

## Habitat Quality of the Woolly Spider Monkey (*Brachyteles hypoxanthus*)

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### Key Words

Ranging ecology · Atelinae, conservation · Tropical forest, structure ·  
Successional functional groups · Protein-to-fibre ratio

### Abstract

This study examines how habitat structure affects the home range use of a group of *Brachyteles hypoxanthus* in the Brigadeiro State Park, Brazil. It has been reported that most of the annual feeding time of woolly spider monkeys is spent eating leaves, but they prefer fruits when available. We hypothesise that the protein-to-fibre ratio (PF; best descriptor of habitat quality for folivorous primates) is a better descriptor of habitat quality and abundance for these primates than the structural attributes of forests (basal area is the best descriptor of habitat quality for frugivorous primates of Africa and Asia). We evaluated plant community structure, successional status, and PF of leaf samples from the dominant tree populations, both within the core and from a non-core area of the home range of our study group. Forest structure was a combination of stem density and basal area of dominant tree populations. The core area had larger trees, a higher forest basal area, and higher stem density than the non-core area. Mean PF did not differ significantly between these sites, although PF was influenced by differences in tree regeneration guilds. Large-bodied monkeys could be favoured by later successional stages of forests because larger trees and denser stems prevent the need for a higher expenditure of energy for locomotion as a consequence of vertical travel when the crowns of trees are disconnected in early successional forests. Forest structure variables

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(such as basal area of trees) driven by succession influence woolly spider monkey abundance in a fashion similar to frugivorous monkeys of Asia and Africa, and could explain marked differences in ranging behaviour and home range use by *B. hypoxanthus*.

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## Introduction

The impact of human activities on forest ecosystems has been extensively mentioned as a major threat to many primate species [Chapman and Peres, 2001]. Several researchers have attempted to develop effective strategies for primate conservation and a number of studies emphasise the importance of forest structure and phytochemistry as key determinants of primate abundance [Chapman et al., 2003; Felton et al., 2003; Wasserman and Chapman, 2003].

The Brazilian Atlantic forest is one of the most disturbed and fragmented tropical forests of the world [Oliveira-Filho and Fontes, 2000]. The woolly spider monkey (*Brachyteles* spp.) is one of two primate genera that are entirely restricted to the Atlantic forest along eastern Brazil. There are two species within the *Brachyteles* genera and both are classified as critically endangered in the IUCN red list [IUCN, 2008]. Although *Brachyteles* had long been considered a primary forest specialist [Aguirre, 1971], most remaining populations currently inhabit secondary forest remnants in patches of different successional status. For example, the Caratinga Biological Station, an 800-ha forest fragment supporting the best studied population of woolly spider monkeys [Strier and Boubli, 2006], is largely comprised of secondary forests, while the remaining primary forest was historically logged to a varying extent [Strier, 1992]. Most *Brachyteles* studies to date have addressed the behavioural ecology and social organization of a few remnant populations [Mendes et al., 2005], with little attention devoted to the importance of forest structure and foliage phytochemistry on the ecology of their range.

It has been hypothesised that community-wide and individual-level plant life history traits, including phytochemical profiles, vary uniformly along successional gradients [Reich et al., 1985]. As a general trend, the trees of a community become increasingly larger in more advanced secondary forest sites even when growth rates are constrained by phylogeny and edaphic conditions [Sheil, 2001; Howorth and Pendry, 2006]. For foliar chemical attributes, the relative amounts of nitrogen and fibre seem to be inversely related, with earlier successional stages characterised by higher levels of foliar nitrogen and fewer structural tissues [Woodwell et al., 1975; Coley, 1983; Bigelow, 1993]. Thus, at the community level, one may expect that the average protein-to-fibre ratio (PF) within leaves will decrease along successional gradients. Such structural and chemical-based leaf attributes may have a strong influence on the ecological distribution and abundance of large herbivores, due to both quantitative and qualitative changes in food resources. These factors may be particularly important to dietary and habitat choices of facultative arboreal folivores, such as woolly spider monkeys.

