

Effect of landscape modification on primate assemblages of the Magdalena River Valley, Colombia

Efecto de la modificación del paisaje sobre el ensamblaje de primates en el valle del río Magdalena, Colombia

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ABSTRACT

Population and community dynamics are affected by local landscape disturbances, and the answer of each species to these changes could differentially affect species survival. Natural land cover in the Magdalena River valley, Colombia, has been reduced by almost 70 % and fragmented. There inhabit isolated and reduced populations of *Alouatta seniculus*, *Ateles hybridus*, *Cebus versicolor*, and *Saguinus leucopus* (Primates). To understand the effect of fragmentation over these species, the relationship between altitude, landscape and class metrics, and plant structure and diversity with the population density of these four primates in 20 localities were assessed. Additionally, the relationship between the density of *A. hybridus*, assumed as a better competitor, and the density of the other primates was assessed. Mean shape index was the most related variable and affected positively the density of *A. hybridus*, *C. versicolor*, and *S. leucopus* and negatively that of *A. seniculus*. Weight class index was the second more important variable, the four primates increased their density where more mature is the plant cover. Diameter at breast height was positively related with the density of *A. hybridus* and *C. versicolor*, negatively related for *A. seniculus* and not related to *S. leucopus* density. Tree density was related negatively with the density of *A. seniculus* and positively with *S. leucopus*. *A. hybridus* was related to the density of the other primates, positively to *A. seniculus* and negatively to the other two species.

Keywords. New World monkeys, relative abundance, habitat transformation



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RESUMEN

Las dinámicas poblacionales y de las comunidades son afectadas por los disturbios en los paisajes locales, y las respuestas de cada especie a esos cambios podrían afectar diferencialmente su sobrevivencia. La cobertura vegetal natural en el valle del río Magdalena en Colombia ha sido reducida casi en un 70 % y está fragmentada. En este paisaje habitan en poblaciones reducidas y aisladas *Alouatta seniculus*, *Ateles hybridus*, *Cebus versicolor* y *Saguinus leucopus*. Para evaluar el efecto de la fragmentación sobre estas especies se evaluó la relación de la altitud, métricas de paisaje y clase, y estructura y diversidad de plantas con la densidad poblacional de los cuatro primates en 20 localidades. Adicionalmente, se evaluó la relación entre la densidad de *A. hybridus*, asumiéndolo como mejor competidor, con la de los otros primates. El índice medio de forma fue la variable más relacionada con la densidad y afectó positivamente a *A. hybridus*, *C. versicolor* y *S. leucopus* y negativamente a *A. seniculus*. El índice ponderado de coberturas fue la segunda, los cuatro primates incrementan la densidad cuando más madura es la cobertura vegetal. El diámetro a la altura del pecho estuvo relacionado positivamente con la densidad de *A. hybridus* y *C. versicolor*, negativamente con *A. seniculus* y no tuvo efecto para *S. leucopus*. La densidad de árboles estuvo relacionada negativamente con la densidad de *A. seniculus* y positivamente con la de *S. leucopus*. La densidad de *A. hybridus* resultó relacionada con la de los otros primates, positivamente con *A. seniculus* y negativamente con las otras dos especies.

Palabras clave. Primates del nuevo mundo, abundancia relativa, transformación de hábitat.

INTRODUCTION

Anthropogenic disturbances such as logging and forest clearing constitute major threats to biodiversity (Michalski and Peres 2005). When a disturbance changes environmental conditions, the natural community can suffer profound, immediate, and cumulative effects (Allesina *et al.* 2006). However, as different species have different ecological attributes—their scale of movement, life history, longevity, and what constitutes its habitat—that determine their niche and their capacity to survive in a modified landscape. Thus, some become more abundant or expand their range, while others may drop and even become locally extinct (Boyle and Smith 2010, Chapman *et al.* 2010). The loss of a species or a change in its abundance, particularly for those that interact with many other species, can have a considerable effect on ecological processes (Lindenmayer and Fischer 2013). It is, therefore, important to consider multiple anthropogenic factors when assessing the synergistic effects of human activities, in order to understand how species respond in fragmented landscapes (Benchimol and Peres 2013).

The west margin of the Magdalena River valley and east slope of the Cordillera Central have a history around

150 years of intensive transformation, and the natural land cover has been reduced by almost 70 %, transforming it into a highly fragmented landscape (IDEAM 2009). The floral association in the forest remnants have been impacted at different levels and different ways, affecting successional processes.

