

Conserving primates in Colombian bamboo forest fragments:
logging and landscape impacts on Red Howler Monkeys

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Abstract

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Increasingly, conservation of tropical forest-dwelling species depends on maintaining their populations in human-dominated landscapes. Often, extensive deforestation has left only fragmented forests that are subject to human use, such as logging, and this is the case in the central Andes of Colombia, where 200 years of human use has left only 15% of the forest, scattered in mostly very small, narrow fragments. This study evaluates the relationship impacts of both fragmentation and current bamboo forestry practices on red howler monkeys (*Alouatta seniculus*), the largest mammal remaining in this landscape. The underlying purpose of this study is to evaluate whether bamboo logging could be compatible with howlers' persistence in these forests, and if any changes in logging practice could improve prospects for howlers. A further goal is to identify opportunities to ameliorate the consequences of extreme habitat

fragmentation, while providing benefits to the owners. Due to the fast growing characteristics of the bamboo, these forests could be used to increase habitat and to promote connectivity among fragments. Results of this study show both reasons to be optimistic and to be cautious about the prospects for bamboo forestry to be compatible with conservation of red howler monkeys.

Bamboo logging does not directly impact the monkeys, who appear widely tolerant of logging activities since they do not impact their feeding trees. However, bamboo extraction damages seedling and sapling trees, which appear to recruit poorly in these forests, threatening the regeneration of the key food resources for the howlers. Combined with the impacts of fragment isolation, persistence of the howlers in this landscape likely depends on enhancing tree regeneration within logged bamboo fragments and expansion of existing fragments and creation of corridor or stepping stone habitats to promote movement of the monkeys among fragments.

With relatively small changes in the implementation of management regulations, conservation of red howler monkeys could be greatly enhanced in this landscape.

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Introduction

The rapidly growing human population and increases in local and global market demands exert an extreme burden on natural resources. Ecosystems around the world are being transformed into a mosaic of human dominated land uses with smaller forest fragments embedded in, mostly, an agricultural and grazing matrix (Estrada et al. 2012).

Fragmentation of tropical forests raises major ecological concerns at local, regional, and global scales. Today's tropical landscapes are characterized by a mosaic of large plantation-type agriculture (intensive and extensive, including pastures) interspersed with various sized family farms and forest patches of different shapes and sizes (Perfecto and Vandermeer 2008), thus resulting in highly fragmented natural habitats for forest dwelling wildlife, such as primates. Accelerated deforestation in the tropical rain forests around the world has led to the destruction of suitable habitat for primates (Marsh 2003). As deforestation increases, there is a reduction in fragment size, floristic composition, plant species diversity, and, increasingly modified vegetation structure, potentially decreasing the quality and quantity of food resources for primates (Cristobal-Azcárate et al. 2005, Arroyo-Rodríguez and Mandujano 2006). Furthermore, the magnitude of the negative fragmentation effects on the surviving fauna is increased in small forest fragments due to anthropogenic extractive activities (Chapman et al. 2000).

Less than 5% of tropical forests are legally protected from human exploitation (Chapman et al. 2000) and approximately 70% of the land has been transformed into pastures, agriculture, or a mixture of managed landscapes (McNeely and Scherr 2003). The critical role of parks and reserves in conservation is undisputed; however, protected areas alone cannot meet conservation goals (Pimentel et al. 1992). For example, in primate range countries, many protected areas are

isolated and are relatively small and/or so poorly managed that their primate populations may not persist in the long-term (Estrada et al. 2012). As a result, conservation of many primate species depends on the capacity of non-protected forest to support their populations. In addition to protecting relatively undisturbed forests, conservation biologists have to develop strategies to make human-dominated areas more hospitable for biodiversity, and active conservation efforts are therefore required within and outside of parks and reserves (Perfecto and Vandermeer 2008, Williams-Guillén and Perfecto 2010). Although agricultural activities and forest use are the main threat to the primate diversity, there are some agroecosystems and forestry practices that are compatible with supporting wildlife and these merit study and evaluation (Estrada et al. 2012).

Bamboo forests are recognized by their ecological services (e.g., erosion prevention, carbon sequestration, biodiversity protection) and their great potential to support local economies (INBAR 2014). In the last decades, bamboo forestry has been promoted around the world as an opportunity to reduce poverty in an environmentally sustainable manner. Bamboo silvicultural research has been developed extensively in tropical countries; however, there is almost a complete lack of information about the bamboo logging impact on the wildlife. For instance, in Central Colombia, bamboo forests are the last forest remnants in the premontane region of the Central Cordillera. The Andes of Colombia is one the most biodiverse regions in the world, unfortunately also one of the most endangered due to extensive conversion of the original land cover (Myers et al. 2000). The actual landscape of the premontane region (known as Eje Cafetero) is composed of small and isolated native bamboo forest remnants within a matrix of pastures and crops. These forest remnants are privately owned and under extractive activities. The original fauna and flora persisting in this landscape may be threatened by bamboo harvesting and the extreme fragmentation in the region. However, few studies have addressed the effects of

fragmentation (Kattan et al. 1994, Muriel and Kattan 2009, Roncancio and Gómez-Posada 2009) and none have evaluated the impact of bamboo logging activities on wildlife.

This dissertation focuses on the impact of bamboo logging on a target primate species, the red howler monkey, *Alouatta seniculus*. Howlers are a charismatic primate in the region, due to their size, color and strong vocalizations. Howlers are also one of the last diurnal large mammals found in the Eje Cafetero region. Therefore, protection of the red howler could be an important tool for conservation more broadly, because their conservation will require maintaining these last remnant Andean forests, and along with them the other species persisting in this fragmented ecosystem.

Howlers are forest dependent primates known by its versatility in using different habitat types, and ability to survive in disturbed forest fragments (Bicca-Marques 2003). However, logging activities in the bamboo forest fragments may negatively impact howler populations. Further, howlers have a low capacity for movement through agricultural habitats that lack trees and some canopy cover (Mandujano et al. 2006), and thus may be strongly isolated by prevailing conditions in the Eje Cafetero.

The first two chapters of this research focus on the comparison of howler behavioral ecology and the floristic composition and structural characteristics of their food resources, between the two bamboo logging management types that occur in this region, commercial (regulated intense and continuous logging) and domestic (sporadic and less supervised logging). The third chapter analyses the habitat characteristics that determine the presence/absence of howlers in those bamboo fragments.

The underlying purpose of this study is to understand if bamboo logging could be compatible with howlers' persistence in these forests, and if any changes in logging practice

could improve prospects for howlers. A further goal is to identify opportunities to ameliorate the consequences of extreme habitat fragmentation, while providing benefits to the owners. Due to the fast growing characteristics of the bamboo, these forests could be used to increase habitat and to promote connectivity among fragments. Due to the economic benefits of bamboo forestry, the Colombian government is actively promoting bamboo harvesting, but recognition of the ecosystem benefits of forested systems and pride in the nation's biodiversity have also encouraged the development of sustainable management strategies and habitat conservation plans for native species. Thus, the results of this dissertation are likely to be influential, both in Colombia and in other tropical countries investing in bamboo forestry, in guiding improvements to bamboo forest management strategies that could make bamboo forestry more compatible with conservation while continuing to improve the livelihoods of regional human populations.

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Chapter 1. Behavioral ecology of red howler monkeys in bamboo forests under short logging cycles

Abstract

Bamboo forests are promoted as an environmentally sustainable resource that generates income for farmers and that holds great biodiversity. Despite numerous wildlife inventories and silvicultural studies, the effect of bamboo logging on the wildlife has not been well studied. In a highly fragmented montane region in Colombia, we studied for 6-12 months the behavioral ecology of six red howler monkey groups (*Alouatta seniculus*) inhabiting remnant bamboo forest under two types of logging management: commercial (regulated intense and continuous logging) and domestic (sporadic and less supervised logging). We also described the immediate response to bamboo logging of two howler groups. Howler behavioral ecology was not different between the two management types, nor did it differ from patterns reported in unlogged forests. Logging in these fragments is focused only on bamboo, which is not eaten by the howlers, and no other trees are harvested. Thus, in both types of logging management, the main food resources for howlers were not impacted, regardless of the intensity and frequency of the logging. Howlers' diet in these fragments was species-poor, likely due to a combination of the natural low plant diversity of bamboo forest, particularly in small fragments, as well as the howlers' strong preference for *Ficus* species, and the maintenance activities associated with logging. The ranging patterns of the howlers shifted slightly during logging periods, but because bamboo grows fast and recovers prior height within about six months, we suggest this may be only a temporary effect. Colombian regulations of the bamboo logging limit the harvest up to 35% of stems, which maintains canopy connectivity. All of these characteristics suggest that under careful

management regulations, bamboo forest logging could be used to enhance red howlers conservation at both the local and the landscape level (connecting and expanding available habitat), while providing benefits to the landowners.

Key words: sustainable selective logging, productive systems, *Alouatta seniculus*

Introduction

One of the great challenges for conservation ecologists is to understand where and how wildlife conservation can be made compatible with significant economic activities. Forests worldwide are on the decline; half the forest cover on Earth has been lost since the industrial revolution, replaced primarily by agricultural lands, and only 12% of tropical forests are legally protected from human exploitation (FAO 2010). Remaining forest tracts are often fragmented and heavily utilized, and accordingly, many animal species rely on managed forests for their survival (Chapman and Peres 2001, ITTO/IUCN 2009) and their conservation depends on the capacity of these privately-owned forests to support their populations into the future (Chapman et al. 2010, Melo et al 2013). Increasingly, conservationists are focusing on how to maintain species in production landscapes, recognizing that despite the substantive increase in protected area networks in recent decades, the majority of conservation must take place on private lands (Perfecto and Vandermeer 2008, Putz et al. 2012). However, there is a limited understanding of how production forests can meet both economic and conservation goals, and more studies are needed to understand the effect of extractive activities on biodiversity.

Bamboo is a major non-wood forest product and is widely used as a wood substitute. In recent decades, bamboo has been recognized for its huge potential to provide a sustainable source of income for small and medium-sized enterprises, and it is promoted as an excellent opportunity to reduce poverty in an environmentally sustainable manner (INBAR 2014). As a

result, the bamboo industry is thriving across continents. The total area of bamboo forest (natural and planted) increased worldwide by about 11% between 1900 and 2000 (FAO 2010). The environmental benefits of bamboo forestry include rehabilitation of degraded forestlands, biomass generation, carbon sequestration, erosion prevention and watershed protection (INBAR 2014). Bamboo forests are also important habitat to wildlife. For example, many species of primates, some of them endangered, live in or use bamboo forest (Sheil et al. 2012, Olson et al. 2013). Given the rapid expansion of bamboo forestry across the world, it is a priority to understand the responses of wildlife to the selective logging of bamboo (where only bamboo stems are extracted), and to incorporate that information in bamboo forest management policies (Morgan and Sanz 2008, Sheil et al. 2012).

Extractive activities usually result in a reduction of biodiversity and multiple changes in the ecosystem (Bawa and Seidler 1998, Chapman et al 2000). Selective logging involves alterations in the physical structure of the vegetation, as well as availability of food resources for wildlife. Reduction of food availability may have considerable impacts on primates, potentially worsening body condition, increasing vulnerability to diseases or parasites, and/or nutritional deficiency, which ultimately leads to higher mortality rates and population decline (Johns 1986, Johns and Skorupa 1987, Rode et al. 2006, Felton et al. 2010). The most immediate common response of primates to logging disturbance is to avoid logged areas and human activities, and find new food resources when their favored food species are eliminated. The responses entail major changes in group ranging, feeding behavior, diet, and activity patterns (Singh et al. 2001, Arnhem et al. 2008, Guo et al. 2008, Gerber et al. 2012). In cases of severe reduction of food resources, the species may fail to persist in the forest (Johns and Skorupa 1987, Plumptre and Grieser Johns 2001). For example, almost half of the diet of spider monkeys (*Ateles chamek*) inhabiting a

certified forestry concession in Bolivia is based on timber species. Post-logging population declines of up to 75% of this species have been observed, compared to unlogged forest areas (Felton 2010).

Despite such negative impacts, logged forests also have potential for conservation, as they generally contain a great proportion of native fauna, including primates (Grieser Johns and Grieser Johns 1995, Clark et al. 2009) than do many other alternative land uses (Putz et al. 2012). In general, the extent to which selective logging impacts primates depends mainly on the type, periodicity and intensity of the logging, and the timber species removed (Chapman et al. 2000, Bicknell and Peres 2010). Some studies suggest that moderate to low-intensity logging could be compatible with primate conservation, for example, when there is low overlap between tree species that are harvested and those used as food sources by primates (Johns and Skorupa 1987), and when logging cycles are long enough to allow sufficient time for recovery of vertebrate and plant populations (Chapman and Peres 2001, Hunth and Ditzer 2001, Chapman et al. 2010). Some primate species exhibit similar or only slightly lower population characteristics in a logged than in an unlogged forest, even over the long time scales, suggesting that logged forest can extend the conservation estate for many species if it is managed appropriately (Grieser Johns and Grieser Johns 1995, Clark et al. 2009, Putz et al 2012).

In the premontane range on the Central Cordillera (900 to 1800 m altitude) of Colombia, in an area also known as Eje Cafetero (the main coffee growing region), only ~15% of the original cover remains (Wild et al. 2006), almost all of which exists in fragments dominated by native bamboo (*Guadua angustifolia*) (Camargo et al. 2010). In the region, there are approximately 40,000 ha of bamboo forest, which are fragmented into relatively small (< 10 ha) and irregularly shaped forest islands within an agricultural mosaic (Kleinn and Morales-Hidalgo 2006). The

majority of these fragments are privately-owned, and are under bamboo logging pressure. Bamboo plays an important role in the livelihoods of numerous rural communities as traditional raw material for manifold construction purposes, as well as for handicrafts, and a variety of other uses. Because these bamboo fragments are the last forest remnants in the region, their conservation and sustainable management are of an interest of the Colombian government. There is a legislative framework and guidelines for management and harvesting of bamboo stands (Camargo et al. 2010). Bamboo extraction is regulated by environmental authorities, and only a specific number of mature and over mature stems can be extracted to maintain bamboo stem productivity. For commercial purposes, up to 35% of the stems can be harvested every 1 or more years (Bosques FLEGT/Colombia 2008). Where landowners use bamboo to meet the needs of their farm, the extraction is considered domestic use, and extraction occurs sporadically and without supervision. In this case, only 20m³ of stems can be legally extracted per year. We will refer to these two types of logging management as “commercial” and “domestic” respectively (see the “study area” section for details).

These bamboo forests preserve a large proportion of the original vegetation of the region and provide a refuge for the local fauna (Ospina and Finegan 2004, Camargo et al. 2010), including, the red howler monkey (*Alouatta seniculus*). This is one of the few large mammal species that persists in the highly-converted Eje Cafetero. Although this species is not considered threatened by the IUCN, red howlers may be vulnerable in the Eje Cafetero, as their habitat has been so severely reduced (Defler 2004, Gómez-Posada 2006). In this region, the red howler is a charismatic and widely-loved primate. Therefore, howlers can be used as flagship species for conservation because protection of the howlers would result in protection of the remnant Andean forest and other species of this endangered ecosystem.

Howler monkeys have been widely studied in lowland forests, and they are well known for their versatility in using different habitat types, including their ability to survive in disturbed forest fragments (Bicca-Marques 2003, Arroyo-Rodríguez and Dias 2010). Howlers exhibit considerable dietary flexibility and use energy-saving strategies; both types of adaptation likely contribute to their ability to survive in human-modified forests (Crockett 1998, Bicca-Marques 2003). Howlers are found in forests under logging pressure, but few studies have quantified their response to the extractive activities (DeLuycker 1995, Pinto et al. 2003, Zunino et al. 2007). More studies are necessary to evaluate to what extent logging affects howler populations, and their responses to different intensities of selective logging (Arroyo-Rodríguez and Dias 2010).

The purpose of this study was to describe the behavioral ecology of howlers living in logged bamboo forest fragments in the Colombian Coffee region and to compare their responses to two logging managements, commercial and domestic. Logging episodes in fragments under commercial use enabled us to evaluate the short-term responses of howlers to bamboo logging. It is reasonable to expect that howlers' behavioral flexibility would improve their ability to survive in logged habitats, perhaps irrespective of the bamboo harvest intensity, as long as the habitats retain species on which they feed, and these trees are not affected by the logging. The potential implications for the bamboo industry are large, as this study allows a test of the degree to which commercial bamboo logging, as well as the sporadic domestic bamboo harvests, can be compatible with howler conservation.

Methods

Study area

The study took place in six bamboo forest fragments located in the premontane range on the western slope of the Cordillera Central of Colombia (fig. 1), about 1100 m of altitude. All the fragments are narrow corridors located in Quindío and Valle del Cauca Departments on privately owned farms. The climate is dry-wet transitional, with a bimodal pattern of precipitation, average annual rainfall of 1800 mm, and average temperature of 18-24 °C (CVC 2000). The fragments are immersed in a matrix of livestock pastures, corn and fruit crops.

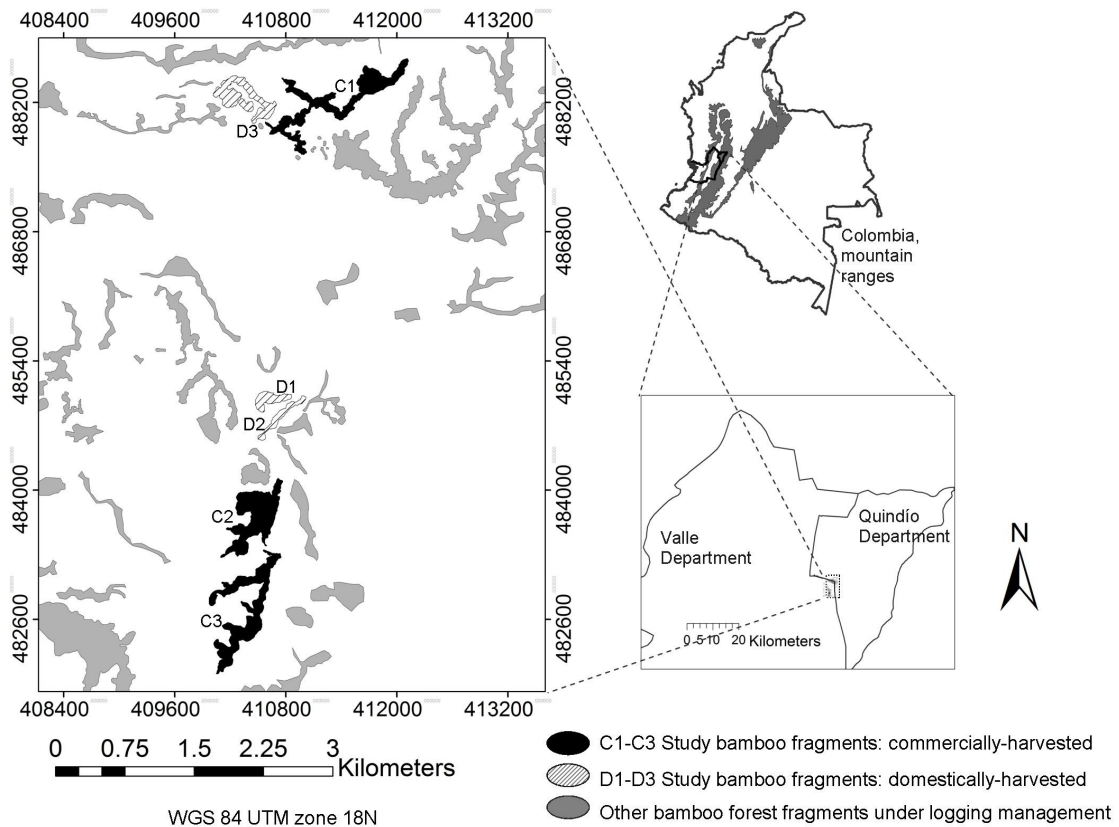


Figure 1. Study site at the Colombian Eje Cafetero region, indicating the 6 focal bamboo forest fragments.

Guadua (*Guadua angustifolia* Kunth, Poaceae) is a native, thorny, woody bamboo that tend to form monospecific stands, called ‘guadales’. Bamboo grows about up to 21 cm per day, and

emerge from the ground with a constant diameter up to 22 cm and will reach its final height (18-30 m) in about 6 months of growth (Riaño et al. 2002). *Guadua* stems are very flexible - their tops tend to arch, providing a relatively continuous canopy pathway for primates and other animals. The stems are highly resistant to rot and thus are appreciated for a wide variety of uses, including as live fences, fuel wood, timber (building material for houses, bridges, and fences, furniture, jewelry, handicraft, kitchen utensils, musical instruments, etc.), and also for watershed and erosion protection (Castaño and Moreno 2004).

Natural bamboo forests have a mean bamboo stem density around 6,500 ha⁻¹, across all states of maturity (Camargo et al. 2010). The canopy stratum of a bamboo forest is formed by the intersection of branches and leaves of fully developed bamboos stems between 18-30m in height, and scattered emergent trees, which are taller than the bamboo. Bamboo forest fragments are dominated by bamboo, with low plant species richness within each fragment, but characterized by a diverse floristic composition across fragments (Ospina and Finegan 2004). Moraceae, Fabaceae, Anacardiaceae are among the most abundant families represented in guadales, and among the most abundant tree species are *Anacardium excelsum* (Anacardiaceae) and *Trophis caucana* (Moraceae) (Gómez-Posada chapter 2).

Bamboo forests support a diverse fauna, which includes night monkey (*Aotus cf. lemurinus*), sloth (*Choloepus hoffmanni*), kinkajos (*Potus flavus*), tayra (*Eira barbara*), among many others. Red howler monkeys and night monkeys are among the few primate species that have survived in these highly fragmented landscapes. Hunting of red howler monkeys in the Eje Cafetero is rare. Also, there is no recent documentation of attacks and killings of howlers by natural predators (mostly locally extinct from these forest fragments), but domestic dog attacks have been reported.

Bamboo logging

In Colombia, there have been numerous studies on bamboo silviculture and bamboo forestry development (e.g. Castaño and Moreno 2004, Camargo et al. 2008, review in Mejía and Moreno 2013), and the regional environmental authorities (known as regional corporations) have worked together to develop regulations and strategies to promote the sustainable management of bamboo forest called the *Unified Norm for Bamboo's Management and Use (Norma Unificada para el Manejo y Aprovechamiento de la Guadua)* (Bosques FLEGT/Colombia 2008), through projects funded by the German Development Cooperation Agency GTZ and the European Union (Gobernanza Forestal, Bosques FLEGT/Colombia) (Camargo et al. 2010). These regulations are very detailed and carefully describe every step to grow and sustainably manage natural and planted bamboo forest, to improve productivity, and to commercialize bamboo forest resources. Much effort is focused on aiding and educating small farmers, with the purpose to help improving their livelihoods. Governmental authorities emphasize how unsustainable harvesting may cause environmental damage, and decreased the productivity and quality of the forest. It also highlights the environmental benefits of bamboo forest and includes recommendations to diminish the damage to the native flora and fauna during the harvesting activities (Ospina and Vega 2004, Camargo et al. 2010).

