

## Effects of Fragment and Vegetation Structure on the Population Abundance of *Ateles hybridus*, *Alouatta seniculus* and *Cebus albifrons* in Magdalena Valley, Colombia

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### Key Words

Endangered species · Fragmentation · Population abundance · Vegetation structure

### Abstract

Many primate species currently subsist in fragmented and anthropogenically disturbed habitats. Different threats arise depending on the species' life history strategy, dietary requirements and habitat preference. Additionally, anthropogenic disturbance is far from uniform and may affect individual forest fragments in a single landscape in differing ways. We studied the effects of fragmentation on three species of diurnal primate, *Cebus albifrons*, *Alouatta seniculus* and *Ateles hybridus*, in Magdalena Valley, Colombia. We tested the assumption that generalist species are more resilient than specialist species to habitat degradation by examining the fragments' vegetation and spatial structure and how these affected primate presence and abundance patterns. We found *C. albifrons*, a generalist, to be the most abundant species in 9 of 10 forest fragments, regardless of the level of habitat disturbance. *A. hybridus*, a large-bodied primate with a specialist diet, was either absent or low in abundance in fragments that had experienced recent disturbances and was found only in higher-quality fragments, regardless of the fragment size. *A. seniculus*, a species considered to have a highly flexible diet and the ability to survive in degraded habitat, was found in intermediate abundances between those of *Cebus* spp. and *Ateles* spp., and was more frequently found in high-quality fragments.

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## Introduction

Anthropogenic effects, including habitat loss and fragmentation, hunting and disease transfer, are leading causes of the pervasive loss of global biodiversity [Chapman and Peres, 2001; Michalski and Peres, 2005; Goldberg et al., 2008]. Primate species in particular are affected by habitat fragmentation [Arroyo-Rodríguez et al., 2013; Benchimol and Peres, 2014]. Despite this, continuous forest is rapidly being divided into small and isolated fragments in order to create farmlands and extract wood, minerals and oil from the land [Cowlshaw and Dunbar, 2000; Marsh and Chapman, 2013]. This creates a drastically different landscape in the habitat, and any organisms that cannot quickly adapt their behaviour to these emerging changes are ultimately faced with extinction [Chapman and Peres, 2001]. Despite numerous studies on the effects of habitat fragmentation and anthropogenic disturbance on primate populations [Marsh and Chapman, 2013], new findings frequently arise with each additional study [Benchimol and Peres, 2014]. The growing understanding of primates' flexibility within and across species necessitates further investigation of the effects of habitat fragmentation on individual primate species [Ewers and Didham, 2006].

While some primate species exhibit morphological adaptations and behavioural plasticity that allow them to continue to subsist in these habitats (howler monkeys, *Alouatta palliata* [Cristobal-Azkarate and Arroyo-Rodríguez, 2007]; collared lemur, *Eulemur collaris* [Donati et al., 2011]; diademed sifaka, *Propithecus diadema* [Irwin 2008a, b]; black and white colobus, *Colobus guereza* [Gillespie and Chapman, 2008]; moustached guenon, *Cercopithecus* [Tutin, 1999]), others appear to be more vulnerable due to greater specialization both morphologically and behaviourally (red colobus, *Procolobus rufomitratus* [Gillespie and Chapman, 2008]; bearded saki monkeys, *Chiropotes satanas chiropotes* [Boyle and Smith, 2010; Schwitzer et al., 2011]). Factors that enable some species to persist in fragmented forests include a small home range, broad-ranged diet and small group size [Purvis et al., 2000] (howler monkeys, genus *Alouatta* [Bicca-Marques, 2003]; mantled howler monkeys, *Alouatta palliata* [Es-trada, 1999]; white-faced capuchins, *Cebus capucinus* [Panger et al., 2002]), whereas primate species with large home ranges, specialist diets and large group sizes can be more severely and immediately affected by forest fragmentation [Andrén, 1994] (southern gentle lemurs, *Hapalemur meridionalis* [Eppley et al., 2011]; brown spider monkeys, *Ateles hybridus* [Link et al., 2012]; spider monkeys, family Atelidae [Rimbach et al., 2012]). However, degradation can vary greatly, and fragment size and quality are important factors to consider [Arroyo-Rodríguez et al., 2007].

