



Tree community structure reflects niche segregation of three parapatric squirrel monkey species (*Saimiri* spp.)

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Abstract

Integration between ecology and biogeography provides insights into how niche specialization affects the geographical distribution of species. Given that rivers are not effective barriers to dispersal in three parapatric species of squirrel monkeys (*Saimiri vanzolinii*, *S. cassiquiarensis* and *S. macrodon*) inhabiting floodplain forests of Central Amazonia, we tested whether forest structure and tree diversity may explain species differences in niche specialization and spatial segregation. We sampled 6617 trees of 326 species in three habitats (high várzea, low várzea and chavascal) used by three *Saimiri* species, and estimated tree species richness in each of them. For each tree, we measured variables known to influence habitat use in primates, such as crown area and presence of lianas, epiphytes and hemi-epiphytes. We used ANOVA to compare these variables and performed multivariate analyses (NMDS, ANOSIM and SIMPER) to evaluate dissimilarities in forest structure among each habitat inhabited by the three *Saimiri* species. We identified differences in the tree species richness, crown area and presence of lianas, epiphytes and hemi-epiphytes between the three habitats for all *Saimiri* species. NMDS demonstrated that areas of high and low várzeas occupied by *S. vanzolinii* were clearly separated from the other species. We also found that different plant species contributed to dissimilarity among *Saimiri* ranges. Our findings support the hypothesis that tree community structure may promote niche specialization and spatial segregation among primates. We discuss how these patterns could have been favored by historical changes in forest flood patterns, the evolutionary history of *Saimiri* spp., and past competition.

Keywords Amazon · Forest structure · Geographic barriers · Habitat similarity · Threatened species

Introduction

Theories from ecology and historical biogeography provide insights regarding the evolutionary importance of habitat differentiation in speciation (Cadotte et al. 2010; Jenkins and Ricklefs 2011; Wiens 2011). Identifying ecological differences in habitats used by closely related species can help to determine the local processes driving the limits of modern geographical species distributions such as dispersal and the putative suite of past environmental conditions inhabited by ancestral clades (Francis and Currie 2003; Wiens and Donoghue 2004). It is difficult to infer whether similar species that currently coexist competed in the past, or have more recently come to overlap in their distribution, and which particular extant phenotypes result from adaptations to past competition (see the ghost of competition past theory, Connell 1980). In general, geographical distribution of species are influenced by (1) the ancestral ecological niche of the clade; (2) the geographical starting point of dispersal; (3)

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interspecific competition; (4) the amount of time elapsed since clade origin and time to dispersal (Wiens and Donoghue 2004) and (5) past competition (Connell 1980), as well as random historical factors.

Riverine barriers (Wallace 1852) and the Pleistocene forest refuge hypotheses (Haffer 1969) represent key theories used to explain patterns of species diversity, particularly in the Amazon. For a number of Amazonian birds, riverine barriers play a strong role in species diversification (Ribas et al. 2012). Similarly for Amazonian primates, rivers play an important role in constraining dispersal and diversification, which are influenced by a species' ability to cross this ecological barrier and the size and rate of flow of the rivers (Ayres and Clutton-Brock 1992). For black-water rivers (those located in unflooded forests), species which occur on one river bank are not often found on the opposite one (Ayres and Clutton-Brock 1992). In contrast, primate communities are often distributed on both banks in areas with white-water rivers, located in flooded forests (Ayres and Clutton-Brock 1992). This has been reported across several primate taxa which inhabit both forests types, including species of the genera *Alouatta*, *Cacajao*, *Cebus*, *Sapajus* and *Saimiri*, which present larger geographical distributions than species of genera inhabiting only unflooded forests, such as *Saguinus*, *Mico* and *Plectorucebus* (Ayres and Clutton-Brock 1992).