Bamboo forests are managed either for domestic production or commercial sale. Both types of management are subject to regulation, but only commercial production is supervised. The designation of domestic vs. commercial logging management is determined by the intensity and logging cycle (Bosques FLEGT/Colombia 2008):

- Domestic logging (“*entresaca doméstica*”): This is a type of harvesting that takes place exclusively to meet the basic needs of a farm and its inhabitants. Fragments under domestic use

are harvested sporadically, with extraction of bamboo restricted to a volume of 20m³ (2000 stems) per year. Although the farmers need a permit for domestic extraction, landowners do not always apply for permits, as they remove stems sporadically whenever they need bamboo. For that reason, it is difficult to find records of the periodicity and the number or volume of stems extracted from those fragments. Bamboo stems taken via domestic extraction cannot be sold.

- Commercial logging (“*entresaca comercial persistente*”): This type of harvest aims to generate economic benefits from its exploitation; these stems are sold in the market. The logging intensity shall not exceed 35% of the commercial stems (mature and over mature); however, the intensity of harvest may be higher than originally authorized as long as it is determined by a forestry technician (according to the forest stem density) and approved by regional environmental authorities. These authorities grant the logging permits, coordinate the harvest, and estimate the volume of stems that can be extracted, as well as indicate specifically which stems can be cut (which are marked in advance). Cutting cycles may not be less than twelve (12) months, but the periodicity can vary according to the farmers’ will. Workers usually cut the bamboo with machetes, but in recent years, also chainsaws have been used (Camargo et al. 2010). Commercial logging is regulated by criteria that were designed to ensure sustainability and profitability of bamboo forestry, including the natural renewal of sufficient stems with commercial characteristics.

Study fragments

Three of the six bamboo forest fragments in this study were under commercial use (C1 - C3) while the other three were under domestic use (D1 - D3). The fragments were all small, ranging in size from 3.69 to 25.5 ha, with similar narrow shapes (table 1). We chose fragments that had

been harvested in a consistent manner for at least the last past 12 years, according to the owners. Although we tried to match fragment sizes for the two management types, fragments under domestic management tend to be of smaller size, and we were restricted to access only those fragments whose owners allowed us to carry out the study.

According to the owners, the three fragments under commercial logging are harvested regularly, with a minimum of two years between harvests, but the cycle could vary. The three commercial fragments differed somewhat in their use during this study. Fragment C1 has multiple owners, so the extractive activities usually involved only a section of the fragment at any one time. Fragments C2 and C3 each have only one owner, thus the extraction usually took place over the majority of the fragment. We chose these 3 fragments for the study, as the owners told us that a logging event would happen in about six months after the start of our study, so we would have similar sample effort before, during and after the logging. However, the owner of fragment C3 did not harvest the forest during the study, fragment C1 was logged after the second month of the study, for 12 weeks, and, for fragment C2, logging took place after the third month and for 8 weeks. In both cases, C1 and C2, the environmental authority reported that about 35% of the mature stems were removed. In the case of C1, we have complete logging records: prior to logging there were 14,057 mature stems and a density of 2,163 stems per ha. The local authority allowed the owner to extract 4,920 mature stems (714 m³), for a final density of 1,800 stems per ha (Lozano 2010). We observed incidental damage of bamboo stems during the extractive activities in both fragments, and after the logging, some stems fell, which means that the loss of bamboo stems may be a little higher than 35%. During the last month of study in C1, bamboo was logged from 0.75 ha of the focal group's home range. As this was a small area and

represented less than 2% of home range use, we did not include this logging event in our data analyses.

During commercial logging activities, there was noise in the forest, caused by the presence of workers (whose footfalls, talking, and music could be widely heard), the sounds of the saws, machetes and axes, and the fall of the bamboo stems. In addition, workers opened harvesting trails and brought horses and mules within the forest to carry the stems.

We did not witness domestic logging during our study, although in fragment D3, we did note that 10 bamboo stems had been cut with a machete. For that particular case, no trails were opened in the forest and we did not observe horse or mule tracks. This extraction was outside the home range of the focal howler group in this fragment. In general, domestic logging is less noticeable. Typically, no more than a few workers go into the forest to cut stems, and extract as many stems as needed, as often as is needed. The intensity and frequency of domestic logging varies according to the owner's will. Thus, domestic logging management is difficult to describe, as there are no official records, and the owners do not take notes regarding harvesting activities.

Primate observations

In each of the fragments, one group of howlers was selected, habituated and studied for 6 months to one year during 2010 and 2011 (table 1). We assigned to each group the same name as the fragment it inhabits. The size of the focal groups was on average (\pm SD) 8 ± 1 for groups inhabiting forest under commercial logging and 8 ± 3 for the domestic ones (table 1). All group members were individually recognized, using facial features, sex, and body size. Four of the six study fragments have a high howler population density (table 1). Groups C2, C3, D1, and D2 have been monitored since 2004 (Gómez-Posada et al. 2010).

The commercial logging events in fragments C1 and C2 allowed us to describe the immediate direct response of howlers to extractive activities. For group C1, we had one month of observations before the logging took place, three months during the logging, and 8 months after the extraction. For group C2 we had two months of observations before, during and after the bamboo logging.

Each month, each focal group was followed continually over 5 complete days (12 hours per day: 6:00–18:00). We collected data on activity and diet using slow scan sampling (Altmann 1974, Robinson 1986). Every 15 minutes we scanned the group for ten minutes, and for each monkey, we noted its first activity (resting, traveling, feeding or social interactions). If the individual was feeding, we also noted the type of food eaten (leaves, fruits, and other items - which were primarily flowers, stems of vines, roots of epiphytes, exudates, tree bark, and mineral soil).

We recorded the location of the groups every 15 min on a previously established trail system. To determine the area of each group's home range, a 50 m x 50 m grid was superimposed on our site map. All quadrants visited by the monkeys at least once were considered part of their home range (NRC 1981). We plotted all group locations to obtain frequencies and percentage of use of each $\frac{1}{4}$ ha quadrant within their home ranges. We calculated daily path lengths for each howler group as the sum of the straight distances between consecutive locations taken every 15 min. We use AutoCad 2009 version 17.2 for Windows for all home range, quadrant use, and daily path length calculations.

To calculate the density of feeding trees and their relationships with patterns of habitat utilization, we marked all feeding trees used by the groups during the study. To estimate the fruit biomass and new leaves production by *Ficus* trees, in each fragment, we identified all *Ficus*

trees with a DBH > 10 cm in 3 ha, and checked these trees every 15 days through out the study (*F. insipida*, *F. killipii*, *F. giganticus*, *Ficus* sp1 and *Ficus* sp2). We calculated the approximate number of fruits in the selected trees by counting the number of fruits present on some branches (using binoculars), estimating an average and multiplying this by the number of similar-size branches on each tree. We measured the dry weight of at least five fruits of each species to obtain an average dry weight, and used these values to estimate the fruit biomass produced by each tree (Palma et al. 2011). We calculate the mean fruit biomass production by a *Ficus* tree, by averaging the production of each tree every two weeks. To estimate the production of new leaves, we visually estimated the percentage of the crown with young leaves of the selected trees. We calculate the mean percentage of new leaves production by a *Ficus* tree by averaging the production of each tree every two weeks.

Table 1. Characteristics of the six studied fragments (C: under commercial use, D: under domestic use).

<i>Howler group</i>	<i>Fragment size (ha)</i>	<i>Fragment shape (area/perimeter)</i>	<i>Howler density^a Ind/km²</i>	<i>Size of howlers' focal group</i>	<i>Sample effort h/months^b</i>
C1	25.50	0.03	58.82	8	720/12
C2	21.94	0.06	241.54	9	360/ 6
C3	25.09	0.04	302.89	7	720/12
D1	4.22	0.03	166.02	8	720/12
D2	3.69	0.03	297.57	11	360/ 6
D3	13.42	0.03	37.25	5	720/12

^a Direct count of all the red howlers monkeys living in each fragment / fragment size (Gómez-Posada et al. 2010)

^b Accumulated hours of observation/number of study months

Statistical analyses

Diet and activity data are presented as a percentage of the overall observations in each behavioral category over the study period. To investigate differences in howlers' activity patterns

and diet between logging types, we employed Mann-Whitney tests due to the lack of normality in the distribution of the data and small sample sizes of this study.

The diet diversity for each group was calculated by a Shannon's diversity Index. To analyze the similarity of the diets across study groups, we performed a cluster analysis using the Morisita-Horn index, which takes into account both species richness and frequency of consumption by species. The index was calculated in a group paired-analysis. This analysis was performed using the EstimateS 9.1.0. program for Windows. To investigate if the density of feeding trees per howler group varied among logging types, we used Mann-Whitney tests.

To examine differences in howlers' home range size and daily path length between logging types, we employed Mann-Whitney tests. In the case of daily path length, we reported also the value of a Kruskal-Wallis test, which was the most appropriate test given the lack of normality in the data, as in this case there were differences among all the groups.

To investigate the differences before, during and after the logging in howler activity patterns, diet, home range size and daily path length, we employed chi square tests for group C1 (because we have only one sample before the logging) and Kruskal-Wallis tests for group C2. The frequency of use of each quadrant before, during and after the logging was compared using a Friedman test.

To analyze the differences between logging types in *Ficus* fruit biomass and production of new leaves, we used Mann-Whitney tests, and for C1 and C2, we used Kruskal-Wallis test to compare these variables before, during and after the logging.

We used Spearman's correlations to determine (1) if each activity, consumption of each food item in diet, home range size and daily path length were related to the fragment size or to

the howler population density, and (2) if the frequency of use of each quadrant in the home range was correlated with the number of feeding trees per quadrant.

All tests were performed using Statistica 6.1 program. We considered statistical tests significant at the $p < 0.05$ level.

Results

Behavioral ecology in bamboo logged fragments

Activity Patterns

Across groups, red howlers spent most of their time resting ($X \pm SD = 48.94 \pm 2.16\%$ of scan samples; range = 47.17-53.05%), followed by feeding ($29.64 \pm 6.17\%$; range = 22.89-39.17%), traveling ($14.14 \pm 6.50\%$; range = 8.52-22.38%), and engaged in social interactions ($7.27 \pm 3.36\%$; range = 2.91-11.5%) (fig. 2). The time budgets were highly similar among groups living in fragments with commercial or domestic use (resting, $U=426$ $p=0.73$; feeding, $U=380.5$ $p=0.32$; traveling, $U=329$ $p=0.07$; social int, $U=387$ $p=0.35$). Activity patterns were not related to either red howler population density or fragment size.

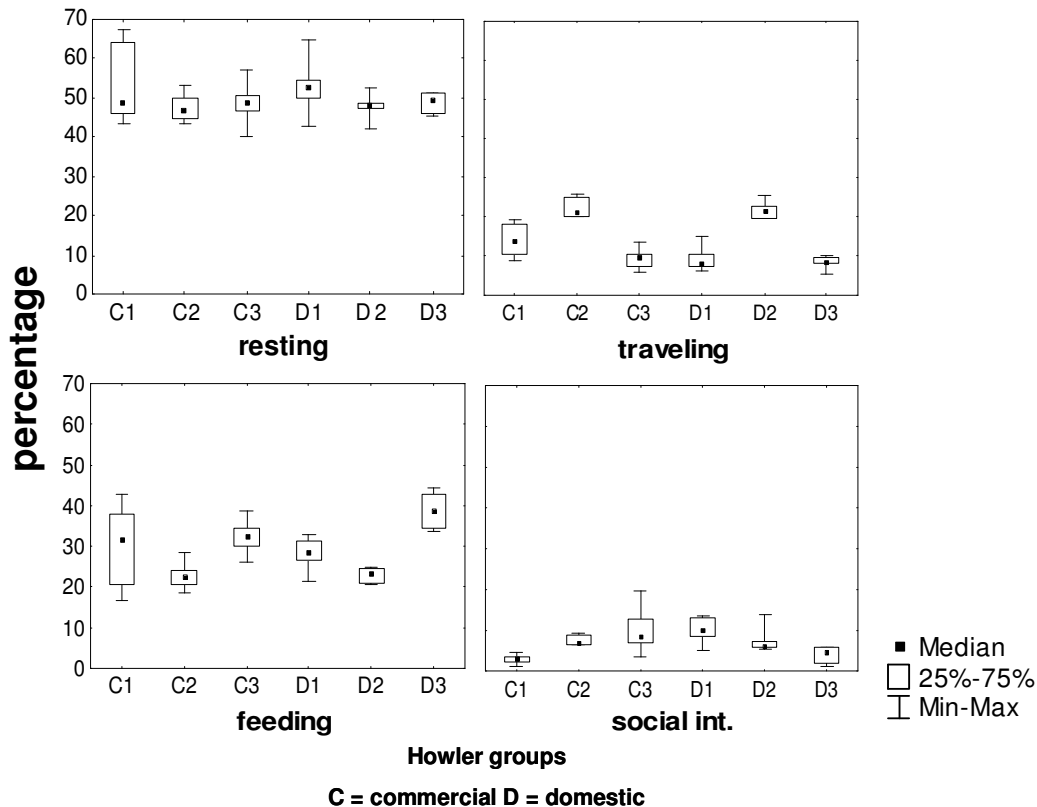


Figure 2. Activity patterns of six red howler groups. C1-3=commercially-harvested bamboo fragments, D1-3=domestically-harvested bamboo fragments. The Y-axis depicts the proportion of individuals doing each activity

Diet

In general, the red howlers' diet was species-poor: the six groups fed from 33 plant species, ranging from 6 to 20 species eaten by each group (table 2). Most plant species were represented in fewer than 5% of the feeding observations. Moraceae was the most important family in the howlers' diet, with 11 genera represented in the diet across the study groups. Six *Ficus* species were the most important in the diet (howlers ate fruits, flowers, and leaves of *Ficus*) and two of them, *F. killipi* and *F. insipida*, comprised 76.59% of the diet for five of the groups (range 66.55-89.39%). For group D3, the most consumed species was *A. excelsum* (Anacardiaceae, 53.18% of the diet), with the howlers eating mostly new leaves, and in rare occasions, the peduncle of the fruit.

Most of the plants eaten by howlers were big canopy trees, with DBH larger than 90 cm, except *S. trophoides* and *T. caucana* (mid-size trees which were minor items in the diet).

Howlers ate leaves and stems of lianas and epiphytes, which were difficult to identify; only four species were identified, two from the Cucurbitaceae (*Cayaponia racemosa* and *Thladiantha dubia*), one epiphyte Araceae (*Philodendron elegans*) and one epiphyte cactus (*Rhipsalis baccifera*). The consumption of lianas and epiphytes was in general very low, less than 4% of the diet. Howlers did not eat bamboo.

Table 2. List of plant species consumed by the six red howler study groups, and percentage of observations consuming each species. C = commercially harvested fragments. D = domestically harvested fragments.

Family	Plant species	C1	C2	C3	D1	D2	D3
Anacardiaceae	<i>Anacardium excelsum</i>	7.32	10.23	7.28	12.99	1.73	53.18
Araceae	<i>Philodendron elegans</i>	0.9					
Araliaceae	<i>Dendropanax</i> sp			0.69			
Bombacaceae	<i>Ochroma pyramidale</i>		0.99			1.59	
Cactaceae	<i>Rhipsalis baccifera</i>		0.1				
Cecropiaceae	<i>Cecropia angustifolia</i>	0.9		0.12		0.19	1.5
Cucurbitaceae	<i>Cayaponia racemosa</i>			1.88	2.21		
	<i>Thladiantha dubia</i>			0.52	0.86		
Fabaceae	<i>Erythrina poeppigiana</i>	12.12	0.47		2.94	7.22	17.01
	<i>Inga densiflora</i>					0.23	
	<i>Inga edulis</i>					0.23	
	<i>Inga</i> sp		0.63				
Lauraceae	<i>Nectandra</i> sp	0.54					
Malvaceae	<i>Helioarpus</i>	0.18					2.71
	<i>popayanense</i>						
Moraceae	<i>Clarisia biflora</i>	0.72					
	<i>Ficus giganticus</i>					6.94	
	<i>Ficus insipida</i>	12.39	54.05	65.11	59.18	76.24	15.98
	<i>Ficus killipii</i>	54.16	14.2	24.29	21.82	1.5	0.19
	<i>Ficus</i> sp1		5.22			1.41	
	<i>Ficus</i> sp2		4.96				
	<i>Ficus</i> sp3		6.68				
	<i>Poulsenia armata</i>	0.72					
	<i>Sorocea trophoides</i>	3.44				0.7	
	<i>Trophis caucana</i>	0.09					
	<i>Naucleopsis glabra</i>	0.18					
Sapindaceae	<i>Cupania macrophila</i>						1.59
Unidentified species		6.33	2.45	0.12		2.01	7.85
Total # species in diet		20	11	8	6	13	9
Shannon Index		1.67	1.53	0.97	1.14	1.00	1.41

Groups inhabiting forest under commercial and domestic bamboo production tended to use a similar number of species in the diet ($X \pm SD$ commercial 14.33 ± 8.5 species, domestic 9.33 ± 3.51 species, $U=3$, $p=0.66$). Only three species were consumed by all six howler groups (*F. insipida*, *F. killipii* and *A. excelsum*), but 11 species were shared between the two logging types (table 2).

When comparing the percentage of observations per species consumed by red howlers across the six groups, we found that on average (\pm SD), Morisita-Horn similarity index was 0.61 ± 0.29 (range 0.23–0.99). Cluster analysis showed no tendency for groups from one type of management to be grouped together (fig. 3).

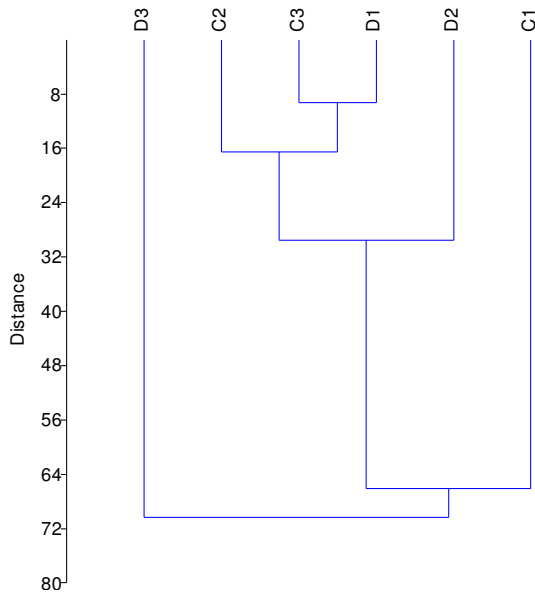


Figure 3. Diet similarity estimated with a Morisita-Horn Index for six red howler groups. C1-C3=commercially-harvested bamboo fragments, D1-D3=domestically-harvested bamboo fragments.

The density of feeding trees within the home range of each group was on average (\pm SD) 7.22 ± 3.58 trees/ha, with no differences in density between commercial (6.36 ± 1.75 trees/ha) and domestic use (8.09 ± 5.16 trees/ha) ($U=3$ $p=0.51$). The density of *Ficus* feeding trees was similar between groups in commercially and domestically harvested fragments ($U=4$ $p=0.82$), being on average (\pm SD) 4.40 ± 1.89 trees/ha, excluding D3 which had only 0.24 *Ficus* tree/ha. The fruit biomass produced by *Ficus* was on average (\pm SD) 90.25 ± 158.70 g/tree, and there were no differences between the two logging types (commercial 120.82 ± 180.84 , domestic 99.29 ± 152.52

g/tree, $U=1031.50$ $p=0.71$), excluding D3 that had a very low *Ficus* fruit production throughout the study (5.54 ± 0.87 gr/tree).

Leaves were the most consumed plant item for all the groups, comprising $70.61\pm 15.17\%$ (range 51.75-94.02%) of the feeding bouts, followed by fruits ($25.04\pm 13.70\%$; range 5.54-48.88%) and other items (4.35 ± 4.11 ; range 0.44-11.67%). Group D3 had the lowest fruit consumption ($X\pm SD$ $5.54\pm 7.8\%$) and the most folivorous diet ($94.02\pm 7.86\%$). There were no differences among groups living in fragments with commercial or domestic use for each of the main items consumed by the red howlers (leaves $U= 361$ $p=0.19$, fruits $U=378.50$ $p=0.29$, others $U=298$ $p=0.06$) (fig 4). We did not find any significant relationship between either howler population density or fragment size with the proportion of different food types eaten, the diet breadth, the diet diversity and the number of feeding trees.

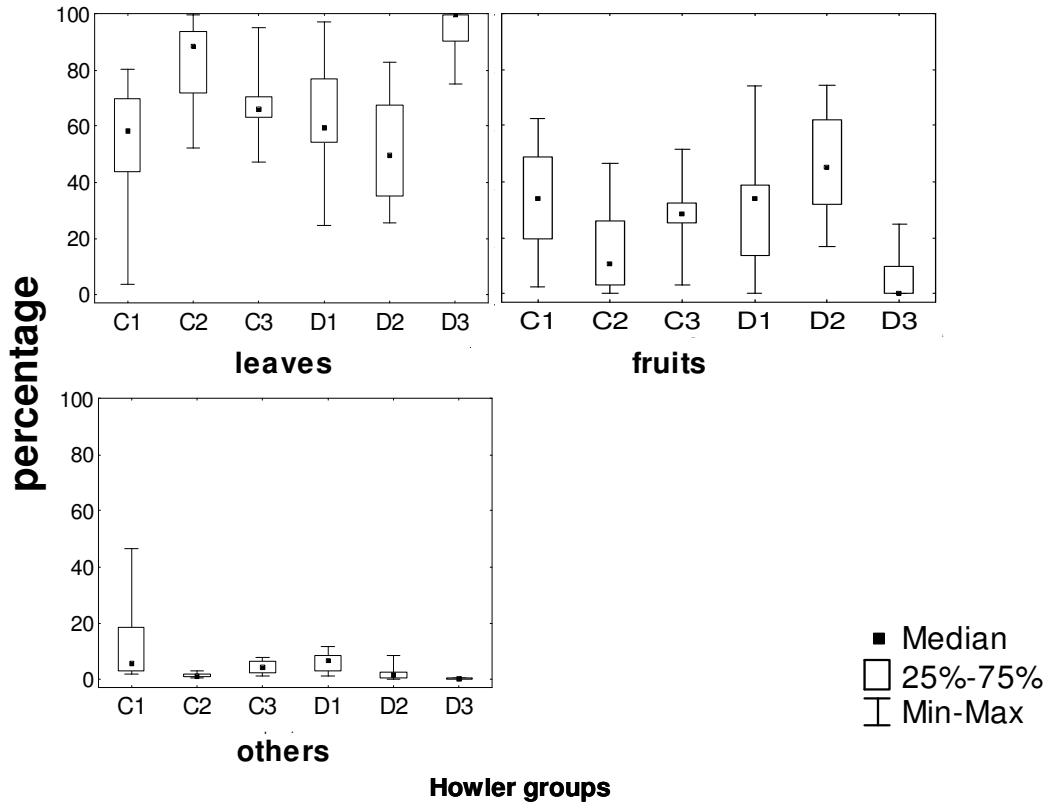


Figure 4. Percentage of plant items (leaves, fruits, other) in the diet of six red howler groups. C1-C3=commercially-harvested bamboo fragments, D1-D3=domestically-harvested bamboo fragments.