Since fragmentation is at the landscape level, studies focussing on single fragments, often compared with continuous forest, are unable to take into consideration the continuous, rather than discrete, variation that occurs between fragments within a single landscape [Arroyo-Rodríguez et al., 2013]. Fragment quality can vary greatly based on the amount of time that has passed since isolation, the shape and size of the fragment, and the degree to which it has been exposed to other anthropogenic disturbances [Fahrig, 1999; Benchimol and Peres, 2014]. The 'quality' of the fragment, as measured through vegetation structure, is predicted to impact its ability to sustain larger populations or even multiple primate species [Mbora and Meikle, 2004; Wicz-kowski, 2004]. Thus, by measuring population response to fragment geometry, vegetation structure and anthropogenic effects, we can predict species' responses in other habitats, aiding the development of targeted conservation efforts in the future.

In this study we assessed the effects of fragmentation on the abundance of three diurnal sympatric primates: brown spider monkeys (*A. hybridus*), red howler monkeys (*Alouatta seniculus*) and white-fronted capuchins (*Cebus albifrons*) in a fragmented landscape in Magdalena Valley, Colombia. *A. hybridus*, a relatively understudied primate, is considered to be one of the 25 most endangered primates, necessitating an immediate and better understanding of the species' response to habitat disturbance [Mittermeier et al., 2012]. We analysed the influence of fragment quality, fragment spatial structure and anthropogenic disturbance (selective logging) on the abundance of these three platyrrhines. Given that high-quality habitat has been empirically linked to high fruit production [Chapman et al., 1992], we hypothesized that omnivorous, generalist *C. albifrons* and folivorous *A. seniculus* would be more resilient to habitat degradation. In contrast, ripe-fruit specialist *A. hybridus* would require larger and less degraded fragments and be less abundant in low-quality and small fragments.

## Methods

### Study System

Our study took place near the Magdalena River, between the eastern and central cordilleras of Andean Colombia in and around the private cattle ranch 'Hacienda San Juan del Carare' (hereafter 'San Juan'; 06°43' N, 74°09' W). The area is seasonally flooded tropical rain forest, with a mean annual rainfall of 2,070 mm [Link et al., 2010], and the average temperature is around 28°C. The primates have been studied there since 2007. Most forest fragments are inaccessible during the wet season (October to December) due to flooding, making it most efficient to conduct censuses during the dry months, in which this study took place. The area is made up of a matrix of forest fragments within naturally occurring and cleared pasture for cattle. Selective logging took place in and around the fragments, though large trees (e.g. *Ficus insipida*) are still present [Link et al., 2010].

We investigated 10 forest fragments (F1, F2, F3, FA, FT, FN, FC, FTF, FP, FDU) ranging in size from 0.7 to 171 ha (mean = 51.9 ha; table 1). Each fragment exists in isolation from both continuous forest and other fragments. The edges are defined by naturally occurring savanna, pasture for cattle ranching, and the San Juan River itself. The study area supports three diurnal primate species (*A. hybridus*, *A. seniculus* and *C. albifrons*) and one nocturnal species (*Aotus griseimembra*) [Link et al., 2010].

The white-fronted capuchin, *C. albifrons*, is a medium-sized primate (mean = 3.2 kg, n = 12 [Russo and Young, 2011]) with highly adaptable behaviour. Untufted capuchin monkeys (*Cebus* spp.) engage in both arboreal and terrestrial foraging [Terborgh, 1983] and exploit an ample variety of food resources including ripe fruits, roots and flowers, insects, arthropods, eggs and mammalian prey, and engage in crop raiding in some areas [Buckley, 1983; Panger et al., 2002; Sabbatini et al., 2006]. These primates have medium-sized home ranges (median = 130 ha, n = 4 [Defler, 1979; Terborgh, 1983; Matthews, 2009]) and are found in groups ranging in size from 8 to 35 individuals (mean = 13.8, n = 5 [Defler, 1979; Terborgh, 1983]). *Cebus* spp. have relatively long interbirth intervals (interbirth interval unknown in *C. albifrons*; 2.25 years in wild *C. capucinus* [Fedigan et al., 2008]) and slow rates of maturation when controlling for body size [Fedigan and Rose, 1995]. This slow development is theorized to be part of a strategy to increase individual learning and ability to adjust to environmental variation [Janson, 1998]. *C. albifrons* is currently listed as 'Least Concern' by the IUCN [2014].