Seasonal white-river flooded forests (hereafter várzeas) are a major vegetation type in the Amazon (Prance 1979) and are annually covered by up to 10 m of nutrient-rich white water (Furch 1984; Klammer 1984; Junk et al. 1989, 2012). This annual flooding influences plant phenology (Schöngart et al. 2002; Haugaasen and Peres 2005; Parolin et al. 2011; Paim et al. 2017) and therefore food availability for primates (Paim et al. 2017). Water levels are a crucial factor determining the floristic composition of the várzeas, driving differences among local habitats (Ayres 1993; Wittmann et al. 2006). Várzeas have the highest density of primate species in the Amazon, showing higher densities relative to unflooded forests (Haugaasen and Peres 2005). For *Saimiri ustus*, for example, density can be six times higher in várzeas compared to unflooded forests (Peres 1997). This forest type is nutrient-poor due to the absence of rich alluvial sediments (Klammer 1984; Irion et al. 2010), producing less biomass, which is crucial to consumers (Junk and Piedade 1997; Peres 1997). Thus, due the high biomass production, várzeas seem to be an important environment for primates, making them useful to investigations examining the set of ecological factors that promote interspecific segregation.

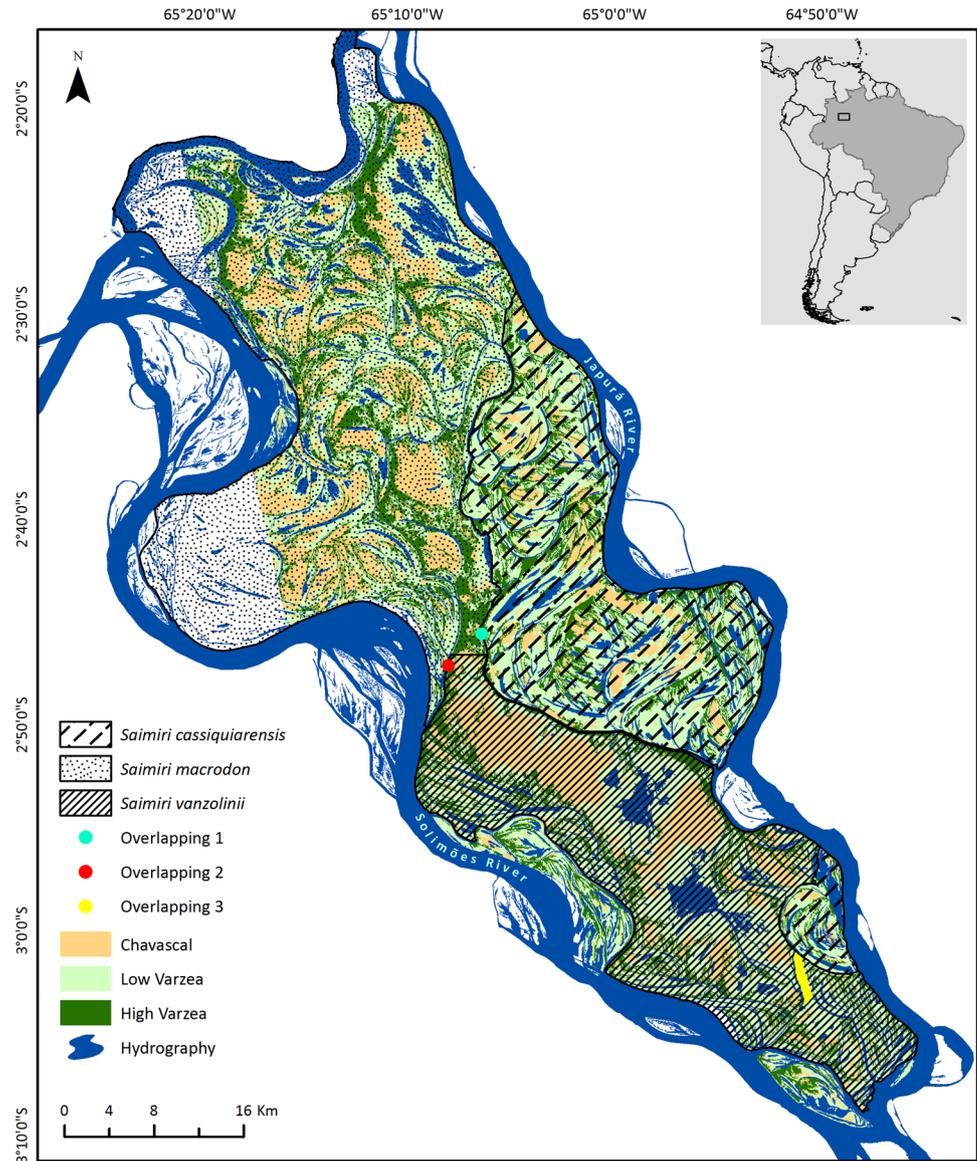
Reserva de Desenvolvimento Sustentável Mamirauá (RDSM) is the largest protected area (11,240 km²) devoted to the conservation of Amazon floodplain forests. This reserve is home to three of the seven species of squirrel monkey (*Saimiri vanzolinii*, *S. cassiquiarensis* and *S. macrodon*;