Home range size

Home range of the red howler groups varied from 3 to 15.75 ha (table 3). The number of hectares used each month was on average (\pm SD) 3.75 ± 2.41 ha (table 3). Home range sizes did not differ for groups living in commercial vs domestic forest ($U=3.50$ $p=0.66$) (table. 3). The number of hectares that each group used per month was also similar between the two logging types ($U=363$ $p=0.20$) (table 3). Neither the fragment size, nor the density of red howlers were related to home range size.

Table 3. Home range for the six red howler study groups

Group	Home range (ha)	Ha used per month mean (SD)
C1	15.75	7.88 (2.05)
C2	3.00	1.96 (0.29)
C3	5.25	2.56 (0.71)
D1	3.50	2.33 (0.76)
D2	3.00	2.33 (0.47)
D3	8.50	3.85 (0.65)

Daily path length

Red howlers moved mainly between feeding trees and sleeping trees/bamboo stems. All the groups used predetermined canopy pathways within their home ranges, which would have some variation according to the food availability in different feeding trees. In these bamboo forests, trees are scattered and red howler used the thick bamboo stems during their movements. When there was no connectivity among stems, howlers climbed to the upper part of the stem and bent the tip, using their own weight, until the stem touched the next one. Howlers slept at night in thick horizontal bamboo stems or large branches of trees.

Daily path length ranged from 68.3 m to 1387 m with an average (\pm SD) of 552.1 m \pm 259.8. This distances varied among groups ($H=98.37$ $p<0.01$) (fig. 5) and among logging types ($U=6683$ $p<0.01$), but the variances were large. No significant relationships were found between fragment size and density of howlers with the daily path length.

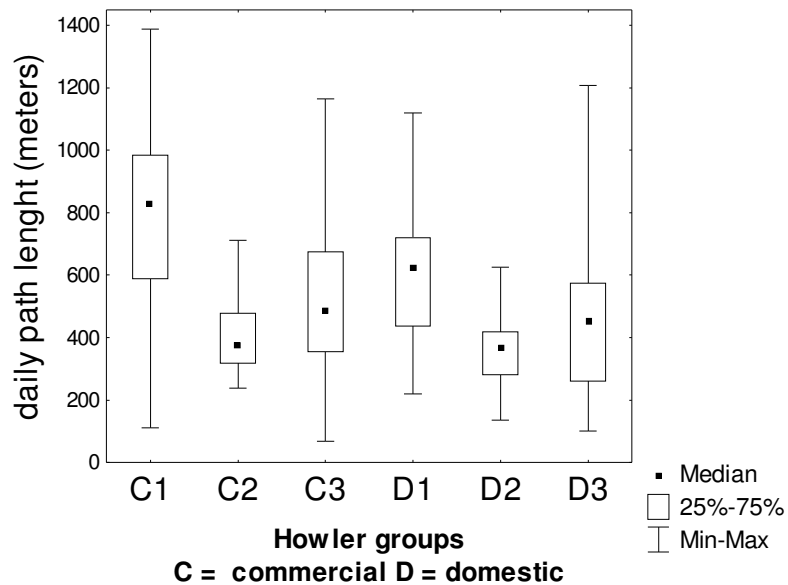


Figure 5. Daily path length of six red howler groups inhabiting bamboo fragments with different logging intensity. C1-3=commercially-harvested bamboo fragments, D1-3=domestically-harvested bamboo fragments.

Immediate response to commercial logging activities

Activity patterns

During the logging period, howlers did not vocalize or show aggression towards the workers, nor did they overtly respond to the sound of the saws. However, on some occasions the groups altered their behavior for a short time in response to the presence of workers. For example, a group might wait in a single tree until the workers were gone before moving to a target tree, or the members of the group might follow a different canopy path to access the trees. Howlers were never observed moving away from the foci of logging activities, or avoiding areas affected by harvesting trails and stem removal. Howler activities did not differ before, during and after the logging in either group C1 or C2 (fig. 6).

No individuals died or presented signs of injuries during or after the extractive activities, except a new born male infant from group C2, who died three months after logging. However, as this individual was apparently sick since its birth (crying continuously, as if in pain), we assume its death was not directly related to the logging activities.

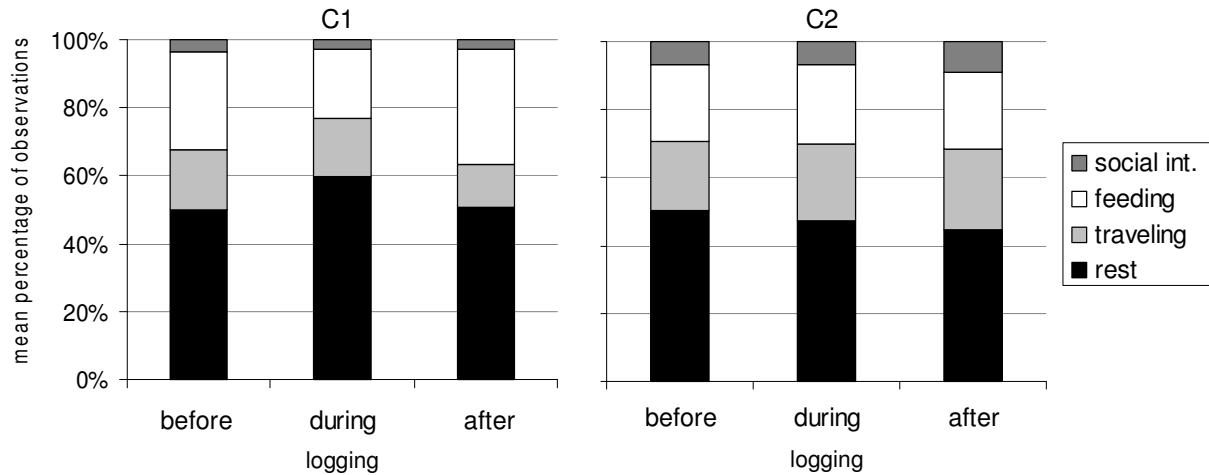


Figure 6. Activity patterns for two red howler groups, before, during and after commercial bamboo logging. (group C1: resting, $X^2=1.12$ $p=0.57$; traveling, $X^2= 1.03$ $p=0.60$; feeding, $X^2=3.47$ $p=0.18$; social interactions, $X^2=0.12$ $p=0.94$; group C2: resting, $H=2.57$ $p=0.28$; traveling, $H=2.56$ $p=0.27$; feeding, $H=0.01$ $p=0.99$; social interactions, $H=3.71$ $p=0.16$)

Diet

For both groups, none of the feeding trees were isolated due to the logging activities, as howlers were able to access them using the bamboo stems that were left standing. None of the mature feeding trees were damaged incidentally during logging, nor were any cut, as only bamboo stems were targeted for extraction. Group C1 decreased consumption of fruits and other items during and after logging, while increasing consumption of leaves (leaves $X^2=48.68$ $p<0.01$, fruits $X^2=14.28$ $p<0.01$, other $X^2=18.47$ $p<0.01$) (fig. 7). Flowers of *E. poeppigiana* (component of “other items”) were available primarily for C1 before logging, thus howlers had a high consumption of them during that month. The species finished flowering right before logging

started (unpublished data). In contrast, the composition of the diet of group C2 did not differ before, during and after the logging (leaves $H=0.28$ $p=0.86$, fruits $H=0.29$ $p=0.87$, other $H=2.00$ $p=0.37$) (fig. 7).

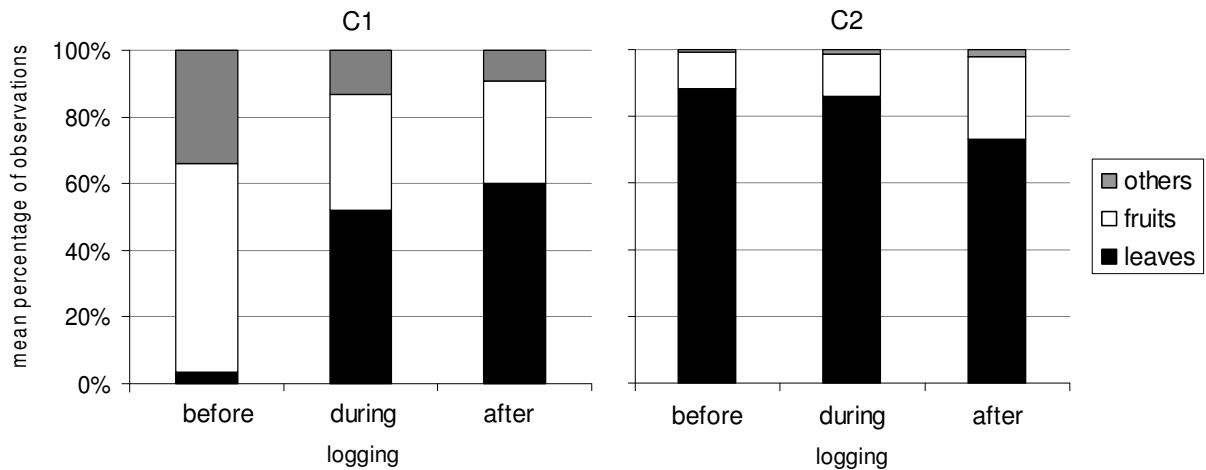


Figure 7. Diet composition (leaves, fruits, other items) for howler groups C1 and C2 observed before, during and after bamboo logging.

Ficus fruit biomass production in both fragments C1 and C2 tended to increase after the logging ($x \pm SD$, C1: before 10.88 ± 15.39 g/tree, during 6.48 ± 15.55 g/tree, after 168.95 ± 264.44 g/tree, C2: before 30.20 ± 21.91 g/tree, during 13.10 ± 15.62 g/tree, after 227.86 ± 240.39 g/tree), however these differences were not significant (C1 $H=1.98$ $p=0.37$, C2 $H=2.00$ $p=0.36$). New leaves production in *Ficus* was not affected by the logging in C1 (before 60.42 ± 7.66 , during 11.56 ± 7.97 , after 12.01 ± 10.71 % of a tree crown, $H=5.32$ $p=0.08$), but increased during and after the logging in C2 (before 15.95 ± 1.45 , during 21.31 ± 4.38 , after 23.63 ± 5.03 % of a tree crown, $H=6.27$ $p=0.04$).

Home range and daily path length

The harvest area within both fragments was large; approximately 40% of the home range for group C1 and 83% for C2. For both groups, howlers used the logged quadrants as frequently before, during and after the logging (C1: Friedman $X^2=0.81$ $p=0.67$; C2: Friedman $X^2=1.80$ $p=0.41$) (table 4). However, following the logging, howlers from group C1 increased the use of quadrants that were not harvested, but this was not seen in group C2 (C1: Friedman $X^2=18.23$ $p<0.01$; C2: Friedman $X^2=0.99$ $p=0.6$) (table 4). Quadrants use was dictated by the presence of feeding trees, as the frequency of use of each quadrant was correlated with the number of feeding trees, strongly in the case of C1 ($r_s=0.73$ $p<0.01$), and more weakly in the case of C2 ($r_s=0.55$ $p=0.06$).

Table 4. Percentage of use per quadrant ($X\pm SD$) within each home range, and total use of not logged and logged area by two groups of red howler monkeys, comparing before, during and after commercial bamboo logging.

Quadrants		Red howler groups					
		C1			C2		
		Before	During	After	Before	During	After
Not logged	X \pm SD	0.87 \pm 2.3	1.43 \pm 2.4	1.67 \pm 3.4	16.95 \pm 14.0	10.61 \pm 3.1	16.63 \pm 11.1
		9	2	4	8	7	1
	Total use	33.06	54.29	63.57	33.90	21.22	33.27
Logged	X \pm SD	2.68 \pm 5.7	1.83 \pm 2.5	1.46 \pm 2.1	6.61 \pm 9.29	7.88 \pm 9.08	6.67 \pm 8.34
		6	1	4			
	Total use	66.94	45.71	36.59	66.95	86.73	67.35

The number of hectares that each group used per month was not influenced by the logging activities (C1: $X^2=0.004$ $p=0.99$, C2: $H=0.25$ $p=0.88$) (table 5). Similarly, the daily path length

was not affected by logging for group C1 ($H= 0.37$ $p=0.07$), however, group C2 increased its daily movements following the logging ($H=5.59$ $p=0.05$) (fig. 8).

Table. 7. Number of hectares used per month by two groups of red howler monkeys, before, during and after commercial bamboo logging.

	C1			C2		
	before	during	after	before	during	after
Mean	8.00	7.75	7.91	1.88	1.88	2.13
SD	0.00	1.00	2.51	0.18	0.18	0.53

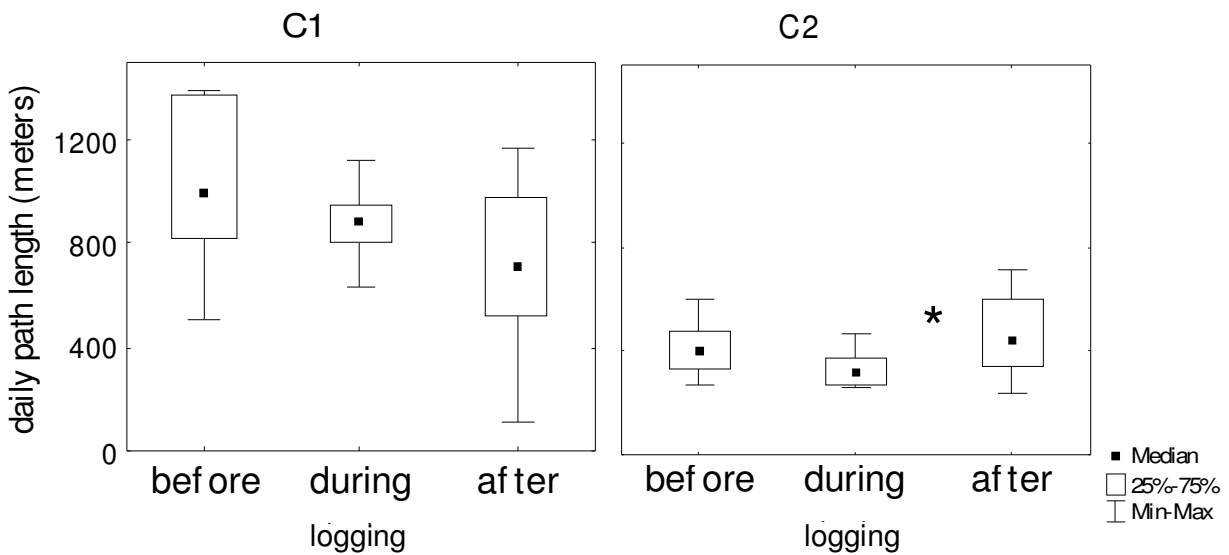


Figure 8. Daily path length for two red howler groups (C1 and C2) before, during and after commercial bamboo logging. (* $p=0.05$)

Many of the bamboo stems that red howlers used for their canopy movements were removed during the logging, and in some cases, the groups were forced to modify their usual canopy paths, using the remainder of stems left standing. After the logging, individuals from group C1 seemed to jump more frequently from one bamboo stem to another when there was not complete canopy connectivity, although we did not collect systematic data on this behavior. In some cases, for young individuals, the jump was difficult, and they seemed stressed. Some times the mother

returned and helped or encouraged the young ones to jump, and they were delayed from the rest of the group. This was not observed for group C2.

Discussion

The diet, ranging, and activity patterns of the 6 howler monkey groups we studied in logged bamboo forest fragments, were similar to reports for the genus elsewhere, including studies from fragments, as well as protected and those from continuous forests (reviewed in Crockett and Eisenberg 1987, Neville et al. 1988, Bicca-Marques 2003, Di Fiore and Campbell 2006, Cristobal-Azacarate and Arroyo-Rodriguez 2007, Chaves and Bicca-Marques 2013). This is not surprising, as howlers display a conservative activity budget, and in general, similar diet and ranging patterns across habitats with different quality, as has been seen in studies from degraded forests (De Thoisy et al. 1996, Pavelka et al. 2003), small fragments (Rivera and Calmé 2006, Asensio et al. 2007, Dunn et al. 2010), small islands (Rodríguez-Luna et al. 2003, Orihuela et al. 2005), shaded cocoa plantations (Williams-Guillen et al. 2006, Zarate et al. 2014), eucalyptus plantations (Bonilla-Sánchez et al. 2012), logged forests (DeLuycker 1995, Pinto et al. 2003), among others. Howlers are animals that behaviorally constrain their energy expenditure (Milton 1980, Silver and Marsh 2003), which may be a consequence of their highly folivorous diet (Bicca-Marques 2003). These adaptations may foster an ability to persist in highly human-modified environments.

In general, logging affects primates mainly through reduction of food resources, which may reduce their nutrition (Rode et al. 2006), which in turn decrease their ability to overcome parasites (Gillespie et al. 2005), force them to use different resources (Guo et al. 2008), modify their habitat use (Singh et al. 2000), avoid logged areas (Arnhem et al. 2008), and could

eventually lead to a population reduction (Plumptre and Grieser Johns 2001, Felton 2010). In our study, we did not find a strong negative effect of the bamboo logging on the behavioral ecology of howlers living in bamboo forest fragments. This could be related to the fact that their food resources are not harvested. In these bamboo fragments, only bamboo stems are harvestable under Colombian regulations (Bosques FLEGT/Colombia 2008), and howlers did not eat bamboo. Thus, howlers' feeding trees were not impacted directly by the logging. Further, we saw no damage to mature trees that the howlers used for feeding. The main variables that determine the activity budget, diet and the spatial use patterns of primates are, in general, the distribution, quality and abundance of food resources (Milton 1980, Crockett and Eisenberg 1987, Terborgh 1983), and in the case of howlers, also the availability of big large trees (DBH > 60 cm) (Dunn et al. 2009). As the bamboo logging does not directly affect the adult trees that are the main food resources for howlers in these bamboo forests, their behavioral ecology did not seem to be significantly altered by the extractive activities, and was similar to what has been reported in another study in unlogged bamboo forest (Londoño and Gómez-Posada submitted), and protected montane forest in Colombia (Gaulin and Gaulin 1982, Giraldo et al. 2007, Gómez-Posada et al. 2007, Palma et al. 2011).

It is important to note that trees with commercial value or any important use for humans most probably had been removed from these bamboo fragments in Colombia long before, as the region has been under heavy agricultural and livestock activities for more than a century. *Ficus insipida* and *F. killipii* which are used in other countries (Castaño et al 2007, Felton et al 2012), are not harvested in the region.

The activity patterns, diet and home range size for howlers inhabiting fragments under the two different logging managements were also similar, which could be explained by the fact that

both types of logging, regardless of the intensity and periodicity of the extractive activities, are only focused on bamboo stems and do not affect the howlers' primary food resources. In commercially and domestically logged fragments, no adult trees were impacted by the logging, and both had a similar density of feeding trees, *Ficus* trees and *Ficus* fruit biomass production. Fragments under both logging types also have a similar resource availability for howlers (see Gómez-Posada chapter 2), which may explain the similar activity budget, diet and home range size, across the six study groups, regardless of the logging type.

The same explanation may serve to account for the lack of relationship between logging intensity and daily path length. As a general rule, the location of the main food resources influences primates' ranging behavior (Terborgh 1983). Howler movements are dictated by the location of their primary feeding trees; they travel almost solely to access food resources, and are considered travel minimizers (Milton 1980). In our study, differences among the groups were most likely explained by the relative separation of their feeding trees, which were not affected by the logging, regardless of its type.

Howlers' diet has low diversity in plant species in these bamboo forests. Across the six groups, only 33 species were recorded in their diet, and three groups used fewer than 10 species. This low diversity of species in the diet could be related to the natural low plant diversity of the bamboo forest, given the predominance of bamboo (Ospina and Finegan 2004, Gómez-Posada Chapter 2).

The low number of species in the howlers' diet in this study could also be related to the high consumption of *Ficus* species. If a preferred food is relatively abundant in a forest, howlers could concentrate their feeding activities on a small number of those preferred trees, as has been seen in the case of *Ficus* (Serio-Silva et al. 2002). For example, in Mexico, groups of black howlers

(*A. pigra*) living in a diverse and large reserve in Mexico (the largest tropical reserve in the country), ate from only 10 species and 50% of feeding time was devoted to a single *Ficus* species (Rivera and Calmé 2006). Rivera and Calmé (2006) suggest that howler monkeys showed strong selection for the consumption of plant foods of particular tree species, limiting their diet to a small number of preferred species, relatively independent of their availability, and the availability of non-preferred species. In general, *Ficus* make up a very high proportion of the diet of different species of howlers; *Ficus* are relatively abundant in secondary environments (Julliot and Sabatier 1993, Bicca - Marquez 2003, Cristobal-Azcarate and Arroyo-Rodríguez 2007). The preference of *Ficus* in the diet of howlers can be explained by their nutritional content, their abundance, their big size, and their continued supply of fruits and other items such as flowers, bark, exudates, and leaves (Serio-Silva et al. 2002, Bicca - Marquez 2003).

Another explanation for the low number of species in the howlers' diet in these bamboo fragments could be related to the long term nature of the logging activities. In a parallel study, it was found that species richness and abundance of howlers' food plants in fragments under commercial and domestic logging were lower compared to a protected bamboo forest that has not been logged in over 20 years (see Gómez-Posada Chapter 2). This lower diversity may be the result of an arrested succession of some species due to mechanical damage to saplings as a consequence of the bamboo logging (e.g. during stem dragging and workers activity). In a study conducted in the same protected bamboo forest, 30 plant species were consumed by two groups of red howlers over six months (Londoño and Gómez-Posada submitted). This could suggest that logging, regardless of its periodicity and intensity, has reduced the diversity of food resources for howlers in such bamboo forests (see Gómez-Posada Chapter 2). Nevertheless, the protected bamboo forest studied by Londoño and Gómez-Posada is 148.84-ha in size, much larger than the

logged fragments. The low number of species reported in the red howlers' diet in this study, may be caused by a combination of the natural low plant diversity of bamboo forest, the howlers' strong preference for *Ficus* species, the small size of the fragments, and the on-going logging activities.

