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PATTERNS OF HABITAT USE BY PRIMATES IN EASTERN ECUADOR

by

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ABSTRACT

Lowland tropical rain forests of western Amazonia are characterized by the most speciose primate communities in the Neotropics, immediately leading to the question of to what extent does niche partitioning by primate species serve as a mechanism to promote species co-existence. Because the primate assemblages that we observe today reflect a combination of ecological and evolutionary processes, this study examines habitat occupancy and its relationship to phylogeny and space in a diverse diurnal primate community in an undisturbed lowland rain forest of Amazonian Ecuador. Specifically, the following null hypotheses are explored as potential factors that shape community structure: (1) mean height in the forest strata does not differ among species; (2) species occupy habitat types at frequencies proportional to their overall availability; (3) species do not segregate in ecological space; (4) there is no relationship between phylogenetic distance and ecological distance among species; and (5) there is no relationship between ecological distance and geographic distance among species.

.   The results of this study reveal that ecological differences among the species in this primate community facilitate their coexistence. Larger species generally occupied higher strata than smaller ones. Furthermore, although they generally tended to occupy habitat types at frequencies proportional to their availability in the study area, species segregated in ecological space defined by dissimilarity in habitat occupancy. Finally, in this community, a clear relationship was not observed between phylogenetic and ecological distances or ecological and geographic distances. This study elucidates the spatial distribution and the habitat partitioning of the diurnal primate community at the Tiputini Biodiversity Station in Ecuadorian Amazonia.

ACKNOWLEDGMENTS

INTRODUCTION

Coexistence of species in time and space, as well as the processes involved in maintaining specific community assemblages, are central questions in community ecology. Coexistence and community assemblage processes are particularly interesting when examined in areas of high species diversity, such as the lowland tropical rain forests of western Amazonia, which can contain over 200 tree species in a single hectare (Pitman et al. 2002) and are characterized by the most species-rich primate communities in the Neotropics (Peres & Janson 1999). Despite their high species richness in certain regions, Neotropical primate communities have generally been described as exhibiting a "relatively low adaptive diversity" when compared to their African and Asian counterparts (Fleagle & Reed 1996). Early platyrrhines (New World monkeys) first appear in the South American fossil record around 26 million years ago (MacFadden 1990) and have since undergone explosive adaptive radiations over a relatively short period of time (Fleagle & Reed 1999). Although platyrrhine communities, unlike those of Asia and Africa, tend to consist primarily of small-bodied, arboreal frugivore-insectivores, with no terrestrial and very few folivorous or nocturnal species (Fleagle & Reed 1996, Reed & Bidner 2004, Terborgh & van Schaik 1987), up to 14 species of primates have been observed in a single one-km^2 plot (Peres 1988, Peres 1993). This tremendous diversity in primates immediately leads to questions of what environmental and biogeographic factors shape such communities and to what extent does niche partitioning by primate species serve as a mechanism to promote species co-existence.

Given that platyrrhine species are relatively similar in their dietary, activity, and arboreal patterns, it is possible that interspecific differences in phylogeny, microhabitat

use and spatio-temporal factors can potentially help explain species coexistence, particularly at local scales. Studies of primate communities suggest differentiation among co-occurring species along at least one dimension of the ecological niche, and emphasize evolutionary history, partitioning of resources such as food and habitat, interspecific competition, and food availability as important factors that influence community structure (Bourliére 1985, Reed & Bidner 2004, Stevenson et al. 2000, Terborgh 1983). To elucidate patterns of species coexistence, many studies have investigated both differences in habitat use among Neotropical primate species, as well as influences of different habitat parameters on the species distribution patterns (Bobadilla & Ferrari 2000, Buchanan-Smith et al. 2000, Haugaasen & Peres 2005, Heymann et al. 2002, Lehman 2000, Lehman 2004, Mittermeier & van Roosmalen 1981, Peres 1988, Peres 1993, Peres 1997, Pontes 1997, Pontes 1999, Pozo 2004, Soini 1986, Stevenson & Quiñones 1993, Stevenson et al. 2000, Terborgh 1983, Wallace et al. 1998, Warner 2002, Yoneda 1988, Youlatos 1999, Youlatos 2004). For example, when Sorensen and Fedigan (2000) examined the impact of a forest regeneration gradient on the distribution and densities of capuchins (*Cebus capucinus*), howler monkeys (*Alouatta palliata*), and spider monkeys (*Ateles geoffroyi*) in a tropical dry forest, they found that densities of all three species were highest in the oldest regenerating forest. Another study of habitat preferences of primate species at two sites in Bolivia found that whereas capuchins (*Cebus apella*) showed no habitat preferences among five different forest types and also used all levels of forest strata, spider monkeys (*Ateles paniscus chamek*) preferred upper strata of tall forests. Moreover, the marmoset species (*Callithrix argentata melanura*) preferred vine forest, and two species of howler monkeys (*Alouatta caraya* and *A.*

seniculus) were restricted to a flooded forest, thereby stressing the relationship between habitat partitioning and species coexistence (Wallace et al. 1998).

The potential importance of niche partitioning has also been highlighted in primate communities in Amazonian Ecuador, where species have shown different preferences for food, vegetation types, and forest strata (Pozo 2004, Youlatos 2004). The work of Youlatos (1999) on six sympatric primates (excluding Atelidae) in Ecuadorian Amazonia linked physical characteristics such as anatomy and size to selection of forest strata, finding that smaller species generally utilized lower strata while larger ones used upper layers of the forest. Furthermore, in a subsequent examination of the relationship between habitat (e.g. forest type, forest layer, and support size) and organismal (e.g. body mass, diet, and locomotor mode) parameters in primate communities (including Atelidae) in Ecuador and French Guiana, Youlatos (2004) concluded that *Alouatta*, *Ateles*, *Lagothrix*, and *Pithecia* were associated with canopy, mature forest, frugivory, and climb/suspensory locomotion. Similarly, Pozo (2004) found that six sympatric primates (excluding Atelidae) primarily used high forests on ridges, but in frequencies disproportional to available habitat.

While the primate assemblages that we observe today reflect a combination of ecological and evolutionary processes, these processes are often considered independently; thus, an approach that incorporates available data from published molecular phylogenies is crucial to the understanding of species coexistence in primate communities (Fleagle & Reed 1999, Webb et al. 2002). When examining species coexistence in a given community as a function of evolutionary history (phylogeny) and present-day ecological factors, one can envision three possible scenarios. First, if niches

are conserved within evolutionary lineages, we should observe a positive relationship between phylogenetic distance and ecological distance ("phylogenetic niche conservatism;" Harvey & Pagel 1991, Lord et al. 1995). Alternatively, if natural selection promotes ecological differentiation to avoid competitive exclusion among closely related species, we would expect a negative relationship between phylogenetic distance and ecological distance (Hardin 1960, Losos et al. 2003, Silvertown et al. 2001). Finally, if species are randomly dispersed in ecological space, no relationship would be detected between phylogenetic distance and ecological distance (Davis 2005, Losos et al. 2003, Rice et al. 2003, Silvertown et al. 2006).

In addition to differentiation in ecological space, co-occuring species may also segregate in geographic space. Thus, it is worthwhile to assess the relationship between interspecific ecological and geographic distances within communities. If interspecific competition is important in shaping community structure, we expect that as ecological distance decreases, geographic distance increases, such that species with highly overlapping ecological niches should have low spatial overlap (Hofer et al. 2004). On the other hand, if we observe a positive relationship between ecological distance and geographic distance, there may be a situation in which ecologically similar species overlap in space because they share resources, suggesting that competitive exclusion will eventually occur (Hofer et al. 2004). Finally, if we fail to detect a relationship between ecological distance and geographic distance within a community, there may be other mechanisms of coexistence that need to be further examined.

In this study, habitat occupancy and its relationship to phylogeny and space are evaluated in a diverse diurnal primate community in an undisturbed lowland rain forest of

Amazonian Ecuador. Specifically, the following null hypotheses are explored as potential

factors that shape community structure: (1) mean height in forest strata does not differ

among species; (2) within each species, habitat occupancy is proportional to habitat

availability; (3) species do not segregate in ecological space defined by dissimilarity in

habitat occupancy; (4) there is no relationship between phylogenetic distance and

ecological distance among species; and (5) there is no relationship between ecological

distance and geographic distance among species.

METHODS

Study site

This study was conducted at Tiputini Biodiversity Station (TBS) in the Orellana

Province of eastern Ecuador (~0° 38' S, 76° 08' W). Established in 1994 by the

Universidad San Francisco de Quito, the station comprises a 650-hectare tract of

undisturbed lowland Amazonian rain forest located within the 1.5 million hectare Yasuní

Biosphere Reserve, one of the most biologically diverse places on Earth (Karubian et al.