Four primates are found in this region: Red howler monkeys (*Alouatta seniculus* Linnaeus, 1766), brown spider monkeys (*Ateles hybridus* Geoffroy, 1829), white fronted capuchins (*Cebus versicolor* Pucheran, 1845) and white footed tamarins (*Saguinus leucopus* Günther, 1877). *A. seniculus* is an atelid that weights around 7 kg that inhabits a broad range of forest covers from transitional vegetation until riparian and mature forest up to 3200 masl. It is a facultative leaf-eater monkey when the fruit is scarce (Link *et al.* c2021c). *A. hybridus* is an atelid primate too around that weights 7.5 kg. It is dependent of mature forest, but some groups could be found in fragmented forests. It is highly frugivorous and feed largely on ripe fleshy fruits, which comprise approximately 80 % of its diet (Link *et al.* c2020b). *C. versicolor* is a cebid primate that weights around 2.5 kg that inhabits tropical lowland forests and seasonally flooded forests. It has an omnivorous diet, eating predominantly

ripe fruits and invertebrates, but also other vegetative parts of plants, vertebrate prey and eggs (Link *et al.* 2021d). *S. leucopus* is a small (460 g) callitrichid that inhabits from transitional to mature, mainly humid, and subhumid forests. Its diet is based on fruits and is supplemented with invertebrates, bark, and flowers (Roncancio *et al.* 2012). and *S. leucopus* are endemic to Colombia. *C. versicolor* is Endangered (Link *et al.* 2021d) and *S. leucopus* is Vulnerable (Link *et al.* 2021a). *A. hybridus* is categorized as Critically Endangered (Link *et al.* 2020b). *A. seniculus* is categorized as Least Concern even though its populations are decreasing (Link *et al.* 2021c). The main threat to these taxa is the reduction and fragmentation of their habitat resulting from the combined effects of selective extraction, hunting and trade, and the lack of no-take protected areas as National Natural Parks (Londoño and Gómez-Posada 2010, Roncancio *et al.* 2011, Defler *et al.* 2013).

The responses of these primates to disturbances, and their specific tolerance thresholds to the resulting landscape configuration are, however, not well understood (French and Smith 2005, Ewers and Didham 2007) due to the lack, among other things, of a landscape model grounded on a robust mathematical approach (Reckhow 1990, Wade 2001, Fahrig 2003, Arroyo-Rodríguez *et al.* 2013). In this study, I estimated the relationship of different traits such as size, shape, isolation distance and land cover composition, plant structure, and plant diversity, with the population density of these four primates. I also estimated the relationship between the population densities of these primates under a theoretical framework of compensation density (Peres and Dolman 2000). I assumed that *A. hybridus* is a better competitor than other species due to its large size and specialized frugivorous diet (Defler 2010). My hypothesis was that the changes in the population density of primates could be explained by changes in size, shape, isolation distance, composition of plant covers and plant structure and diversity, although, differentially in type and intensity and affected by the interspecific interactions of the assembly.

MATERIALS AND METHODS

Study area

I conducted fieldwork in 20 localities (local landscape), randomly selected with respect to the primate presence. In other words, the presence of the primates was not

a criterion to select the localities (WGS 84 – decimal degrees: Amaní -74.88611W, 5.56083N; Berlin -74.57354W, 6.52191N; Cerro Las Campanas -74.45416W, 8.23381N; Cerros de Corcovado -74.46314W, 8.46191N; Charca de Guarinocito -74.73472W, 5.33972N; EL Pajuil -74.69466W, 5.88033N; Falan -74.97000W, 5.11889N; Fresno -75.01475W, 5.20222N; Guamo 2 -74.69180W, 5.86057N; Guamo1 -74.70102W, 5.86893N; La Florida -74.19829W, 8.57968N; La Pedrera -74.95722, 5.57611; La Primavera -74.96667W, 5.51667N; Las Margaritas -74.59761W, 6.56341N; Mariquita -74.94606, 5.22742N; Playas -74.92331W, 6.26989N; Porce III -75.18909W, 6.83280N; Río Manso -74.77361W, 5.67556N; Venecia -74.83861W, 5.64278N; Yalí -74.87281, 6.67851N). These areas are located in the middle Magdalena River valley in Colombia, distributed from the north of the department of Tolima to the south of the department of Bolívar, extending through the eastern parts of the departments of Caldas and Antioquia (Fig. 1). The altitude of the locations ranged from 190 to almost 1400 m (Table 1), with mean temperatures of 19 to 27 °C and mean annual precipitation

