the study, as we focused on primary forest. All sites within “forest” fragments that were identified as palm oil plantations were eliminated and verified in the field by direct observation. All the pre-selected areas that were eliminated were replaced by fragments in similar categories. For consistency, these were located at least 1 km from fragments already
140 sampled. A total of 81 fragments were surveyed within all the combinations of classes present (Appendix 1).

One transect was located in each fragment, except for the largest fragment (1080 ha) where three transects were surveyed. Transect direction was randomly chosen and where possible, transects were straight, although in fragments with irregular shapes, the
145 direction varied according to the fragment form.

Primate surveys

Count data were collected by recording every primate group and individual of each group observed along a transect during each survey. Field data collection was conducted between August 2013 and May of 2014 (this period includes the wet and dry season for
150 the study area). Counts were conducted from 0600 to 1100 hours and again at 1330 to 1630 hours on the same day, and repeated on consecutive days. Each transect was surveyed three to six times, with a minimum of three surveys per transect. Surveys were

not conducted in heavy rain. Transects were walked at approximately 0.5 km/h and when a primate group was visually detected, a minimum of 15 minutes were taken to count the group members and determine group composition (number of males, females and immature). The time of detection and the coordinates of the location of each observation based on a GPS reading were also recorded. All observations and species identifications were aided by binoculars, and primate species' classification followed Defler (2010), Ruiz-Garcia and Castillo (2016) and Mittermeier et al (2013). Primate surveys were carried out by the first author.

Vegetation surveys

Vegetation surveys were conducted in four 10 x 50 m plots, located every 250 m along the length of each transect. In each plot, all trees with a diameter at breast height (DBH) >10 cm were recorded to species level. Species identifications were based on vegetative and reproductive material using the guide "Guia de frutos de La Macarena" (Stevenson et al 1998) as well as expert identification by Francisco Castro (Botanist of Los Llanos University). For each tree, the DBH and the presence or absence of fruits, flowers and young leaves during survey time was recorded. Finally, the percentage of canopy cover and canopy height were recorded from one single point every 200 m along the transect. Presence of natural fence rows (defined as tree-lines used to separate adjoining pastures, Carretero-Pinzon et al 2010) and the type of land use directly adjacent to the patch were recorded by direct observation for each fragment. The types of land use in the matrix adjacent to each forest fragment were categorised as *pastures* (including introduced pastures or natural savannahs) or *plantations* (crops and palm oil plantations, alone or combined with exotic pastures). Vegetation surveys were conducted by the first author with the assistance of Francisco Castro.

Variable selection

A range of ecologically relevant site-scale, patch-scale and landscape-scale variables were selected, based on a primate literature review (Table 1). Four site-scale variables were selected that were canopy cover, canopy height, number of food trees and number of trees with fruits. The variable, number of food trees, was based on each primate species' diet (see Table 2 for sources of this information). Four patch-scale variables were also selected: patch size, patch shape index (a measure of complexity of the patch shape, see Table 1 for calculations), presence/absence of natural fence rows and the type of matrix adjacent to the patch. The presence/absence of natural fence rows and the type of matrix were considered in our analysis as patch variables because they were measured directly adjacent to the focal fragment, rather than being reflective of the broader landscape. The percentage of forest cover and patch density were selected as respective measures of landscape composition and configuration. Site-scale variables were measured based on the vegetation plot data aggregated along each transect. Patch-scale variables were measured for the whole patch in which a transect was located. Landscape-scale variables were measured at five buffer distances (500 m, 1000 m, 2500 m, 3000 m and 3500 m) surrounding each forest fragment. The range of buffer sizes were chosen in relation to the range of recorded dispersal distances available in the literature for the species. These dispersal distances range from a dispersal distance of 500 m for *Callicebus* to a dispersal distance of >3000 m for *Alouatta* (Crockett 1998, Carretero-Pinzon, unpublished data). No information was available on the dispersal distances for the other species. Although we recognise the considerable uncertainty in these dispersal estimates, our choices of buffer size do likely broadly capture the range of dispersal scales for the study species. Prior to the calculation of patch- and landscape-scale variables, the mapping of the selected fragments was

improved using a more recent forest and non-forest map of Colombia produced by IDEAM (2014) which is derived from satellite images captured in 2010.