Given that the process of secondary succession reflects changes in both forest structure and the phytochemical content of leaves, a successional gradient within a forest mosaic provides a suitable system to examine the effects of these traits on the habitat selection of *Brachyteles*. Studies of habitat selection by other vertebrate spe-

cies have shown that more precise information can be obtained by assessing typical differences between alternative habitat types and areas uninhabited by the species [Bright et al., 1994; Austin et al., 1996; Bellamy et al., 1998].

In order to assess the habitat preference of woolly spider monkeys and the more favourable successional stages for these primates, we investigated the ranging ecology of this highly endemic ateline primate species on the basis of forest successional stage, forest structure, and the PF of leaves between intensively and rarely used portions of the home range of a habituated group of *Brachyteles hypoxanthus* in the Brigadeiro State Park (BSP), state of Minas Gerais, Brazil. This park supports a large remaining population of *B. hypoxanthus* [Boubli et al., 2006], and the forest is thus very important for the persistence of this species.

Since the biomass of arboreal folivorous primates in Asia and Africa is positively related to the PF [Chapman et al., 2002], these primates are supposed to prefer and to be positively related to late-successional forests with higher basal areas [O'Driscoll-Worman and Chapman, 2006]. Considering that *B. hypoxanthus* is more folivorous (51% of annual feeding time) than frugivorous (32% of annual feeding time) [Strier, 1991; Strier and Boubli, 2006], one working hypothesis has been that woolly spider monkeys prefer the higher PF of early-successional community leaves than the lower PF of later stages of succession. We also hypothesise that *B. hypoxanthus*, as a predominantly folivorous species [Strier, 1991; Strier and Boubli, 2006], prefers early secondary forests with higher PF levels than late-successional forests with higher basal areas and with less pioneers and initial successional species. Thus, it is proposed that PF is a better descriptor of habitat quality and abundance for these primates than the structural attributes of forests.