2005). Bordered to the south by the Tiputini River, a tributary of the Napo River, TBS

encompasses various habitats, including terra firme (unflooded) and várzea (periodically

flooded) forests, palm swamps and other wetlands, and areas in different stages of natural

regrowth, hereafter called second-growth. Mean annual rainfall at TBS is 2740 mm with

a drier period between October and February (J. Guerra, unpubl. data from 1998 to 2002,

in Karubian et al. 2005), and mean temperature is 25° C (Kreft et al. 2004). Elevation

ranges from approximately 200 to 235 m above sea level (Loiselle et al., in press). The

station includes over 30 kilometers of well-marked trails (Universidad San Francisco de

Quito 2003) as well as two 100-ha gridded plots (~1 km x 1 km each with 100 x 200 m

grid lines) established in 2001 by J.G. Blake and B.A. Loiselle (Figure 1). The Harpia

and Puma plots, each containing 16 km of transects, are largely in terra firme forest,

although some portions of each are in flooded hardwood and flooded palm swamp

forests. The Harpia plot, ranging from 201 to 233 m elevation, contains upland forest

with relatively heterogeneous topography, while the Puma plot, ranging from 209 to 235

m elevation, is flatter and dissected by more streams, thereby including more periodically

flooded forest than Harpia (Loiselle et al., in press). GIS databases for grid markers

(every 50 m on each transect), streams, slope, aspect, and elevation have been compiled

for these plots by J.G. Blake and B.A. Loiselle (see Loiselle et al., in press for further

descriptions of plots).

Study species

Of the fifteen total primate species that inhabit Ecuadorian Amazonia, at least ten

have been documented at TBS, making it one of the most species-rich sites for primates

globally (Marsh 2004). Based on Schneider et al. (2001, Figure 2), these species belong

to three monophyletic families: *Cebidae* (marmosets, tamarins, capuchins, and squirrel

and owl monkeys), *Pitheciidae* (titi monkeys, sakis, and uakaris), and *Atelidae* (muriquis

and howler, spider, and woolly monkeys). The species included in this study were

golden-mantled tamarins (*Saguinus tripartitus*), common squirrel monkeys (*Saimiri

sciureus*), white-fronted capuchins (*Cebus albifrons*), sakis (*Pithecia* sp.), dusky titi

monkeys (*Callicebus discolor*, van Roosmalen et al. 2002), lowland woolly monkeys

(*Lagothrix poeppigii*; Fooden 1963, Di Fiore 1997), white-bellied spider monkeys (*Ateles

belzebuth*), and red howler monkeys (*Alouatta seniculus*). The owl monkey (*Aotus

vociferans*), because it is nocturnal, and the pygmy marmoset (*Callithrix pygmaea*),

which has not been documented in the study plots, were not examined. Because each of the eight species in this study belongs to a unique genus, each study species will hereafter be referred to by genus.

Data collection

Primate censuses, generally following methods outlined by Peres (1999), were conducted by two independent observers (the author and a trained field assistant) from December 2004 through March 2005. In each 100-ha plot, 10 one-kilometer transects that are 100 m apart were used for censuses by alternating daily between the five even-numbered and the five odd-numbered transects. Thus, on a given census day, each observer surveyed a different plot by walking five one-kilometer transect lines (200 m apart) on one-meter wide foot trails at a pace of 1-1.25 km per hour. During census walks, observers stopped for a few seconds periodically to look and listen for primate activity. Two or three of the five transects were censused each morning from 0600-0630 h to 1000-1030 h, and each afternoon the remaining transects were walked from 1400-1430 h to 1700-1730 h. In addition, transects were visited in a systematic order to ensure that each morning and afternoon censuses began and ended at different locations within each plot as well as to prevent a single transect from being censused more than once in a three day period. To avoid potential biases in detectability, censuses were terminated during heavy rain and were paused during brief periods of rain. A full census of the Harpia and Puma plots was repeated 15 times, yielding a cumulative transect distance of 300 km. Although primate censuses were primarily conducted within these plots, the entire trail system of TBS was regularly surveyed to obtain data from periodically

flooded forest habitat (which is not represented in the plots) as well as to assess the

distribution of primate species throughout the TBS area.

For each encounter with primates, the following standard information

(Brockelman & Ali 1987, Mittermeier & van Roosmalen 1981, Peres 1999) was

recorded: date, time, weather, detection type (visual or aural), location with respect to

transect marker, distance between observer and first-sighted individual, perpendicular

distance from first-sighted individual to trail, primate species, minimum number of

individuals in group, sex and age class of each individual (when possible), general

activity, direction of movement, vertical position of individual in forest strata (i.e. height

where first-sighted individual was observed), height of the canopy, and characteristics of

surrounding habitat (e.g., canopy height, liana density, palm density, proximity to stream,

relief, and canopy density). Subsequent to inter-observer standardization of distance

estimates using a laser rangefinder, each observer either estimated distances by sight or

measured them directly with a rangefinder. To maximize sampling effort, an encountered

group of primates was generally tracked for no longer than 15 minutes.

Habitat characterization and habitat occupancy by primates

To quantify the relative availability of habitats on the Harpia and Puma plots, I

used detailed habitat descriptions from J.G. Blake to construct a habitat map of each plot

in ArcGIS 9. Within each plot, habitat was classified into one of six categories (Table 1)

at each transect marker (every 50 m) along the ten one-kilometer transects included in the

primate censuses (Figure 3). The habitat type characterizing a given transect marker was

considered to be the dominant habitat type within a 25 m radius of that point, thereby

comprising a circular habitat subplot. The location of each primate sighting was mapped

in ArcGIS 9 and subsequently assigned to the habitat type of its nearest transect marker.

The habitat types assigned to any primate sightings located farther than 25 m from a

transect marker were then verified against field notes taken on the surrounding habitat.

Finally, for each primate species, I assessed the habitat occupancy of the area around

each transect marker by simply scoring the species' presence as one and the species'

absence as zero and summing up the number of subplots of each habitat type occupied

per species. Thus, if a species was observed multiple times within a given habitat subplot,

it still received a score of one.

Analyses

While the other analyses in this study are based solely on census data from the

two study plots, the determination of differences in mean height among species using a

Welch ANOVA for unequal variances (JMP v. 5.1.2, 2004) also includes census data

from trails. The relationship between mean height and mean body mass (from Smith &

Jungers 1997) across species was explored with a Spearman's rank correlation test (JMP

v. 5.1.2, 2004). To assess whether each species occupied habitat types disproportionately

to their availability, I conducted log-likelihood ratio goodness-of-fit (G) tests (Zar 1999)

in which the observed frequencies were the number of subplots of each habitat type a

given species occupied in the Harpia and Puma plots combined, and the expected

frequencies were based on the proportional availability of habitat types in the two plots.

Nonmetric multidimensional scaling (NMS, PC-ORD v. 4.01, McCune & Mefford 1999),

a type of ordination that depicts the relationships among community members using

ranked distances between samples (Clarke 1993), was used to examine the position of

species in ecological space, defined by the interspecific dissimilarities in habitat

occupancy. Nonmetric multidimensional scaling (Kruskal 1964, Mather 1976), an

iterative optimization procedure, found the best positions of the species along k axes such

that stress (a measure of how much distance in the original space deviates from distance

in the reduced ordination space) was minimized (McCune & Grace 2002). Subsequently,

a Monte Carlo test was implemented to determine whether the structure in the species

matrix (in terms of habitat occupancy) was stronger than expected by chance (McCune &

Grace 2002). Thus, the initial dataset was a species-by-habitat matrix (same as the

species-habitat matrix shown in Table 2) of habitat occupancy in which rows were

species and columns were habitat types (based on Table 1). From this initial matrix,

which was first relativized by column (habitat) totals to reduce effects of unequal habitat

availability, I constructed a species dissimilarity matrix using the Sorensen distance index

to conduct the NMS using a random starting configuration and performing 40 runs with

the real data, thus yielding an ordination of species in ecological (habitat) space.

To examine the relationship between phylogenetic and ecological distance, I

calculated the pairwise genetic distance between genera using a molecular phylogeny of

platyrrhine genera with branch lengths estimated by maximum likelihood (Schneider et

al. 2001, Figure 2) and created a species matrix of genetic distance. I subsequently

implemented a Mantel test (PC-ORD v. 4.01, McCune & Mefford 1999) with a

randomization (Monte Carlo test) method to compare the genetic distance matrix to the

ecological dissimilarity matrix used in the species ordination. Finally, to obtain a matrix

of geographic distance between species pairs, I calculated the mean nearest-neighbor

distance between each pair of species across the two plots in ArcGIS 9. Specifically,

within each plot, I computed the mean minimum distance between the mapped

observations of each pair of species by peforming bi-directional spatial joins between the observations of each of the 28 species pairs. Again, a Mantel test was used to compare the resulting geographic distance matrix to the matrix of ecological distance defined by dissimilarity in habitat use. In addition, using all observations throughout the study period (opportunistic and census data from trails and plots,) I tallied the number of times each pair of species was observed to overlap spatially and temporally (i.e. cases in which both species were visible to the observer at a given time). Because primates were not followed, data on the specific nature of the spatio-temporal overlap between species pairs are not available.