205 # Table 1 approximately here#

Statistical Analysis

To model the occupancy and abundance of each species, we used zero-inflated Poisson generalized linear models (Lambert 1992; Martin et al 2005; Zuur et al 2009; Rhodes
210 2015). These models allow for the simultaneous modelling of an occupancy component and an abundance component, given occupancy, and are ideally suited for dealing with zero-inflated count data (Martin et al 2005; Rhodes 2015). Each species was modelled separately and the response variable was the number of individuals observed per transect. Note that the modelled counts are indices of abundance rather than true
215 abundances because we do not account explicitly for detection error. They are therefore interpreted as such. Ignoring detectability essentially assumes that detectability is constant among sites and this may be an issue if detectability actually varies strongly among sites. However, given that forest structural characteristics do not vary strongly among sites, except for some variation in canopy height and closure, we do not expect
220 this to be a major issue. Nonetheless, this may be a limitation of the approach we took. The study area is a part of the piedmont and dissected savannas found in this region, with an uneven topography (Lasso et al 2010), that can be a factor for the varied canopy height observed in our study sites. We modelled the occupancy and abundance components of the model as functions of the site, patch and landscape variables with
225 variation in sampling effort controlled for in the models as an offset (Zeileis et al 2008). We formulated a range of alternative hypotheses about the effects of landscape, patch

and site scale variables on the occupancy and abundance and tested the support for these based on an information theoretic approach (Burnham and Anderson 2002). To reduce the number of models to a manageable level, we first determined the best buffer size at which to represent the landscape variables for each species. To do this, we modelled the occupancy and abundance of each primate species with only the landscape variables measured at each buffer size separately. We chose the buffer size for each species that had the lowest AIC. Then, we constructed alternative models of the site, patch and landscape variables using landscape variables measured at the chosen buffer size. We constructed our alternative models based on all combinations of site, patch and landscape variables, but keeping variables within a scale grouped together. We assumed that the same variables influence occupancy and abundance in each model. For each species, we also included a null model that included no predictor variables. For each species this resulted in a consideration of 8 models.

All statistical analyses were performed using the R software (www.r-project.org) and the package pscl (Zeileis et al 2008). We ranked all models for each species according to their AIC values and calculated their Akaike weights (Burnham and Anderson 2002). For each species, a 95% confidence set of models was constructed using the cumulative Akaike weight for each model, starting with the highest and adding the next model until the cumulative sum of weights exceeded 0.95 (Burnham and Anderson 2002). In addition, the average relative importance of each set of variables (site, patch and landscape) was calculated to evaluate the importance of each set of variables for explaining the occupancy and abundance of each species. In order to calculate the relative importance, we controlled for the number of variables by taking the importance of the set of variables rather than each variable separately and then summing the relative importances (see Rhodes et al. 2009).

Finally, to test for spatial autocorrelation in the final model residuals, we created spline correlograms of the residuals of the highest ranked model for each species using the *ncf* package in R (Bjørnstad 2013). The spline correlograms estimated spatial correlation using a smoothed spline with 95% confidence intervals calculated by bootstrapping (Bjørnstad and Falck 2001). Splines that are centred on zero indicate spatial randomness (i.e., the data are spatially independent), while splines where the 95% confidence intervals do not overlap zero indicate spatial autocorrelation (Bjørnstad and Falck 2001).

Results

All four species were observed in 22 % of the patches surveyed with only 1 % of the patches surveyed having no primate species present. A total of 271 dusky titi monkeys, 627 howler monkeys, 1092 black-capped capuchin monkeys and 2799 Colombian squirrel monkeys were observed, including adults and immature (sub-adults, juveniles and infants).

Ranking of explanatory variables

The 95% confidence sets of models showed some model uncertainty with one or two models within the 95% confidence set for all primate species studied (Table 2).

However, in general the best model was well supported with Akaike weights > 0.8 (Δ_i (w_i)): dusky titi monkeys: 7.05 (0.95); black-capped capuchins 5.3 (0.98); red howler monkeys: 3.02 (0.99); Colombian squirrel monkeys: 17.35 (0.99)), and all substantially better than the null model. The difference between the best model and the null model for all species range from 21.67 – 229.36 (Δ_i : dusky titi monkeys: 21.67; black-capped capuchins 60.54; red howler monkeys: 83.83; Colombian squirrel monkeys: 229.36) indicating very little support for the null models. The best model explaining the occupancy and abundance of Colombian squirrel monkeys, red howler monkeys, and

black-capped capuchins contained the variables at the site, patch and landscape scales (500 m buffer for Colombian squirrel monkeys and red howler monkeys and 1000 m buffer for black-capped capuchins). For dusky titi monkeys, the best model explaining occupancy and abundance contained the variables at the site and landscape scales (1000
280 m buffer). There was no evidence of spatial autocorrelation in the model residuals for any of the best models (Appendix 2).

Table 2 approximately here#

285 The relative importance of the site-scale and patch-scale variables was high relative to the landscape-scale variables for red howler monkeys, black-capped capuchins and Colombian squirrel monkeys. On the other hand, landscape-scale variables showed a high importance relative to site-scale and patch-scale variables for dusky titi monkeys (Figure 2).