Red howler monkeys, *A. seniculus*, are large-bodied (mean = 6.75 kg [Peres, 1997]), slow-moving primates that use relatively small home ranges (median = 21 ha, n = 12 [Barbisan-Fortes et al., 2014]) and are characterized as energy minimizers [Strier, 1992]. *Alouatta* spp. have high levels of dietary flexibility, opportunistically eating fruit when it is available, with leaves serving as their primary food source when preferred foods are not available [Marshall et al., 2009]. They

**Table 1.** Vegetation structure results

Fragment ID	Ecological vegetation variables				Spatial structural variables			
	edge proportion	tree density, trees/ha	mean DBH, cm	canopy density, %	fragment size, ha	fragment isolation	C-to-C coefficient distance, m	BZ land type coefficient proportion
FP	432.84	2,007	9.9±4.2	70.9	0.67	673	1,464	1.11
F1	170.45	1,718	16.8±17.5	76.1	13.4	578	925	1.22
F2	138.92	1,749	12.6±8.3	72.8	16.6	588	925	1.21
FT	200.12	1,740	11.6±11.2	73.8	16.8	584	829	1.22
FDU*	74.62	2,941	10.7±8.6	68.4	39.8	984	815	1.41
F3	102.72	1,685	12.2±7.4	74.3	48.6	566	1,238	1.27
FA	114.97	1,805	13.4±8.5	71.8	58	606	1,238	1.43
FC*	76.57	2,230	9.0±4.7	74.0	70.9	747	1,897	1.33
FN	117.50	1,393	16.5±11.0	72.6	83.3	470	3,460	1.25
FTF*	39.60	1,043	9.1±3.5	75.3	171	351	1,553	1.40

Asterisks denote the presence of selective logging within fragments. C-to-C = Target fragment centroid to nearest fragment centroid; BZ = buffer zone; ± = standard deviation.

have shorter interbirth intervals (17 months [Crockett and Sekulic, 1982; Crockett and Rudran, 1987]) compared to *Cebus* spp. and other ateline primates, and exhibit faster maturation rates [Ross, 1989]. *A. seniculus* is currently classified as 'Least Concern' by the IUCN [2014].

Brown spider monkeys, *A. hybridus*, are large-bodied (mean = 8.9 kg [Di Fiore and Campbell, 2007]) energy maximizers [Strier, 1992]. They are fast-moving, wide-ranging, highly arboreal frugivores. Their high degree of fission-fusion sociality allows large groups to disperse widely in the pursuit of high-energy ripe fruit, whilst minimizing intragroup feeding competition [Symington, 1988, 2000; Asensio et al., 2008; Link et al., 2012]. Spider monkeys have long interbirth intervals (~36 months [Shimooka et al., 2008, Vick, 2008]). As a result of deforestation and fragmentation, populations have declined in a number of *Ateles* spp., and many populations are now limited to forest fragments and degraded habitats [Ramos-Fernández and Ayala-Orozco, 2002; Ramos-Fernández and Wallace, 2008; Rangel-Negrín et al., 2009; Link et al., 2010; Abondano and Link, 2012; Rimbach et al., 2012]. *A. hybridus* is currently classified as 'Critically Endangered' by the IUCN [Urbani et al., 2008].