Group D3 used a very low number of *Ficus* trees within their home range, perhaps because these trees were not numerous in the fragment, and overall, those trees had a low *Ficus* fruit biomass production, which resulted in a low consumption of these species. The group relied on leaves of the most abundant species in the fragment, *A. excelsum* (Gómez-Posada chapter 2) which was consumed in a low percentage by the other groups. One of the dietary adaptations of howlers when preferred food resources are not available, is to feed on plants that are not a common part of their diet (Asensio et al. 2007, Cristobal-Azcarate and Arroyo-Rodríguez 2007, Zunino et al. 2007). Serio-Silva et al (2002) suggest that when few *Ficus* trees are present within the howlers' home range, folivory is the dominant tendency in the diet, as was seen for group D3. We have no information to explain the low abundance of *Ficus* in this fragment.

Howler monkeys in fragments and disturbed habitats complement their diet with secondary fallback sources of food, which are typically items that are abundant but low in nutrients, such as the fruits and leaves of lianas (De Thoisy et al. 1996, Pavelka et al. 2003, Asencio et al. 2007). All the groups in our study site consumed liana fruits and leaves, but due to the nature of lianas' growing habit, their species identification was difficult. In general, lianas did not make up a high percentage of the red howlers' diet. Lianas grow on trees and on bamboo stems, and with the removal of bamboo stems, this resource was probably diminished. We do not have data to quantify changes in the availability of lianas for howlers, but due to their low percentage in howlers' diet, we assume the impact of any decrease was low. However, the low consumption of

lianas could be the result of the short logging cycles, as it may not be enough time among logging periods for lianas to re-grow, limiting their availability.

Short-term responses of commercial logging activities:

Our results did not show a clear pattern for the immediate response of the two howler groups to the logging activities; but in general we did not observe any dramatic alterations due to harvesting activities. In Costa Rica, a group of mantled howlers (*A. palliata*) lost important feeding trees due the construction of an irrigation canal system. The immediate response to this deforestation was a change in the daily activity patterns, in the shape and size of the home range, and an increase in daily path length. Further, their social interactions decreased and foraging time increased, related with the search of new food resources. Howler fed in new areas displaying unusual behaviors (like foraging on the ground and eating small plants) (Clarke et al. 2002). In our study, activity patterns did not change during or after harvest periods; but there was a decrease in fruit consumption in the case of group C1 (however the fruit consumption value was within the range of documented howler patterns for the other five groups and in variable habitats, Di Fiore and Campbell 2006). We think the logging may not cause this change, as we did not detect a decrease in *Ficus* fruit production after the extractive activities. It may be more likely related to phenological changes in fruit and new leaf availability within each home range. In montane forest, intra- and interspecific asynchrony in the phenology of forest trees has been reported (Ataroff 2001, Cavelier et al. 2001). Instead of having a fruiting season, each individual tree produces fruits during a different period of time, and localized scarcities within a howler group's home ranges may occur (Giraldo et al. 2007). In these forests, new leaves are produced continuously (Cavelier et al. 2001), and offer a constant source of food for howler monkeys,

whose consumption increased when fruits are not abundant within the home range (Milton 1980, Julliot and Sabatier 1993).

Even though no significant behavioral changes were found in response to the commercial logging in our study, there were some effects on the howler's ranging patterns. In some cases, the stems that were part of the canopy pathways were removed, forcing the howler groups to alter their usual travel paths. These disruptions could lead to an increase in daily movements, as was the case for group C2, or to a decrease in the use of logged area, as was the case for group C1. Although we do not have data, it is possible that larger gaps between stems formed as a result of the logging, made travel more difficult for young individuals; and may have increased their likelihood to become temporary dislodged from their mothers and the group. The reduction of canopy travel pathways may cause an increase in energetic demands and the risk of falling, increasing infant and juvenile injury and mortality (Johns 1986, Chapman et al. 2000). However, we did not witness injuries and accidents, and the only death observed appeared unlikely to be attributable as a direct effect of logging. Also, neither group of howlers stopped using the logged area in their fragment, or visiting feeding trees located there, either during or after the logging. When stems were removed, howlers found other stems for their movement. As howlers established new canopy pathways using the bamboo stems left standing, we suggest that the disruption in their routines was temporary.

Guadua angustifolia is a fast growing species, with stems growing up to 21 cm per day, reaching its final height only six months after emerging (Riaño et al. 2002). Thus, after the logging, in about 6 months, the forest approaches the same density of stems as before the extraction. This is another reason to suggest that the disruption on the daily routine and habitat use for howlers in this bamboo forests may be temporary.

Due to the Colombian restriction on the percentage of bamboo stems that could be extracted over each one year interval (Bosques FLEGT/Colombia 2008), many standing stems are left after logging, which allow red howlers to move throughout their home range and access their feeding trees. Thus, despite the large volume of bamboo stems removed during commercial logging, red howlers' activity patterns and diet did not change dramatically during or after the logging events that took place in fragments C1 and C2. In cases where feeding trees were isolated or removed by logging, the behavioral ecology of primates was severely impacted and nutritional deficit may occur (Johns and Skorupa 1987, Chapman et al. 2000). Maintaining the canopy connectivity and the feeding trees mitigates the negative impacts of bamboo logging in our study site (Putz et al 2001). For both groups there were some areas within the home range that were not harvested. It has been suggested that adjacent unlogged sites can act as a refuge for monkeys, potentially minimizing harsh conditions introduced by logging activities, such as climate changes, or injuries from falling trees (Johns 1986, Pinto et al. 2003).

These bamboo forests have been harvested in Colombia since the beginning of the 20th century, thus howlers have been under logging pressure for at least 100 years, and for a long time before the logging was supervised and controlled by the environmental authorities. In the case of commercial logging, although the extraction is carried in periods as short as one year, the forest is continuously monitored to check the bamboo forest health. Additionally, both, bamboo forests under domestic and commercial use, are surrounded by crops (coffee, orange, tangerine, papaya, avocado, mango, lime, banana, plantain, corn, among others) and pasture for livestock. This means there is continued presence of workers in and around the forest. In this area, howlers are not hunted and these monkeys may not perceive humans as an important threat. We suggest that these monkeys are habituated to human presence, and up to some degree, to the logging activities.

Physiological stress (associated with glucocorticoids level elevations) has been reported for howlers facing anthropogenic disturbances (Martínez-Mota et al. 2007), which in the long term could potentially limit the future viability of populations. In our study site, fecal samples taken from groups C1 and D1 showed similar glucocorticoid levels between them and with howlers' fecal samples from larger unlogged forest (Rimbach et al. 2013), which could indicate that this species may not be negatively influenced by the logging activities. However, additional studies are needed to assess whether and to what extent the potential increases in physiological stress of individuals inhabiting bamboo logged patches affects their health and their population persistence.

There is a lack of information on the responses of the genus *Alouatta* to selective logging, particularly for *A. seniculus*, which makes it difficult to compare and generalize from our results. We did not find other studies of primates in logged bamboo forest. Red-handed howlers (*A. belzebul*) and black and gold howlers (*A. caraya*) in Brazil and Argentina, adjusted their diet, habitat use and home range to the new conditions created by selective logging (DeLuycker 1995, Pinto et al. 2003). For example, as a response to the harvesting activities, howlers fed on new resources from the secondary forest vegetation that grew in the tree fallen gaps, due to the extraction of the most important species in their diet (howlers have been characterized as opportunistic feeders, taking advantage of colonizing pioneer trees). In the case of *A. caraya*, the howlers' ecological density remained stable after 22 years of the logging activities (Zunino et al. 2007). In both studies, it is suggested that howlers' persistence may be compatible with moderate and selective logging, as long as logging is under careful management plans.

The results of this study suggest that logging of bamboo forest has no systematic effect on howler behavioral ecology. The present logging model regulated by the Colombian authorities

seems to work for howler persistence, allowing the fragments' owners to profit from the bamboo extractive activities, either commercial or domestic. This compatibility between economic and conservation activities may be due to a combination of characteristics, such as the fast growing habit of the bamboo (forest structure is recuperated in short time after logging), the timber species is not consumed by howlers (which means feeding trees are not affected by the logging), the restriction of the amount of stems that can be extracted (which maintains the canopy connectivity). However, the extremely short logging cycle could be negatively impacting the recruitment of some plant species, threatening the availability of food resources in the future (howlers are eating from adult trees, and the repeated bamboo logging may not allow saplings from other plant species, even secondary vegetation, to reach sizes large enough to escape from incidental mechanical damage during extractive activities). This implies that bamboo logging in the Colombian Eje cafetero needs a more careful management planning in order to secure food for howlers in the long term (see Gómez-Posada chapter 2).

There is still more information needed to have a complete portrait of the bamboo logging impact in these fragments. We studied howler groups over only one year, and evaluated the direct effect of the logging on only two troops with a short sample time before logging. The immediate response of primates to logging may not predict the long-term impact of such disturbances. Thus, it is important to evaluate a longer-term effect of selective logging on howler populations and on other animals in the area (Chapman et al. 2000). Also, it is important to evaluate the physiological responses of howlers to logging, as well as the potential impacts of continuous contact with humans and domestic fauna, which could increase howlers' vulnerability to parasites and diseases (Gillespie et al. 2005).

These howler populations have been isolated for at least 70 years (Gómez-Posada et al. 2010) and have persisted under logging pressure for even longer. There are few options to protect the remaining forest tracks in this private agricultural landscape. We suggest that well-managed bamboo forestry could be used as a tool to enhance howler conservation in fragments in the Colombian Andes at both the local and the landscape level, for example, adding fast growing bamboo forest corridors to facilitate the dispersal of howlers and other animals or to expand available habitat. Bamboo forestry could potentially serve as a sustainable practice that supports red howlers as well as human livelihoods.

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Chapter 2. Effects of bamboo logging under short rotation cycles on the floristic composition and regeneration potential of food resources for red howler monkeys in Central Colombia

Abstract

Bamboo is an important forest product that has the potential to support the livelihoods of rural communities. These forests harbor considerable biodiversity, and due to the frequent selective logging of bamboo, a careful analysis of their potential to support wildlife is needed to promote best management policies. In a highly fragmented montane region in Colombia, native bamboo forests are the last forest remnants, which provide refuge for the original fauna and flora. These forest are privately owned and are under logging activities that the government promote as environmentally sustainable sources of income for farmers. Using the red howler monkeys as a target species, we evaluated the effect of bamboo logging on the floristic composition and structure of food resources for red howlers (*Alouatta seniculus*) in 14 bamboo forest fragments, comparing impacts from two commercial (regulated, frequent) and domestic (sporadic and less supervised) logging that dominate in this region. We also compared the logged fragments with the only protected bamboo fragment that has been unlogged for at least the past 20 years. We found a severe negative impact of bamboo logging on the abundance and floristic composition of food resources for howlers. The floristic composition of logged fragments was highly similar between logging types, but different from the protected forest. Logged fragments had a lower species richness and abundance of seedlings and saplings compared to the protected fragment, most probably due to the mechanical damage of the logging activities, including site preparation. In logged fragments, the recruitment into sapling size classes was low for many species, particularly for two of the most important food species for red howlers and other fauna, *Ficus insipida* and *F. killipii*. Succession of these two species appears to be arrested, probably due to the low ability of seedlings and saplings to germinate and establish, and due to failure to recruit into mature size classes. Bamboo forests support howler populations and other fauna, which are currently relying on adult trees with low regeneration potential. The silvicultural regulations and techniques for bamboo logging must include the ecological requirements of other species if they are to provide an environmentally friendly alternative to commercial wood production.

Introduction

Bamboo is one of the most productive and fastest growing plants in the world with characteristics that make it a sustainably harvestable resource that can support economic development in developing countries (Londoño 2001, INBAR 2014). In the last decades, there has been an increase in the bamboo industry, promoted around the world as an opportunity for environmental sustainability combined with poverty reduction (Held 2005, INBAR 2014). This has led to a worldwide increase in the total area of bamboo forest, with natural and planted bamboo forest increasing by about 11% between 1990 and 2000, (FAO 2010). Bamboo is a component of tropical forests, and bamboo forests harbor great biodiversity providing habitats for highly specialized endangered animal species (such as giant panda (*Ailuropoda melanoleuca*), mountain gorilla (*Gorilla beringei*) and several species of bamboo lemurs (members of *Hapalemur* and *Prolemur simus*)). Bamboo forests can play an important role in rehabilitation of degraded forest lands, reforestation, watershed protection, erosion prevention, carbon sequestration, and biomass generation (INBAR 2014). Consequently, it is important to develop management protocols for bamboos that protect biodiversity without compromising economic productivity.

Bamboo stems serve as an excellent wood substitute. Selective logging of bamboo stems is increasing around the world (INBAR 2014), and although there are numerous studies on silvicultural management practices, little is known about the effect of selective logging or removal of bamboo stems on biodiversity. It is a priority to understand the responses of wildlife to bamboo selective logging, and to incorporate this information into management policies of these logged forests.

Selective logging may impact the forest and cause multiple changes in ecosystems, such as changes in species composition, physiognomy, and forest structure (Silva et al. 1995, Castro-Luna et al. 2011). For example, species richness and abundance of the regeneration pool can be reduced in selectively logged forest, due to a combination of causes as mechanical damage and soil compaction (Gutiérrez-Granados et al. 2011). Considerable incidental damage can be done to the adult trees adjacent to the fallen tree, e.g. neighboring, non-target trees may be pushed over or lose branches as the timber tree is felled, or may be pulled down if linked to the timber tree via lianas (Verburg and van Eijk-Bos 2003, Chapman and Chapman 1997). For example in Brazil, for each timber tree felled, 20 to 29 additional, non-target trees > 10 cm of DBH were damaged; damage was most severe when selective logging was unplanned (Johns et al. 1996). In general, the intensity of the disturbance caused by selective logging is related to the number of trees harvested, the silvicultural system, and the duration of the logging cycle (Hunth and Ditzer 2001, Villela et al. 2006, Putz et al. 2008). Therefore, depending on how it is managed and the ecological context, selective logging can have either little or large impacts on forest structure, composition and dynamics (Peres and Barlow 2004, Putz et al. 2012, Gourlet-Fleury et al. 2013). Twenty years after experimental selective logging in a Suriname forest, the effects of the extraction and silviculture were still visible, but species abundance and richness values were still within the range of unlogged forest. These impacts were less noticeable in light to moderate logging intensity (Dekker and de Graaf 2003). Under sustainable silvicultural management and responsible forestry, logged forest has great potential for timber production and conservation value, retaining substantial biodiversity, carbon and timber stocks (Putz et al. 2012).

The main coffee growing region in Colombia (called Eje Cafetero) is highly fragmented, with less than 15% of the original cover remaining (Wild et al. 2006). In the region, Bamboo

forests are the last remnant between 900-1800 m of altitude, most are small (< 10 ha) and privately owned (Castaño et al. 2010). As these bamboo forests are the last remnants in the Colombian Eje Cafetero, their conservation and sustainable management are a government priority. Colombia is one of the few countries in Latin America where bamboo have played a notable role in local economy and traditional culture (Londoño 2001). In the last 20 years there has been great progress in research on silvicultural management practices and regulation legislation of bamboo logging in the country (review in Mejía and Moreno 2013), promoting the use of bamboo as an environmentally sustainable resource that generates income for farmers. The country has developed detailed silvicultural studies and guides describing the entire production and utilization process (e.g. Espinal et al. 2005, Moreno 2006, Bosques FLEGT/Colombia 2008). Bamboo extraction is restricted and regulated by regional environmental authorities, only a low percentage of mature and over mature stems can be extracted to maintain bamboo stem productivity. Where landowners use bamboo to meet the needs of their farm, the extraction is considered domestic use and only 20m³ of stems can be extracted per year. This logging occurs sporadically and without supervision. If the landowners want to sell the stems for commercial purposes, up to 35% of the stems can be harvested every 1 or more years, and it is called persistent commercial logging (Bosques FLEGT/Colombia 2008). We refer to these two types of logging management as commercial and domestic, respectively (see Study Area section for details).

Almost every study on bamboo logging in Colombia highlights its important role in preserving the original wildlife and their environmental services. Despite numerous inventories of fauna and flora (review on Mejía and Moreno 2013), only two studies have evaluated the impact of logging on plant communities associated with bamboo (Ospina 2002, Gómez and

Orozco 2006), and no studies have assessed its impacts on vertebrates, insects, or other animals (except on red howlers monkeys, see Gómez-Posada chapter 1). The silvicultural techniques were carefully developed based on the growth habits and “needs” of bamboo. From a conservation point of view, it is important to develop management models based on a sound understanding of the regeneration, growth and mortality patterns of other native plant species, both for their conservation, as well as for those animal species that depend on these components of the plant community.

The red howler monkey (*Alouatta seniculus*) is one of the few large-mammals that persist in the highly-converted Eje Cafetero region and that live in bamboo forest. In this region, it is a charismatic and widely-loved primate. Because of their popularity, howlers could function as an important tool for conservation, as protection of howlers can extend to remnant bamboo forests and their inhabitants (analogous to efforts to conserve flagship or focal, landscape species: Heywood 1995, Lambeck 1997, Sanderson et al. 2000). Although this species is not considered threatened by the IUCN, red howlers may be highly vulnerable in the Eje Cafetero as their habitat has been severely reduced (Defler 2004, Gómez-Posada 2006). Thus, howler monkeys are a good target species to study the suitability of bamboo forest as a conservation tool. Their herbivorous-frugivorous diet overlaps with many vertebrates that live in those fragments.

In this study, we asked what are the impacts of bamboo logging of the floristic composition (both diversity and abundance) and regeneration potential of key tree species that are components of the diet of red howler monkeys. We predict that the logging activities may have relatively little impact on adult trees, but that they will negatively impact seedlings and saplings. Although the logging does not target any species beside bamboo, incidental mechanical damage from the logging process likely impacts growing trees. We compared the logged fragments to

the only protected bamboo fragment that remains in this region, which has been unlogged for at least 20 years. We predict that tree diversity and abundance, as well as basal area, will be higher in the protected fragment than in the logged fragments, and that recruitment of seedling and sapling stage classes will be poor in the logged fragments, and lower than what is seen in the protected forest. In addition, we compared the impacts of two different forest management types that dominate the region: commercial vs. domestic logging. Because commercial logging is more intensive than domestic use of bamboo, we predict that commercially logged fragments will have lower tree diversity, abundance, and basal area than the domestic ones, and that they will have lower natural regeneration, with more adults than juveniles, due to the effects of the logging on the survival of young individuals.

Study Area and Bamboo Logging Context

Study area

The study area is located in the Departments del Valle and Quindío, in the Eje cafetero, between 900 to 1100 m of altitude (Fig. 1). The study sites are in the premontane range on the western slope of the central mountain range of Cordillera de los Andes. Mean annual precipitation is 1,800 mm, and mean annual temperature is around 23°C (CVC 2000).

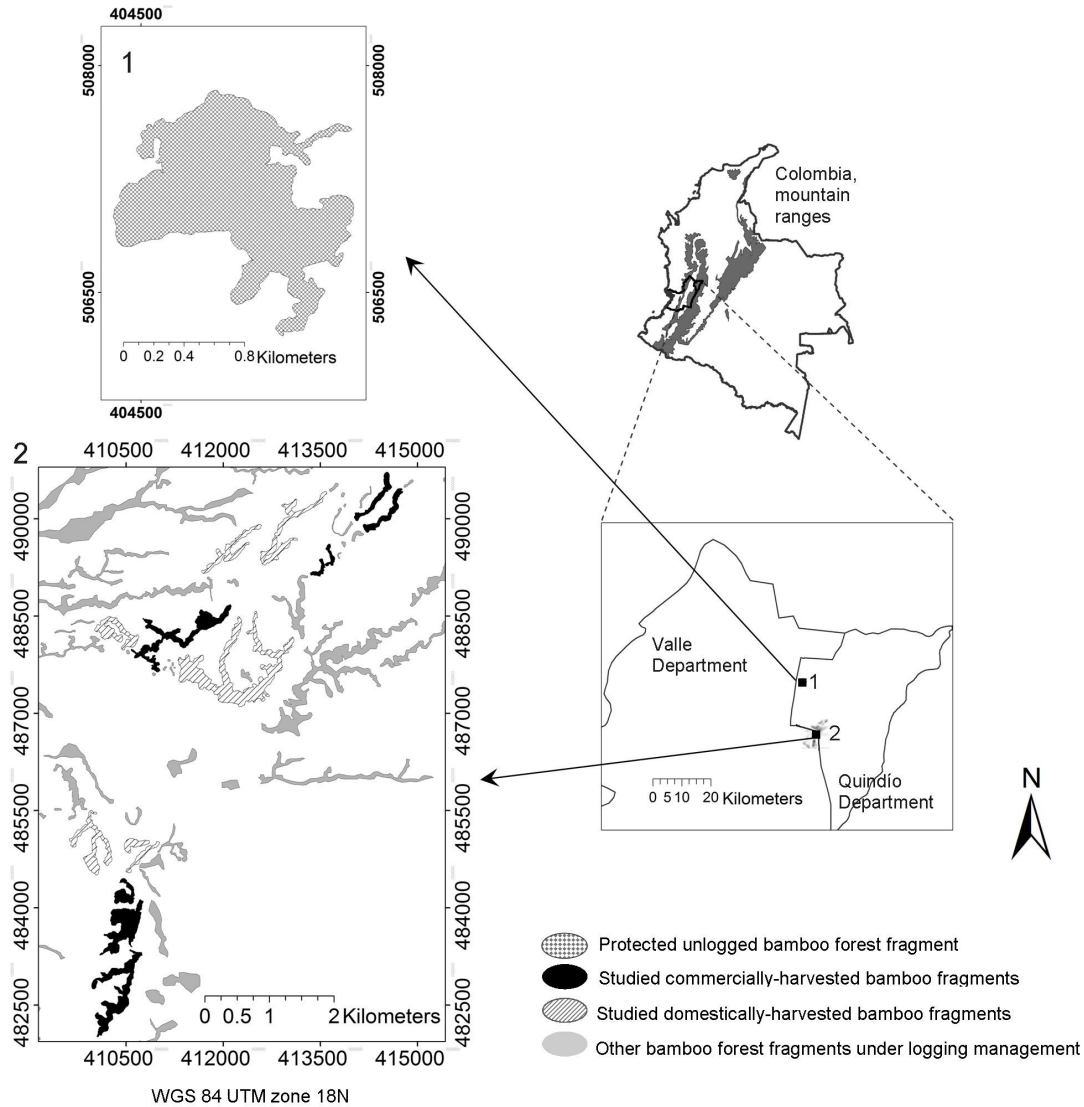


Figure 1. Study site at the Colombian Eje Cafetero region, indicating the focal bamboo forest fragments.