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Figure 2 approximately here#

Effect of explanatory variables

The occupancy and abundance of primate species were significantly influenced by some
295 variables at all spatial scales, but with some differences among species (data based only in the best model for all species, Figure 3). For red howler monkeys, variable patch density and canopy height had significant effects on occupancy, variables canopy height, canopy cover, presence of natural fence rows, patch density and patch shape index had significant effects on abundance. For black-capped capuchins canopy height and the
300 number of food trees had significant effects on occupancy, while the variables canopy cover, number of food trees, matrix, presence of natural fence rows and patch density

had significant effects on abundance. For Colombian squirrel monkeys, percentage of forest cover variable had significant effect on occupancy, variables canopy height, number of trees with fruits, patch shape index, presence of natural fence rows and the
305 percentage of forest cover had significant effects on abundance. For dusky titi monkeys, the percentage of forest cover had significant effect on occupancy, variable number of trees with fruits had significant effects on abundance. Fragment size was no significant for any of the primate species studied here.

The direction of the effect of the explanatory variables also varied among species
310 (Figure 3). For red howler monkey, occupancy was influenced positively by patch density, while their abundance was negatively influenced by canopy height and the patch shape index. Dusky titi monkeys' occupancy was positively influenced by the percentage of forest cover at the landscape scale, while the number of trees with fruits had a positive effect on the abundance of this species. The occupancy of black-capped
315 capuchin was negatively influenced by canopy height and the number of food trees, while its abundance was positively influenced by canopy cover, number of food trees and matrix and negatively influenced by presence of natural fence rows and patch density. The percentage of forest cover at the landscape-scale had a positive effect on Colombian squirrel monkey occupancy. The abundance of this species was also
320 negatively influenced by the presence of natural fence rows and the percentage of forest cover in the landscape and positively influenced by canopy height, the number of trees with fruits and the patch shape index.

Figure 3 approximately here#

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Discussion

In this study, we applied a multiscale approach to assess the importance of landscape-scale variables relative to site-scale and patch-scale variables for four primate species in the Colombian Llanos. The main contribution is the identification of key spatial scales at which habitat variables influence primate occupancy and abundances and the variation in the influence of these scales among species. It highlights the importance of site-scale and patch-scale variables for three of the studied species (red howler monkeys, black-capped capuchins and Colombian squirrel monkeys), but quite differently, landscape-scale variables for dusky titi monkeys in the same study area. The multiscale approach allowed us to disentangle the relative importance that variables measured at different spatial scales have on primate species occupancy and abundance, improving our understanding on how primate species are distributed. The importance of spatial scale on the distribution and abundance of primate species has been highlighted by other authors (Arroyo- Rodriguez et al 2013b and Thornton et al 2011), but few studies have empirically tested this importance. Our study demonstrates the need for primate studies to focus at multiple spatial scales of analysis to better understand how site, patch and landscape-scale variables affect species occupancy and abundance for different species to make informed conservation and management decisions.

Our finding that the relative importance of the site, patch and landscape scales is different for each species is likely related to specific life-history strategies of those species. For example, red howler monkeys, black-capped capuchins and Colombian squirrel monkeys are able to use the matrix and disperse through it across a diverse range of habitats (Defler 2010; Carretero-Pinzón 2013, pers. obs.). Therefore, these species are likely to be less influenced by the landscape context than their specific habitat requirements at patch- and site-scales. In contrast, the dusky titi monkey is a more restricted species in terms of dispersal movements through the matrix (only a few

anecdotic observations of this species crossing pastures apparently to disperse have been noted, Carretero-Pinzón unpublished data). Therefore, variables describing the structure of the landscape, such as percentage of forest cover, are more significant because it will
355 restrict their dispersal. Nonetheless, data on dispersal patterns for the species studied here are scarce, except for red howler monkeys (Crockett 1996). This is because dispersal events are difficult to observe in primate species. Below we expand on pattern-process-scale inferences for the species studied here.

Site-scale processes

360 The study highlights the importance of site-scale variables in explaining primate occupancy and abundance. Our site-scale variables are related to forest structural attributes such as canopy height and canopy cover and measures of resource availability during the survey such as number of trees with fruits. However, the influence of these variables varied substantially among species. For example, a negative effect of canopy
365 height on the occupancy of red howler (non-significant) and black-capped capuchin monkeys (significant) was unexpected. Canopy height has been used as a measure of habitat quality for species of *Alouatta* (*A. palliata*, Anzures-Dadda and Manson 2007; *A. pigra*: Pozo-Montuy et al 2008). However, this interpretation may not be true for other types of forest which have different canopy heights and structures. The negative effect
370 observed in our study may be related to the variable canopy height of Colombian Llanos forests (ranging from 10-25 m in height), which may not necessarily relate to habitat quality, but rather to other features such as topography and forest composition (Lasso et al 2010). While the positive effects of the number of trees with fruits showed for dusky titi monkeys and Colombian squirrel monkeys emphasise the importance of this resource
375 availability in the abundance of these endemic taxa in fragmented areas. For the Colombian squirrel monkey, the importance of resource availability on activity patterns

