Phylogenetic constraints on fine-scale patterns of habitat use by eight primate species in eastern Ecuador

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Abstract: Lowland forests of western Amazonia contain the most species-rich primate communities in the Neotropics, which begs the question of what mechanisms operate to promote species coexistence. This study examines habitat occupancy and its relationship to phylogeny in a primate community in Amazonian Ecuador. First, as potential factors that shape community structure, we determined whether (1) mean height in the forest canopy differed among species; (2) within each species, habitat occupancy was disproportional to habitat availability; and (3) species diverged in habitat occupancy. We then tested hypotheses regarding ecological distance and its relationship to phylogenetic distance among species pairs within this community. We tested these hypotheses primarily with data derived from 15 censuses of primate species on two 100-ha plots in eastern Ecuador. In these censuses, we observed eight primate species over nearly 200 encounters. We observed larger species at greater heights in the forest canopy than smaller ones. Although they occupied habitat types at frequencies proportionate to their availability in the study area, species diverged in habitat occupancy. Although a clear relationship was not observed between phylogenetic and ecological distances among species pairs, this study suggests that ecological differences among the species in this community facilitate their coexistence.

Resumen: Los bosques de tierras bajas de la amazonía occidental se caracterizan por albergar a la comunidad de primates más diversa de los neotrópicos dando pauta a investigar a qué nivel la partición del nicho sirve como un mecanismo para promover la coexistencia de las especies de primates. En este estudio examinamos la ocupación del hábitat y su relación con la historia evolutiva en una comunidad de primates en la amazonia ecuatoriana. Primero como factores potenciales que influyen en la estructura de la comunidad determinamos si (1) la altura promedia en los estratos del bosque varía entre las especies; (2) las especies ocupan los tipos de hábitat en frecuencias desproporcionales a su disponibilidad en el área de estudio; y (3) hay diferencias entre especies en la ocupación del hábitat. Luego examinamos hipótesis alternativas en cuanto a la distancia ecológica y su relación con la distancia filogenética entre pares de especies en esta comunidad. Mostramos que las especies más grandes generalmente ocupan estratos más altos que las especies pequeñas. A pesar de ocupar los tipos de hábitat en frecuencias proporcionales a su disponibilidad en el área del estudio las especies se segregan en el espacio ecológico. No observamos una relación clara entre las distancias filogenéticas y ecológicas entre pares de especies. Este estudio sugiere que las diferencias ecológicas entre las especies de esta comunidad facilitan su coexistencia.

Key Words: Amazon, Atelidae, Cebidae, community structure, habitat use, neotropical primates, niche conservatism, Pitheciidae, species coexistence

INTRODUCTION

Coexistence of species in time and space, as well as the processes involved in maintaining community assemblages, are central questions in community ecology. Many ecologists have aimed to understand processes of species coexistence 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 which 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 exhibit relatively low adaptive diversity when compared with their African and Asian counterparts (Fleagle & Reed 1996). Early platyrrhines (New World monkeys)

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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 consist primarily of small-bodied, arboreal frugivore-insectivores, with no terrestrial and few folivorous or nocturnal species (Fleagle & Reed 1996, Reed & Bidner 2004, Terborgh & van Schaik 1987), up to 14 species of primate have been observed in a single 1-km^2 plot (Peres 1988, 1993). This tremendous diversity immediately leads to questions of what ecological factors shape such communities and what mechanisms operate to promote species coexistence.

Given that platyrrhine species are relatively similar in their dietary, diurnal and arboreal habits, interspecific differences in microhabitat, spatio-temporal factors, and evolutionary history can potentially help explain species coexistence. 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). Particularly, the importance of niche partitioning in shaping community structure has been highlighted in primate communities in Amazonian Ecuador, where species differ in their preferences for food, vegetation types and forest strata (Pozo 2004, Youlatos 2004).

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 can contribute to the understanding of species coexistence (Fleagle & Reed 1999, Webb *et al.* 2002). To examine species coexistence in a community as a function of evolutionary history and present-day ecological factors, we explore three alternative hypotheses. First, if niches are conserved within evolutionary lineages, then closely related species should exhibit less ecological divergence than more distantly related species (Harvey & Pagel 1991, Lord *et al.* 1995). Alternatively, if natural selection promotes ecological differentiation to avoid competitive exclusion among closely related species, then closely related species should exhibit more ecological divergence than more distantly related species (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 relatedness and ecological divergence among species pairs in a community (Davis 2005, Losos *et al.* 2003, Rice *et al.* 2003, Silvertown *et al.* 2006).

In this study, we examine habitat occupancy and its relationship to phylogeny in a diverse primate community in an undisturbed rain forest of Amazonian Ecuador. First, as potential factors that shape community structure, we determine whether (1) mean height in the forest canopy differs among species; (2) within each species, habitat occupancy is disproportionate to habitat availability; and (3) species segregate in ecological space defined by dissimilarity in habitat occupancy. We then test the above hypotheses regarding ecological divergence and its relationship to phylogenetic relatedness between species pairs within this community.