## Methods

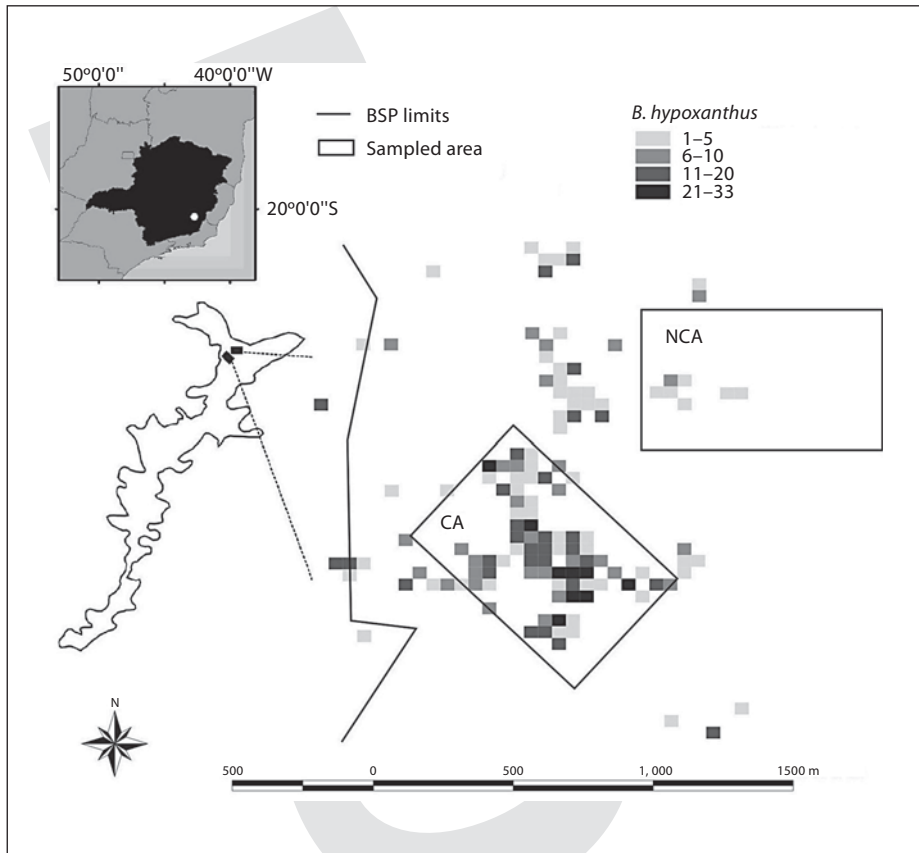
### *Study Site*

This study was carried out in the BSP, state of Minas Gerais, south-eastern Brazil (20°35'S; 42°24'W; fig. 1), one of the last remaining strongholds of *B. hypoxanthus*. The BSP is a 13,210-ha area composed predominantly of seasonal semideciduous forest [Velooso et al., 1991] abutting rock outcroppings along the highest elevations, and croplands and pastures in the surrounding landscape. Currently, the BSP forest matrix consists largely of 40- to 50-year-old patches. Elevation ranges between 880 and 1,985 m ASL and the predominant soil types consist of dystrophic latosols. There are two well-defined seasons, with a dry winter usually extending from April to September. The annual mean rainfall ranges between 1,200 and 1,500 mm, and mean temperature ranges monthly between 14 and 28°C [Gjorup, 1998].

### *Ecology of Brachyteles in the BSP*

The *Brachyteles* data set examined in this study was based on scan sampling employed during the systematic observation of a previously habituated study group of *B. hypoxanthus*, between May 2004 and November 2005. Six parallel transects in the BSP, 1 km in length and 200 m apart, were used. Two observers followed the study group from the onset of group activity early in the morning until the group retired to any given sleeping site late in the day. Continuous dawn-to-dusk group follows were conducted for 5 consecutive days per month. During scan sampling, a number of group structure, behavioural, and positional variables, including the number of individuals sighted and their georeferenced locations, were recorded every 15 min (quarter-hour group scans).

On the basis of the spatial data obtained from scan sampling, a number of forest sites were consistently identified as part of the core home range of the resident *B. hypoxanthus* group,

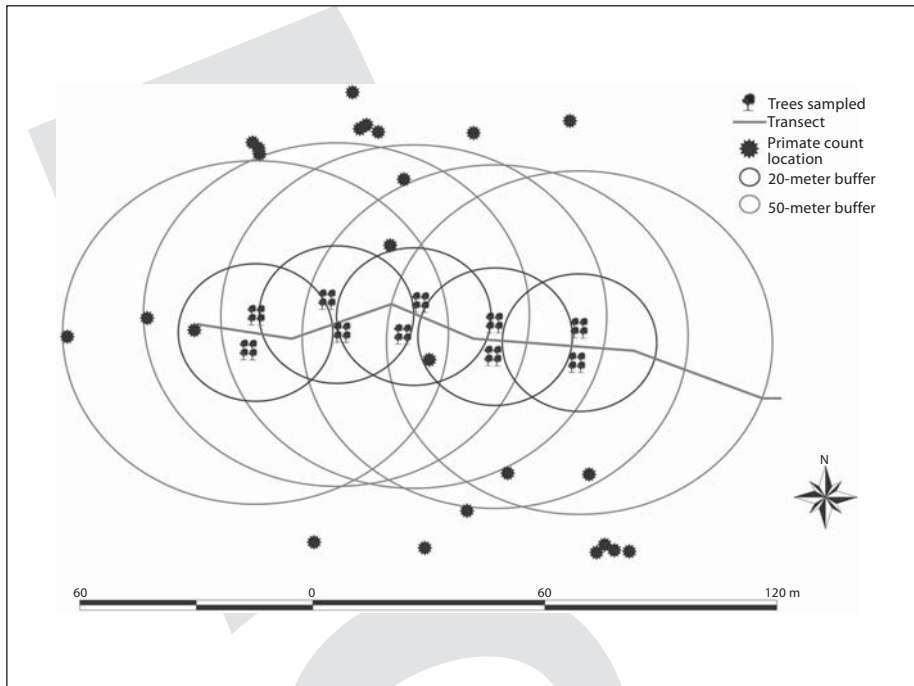


**Fig. 1.** Upper left corner: the BSP location (white dot) in Minas Gerais (black), Brazil, showing the home range use by a group of *B. hypoxanthus*. Squares represent the total number of quarter-hour group locations (see label in the upper right corner) obtained during the study.

whereas another home range area was rarely or never used. These two areas were therefore targeted for detailed habitat sampling and are hereafter denoted as the core area (CA) and non-core area (NCA), respectively (fig. 1). One of the major distinguishing phytophysognomic traits of the NCA was the abundance of bamboo (*Chusquea capitata* Nees) clumps (online suppl. fig. 1 and 2, for all online supplementary material, see [www.karger.com/doi/10.1159/00011159](http://www.karger.com/doi/10.1159/00011159)).