RESULTS

During the 15 censuses of the study plots, all eight species of primates were encountered on both plots, 93 times on Harpia and 103 times on Puma (Figure 4). On Harpia, *Lagothrix* was seen most (25 times), and *Callicebu*s and *Ateles* were the least sighted species (six times each). *Saguinus* was the most commonly observed species on Puma (28 times), while *Pithecia* was the least detected species (five times). Overall, *Lagothrix*, *Saguinus*, and *Cebus* were encountered the most, and *Pithecia* was the least encountered species.

Habitat characterization

Harpia plot is dominated by mature and mixed upland forest habitats, while Puma plot primarily contains second growth and mixed upland forest (Figures 3, 5). Puma plot, due to the presence of *Mauritia* palm swamp and palm hardwood swamp, has more habitat types than Harpia. Overall, mixed upland forest is the most abundant habitat type across both plots.

Height in forest strata

Alouatta, *Ateles*, *Lagothrix* and *Pithecia* occurred at significantly higher strata in

the forest than *Callicebus*, *Cebus*, *Saguinus* and *Saimiri* (Welch ANOVA: $F_{7, 111.9} =$

70.77, $P < 0.001$; Tukey test: $P = 0.05$, Figure 6). Mean body mass and mean height were

positively correlated ($r^2 = 0.738$, $P = 0.037$, n = 8, Figure 7).

Habitat occupancy compared to habitat availability

Each primate species was encountered in 12 to 43 of the 420 total habitat subplots

in the Harpia and Puma plots combined. Within each primate species at TBS, habitat

occupancy was proportional to habitat availability (G-tests: df = 5 and $P > 0.05$ for all

species, Table 2). Subsequently, G-tests were repeated with the number of observations

in each habitat type (rather than the number of subplots of each habitat type occupied)

using (1) all observations during censuses, and (2) all visual observations, including those

that did not occur during censuses, and results did not change.

Ordination of species in ecological space

Primate species at TBS segregated in ecological space (final stress $< 1 \times 10^{-7}$). The

NMS yielded a final solution of three dimensions after 113 iterations, with the first

(38%), second (34%), and third (2%) axes representing a greater percentage of variance

among species in ecological space than expected by chance (Monte Carlo test, $P<0.05$,

Figure 8). Occupancy of palm swamp and palm hardwood swamp habitats explained

much of the variance described by the first axis, while mixed upland forest, gap, palm

hardwood swamp, and second-growth explained much of the variance accounted for by

axis two (Table 3). The three Atelidae species separated considerably along both axes,

with *Alouatta* being the most ecologically distinct (Figure 8). The two Pitheciidae species

segregated to some extent along axis two but not along axis one. *Saimiri* appeared to be the most ecologically different species in the Cebidae family.

Relationships between phylogenetic, ecological, and geographic distance

Genetic distance, as estimated by branch lengths from Schneider et al. (2001), ranged from 0.03 (between *Ateles* and *Lagothrix*) to 0.141 (between *Callicebus* and *Saimiri*). Ecological distance ranged from 0.23 (between *Saimiri* and *Ateles*) to 0.68 (between *Lagothrix* and *Pithecia*). Genetic distance and ecological distance (measured as dissimilarity in habitat occupancy) were not correlated (standardized Mantel statistic r = -0.04, P = 0.309). Mean geographic distance was smallest between *Callicebus* and *Saguinus* (118 m) and largest between *Pithecia* and *Saguinus* (295 m, Table 4). Ecological distance and geographic distance were not correlated in the diurnal primate community at TBS (standardized Mantel statistic r = -0.000092, P = 0.528). The most commonly observed pair of species (Table 4) was *Cebus* and *Saimiri* (18 times), followed by *Callicebus* and *Saguinus* (15 times).

DISCUSSION

This study provides a fine-scale, seasonal snapshot of the distribution and habitat occupancy of the diurnal primate community at Tiputini Biodiversity Station. Within the duration of the study, all eight study species were observed in each of the two 100-ha plots. The results of this project provide preliminary information regarding the habitat use and distribution of the primate community at TBS and, consequently, offer clues as to how it is possible for various species of primates to coexist.

Height in forest strata

Vertical stratification among primate species at TBS appears to be a significant

mode of ecological segregation, with larger-bodied species generally occurring at greater

heights than smaller-bodied ones. Interspecific differences in mean height have been

well-documented in previous studies of platyrrhine communities (Bobadilla & Ferrari

2000, Buchanan-Smith et al. 2000, Heymann et al. 2002, Mittermeier & van Roosmalen

1981, Peres 1993, Terborgh 1983, Wallace et al. 1998, Youlatos 1999, Youlatos 2004).

Furthermore, many of these studies have also drawn attention to the positive relationship

between body mass and height (Buchanan-Smith et al. 2000, Heymann et al. 2002, Peres

1993, Terborgh 1983, Youlatos 1999). In fact, body mass, due to its connection to diet,

foraging techniques, locomotion, antipredator strategies, and habitat use, is of utmost

influence on the structure of platyrrhine communities (Terborgh 1983, Youlatos 1999). It

has been proposed that this positive relationship between body mass and height is linked

to the degree of vulnerability to aerial predators (Youlatos 1999). According to Terborgh

(1983), large raptors represent the primary diurnal threat to arboreal primates, which

avoid predation by crypticity, forming groups, and escape in size. Thus, it is plausible

that smaller primates, which can be preyed upon by more raptor species than larger ones,

use lower forest strata more frequently than large primates such as *Ateles* and *Lagothrix*

to reduce exposure to predators. Larger primates, on the other hand, are far less

vulnerable to aerial predators, and are hence able to occupy higher forest layers.

Interestingly, an ordination of co-occurring primate species in Yasuní National Park,

Ecuador, based on organismal and habitat parameters revealed that *Alouatta*, *Ateles*,

Pithecia, and *Lagothrix* formed a tightly clustered group, primarily associated with

mature forest, canopy, and frugivory (Youlatos 2004). Similarly, in the study of primates

at TBS, these four genera were observed at significantly higher forest strata than

Callicebus, *Cebus*, *Saguinus*, and *Saimiri*, thus confirming their ecological similarity.

Habitat occupancy and ordination of species in ecological space

In contrast to other studies, I found that habitat occupancy by the TBS primate

community was proportional to the overall availability of habitat types in the two study

plots. Most other synecological studies of Amazonian primates have documented marked

differences in habitat use among species (Haugaasen & Peres 2005, Mittermeier & van

Roosmalen 1981, Peres 1997, Pozo 2004, Terborgh 1983, among others). There are

several reasons why these differences were not supported by G-tests, the most obvious

being related to sample size. Species were observed in 12 to 43 habitat cores out of a total

of 420 available in the two study plots. Given the magnitudes of home range sizes and

daily movement patterns of primates in general, clearly they occupied a greater area in

the plots than solely the areas where they were observed during censuses. It is probable

that further dividing the small sample size of each species among six potential habitat

types prevented the statistical detection of interspecific differences in habitat occupancy.

Additionally, because all of these previous studies were conducted at a larger spatial scale

than the TBS study, they tended to represent a greater variety of habitats among which

differences were likely more evident.

It is widely recognized that habitat use is influenced by seasonality and food

availability (Peres 1994, Stevenson et al. 2000). If this study were to cover multiple

seasons (rather than only the drier portion of the year), or if a measure of fruit availability

had been included, a better understanding of habitat use may have been possible. Finally,

overall availability of the six habitat types was quite unequal—for example, very little palm swamp and palm hardwood swamp occur in the study plots. Even though this was accounted for in the analyses, it is possible that a more exhaustive sampling of these uncommon habitat types could result in a greater number of primate observations in them. In addition, given that some species of primates have been observed in palm swamp habitat primarily while feeding on palm fruits (Stevenson et al. 2000, Terborgh 1983), again knowledge of fruiting phenology is important.