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-ha tract of relatively undisturbed lowland Amazonian rain forest located within the 1.5-million-ha 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. The station includes two 100-ha plots approximately 1.5 km apart (Blake 2007) that were established in 2001 by J.G.B. and B.A.L. 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 generally flatter and dissected by more streams, thereby including more periodically flooded forest than Harpia (Loiselle *et al.* 2007). GIS databases for grid markers (every 50 m on each transect), elevation and streams have been compiled for these plots by J.G.B. and B.A.L.

Study species

At least ten primate species belonging to three families (*Cebidae*, *Pitheciidae* and *Atelidae*; Schneider *et al.* 2001, Figure 1) have been documented at TBS (Marsh 2004). The species included in this study were golden-mantled tamarin (*Saguinus tripartitus*; Milne-Edwards, 1878), common squirrel monkey (*Saimiri sciureus;* Linnaeus, 1758), white-fronted capuchin (*Cebus albifrons*; Humboldt, 1812), equatorial saki (*Pithecia aequatorialis*;
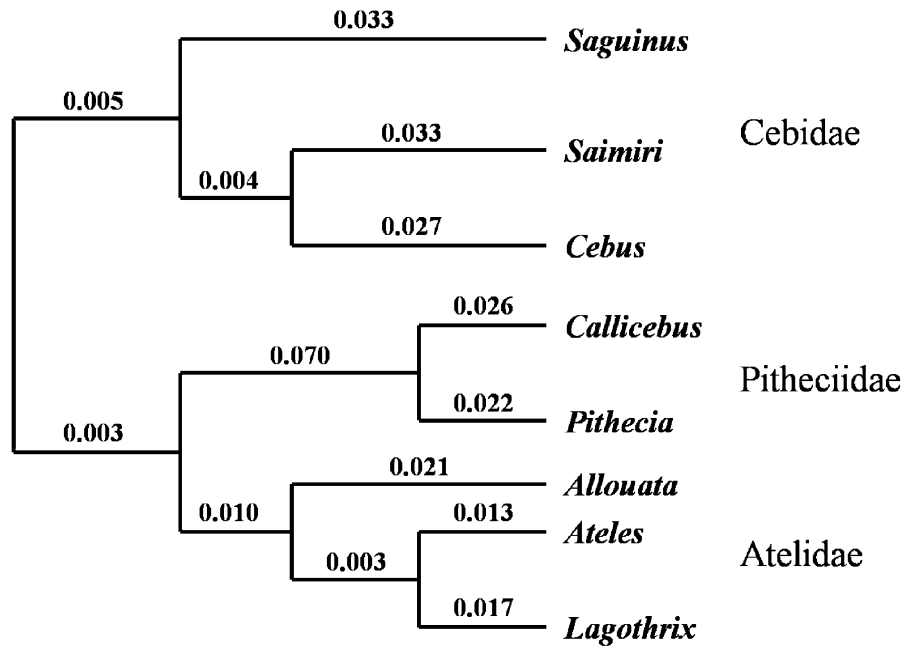
Figure 1. Molecular phylogeny (based on four tandemly aligned DNA datasets) of eight study genera in three families, redrawn from Schneider *et al.* (2001) to include only the genera in this study. Branch lengths (numbers above branches) were estimated by Schneider *et al.* (2001) using maximum-likelihood with Modeltest selected parameters.

Hershkovitz, 1987; Di Fiore *et al.* 2007), dusky titi monkey (*Callicebus discolor*; I. Geoffroy & Deville, 1848; van Roosmalen *et al.* 2002), lowland woolly monkey (*Lagothrix poeppigii*; Schinz, 1844; Di Fiore 1997, Fooden 1963), white-bellied spider monkey (*Ateles belzebuth;* É. Geoffroy, 1806), and red howler monkey (*Alouatta seniculus*; Linnaeus, 1766). The owl monkey (*Aotus vociferans*; Spix, 1820), because it is nocturnal, and the pygmy marmoset (*Callithrix pygmaea*; Spix, 1823), which has not been documented in the study plots, were not examined. Because no two species in this study belong to the same genus, we hereafter refer to each species by only its genus name.

Data collection

Primate censuses, following methods outlined by Peres (1999), were conducted by two independent observers (the author and a trained field assistant) from December 2004 to March 2005. In each plot, 10 1-km 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 transect lines (200 m apart) on 1-m-wide foot trails at a pace of $1–1.25$ km h^{-1}. During censuses, 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 06h00–06h30 to 10h00–10h30, and each afternoon the remaining transects were walked

from 14h00–14h30 to 17h00–17h30. Transects were visited in a systematic order to ensure that each morning and afternoon censuses began and ended at different locations within each plot and to prevent a single transect from being censused more than once in a 3-d period. To avoid potential biases in detectability, censuses were terminated during heavy rain and were paused during brief periods of rain. We conducted 15 full censuses of the Harpia and Puma plots, yielding a cumulative transect distance of 300 km. Although censuses were primarily conducted within these plots, the entire trail system of TBS was regularly surveyed to assess the distribution of primate species throughout the TBS area.