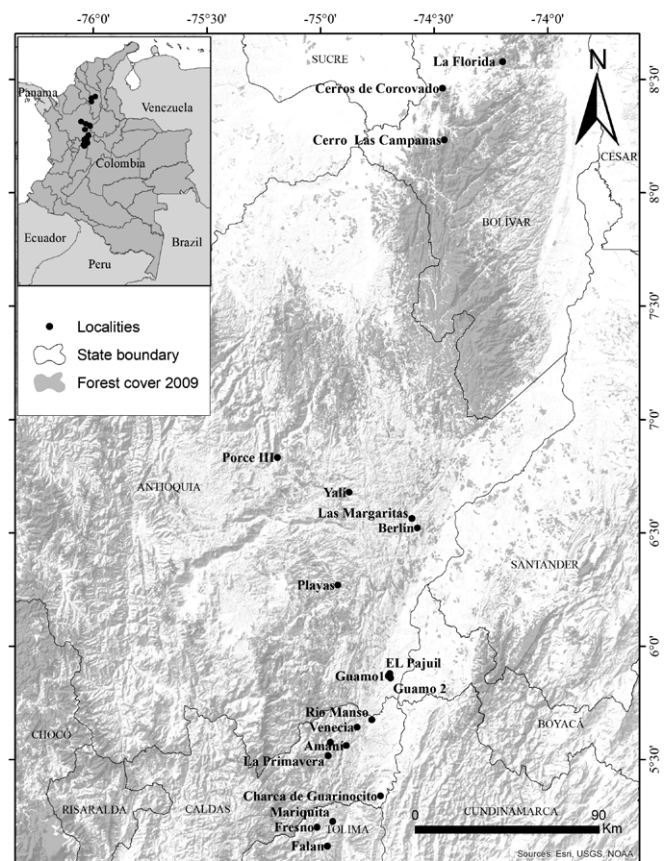


Figure 1. Location of the sampling localities along the Magdalena River valley, Colombia

Table 1. Local features, landscape and class metrics selected as explanatory variables.

Locality	Altitude	Weighted class index (WCI)	Interspersion juxtaposition index (IJI)	Mean shape index (MSI)	Landscape area (ha)	Forest proportion in local landscape
Falán	983	3.71	16.30	2.08	4213	0.21
Fresno	1385	3.57	1.00	2.29	1428	0.18
Mariquita	885	3.89	48.79	2.06	3382	0.22
Guarinocito	191	2.81	67.65	1.80	520	0.22
Primavera	679	3.89	55.36	2.58	742	0.35
Amaní	534	5.97	81.39	2.11	944	0.58
Pedreira	814	5.66	66.39	3.14	664	0.59
Venecia	416	5.29	60.49	1.30	142	0.49
Río Manso	212	6.15	1.00	1.89	461	0.70
Guamo 2	187	4.42	1.00	1.28	71	0.80
Guamo 1	223	4.75	1.00	1.21	10	0.91
Pajuil	192	3.63	37.12	1.32	45	0.54
Playas	1003	6.91	59.55	1.46	412	0.77
Berlín	568	6.89	87.69	1.96	755	0.81
Margaritas	606	7.24	95.87	1.57	639	0.80
Yalí	1133	5.04	70.37	2.05	189	0.35
Porce III	934	3.72	86.31	1.36	576	0.54
Campanas	354	7.58	46.01	2.33	881	0.99
Corcovado	414	7.81	1.00	1.56	573	1.00
La Florida	200	6.70	71.84	1.59	483	0.84

ranging from 1800 to 4200 mm (Hijmans *et al.* 2005). The region is approximately 48 000 km², comprising crops (23 %), pasture (22 %) and natural vegetation (32 %) (the remaining 23 % is for other land use). Natural vegetation includes dense forest fragments of less than 0.1 to 300 and 6000 km² (mean = 60 km² ±1640), with shapes that tend to be irregular (Mean Shape Index = 1.8) and medium connectivity (interspersion juxtaposition index = 52, range: 0 < IJI ≤ 100) (Statistics estimated for author from IDEAM 2009).

Primate population density

Sampling was done between 2005 and 2011. To estimate primate population densities, I used distance sampling along linear transects (Buckland *et al.* 2001) and censuses in two localities where I could assume that complete counts were possible. With this method, transects can be resampled to increase the sample size to calculate encounter rate, and individual recognition is not necessary. The number and length of transects varied depending on the extension, shape and topography of each site (Table 2). Transects were distributed throughout each site to obtain

a representative density estimation. In two localities, Guarinocito and Guamo 1, population density was estimated using censuses, because these localities are fragments without structural connectivity of forest, of 0.21 and 0.1 km², respectively, and are elongated. I therefore, assumed that it was possible to evaluate the entire area of interest and count all its primates individually. Population densities of *A. seniculus*, *A. hybridus* and *C. versicolor* in Florida, *A. seniculus* in Pedreira and Río Manso, and *A. hybridus* and *C. versicolor* in Margaritas, were estimated using the detection function obtained in similar localities of this study, because the number of detections were too low (<10) in these localities to enable a robust analysis in Distance. Some population densities were taken from secondary information (Santamaría *et al.* 2007, Rojas-V. 2009). I assumed that the results are comparable given that they used the same methodology.