#### *Plant Community Structure and Successional Stage*

The NCA and CA were inventoried between May 2004 and November 2005 by means of the point-centred quarter method [Cottam and Curtis, 1956]. A total of 200 centre points (and 800 trees) were sampled in each area. A single path was used in the CA, across an area with the highest density of the woolly spider monkey group's quarter-hour locations. Centre points were applied on each side of this path, 20 m apart from one another. In the NCA, 2 out of 6 transects that had previously been used during *B. hypoxanthus* population censuses were randomly chosen for the forest inventory (fig. 1, 2). The 4 nearest stems  $\geq 15$  cm in circumference at breast height of each centre point were tagged, identified, and measured (circumference at breast



**Fig. 2.** Spatial configuration of the sampling design employed in this study. Circular buffers with a radius of 20 and 50 m were placed at equidistant segments along each transect, and centred half-way between neighbouring centre points on either side. The location of aggregate group counts are indicated by an asterisk.

height and height), and the distance between each stem and the centre point was also measured [Newton, 2007]. Each area was structurally evaluated using the Simpson diversity index ( $D = 1/C$ ) [Magurran, 2004], and stem density (stems/ha) and basal area ( $m^2/ha$  or  $cm^2/m^2$ ) of all 800 trees were sampled.

Successional stage was analysed by classifying species into successional functional groups (pioneer, early successional and late successional) of each Atlantic forest species according to the literature [Gandolfi et al., 1995; Rolim et al., 1999; Nakazono et al., 2001; Salimon and Negrelle, 2001; Nunes et al., 2003; Ribas et al., 2003; Silva et al., 2003; Oliveira-Filho et al., 2004; Paula et al., 2004; Silva-Junior et al., 2009]. An assessment of the successional stage was based on the number of species present of each functional type, the number of individuals per functional group, and their respective (plant species) contribution to an importance value (IV) [Newton, 2007] in each site:

$$IV = \text{relative abundance} + \text{relative frequency} + \text{relative basal area} \quad (1)$$

where 'relative abundance' is the ratio of the number of individuals of the species to the total number of individuals of the sample; 'relative frequency' is the ratio of the number of sampling units where the species is present to the total number of sampling units, and 'relative basal area' is the ratio of the sum of the basal area for the species to the total basal area of the sample. The IV is one of the most principal parameters used to rank the dominance of plant populations in community ecology [Newton, 2007].

### Phytochemical Profiles

We follow Kappelle and Leal [1996] and define the phytochemical profile of each site as the PF of leaves from only those species comprising more than 80% of the IV [Newton, 2007] between April 2004 to November 2005. A combination of an equal proportion of young and mature leaves was taken (approx. 50 g) from the upper layer of tree crowns sampled by the point-centred quarter method in 3 different individuals of each species in each site. Thus, 333 samples of leaves were collected, each from one different tree. When a species had fewer than 3 individuals in our 400 centre-point samples, leaves were randomly taken from individuals of the same species found immediately adjacent to the site to complete the leaf samples.

Once collected, fresh leaf samples were placed into paper bags and air-dried for 2 days at 28°C until they had no changes in weight. Desiccated samples were then taken to the Animal Nutrition Laboratory, Animal Science Department, University of Viçosa and chemical analysis was conducted within the following 2 days. We defined the PF content of dried and milled samples as the ratio between the crude protein and neutral detergent fibre, in terms of the dry matter weight of each sample. Crude protein was assessed using the Kjeldahl procedure [Windham, 1995] in the same laboratory using copper sulphate as catalyst and using a 1-mm grinder for total nitrogen, multiplied by 6.25 [Chapman et al., 2003]. Neutral detergent fibre values were calculated following the methods proposed by Van Soest et al. [1991].