For each encounter with primates, we recorded the following information (Brockelman & Ali 1987, Mittermeier & van Roosmalen 1981, Peres 1999): date, time, weather, location with respect to transect marker, perpendicular distance from first-sighted individual to transect, species, direction of movement, height in the forest canopy (i.e. height in canopy where the first-sighted individual was observed), 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, we tracked an encountered group of primates for no longer than 15 min.

Table 1. Habitat occupancy, defined as the number of habitat subplots occupied out of the total 415 habitat subplots on the Puma and Harpia plots, of each primate species observed at Tiputini Biodiversity Station. 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 seniculus*, ATE = *Ateles belzebuth*, CAL = *Callicebus discolor*, CEB = *Cebus albifrons*, LAG = *Lagothrix poeppigii*, PIT = *Pithecia aequatorialis*, SAG = *Saguinus tripartitus*, SAI = *Saimiri sciureus*.

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
Total number of subplots	99	142	8	13	50	103	415	NA

Above "Habitat type" spans the six habitat columns.

Habitat characterization and habitat occupancy

To quantify the relative availability of habitats on the study plots, we used detailed habitat descriptions (J.G.B., unpubl. data) to construct a habitat map of each plot in ArcGIS 9.1 (ESRI, Redlands CA 92373-8100, USA). Within each plot, we classified habitat into one of six categories at each transect marker (every 50 m) along the ten transects included in the censuses (Figure 2). 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. Each primate sighting was mapped in ArcGIS 9.1 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 verified against field notes taken on the surrounding habitat. Finally, we assessed the habitat occupancy of the area around each transect marker by scoring species presence as 1 and absence as 0 and summing up the number of subplots of each habitat type occupied per species.

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 in the forest canopy 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 in the canopy and mean body mass (from Smith & Jungers 1997) across species was assessed with a Spearman's rank correlation test (JMP v. 5.1.2, 2004).

To evaluate whether each species occupied habitat types disproportionately to their availability, we 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 two plots and the expected frequencies were based on the proportional availability of habitat types in the plots. We used non-metric multidimensional scaling (NMDS, PC-ORD v. 4.01, MjM Software, Gleneden Beach, Oregon), a type of ordination that depicts the relationships among community members using ranked distances between samples (Clarke 1993), to examine the position of species in ecological space, defined by interspecific dissimilarities in habitat occupancy. Non-metric 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). A Monte Carlo test was then implemented to determine whether the structure in the species matrix was stronger than expected by chance (McCune & Grace 2002). The initial dataset was a matrix of habitat occupancy (Table 1) in which rows were species and columns were habitat types. From this initial matrix, which was first relativized by column totals to reduce effects of unequal habitat availability, we constructed a species dissimilarity matrix using the Sørensen distance index to conduct the NMDS using a random starting configuration and performing 40 runs with the real data, thus yielding an ordination of species in ecological space.

To test hypotheses about the relationship between phylogenetic relatedness and ecological divergence among species pairs in this community, we calculated
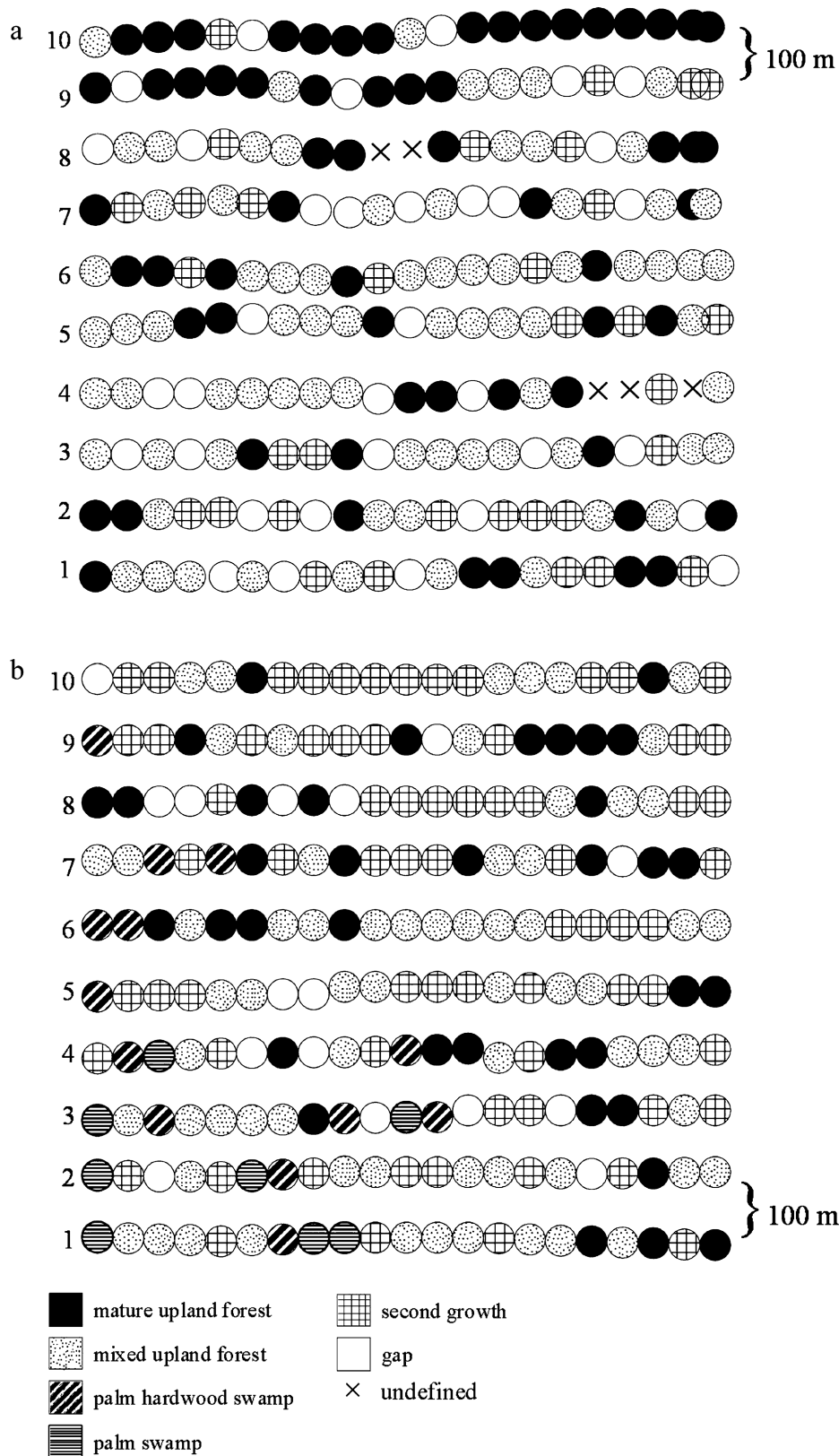
Figure 2. Habitat characterization of Harpia (a) and Puma (b) plots based on detailed habitat descriptions every 50 m on the ten transect lines. Habitat categories are mature upland forest (dominated by tall, large-diameter trees, few lianas and regrowth, open understorey, dense canopy, unflooded), mixed 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), and undefined (habitat descriptions of these points were unavailable).