Despite the low proportion of palm swamp and palm hardwood swamp in the study plots, these two habitat types explained much of the variation among primate species in ecological space. This is likely due to the relativization of the species-habitat matrix by habitat totals. Whereas the G-tests were unable to elucidate patterns of habitat differentiation among species due to small sample sizes, the NMS revealed several differences among species. First, the spacing among Atelidae species supports the prediction of competitive exclusion, suggesting that due to their shared evolutionary history, they have diverged ecologically to avoid competing with one another. Stevenson et al. (2000), in a study of fruit overlap among primate species in Colombia, found the highest overlap between *Ateles* and *Lagothrix*, and even observed *Lagothrix* displaying aggressive behaviors toward *Ateles* and *Alouatta* in fruiting trees. They propose that coexistence of *Lagothrix* and *Ateles* is facilitated by *Lagothrix* feeding on arthropods and *Ateles* consuming palm fruits. Hence, the results of Stevenson et al. (2000) reveal evidence of ecological segregation in the context of direct and indirect competition among Atelidae species.

Cebus and *Saimiri*, which comprise a monophyletic clade nested within Cebidae, are spread apart in ecological space. This is particularly interesting in light of the associations observed between these two genera both at TBS and elsewhere (Mittermeier & van Roosmalen 1981, Terborgh 1983). The two Pitheciidae species are relatively close together in ecological space along the first axis; however they differ along axis two as well as in mean height, implying some degree of ecological differentiation between them. In general, the NMS ordination displays three main species clusters which for the most part exclude *Lagothrix*: one with *Pithecia* and *Alouatta*, another including *Saimiri* and *Ateles*, and a third encompassing *Cebus*, *Saguinus*, and *Callicebus*. In all three of these clusters, species that are close together in habitat occupancy differ either in diet and/or use of vertical forest strata. For example, *Pithecia* primarily consumes seeds and fruits, while *Alouatta* is a folivore/frugivore (Youlatos 2004). *Saimiri* and *Ateles* differ both in height and diet, with *Saimiri* feeding more on insects (Youlatos 2004) and *Ateles* mainly exhibiting frugivory (Dew 2005). While *Cebus*, *Saguinus*, and *Callicebus* do not differ in height, *Cebus* is an omnivore (Youlatos 2004), while *Callicebus* primarily consumes fruit and leaves (Youlatos 2004) and *Saguinus* feeds on fruit, insects, and gums (Heymann 2000). The latter two species were observed together a number of times during this study as well as in others (Terborgh 1983). Consequently, the primate species at TBS are ecologically segregated in terms of habitat use, height, and probably diet as well.

Relationships between phylogenetic, ecological, and geographic distance

The finding that there is no relationship between phylogenetic distance and ecological distance among the primate species at TBS does not strongly support phylogenetic niche conservatism (i.e., ecological similarity was not higher for more

closely related species than expected by chance) or competitive exclusion (phylogenetic repulsion of ecologically similar species). However, the ordination reveals that species are not randomly dispersed in ecological space. Species that were clustered in ecological space belonged to different families, with the exception of *Cebus* and *Saguinus*, which are in the same family but in different clades. This result provides more evidence for the competitive exclusion hypothesis.

In their examination of birds, mammals, and butterflies in Mexico, Peterson et al. (1999) demonstrated conservatism of climate niches among sister-species pairs but not at the family level. These results imply that niche differentiation likely occurs at the time scale of higher taxonomic levels such as genera or families (Peterson et al. 1999); thus, it makes sense that niche conservatism (along the axis of habitat occupancy) was not observed given that there are no congeners in the TBS primate community. Despite strong empirical support for niche conservatism, many studies assessing associations between ecological traits and phylogeny among a variety of taxa have failed to detect a phylogenetic signal in niche structure (anoles, Losos et al. 2003; jays, Rice et al. 2003; plants, Silvertown et al. 2006). As Wiens and Graham (2005) remark, rather than focusing on the question of whether niches are conserved, it is more constructive to concentrate on the patterns that niche conservatism or a lack thereof may produce. In the case of this study, the lack of support for niche conservatism reflects a pattern of more-related species differing in habitat occupancy. In addition, it must be stressed that while this study focused on one dimension of a niche, habitat, niches are multidimensional (Hutchinson 1957). Therefore, in order to adequately evaluate niche conservatism and its influences on community structure, measures of other niche dimensions are necessary.

Fleagle and Reed (1996), in their cross-continental comparison of primate community ecology, found that Neotropical primate communities were more tightly clumped in ecological space than those studied in Asia, Africa, and Madagascar. Moreover, subsequent analyses indicate a positive relationship between ecological similarity and phylogenetic relatedness among species at a global scale (Fleagle & Reed 1999). In contrast, the habitat occupancy dimension of the niche was not phylogenetically conserved in this study of the TBS primate community, which was conducted at an extremely local scale (two 100-ha plots), perhaps suggesting that the relationship between phylogenetic and ecological similarity varies across spatial scales. Thus, further examination of this relationship in platyrrhine communities across different spatial scales is merited, particularly given that the number of species should increase at larger geographic scales (Arrhenius 1921). However, before such an investigation can be undertaken, a fully resolved phylogeny of extant platyrrhines is required. Although Schneider et al. (2001) were able to roughly estimate branch lengths in a molecular phylogeny of extant Neotropical primate genera using maximum likelihood, the validity of these estimates are somewhat uncertain. While multiple DNA datasets and molecular approaches reveal three monophyletic platyrrhine families, thereby permitting assessments of niche conservatism within each of the three clades, there are discrepancies in the reconstructed relationships among these families, particularly in which two of the three are more closely related (Schneider et al. 2001, Opazo et al., in press). According to branch lengths estimated by Schneider et al. (2001), Pitheciidae and Atelidae are more closely related, but this grouping is not strongly supported. Hence, it is difficult to ascertain whether the lack of relationship between ecological distance and phylogenetic

distance is truly due to a lack of phylogenetic niche conservatism (along the dimension of

habitat occupancy) or merely a result of inadequate estimates of interspecific genetic

distances. It is important to evaluate the potential of using alternative methods for testing

for phylogenetic independence that do not require branch lengths and can deal with

unresolved nodes (Abouheif 1999).

In this study, a significant linear relationship between ecological distance and

geographic distance was not detected. If this relationship is assessed in the context of a

community shaped by competition, species that are ecologically similar should differ in

their spatial patterns, but species that are ecologically different may or may not overlap

spatially (Hofer et al. 2004). Thus, perhaps testing for a linear relationship is not

appropriate in this case, and other types of analyses need to be explored (Hofer et al.

2004). Nevertheless, if we examine the geographic distance between ecologically similar

species (i.e. those forming clusters in the NMS ordination, see Figure 8), there are species

pairs such as *Callicebus* and *Saguinus* that are relatively close together (mean distance =

118 m), as well as pairs such as *Pithecia* and *Alouatta* (mean distance = 268 m) that are

far apart.

Conclusions

In conclusion, the results of this study reveal that ecological differences among

the primate species at TBS assist in promoting their coexistence. This study, unlike

previous studies of habitat use by Neotropical primates which have generally been

conducted at larger spatial scales, detects ecological differences among species at a fine

scale (two 100-ha plots). First, larger species occurred at greater heights than smaller

ones. Second, although they generally tended to occupy habitat types at frequencies

proportional to their availability in the study area, species segregated in ecological space as measured by dissimilarity in habitat occupancy. Specifically, species differ in their occupancy of rare habitat types such as palm swamp and palm hardwood swamp (which were primarily occupied by *Ateles*, *Saimiri*, and *Lagothrix*), and also to a lesser degree mixed upland forest, gap, and second-growth. Finally, although a clear relationship between ecological distance and phylogenetic distance was not observed in this community, species within the same families tended to segregate in terms of habitat occupancy. Furthermore, species that clustered together in habitat occupancy generally diverged along other ecological axes such as mean height or diet. Nevertheless, a relationship was not detected between ecological distance (dissimilarity in habitat occupancy) and geographic distance.

Conservation

As humans continue to exploit natural systems through activities such as deforestation and harvesting of organisms, a better understanding of how ecosystem changes affect natural communities is becoming increasingly important. Of particular concern are the effects of habitat loss and human disturbance on tropical forest ecosystems, which sustain a large portion of the world's biodiversity, including the majority of primate species. In fact, the Neotropics alone contain more than half of the world's tropical forests and one third of its primate species, many of which are threatened (Mittermeier 1987). A clear understanding of the spatial distribution and the habitat partitioning of primate communities in the Amazon is necessary to ensure that well-informed conservation strategies are designed to effectively protect these animals and the variety of habitats on which they depend. Moreover, the value of examining primate

communities in undisturbed environments should not be overlooked. On the contrary, it is important that we comprehend primate community structure in the context of natural disturbances and inherent differences in habitat quality before evaluating primate community structure as a function of human disturbance. As a result, decisions regarding the primate conservation in this area should take into account the various habitat types used by the primate community. In addition, as hunting pressures, oil exploration, road construction, and other human disturbances continue to affect primates in areas close to the study site, knowledge of habitat use by these various primate species becomes increasingly important in guaranteeing their persistence (Fabara Rojas 2005).