Local features and landscape and class metrics of each site

Initially, I defined a local landscape for each locality through a circle that was the smallest perimeter containing the transects used to estimate primate population

Table 2. Sampling design and sampling effort to estimate the population density of the four primate species using distance sampling with line transects. Guarinocito and Guamo 1 are not in this table because no distance sampling line transects were used there.

Locality	No. of transects	Transect length (km) Mean (SD)	Mean number of repetitions	Total sampling effort (km)
Falan ¹	10	1.2 (0.1)	5	57.9
Fresno ¹	10	1.1 (0.04)	5	56.8
Mariquita ¹	12	1.1 (0.1)	5	69.04
Primavera	8	0.8 (0.1)	13	84.9
Amaní ²	5	1.4 (0.5)	25.2	180.6
Pedraera	8	1.3 (0.3)	5.6	86.7
Venecia	6	0.8 (0.2)	16	70.5
Rio Manso	9	1.0 (0.2)	6.5	58.1
Guamo 2	18	0.2 (0.03)	17.4	55.8
Pajuil	10	0.4 (0.1)	58.5	202.7
Playas	44	0.3 (0.03)	8.1	109.8
Berlin	26	0.38 (0.06)	15.6	148.07
Margaritas	31	0.3 (0.01)	17.9	191.9
Yalí	40	0.3 (0.05)	21.6	228.5
Porce III	31	0.3 (0.03)	12.7	122.9
Campanas	34	0.5 (0.09)	16.9	283.0
Corcovado	16	0.5 (0.1)	15.7	133.5
La Florida	28	0.3 (0.02)	20.5	170.3

¹Rojas-V. (2009); ²Santamaría *et al.* (2007)

densities (Fig. 2). For Guarinocito and Guamo 1, the entire fragments were contained in the smallest perimeter. This circle was overlaid with a raster of land cover (IDEAM 2009), a raster of mean annual temperature and mean annual precipitation from BIOCLIM (Hijmans *et al.* 2005), and with a Digital Elevation Model (USGS 2000). For each locality I measured three local features, two landscape metrics and twelve class metrics (in the class where the population density was estimated). Local features included: mean altitude, mean annual temperature, and mean annual precipitation. Landscape metrics included: Shannon index (SI) and a weighted class index (WCI). I developed the WCI to integrate an index that allowed to measure the land cover composition and structure, not only the land cover structure as SI (Fahrig *et al.* 2011). To estimate the WCI, I qualified class types as follows: Dense forest = 8, Open forest = 7, Fragmented forest = 6, Scrubland = 5, Grassland (natural) = 4, Crops = 3, Pasture = 2, and wetland, open soil and urbanized area = 1. Then, I multiplied the value of each class type by its relative size in the local landscape. Finally, I added the results of the multiplication to obtain the index values. In this way, the value for

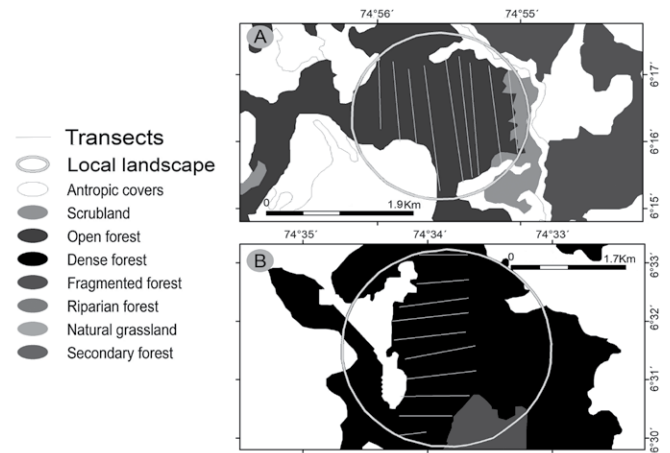


Figure 2. Example of the local landscapes delimitation to estimate the local features, landscape and class metrics. A = Playas, B = Berlin.

a local landscape with predominantly dense forest, was close to eight, while for one with more pasture and crops, the values were between two and three. Class metrics, for the class in the local landscape where the population density estimation was done, were as follows: mean core area (MCA), total core area (TCA), total core area index (TCAI), core area density (CAD), interspersed juxtaposition index (IJI), area weighted mean shape index (AWMSI), mean shape index (MSI), mean patch fractal dimension (MPFD), area weighted mean patch fractal dimension (AWMPFD), total edge (TE), mean patch size (MPS) and core area (CA). All analyses were done using ArcGis 10.5, Patch Grid tool.

Plant structure and diversity

In the forest where the primate densities were estimated of each locality, six or seven rectangular plots of 0.20 ha (50 m × 4 m) were randomly placed. I stopped sampling when the standard deviation of the diameter breast height (DBH) was stable. I took samples for species identification, and determinations were carried out in the herbaria of the Antioquia –HUA-, and Caldas –FAUC- universities. Mean DBH and height, tree density, and the Inverse Simpson Index (ISI) were estimated for each locality as explanatory variables.