and home range use has been previously observed (Carretero-Pinzón 2016). This study found that forest fragment was used depending on fruit production available on that fragment at that time (Carretero-Pinzón 2016). Also, Data for dusky titi monkeys is limited (Ospina 2006). This variation on site-scale effects on primate species occupancy and abundance highlight the importance of forest structure and resource availability within forest fragments, depending on species traits. For example, medium and large species such as black-capped capuchins and red howler monkeys seem to be more affected by forest structure, whilst small body size species such as dusky titi monkeys and Colombian squirrel monkeys seem to be more effected by resource availability variables.

Patch-scale processes

An interesting result was that fragment size did not have a significant effect for any of the species studied, contrary to the findings of other studies (Cristobal-Azkarate and Arroyo-Rodriguez 2007; Anzures-Dadda and Manson 2007; Arroyo-Rodriguez et al 2008; Arroyo-Rodriguez et al 2013b). The species studied here are a subset of all primate species present in the Llanos. They are typical of naturally fragmented gallery forest of the Colombian and Venezuelan Llanos and adapted to other different habitats (Carretero-Pinzon and Defler 2016). Their adaptation to edge habitats may explain their persistence in anthropogenic forest fragments typical of the study region and the limited role of fragment size. On the other hand, the significant negative effect of the presence of natural fence rows on black-capped capuchins and Colombian squirrel monkeys' abundances can be related with a reduction of dispersal opportunities for these two species which use these landscape elements. This finding highlights the importance that matrix elements such as natural fence rows have on some primate species distributions in these fragmented landscapes. This finding has been reported previously by other

authors who note the use of natural fence rows for dispersal movements (Zunino et al. 2007; Asencio et al. 2009; Pozo-Montuy and Serio-Silva 2007, Carretero-Pinzón et al 2010).

405 **Landscape-scale processes**

The significant effect of the landscape-scale percentage forest cover, for dusky titi monkeys and Colombian squirrel monkeys and patch density for black-capped capuchins and red howler monkeys highlights the need to also consider the landscape-scale in understanding the spatial distribution and abundance of some primate species. This is particularly important for the dusky titi monkey, an endemic species to the study area, whose small body size may limit its ability to successfully disperse in fragmented landscapes where there is a higher risk of domestic dog predation. The influence of percentage of landscape-scale forest cover for another primate species has been reported by Arroyo-Rodriguez et al (2008). They compared landscapes with different compositions, identifying a positive relationship between the total amount of forest and the occurrence of Mexican mantled howlers (*Alouatta palliata mexicana*). In our study, the strong positive influence of patch density on the red howler monkeys' occupancy and negative influence on black-capped capuchins' abundance also highlights the importance of considering the spatial configuration of the landscape for species persistence. The black-capped capuchin, as for other species of capuchins, is an opportunistic species that uses the matrix and has a varied diet and can utilize a range of habitat types. However, this adaptability may also make it susceptible to a higher predation risk while exploiting fragmented resources in the matrix (= *Sapajus* spp.; Chiarello 2003; Fragaszy et al 2004a, c; Pyritz et al 2010). Therefore, more fragmented landscapes with a higher density of patches may have a higher risk of predation. Although a high predation risk is also true for red howler monkeys, their large body size

as well as their minimizing energy strategy (reduced daily travel distance and a diet dependent on a higher proportion of leaves in forest fragments, Arroyo-Rodriguez and Dias 2010), and their suggested use of different fragments and matrix landscape elements to supplement their diet (Pozo-Montuy et al 2012) could explain the positive effect of patch density in this species occupancy in our study area.

Implications for conservation

This study highlights the importance of considering multiple spatial scales for the conservation and management of species of primates in highly fragmented forest landscapes. Our findings also highlight the value of jointly applying landscape ecology and spatial distribution modelling to inform management actions for species that persist in fragmented tropical forest landscapes. It emphasises the need to focus conservation actions on avoiding habitat loss and increasing the amount of suitable habitat available in the landscape to increase the probability of occupancy of the dusky titi monkeys and Colombian squirrel monkeys. There also needs to be an increase in within-patch habitat quality to increase species abundance. This is particularly important for the two endemic species (the dusky titi monkey and the Colombian squirrel monkey) because their distributions occur in areas where habitat loss is increasing (Carretero-Pinzón 2013b; Carretero-Pinzón et al 2009, 2013). For example, maintaining and increasing percentage of forest cover is an important for conserving the dusky titi monkey while also increasing resource availability within forest patches. For the Colombian squirrel monkeys, variables at all scales need to be considered to manage its abundance and occupancy. Some specific actions that could be beneficial for these two species are the implementation of reforestation and regenerating projects, to increase the amount and connectivity of suitable habitat in the landscape.