Paim et al. 2013; Rylands et al. 2013; Lynch-Alfaro et al. 2015). These three species overlap at the borders of their geographical distributions, but their borders lack clear geographical barriers such as large rivers (Paim et al. 2013) that otherwise appear to separate some primate species (Ayres and Clutton-Brock 1992). Based on phylogeographical evidence, over the past 150,000 years *S. vanzolinii* diversified in the Mamirauá region, *S. cassiquiarensis* expanded its distribution and crossed the Japurá River into Venezuela and *S. macrodon* expanded to the South of the Solimões River and into Peru and Colombia (Lynch-Alfaro et al. 2015). Thus, a study focusing on forest structure and tree species richness at RDSM may provide biogeographical insights into the dispersal and evolutionary history of these three squirrel monkey species (Fig. 1).

Saimiri vanzolinii shows strong endemism and inhabits the smallest geographic distribution of any Neotropical primate with a range of only ~870 km². In contrast, *S. cassiquiarensis* and *S. macrodon* inhabit larger areas (Paim et al. 2013; Lavergne et al. 2010; Chiou et al. 2011), although at present, we lack knowledge of the extent of their geographical distributions. In RDSM, there are small white-water channels that are thought to act as dispersal barriers to squirrel monkeys, as they were believed to define the limits of the species' distributions (Ayres 1985; Ayres and Clutton-Brock 1992). However, recent direct contact among the species was documented—mixed groups of *S. cassiquiarensis* and *S. vanzolinii*, *S. macrodon* and *S. vanzolinii*, and *S. cassiquiarensis* and *S. macrodon* have been reported (Paim et al. 2013; Lynch-Alfaro et al. 2015; Paim and Rabelo, 2015). Despite this contact, there is no evidence of hybridization based on the fact no animals with intermediate traits have been observed (F.P. Paim, personal observation). However, in the absence of genetic information, this cannot be confirmed. In cases where hybridization has not occurred under conditions of sympatry, habitat segregation may be the mechanism by which species separation is maintained. For example, in Colombia, *A. seniculus* and *A. palliata* are present in the same forests, but inhabiting different vegetation types and height (Leal and Defler 2013).

Patterns of use of space (e.g. home range and habitat selection), either when sympatric species use distinct habitats with different intensities, or regional spatial segregation, can help illuminate the relative importance of the mechanisms permitting coexistence, and factors leading to separate species distributions. For example, *Sapajus libidinosus* and *Callithrix jacchus*, with overlapping geographical distributions, differ in diet and the vertical use of space (Cunha and Vieira 2004). Differences in habitat selection were observed among *Saimiri* species in the RDSM. While *Saimiri vanzolinii* selects chavascal (i.e. areas mainly dominated by shrub vegetation that are flooded for 6–8 months annually), both *S. cassiquiarensis* and *S. macrodon* select low várzeas (i.e.

Fig. 1 Study area showing areas inhabited by the three *Saimiri* species and their habitat types associated. Overlapping 1 = mixed groups of *S. cassiquiarensis* and *S. macrodon* observed; overlapping 2 = mixed groups of *S. macrodon* and *S. vanzolinii* observed; overlapping 3 = mixed groups of *S. vanzolinii* and *S. cassiquiarensis* observed; unpainted spaces in *S. macrodon* distribution represent areas where classified images were not available



areas with open canopies, flooding to a depth of 2.6–5 m; Paim 2008). Moreover, it remains unclear why *S. cassiquiarensis* and *S. macrodon* select low várzeas and while *Saimiri vanzolinii* selects chavascal.