### Data Analyses

In November 2005, the last month of this study, the *B. hypoxanthus* group studied had 42 monkeys: 9 adult males, 13 adult females, 1 subadult male, 4 subadult females, 2 juvenile males, 6 juvenile females, and 7 infants [Moreira, 2008]. To correlate the spatiotemporal use of the home range by woolly spider monkeys with vegetation variables, all georeferenced primate group locations were layered onto a digital map at the same spatial scale. Because each quarter-hour group location [Altman, 1974] was associated with a group count (here defined as the total number of adults and independent juveniles observed in the group), group locations were expressed in terms of the total party size. Using GIS (Arcview), a total of 100 circular buffers of two sizes (20 and 50 m in radius) were then overlaid along forest paths and centred half-way between any pair of centre points sampled (fig. 2). An aggregate group size (AGS), defined as the total number of group locations considering the party size of each location, was then computed for each circular buffer. Group locations recorded within more than one buffer were considered for each overlapping buffer. The stem density and basal area were calculated for each buffer based on the trees in centre points. The PF values per buffer were represented by the sum of the PF of species for each tree sampled by the set of points in the buffer. We then calculated the ratio of the sum for the buffer to the number of sampled trees.

All statistical analyses were performed using the R statistical environment [R Development Core Team, 2007]. We examined between-site differences in stem density, basal area, foliar PF content, and tree guild composition using ANOVAs followed by F tests ( $p > 0.05$ ). Successional status was assessed by comparing the number of species and individuals of each tree guild between sites using  $\chi^2$  tests. To investigate the relationship between the use of space by *Brachyteles* and the structural and phytochemical characteristics of the forest sites, multiple regressions were performed in which the AGS was entered as a response variable and stem density, basal area, and mean PF per buffer as explanatory variables. These analyses were carried out using generalised linear modelling with a Poisson error structure and a log link, followed by residual analyses to verify the error distribution and model suitability, including checks for overdispersion [Crawley, 2007]. Full models were built by including explanatory variables and their interactions, according to term complexity, starting from the simplest one. Model simplification was achieved by extracting non-significant terms ( $p > 0.05$ ) from the model according to their respective complexity, starting from the most complex. When two non-significant terms represented the same complexity, the one explaining the least amount of variance was extracted first. Each term deletion was followed by an ANOVA and F test to recalculate the variance explained by the remaining terms.

**Table 1.** Summary of forest structure and composition, and foliar PFs (mean  $\pm$  SD) in the CA and NCA sampled within the BSP

Variables	CA	NCA	Test	p
Tree species diversity (D)	43.48	25.0	–	–
Tree species, n	106	121	$\chi^2 = 0.99$	0.32
Tree families, n	38	39	$\chi^2 = 0.013$	0.091
Tree density, ind./ha	3,714.8 $\pm$ 1,849.64***	1,559 $\pm$ 1,147.7	F = 98.08	<0.001
Basal area, m <sup>2</sup> /ha	9.37 $\pm$ 14.55***	2.80 $\pm$ 2.46	F = 19.83	<0.001
PF	0.27 $\pm$ 0.09	0.28 $\pm$ 0.10	F = 1.69	0.2

\*\*\* p < 0.001.

## Results

### *Plant Community Structure and Successional Stage*

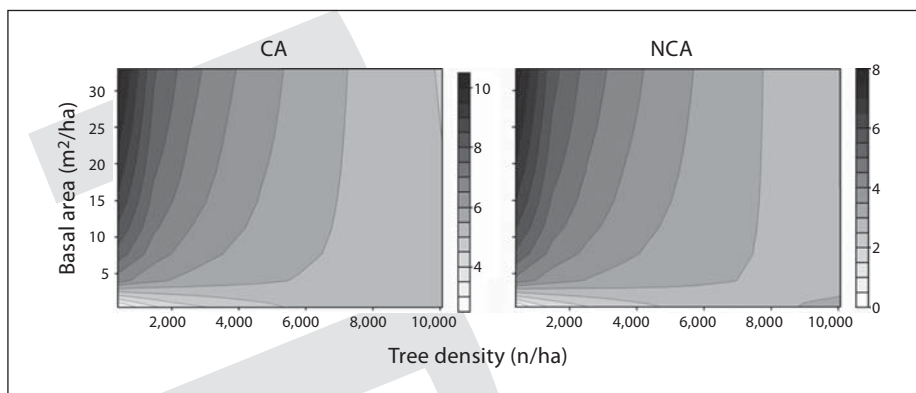
Variables describing the forest structure in the CA and NCA of the study group are summarised in table 1. The CA was more diverse than the NCA, as expressed by the Simpson diversity index ( $D_{ca} = 43.48$  and  $D_{nca} = 25.0$ ), despite richness not being significantly different between both forests. Both the stem density and basal area were significantly greater in the CA ( $F_{1, 198} = 98.08$ ,  $p < 0.001$ ,  $F_{1, 198} = 19.83$ ,  $p < 0.001$ , respectively; table 1). Although not quantified, bamboo (*C. capitata* Nees) clumps were present in both areas. They were smaller and less frequent in the CA (author's observation). Conversely, the NCA understory was almost entirely dominated by large clumps of bamboo (online suppl. fig. 1 and 2).