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455 Ethics Regulations from The University of Queensland (AEC No. GPEM/096/13). The first author wishes to thank the local people and landowners who supported the fieldwork.

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475 **Table 1 Summary of site, patch and landscape variables selected from primate literature as predictive variables of primate occupancy and abundance.**

Variable Name	Description	Reference
Landscape Scale		
Patch density	The number of patches present divided by the area of the buffer (500 m, 1000 m, 2500 m, 3000 m and 3500 m).	Arroyo-Rodríguez et al 2013b
Percentage of forest cover	Percentage of forest present in each buffer area (500 m, 1000 m, 2500 m, 3000 m and 3500 m)	Arroyo-Rodríguez et al 2013b
Patch Scale		
Patch size	Size in hectares of each fragment surveyed	Arroyo-Rodríguez et al 2013b
Patch Shape Index	Index of patch shape is a measure of complexity of the patch shape. This index is calculated with the formula: $SI = P / \sqrt{A\pi}$; where P is the patch perimeter and A is the area measured in meters, respectively. Higher values of SI, means a higher shape complexity (perfect circle, SI = 1.0).	Forman and Godron 1986; Arroyo-Rodríguez et al 2013b
Matrix type	Presence of crops, African palm oil plantations and pastures surrounding the focal fragment. Only two categories were used for the analysis: pastures (includes natural savannahs and small crops) and African palm oil plantations	Anderson et al 2007; Blair and Melnick 2012
Presence of natural fence rows	Presence of natural fence rows adjacent to the focal fragment (unplanted lines of native trees	Carretero-Pinzón et al 2009, 2010

left standing during forest clearance to divide pastures

Site Scale

Canopy Cover	Mean percentage of canopy cover measured every 200 m on each transect	Wieczkowski 2004
Canopy Height	Mean of canopy height measured every 200 m in each transect	Pozo-Montuy et al 2008; Anzures-Dadda and Mason 2007
Presence of trees with fruits, flowers or young leaves	Number of trees with fruits, flowers or young leaves present in the vegetation strips on each transect	Chapman and Onderdonk 1998
Number of food plants consumed by each primate species	Number of all plant species consumed by each primate species in the vegetation strips on each transect	Chapman et al 2006 ¹

¹The list of plant species consumed by each primate species studied here was based on the following references by primate species: *Alouatta seniculus*: Escudero 2005, Beltran 2005, Santamaria 2005, Ramos 2007; *Sapajus apella*: Torres 2005, Ramos 2007, Fragaszy et al 2004b, Gomez-Posada 2012a, 2012b; *Saimiri cassiquiarensis albigena*: Carretero-Pinzon 2000, 2008; *Calliebus ornatus*: Ospina 2006.

490 **Table 2 Summary of model rank, Akaike's information criteria (AIC) for the 95 % confidence set of models for the four primate species in Colombian Llanos. The buffer distance refers to the radius distance in which landscape variables were measured.**

Rank	Model name	AIC	Δ_i	Wi
Red howler monkeys (<i>Alouatta seniculus</i>)				
1	All variables 500	568,61	0	0,8166
2	Site and Patch variables	571,63	3,02	0,1804
Dusky titi monkey (<i>Callicebus ornatus</i>)				
1	Landscape variables 1000m	353,78	0	0,9285
	Patch and Landscape variables			
2	1000m	360,83	7,05	0,0273
Black-capped capuchins (<i>Sapajus apella</i>)				
1	All variables 1000m	879,03	0	0,9953
Colombian squirrel monkey (<i>Saimiri cassiquiarensis albigena</i>)				
1	All variables 500m	1301,7	0	0,9998