RDSM presents three species of *Saimiri* and there are no geographical barriers separating them. This offers an excellent opportunity to study how ecological factors contribute to species-specific differences in the geographic distribution, potentially indicating the importance of niches in maintaining species coexistence. The three different habitat types differ in flooding time and forest structure. Based on differentiation in habitat use by the three *Saimiri* species, and spatial separation without clear barriers among them, we hypothesized that forest structure provides a mechanism for niche segregation among these three closely related species. We predicted that richness and abundance of tree species, presence of lianas, epiphytes and hemi-epiphytes, and crown

area will differ among the habitat types in each of the areas inhabited by each species of squirrel monkeys.

Methods

Study area

The study was carried out in a 2600-km² area in the southern portion of RDSM (03°08'–02°36'S, 65°45'–67°13'W). This area has four seasons, distinguished by water levels: the flooded season (May to July); the water recession season (August to October); the dry season (November to January); and the rising water season (February to April; Ramalho et al. 2009). RDSM is comprised of three main habitats (i.e. forest types). The highest forest type (high várzea) floods for 2–4 months to a depth of 1 to 2.5 m; the intermediate

(low várzea) floods for 6 months to a depth of 2.5–5 m; and the lowest forest type (chavascal), which remains flooded 6–8 months of the year at a depth of up to 5 m (Ayres 1993).

Data collection

Within the previously determined distribution of each species of *Saimiri* (Paim et al. 2013), we sampled 24 randomly located 25 × 25-m plots in each habitat (high várzea, low várzea and chavascal; 216 plots in total); if two plots were within 25 m of one another, a new random location was selected. We chose this method to facilitate access to the plots in all seasons, by foot or canoe. Habitat classifications follow Ferreira-Ferreira et al. (2014; Fig. 1). All sampling was done during the low-water period in 2013 and 2014.

We located all woody stems with a diameter at breast height (DBH) ≥ 10 cm and recorded: (1) DBH, (2) crown area (by multiplying the longest axis of the crown by the shortest perpendicular axis) and (3) presence of lianas, epiphytes and hemi-epiphytes (LEH) for each tree and palm in each plot. For the presence of LEH, we considered three categories: 0 = no presence; 1 = one specimen present; and 2 = two or more specimens present. To avoid inter-observer variability, all estimation was made by the same person (F.P. Paim). We calculated the mean values for all variables for all measured trees, to express a general index for each plot. For trees with multiple trunks, we measured only trunks with DBH ≥ 10 cm and considered each one as a single tree (Following Chapman et al. 1992). Voucher specimens were collected for all trees and palms and were identified at the Herbarium of the Instituto Nacional de Pesquisas da Amazônia (INPA). We used the website Taxonomic Name

Resolution (<http://tnrs.iplantcollaborative.org/>; Boyle et al. 2013) to confirm the species identities and nomenclature.

Data analysis

For each plot, we calculated the mean for presence of LEH and crown area. After testing for normality and homoscedasticity, we contrasted these values among the habitats in each *Saimiri* species distribution using a one-way analysis of variance (ANOVA). To evaluate differences between pairs of habitat types for each species' range, we used Tukey's post hoc test. Each plot was considered as an independent unit. All analyses were performed using SPSS 22 (2013).

We performed non-metric multidimensional scaling (2D NMDS), based on the Bray–Curtis index of similarity to evaluate the influence of tree and palm species richness and abundance in each of the three habitat types in each of the area inhabited by the three species. For this analysis, we considered the total number of species registered in each plot. The stress value represents distortion of distance, where values close to zero mean the distances on the graphic representation are more accurate (Legendre and Legendre 1998; Clarke and Warwick 2001).