Data Analyses

Population density. I analysed data using Distance 7.1 software (Thomas *et al.* 2010). Analyses were performed separately for each locality. Detection functions were selected according to the fit between the frequency distribution of detection distances and theoretical models (Key functions and adjustment terms). The models tested were:

Half-normal (Cosine, Hermite polynomial), Uniform (Cosine, simple polynomial), and Hazard rate (Cosine, simple polynomial). I chose the best fitting model according to the Akaike Information Criterion. Population density variance (CV) was empirically calculated as the sum of the sampling variances of encounter rate, estimates of detection probability, and group size. I used the expected group size estimated from the regression between group size and detection probability to estimate the density (Buckland *et al.* 2001). In Guarinocito and Guamo 1 where I used censuses, the density was estimated divided the number of individuals over the size of the fragments. Distance sampling is one of the most often used methods to obtain precise and unbiased estimations with a given sampling effort, so I assumed that the results obtained with distance sampling and the censuses are comparable (Cassey and McArdle 1999, Norvell *et al.* 2003).

Relationship of the explanatory variables in primate density. Because the vegetation was sampled in only fifteen out of the 20 localities, I analysed the relationship of the density of primates and the local features, landscape, and class metrics of the localities independent of the plant structure and diversity. First, I performed analyses of association between the explanatory variables in order to eliminate collinearity (Autocorrelation) (Cushman *et al.* 2008). I used the Spearman coefficient of correlation to evaluate this association (data did not distribute normally, Shapiro-Wilk test: $W = 0.90$, $P = 0.04$). When two variables were correlated (Spearman rank correlation coefficient: $P-r^s < 0.05$), one of them was eliminated (Sokal and Rohlf 1995), considering the precision of the measurement. However, the main criterion was mathematical. Finally, four out of the 17 local features, landscape and class metrics were considered (altitude, interspersed juxtaposition index, mean shape index and weighted cover index) and, likewise, only the density of the Variegated spider monkey out the four primates and the four plant structure and diversity variables were considered as explanatory variables.

Given that the population density is a variable expressed in area, I assumed that it has Poisson probability distribution and, thus, the relationships were evaluated using Poisson regressions. This was done using a Bayesian approach and using an uninformative prior distribution to the precision of the explanatory variable effects, and an uninformative prior distribution to the intercept (alpha)

and slopes (beta). I assumed that the posterior distributions of the intercept and the slope of each variable had a normal distribution (McCarthy 2007, Pfeiffer *et al.* 2008). I did not consider the interaction (multiplicative effects) between the explanatory variables. In order to select the best model, the Deviance Information Criterion (DIC) was used. Initially, I ran the model with all of the possible explanatory variables and estimated the DIC. Later, I extracted one variable, ran the model and estimated de DIC again. If the DIC was higher, I returned the variable and extracted another. If the DIC resulted lower, I removed definitely that variable and extracted another, until I got the model with the lowest DIC. Estimation of the intercept and slopes was done using Markov chains with 100 000 iterations, and taking account from the 10 001 iteration to the final estimation. The DIC was estimated with 100 000 additional iterations. The analyses were performed using OpenBugs 3.2.2 software (Lunn *et al.* 2000).

RESULTS

Population densities

Saguinus leucopus was found in 20 localities with densities of 6.0 to 149 ind/km². *A. hybridus* was found in seven localities with densities of 0.62 to 58 ind/km². *C. versicolor* was found in six localities with densities of 1.04 to 103 ind/km², and *A. seniculus* was found in nine localities with densities of 0.21 to 75 ind/km² (Table 3).

Local features, landscape, and class metrics

The localities were at elevations between 191 m and 1385 m. Corcovado, Campanas and Margaritas had the largest area of dense forest while Guarinocito and Fresno were the localities with largest areas of crops and pastures (Table 1; WCI). The localities with the more aggregated forests were Fresno, Río Manso, Guamo 1, Guamo 2, and Corcovado (One fragment with all pixels together), while Margaritas had the most disaggregated forest patches (Table 1; IJI). The localities with the most regular shaped forests were Guamo 1, Guamo 2 and Pajuil, while the forests of Pedrera and Primavera were the most elongated (Table 1; MSI).

Regarding plant structure and diversity, Guarinocito showed the highest mean DBH following by Corcovado and Río Manso. Playas had the smallest mean DBH. Río Manso, Amaní and Berlín had the tallest trees. The highest

Table 3. Population density (individuals/km²) of the four primate species recorded in the surveys. D= Population density, CI= Confidence interval 95%, CV= Coefficient of variation.