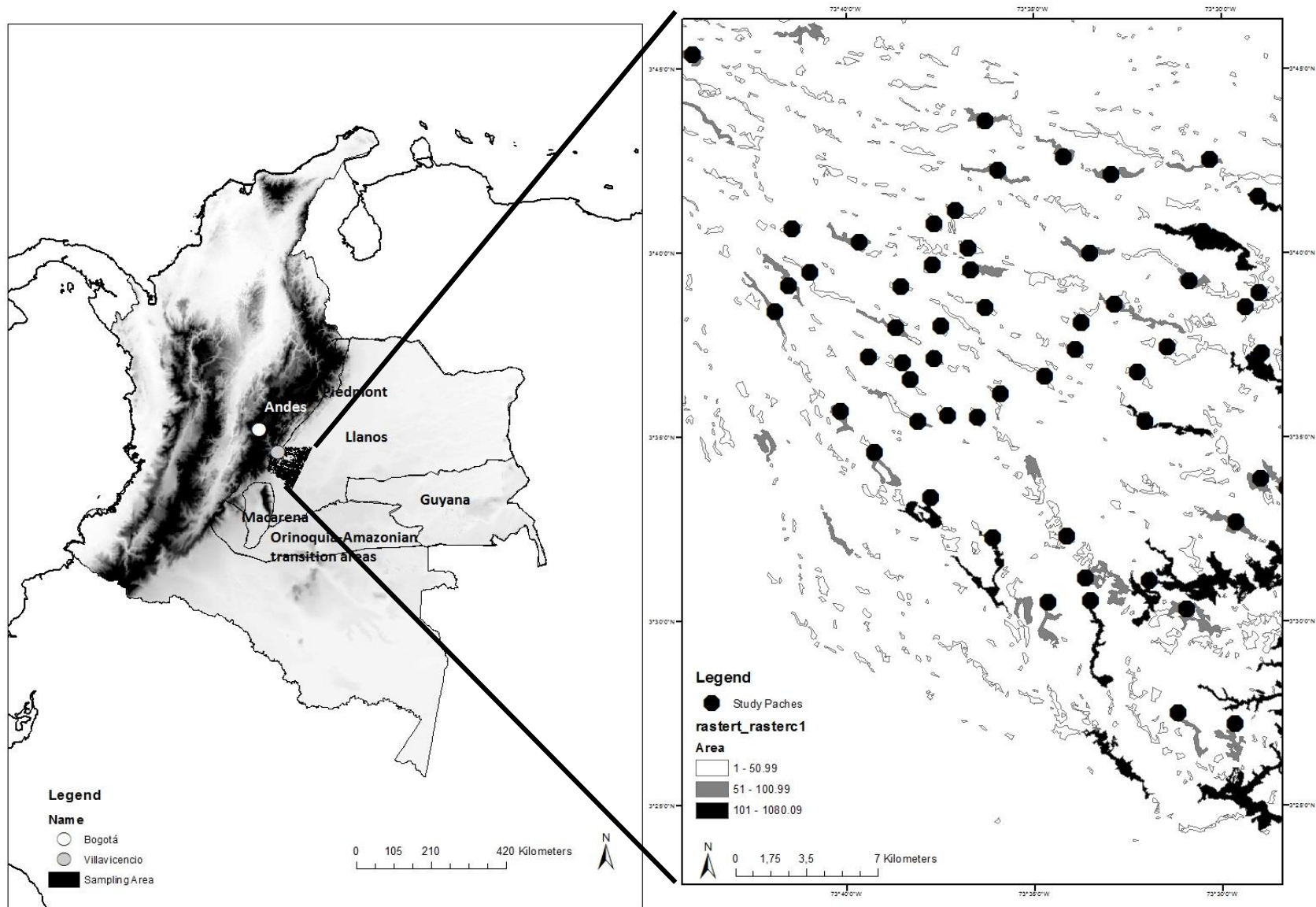
495 **Figure Captions**

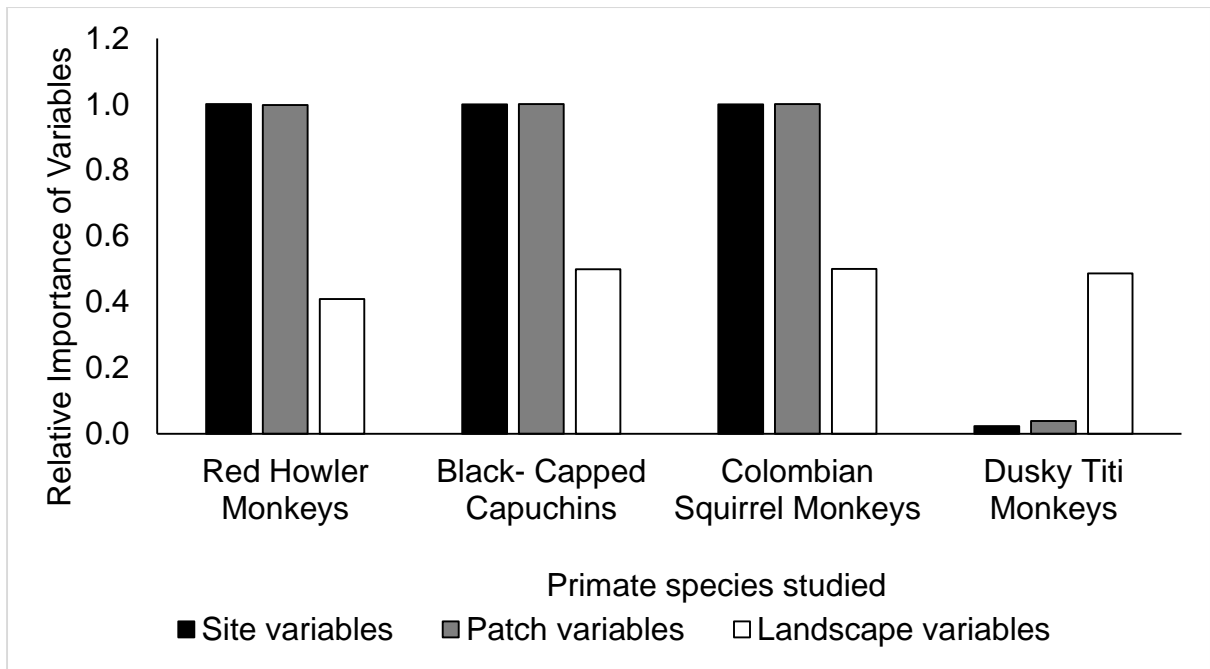
Figure 1 Location of the study area in Los Llanos bioregion (Colombia). Detailed map shows the forest fragments surveyed.