#### Data Collection

##### Ecological Vegetation Variables

Ecological variables of each fragment were measured using the methods suggested by Ganzhorn et al. [2011]. The fragment size (hectares), total length of the perimeter of the fragment (metres), tree density (trees per hectare), the mean diameter at breast height (DBH; centimetres), and the canopy density (percent; table 1) were measured for each fragment. Fragment size and length of fragment perimeter were determined using Landsat 5 imagery and processed with GIS (ArcGIS 10.1). The edge proportion was calculated by dividing the fragment perimeter length (metres) by the size of the fragment (hectares). Tree density, DBH and canopy density were measured using the quarter-point plotless sampling method [Ganzhorn et al., 2011]. Sampling points were randomly selected within each fragment using a dice and grid system. At each starting point we took a digital photograph of the tree canopy from breast height for canopy density analysis. CanopyDigi software [Goodenough and Goodenough, 2012] was used to estimate the percent of canopy coverage. After the initial point had been selected using dice, subsequent points were randomly selected in a direction dictated by the second hand of an analogue watch 5 m from the previous point. The distance to the nearest 4 trees (≥5 cm DBH), with 1 tree within each quarter point of a grid system, was measured along with their DBH. We used a DBH threshold lower than

the standard 10 cm since the low occurrence of large trees would have prevented us from carrying out quantitative habitat surveys in heavily disturbed fragments. Fifty sampling points were completed in each fragment [Ganzhorn et al., 2011].

#### Fragment Spatial Structure

Using spatial data collected from satellite imagery which were ground-truthed and processed in ArcGIS, three separate landscape variables were generated. Isolation of forest fragments was examined in terms of their proximity to surrounding forests. A single multidirectional proximity figure was calculated for each fragment within ArcGIS. The figure was derived as the mean distance from the target fragment edge to the next nearest fragment edge as calculated across 4 quadrants delimited by the cardinal compass directions [Hill and Curran, 2004]. The data ranged from 140 to 515 m, and the error was defined by the GIS raster resolution as 5 m. The surrounding matrix of each fragment was measured to quantify the ease of primate dispersal using two separate methods. Firstly, a 250-metre 'buffer zone' was measured from the target fragment edge and the total area of land type (forest, pasture, water) was calculated [Bender et al., 2003; Tischendorf et al., 2003]. To estimate the relative ease of primate travel through these differing land types [Arroyo-Rodríguez and Mandujano, 2009], the area of these differing land types was multiplied by coefficient values (forest = coefficient 1, pasture = coefficient 2, water = coefficient 3). The proportion of these values to the total area within 250 m of the fragment edge, or buffer zone, was a product of this calculation. Secondly, the distance from the target fragment centroid (obtained using ArcGIS 'calculate geometry' function) to the nearest fragment centroid was measured in metres, and the same coefficient values were applied to the total distance. We included this second measurement because, whilst similar to the land type buffer zone coefficient proportion value, it is also an approximation of the likelihood that primate dispersals are occurring. For instance, FTF is a large, degraded fragment that satellite imagery shows has become isolated from the surrounding forest at some point between the years of 1970 and 2011. Because of its relatively large size, the likelihood that a primate would disperse from this area to a smaller fragment is low. This is reflected in the 'centroid-to-centroid coefficient distance', but not the 'land type buffer zone coefficient proportion' as the distance between two fragment centroids will be large, but the area surrounding the fragment is largely pasture with some forest cover.