	<i>Saguinus leucopus</i>			<i>Ateles hybridus</i>			<i>Cebus versicolor</i>			<i>Alouatta seniculus</i>		
Locality	D	CI	CV	D	CI	CV	D	CI	CV	D	CI	CV
Falán ¹	19	8–46	10.74	0	–	–	0	–	–	0	–	–
Fresno ¹	9	2–32	63.55	0	–	–	0	–	–	0	–	–
Mariquita ¹	103	55–191	30.6	0	–	–	0	–	–	0	–	–
Guarinocito	67	–	–	0	–	–	0	–	–	0	–	–
Primavera	149	78–284	31.9	0	–	–	0	–	–	0	–	–
Amaní ²	54	35–84	18.6	0	–	–	0	–	–	0	–	–
Pedraera	101	58–177	27.4	0	–	–	0	–	–	1.1	–	–
Venecia	125	55–286	37.6	0	–	–	0	–	–	0	–	–
Río Manso	142	103–196	15.8	0	–	–	0	–	–	2.9	–	–
Guamo 2	148	69–316	38.4	35	21–59	26	103	57–189	31	75	44–128	27
Guamo 1	67	–	–	0	–	–	0	–	–	0	–	–
Pajuil	24	15–39	21.8	39	21–73	31	0	–	–	35	24–52	20
Playas	46	32–68	19.2	0	–	–	0	–	–	0	–	–
Berlin	51	36–72	15	5.4	3–11.3	40	31.5	14–74	40	4	1.5–10.4	50
Margaritas	110	7–160	18.9	1.1	–	–	1.04	–	–	12	5–29	45
Yalí	6	3–10	31.5	0	–	–	0	–	–	0	–	–
Porce III	11	5–26	41.9	0	–	–	0	–	–	0	–	–
Campanas	69	44–107	22.5	58	33–103	29	20	9–46	43	0.5	–	–
Corcovado	47	32–69	19.2	32	19–53	25	10	5–22	37	17	9–31	31
La Florida	63	45–88	17.4	0.62	–	–	1.5	–	–	0.2	–	–

¹Rojas-V. (2009); ²Santamaría et al. (2007)

tree densities were found in Primavera and Berlín, and the lowest in Porce III (Table 4). The localities with the highest tree diversity were Río Manso and Berlin, while Porce III, Playas and Guarinocito showed the lowest tree diversity values.

Relationship of the explanatory variables in primate densities

Higher population densities of *S. leucopus* were recorded in localities with elongated, denser, and taller forests, in localities at lower elevations and with higher structural connectivity. These results also show that *S. leucopus* densities decrease when the density of *A. hybridus* increase (Table 5). Population densities of *C. versicolor* and *A. hybridus* tended to be higher when there was less connectivity. Regarding with plant structure and diversity, these results suggest that *C. versicolor* densities are positively affected only by tree DBH, while *A. hybridus* populations tend to increase in forests with higher DBH values, lower tree-height, and higher plant diversity (Table 5).

Population densities of *A. seniculus* were higher with denser forests, and lower in more elongated forests. Contrary to the pattern found for *S. leucopus* and *C. versicolor*, the population densities of *A. seniculus* increase when the density of *A. hybridus* increase and decrease when the lower DBH and tree density increase (Table 5).

DISCUSSION

These results show that the population densities of the four studied species are very variable among different localities, from local extinction, for example to *A. hybridus* in all localities in Caldas, to some of the highest population densities estimated for the taxon or congeneric species (Crockett et al. 1987, Chapman and Balcomb 1998, Gómez-Posada et al. 2007, 2009, Roncancio and Gómez-Posada 2009, Gómez-Posada et al. 2010, Williams-Guillén et al. 2013, De Luna and Link 2018). This indicates that different zones in the Magdalena River valley have been affected in different

ways. Differences in the local occupation between species indicate that *S. leucopus* in this landscape could resist better the degradation, reduction and fragmentation of its habitat and synergic threats such as trade, given that, in spite of the large variation in its densities, it was found in all 20 localities. The other three species, in contrast, show less tolerance to changes in their habitats, and face a local extinction probability close to 60 % even though there are remnant forests, based in proportion of the occupied localities to each primate species.

Results obtained for *C. versicolor* and *A. hybridus* are consistent with the patterns found for *Cebus capucinus* (Linnaeus, 1758) and *Ateles geoffroyi* (Kuhl, 1820) in Nicaragua and with *Cebus libidinosus* (Spix, 1823) in Bolivia (Pyritz *et al.* 2010) where they have suffered local extinctions. Usually, *A. seniculus* and other howlers are recognized as being able to tolerate relatively higher levels of habitat fragmentation, as in many areas it is the only primate taxon to persist and in some it can be found at very high densities (Crockett *et al.* 1987, Chapman and Balcomb 1998, Gómez-Posada *et al.* 2007, 2009, Roncancio and Gómez-Posada 2009, Gómez-Posada *et al.* 2010, Williams-Guillén *et al.* 2013, De Luna and Link 2018). Red howlers have been locally extirpated in a number of localities in the Magdalena valley, and their densities are very variable in the localities where they are still present. A study of *Alouatta guariba* (Humboldt, 1812) carried out in southern Brazil showed a similar situation to that found for red howler populations in this study (Silva and Bicca-Marques 2013). The population depletion of howler monkeys could become driven by synergic threats and the degradation of the ecological conditions in the forest fragments.