Bamboo and the context of bamboo logging

Guadua angustifolia (Kunth, Poaceae) is a thorny, woody bamboo, native to the tropical regions in Central and South America, and occurs mainly in the central-western region of Colombia, in the three mountain ranges. Its stems grow up to 21 cm per day, which emerge from the ground with a constant diameter of up to 22 cm, and reach a final height of 18-30 m in about 6 months (Londoño 2001, Riaño et al. 2002). This bamboo grows in natural stands,

predominantly along rivers, and in the coffee region, the stands are relatively small (< 10 ha) and irregular in shape, thus forming a highly fragmented pattern. In the last bamboo inventory, the total area in the coffee region was estimated to be ~40,000 ha (Kleinn and Morales 2006).

Bamboo is the dominant species in these forests, with a mean stem density of 6500/ha across all states of maturity. More than 400 plant species have been identified in these bamboo forests, although with a relatively low plant diversity within each stand (Ospina and Finegan 2004, Gómez and Orozco 2006, Camargo et al. 2010). The canopy stratum of a bamboo forest is formed by the thick intercross of branches and leaves of fully developed bamboos (which are highly bent in the upper sections), and scattered emergent trees, which are taller than the bamboo.

This bamboo has been used in Colombia since pre-Hispanic times due to the characteristics of the stems, flexible, tall, and very resistant to breakage and rot. It is a significant product in construction (housing, bridges, canals, aqueducts, fences, etc), furniture, jewelry, handicraft, cooking utensils, musical instruments, fuel wood, live fences, and also for watershed and erosion protection (Espinal et al. 2005). The bamboo stands are the last forest remnants in the region and provide refuge for the original fauna and flora (Camargo et al. 2010).

The Colombian government has been developing standards for sustainable management of bamboo forest since the 1990s, in an attempt to stop overexploitation and misuse of these forests (Bosques FLEGT/Colombia 2008). In addition, and equally important, this effort has included encouraging the use of bamboo as an economic alternative for rural communities, especially small farmers (Camargo et al. 2008). There has been significant research on management, production, marketing and industrial uses of *G. angustifolia* (review in Mejía and Moreno 2013). The regulations for bamboo logging (the *Unified Norm for Bamboo's Management and Use* (*Norma Unificada para el Manejo y Aprovechamiento de la Guadua*) are very explicit and

carefully describe every step to grow and sustainably manage natural and planted bamboo forest, to improve productivity, and to commercialize bamboo forest resources (Bosques FLEGT/Colombia 2008). The regulations were developed by the regional environmental authorities, through projects funded by the German Development Cooperation Agency GTZ and the European Union (Gobernanza Forestal, Bosques FLEGT/Colombia, <http://www.bosquesflegt.gov.co>) (Camargo et al. 2010). The government also created guidelines for capacity building of local institutions and communities, so they can harness the “immense economic and environmental potential” of bamboo forests, both in the production of raw materials and the industrial field (Moreno 2014, Bosques FLEGT/Colombia 2013a, b). In these guidelines, sustainability of logging is stressed because unsustainable harvesting may cause environmental damage and decrease productivity and quality of the forest. The guidelines also include recommendations on how to harvest the bamboo to reduce impact on other species (Ospina and Vega 2004, Camargo et al. 2008), for example, avoiding cutting down threatened plant species, avoiding logging near rivers and creeks, among others.

Bamboo forests are managed either for domestic production or commercial sale. Both types of management are subject to regulation, but only commercial production is supervised. The designation of domestic vs. commercial logging management is determined by the intensity and frequency of the logging cycle (Bosques FLEGT/Colombia 2008):

- Domestic logging: This type of harvest takes place exclusively to meet the basic needs of a farm and its inhabitants. Fragments under domestic use are harvested sporadically, with extraction of bamboo restricted to a volume of 20m³ (2000 stems) per year. Although farmers need a permit for domestic extraction, landowners do not always apply for it, and they remove stems every time they need bamboo. For that reason, it is difficult to find records of the

periodicity and the number or volume of stems extracted from those fragments. Bamboo stems taken via domestic extraction cannot be sold.

- Commercial persistent logging: This type of harvest is conducted to generate economic benefits from its exploitation; these stems are sold in the market. The logging intensity shall not exceed 35% of the commercial stems (mature and over mature); however, the intensity of harvest may be higher as determined by a forestry technician (according to the forest stem density) and the approval from the regional environmental authorities. These authorities granted the logging permits, coordinate the harvesting, estimate the volume of stems that can be extracted, as well as which stems can be cut. Cutting cycles may not be less than twelve (12) months, and the periodicity varies according to the farmers' will. Workers usually cut the bamboo with machetes, but in the last years, also chainsaws have been used (Camargo et al. 2010). Commercial logging is regulated by criteria that were designed to ensure sustainability and profitability of bamboo forestry, including the natural renewal of sufficient stems with commercial attributes.

Methods

Study fragments

We had three bamboo forest management treatments in this study: commercial management (commercial bamboo extraction, for sale), domestic management (domestic bamboo extraction, solely for landowner use), and protected management. When we use “logging management”, we are referring specifically to commercial and domestic logging. We confirmed by direct observations the presence of resident groups of red howler monkeys in all the fragments (n=15, 7 commercial, 7 domestic and 1 protected management) used in this study.

The bamboo forest fragments are immersed in a matrix of coffee, fruits and corn crops, and livestock pastures. We identified the type of management of each fragment by interviewing the owners of the land. We selected logged fragments that represented a three year span in logging history, selecting those recently harvested (within 6, 12, 24, or 26 months of sampling), or that were harvested during the sample period, ensuring a comparable range of harvest dates in both logging treatments. The bamboo forest fragments under logging management were similar in size (Mann Whitney Test, $U=13$ $p=0.14$; See Gómez-Posada Ch. 1). Those under commercial management ranged from 4.4 – 25.5 ha in area with an average size of 13.64 ± 9.98 ha, while those under domestic management ranged from 3.1 to 30 ha in area with an average size of 7.51 ± 7.89 ha.

We also selected the only protected bamboo forest fragment (called La Montaña del Ocaso) that exists in this region. It is also the largest forest fragment (148.84 ha) in this altitudinal range of the Central Cordillera. This site has not been subject to logging activities within at least the past 20 years. The protected areas is administrated by a local University that has carried out conservation programs that have increased the area of this bamboo forest fragment by about 30% since 2000 (Aguilar-Isaza et al. 2010). This site provided our only comparison to unlogged conditions in this region.

Vegetation sampling

Within each of the 15 bamboo forest fragments (7 commercial, 7 domestic and 1 protected), we randomly established 5 plots of 30 x 30 m ($900 \text{ m}^2/\text{plot}$, $4500 \text{ m}^2/\text{fragment}$) for a total of 75 plots. Within each plot, we recorded all plant individuals that were part of the howlers' diet in

the region. The list of species was based on diet data collected in both logged (Gómez-Posada, Ch 1) and protected (Londoño and Gómez-Posada, submitted) bamboo forest, supplemented by findings from other studies in Andean forest (Giraldo et al. 2007, Palma et al. 2010). We identified each plant individual and assigned a stage (sapling, seedlings and adults) according to the species' growth habit. For individuals taller than 1.4 m, we measured the diameter at breast height (DBH), height, and crown spread. Species not identified in the field were collected for subsequent identification at the Herbarium of Universidad del Quindío. We also recorded the number of bamboo stems found within each plot.

Floristic composition

The plant diversity in each fragment was calculated using Shannon's diversity index, pooling all the individuals per species, per fragment. Floristic similarities among fragments were assessed using the Morisita-Horn index, which takes into account both species abundance and richness. The index was calculated as a paired-analysis of each fragment. This analysis was performed using the EstimateS 9.1.0. program for Windows.

The importance value index (IVI) is used to determine the overall importance of each species in the community. The IVI ranks species based upon the total number of individuals of the species, the total amount of forest area occupied by the species, and how commonly a species occurs across the entire forest, allowing comparisons of the floristic composition among treatments. We calculated the IVI for each species per management treatment, including all individuals more than 1.4 m in height. The IVI was estimated from values of relative species density ($RD = \text{no. of individuals of the } i\text{th species} / \text{total number of individuals} * 100$), relative dominance ($RDo = \text{sum of the basal area of all plants of the } i\text{th species} / \text{total basal area} * 100$),

and relative frequency (RF = frequency of the *i*th species/total sum of frequencies*100, where frequency F = number of sites occupied by the *i*th species/total number of sites*100), as IVI = RD+RDo+RF (Curtis and McIntosh 1950, 1951).

Structural characteristics and richness

To evaluate structural characteristics and richness, we compared 10 vegetation attributes (species richness: total, seedling, sapling and adult; density: total, sapling, and adult; and basal area) among the three management types using data from plots. Analyses of plant species richness and density were conducted for all individuals found (total), as well as for each life history stage (seedling, saplings, and adults). Basal area per plot was calculated as the sum of the basal area from all individuals taller than 1.4 m in each plot. Comparisons between management treatments for each of the 10 vegetation attributes were made in paired analyses with mixed effects models. Fragments were designated as a random effect (intercept-only structure) to control for fragment effect. Count data (density and species richness) were fit with Poisson response variables (with a log-link function), whereas continuous data (basal area) were fit as normally distributed response variables. P-values were calculated from Z post-hoc tests examining if the differences between management regimens were statistically significant. In addition, to evaluate whether the number of bamboo stems were correlated with the density and abundance of individuals in each stage per plot, we used a Spearman Coefficient correlation test.

To compare the vegetation attributes of the two most important species in the howlers' diet in the region (Gómez-Posada chapter 1): *Ficus insipida* and *F. killipii*, between commercial and domestic fragments, we ran the same models and analyses as above for just these species. In

addition, we evaluated whether *Ficus* differed in either of the two size attributes - height and crown spread of adult trees (continuous data) – between commercial and domestic logging. The protected bamboo forest was not included in these comparisons because we only found two *Ficus* individuals in the plots there.

All analyses were performed using R-package version 2.15.1. The statistical threshold was set at $P \leq 0.05$.

Regeneration analysis

Logging often damages non-target tree species, particularly individuals in the early stage classes. We expected that logging could reduce regeneration of the tree species common in the howler's diet. To evaluate this possibility we analyzed the natural regeneration in each of the management types using a diameter-size class approach per fragment (class intervals of 10 cm). We pooled the number of individual taller than 1.4 m from all species, in each diameter-size class per fragment, and plotted the distribution of frequencies for each management type (average per fragment). Differences in the diametric distribution across treatments were tested using an Anderson-Darling k-sample test. The same analyses were run to study the natural regeneration of *F. inspida* and *F. killipii* in particular.

Results

Floristic composition

Among the 15 fragments, a total of 2224 plants were sampled (summed over five 30x30m plots per fragment), of which 879 (39.52%) were present in fragments under commercial use, 970 (43.62%) in fragments under domestic use, and 375 (16.88%) in the protected bamboo forest. These individuals represented 34 species that are consumed by red howlers, of which 26 were identified to the species level, 5 to genus, 1 to family, and two were unidentified. Taking all fragments together, commercial fragments had 24 species (range 9 – 12), domestic 26 species (range 8-17), and the one protected forest site had 17 (Table 1). Commercial and domestic fragments shared most of their species (21 species), while only 9 and 11, respectively, were shared with the protected forest. The mean Shannon index was $H' = 1.54 \pm 0.29$ for commercial fragments, $H' = 1.53 \pm 0.35$ for the domestic ones, and $H' = 1.84$ for the protected forest.

Table 1. Plant species consumed by red howler monkeys found in the three management treatments: commercial, domestic, and protected bamboo fragments, at the Eje Cafetero, Colombia. Values are percentages of individuals of all stage classes (total abundance of seedlings, saplings, adults) in each treatment (commercial N = 879, domestic N = 970, protected = 375).

Family	Species	Commercial fragments	Domestic fragments	Protected fragment
Anacardiaceae	<i>Anacardium excelsum</i>	29.47	30.41	14.93
Araceae	<i>Philodendron elegans</i>	3.19	2.78	
	<i>Philodendron rigida</i>		0.41	
Araliaceae	<i>Dendropanax</i> sp.	1.71	0.10	
Bombacaceae	<i>Ochroma pyramidale</i>	0.46	1.24	
Cecropiaceae	<i>Cecropia angustifolia</i>	2.96	5.26	12.00
Fabaceae	<i>Erythrina poeppigiana</i>	0.57	0.52	
	<i>Inga edulis</i>	7.62	2.99	
	<i>Inga densiflora</i>		0.21	
	<i>Inga</i> sp	1.14	0.21	5.07
Lauraceae	<i>Ocotea</i> sp	1.02	2.06	
Malvaceae	<i>Quararibea foenigracea</i>			1.33
	<i>Theobroma cacao</i>		1.24	
Meliaceae	<i>Cedrela odorata</i>	0.57	0.62	
	<i>Guarea gigantean</i>	1.14		
	<i>Guarea guidonia</i>	1.93	1.44	1.07
Moraceae	<i>Clarisia biflora</i>	1.71	2.47	0.80
	<i>Ficus insipida</i>	3.53	1.75	
	<i>Ficus killipii</i>	2.05	2.58	0.53
	<i>Ficus subandina</i>	0.11	0.21	
	<i>Ficus</i> cf. <i>giganticus</i>	1.48	0.52	
	Moraceae sp	1.48	0.72	
	<i>Naucleopsis glabra</i>	0.46	0.72	
	<i>Pseudolmedia rigida</i>		0.52	44.27
	<i>Sorocea trophoides</i>	3.87	0.52	1.07
	<i>Trophis caucana</i>	31.85	38.14	11.47
	<i>Trophis racemosa</i>	1.14	1.96	2.13
Rubiaceae	<i>Genipa Americana</i>			1.33
Sapindaceae	<i>Cupania Americana</i>			0.27
	<i>Paullinia bracteosa</i>		0.41	1.87
Siparunaceae	<i>Siparuna</i> sp			0.27
Urticaceae	<i>Coussapoa</i> sp			0.80
Sp. 5		0.34		0.80
Sp 7		0.23		

Altogether, tree species from 9 families were recorded in the commercial fragments, 11 in the domestic ones and 10 in the protected forest. The majority of individuals in the fragments were from Moraceae (50.85% of all plants recorded, from 11 species of 6 genera), followed by Anacardiaceae (27.43%), Cecropiaceae (5.49%) and Fabaceae (6.25); and these four were the most abundant families in all the 15 fragments.

Anacardium excelsum and *Trophis caucana* were the most abundant species in commercial and domestic bamboo fragments, each species with about 30 to 40% of the individuals (Table 1). These two species were the most abundant in each stage (seedlings, saplings and adults). The remaining species each had fewer than 8% of the individuals, with 16 and 18 species representing fewer than 2% of the individuals in commercial and domestic fragments, respectively. In the protected forest, the most abundant species were *Pseudolmedia rigida* (44.27%) and *A. excelsum* (14.93%).

Floristic similarities among fragments were high in general terms between commercial and domestic fragments, with a Morisita index of 0.77 ± 0.14 (range 0.40-0.99), suggesting high floristic homogeneity. The logged fragments clustered without tendency for fragments from one type of management to be grouped together. These fragments presented similar species composition, with a high number of common species, and the same set of dominant species (*A. excelsum* and *T. caucana*). The protected forest was less similar to any of the commercial and domestic fragments, as indicated by a low Morisita index of 0.35 ± 0.04 (range 0.28–0.44), with fewer common species among them, and a different dominant one, *P. rigida*.

Overall, most of the species in the fragments had a low IVI, with only 5 species with values above 20 in each management type (Fig. 2). *A. excelsum* and *T. caucana* presented highest values in both commercial and domestic logged fragments. *Ficus killipii* and *F. insipida* also

had high IVI in the logged fragments, but were not important in the protected forest. *P. rigida* had the highest IVI in the protected forest, but was not important in the logged fragments. In general, in commercial and domestic logged fragments, 5 species occupied the same position, and 5 were located in comparable positions (Fig. 1). For the protected forest, except *P. rigida*, the species with higher IVI are in similar positions to those in the logged fragments.

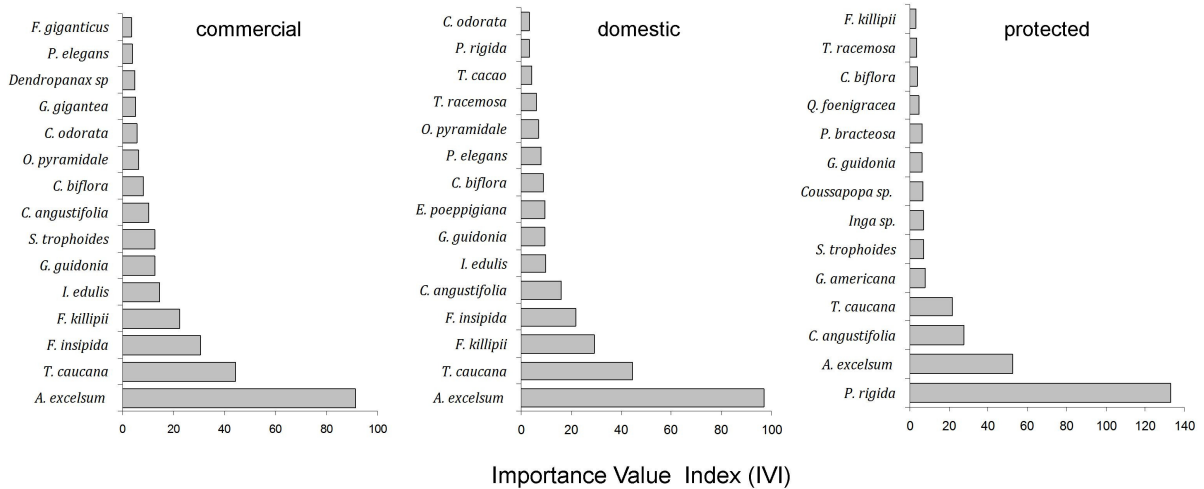


Figure 2. Importance Index Value for the 15 species with the highest index, for plant species consumed by red howler monkeys, in three management treatments: commercial, domestic and protected bamboo forest fragments, at the Eje Cafetero, Colombia.

Plot level analysis: Structural characteristics and richness

Domestic and commercial management types did not differ in any of the 10 vegetation attributes compared (Table 2). Density and species richness in all stage (seedlings, saplings and adults trees), basal area, and number of bamboo stems had similar values between the two logging types. In contrast, most of those attributes were significantly lower (by two to three times) in both logging treatments compared to the protected forest, except density and species richness of adults, and total basal area (Table 2).

The number of bamboo stems per plot was negatively correlated with the density of adults ($r_s=-0.21$ $p=0.05$), adult species richness ($r_s=-0.32$ $p<0.01$) and basal area ($r_s=-0.20$ $p<0.01$). No other attributes showed a correlation with the number of bamboo stems.

Table 2. Structural characteristics and richness of plants in three management treatments: commercial, domestic and protected bamboo forest fragments, at the Eje Cafetero, Colombia. Values are mean (SD) per plot per management regimen. P-values were calculated from mixed effects models. C = commercial, D = domestic, P = protected. ns= non significant differences, ** significant differences.

Vegetation attribute	Commercial	Domestic	P-value C vs. D	Protected	P-value C vs. P / D vs. P
Total species richness	5.71 (1.72)	5.17 (2.51)	0.82 ns	10.56 (2.51)	<.01 / 0.01**
Species richness of seedlings	3.12 (1.49)	3.00 (1.53)	0.99 ns	7.20 (2.17)	<0.01 / <0.01**
Species richness of saplings	3.06 (1.26)	3.94 (1.89)	0.25 ns	6.60 (1.82)	0.01 / 0.01 **
Species richness of adults	2.86 (1.73)	2.88 (1.81)	0.99 ns	4.20 (2.17)	0.61 / 0.62 ns
Density (plants/plot)	26.26 (18.43)	23.80 (10.87)	0.74 ns	75.60 (31.48)	<0.01 / 0.01 **
Density of seedlings	11.51 (13.48)	10.22 (7.68)	0.91 ns	33.00 (17.76)	0.03 / 0.05 **
Density of saplings	8.57 (5.63)	8.61 (5.79)	0.62 ns	29.00 (9.19)	0.01 / 0.03 **
Density of adults	6.17 (5.10)	5.95 (4.83)	0.99 ns	13.60 (7.09)	0.17 / 0.18 ns
Basal area (m ²)	1.85 (1.94)	1.84 (1.62)	1.00 ns	2.76 (1.15)	0.64 / 0.64 ns
Number of bamboo stems	20.09 (11.20)	14.86 (9.80)	0.13 ns	17.40 (3.85)	0.53 / 0.24 ns

Ficus insipida and *F. killipii*

Because of their importance in the diet of howlers, we separately evaluated whether the logging practices influenced the vegetation attributes of two species, *F. insipida* and *F. killipii*. We recorded 48 individuals of *F. insipida* among all the fragments, of which 13 were seedlings, 6 juveniles, and 29 adults. In commercial fragments, we found 31 individuals of this species, 17 in the domestic fragments, and none in the protected forest. We found 45 individuals of *F. killipii* among all sites, of which 7 were seedlings, 8 juveniles, and 30 adults. In commercial fragments, we found 18 of the individuals of this species, 25 in the domestic fragments, and 2 in the

protected forest. Overall, the two species accounted for 4.18% of the total number of individuals reported in this study.

Ficus vegetation attributes measured per plot for both species did not differ between commercial and domestic fragments (Table 3). Structural characteristics, such as basal area, height and crown spread of adults, had similar values in both logging regimens, as did the density of individuals in each stage class.

The number of bamboo stems per plot was negatively correlated with the density of adults *Ficus* (*F. insipida* + *F. killipii*) ($r_s = -0.32$ $p < 0.01$), and with *Ficus* basal area ($r_s = -0.29$ $p < 0.01$).

No other *Ficus* attributes were correlated with the number of bamboo stems.

Table 3. Vegetation attributes for *F. insipida* and *F. killipii* in commercially and domestically harvested fragments at the Eje Cafetero, Colombia. Values are mean (SD) per plot, per logging regimen. P-values were calculated from mixed effect models. ns= non significant differences.