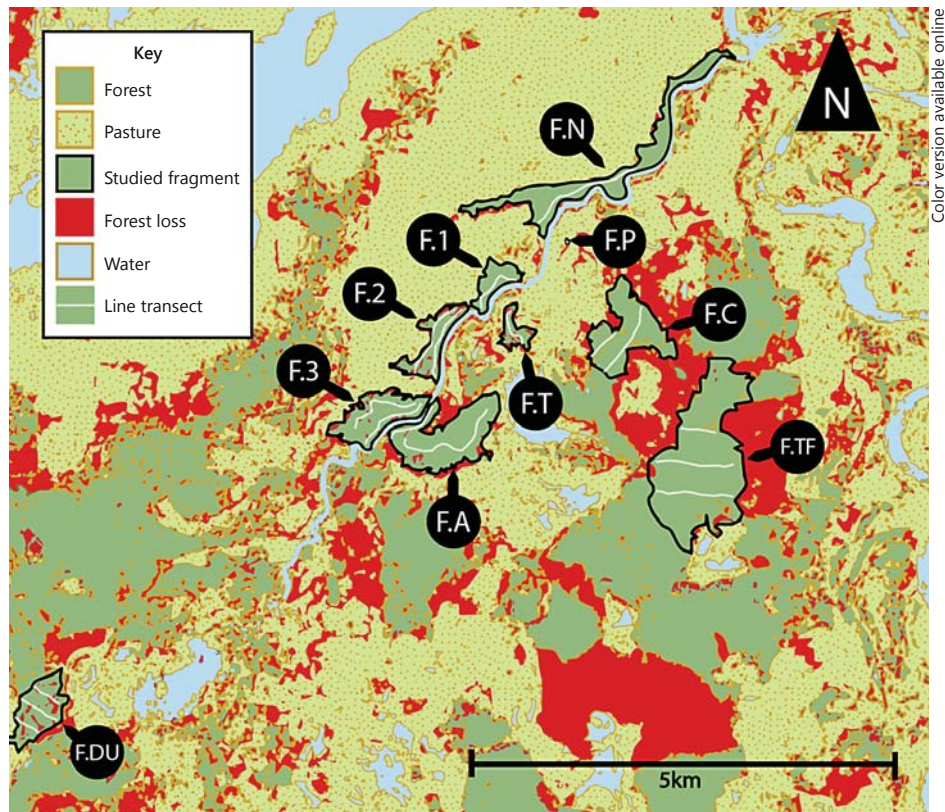
We determined whether fragments had recently been reduced in size using LANDSAT 5 and LANDSAT 7 mosaic images from 1970 and 2011. Fragments were denoted as degraded if they had been reduced in size and/or connectivity since 1970 (fig. 1). We assessed recent logging activity in individual fragments based on visual evidence of cut wood found in the fragment (table 1).

#### Line Transects

Three researchers conducted surveys between May and August of 2014. In order to assess the density of *A. hybridus*, *A. seniculus* and *C. albifrons*, we used the line transect method, following recommendations suggested by Buckland et al., [2001, 2010] and Peres [1999]. Five of the studied fragments (F1, F2, F3, FA, FT) had previously been used for research, and the established trails were used for this study. We randomly superimposed sets of equally spaced (>100 m) parallel transect lines on a map of each of these 5 fragments, where fragment size allowed [Buckland et al. 2010]. We then uploaded these maps and used GPS devices (Garmin GPSMAP 64s GPS) to follow the lines in order to cut and mark the trails.

Overall, we sampled 127 km of line transects, with individual line transect length ranging from 96 to 1,440 m (mean transect length  $\pm$  SD = 753.9  $\pm$  277.1 m, n = 19). Transects were walked between 6:00 and 18:00 h at speeds of approximately 1 km/h stopping every 100 m and waiting 5 min in silence in order to detect any signs of movement or sound. Upon detecting a primate group, we waited 5–20 min if audio cues (movement sounds, calls) suggested that unseen primates were in close proximity in order to increase the chances of detecting all members of the group. Primate group centre location (distance and angle from line transect) was taken from first sighting of a primate, then amended to include accurate group centre estimates [Marshall et al., 2008]. Due to their variable size, transect effort was unequal between fragments, and ranged from 1,056 m (FP) to 20,282 m (FA), with a mean of 12,958 m. A single transect in each fragment was





**Fig. 1.** Description: composite vegetation classification map of study area comparing forest structure from 1970 and 2011.

walked approximately once every 3 days. Upon encountering primates we recorded the time of day, the number of individuals, the perpendicular distance of the group's centre to the line transect, the location of the encounter, and the sex-age category of each individual, when possible. Cluster size was defined as the total number of individuals in a group. For *C. albifrons* and *A. seniculus*, cluster size corresponds to the size of the cohesive social group, while for *A. hybridus* it corresponds to the size of the subgroup (given their fission-fusion social dynamics). Group spread was recorded for each cluster, but not for sightings of individual primates. Before data recording took place, interobserver bias was tested and found to be within a 95% threshold [Rovero et al., 2006].