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Table 1. Habitat types defined for Harpia and Puma plots.

Habitat category	Definition
Mature upland forest	Dominated by tall, large diameter trees, few lianas and regrowth, open understory, dense canopy, unflooded
Mixed upland forest	Mix of young and older growth, unflooded
Palm hardwood swamp	Periodically flooded area with palms and hardwood, flat
Palm swamp	Very open, wetland area with *Mauritia flexuosa*, flat
Second-growth	Liana tangle, regrowth, regenerating gaps, short canopy
Gap	New treefall gap with little regeneration
Undefined	Habitat descriptions of these points were unavailable

Table 2. Habitat occupancy, defined as the number of habitat subplots occupied out of the total 420 habitat subplots on the Puma and Harpia plots, of each of the eight primate species observed at TBS. None of the species occupied habitat types disproportionately to their overall availability in the study plots (log-likelihood ratio G-tests: df = 5 and *P* > 0.05 for all species). ALO=*Alouatta*, ATE=*Ateles*, CAL=*Callicebus*, CEB=*Cebus*, LAG=*Lagothrix*, PIT=*Pithecia*, SAG=*Saguinus*, SAI=*Saimiri*.

| | Habitat type | | | | | | | |
Species	Mature upland forest	Mixed upland forest	Palm hardwood swamp	Palm swamp	Second-growth	Gap	Total	*G*
ALO	6	5	0	0	2	1	14	4.20
ATE	3	4	1	2	3	1	14	5.65
CAL	2	7	0	0	6	2	17	3.89
CEB	3	9	0	0	10	6	28	8.26
LAG	11	18	3	2	4	5	43	8.92
PIT	4	3	0	0	2	3	12	3.58
SAG	5	14	2	0	10	4	35	4.04
SAI	3	4	1	1	6	3	18	9.77

Table 3. Percent of variance explained by each axis in NMS ordination of primate species in ecological (habitat) space. *R*-squared values for each habitat type indicate its correlation with the ordination axes.

Axis	1	2
% variance in distance matrix	38%	34%
Correlations with main matrix	r^2	r^2
Mature upland forest	0.043	0.119
Mixed upland forest	0.003	0.686
Palm hardwood swamp	0.318	0.438
Palm swamp	0.861	0.118
Second-growth	0.054	0.423
Gap	0.019	0.517

Table 4. Mean (± SE) geographic distance between species pairs in Harpia and Puma plots and number of times each species pair was observed in the same place at the same time.

| Species pair	Mean geographic distance (m)	n	Number of observations together
ALO-ATE	265 ± 30	30	1
ALO-CAL	246 ± 27	37	0
ALO-CEB	164 ± 18	46	1
ALO-LAG	169 ± 14	64	2
ALO-PIT	268 ± 29	28	3
ALO-SAG	224 ± 19	55	0
ALO-SAI	212 ± 15	36	0
ATE-CAL	230 ± 21	35	0
ATE-CEB	214 ± 28	44	1
ATE-LAG	190 ± 22	62	2
ATE-PIT	239 ± 31	26	1
ATE-SAG	257 ± 20	53	1
ATE-SAI	225 ± 31	34	1
CAL-CEB	197 ± 23	51	0
CAL-LAG	243 ± 22	69	2
CAL-PIT	286 ± 27	33	1
CAL-SAG	118 ± 14	60	15
CAL-SAI	218 ± 29	41	1
CEB-LAG	133 ± 9	78	1
CEB-PIT	236 ± 19	42	2
CEB-SAG	184 ± 13	69	0
CEB-SAI	189 ± 25	50	18
LAG-PIT	208 ± 20	60	4
LAG-SAG	168 ± 11	87	3
LAG-SAI	159 ± 16	68	2
PIT-SAG	295 ± 25	51	5
PIT-SAI	246 ± 25	32	0
SAG-SAI	216 ± 20	59	2
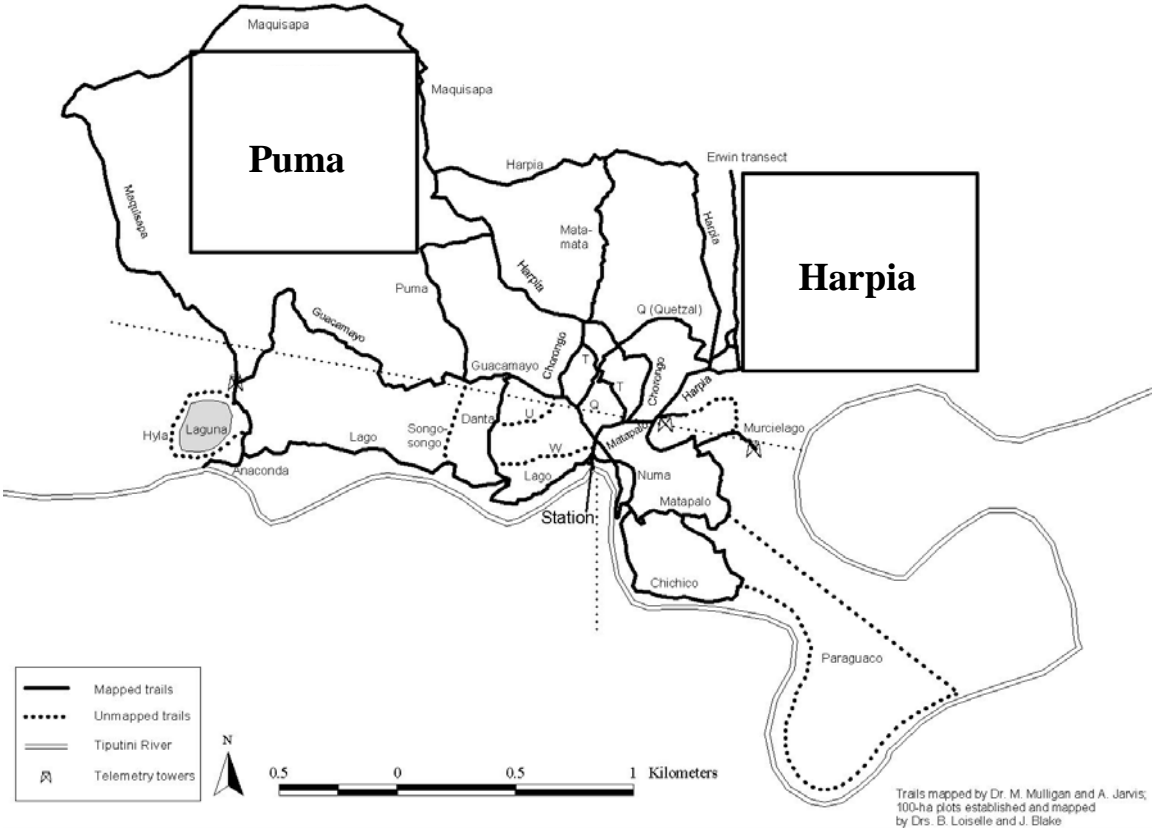
Figure 1. Map of study plots, Harpia and Puma, in relation to Tiputini Biodiversity