The CA was more advanced in terms of secondary succession than the NCA. Considering the number of tree species per guild, both areas were equally represented, although the overall tree abundance in each guild differed (table 2). There were significantly fewer individuals from pioneer ( $\chi^2 = 0.194$ , 2 d.f.,  $p < 0.001$ ) and early-successional functional groups in the CA ( $\chi^2 = 5.56$ , 2 d.f.,  $p < 0.05$ ), whereas late-successional trees were more abundant in the CA ( $\chi^2 = 70.04$ , 2 d.f.,  $p < 0.001$ ).

### *Leaf Fibre and Protein Profiles*

A total of 54 and 56 tree species were sampled in the NCA and CA, respectively, but no significant differences could be detected between areas (table 2) or species. For example, *Clusia arrudea* (Clusiaceae) and *Sapium glandulatum* (Euphorbiaceae) had the lowest (8.31% of crude protein : 63.77% of fibre = 0.131 PF) and highest (20.18% of crude protein : 34.71% of fibre = 0.581 PF) PFs, respectively. While *C. arrudea* occurred exclusively in the NCA, *S. glandulatum* occurred in both areas. However, PFs of *S. glandulatum* were similar, regardless of where they were sampled (online suppl. table 1 and 2).

PFs differed among regeneration guilds ( $F_{2, 155} = 5.96$ ,  $p < 0.01$ ) only in the NCA, where late-successional species had the lowest mean PF (14.57% of crude protein : 66.07% of fibre = 0.220 PF), whereas early-successional species (16.26% of crude protein : 60.11% of fibre = 0.270 PF) and pioneers (18.33% of crude protein : 66.04% of fibre = 0.277 PF) had higher values. The proportions were similar but not significant



**Fig. 3.** Effects of basal area and tree density on patterns of home range use by *B. hypoxanthus* at the CA and NCA. The grey scales on the right of each respective graph represent the AGS (log<sub>e</sub> AGS) of quite different values, with darker areas representing more frequent group locations and larger group sizes.

**Table 2.** Total tree abundance, species richness, and relative contribution to the IV (%) of 3 regeneration guilds for each study area (n = 800)

	CA				NCA			
	P	ES	LS	UNC	P	ES	LS	UNC
Individuals, n	39	430	274***	57	155***	502*	110	33
Species, n	11 (n.s.)	45 (n.s.)	34 (n.s.)	16 (n.s.)	18 (n.s.)	61 (n.s.)	22 (n.s.)	20 (n.s.)
IVI, %	6.35	52.2	33.23	8.22	20.48	60.15	12.55	6.82

P = Pioneer; ES = early-successional; LS = late-successional; UNC = poorly known species that could not be classified; IVI = IV index (see text); n.s. = non-significant.

\* p < 0.05; \*\*\* p < 0.001; n.s. = non-significant.

in the CA. There, late-successional species had a lower mean PF (14.17% of crude protein : 62.56% of fibre = 0.226 PF), whereas early-successional species (15.76% of crude protein : 62.04% of fibre = 0.273 PF) and pioneers (18.29% of crude protein : 66.03% of fibre = 0.276 PF) had higher ratios.