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 1) and created a species matrix of genetic distance. We subsequently implemented a Mantel test (PC-ORD v. 4.01, MjM Software, Gleneden Beach, Oregon) with a randomization method to compare the genetic distance matrix to the ecological dissimilarity matrix used in the species ordination. Further, because a Mantel test can only detect linear relationships between distance matrices, we performed an additional analysis (in R version 2.8.1, R Foundation for Statistical Computing, Vienna, Austria) to determine whether pairwise ecological distances among species pairs from a single monophyletic family were greater, less than, or no different from pairwise distances among species pairs from different monophyletic families. In this analysis, we performed the following procedure: (1) based on the observed number of species per family, we randomly assigned a family to each species in the ecological dissimilarity matrix used in the species ordination and Mantel test. (2) We then computed the pairwise ecological distances among species pairs from a single monophyletic family and the pairwise distances among species pairs from different monophyletic families. (3) We calculated the mean difference between the pairwise ecological distances among species pairs from a single monophyletic family and pairwise distances among species pairs from different monophyletic families. (4) We carried out steps 1 through 3 a total of 1000 times. (5) We created a null distribution of the 1000 mean differences from step 3 and obtained the 2.5% and 97.5% quantiles of this null distribution. (6) We compared the 'observed' mean difference between the pairwise ecological distances among species pairs from a single monophyletic family and pairwise distances among species pairs from different monophyletic families to the null distribution of mean differences created in step 5. An observed mean difference less than the 2.5% quantile of the null distribution of mean differences would lend support to the niche conservatism hypothesis (i.e. species within families are less divergent in ecological space than species among families), while an observed mean difference greater than the 97.5% quantile of the null distribution of mean differences would lend support to the hypothesis that natural selection promotes ecological differentiation to avoid competitive exclusion among closely related species (i.e. species within families are more divergent in ecological space than species among families).

RESULTS

During the 15 censuses of the study plots, we encountered eight species of primate on the two plots, yielding a total of 93 observations on Harpia and 103 observations on Puma (Figure 3). On Harpia, *Lagothrix* was seen most (25 times), and *Callicebus* 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 (5 times). Overall, *Lagothrix*, *Saguinus* and *Cebus* were encountered the most, and *Pithecia* was the least-encountered species. Harpia is dominated by mature and mixed upland forest habitats, while Puma primarily contains mixed upland forest and second growth (Figure 2). Puma, due to the presence of *Mauritia* palm swamp and palm-hardwood swamp, has more habitat types than Harpia. Mixed upland forest is the most abundant habitat type across both plots.

Height in forest canopy

Of the eight species detected at TBS, *Saguinus* and *Callicebus* were observed at the lowest mean heights in the canopy (10.2 m and 10.6 m, respectively), and *Lagothrix* and *Ateles* were observed at the largest mean heights in the canopy (21.9 m and 22.5 m, respectively). On average, *Cebus* and *Saimiri* were seen at relatively low heights in the canopy (11.7 m and 12.4 m, respectively), while *Pithecia* and *Allouata* were typically detected over 6 m higher in the canopy (19.1 m and 19.6 m, respectively). *Alouatta*, *Ateles*, *Lagothrix* and *Pithecia* occurred at significantly greater heights in the canopy than *Callicebus*, *Cebus*, *Saguinus* and *Saimiri* (Welch ANOVA: $F_{7, 111.9} = 70.8$, P < 0.001; Tukey test: P $= 0.05$, Figure 4). Mean body mass and mean height in the canopy were positively correlated ($r^2 = 0.738$, P $= 0.037$, n $= 8$, Figure 4) with the smallest species (*Saguinus*) typically being observed at the lowest heights in the canopy, and the largest species (*Ateles*) generally being detected at the greatest heights in the canopy.