Table 4. Plant structure and diversity for each locality. DBH=Diameter breast height

Locality	DBH	Height	Tree density	Inverse Simpson Index
Falán ¹	–	–	–	–
Fresno ¹	–	–	–	–
Mariquita ¹	–	–	–	–
Guarinocito	32.95	13.95	325	11.95
Primavera	18.34	12.79	1087.5	18.68
Amaní ²	20.2	15.32	730.26	–
Pedraera	17.24	11.53	608.33	21.54
Venecia	20.3	13.25	525	27.13
Río Manso	23.38	15.67	558	85.04
Guamo 2	–	–	–	–
Guamo 1	21.89	12	458.33	23.023
Pajuil	19.67	10.25	383.33	14.38
Berlin	20.4	14	841	46.16
Playas	17	11.5	516.66	10.33
Margaritas	18.53	9.78	650	12.51
Yalí	18.46	12.96	533.33	27.67
Porce III	21.04	8.66	525	10.15
Campanas	21.9	11.3	657.14	31.1
Corcovado	27.41	13.64	542.86	21.71
Florida	17.5	10.7	630	29.15

¹Rojas-V. (2009); ²Santamaría *et al.* (2007)

Different features, landscape and class metrics are related differently the population densities of the four studied primate species, even though forest shape had the most significant effect on population density for all species. This situation was also found in Mexico, where the occupancy

Table 5. Relationship between the explanatory variables and the density of the studied species. WCI = Weighted core index; IJI = Interspersion juxtaposition index; MSI = Mean shape index; TD = Tree density; DBH = Diameter at breast height; SI = Shannon index.

	<i>Alouatta seniculus</i>		<i>Ateles hybridus</i>		<i>Cebus versicolor</i>		<i>Saguinus leucopus</i>	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Altitude			-0.005	0.001	-0.006	0.002	-0.001	0.001
WCI	0.221*	0.079	0.664*	0.085	2.064*	0.657	0.080*	0.021
IJI			0.001	0.003	0.033	0.007	-0.001	-0.003
MSI	-4.672**	0.598	1.437**	0.271	3.609**	1.335	0.640**	0.063
<i>Ateles</i> density	0.072	0.007			-0.018	0.222	-0.021	0.002
Height			-0.437**	0.068			0.110**	0.017
TD	-0.008*	0.001					0.001	0.001
DBH	-0.078**	0.020	0.161*	0.024	2.382**	0.079		
SI			0.024	0.006				

**Main effect; *Secondary effect; Blank = no significant effect

of all primates was negatively affected by shape irregularity (Arroyo-Rodríguez *et al.* 2008). In this study the effect of the shape was not the same for the four primates. While the population density of *A. seniculus* tended to decrease in elongated forests, the densities of the other three primates tended to increase (Lenz *et al.* 2014). High densities, however, do not always mean high abundance or better conditions for the population. High densities in forest remnants have been explained as a crowding effect (Chiarello and de Melo 2001, Peres 2001, Baranga 2004, Martins 2005, Rode *et al.* 2006). If the crowding is the first effect that suffer these primates, probably, the howler monkeys become affected later than the other species given that it could use some types of forest land cover that the other species do not use and in this way the population is diluted in a more extended area (Crockett 1998, Gómez-Posada and Londoño 2012). On the other hand, depending on the moment of the fragmentation process and the regeneration dynamics, early fragmentation, reversal isolation by regeneration in transitional crops, the smaller or more mobile species could or must use the elongated fragments to satisfy their ecological requirements, increasing their relative abundance, while the howler just need a small home range in the core areas (Matthews 2009, Spehar *et al.* 2010, Palma *et al.* 2011, Alba-Mejia *et al.* 2013). In this sense the fragment shape is an important factor that determines population size in fragmented landscapes, thus, habitat restoration efforts may be more effective if they focus on saving the forest fragments with less elongated shapes and keep a minimal width in the corridors (Ewers and Didham 2007).