Due to a low number of observations per fragment (mean =  $28.6 \pm 14.7$ , range = 0–50, n = 250 observations) population density for each of the three primate species was calculated only for the entire area using Distance software [Thomas et al., 2006]. We selected the best fit model using the lowest Akaike's information criterion [Buckland et al., 2001]. Cluster size was calculated using the cluster-biased regression method. Data were truncated at 5% as suggested by Buckland et al. [2001] to exclude potential outliers. Encounter rate was then calculated for each fragment by dividing the entire number of encounters for a single species by the number of kilometres of transect walked (table 2). Primate encounter rates were grouped into 4 time periods of 3 h each (6–9 a.m., 9 a.m. to 12 p.m., 12–3 p.m., 3–6 p.m.) for later analysis.

**Table 2.** Encounter rates per kilometre of primate species by fragment

Fragment ID	<i>Ateles</i>	<i>Alouatta</i>	<i>Cebus</i>
FP	0	0	0
F1	0.98	1.16	0.89
F2	0	1.18	0.79
FT	0.31	0.93	1.96
FDU	0	0.29	0.68
F3	0.14	0.82	0.77
FA	0.15	0.35	0.84
FC	0	0.28	1.67
FN	0.31	0.69	0.46
FTF	0	0.09	1.63

### Statistical Analyses

We used multiple linear regressions to predict population abundance using ecological vegetation variables (canopy density, mean DBH, tree density, edge proportion) and spatial/structural vegetation variables (fragment size, fragment isolation, centroid-to-centroid coefficient distance, buffer zone land type coefficient proportion) separately and selected the best predictors. Since we used the fragment as the unit of analysis, we ran two separate models due to sample size limitations. Before this model was run, vegetation variables and spatial/structural vegetation variables were checked for multicollinearity using Pearson's correlation. No variables were found to be significantly correlated ( $p > 0.05$ ). Residual errors of this analysis were tested for normality using the Kolmogorov-Smirnov test in order to check the assumptions of general linear models, and the residual errors were found to be normally distributed. Vegetation structure differences between fragments were tested using a Kruskal-Wallis test, and qualitative disturbance cues (binary; presence of logging) were tested against quantitative vegetation data using a Mann-Whitney U test. Temporal differences in encounter rates of each primate species were tested for significant differences with a non-parametric Friedman's ANOVA test. All statistical analyses were performed with SPSS 20.

## Results

### Vegetation Structure

Mean DBH was highly variable between fragments (K-W:  $\chi^2 = 31.55$ , d.f. = 9,  $p < 0.001$ ). Canopy density also varied significantly between fragments (K-W:  $\chi^2 = 20.35$ , d.f. = 9,  $p = 0.016$ ). We found evidence of selective logging (cut and prepared wood ready for extraction) in 3 of the study fragments (FC, FTF, FDU) and a single fragment had indications that hunting had taken place (FDU, hunting platforms), though we cannot quantify the use of the platforms or the targeted prey. We found that fragments which had recently been reduced in size (FC, FTF, FDU; fig. 1) and showed visual evidence of recent logging exhibited lower mean DBH values (Mann-Whitney U test,  $Z = -3.437$ ,  $p = 0.001$ ,  $n = 1,880$ ).

### Density Estimates

In total, we recorded 250 sightings of primate groups. We encountered *C. albifrons* the most ( $n = 130$  encounters), followed by *A. seniculus* ( $n = 87$  encounters) and *A. hybridus* ( $n = 33$ ). No differences between the number of sightings between differ-

ent time periods were found for any species (*Alouatta*,  $\chi^2 = 4.744$ , d.f. = 3,  $p = 0.192$ ; *Ateles*,  $\chi^2 = 0.625$ , d.f. = 3,  $p = 0.891$ ; *Cebus*,  $\chi^2 = 3.989$ , d.f. = 3,  $p = 0.263$ ).

*C. albifrons* mean group size was  $3.2 \pm 2.4$  individuals and ranged from 1 to 11 individuals. Average cluster/group spread was 16.1 m, and highest group spread was recorded as 40 m. They were found in all but the smallest fragment (FP; table 2). Density of *C. albifrons* was 62.2 individuals/km<sup>2</sup> (95% CI = 42.5–90.9). No ecological or spatial/structure vegetation variables were found to be significantly good predictors of encounter rates of *C. albifrons*.