#### *Habitat Effects on Brachyteles Home Range Use*

All models describing the effects of plant community variables (forest structure, composition, and phytochemical profile) on the AGS of *B. hypoxanthus* converged into one, in which forest basal area was a significant explanatory variable ( $\chi^2 = 2.805$ ,  $p < 0.01$ ). In addition, there was a significant interaction between basal area and stem density ( $\chi^2 = 2.420$ ,  $p < 0.05$ ). In other words, the ranging ecology of *B. hypoxanthus* in the BSP was clearly associated with large trees and stem density (fig. 3).

## Discussion

### *Primate Persistence in Regenerating Secondary Forests*

Tropical deforestation is widely considered to be the greatest threat to tropical forest vertebrates [Laurance and Peres, 2006]. The wholesale historical conversion of the Brazilian Atlantic forest such that only approx. 7% of its original extent remains [Dean, 1996] has greatly reduced the geographic range size of many endemic vertebrates, including both extant species of *Brachyteles*. It is estimated that the geographic range of *B. hypoxanthus* has contracted to less than 5% of its original pre-Columbian extent (300,000 km<sup>2</sup>) [Aguirre, 1971]. It has been proposed that the regeneration of secondary forest in degraded tropical landscapes may provide a key opportunity to rescue many primary forest species that would otherwise be confined to isolated native forest fragments [Wright and Muller-Landau, 2006]. The domination of forest areas by bamboo has a strong influence on the ranging ecology of *B. hypoxanthus*. Bamboo does not provide a nutritious food resource for this species, and the unchecked proliferation of bamboo through reproductive or vegetative propagation can inhibit or suppress the regeneration process. A similar phenomenon may also be true for the Rio Doce State Park, a neighbouring reserve in the State of Minas Gerais that also safeguards a potentially significant population of *B. hypoxanthus*. Recurrent historical fires in Rio Doce have generated a complex forest mosaic in which *Senefeldera multiflora* Mart. (Euphorbiaceae) has become hyperabundant at specific sites [Silva-Junior et al., 2009]. This tree species has never been observed to serve as a food resource for *B. hypoxanthus* [L.G. Dias, pers. commun.] and that study site supports a low population density of *B. hypoxanthus* [Biodiversitas, 2006].

### *Forest Structure and Plant Community Habitat Traits*

Our results show structural differences between both forest communities in the BSP, despite the relative proximity of the sampling sites (<1 km). In the NCA, trees in the area least used by *Brachyteles* were mainly of smaller size classes and were thinly spread among dense bamboo (*C. capitata* Nees) clumps.

Bamboo species are natural components of tropical and subtropical forests [Martins et al., 2004]. Following canopy disturbance, their architectural plasticity and clonal propagation make them efficient colonisers; they rapidly expand to occupy new sites, persist for prolonged periods and compete with other woody species for resources (e.g. light and space), eventually suppressing natural regeneration [Martins et al., 2004; Wang et al., 2006]. Decreases in basal area and stem density promoted by bamboo interference have been observed in both temperate and tropical forests of China [Wang et al., 2006; Taylor and Qin, 1989], Japan [Nakashizuka and Numata, 1982], South-Central Chile [Veblen, 1982], and the Peruvian Amazon [Griscom and Ashton, 2003]. The bamboo interference could have a negative effect on the conservation of woolly spider monkeys, but this has not been confirmed. The episodic mortality of entire populations of bamboo after reproductive periods provides a timely opportunity for growth and establishment of fast-growing and shade-intolerant species, explaining the higher abundance of these guilds in other Atlantic forest sites in Brazil [Tabarelli and Mantovani, 1999; Martins et al., 2004].

The regeneration processes are quite different between the CA and NCA. Our results suggest that a more shaded environment underneath the canopy of the CA was the prevailing force in promoting the recruitment of late-successional species,

while preventing pioneer regeneration. In contrast, the more open canopy in the NCA, generated by a developing bamboo stand, has enabled the establishment of pioneers. However, the effects of shade and physical damage from fallen culms of bamboo are potentially important factors positively affecting the recruitment and negatively affecting growth of large trees, which this study shows are the most important habitat feature for woolly spider monkeys. Early-successional species are probably well established in both secondary forest areas, due to their partial tolerance to shade, rapid growth, and ability to compete with younger bamboo stands. Regardless of the factors driving forest dynamics in each area, we conclude that secondary succession is arrested in the NCA in a fashion similar to that proposed by Griscom and Ashton [2003].