We conducted an analysis of similarity (ANOSIM) with 9999 permutations to verify differences in habitat based on tree species richness and abundance among the squirrel monkey distributions. *R* values indicate the biological importance of differences, ranging between -1 and 1 . Values greater than zero indicate differences between groups, while zero represents the absence of differences between groups. Negative *R* values indicate that dissimilarities within groups are greater than dissimilarities between groups (Clarke and

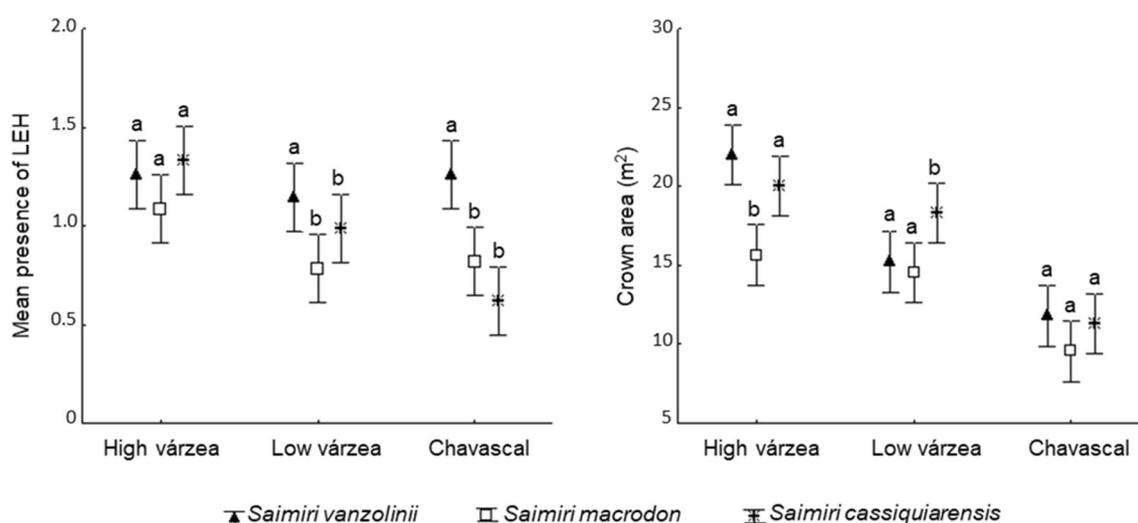


Fig. 2 Mean (\pm confidence interval) presence of lianas, epiphytes and hemi-epiphytes (LEH), and mean (\pm confidence interval) crown area (m²) for trees and palms in three habitats in areas inhabited by

Saimiri vanzolinii, *S. cassiquiarensis* and *S. macrodon*. For the same independent variable, a different letter indicates significant difference at $P < 0.05$

Warwick 2001). We set the alpha value to 0.05 and used a Bonferroni correction (Zar 2010).

We used similarity percentage (SIMPER) analyses to quantify the relative contribution of each tree and palm species among *Saimiri* distributions (Clarke 1993). This analysis was done by pairing squirrel monkey species' habitats and determining which species contribute most to the dissimilarity between different habitat types for each *Saimiri* species distribution. For example, we compared dissimilarity between high várzeas in areas inhabited by *S. macrodon* and *S. cassiquiarensis* and the same procedure was applied for all combinations of all three *Saimiri* distributions for the three habitat types. We ran SIMPER in each habitat to identify the top three ranked species and their respective percentage effects on dissimilarity among *Saimiri* species distributions. We also selected the top ten ranked plant species to identify their contribution to habitat dissimilarity in multiple comparisons.

Comparisons in both ANOSIM and SIMPER were made using a Bray–Curtis index of similarity and used the number of tree and palm specimens sampled, considering their abundance (i.e. number of specimens by species) for the three habitats. NMDS, ANOSIM and SIMPER tests were analyzed using PAST 2.16 software (Hammer et al. 2001).