Forest cover (WCI) was the second most important factor, when WCI was higher the population densities of all four species tend to be higher. Similarly, forest land cover was one of the main predictors of species persistence in isolated forests in a continental-scale analysis of neotropical primates (Benchimol and Peres 2013) and in two primate-assemblages in French Guiana and Ecuadorian Amazonia (Youlatos 2004). Forest land cover could be a determinant factor in the survival of these species (Sorensen and Fedigan 2000). Additionally, the general structure of the land cover landscape, associated with the matrix has been recognized as a factor that determines the presence of some primates in a fragment (da Silva *et al.* 2015).

Regarding plant structure, DBH was the main determining factor but, while the howler densities tend to be lower in forest with higher densities of large-trunked trees, densi-

ties of spider monkeys and capuchins tends to higher. In contrast, *Alouatta palliata* (Gray, 1849) has been shown to prefer fragments with a greater density of large trees (DBH > 60 cm) (Arroyo-Rodríguez *et al.* 2008). The equitability in the plant diversity was important for *A. hybridus* only, highlighting the high ecological requirements to this species and determine the necessity of focal intervention as specific plant enrichment to habitat restoration (Boyle and Smith 2010).

There is broad evidence that some types of agro-ecosystems in a fragmented landscape could be useful as temporary or additional habitat for different taxa (Estrada *et al.* 2006, Guzmán *et al.* 2016). However, I found that the primates in the Magdalena River valley are concentrated in zones with considerable areas of mature forest (WCI), including *S. leucopus*, even though tamarins and marmosets have preferences for regenerating forest (Snowdon and Soini 1988, Rylands 1996, Garber 1998, Defler 2010). This pattern is probably related to the ecological stability and resilience provided by mature forests. Thus, the biodiversity conservation at a landscape scale requires considerations regarding a minimum proportion of dense forest in the mosaic.

The densities of *A. hybridus* were significantly related to those of the other three primates, but, while howlers tend to be found in higher densities in forests with higher densities of *Ateles*, the other two species tend to be less abundant. The reason may be related to hunting pressure. Howler monkeys come second to spider monkeys as preferred game by hunters (Freese *et al.* 1982, Rodríguez-Luna *et al.* 1996, Sorensen and Fedigan 2000, da Silva *et al.* 2005). So, it could be possible that the populations of *A. seniculus* will not start to decline by hunt until the density of *A. hybridus* is impacted by overhunting.

Ateles hybridus, by size, could be a better competitor than *Cebus versicolor* and *Saguinus leucopus*. The three species are overlapping in some niche dimensions (ecological requirements), so, by a compensation density process (MacArthur *et al.* 1972), the abundance of *A. hybridus* could regulate the density of the smaller primates. As a result, when the density of the bigger primates decreases, the density of the smaller primates increases (Peres and Dolman 2000, Hilário and Ferrari 2015), as has been observed in fragments where there were no spider monkeys, howlers or capuchins, and the density of the tamarins was

of over 100 ind/km². Thus, the high densities of *S. leucopus* reflect a very disrupted assemblage of primates, and I must not interpret them as a good indicator for the whole system.

I therefore suggest the use of *A. hybridus* as a landscape species to play the role as umbrella, keystone and maybe flagship surrogate to guide the priorities in the management of the humid and sub-humid forests of the Magdalena River valley (Sanderson *et al.* 2002). *A. hybridus* was the most affected species and by more factors (local vulnerability) (Rimbach *et al.* 2013) and it is a keystone species in this system (Christianou and Ebenman 2005). Thus, consolidating sustainable conservation scenarios for this primate, will satisfy the requirements for the other species, as a good representative of the ecological integrity of the whole system in a landscape approach.

The landscape approach to the conservation management usually demands the mosaic design that determines the minimal proportion and type of the core areas, their shape and aggregation and landscape composition. The landscape species approach based in the requirements or in the landscape structure effects allow us to plan and monitor the management actions in more cost-effective way.

However, landscape structure needs to be measured at the appropriate scale (Arroyo-Rodríguez and Fahrig 2014). The majority of the studies, including this, quantified landscape predictors within a single spatial scale, potentially missing significant primate–landscape responses (Galán-Acedo *et al.* 2019). Thus, studies on landscape effects on primates need to use a multiscale approach to ensure that landscape–species associations are correctly evaluated (Arroyo-Rodríguez and Fahrig 2014, Jackson and Fahrig 2015, Galán-Acedo *et al.* 2019). This study was done as patch-landscape analysis, and the scales were adjusted to each local landscape for a relative criteria based in the inferential area to primate density estimation. I think that standard measures of scales or direct scales are not applicable since the size of the inferential areas was highly variable, but a multiscale stratified analyses, with enough sampling sites, could be addressed in regions with similar land use patterns such as Caldas western region, Antioquia southeast and Serranía de San Lucas, that allow the use of standard scales, based on ecological criteria, to determine the optimal scale for each species to each region (Jackson and Fahrig 2012, 2015).

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CONFLICT OF INTEREST

The authors declares that they do not have conflict of interest.

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