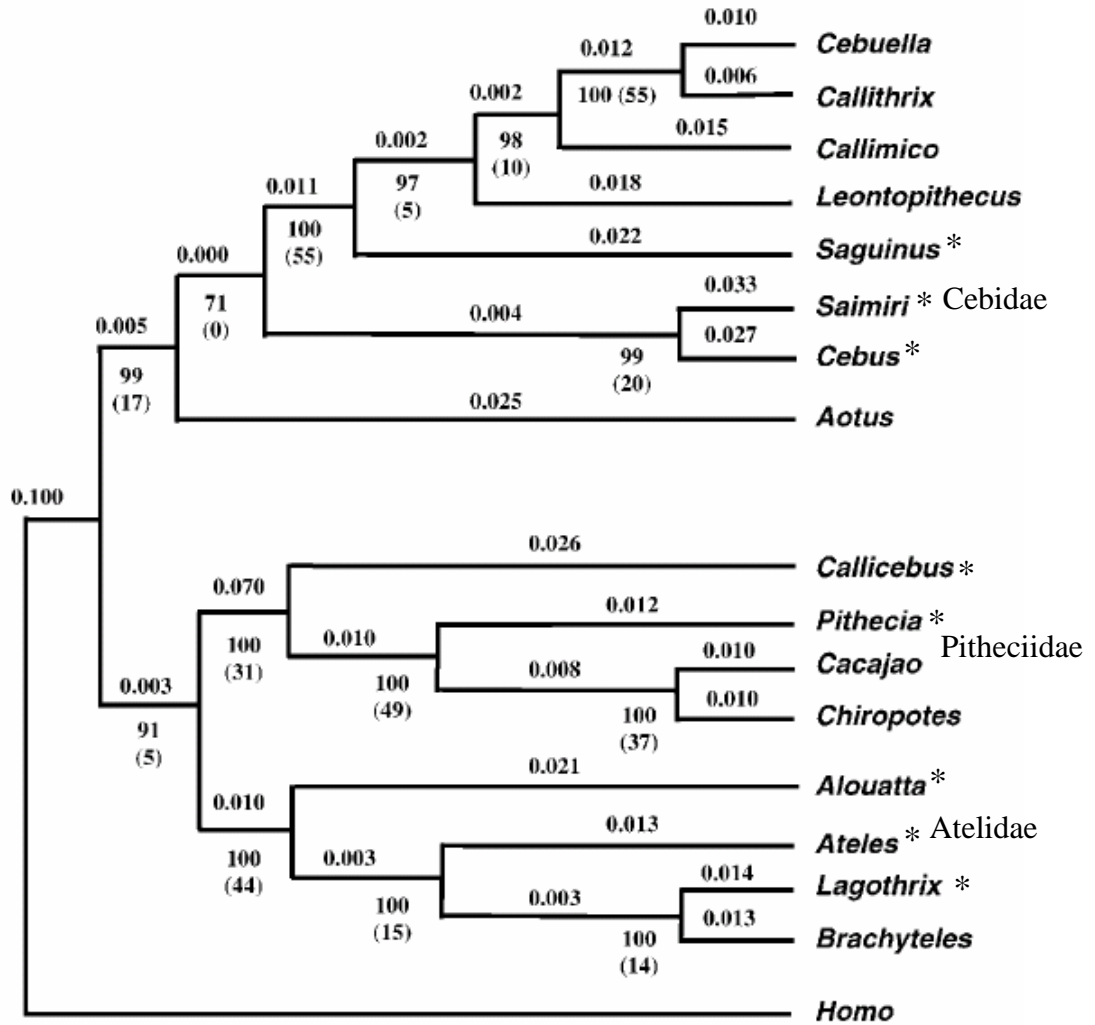Station's trail system (prepared by K.M. Holbrook).

Figure 2. Molecular phylogeny (based on four tandemly aligned DNA datasets) of extant

platyrhhine genera in three families by Schneider et al. (2001). Branch lengths (numbers

above branches) were estimated by Schneider et al. (2001) using maximum-likelihood

with Modeltest selected parameters. Numbers below branches represent bootstrap support

for each node, and parentheses indicate decay index values. Asterisks (*) indicate genera
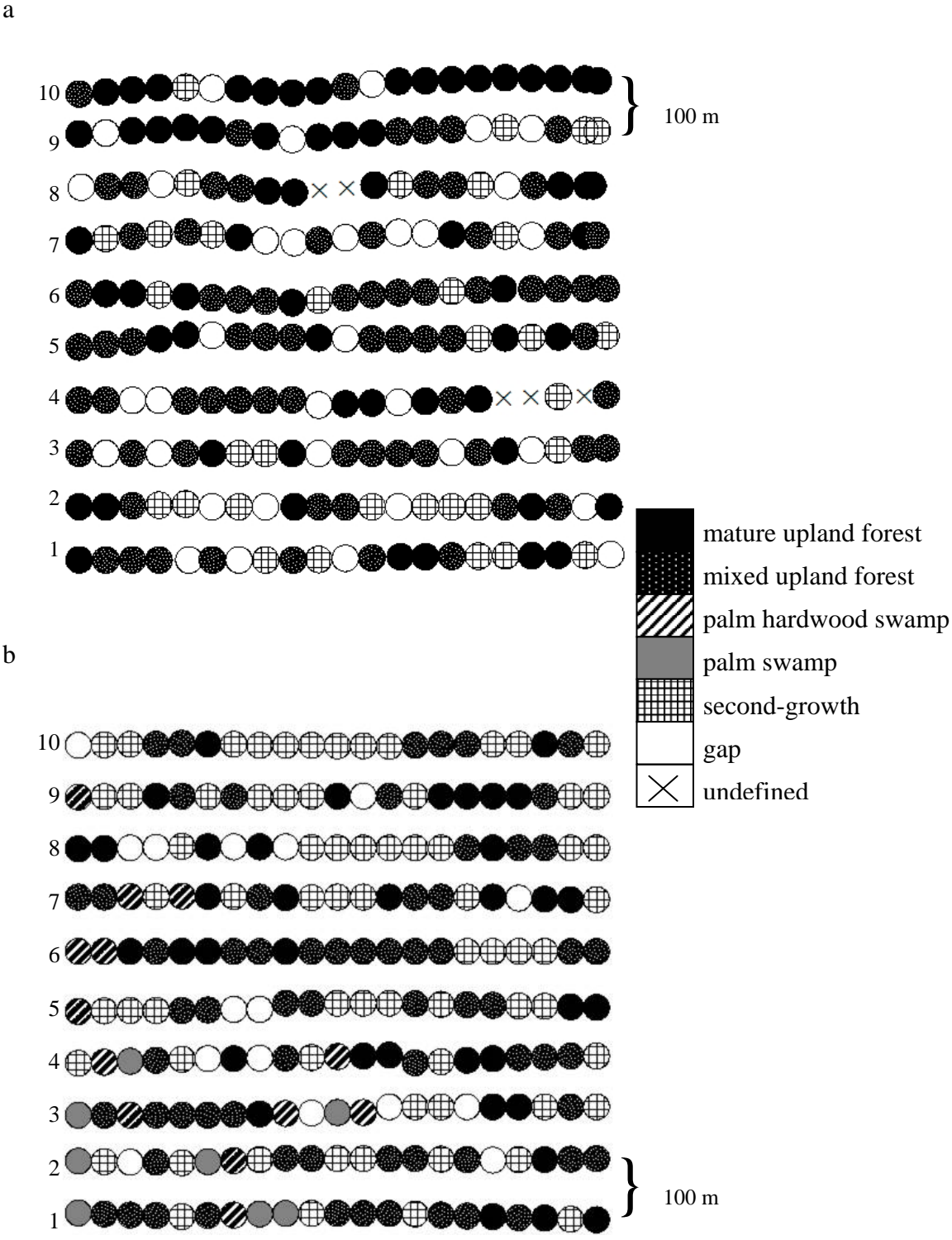
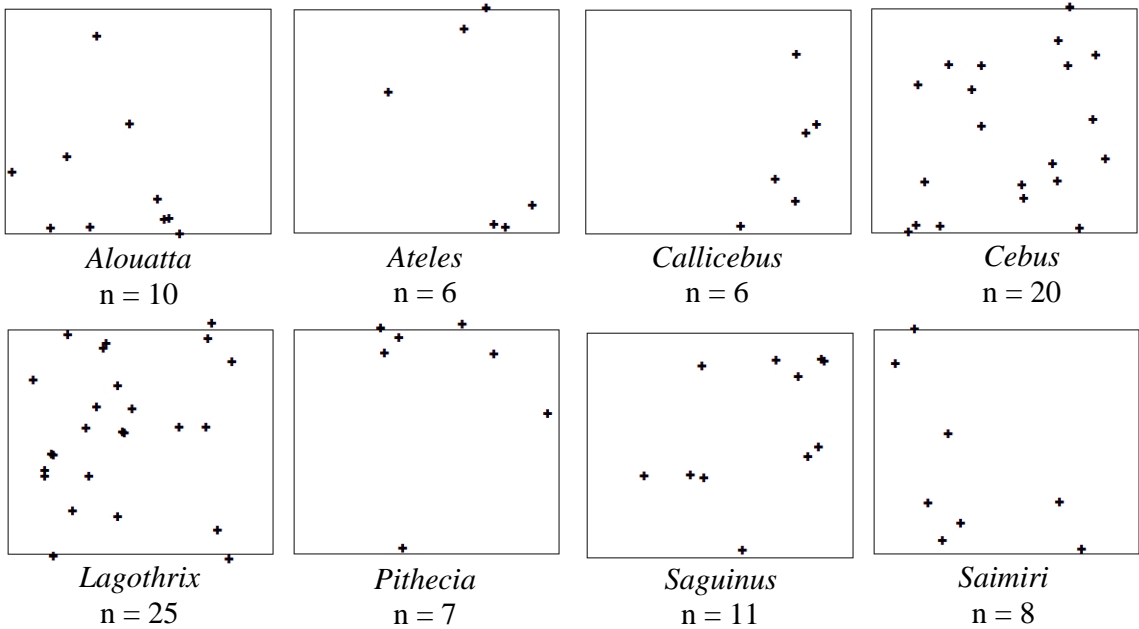included in this study.