Habitat occupancy and ordination of species in ecological space

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 proportionate to habitat availability (G-tests: df = 5 and P > 0.05 for all species, Table 1). However, species segregated in ecological space (final stress $<1 \times 10^{-7}$). The NMDS 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 5). Occupancy of palm swamp and palm-hardwood swamp habitats explained much of the variance described
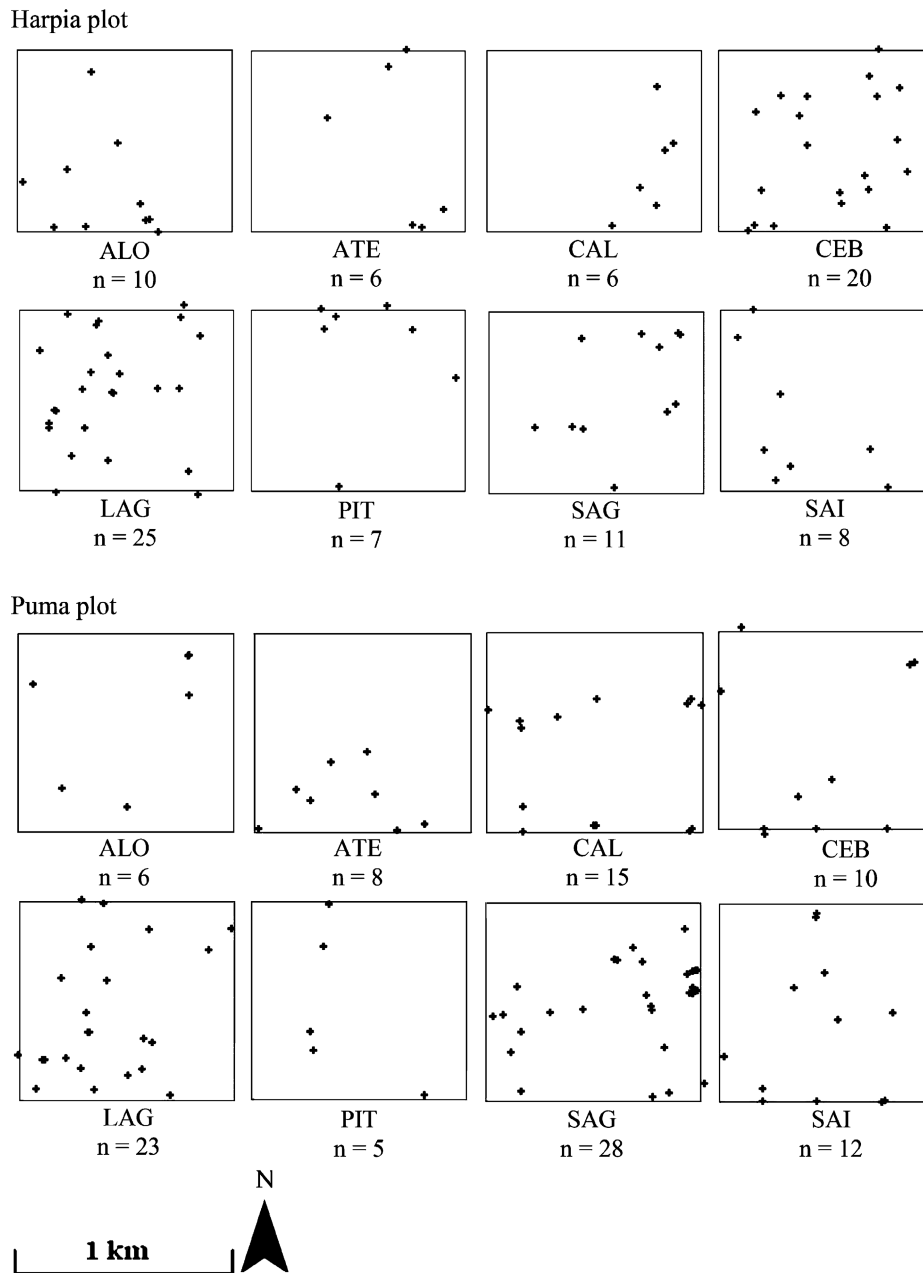
Harpia plot

Puma plot

N

1 km

Figure 3. Distribution of observations of primate species in Harpia (a) and Puma (b) plots. ALO = *Alouatta seniculus*, ATE = *Ateles belzebuth*, CAL = *Callicebus discolor*, CEB = *Cebus albifrons*, LAG = *Lagothrix poeppigii*, PIT = *Pithecia aequatorialis*, SAG = *Saguinus tripartitus*, SAI = *Saimiri sciureus*.

by the first axis, while mixed-upland forest, gap, palm-hardwood swamp and second growth explained much of the variance accounted for by the second axis (Table 2). The three Atelidae species separated considerably along both axes, with *Alouatta* being the most ecologically distinct (Figure 5). The two Pitheciidae species segregated to some extent along the second axis but not along the first. *Saimiri* appeared to be the most ecologically distinct species in Cebidae.