Ficus vegetation attributes	Commercial	Domestic	Pvalue	
<i>Ficus insipida</i>				
Density (plants/plot)	0.89 (1.89)	0.49 (0.92)	0.93	ns
Density of seedlings	0.34 (1.41)	0.03 (0.17)	0.30	ns
Density of saplings	0.06 (0.34)	0.11 (0.32)	0.67	ns
Density of adults	0.50 (0.93)	0.34 (0.76)	0.95	ns
Height of adults (m)	21.06 (2.54)	21.06 (1.32)	0.87	ns
Crown spread of adults (m)	20.00 (8.54)	20.25 (9.52)	0.75	ns
Basal area (m ²)	1.29 (1.36)	0.59 (0.45)	0.12	ns
<i>Ficus killipii</i>				
Density (plants/plot)	0.51 (1.01)	0.71 (1.10)	0.79	ns
Density of seedlings	0.09 (0.51)	0.09 (0.28)	0.98	ns
Density of saplings	0.03 (0.17)	0.17 (0.38)	0.22	ns
Density of adults	0.40 (0.81)	0.46 (0.82)	0.97	ns
Height of adults (m)	23.86 (5.39)	21.75 (2.07)	0.68	ns
Crown spread of adults (m)	18.59 (8.89)	20.12 (9.55)	0.31	ns
Basal area (m ²)	0.82 (0.53)	0.92 (0.89)	0.95	ns

Natural regeneration

Regeneration potential can be inferred from examining the size distribution profile of individuals found in the same fragment. A healthy population will show a higher number of young individuals than adults, so the size distribution would look like an inverted J. Figure 3 shows the size distribution patterns per diameter size class for all the species found per fragment, comparing the three management types. In each management, the size distributions followed a J-reverse pattern characterized by an exponential decreasing in tree abundance with increasing diameter class. The size distribution did not vary among management treatments (Anderson-Darling test $P=0.54$). In each case, the majority of the individuals were in the smallest diameter class, 0-10 cm (protected 60% of individuals, commercial $53.43\pm 16.92\%$, domestic $49.58\pm 26.29\%$), although the protected forest had 4 to 5 times more individuals in the first diameter class than the logged fragments. In this first diameter class, *T. caucana* was the most abundant species in each of the logged fragments (commercial $53.76\pm 20.28\%$ of the individuals in that diameter class, domestic $48.22\pm 16.15\%$), but not in the protected forest (15.69%).

The distribution patterns per diameter class for *F. insipida* and *F. killipii* (Fig. 3) did not follow an inverted J shape. For both species, the number of individuals was very low per fragment, and showed a gap in number of individuals in the middle size classes. For *F. insipida* (Fig. 3), the size distribution was similar between commercial and domestic fragments (Anderson-Darling test, $P=0.44$). In both logging regimes, there were no individuals between 10 to 20 cm of DBH, and only the domestic ones had any individuals in the next two classes (20-30 and 30-40 cm), although very few in each case. Overall, $80.42\pm 14.17\%$ of the individuals had a DBH larger than 50 cm in the commercial fragments, and $68.47\pm 47.41\%$ in the domestic ones. The size distribution of *F. killipii* (Fig. 3) also did not differ between commercial and domestic

fragments (Anderson-Darling test, $P=0.68$). There were no individuals with a DBH between 20-30 cm, in either logging regimes. Overall, $85.00\pm 22.36\%$ of the individuals had a DBH larger than 50 cm in the commercial fragments, and $72.78\pm 33.70\%$ in domestic ones.

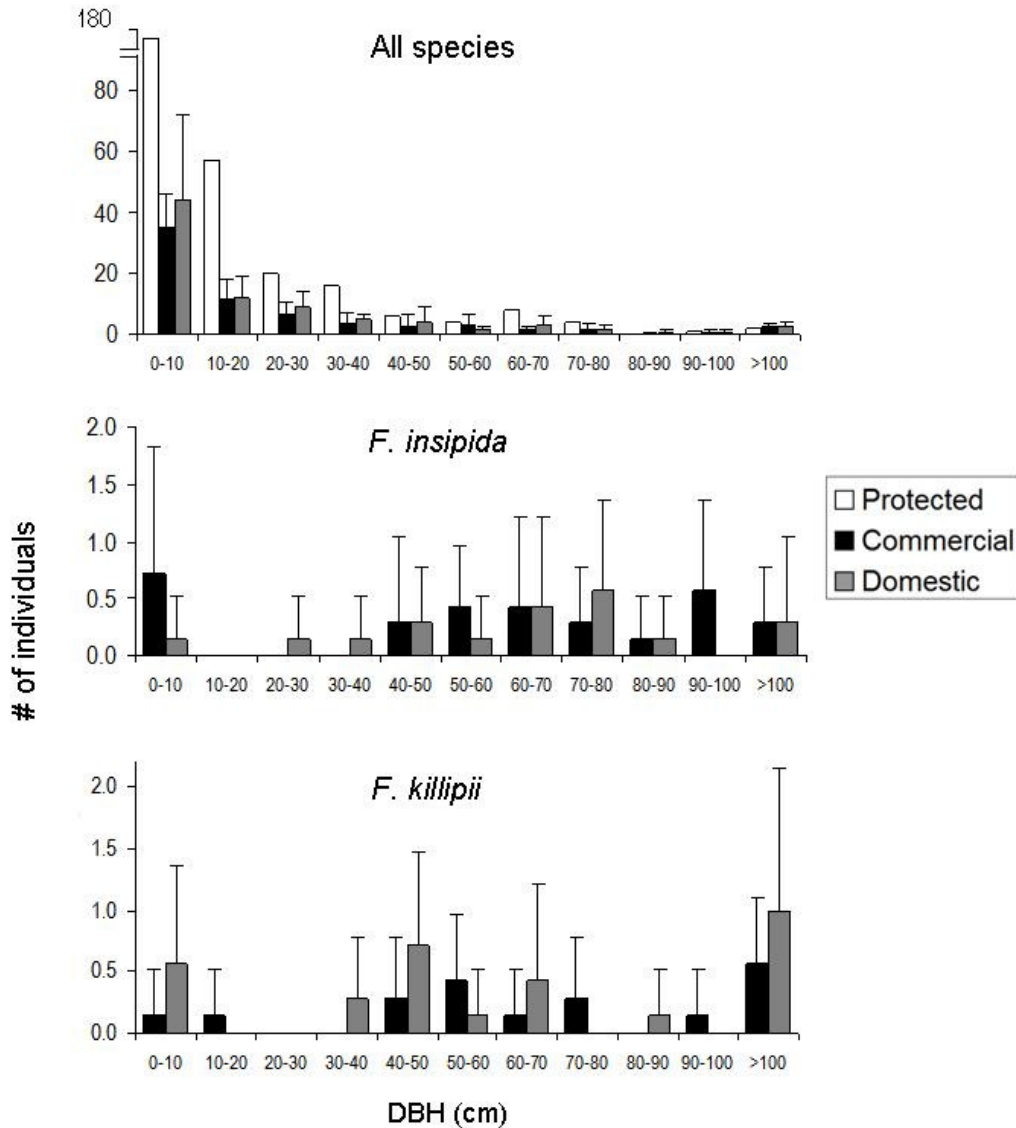


Figure 3. Number of individuals per diameter size class per fragment, in three management treatments: protected, commercial, and domestic bamboo forest fragments, at the Eje Cafetero, Colombia for: all species, *F. insipida*, and *F. killipii*. Error bars represent 1 SD.

Discussion

Bamboo logging has a severe negative impact on the abundance and floristic composition of food resources for howlers in the Eje Cafetero in Colombia, regardless of the logging management. Overall, total species richness and diversity of tree species was lower in fragments under either of the two logging management regimes, and this effect was driven by much lower abundance and diversity in the tree seedling and sapling stages in the logged fragments vs. the unlogged fragment. Tree species diversity and abundance may decline further in the future due to negative impacts of bamboo harvesting on natural regeneration of the most important food resources, such as *Ficus* species. Bamboo forests support howler populations and other fauna, which are currently relying on adult trees with low regeneration potential.

Analysis of the vegetation plots revealed several consistent patterns among the bamboo fragments in this study. First, species richness and diversity are low, particularly in the logged bamboo fragments. Further, the protected forest has a different composition than logged fragments. Second, the logged fragments are remarkably similar in virtually all respects, with comparable composition and characteristics of the vegetation, regardless of the logging type. The fragments were dominated by a small number of species, which were largely shared among the sites. Finally, while recruitment into sapling size classes was notable in the unlogged protected forest, it was low for many species in the logged fragments, particularly for two of the most important food species for red howlers, *F. insipida* and *F. killipii*. Taken together, these data show that the logged bamboo fragments have diminished diversity and capacity for regeneration, despite containing key native tree species within the fragments.

Overall, plant richness and abundance of species consumed by howlers were not high in these bamboo fragments, as was expected due to the dominance of the bamboo (Ospina and

Finegan 2004, Calle and Mendez 2009, Gómez and Orozco 2006). Only 34 species were reported, with a range of 8 to 17 species per fragment, and few of those species were abundant. We found that the density of bamboo was negatively correlated with the basal area, density and richness of adult trees; probably as a consequence of bamboo competition. Bamboo is a fast growing plant and competition in bamboo-dominated forest likely impacts tree seedlings and saplings through competition with bamboo below ground for water and soil nutrients, and above ground for light and space, contributing to an overall low species richness (Griscon and Ashton 2003, Campanello et al. 2007, Lima et al. 2012).

The protected bamboo forest was more diverse than the logged fragments; it has about twice the number of species and three times the abundance of plant individuals per plot compared to the logged fragments, except for adult trees. The reduction in the diversity on seedlings and saplings in logged fragments may be a consequence of two factors at work: the reduction of seedling establishment and the increase mortality of seedlings and saplings.

After each logging event, bamboo stems re-sprout and rapidly grow. This likely enables them to outcompete other species (Peña-Claros 2003, Campanello et al. 2007), causing a reduced establishment rate of non-bamboo seedlings, compared to the unlogged forest (Griscom and Ashton 2003, Lima et al. 2012). Also, after logging, the canopy openings may provide suitable conditions for some shrub and herb species to aggressively colonize disturbed areas. The resulting dense plant cover might directly or indirectly interfere with tree seedling establishment, growth, and survival (Chapman and Chapman 1997, Campanello et al. 2007, Duclos et al. 2013). Indirect impacts may also be important in depressing germination and growth, as the logging may cause soil compaction that may reduce the rooting capacity of seedlings (Gutierrez-Granados et al. 2011).

During the harvest period in logged fragments, the mechanical impacts of the logging activities cause a high mortality rate of seedlings and saplings (Gómez and Orozco 2006, Peña-Claros et al. 2008, Gutierrez-Granados et al. 2011), for example, when opening paths to drag stems to loading points, or during the stem dragging itself (John 1988, Verburg and Van Eijk-Bos 2003). Another cause of seedling and sapling mortality in logged forest is the site preparation, locally called 'socola'. Before the logging, workers removed weeds, herbaceous vegetation, and vines to facilitate later access and mobility throughout the forest during logging activities (Bosques FLEGT/Colombia 2008, Camargo et al. 2008). Pre-logging site preparation has been suggested as the mechanism that has the greatest negative effect on the vegetation in bamboo forests in the region, as many seedlings and saplings are directly impacted (Ospina 2002, Gómez and Orozco 2006). However, there are no studies on the effect of the site preparation on the plant community in bamboo logged fragments.

Low seedling and sapling density in logged fragments suggests that future regeneration could be poor. However, we do not know the minimum seedling density required to maintain the adult tree community in these forests (Benitez Malvido 1998). In addition to the factors listed above, other causes could be directly related to the reduction of diversity in the regeneration pool, such as lower seed production of adult trees in logged fragments. The potential impact of the low seedling and sapling richness and abundance demands further research into its causes.

The protected forest and the logged fragments had similar adult tree attributes, contrary to our expectation. Bamboo stems are smaller than trees typically targeted in selective harvest of tropical species (only up to 22 cm DBH), and are moreover lighter than other woody stems of the same size, as they are hollow and do not have big branches (Riaño et al. 2002). Given bamboo's characteristics, it is likely that fallen bamboo stems are not heavy enough to damage an adult tree,

but they may well will impact smaller ones. Further studies are needed to evaluate tree mortality caused by incidental damage after the bamboo logging.

Floristic similarities between the protected forest and the logged fragments were low. The majority of the species found in the logged bamboo fragments are light demanding and fast growing species (e.g., *A. excelsum*, *C. angustifolia*, *T. caucana*, *F. insipida*, *F. killipii*, *S. trophoides*, *G. guidonia*, among others), as has been reported from other studies in logged bamboo forests (Ospina 2002, Gómez and Orozco 2006). Although many of those species were found in the protected fragment, they were not abundant there. The most abundant species in the protected forest was *P. rigida*, a late successional species that is shade tolerant, and rarely found near roads or forest edges. *Pseudolmedia* species are considered mature forest species (Peña-Claros 2003, Justiniano and Nash 2002). The establishment and growth of this species is probably not favored by both the higher light intensity caused by the repeated extractive activities in the logged fragments (where this species was missing or scarce) and the competition by the bamboo re-sprouting after each logging event. The canopy closure due to succession following a major canopy opening is not occurring in these logged bamboo fragments, as the short cycle of logging repeatedly re-opens the canopy, increasing the light within the forest, which potentially may impact the recruitment of shade tolerant species and favor light demanding species, including bamboo (Peña-Claros et al. 2008, Villela et al. 2008). Thus, only fast growing, light tolerant or demanding species would be able to compete with the bamboo. For the opposite reason, it is possible that *Ficus* species were not abundant in the protected forest, as those are pioneer light demanding/shade intolerant species that require periodic perturbations to germinate (Castaño et al. 2007, Schngart et al. 2007).

Consequently, commercial and domestic fragments had a very similar relative importance (IVI) ranking of species, but different from the protected forest. *A. excelsum* had the highest IVI in both logging managements, because it is an abundant, large tree (up to 299 cm DBH in these fragments) that was present in all the fragments. *T. caucana* had the second highest IVI, even though it is only a medium sized tree, because it was very abundant and was found in all the fragments. *Ficus* species also showed high values of IVI. Although these species were neither as frequent nor abundant as *T. caucana*, their size (biomass) makes them important species in these forests. In many of the fragments, *Ficus* were the largest trees, with DBH ranging up to 245 cm for *F. insipida* and 168 cm for *F. killipi*. These four species are all considered to be light demanding fast growing species (Ospina 2002, Gómez and Orozco 2006, Castaño et al. 2007). In contrast, the species with the highest IVI in the protected forest was the late successional shade tolerant species, *P. rigida*, which was also the most abundant species there. All these results suggest that one possible effect of the bamboo logging is a change in the floristic composition of the logged forest, where shade tolerant, slow growing species, and species with low capacity to survive mechanical damage may have poorer success in an environment that is under regular harvesting activities (Johns 1988, Lima et al. 2012). Several other studies also have shown that disturbance by selective logging reduces the number of shade tolerant species and stimulates fast growing light-demanding species (e.g. Silva et al. 1995, Villela et al. 2006, Gutierrez-Granados et al. 2011).

We should be careful in interpreting the comparisons between logged bamboo fragments and the protected bamboo forest, as we are comparing to only a single protected fragment – which is the only reserve in the region - and it is much larger in size than the logged fragments. For example, small fragments might have a lower abundance of seedling and saplings of shade

tolerant species as a result of stronger edge effects, compared to a larger forest (Norckonk and Gass, Benites Malvido 1998). In México, fragment size was correlated with the richness of plant species consumed by mantled howlers *A. palliata* (Arroyo-Rodríguez and Mandujano 2006). Thus, the lower abundance and richness of seedlings and saplings of red howler food resources found in logged fragments in this study, may be not only caused by the logging activity, but also, as an effect of the small size of all the fragments. However, we did not find differences in richness and abundance of adult trees between logged fragments and the protected forest. In México, fragment size principally affects the presence of large trees, which are less abundant and have smaller basal area in small fragments (Arroyo-Rodríguez et al. 2007). In our study, the logging seems to have affected only seedlings and saplings, but not adults; thus, we suggest that the effect of the bamboo logging could be more important than the fragment size, although both mechanisms may work together to decrease food resources for howlers.

The differences in floristic composition between the logged fragments and the protected forest imply that different dietary opportunities are available for howlers in these two contexts. In the protected forest, the howlers' diet was more diverse than in logged fragments, and not so reliant on only two *Ficus* species. For example, in the protected forest, two howler groups consumed 30 species over six months (Londoño and Gómez-Posada submitted), while in the logged fragments, six howlers groups consumed only 33 species during 6 to 12 months, with three of the groups using fewer than 10 species over one year (Gómez-Posada, Ch 1). The most important species for howlers in the protected forest was *P. rigida* ($45.10 \pm 3.25\%$ of the diet) and 4 species of *Ficus* accounted for $32.50 \pm 16.40\%$ of the diet (Londoño and Gómez-Posada submitted). In the logged fragments, the diet is based on *F. insipida* and *F. killipii*, which together comprised more than 70% of the diet. Despite their high abundance, *T. caucana* and *A.*

excelsum were not important in the howlers' diet (>1% and 15% respectively) (Gómez-Posada, Ch 1). These results agree with other studies that suggest that selective logging may reduce the diversity of food resources for herbivorous primates, even where timber trees are not themselves used by animals (Johns 1988, Peres and Barlow 2004).

Because commercial harvests allow for a greater proportion of the bamboo to be cut, we expected to find that commercially-logged bamboo fragments showed greater impacts from logging than domestically used ones. However, the results showed no differences in any of the vegetation attributes between commercial and domestic logging. Bamboo logging, regardless of the management type, may create conditions that select for the same set of species across the landscape, favoring light demanding, fast growing species, including those with high capacity to survive mechanical damage (Clark and Clark 1991, Guariguata 1998). This would result in a homogeneous tree composition among logged sites (Peres and Barlow 2004, Gutierrez-Granados et al. 2011).

Another explanation for the lack of differences in vegetation attributes between commercial and domestic fragments may be a similar response of the plant community to logging with harvesting percentages smaller than 34% of the stems. A study in the Eje Cafero found that the overall diversity and abundance of plants from canopy species between 1 and 9.9 cm of DBH, were negatively affected only when more than 34% of the bamboo stems were harvested (Ospina 2002). We did not quantify how many stems were harvested in the fragments, but according to the Colombian regulations, regardless of the management type, it should be less than 35%, as it the maximum commonly allowed in Colombia (Bosques FLEGT/Colombia 2008).

However, the similarities in structural characteristics and richness between commercial and domestic logging could also be due to the lack of supervision for domestic extraction.

Commercial logging is carried out often, in cycles of at least 12 months, and under supervision by the local environmental authorities (Bosques FLEGT/Colombia 2008). However, there are no official records for the domestic logging, with no information about the periodicity or extent of extraction, as the owners cut stems every time the need arises, which could be as or more often than for commercial bamboo logging. Low impact logging is an important method to reduce change in forest structure, but the impacts may strongly depend on the logging cycle (Putz et al. 2008). If domestic fragments in our study are harvested very often, the impact could be quite comparable to those of commercial logging effect (Hunth and Ditzer 2001, Verburg and van Eijk-Bos 2003). It is also possible that owners may harvest a high percentage of bamboo stems (in one or many extractive events) for domestic use, cutting higher quantities than are allowed by the regulations, and that silvicultural techniques may not be applied correctly to minimize damage to associated vegetation (Putz et al. 2008).

How has logging impacted natural regeneration?

The size distribution patterns for all the species in the three management types showed a concentration of small sized individuals, especially in the protected forest, which could be interpreted as capable of sustained regeneration. However, in the logged fragments, half of the individuals in the first size class were from one species, *T. caucana*, which is only rarely eaten by red howlers, while the remaining species had few or no individuals in this smallest size class. These results suggest that the regeneration potential for most species in the logged bamboo fragments is low. In the case of the two species of *Ficus* (*F. insipida* and *F. killipii*), there is a concentration of large sized individuals, few small sized individuals, and a gap in the middle sizes classes. These size-class distributions suggest that the succession of these two species is

arrested, due to low ability of seedlings and saplings to germinate and establish, and also, because they are failing to recruit from the smallest size class into a larger size class, most probably as a consequence of the logging.

Ficus are important sources of food for many vertebrate species. They are consumed by up to 50% of the bird and mammal faunas present in a forest (Shanahan et al. 2001, Kattan and Valenzuela 2013), and in some cases are considered keystone plant resources in tropical forest (Díaz-Martin et al. 2014). Their importance for howlers seems to be even higher in secondary forests where *Ficus* tend to be abundant. Howlers rely heavily on the abundant and continuous production of *Ficus* fruits, flowers and leaves (Milton et al. 1982, Serio-Silva et al. 2002 Bicca-Marques 2003). We did not find information about *F. insipida* and *F. killipii* growth rates in bamboo forest; however, in a study in a lowland forest in Peru, it was estimated that *F. insipida* needs at least 5 years to reach 10 cm of DBH (Terborgh et al. 1997). An analysis modeling *F. insipida* tree growth in lowlands forest of Brazil, it was estimated that an individual needs ~3.1 years to reach 10 cm DBH (Schongart et al. 2007). Commercial bamboo logging rotations in Colombia are at least 12 months. Which such a short cycle, it is possible that *Ficus* seedlings that survive the logging or that germinate following logging will not grow large enough to escape being cut during site preparations of the next logging cycle, or to resist the mechanical damage caused by the next logging. The very short cycle of bamboo logging could explain the failure of recruitment in the middle size class for *Ficus*. *Ficus* populations in logged fragments consist of old individuals, and without a cohort of smaller individuals, these mature trees will not be replaced when they die.

Other species may face the same problem. For example, the low abundance of *P. rigida* in logged fragments may not be only due to their shade requirements and bamboo competition, but

rather to the negative impacts of such short logging cycle, as discussed for *Ficus*. We did not find data on *P. rigida* growth rate in bamboo forests or in the region, but some estimates in a lowland forest in Bolivia suggest that a tree may need more than 50 year to grow to 10 cm DBH (Poorter et al. 2001, Justiniano and Nash 2002). Species such as *P. rigida* and *Ficus* are important sources of fruit for howlers and other fauna, yet they may be lost from the logged fragments due to the frequency of harvest and site preparation activities. In the long term, it is possible that only fast growing species, with better capacity to survive mechanical damage and that are light demanding, will remain in logged fragments, which may be the case of *T. caucana*, a species that is not important for howlers.

Howler monkeys prefer big trees as food resources (Arroyo-Rodríguez et al. 2007, Serio-Silva et al. 2002, Dunn et al. 2009), and in Mexico, the loss of big trees (DBH >60 cm) was related with the absence of howlers in a fragment (Arroyo-Rodríguez et al. 2007). The food availability in a forest can be greatly reduced by the loss of big trees (Coates-Estrada and Estrada 1986). In this study, the bamboo logging did not affect adult trees and basal area, suggesting that there is no logging effect on the present quantity of food resources. However, the most important species in their diet, *F. insipida* and *F. killipii*, were not abundant in the fragments and have a low natural regeneration capacity; and the most abundant species were not important for howlers. We can conclude that the extremely short logging cycle could be threatening the availability of howlers' food resources in the future.

One study in the Eje Cafetero that quantified the impacts of logging on richness and abundance of species in bamboo fragments found that one year after the logging, between 25 to 73% of the species were lost (mean 49.82%) and the abundance of individuals was reduced between 30.13 to 63.13% (mean 49.19%) (Gómez and Orozco 2006). The repeated harvesting of

these bamboo fragments will not allow the vegetation to recover, and will gradually result in a loss of plant diversity (Hunth and Ditzer 2001, Makana and Thomas 2005). The ecological and biological complexity of the forest may be profoundly disrupted if the logging is repeatedly in such a short cycle (Makana and Thomas 2005, Campanello et al. 2007). Our results suggest that bamboo logging in very short cycles modifies regeneration and may affect forest composition and structure in the long term.