a

b

Figure 3. Habitat characterization of Harpia (a) and Puma (b) plots based on detailed

habitat descriptions taken by J.G. Blake every 50m on each of the ten transect lines.

a
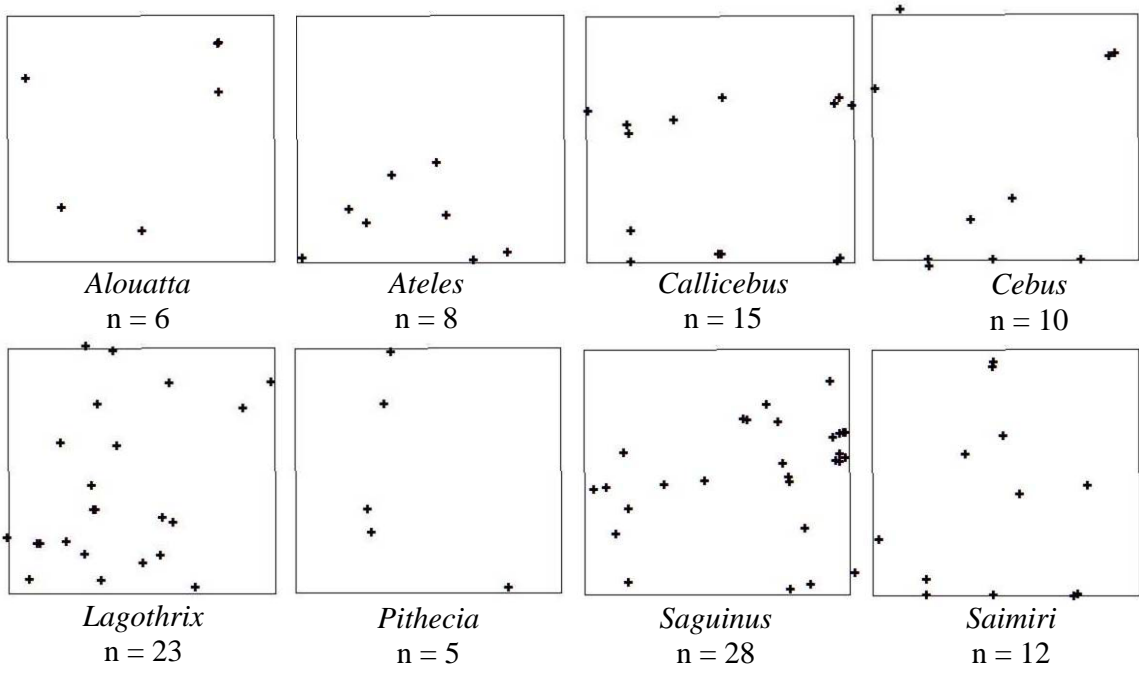

Alouatta n = 10	*Ateles* n = 6	*Callicebus* n = 6	*Cebus* n = 20
Lagothrix n = 25	*Pithecia* n = 7	*Saguinus* n = 11	*Saimiri* n = 8

b

Alouatta n = 6	*Ateles* n = 8	*Callicebus* n = 15	*Cebus* n = 10
Lagothrix n = 23	*Pithecia* n = 5	*Saguinus* n = 28	*Saimiri* n = 12

Figure 4. Distribution of observations of eight TBS primate species in the Harpia (a) and

Puma (b) plots.
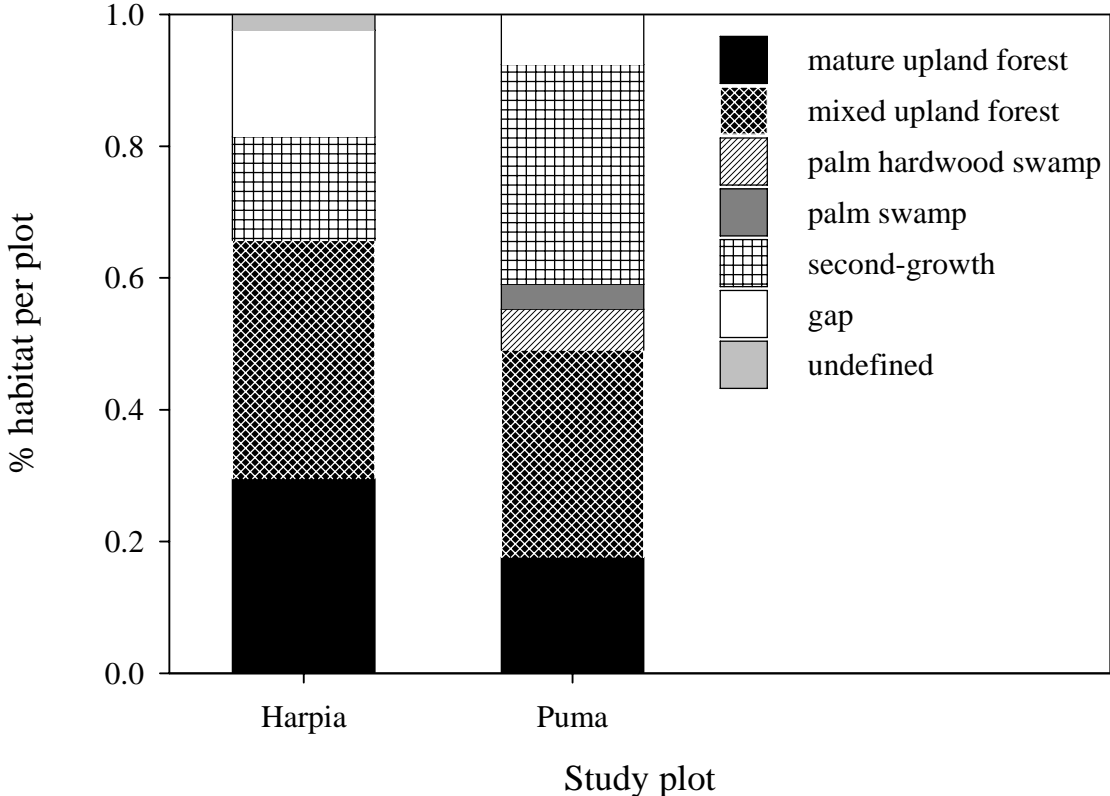
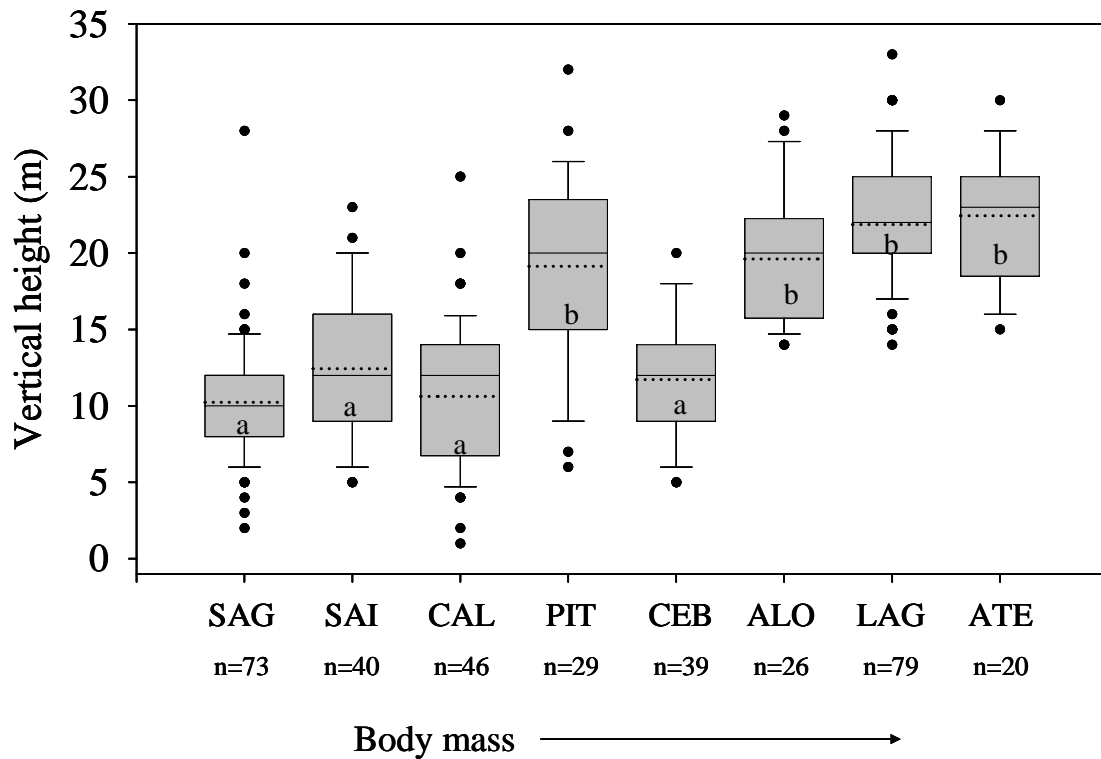Figure 5. Proportion of each habitat type in Puma and Harpia plots.