Relationships between phylogenetic and ecological distance

Genetic distance ranged from 0.03 (between *Ateles* and *Lagothrix*) to 0.141 (between *Callicebus* and *Saimiri*). Ecological distance (measured as dissimilarity in habitat occupancy) ranged from 0.23 (between *Saimiri* and *Ateles*) to 0.68 (between *Lagothrix* and *Pithecia*). Genetic distance and ecological distance were not correlated (standardized Mantel statistic $r = -0.04$, P = 0.309,
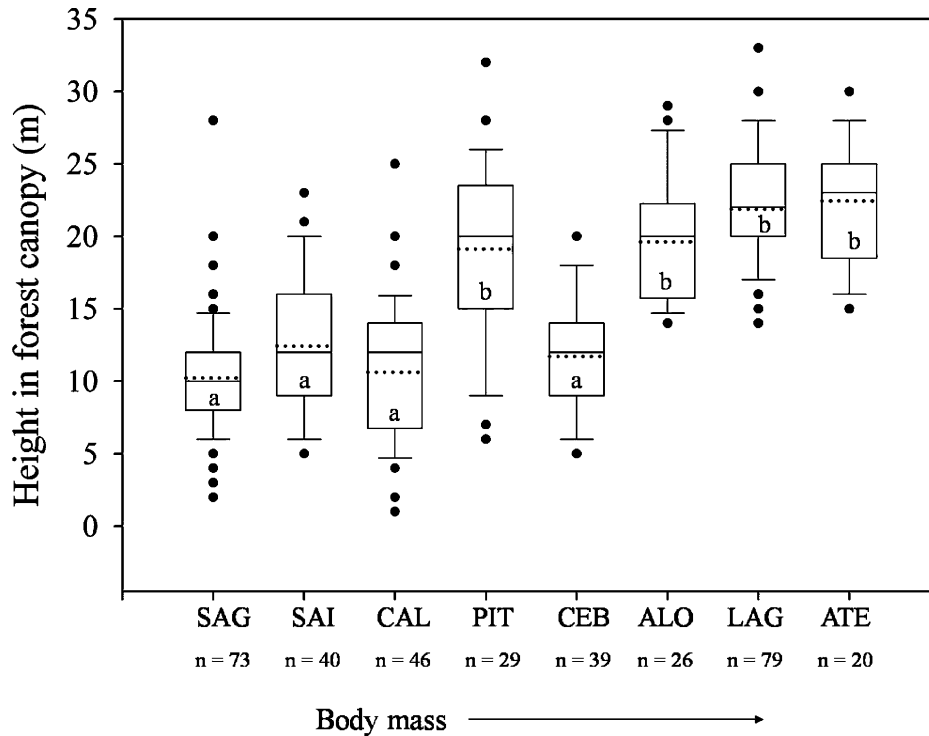
Figure 4. Height (m) in the canopy of each species in order of increasing mean body mass (from Smith & Jungers 1997) estimated as the average of mean male and mean female body mass. Due to the unavailability of body mass estimates for every species and to taxonomic discrepancies, those of the most closely related listed species were used (as in Youlatos 2004): *Saguinus fuscicollis* for *S. tripartitus, Callicebus cupreus* for *C. discolor, Pithecia monachus* for *P. aequatorialis* and *Lagothrix lagotricha* for *L. poeppigii*. Dotted line in box represents mean height in the forest canopy, 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 in the canopy. ALO = *Alouatta seniculus*, ATE = *Ateles belzebuth*, CAL = *Callicebus discolor*, CEB = *Cebus albifrons*, LAG = *Lagothrix poeppigii*, PIT = *Pithecia aequatorialis*, SAG = *Saguinus tripartitus*, SAI = *Saimiri sciureus*.

Table 3). Similarly, the observed mean difference between the pairwise ecological distances among species pairs from a single family and pairwise distances among species pairs from different families (−0.0443) did not differ significantly from that expected by chance (null distribution of mean differences: 2.5% quantile = −0.126, 97.5% quantile = 0.100).

DISCUSSION

This study provides a fine-scale, seasonal snapshot of the distribution and habitat occupancy of the diurnal

Table 2. Per cent of variance explained by each axis in NMDS ordination of primate species in ecological space and *r*-squared values for each habitat type indicating its correlation with the ordination axes.