*A. seniculus* had the largest group size, with an average of  $3.9 \pm 2.0$  individuals, and it ranged from 1 to 12 individuals. Average cluster/group spread was 11.9 m, and highest group spread was recorded as 36 m. They were found in all but the smallest fragment (FP; table 2). Density of *A. seniculus* was 26.2 individuals/km<sup>2</sup> (95% CI = 17.4–39.3). We found a positive trend between number of encounters of *A. seniculus* and mean tree DBH ( $\beta = 0.096$ , adj.  $R^2 = 0.252$ ,  $p = 0.096$ ).

*A. hybridus* were found in subgroups that had an average size of  $2.2 \pm 1.2$  individuals, and it ranged from 1 to 6 individuals. Average cluster/group spread was 15.38 m, and highest group spread was recorded as 28 m. They were found in 5 of the 10 fragments (F1, FT, F3, FA, FN; table 2). Density of *A. hybridus* was 8.2 individuals/km<sup>2</sup> (95% CI = 4.3–15.6). There was a positive correlation between number of encounters of *A. hybridus* and both mean tree DBH and canopy density ( $\beta$  DBH = 0.079,  $p = 0.011$ ;  $\beta$  canopy density = 0.1,  $p = 0.04$ ; model adj.  $R^2 = 0.718$ ).

A possible confounding factor to density estimates was varying habituation levels of primates in separate fragments, some having been previously studied. However, the relatively uniform encounter rates of *C. albifrons* across fragments (table 2) regardless of degree of habituation suggest that the methodology used prevented bias.

## Discussion

Our results indicate that the three diurnal primate species at San Juan differ in their ability to cope with recent fragmentation, and fragment quality may be more important than fragment size or isolation for some large-bodied primates. For *A. hybridus*, higher fragment quality, described in this study as high values in the ecological variables measured, corresponded with higher abundance, while fragment spatial structure variables had no apparent effect on the presence or absence of any primate species. However, all three primate species were found to be absent from the smallest fragment (FN), suggesting there is a minimum fragment size threshold for primate persistence. *C. albifrons* and *A. seniculus* showed no apparent dependence on either vegetation variables or spatial structure variables.

The results of this study support findings of previous research on the effect of forest fragmentation on primates [Garber et al., 2006], namely that ecomorphological adaptations and social structures govern species' ability to survive in disturbed habitat. In Madagascar, the diademed sifaka (*P. diadema*) occurring in forest fragments utilized fallback food sources and reduced daily path length, thus minimizing energy expenditure, when favoured fruit resources were absent [Irwin, 2008a, b]. Conversely, the collared lemur (*E. collaris*) increased time spent travelling and feeding, and reduced group size in response to fragmentation [Donati et al., 2011]. In Gabon, the moustached guenon (*Cercopithecus cephus*) exhibited a high degree of fission-fusion



dynamics to decrease feeding competition when inhabiting forest fragments [Tutin, 1999]. These studies suggest that dietary and behavioural flexibility of some primate species may guarantee some resilience to anthropogenic disturbance.

Given that forest fragmentation in this area is relatively recent [Link et al., 2010] (fig. 1) and all the species that we studied have the ability to cross the intervening matrix [Link, unpubl. data], we can assume that primate species 'choose' favourable fragments which to inhabit, possibly over generational time periods. As hypothesized, the far-ranging, arboreal frugivores *A. hybridus* are adversely affected by the constraints of living in degraded and fragmented forest. The overall population density of *A. hybridus* in this study (8.2 individuals/km<sup>2</sup>) is low when compared to other studies conducted in fragmented habitats (median = 19.6 individuals/km<sup>2</sup>, n = 20 [Ramos-Fernández and Wallace, 2008]) despite the 'condensing' effects of habitat fragmentation [Link et al., 2010], suggesting that individuals are widely spaced within the available quality habitat.