Results

We recorded 6617 trees of 326 species, in a total of 13.5 ha in the 216 plots (Electronic Supplementary Material 1). Presence of LEH did not differ among areas of the three species in the high várzeas ($F=1.59$; $P=0.21$). Low várzeas and chavascal presented differences ($F=8.33$; $P=0.0005$ and

$F=12.262$; $P=0.0003$, respectively). For both low várzeas and chavascal, a post hoc Tukey test demonstrated that presence of LEH in *S. vanzolinii*'s area was higher than the area of *S. macrodon* and *S. cassiquiarensis*, differing significantly at $P<0.05$ (Fig. 2). Crown area did not differ among areas of the three species in the chavascal ($F=2.38$; $P=0.09$). We found difference in the high ($F=6.80$; $P=0.002$) and low várzeas ($F=6.12$; $P=0.003$). For the high várzeas, a post hoc Tukey test showed that areas occupied by *S. macrodon* presented smaller crown area than those occupied by the other species, differing significantly at $P<0.05$. Low várzeas of *S. cassiquiarensis* showed largest crown area, differing from *S. vanzolinii* and *S. macrodon*, at $P<0.05$ (Fig. 2).

NMDS ordinations showed that high and low várzeas occupied by *S. cassiquiarensis* and *S. macrodon* were more similar to one another than those occupied by *S. vanzolinii* (Fig. 3a, b). For the chavascal, areas occupied by the three species were very similar (Fig. 3c). In addition, global analysis using ANOSIM demonstrated differences in the species richness among all *Saimiri* distributions: high várzea ($R=0.304$; $P<0.001$), low várzea ($R=0.385$; $P<0.001$) and chavascal ($R=0.175$; $P<0.001$). We found differences in all possible combination pairs among the habitats of the three *Saimiri* distributions (Table 1). SIMPER indicated that the plant species that contributed the most to dissimilarity among *Saimiri* distributions were: (1) high várzea: *Attalea phalerata* (3.11%), *Xylopia calophylla* (2.58%) and *Guatteria olivacea* (2.27%); (2) low várzea: *Mabea nitida* (3.20%), *Oxandra riedeliana* (2.86%) and *Neea spruceana* (2.54%) and (3) chavascal: *Pseudobombax munguba* (8.71%), *Triplaris weigeltiana* (5.11%) and *Triplaris dugandii* (4.58%; Table 2).