Axis	1	2
% variance in distance matrix	38%	34%
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

primate community at Tiputini Biodiversity Station. Our results support the hypothesis that fine-scale ecological differences among the primate species at TBS may operate to promote their coexistence. Unlike previous studies that have documented interspecific differences in habitat use by neotropical primates at relatively large spatial scales, we detected ecological differences among species at a fine scale (two 100-ha plots). First, larger species occurred at greater heights in the canopy than smaller ones. Second, although they generally tended to occupy habitat types at frequencies proportionate to their availability in the study area, species segregated in ecological space as measured by dissimilarity in habitat occupancy. Specifically, species differed in their occupancy of palm swamp and palm-hardwood swamp, and to a lesser degree mixed upland forest, gap and second growth. Finally, although we did not detect a clear relationship between ecological distance and phylogenetic distance among species pairs in this community, species within the same families tended to segregate in terms of habitat occupancy, supporting the hypothesis that natural selection results in closely related species diverging in patterns of habitat use. Furthermore, species that clustered together in habitat occupancy generally diverged along other ecological axes such as mean height in the canopy or diet.
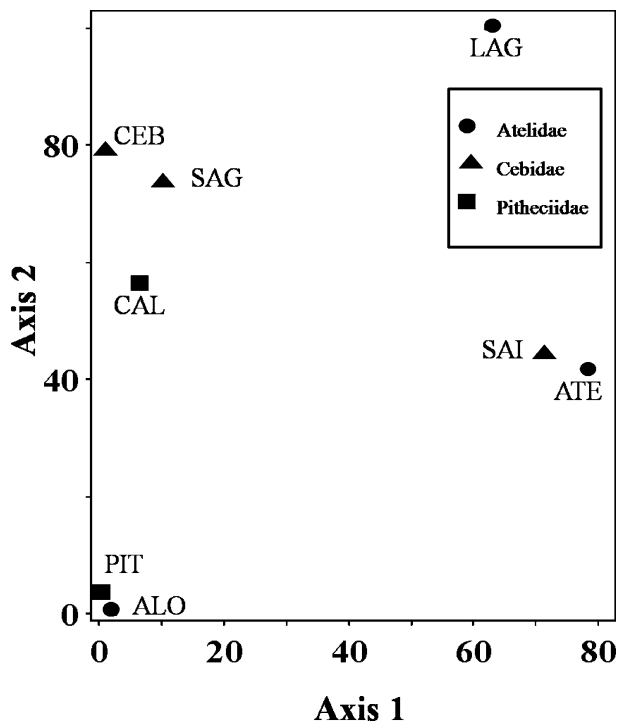
Figure 5. NMDS ordination of primate species in ecological space (final stress < 0.0000001). ALO = *Alouatta seniculus*, ATE = *Ateles belzebuth*, CAL = *Callicebus discolor*, CEB = *Cebus albifrons*, LAG = *Lagothrix poeppigii*, PIT = *Pithecia aequatorialis*, SAG = *Saguinus tripartitus*, SAI = *Saimiri sciureus*.

Table 3. Ecological and genetic distance between each pair of species observed in this study. 'Same' indicates that both species in the pair belong to the same family, and 'different' indicates that each species in the pair belongs to a different family. ALO = *Alouatta seniculus*, ATE = *Ateles belzebuth*, CAL = *Callicebus discolor*, CEB = *Cebus albifrons*, LAG = *Lagothrix poeppigii*, PIT = *Pithecia aequatorialis*, SAG = *Saguinus tripartitus*, SAI = *Saimiri sciureus*.

Species pair	Family	Ecological distance	Genetic distance
ALO-ATE	same	0.590	0.037
ALO-CAL	different	0.384	0.127
ALO-CEB	different	0.519	0.070
ALO-LAG	same	0.678	0.041
ALO-PIT	different	0.255	0.123
ALO-SAG	different	0.559	0.072
ALO-SAI	different	0.571	0.076
ATE-CAL	different	0.616	0.122
ATE-CEB	different	0.660	0.065
ATE-LAG	same	0.362	0.030
ATE-PIT	different	0.616	0.118
ATE-SAG	different	0.567	0.067
ATE-SAI	different	0.227	0.071
CAL-CEB	different	0.289	0.135
CAL-LAG	different	0.677	0.126
CAL-PIT	same	0.354	0.048
CAL-SAG	different	0.459	0.137
CAL-SAI	different	0.405	0.141
CEB-LAG	different	0.570	0.069
CEB-PIT	different	0.420	0.131
CEB-SAG	same	0.288	0.064
CEB-SAI	same	0.440	0.060
LAG-PIT	different	0.682	0.122
LAG-SAG	different	0.347	0.071
LAG-SAI	different	0.428	0.075
PIT-SAG	different	0.525	0.133
PIT-SAI	different	0.448	0.137
SAG-SAI	same	0.386	0.070

Height in forest canopy

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 in the forest canopy than smaller-bodied ones. Interspecific differences in mean height in the canopy have been well-documented in previous studies of platyrrhine communities (Bobadilla & Ferrari 2000, Buchanan-Smith *et al.* 2000, Heymann *et al.* 2002, Peres 1993, Wallace *et al.* 1998, Youlatos 2004). Furthermore, many of these studies have also drawn attention to the positive relationship between body mass and height in the forest canopy (Buchanan-Smith *et al.* 2000, Heymann *et al.* 2002, Peres 1993, Terborgh 1983, Youlatos 1999). It has been proposed that this positive relationship 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 parts of the forest canopy more frequently than large primates, such as *Ateles* and *Lagothrix*, to reduce exposure to predators.