Figure 2 Relative importance of site, patch and landscape-scale variables for each
500 primate species studied.

Figure 3 Effect size and 95 % confidence interval for all the variables included in the top ranked model for all primate species studied. The asterisk (*) in the graphics shows the variables that are significant at $p \leq 0.05$ for the top model.

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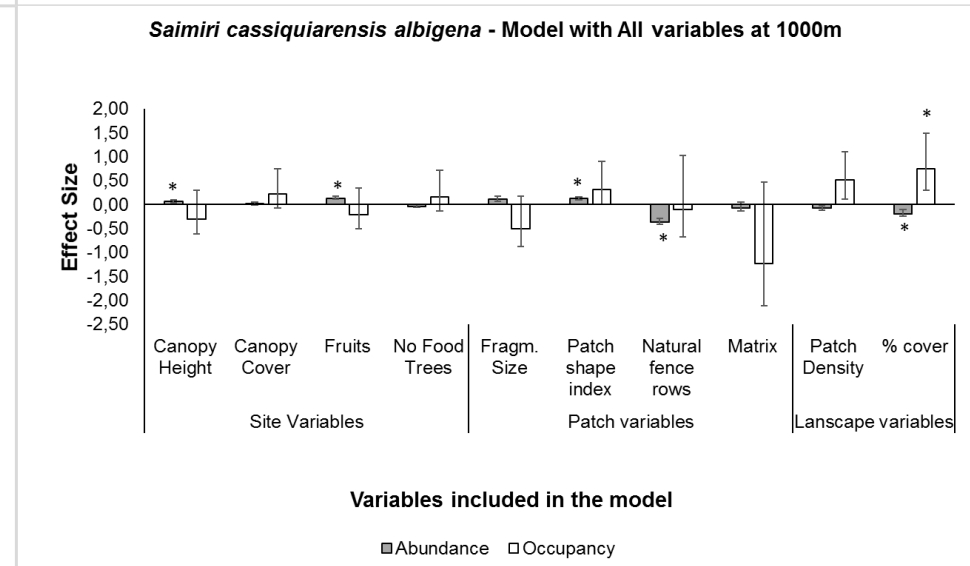
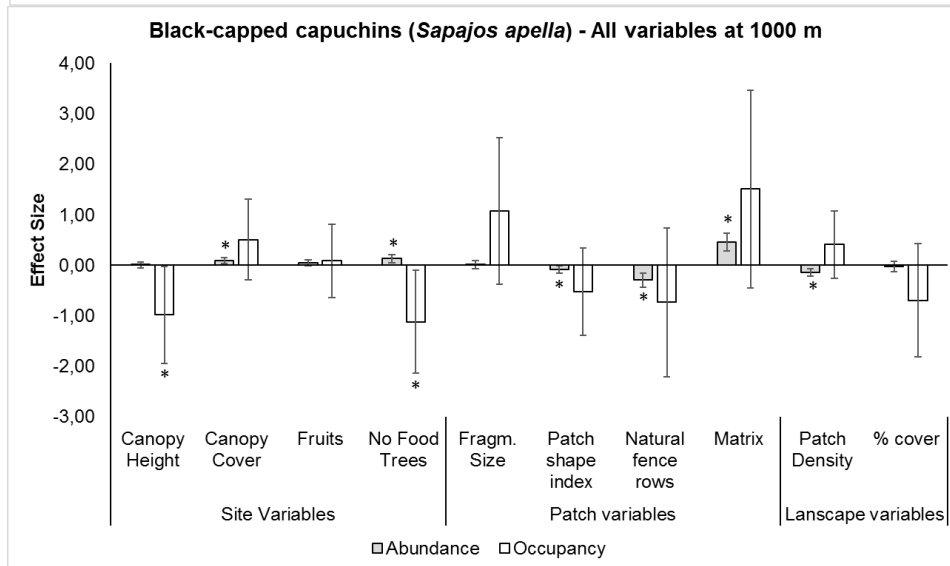
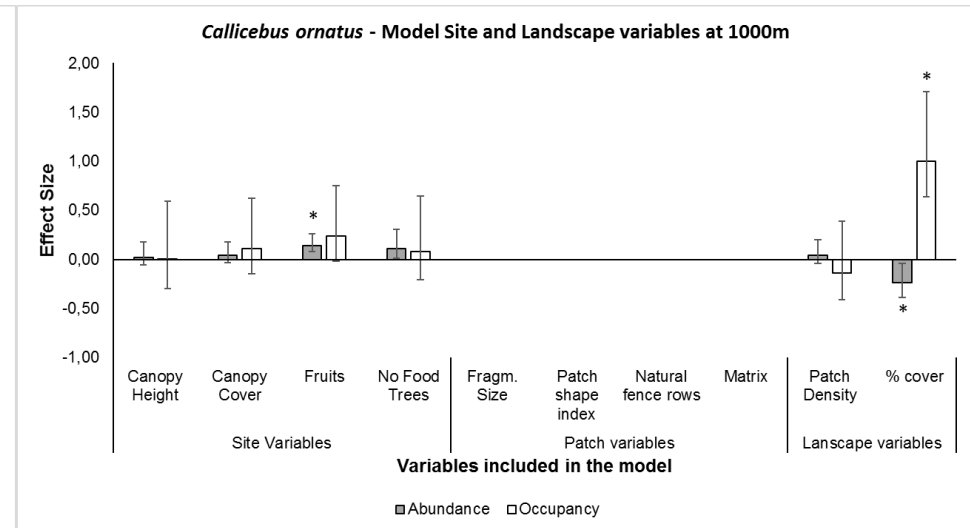
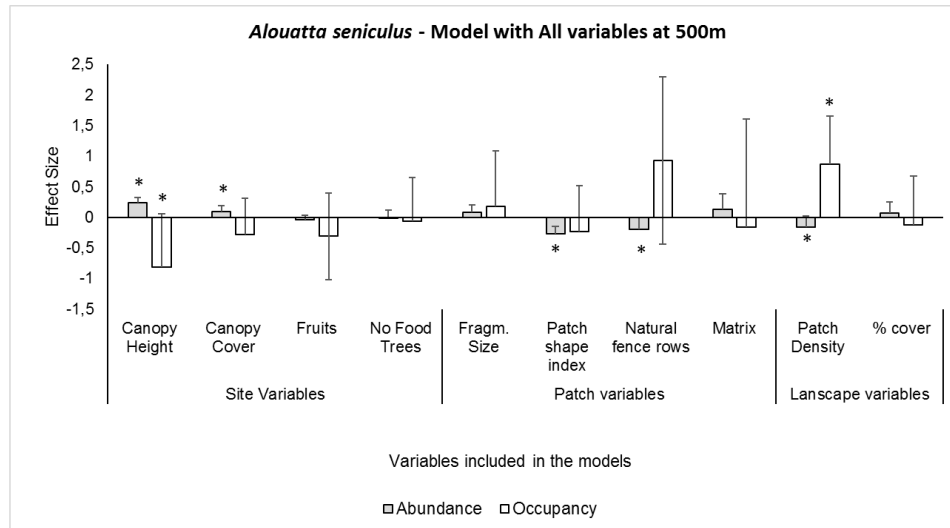




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Appendix 1 Classification of sampling fragments according to a combination of fragment size classes and proportion of forest cover surrounding the fragments within a 1 km buffer.

Fragment size class	Proportion of forest cover class	Combination code	Number of fragments	Number of fragments sampled in each combination of class
1 – 50 ha	0 – 0.33	1	5551	11
1 – 50 ha	0.34 – 0.66	2	90	10
1 – 50 ha	> 0.66	3	37	10
51 – 100 ha	0 – 0.33	4	1275	10
51 – 100 ha	0.34 – 0.66	5	77	10
51 – 100 ha	> 0.66	6	117	10
101 – 1000 ha	0 – 0.33	7	78	10
101 – 1000 ha	0.34 – 0.66	8	0	0

101 – 1000 ha	> 0.66	9	14	10
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Appendix 2. Correlograms for the four primate species studied here. Y-Axis is Moran's Index.