The silvicultural regulations and techniques for the bamboo logging in Colombia have been developed after extensive, rigorous studies to establish an economically and ecologically sustainable management program, and avoid overexploitation of these bamboo forests (e.g., Espinal et al. 2005, Bosques FLEGT/Colombia 2008, Camargo et al. 2008, 2010, among many others). However, those management guidelines do not consider the ecological requirement of other species. As bamboo forests are the last remaining forests in the premontane range of the Central Cordillera, it is urgent to include in the silvicultural management a greater focus on non-target tree species, as these are essential for supporting wildlife. In particular, we need to understand how the logging practices affect the processes of native plant regeneration (e.g., seedling establishment, tree recruitment, growth, fruiting phenology, tree mortality, among others) and evaluate how seedling and sapling recruitment might be boosted through protections of key species. An important result of this study is that the extremely short bamboo logging cycle may be negatively affecting the recruitment rate of important species as *Ficus*. Urgent studies are needed to evaluate the effect of different rotation cycles on the recruitment of key species, and also experimental studies on how to enhance recruitment of those key species.

Regulations of bamboo logging in Colombia have been carefully and intensively planned resulting in a controlled bamboo harvesting to increase the silvicultural value of the forest and

decrease the negative impacts on wildlife. However, in some respects, the regulations may not be sufficiently protective; for example, extractions of more than 35% of the stems are possible if the density of the bamboo is too high. As there are negative effects on the plant community when more than 34% of the stems are harvested (Ospina 2002), the regulations should consider limiting the harvesting intensities to no more than that. Also, emphasis should be made on education and training for both commercial and domestic purposes; and not only for the forest owner, but also the workers. In many cases, the lack of preparation of the workers erased the benefit of adequate silvicultural management (Putz et al. 2008). It is possible that some domestic logging may be higher than the 20m³ of stems per year allowed by the authorities, extracted without silvicultural techniques. As it is not possible to supervise domestic logging, some incentives should be considered, in addition to a strong emphasis in education. For example, tax waivers could be given to forest owners who participate in training activities and who can prove that have domestically harvested their forest following silvicultural regulations.

Bamboo logging takes place around the world and in many countries; and its potential to support local wildlife has been highlighted by a number of NGOs (INBAR 2014). Bamboo logging has been significant in supplying and sustaining small and medium enterprises, thus bamboo logging has a great potential to support local economies and wildlife. However, this potential depends on adequate forest management regulations that consider the ecological requirements of key food resources for wildlife. This work represents the first study of the impacts of bamboo logging on non-target vegetation, and given the importance of bamboo forestry across the tropics, we hope the findings help encourage other researchers to examine impacts in other locations.

In the case of bamboo forestry in Colombia, the existing regulations should be sufficient to protect the howler's food resources, yet no data had been taken before this study to evaluate the actual impacts of logging on recruitment and regeneration of these key tree species. These results demonstrate that either enforcement of the provisions to avoid damage to non-target tree species is insufficient, or that other supports to protect these young trees need to be added. For example, it may be that improved training could help workers reduce the damage to sapling trees, or that marking of seedling and sapling trees that must be avoided during bamboo felling and removal needs to be added to aid workers in avoiding these young trees. Close collaboration with the environmental authorities should allow improvements in the application of the existing regulations that could make a sizeable difference in allowing more individuals to grow into the adult size classes in these forests.

In addition, experimental plantings of larger saplings of key tree species could be conducted to evaluate if more intervention could accelerate regeneration of these resources. Given the importance of *Ficus* species both to red howler monkeys and to a wide diversity of other species in these forests, restoration efforts with *Ficus* should be a particular priority. Additions of other species, enlarging the range of species found within these forests would also be important to add diversity to the diet of the howlers, and other species. Finally, expansion of these fragments with additional plantings of bamboo that help reduce the impacts of fragmentation on these species (see Gómez-Posada, chapter 3), could be encouraged particularly where such extensions include isolated clusters of mature trees, and experimental restoration of key species. Modest expansions of bamboo forest could both enhance the income of landowners while helping to secure the future for wildlife.

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Influence of biogeographical and vegetation characteristics on patch occupancy of red howler monkeys (*Alouatta seniculus*) in a highly fragmented landscape in Colombia

Abstract

Howler species are known for their ability to live in human dominated landscape. These monkeys are extremely forest-dependent, however, and do not disperse well in matrix without canopy connectivity, thus their plasticity does not make them immune to the negative consequences of living in fragmented landscapes. Little is known about the factors that govern patch occupancy by red howler monkeys, *Alouatta seniculus* in fragmented landscapes. This study analyses how the presence/absence of red howler monkeys in forest fragments is related to biogeographical variables (fragment size, shape and isolation: distance to the nearest fragment and amount of habitat area within 100, 200 and 400 m threshold distance of a focal patch) and vegetation characteristics (species richness, abundance, tree height and basal area of food resources for howlers) in a highly fragmented landscape in Central Colombia. The study was conducted in 27 bamboo forest, 14 occupied by howlers and 13 unoccupied, ranging in sizes from 2.4 to 74.8 ha. Only the amount of habitat area within 100 m from the home fragment, and marginally 200 m, showed a significant relationship with the presence of howler monkeys in a fragment. More habitat area available in the near vicinity of the home fragment may imply higher potential sources of food and migrant howler individuals, which may increase their chances of persistence. These results suggest that howlers may persist via a metapopulation dynamic in this landscape, supported also by the lack of relationship between fragment size and abundance of the main food resources, *Ficus* trees, with the presence of howlers. These monkeys can persist in small forest patches with scarce resources if they can supplement their

diet with sources located in neighboring patches. Occupied fragments had taller trees than unoccupied fragments, in agreement with studies in other howler species where canopy height is an important requirement for howlers' presence. The results showed that spatial patch configuration needs to be taken into consideration when designing management strategies for the conservation of red howler monkeys in the Colombian mountains.

Introduction

Habitat fragmentation is a landscape scale process that implies habitat loss and division of remaining habitat into small patches dispersed in a matrix of anthropogenic modified habitat Kattan and Murcia 2003. Thus, fragmentation results in the reduction of forest coverage and in changes of landscape attributes, such as an increase in the number of forest patches, a decrease in patch size and increased isolation (Fahrig 2003, Kattan and Murcia 2003). Species distribution in a fragmented landscape is initially a random process. However, over time species may disappear from some patches due to their small size and limited resources, whereas they may recolonize other suitable patches. Thus, the distribution and abundance of animals in fragmented landscapes may depend on preferences for habitat fragments of higher quality and the degree to which individuals are capable of moving between them (Marsh 2003, Mandujano et al. 2006).

Large canopy dwelling species, such as primates, are typically isolated by the forest fragmentation processes and their survival depends on the population dynamics at the fragment level. Thus, at a local scale, the effects of fragment size, edge, and isolation may be the primary mechanisms driving patch-level extinction (Estrada and Coates- Estrada 1996, Kattan and Alvarez-López 1996). Dispersion of individuals among isolated forest fragments will ameliorate the effect of fragmentation on primate populations; thus dispersal probabilities are negatively

influenced by factors such as the distance between fragments, whereas the degree of connectivity enhances movements among them (Mandujano et al. 2004, 2006, Anzures-Dadda and Manson 2007). Dispersal capacity in fragmented landscapes will depend on the specific characteristics of each primate species, as well as the spatial configuration of the landscape (Kattan and Murcia 2003). Other habitat attributes, such as food resource availability, play an important role in the survival of primate species in fragments, and some studies have shown that the presence and abundance of primates are related to vegetation attributes, such as the diversity, abundance, and basal area of critical food resources (Estrada and Coates Estrada 1996, Cristobal-Azkarate et al. 2005, Arroyo-Rodríguez et al. 2007).

Howler monkeys are recognized for their versatility in using different habitat types, including their ability to survive in small and disturbed forest fragments (e.g., Bicca-Marques 2003, Arroyo-Rodríguez and Dias 2010). Nonetheless, habitat loss and fragmentation negatively impact their distribution in fragmented landscape as isolation distance increases and fragment size decreases (Mandujano and Estrada 2005, Mandujano et al. 2006). Thus, these monkeys may be more sensitive to the fragmentation and habitat loss than is sometimes thought, as howlers are high canopy, forest dependent animals, and their ability to move between forest patches is limited, particularly when the surrounding matrix is mostly livestock pastures or croplands (Mandujano et al. 2004, Anzures-Dadda and Manson 2007, Arroyo-Rodríguez and Dias 2009).

In Mexico, howlers' distribution in fragmented landscape has been widely studied (*Alouatta pigra* and *A. palliata*) (review in Arroyo-Rodríguez and Dias 2009). These occupancy studies imply that to enhance persistence of these endangered primates priorities should be placed on increasing area of habitat fragments and connectivity (Mandujano et al. 2006, Arroyo-Rodríguez and Dias 2009). For instance, occupancy studies have indicated that the presence of

howlers in forest fragments is related to fragment size and shape, distance to closest fragments, abundance of connection corridors, canopy height, diversity of food resources, and percentage of forest cover at the landscape level (e.g., Estrada and Coates-Estrada 1996, Rodríguez-Toledo et al. 2003, Cristobal-Azkarate et al. 2005, Anzures-Dadda and Manson 2007, Arroyo-Rodríguez et al. 2007, 2008, 2013b).

In Colombia, in the premontane range of the Central Cordillera (known as the Eje Cafetero), only 15% of the original forest covers remains (Wild et al. 2006). The current landscape is composed of small and irregularly shaped forest fragments dominated by a native bamboo (*Guadua angustifolia*), forming a highly fragmented pattern within a matrix of pastures and fruit crops. Red howler monkeys (*Alouatta seniculus*) inhabit some of these forest fragments, but little is known about their responses to forest fragmentation (Gilbert 2003). Although this species is not considered threatened by the IUCN, red howlers may be highly vulnerable in this region, as their habitat has been so severely reduced (Defler 2004, Gómez-Posada et al. 2006). Howlers are a charismatic primate, much beloved in the Eje Cafetero of Colombia. Because of the local people's affection for howlers, the conservation of this species in the region may serve as a powerful tool to conserve the last relics of Andean forests and their associated fauna.

A key element for making appropriate conservation decisions is the identification of the environmental variables that allow or impede howler monkey persistence in fragmented habitats (Arroyo-Rodríguez and Mandujano 2009). In this study we asked what biogeographical or vegetation characteristics influence occupancy of bamboo fragments by howlers located at the Eje Cafetero in Colombia. We predicted that fragment occupancy by howlers is positively correlated with fragment proximity and fragment size. Further, we expected that fragments with less edge area would be more likely to be occupied than narrow fragments with highly irregular

shapes. With respect to vegetation characteristics, we expected that occupancy of fragments by howlers would be positively related to the diversity and abundance of food tree species, as well as their combined basal area. In addition, because howlers use large trees for resting areas and feeding, we expected that occupancy of fragments by howlers would be positively correlated with tree height.

Methods

Study area

The study was conducted in the Quindío and Valle del Cauca Departments of the Eje Cafetero, the main coffee growing region in Colombia, in the premontane range on the western slope of the central mountain range of Cordillera de los Andes, between 900 to 1100 m of altitude (Fig. 1). Mean annual precipitation is 1,800 mm, and mean annual temperature is around 23°C (CVC 2000). The region is highly fragmented and only about 15% of the original forest cover remaining (Wild et al. 2006). Current forests remnants are small and irregular bamboo forest fragments dominated by a native bamboo (*Guadua angustifolia*), within a matrix composed of livestock pastures, and coffee, fruits and corn crops (all the crops without canopy cover). These fragments provide refuge for the original fauna and flora of the region. Most of the fragments run along rivers and streams, forming narrow, linear fragments of irregular shape and branching patterns.

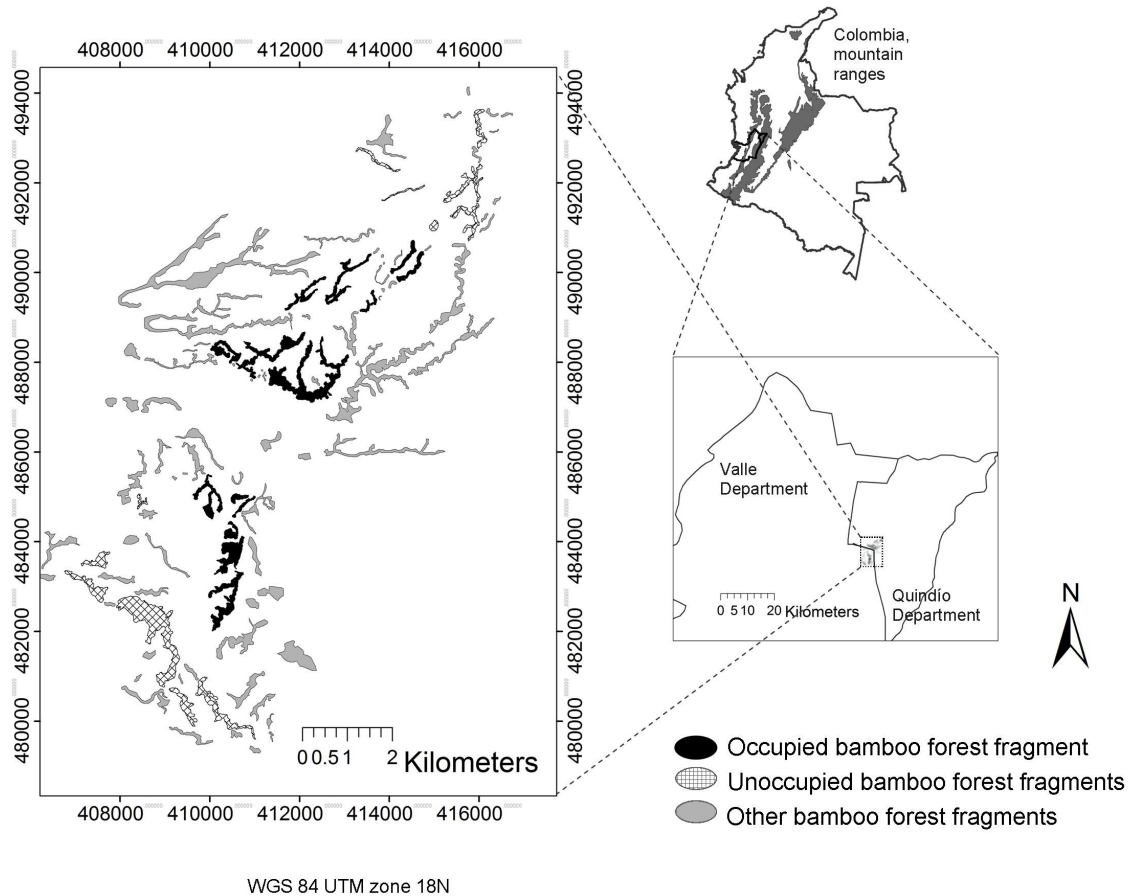


Figure 1. Study site at the Colombian Eje Cafetero region, indicating the focal bamboo forest fragments, occupied by red howler monkeys: black, unoccupied: striped.

Predictor variables to explain presence/absence of red howler monkeys in study fragments

In selecting potential variables for evaluating the factors that promote occupancy of forest fragments by red howler monkeys, we selected the suite of biogeography and vegetation variables that have been shown to be most important in occupancy studies with other species of howlers in the Neotropics. In addition, we used the information from the other portions of this study (see Gómez-Posada Chapters 1 & 2) to select key vegetation variables that are likely to be most important to red howler monkeys in this region. The following explains the specific variables chosen in this study, and the rationale for their selection:

Biogeographical variables:

- **Fragment size:** The size of a forest fragment is important because it may influence the diversity and density of food resources available for howlers. Also, it could be related with the howlers' population size.
- **Fragment shape:** Elongated and narrow fragment will suffer from a stronger edge effect, which may influence diversity and density of food resources available for howlers.
- **Distance to nearest fragment –** The distances among fragments are also a measurement of connectivity that may influence the dispersal process.
- **Proximity index.** The proximity index is a distance-weighted area-based metric to estimate the amount of habitat area within a threshold distance of a focal patch (Fig. 2). When more area is available within a close distance radius, there is a higher potential source of food for howlers (Arroyo-Rodriguez and Dias 2009). Large patches, which are close to the focal patch, have a stronger effect on reducing isolation than small remote patches. Isolation is expected to decrease with increasing index (Tischendorf et al. 2003). We selected three threshold distances for this analysis: 100, 200, and 400 m. These values were chosen based on the distances that a howler would travel across an intervening matrix between forest fragments, as reported for other howler species. For example, mantled howlers (*A. palliata*) most commonly moved between patches that are less than 100 to 200 m apart (Mandujano et al. 2004, Mandujano and Estrada 2005, Palacios-Silva and Mandujano 2007), while it has been found that uninhabited fragments are completely isolated from other fragments when more distant than 200 m (Mandujano and Estrada 2005, Arroyo-Rodriguez et al. 2008).

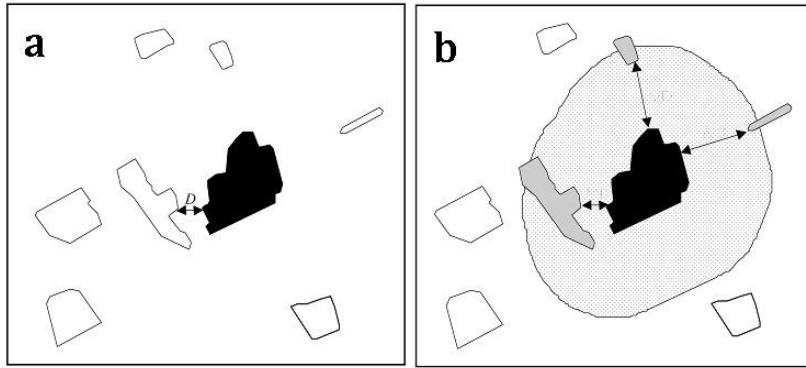


Figure 2. Illustrations of the two isolation metrics used in this study: a) nearest-neighbor distance D ; and b) the proximity index which sums the ratios of patch area/distance for all patches of habitat (gray polygons) located within a threshold distance of a central patch of interest (black polygon). Images from Bender et al. 2003

Vegetation variables:

- Plant species richness and abundance - Both variables are related to fragments' plant species composition and may affect their capacity to sustain red howler monkey populations because these primates need to feed on a balanced diet composed of fruits and leaves of several species on a daily basis (Milton 1980). We expect that howlers will be more likely to occupy fragments with higher tree species richness and density.
- Tree height and basal area- The height and basal area of the trees are an indicator of the structure of the vegetation of the study sites and the availability of howler's food resources. Because howlers are medium-sized arboreal mammals we hypothesize that fragments containing larger trees are more likely to sustain groups of howlers (According to Rodriguez- Toledo *et al.* 2003, Arroyo et al. 2007). In addition, fragments with a greater basal area of trees consumed by howlers are more likely to sustain howler populations.
- Abundance and basal area of *Ficus* species - *Ficus* trees are the most important species for howlers in the region, comprising more than 70% of their diet (Gómez-Posada Ch 1).

Their abundance and basal area provides an approximation of the availability of preferred food species in a fragment.

Data Collection

We selected 27 fragments, 14 with howlers (occupied/inhabited) and 13 without howlers (unoccupied/uninhabited) that differed in size, shape and degree of isolation from other fragments (Fig. 1). For the purpose of this study, we defined forest fragments as remnants of bamboo forest with an area of ≥ 0.5 ha that was isolated from the nearest fragment by at least 20 m, irrespective of its shape. All the fragments were privately owned and actively logged for bamboo (Gómez-Posada Ch 2). To determine the occurrence of howler monkeys, the fragments were sampled between June 2011 and April 2013. Fragment occupancy was defined as the presence of at least one individual in a given fragment (Arroyo-Rodríguez et al. 2008). To determine occupancy, we first interviewed local people who own and/or lived in the proximity of a fragment, about the presence/absence of howlers in the area. Then, two researchers confirmed the occurrence of the species, by waking slowly throughout the day, around and inside the fragments, looking for the monkeys or following their howling until having visual contact. Presence of howlers was generally confirmed in less than a day. If after several days no monkeys were heard/seen in a fragment, and the local people reported that the fragment was not occupied by howlers, it was considered empty. Each site was surveyed only once, but search time was adjusted to site size, with two days being dedicated to small fragments (<10 ha), 3 days to medium size fragments (10-50 ha) and 4 days to larger fragments (>50 ha) (Mandujano et al. 2004).

Aerial photos (1:10,000 scale, SIG-Quindío 2011) of the study area were digitalized and processed with ArcMap GIS software (version 10.0) to create a composite raster photo mosaic of the study area. For biogeographical characteristics, fragment size was calculated with ArcMap 10.0, and fragment shape and isolation were calculated with Fragstat 4.2 (Mcgarigal and Ene 2013). To characterize shape, we used a shape index defined as the patch perimeter divided by the square root of patch area, adjusted by a constant for a square standard. The index is equal to 1 when the patch is square, and increases as patch shape becomes more irregular. To characterize isolation we used two metrics: distance to the nearest neighbor and proximity index. Distance to the nearest neighbor was calculated as the shortest edge to edge Euclidian distance between the focal patch and its nearest neighbor (Mcgarigal and Ene 2013) (Fig. 2). The proximity index was calculated as sum of patch area divided by the nearest edge-to-edge distance between the patch and the focal patch of all patches whose edges are within a specified distance of the focal patch (Whitcomb et al. 1981). The index is dimensionless (has no units) and therefore the absolute value of the index has little interpretive value; instead it is used as a comparative index (Mcgarigal and Ene 2013).

For the vegetation analysis, we inventoried 5 randomly located 30x30m plots within each fragment (a total area of 4500 m² per fragment) between June 2011 and April 2013. Within each plot, we recorded all tree individuals with DBH \geq 10 cm that were part of the howlers' diet. The list of species was based on diet data collected in bamboo forest in the region (see Gómez-Posada Ch 1, Londoño and Gómez-Posada, submitted), supplemented by findings from other studies in Andean forest (Giraldo et al. 2007, Palma et al. 2010). For each individual, we measured the diameter at breast height (DBH) and height. For all plant species together, we quantified species richness, tree abundance, basal area (m²) and tree height per plot, and in

addition, the abundance and basal area (m²) for all the *Ficus* species present in the plots. Across all 27 fragments we found four species in the plots: *F. insipida*, *F. killipii*, *F. subandina* and *F. cf. giganticus*.