Habitat occupancy and ordination of species in ecological space

While most synecological studies of Amazonian primates have documented marked habitat preferences within species (Haugaasen & Peres 2005, Mittermeier & van Roosmalen 1981, Peres 1997, Pozo 2004, Terborgh 1983), we found that habitat occupancy by the TBS primate community was proportionate to the overall availability of habitat types in the two study plots. There are several reasons why our analysis did not detect intraspecific differences in habitat occupancy, the most obvious being related to sample size. Species were observed in 12 to 43 habitat subplots 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, 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 intraspecific differences in habitat occupancy. Additionally, because

previous studies were conducted at larger spatial scales than the TBS study, they represented 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 covered multiple seasons and years (rather than only the drier portion of a single year), or if a measure of fruit availability had been included, we could have had a better understanding of habitat use. Finally, overall availability of the six habitat types was unequal – for example very little palm swamp and palm-hardwood swamp occur in the study plots, and a more exhaustive sampling of these uncommon habitat types might result in a greater number of primate observations in them. Studies that have documented primate species in palm-swamp habitat primarily while feeding on palm fruits (Stevenson *et al.* 2000, Terborgh 1983) highlight the importance of fruiting phenology influencing habitat use patterns.

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. The spacing among Atelidae species supports the hypothesis that natural selection promotes ecological differentiation, 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 overlap in fruit consumption among primate species in Colombia, found the highest overlap between *Ateles* and *Lagothrix*, and even observed *Lagothrix* displaying aggressive behaviours 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. The results of Stevenson *et al.* (2000) reveal evidence of ecological segregation in the context of direct and indirect competition among Atelidae species. The small sample sizes in this study restricted our ability to examine habitat occupancy separately for each plot. Given that the Harpia plot does not contain any palm swamp or palm-hardwood swamp habitat, analysis of habitat occupancy within each plot would reveal what additional habitat types may be important in driving variation among primate species in ecological space.

Cebus and *Saimiri*, which comprise a monophyletic clade nested within Cebidae, are separated in ecological space. This is particularly remarkable in light of the associations observed between these two genera both at TBS (pers. obs.) and elsewhere (Mittermeier & van Roosmalen 1981, Terborgh 1983). A study of mixed groups of *Cebus apella* and *Saimiri sciureus* in central Surinam documents marked differences in diet and use of forest strata between the two species (Fleagle *et al.* 1981). The two Pitheciidae species are relatively close

in ecological space along the first axis but differ along the second axis and in mean height in the canopy, implying some degree of ecological differentiation. The NMS ordination displays three main species clusters which exclude *Lagothrix*: one with *Pithecia* and *Alouatta*, another including *Saimiri* and *Ateles*, and a third encompassing *Cebus*, *Saguinus* and *Callicebus*. In all of these clusters, species that are similar in habitat occupancy differ in diet and/or use of the forest canopy. For example, *Pithecia* primarily consumes seeds and fruits, while *Alouatta* is a folivore-frugivore (Youlatos 2004). *Saimiri* and *Ateles* differ in height in the canopy and diet, with *Saimiri* eating more insects (Youlatos 2004) and *Ateles* mainly exhibiting frugivory (Dew 2005). While *Cebus*, *Saguinus* and *Callicebus* do not differ in height in the canopy, *Cebus* is an omnivore (Youlatos 2004), *Callicebus* primarily consumes fruit and leaves (Youlatos 2004), and *Saguinus* eats fruit, insects and gums (Heymann 2000). Our result that species that were typically observed at similar heights in the canopy are those that have been documented in the literature to diverge in diet is also consistent with the finding that species with similar diets tend to exhibit differences in habitat use and/or height in the forest canopy (Fleagle & Mittermeier 1980). Consequently, the primate species at TBS are ecologically segregated in terms of habitat use, height in the canopy and probably diet.

Relationships between phylogenetic and ecological distance

The finding that there is no relationship between phylogenetic distance and ecological distance among the primate species at TBS does not strongly support the hypotheses of phylogenetic niche conservatism or natural selection promoting ecological differentiation among closely related species to avoid competitive exclusion. 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, though not detected by the analysis of ecological distances between species pairs in the same versus in different families, lends more support to the hypothesis that natural selection promotes ecological differentiation to avoid competitive exclusion among closely related species rather than the niche conservatism hypothesis.

In their examination of birds, mammals and butterflies in Mexico, Peterson *et al.* (1999) demonstrated niche conservatism among sister-species pairs but not at the family level. This finding, which implies that niche differentiation likely occurs at the time scale of higher taxonomic levels such as genera or families (Peterson *et al.* 1999), is consistent with our lack of support for niche conservatism (along the axis of habitat

occupancy) given that there are no congeners in the TBS primate community. 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 & Graham (2005) remark, rather than focusing on 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 differences in habitat occupancy among species within each monophyletic family. 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 & 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 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, suggesting that the relationship between phylogenetic and ecological similarity may vary across spatial scales. Thus, further examination of this relationship in platyrrhine communities across different spatial scales is merited.

ACKNOWLEDGEMENTS

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