*Ateles* spp. exhibit a social system with a high degree of fission-fusion dynamics, and under normal conditions subgroup size is highly flexible. In small fragments with limited food resources, scramble and contest competition may prevent some individuals from gaining adequate nutrition, resulting in physiological stress [Rimbach et al., 2013] and limiting the number of individuals that can subsist in each fragment. In this study *A. hybridus* subgroup sizes were found to be consistently low, suggesting that only 'subgroups' were found in isolated fragments and few fusion events took place. Reduced group size may be used by this species to reduce scramble and contest competition over food resources, and may be successful for the short-term survival of the population. However, the effects of small group sizes may have negative consequences for the long-term survival of this population, potentially leading to inbreeding and limited gene flow [Knapp, 2013].

The two ecological variables found to predict *A. hybridus* encounter rate in individual forest fragments were canopy density and mean DBH values. These variables showed lower values in fragments which showed evidence of selective logging. Whether this is due to selective logging or 'edge effects' related to fragmentation events is unclear [Harper et al., 2005].

Canopy density may be a key factor in allowing highly arboreal brachiators such as *Ateles* spp. to locate food resources efficiently [Skorupa, 1988; Dew, 2005]. In contrast, *Alouatta* spp. are quadrupedal climbers with small home ranges and highly available food resources, thus loss of canopy density may not limit their ability to survive in degraded forest fragments [Bernstein et al., 1976; Youlatos, 1993]. This may enable them to subsist in both small fragments and in fragments where large trees have been removed [Estrada and Coates-Estrada, 1996]. However, this may happen at a cost to overall group survivorship, as suggested by our findings that they still occur in degraded fragments but at reduced numbers (as seen in FC, FTF, FDU) [Schwarzkopf and Rylands, 1989; Palacios and Rodriguez, 2001].

No relationship was found between *A. seniculus* encounter rates, ecological vegetation variables or fragment structure variables. This suggests that *A. seniculus* may not be severely affected by fragmentation and habitat degradation in the short term, a similar result to previous studies at this site [Rimbach et al., 2013]. *Alouatta* spp. exhibit morphological adaptations that allow them to utilize leaves when fruit availability is low [Anapol and Lee, 1994; Fleagle, 2013]. Previous studies have shown *Alouatta* spp. display a broad range of behavioural adaptations to inhabit anthropo-

genically disturbed habitats: from adopting extreme energy-minimizing foraging patterns [Milton, 1980], expanding the range of plant species used as food sources [Bicca-Marques, 2003], even using anthropogenic elements (live fences) to move to new food sources [Asensio et al., 2008]. Adaptations such as these may enable the *A. seniculus* population in this study to subsist in degraded fragments.

*C. albifrons* were found in relatively high numbers in all but the smallest fragment (FN). Fragment quality and fragment spatial structure had no apparent effect on *C. albifrons*, suggesting that this species is not strongly affected by anthropogenic disturbance. Their ability to travel and forage terrestrially, and exploit numerous food sources is likely a contributing factor [Miller, 2002]. During our study we observed groups of *Cebus* travelling terrestrially between forest fragments several times, indicating that their flexible locomotion allows them to exploit a larger range of habitats [De Freitas et al., 2008]. We also found that *C. albifrons* abundance was high in fragments where *A. hybridus* and *A. seniculus* abundance was low, indicating that lower interspecific competition in these fragments may potentially enable this species to fully exploit the resources available in these fragments. This is a phenomenon that has been recorded previously in areas experiencing high levels of hunting activity [Rosin and Swamy, 2013].

Our study builds on the current understanding of how primates are affected by habitat degradation and fragmentation, which is of particular importance for the critically endangered brown spider monkey (*A. hybridus*). Given the long lifespan of *Ateles* spp., and the relatively short time scale in which anthropogenic disturbance can markedly affect primate populations, understanding the needs of the species may prove useful for the implementation of conservation strategies. While it appears in our study that *A. hybridus* has initially fared the worst as a result of the fragmentation of the habitat, *C. albifrons versicolor* and *A. seniculus* will likely experience long-term negative effects that are not yet fully evident.

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