Figure 6. Height (m) above ground of each species in order of increasing body mass.

Dotted line in box represents mean height, solid line represents median. Boundaries of

each box represent 25th and 75th percentiles, and whiskers indicate 10th and 90th

percentiles. Primate species with different letters significantly differed in mean height

(Welch ANOVA: $F_{7, 111.9} = 70.77$, $P < 0.001$; Tukey test: $P = 0.05$). ALO = *Alouatta*,

ATE = *Ateles*, CAL = *Callicebus*, CEB = *Cebus*, LAG = *Lagothrix*, PIT = *Pithecia*, SAG
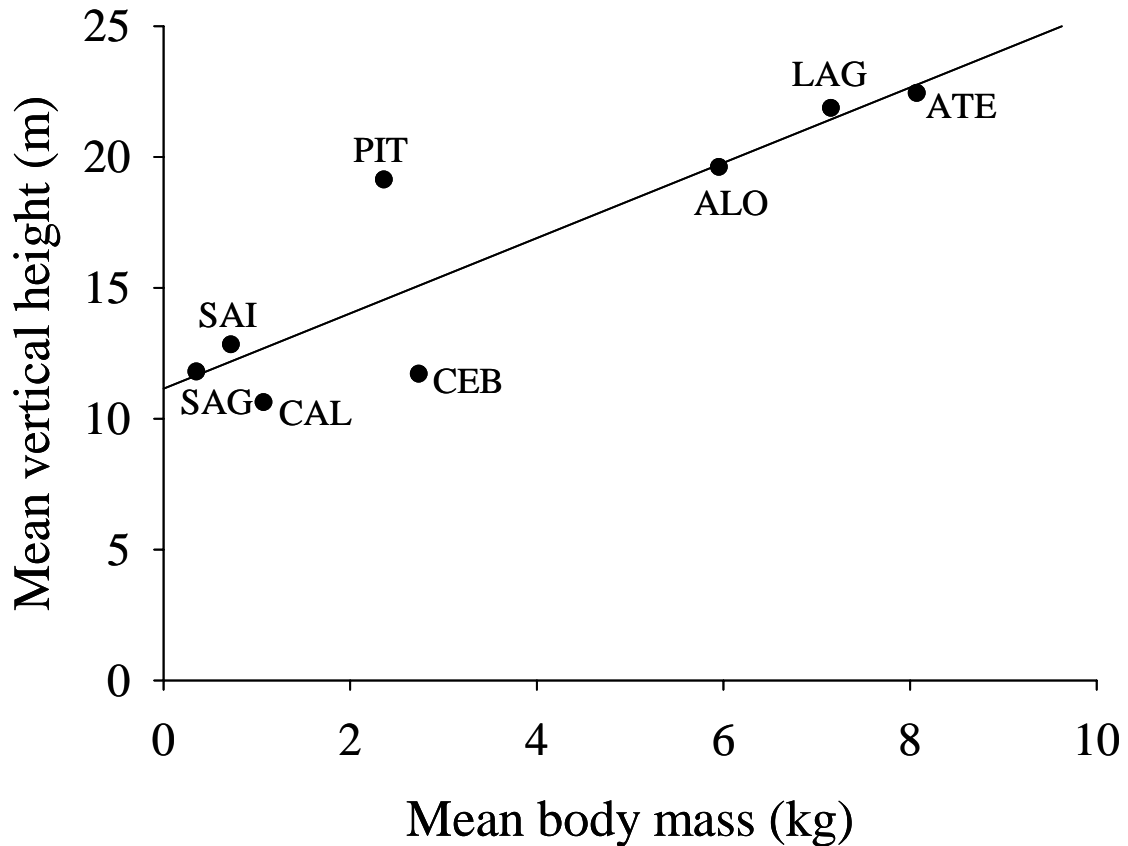
= *Saguinus*, SAI = *Saimiri*.

Figure 7. Mean body mass (from Smith & Jungers 1997), estimated as the average of mean male and mean female body mass, and mean height of the eight primate species observed at TBS ($r^2 = 0.738$, $P = 0.037$). Due to the unavailability of body mass estimates for every species and to taxonomic discrepancies, those of the most closely related listed species were often used (as in Youlatos 2004): *Saguinus fuscicollis* for *S. tripartitus, Callicebus cupreus* for *C. discolor*, *Pithecia monachus* for *Pithecia* sp., and *Lagothrix lagotricha* for *L. poeppigii*. ALO = *Alouatta*, ATE = *Ateles*, CAL = *Callicebus*, CEB = *Cebus*, LAG = *Lagothrix*, PIT = *Pithecia*, SAG = *Saguinus*, SAI = *Saimiri*.
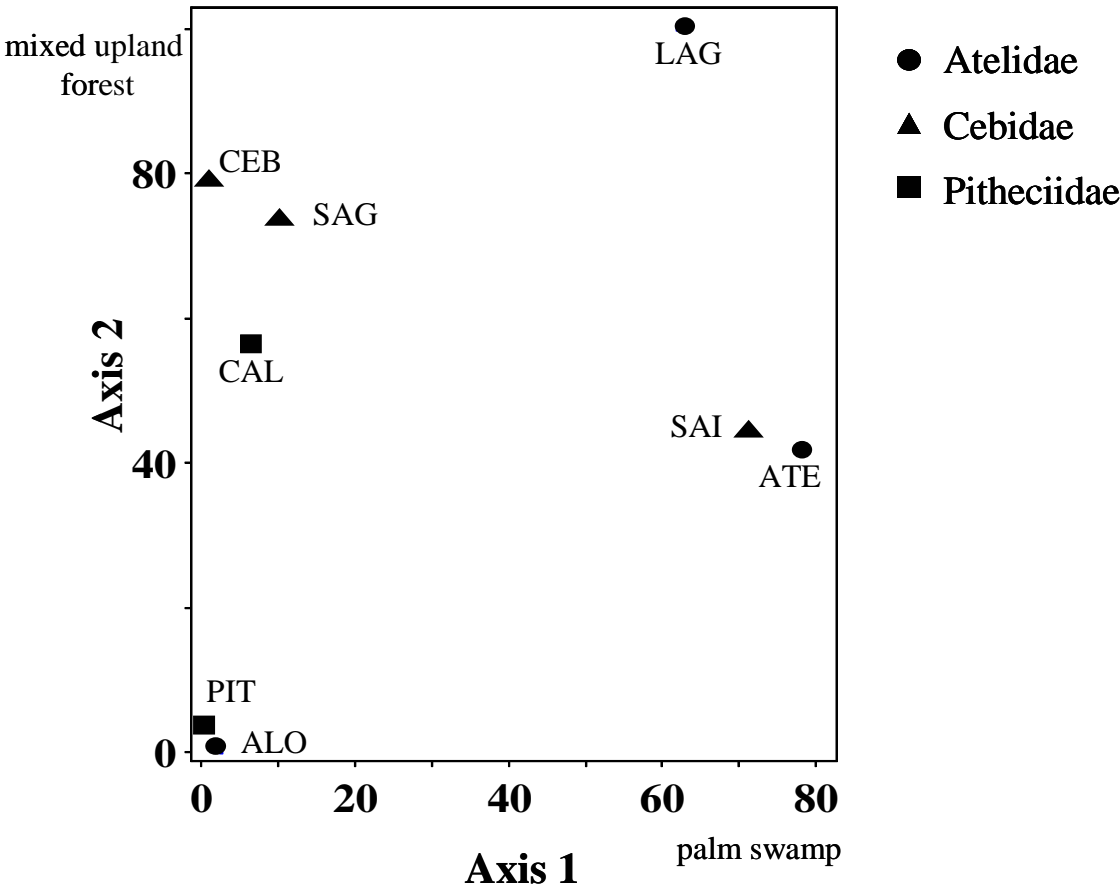
Figure 8. NMS ordination of primate species in ecological space. Axis one represents 38% and axis two represents 34% of the overall variance among species (final stress < 0.0000001). ALO = *Alouatta*, ATE = *Ateles*, CAL = *Callicebus*, CEB = *Cebus*, LAG = *Lagothrix*, PIT = *Pithecia*, SAG = *Saguinus*, SAI = *Saimiri*.