In light of our results, we emphasise the importance of monitoring the course of secondary succession as an additional tool in habitat management programmes designed for critically endangered species. In particular, as a short-term management option we recommend studies regarding the control of large clumps of bamboos in the BSP as a method for appropriate forest management that can facilitate forest regeneration, increase basal area and augment the suitable habitat area available for *B. hypoxanthus*.

#### *Brachyteles Ranging Ecology in Relation to Habitat Features*

Basal area and tree density explained a significant proportion of the variance in the home range use of *B. hypoxanthus*. Accordingly, the habitat quality of the CA apparently favours the energy budget of *B. hypoxanthus* in two ways. First, large tropical trees generally produce large fruit patches [Chapman et al., 1992] that serve as more reliable food sources for larger group sizes [Felton et al., 2003]. As reported by Strier and Boubli [2006], woolly spider monkeys prefer fruits to other food items, despite the larger portion of leaves in their annual diet. Other studies have already shown that foraging parties of *B. hypoxanthus* prefer large food patches [Milton, 1984; Strier, 1987b, 1989]. Second, high physical connectivity between tree crowns enables more efficient locomotion and provides more efficient access to food sources (online suppl. fig. 3); a discontinuous canopy may require more energy expenditure during travel. Because of its large body mass, vertical travel is assumed to be very costly for *B. hypoxanthus* [Milton, 1984] and the energetic costs of locomotion may be an additional constraint faced by large-bodied arboreal primates regardless of dietary choices. On the other hand, woolly spider monkey abundance was related to forest basal area, similar to arboreal frugivorous primates of Asia and Africa [O'Driscoll-Worman and Chapman, 2006]. This is another indicator of preferential frugivory in *B. hypoxanthus*, besides the 32% of annual feeding time of the species on fruits [Strier, 1991; Strier and Boubli, 2006].

#### *Foliar Protein and Fibre Content*

Contrary to our initial prediction, the foliage PF was similar for CA and NCA phytocoenoses (table 1). Thus, our hypothesis that the PF is a better descriptor than structural parameters for habitat quality of *B. hypoxanthus* failed.

Foliar nutrient concentrations can be controlled by a single or multiple interacting factors [Mattson, 1980; Bazzaz, 1996]. Species-rich tropical forests are complex and dynamic ecosystems in which different tree populations, or even the same stem, can experience variable levels of resource availability both above and below ground,

as well as biotic pressures exerted by neighbours, parasites, or herbivores [Mattson, 1980]. Consequently, foliar nutrient concentration and digestibility are also expected to vary among individuals, species, and forest types. For example, Chapman et al. [2003] reported a marked variation in nutrient content, both within and between seasons, within and among species, and between different sites in an Afrotropical forest. Light availability, soil composition, tree phenology, and local microbial activity were all attributed as possible causes of this variation.

Although foliar traits are linked to the availability of key resources (e.g. soil nutrients and light) in a given time along the successional process, such traits are coupled more with the regeneration niche of a given species [Reich et al., 1995]. Pioneers and early-secondary species could therefore take advantage of a more open early-successional canopy, particularly after disturbance events that are usually followed by abrupt changes in light and nitrogen availability [Dominy et al., 2003]. Under these conditions, early regeneration guilds of plants can take advantage of their fast growth rates, high investment in leaf and root biomass production, short leaf life span, and light foliar tissues. These foliar characteristics related to succession have an direct influence on woolly spider monkey habitat quality. These intrinsic traits may allow early-successional species to supply leaves with nutrients, while inhibiting foliar structural tissues and synthesis of quantitative defences (e.g. tannins, phenols, and fibres). The reverse situation may be found in late-successional species [Coley, 1983; Reich et al., 1995; Bazzaz, 1996; Kull and Niinemets, 1998; Guariguata and Ostertag, 2001; Navas et al., 2003]. However, these correlations between plant traits, foliar protein, and fibre content are only consistent with our findings in the NCA, where the PFs of pioneer and early-successional species were statistically greater than those of late-successional species. In the NCA, late-successional species were often represented by smaller-crowned understory trees, where the shaded environment is more closely related to their regeneration niche [Reich et al., 1995].

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