Data analysis

We used descriptive statistics to report the biogeographical and vegetation characteristics of the fragments and applied a Mann-Whitney U test to explore differences in patch occupancy. The occupancy of fragments by howler monkeys was further explored using a stepwise multiple logistic regression analysis with generalized linear models, where significant terms were identified in a stepwise manner, removing terms beyond the null model based on a F statics at each step (following the principle of maximum likelihood). We used Pearson correlations to test and eliminate all but one of each group of intercorrelated variables. All the vegetation variables were highly correlated to each other, except for tree height. We decided to use *Ficus* abundance as the key variable in the models, due to their high importance in the howlers' diet in the region (see Gómez-Posada Ch 1). We included in the model eight explanatory variables for the 27 fragments: fragment size, shape index, distance to the nearest forest, proximity index at 100, 200 and 400 m, tree height and abundance of *Ficus* trees. All analyses were performed using R-package version 2.15.1. The statistical threshold was set at $P \leq 0.05$.

Results

Only three of variables included in this study exhibited significant differences between occupied and unoccupied forest fragments: proximity index at 100 and 200 m, and tree height (Table 1). Occupied fragments had more forest area within a buffer distance of 100 and 200 m

from the edge of the fragment, and taller trees than the unoccupied fragments. None of the inhabited fragments had a proximity index at 100 m with a zero score, while 7 out of the 13 uninhabited had zero for this index. For the other variables that did not have significant differences between inhabited and uninhabited fragments, some trends could be noted. For example, all the occupied fragments had a distance to the nearest fragment less than 90 m, while seven out of 13 unoccupied had distance larger than 125 m to the nearest fragment. All vegetation variables tended to be lower in unoccupied fragments, with narrow ranges; for example *Ficus* abundance was < 5 individuals per plot in all the unoccupied fragments, while 7 of the 14 occupied fragments had > 6 *Ficus* tree per plot.

Table 1. Comparison of the biogeographical and vegetation variables in occupied vs. unoccupied fragments (Values are reported for all fragments combined and separately for fragments occupied and unoccupied by howler monkeys *Alouatta seniculus*. Differences between these latter two types of fragments were compared using Mann-Whitney U test. *significant differences).

Variables	All		Unoccupied		Occupied		U (P)
	Media (SD)	Range	Media (SD)	Range	Mean (SD)	Range	
Area (ha)	15.1 (16.6)	2.4-74.8	15.2 (19.1)	2.4-74.8	15.1 (14.7)	3.6-58.9	71 (0.33)
Shape index	3.0 (0.9)	1.2-4.8	2.9 (0.8)	1.2-4.4	3.1 (0.9)	1.5-4.8	78 (0.53)
Dist. nearest fragment (m)	103.8 (93.05)	50-458.9	137.7 (124.4)	50.0-458.9	76.8 (14.6)	50-90.1	68 (0.13)
Proximity index 100 m	22.6 (29.6)	0-132.8	11.13 (16.9)	0-53.2	31.7 (34.6)	1.6-132.8	37 (0.00)*
Proximity index 200 m	32.4 (34.5)	0-149.3	21.3 (20.1)	0-53.2	41.2 (40.9)	1.6-149.3	48 (0.03)*
Proximity index 400 m	35.3 (34.5)	0-149.4	24.1 (21.6)	0-53.5	44.2 (40.5)	3.9-149.4	55 (0.08)
Species richness (species/plot)	6.1 (2.5)	1-11	5.5 (2.5)	1-9	6.7 (2.4)	3-11	82.5 (0.68)
Tree abundance (indv/plot)	29.5 (19.6)	1-69	25.4 (17.9)	1-54	32.8 (19.1)	13-69	79.5 (0.59)
Basal area (m ² /plot)	8.3 (5.2)	0.03-18.9	7.5 (5.9)	0.03-18.7	8.9 (4.7)	2.3-18.9	65 (0.21)
Tree height (m)	19.6 (2.2)	13.5-22.1	18.2 (2.7)	13.5-21.5	20.5 (1.4)	17.5-22.1	10 (0.05)*
<i>Ficus</i> spp. abundance (ind/plot)	3.3 (3.1)	0-13	2.4 (1.7)	0-5	4.1 (3.9)	0-13	72.5 (0.37)
<i>Ficus</i> spp. basal area (m ² /plot)	2.2 (2.3)	0-9.27	1.8 (1.6)	0-5.15	2.5 (2.8)	0-9.27	74 (0.41)

The variable that best described the distribution of howlers in forest fragments was the proximity index at 100 m ($Z=0.14$ $P=0.04$) (annex 1). According to the stepwise regression, only this single variable explained the variation in the data. Two more variables had marginal effects as predictors of the presence of howlers in a fragment: distance to the nearest forest ($Z=-1.8$ $P=0.06$) and proximity index at 200 m ($Z=1.8$ $P=0.06$). The final model describing the

presence/absence of howlers from bamboo forest fragments = fragment size + shape index + proxi 100 +proxi 200 + proxi 400 + distance nearest fragment + tree height + *Ficus* density. The probability of a fragment to be occupied by howlers is higher than 70% with proximity index scores higher than 31, which was the average index score for occupied fragments (Table 1, Fig. 3).

Table 2. Model parameters and fit for the minimum adequate model describing red howler monkey *Alouatta seniculus* presence in occupied bamboo forest fragments

	Slope	SD	Z	p	Changes deviance	P F-test deviance
Null intercept	-0.81	0.6			47.7	
proxi 100	0.05	0.02	2.1	0.04	9.0	0.05
Residual deviance	31.5				38.7	

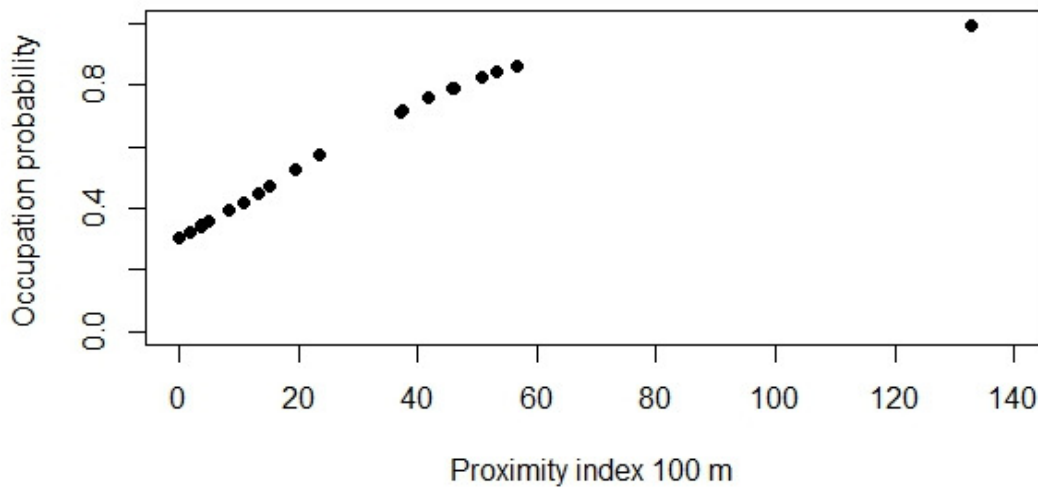


Figure 3. Changes in the probability of howler monkey (*Alouatta seniculus*) occurrence in bamboo forest fragments as a function of the proximity index at 100 m as predicted by a multiple logistic regression model of monkey presence/absence $Y = -0.81 + (\text{proximity index } 100 \times 0.05)$.

Discussion

The fragmentation process reduces and isolates areas of habitat suitable for a species' survival, which can then lead to local extinction (Marsh 2003). Consequently, those habitat patches that present a higher degree of connectivity are more likely to sustain viable populations and avoid extinction (Kattan and Murcia 2003, Mandujano et al. 2006). In this study, the amount of habitat within a close distance of a fragment was a good predictor of the presence of howlers in a fragment.

Howlers are considered specialist dispersers (Mandujano et al. 2004), with a low probability of crossing boundaries from forested habitat into unforested habitat matrices, and a high risk of mortality while in the matrix (Tischendorf et al. 2003). Although there are rare reports of howlers crossing distances between patches as far as 656 m (Mandujano et al. 2004), the majority of the movements made by howlers through matrix habitats are between fragments located very short distances away, mostly <100 m (Mandujano et al. 2004, Mandujano and Estrada 2005, Palacios-Silva and Mandujano 2007). In our study, the occupied fragments were all at distances <90m from other fragments, which may represent distances short enough to facilitate the howlers' dispersal. If the mean distance between fragments is beyond the natural movements of a primate, the monkeys inhabiting a fragment would be dependent perhaps exclusively on resources within that isolated fragment. In contrast, if the distance between fragments is within the dispersal capability of the primates, then the population dynamics could be governed by their use of multiple fragments (Rodríguez-Toledo et al. 2003).

But our results showed that the amount of suitable habitat around a fragment also influenced the presence of howlers in a fragment. The amount of habitat within threshold distances of 100 m and, marginally, 200 m were good predictors of howlers' presence. But once

the threshold distance was increased to 400 m, we did not observe a relationship, suggesting that howlers in this landscape are less likely to disperse >200 m. More habitat area available in the near vicinity of the home fragment may imply higher potential source of food and migrant individuals for howlers (Arroyo-Rodríguez and Dias 2009, Arroyo-Rodríguez and Mandujano 2009), which may increase their chances of persistence (Bender et al. 2003, Tischendorf et al. 2003).

In many fragmentation studies, patch isolation has not been a strong predictor of patch occupancy, perhaps due to the metrics used to define and describe isolation (Arroyo-Rodríguez and Dias 2009, Arroyo-Rodríguez et al. 2013a). Most of the fragmentation studies with howlers have used distance-based isolation metrics, such as the distance to the nearest patch (e.g., Cristobal-Azcarate et al. 2005, Arroyo-Rodríguez et al. 2008, Silva and Bicca-Marques 2013). This isolation metric can underestimate the effects of isolation because it does not consider the size of the closest neighbor fragments, which could be only one and very small. In that case, a small and single close fragment may not significantly increase the suitable habitat for howlers or migrant individuals. Bender et al. (2003) and Tischendorf et al. (2003) demonstrated that area-based isolation metrics such as the amount of available habitat within a given radius of a fragment are the most reliable measure of fragment isolation. In addition, two recent reviews of habitat fragmentation effects on primates suggested that assessing habitat fragmentation requires quantifying the habitat configuration, for instance, quantifying not only fragment size, but also connectivity and forest cover around focal fragments (Arroyo-Rodríguez and Dias 2009, Arroyo-Rodríguez et al. 2013a). In Mexico, it has been found that patches with higher surrounding fragment density and patches in landscapes with a greater proportion of suitable habitat have an increased probability of being inhabited by mantled howler monkeys, *Alouatta palliata*

(Anzures-Dadda and Manson 2007, Arroyo- Rodríguez et al. 2008). A similar trend was found in the present study.

The distribution of howler monkeys in fragmented landscapes may be best explained by a combination of factors affecting monkey dispersal decisions. Howler monkeys are social primates that live in stable groups of differing sizes, where males and sometimes females may disperse to join a different group or to establish new groups elsewhere (Crockett and Eisenberg 1987, DiFiore and Campbell 2006). These groups typically move together throughout their home range, searching for food resources (Milton 1980). Howlers in resource poor, degraded fragments may show a higher probability of dispersing to neighboring forest fragments where habitat quality could be higher. However, dispersal across open habitats may increase mortality risk; for example, due to predation from domestic dogs (Estrada and Coates-Estrada 1996). Thus, howler dispersal probability should decrease with the distance between neighboring fragments, and the closest fragments should have the greatest probability of being inhabited first (Fahrig and Paloheimo 1988). Similarly, the probability that a fragment will be inhabited by howlers should increase with the number of adjacent fragments (Mandujano et al. 2006). In fragments with high quality habitat (e.g., high abundance of food resources), howlers' need to disperse should diminish and they may remain where they are unless conditions of the fragment change (Anzures-Dadda and Manson 2007).

Most of the studies on the effects of forest fragmentation on howlers have found that patch size is the best predictor of population patch occupancy (e.g., Gilbert 2003, Mandujano et al. 2006, Arroyo-Rodríguez et al. 2008). Habitat area may be positively related to food availability (Arroyo-Rodríguez and Mandujano 2006, Cristóbal-Azkarate and Arroyo-Rodríguez 2007), and negatively related to anthropogenic pressures (Peres 2001), physiological stress

(Martínez-Mota et al. 2007) and parasite risk (Gilbert 1994). However, in a review of the effect of forest fragmentation on 19 Neotropical primates, howlers were the least area-sensitive species, exhibiting high occupancy rates even in relatively small forest patches (Benchimol and Peres 2013). In our study, fragment occupancy was not related to patch area. However, considering the relationship observed between the occurrence of howler monkeys in fragments and the amount of habitat within a close radial distance of the focal fragments, we could suggest that these populations are supported in part by metapopulation dynamics. In this regard, metapopulation theory assumes that the processes of dispersal and immigration connect isolated populations into a network—the metapopulation (Rodríguez-Toledo et al. 2003, Mandujano et al. 2006, Silva and Bicca-Marques 2013,). Metapopulation theory has been the focus of much discussion in population and conservation biology in fragmented habitats (Hanski and Gaggiotti 2004). According to predictions based on metapopulation theory, if the landscape has been so severely transformed by deforestation that the number, size, quality, and connectivity of fragments are all low, the probability of persistence on a regional scale will decrease due to limited fragment occupation and reduced colonization of empty fragments (Ovaskainen and Hanski 2004). A simulation of the persistence of mantled howlers' metapopulation in a fragmented landscape in Mexico over a period of 30 years, showed that when fragment size remained stable, howler abundance likewise would remain stable, given a minimal individual dispersal probability among fragments; and howler abundance would increase to about 50% when given a high dispersal probability among fragments (Mandujano et al. 2006). For black howler monkeys, *Alouatta pigra*, in Mexico, smaller patches located in landscapes with lower inter-path isolation distances and higher fragmentation levels showed a higher density of individuals (Arroyo-Rodríguez et al. 2013b). These spatial patterns increase landscape connectivity, facilitating inter-patch

movements, thus favoring several landscape-scale processes that can be critical for population maintenance in fragmented landscapes (Arroyo-Rodríguez and Dias 2009, Arroyo-Rodríguez et al. 2013a).

Ten out of the 14 focal fragments with howlers in our study were less than 10 ha in size, and 4 of these 10 were inhabited by only a single group of howlers (mean group size ~9.5 individuals, Gómez-Posada unpublished data). With such a small population in very small fragments, it is likely that howler monkey populations are far below their minimum viable population size (Dunning et al. 2006). Therefore, metapopulation dynamics might be essential in enabling long-term survival of the howler monkey populations inhabiting these fragments (Ribiera and Bicca-Marques 2003). In such a case, the possible negative effects of fragmentation (e.g., environmental changes and stochastic demographic oscillations, loss of genetic variability and evolutionary flexibility) could be softened (Harrison 1991).

We did not find an effect of the fragment's shape on patch occupancy by the howlers. For howlers, there is not a clear pattern of the effect of fragment shape on their occupancy of fragments, perhaps because patch shape complexity offers advantages and disadvantages to them in fragmented landscapes (Arroyo-Rodríguez and Dias 2010). As fragments become smaller and more irregularly shaped, edge effects increase, whereby environmental changes at the fragment edge may lead to alterations in vegetation structure and composition, as for example an increase in tree mortality (Benítez-Malvido 1998, Rodriguez-Toledo et al. 2003, Arroyo-Mandujano et al. 2008). On the other hand, howlers' highly folivorous diet could be favored by the continuous growing of secondary vegetation at the edges (Rylands and Keuroghlian 1988). Also, complexly shaped patches can be colonized more easily than compact (e.g., round or square) patches due to the fact that their proportionally greater amount of edge increases the likelihood that a fragment

will be encountered by a moving individual, either by chance or deliberately (Boinski and Garber 2000, Arroyo-Rodríguez et al. 2008).

Changes in vegetation in highly fragmented habitats may affect the distribution and abundance of howlers. The presence and abundance of howlers has been positively correlated with the diversity, abundance and basal area of important food resources (Estrada and Coates-Estrada 1996, Cristobal-Azkarate et al. 2005, Arroyo-Rodríguez and Mandujano 2006). For example, in México, fragments inhabited by mantled howlers had some vegetation attributes that differed from uninhabited fragments, such as a higher density of big trees (DAP>60cm) and greater basal area (Arroyo-Rodríguez et al. 2007). Nevertheless, it is still unclear which of these vegetation attributes has the greatest influence on howler populations (Arroyo-Rodríguez and Dias 2009). The lack of relationship between the pattern of presence-absence of howler monkeys and all evaluated vegetation variables in our study (see Table 1) may be related to the ability of *Alouatta* species to adapt their folivorous-frugivorous diet in response to the botanic composition of their habitats. They can feed on a high quantity of leaves (making them less dependent on seasonal fluctuations in the fruit abundance, Mandujano et al. 2006), as well as from different secondary species that are typical of fragment edges (Bicca-Marques 2003, Arroyo-Rodríguez and Dias 2009). Further, primates can persist in forest patches with scarce resources if they can supplement their diet with sources located in neighboring patches and/or in different elements in the landscape matrix (for example isolated trees and live fences), as has been observed in howler monkeys inhabiting fragmented landscapes (Zunino et al. 2007, Asensio et al. 2009, Pozo-Montuy and Serio-Silva 2007). For example, when a fragment is very small but is also very close to another fragment with supplementary resources, individuals may use several patches to meet their dietary requirements. Zunino et al. (2007) observed that some groups of *A. caraya* in

Argentina, inhabiting very small fragments <1 ha, used multiple forest patches that were separated by grasslands. Thus, primates may live in fragments that do not exhibit characteristics required for their long term survival. Some authors have suggested that such fragments may function as sinks, while high quality fragments may act as a source of individuals (Chapman et al. 2003, Arroyo-Rodríguez et al. 2008, Arroyo-Rodríguez and Dias 2009). In those cases, source/sink dynamics may be operating in which populations living in sink habitats may go extinct as food resources dwindle without immigration of individuals from source patches.

We found significant differences in the tree height between occupied and unoccupied fragments. In Mexico, *A. palliata* was in occupied fragments where vegetation was taller than unoccupied fragments (Estrada and Coates-Estrada 1996, Rodríguez-Toledo et al. 2003, Anzures-Dadda and Manson 2007). In Costa Rica, *A. palliata* selectively spent more time in vegetation with canopy > 12 m (DeGamma-Blanchet and Fedigan 2005). Howlers are arboreal quadrupeds, and are considered canopy primates that prefer the upper level of the forest (Schwarzkopf and Rylands 1989, Stevenson et al. 2000). Thus, a tall canopy may be an important habitat requirement for these monkeys.

The long-term persistence of forest animals in fragmented landscapes depends also on the permeability of the matrix to their movements (Perfecto and Vandermeer 2008). If there is no migration between fragments because the matrix is inhospitable (the species cannot cross the matrix), the subpopulation will be restricted to the fragment, being vulnerable to the dangers of a small population size. On the other hand, if migration rates among patches are high, because matrices allow species movement, or because other landscape elements as stepping stones and corridors are present, then the probability that a subpopulation becomes extinct is lowered, favoring the persistence of the overall population at the landscape scale (Perfecto and

Vandermeer 2008). Differences in land management may influence howlers' dispersal throughout the matrix, according to the economic activities in the surroundings of a fragment (Anzures-Dadda and Manson 2007, Pozo-Montoy et al. 2011). In our study area, the matrix is mainly agricultural, and occasionally has arboreal elements such as live fences and isolated trees. We did not include in the analysis the crop types or the presence of live fences and isolated trees that may favor howlers' dispersion among fragments. Further studies could analyze the effect of the matrix and stepping stones landscape features on the distribution of howlers in these fragmented landscapes.

Our results suggest that the spatial configuration of habitat is important for howlers' population persistence in the Eje Cafetero, as location with respect to other fragments determines the presence of howlers in the fragments, with distance between them less than 200 m. Therefore, the long-term persistence of populations of red howler monkeys in the forest remnants of the Eje Cafetero in Colombia needs to focus on maintaining forest fragments within short distance to each other. This could ensure connectivity between subpopulations and may allow the persistence of the metapopulation in the long-term. Livestock and fruit crops are the major economic activity in this region, which compose a non-friendly matrix for howlers. Given that the current forest remnants are native bamboo forests fragments under logging activities, generating income for farmers, we suggest encouraging the use of these fast-growing forests, under proper management (see Gómez-Posada chapter 2) to increase suitable habitat for howlers and decrease distances between patches. Enforcing environmental laws and supporting the supervision of logging activities are also important conservation measures in this region.

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Appendix 1. Description of the stepwise multiple logistic regression model of red howler monkeys presence/absence

	Slope	SE	Z	p	likelihood score	p
Step 1					8.750	0.271
intercept	-1.292	3.209				
Fragment size	0.007	0.033	0.040	0.841		
Shape index	-0.297	0.645	0.211	0.646		
Nearest frag	0.036	0.030	1.437	0.231		
prox 100	0.026	0.069	0.147	0.701		
prox 200	-0.242	0.291	0.692	0.405		
prox 400	0.211	0.260	0.657	0.418		
Ficus abundance	-0.367	0.276	1.764	0.184		
Residual deviance	26.295					
Step 2					8.610	0.197
intercept	-0.279	2.784				
Fragment size	0.019	0.030	0.397	0.529		
Shape index	-0.273	0.636	0.184	0.668		
Nearest frag	0.024	0.021	1.310	0.252		
prox 100	-0.009	0.048	0.037	0.847		
prox 200	-0.010	0.036	0.084	0.772		
Ficus abundance	-0.245	0.200	1.492	0.222		
Residual deviance	26.855					
Step 3					8.610	0.126
intercept	-0.074	2.660				
Fragment size	0.018	0.030	0.380	0.538		
Shape index	-0.316	0.622	0.258	0.611		
Nearest frag	0.021	0.018	1.390	0.238		
prox 100	-0.021	0.025	0.743	0.389		
Ficus abundance	-0.237	0.201	1.391	0.238		
Residual deviance	26.505					
Step 4					8.403	0.078
intercept	-0.034	2.646				
Shape index	-0.178	0.573	0.097	0.756		
Nearest frag	0.020	0.018	1.255	0.263		
prox 100	-0.020	0.024	0.729	0.393		
Ficus abundance	-0.251	0.202	1.548	0.213		
Residual deviance	29.920					
Step 5					8.212	0.042
intercept	0.594	1.631				
Nearest frag	-0.020	0.017	-1.157	0.247		
prox 100	0.024	0.021	1.133	0.257		
Ficus abundance	0.230	0.190	1.214	0.225		
Residual deviance	26.769					

Step						6.514	0.039
6	Intercept	1.031	1.509				
	prox 100	-0.017	0.015	-1.128	0.259		
	Nearest frag	0.029	0.023	1.217	0.224		
	Residual deviance	28.707					
Step						4.482	0.034
7	intercept	-0.814	0.567				
	proxi 100	0.047	0.023	0.144	0.0441**		
	Residual deviance	31.504					