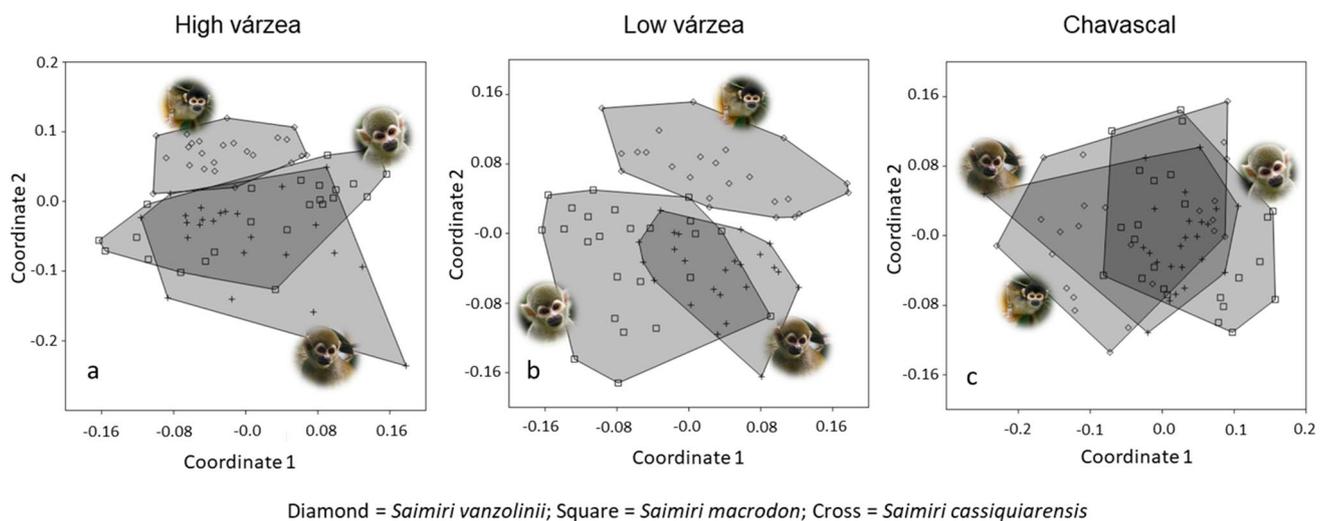


Fig. 3 Two-dimensional NMDS plots of similarity among arboreal community in three types of habitats in three *Saimiri* ranges. Each sampled plot in each habitat is indicated by a different symbol. Diamond=*Saimiri vanzolinii*; square=*Saimiri macrodon*; cross=*Saimiri cassiquiarensis*

Table 1 Analysis of similarity (ANOSIM) among arboreal community in three types of habitats in three *Saimiri* ranges. SV, *Saimiri vanzolinii*; SM, *Saimiri macrodon*; SC, *Saimiri cassiquiarensis*

Species range	High várzea			Low várzea			Chavascal		
	SV × SM	SV × SC	SM × SC	SV × SM	SV × SC	SM × SC	SV × SM	SV × SC	SM × SC
<i>R</i>	0.364	0.394	0.115	0.382	0.407	0.370	0.181	0.236	0.122
<i>P</i>	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

Table 2 Similarity percentage (SIMPER) analysis of top 10 ranked species in each habitat based on comparison between pairs of species ranges

High Várzea			
	vanzolinii/macrodon	vanzolinii/cassiquiarensis	macrodon/cassiquiarensis
1°	<i>Attalea phalerata</i> (3.96%)	<i>Xylopia calophylla</i> (2.84%)	<i>Attalea phalerata</i> (3.42%)
2°	<i>Leonia glycyarpa</i> (2.71%)	<i>Guatteria olivaceae</i> (2.31%)	<i>Xylopia calophylla</i> (3.06%)
3°	<i>Oxandra riedeliana</i> (2.43%)	<i>Pseudolmedia laevigata</i> (2.16%)	<i>Leonia glycyarpa</i> (2.29%)
4°	<i>Guatteria olivaceae</i> (2.36%)	<i>Eschweilera albiflora</i> (2.12%)	<i>Eschweilera albiflora</i> (2.20%)
5°	<i>Inga splendens</i> (2.31%)	<i>Oxandra riedeliana</i> (2.11%)	<i>Guatteria olivaceae</i> (2.14%)
6°	<i>Pseudolmedia laevigata</i> (2.30%)	<i>Molouetia tamaquarina</i> (2.06%)	<i>Virola surinamensis</i> (2.03%)
7°	<i>Eschweilera parvifolia</i> (2.24%)	<i>Ocotea cymbarum</i> (2.02%)	<i>Cecropia membranaceae</i> (1.98%)
8°	<i>Ocotea cymbarum</i> (2.18%)	<i>Attalea phalerata</i> (1.97%)	<i>Gustavia poeppigiana</i> (1.93%)
9°	<i>Theobroma cacao</i> (2.02%)	<i>Garcinia madruno</i> (1.88%)	<i>Molouetia tamaquarina</i> (1.79%)
10°	<i>Molouetia tamaquarina</i> (2.01%)	<i>Eschweilera parvifolia</i> (1.81%)	<i>Sapium glandulosum</i> (1.78%)
Low Várzea			
1°	<i>Licania apetala</i> (9.22%)	<i>Licania apetala</i> (7.45%)	<i>Mabea nitida</i> (3.50%)
2°	<i>Inga splendens</i> (4.15%)	<i>Micropholis trunciflora</i> (6.13%)	<i>Neea spruceana</i> (3.13%)
3°	<i>Maquira coriaceae</i> (3.94%)	<i>Micropholis egensis</i> (5.81%)	<i>Eschweilera albiflora</i> (3.30%)
4°	<i>Licaria armeniaca</i> (3.49%)	<i>Aniba terminalis</i> (4.21%)	<i>Minuartia guianensis</i> (2.82%)
5°	<i>Micropholis egensis</i> (3.21%)	<i>Annona tenuipes</i> (4.15%)	<i>Pouteria procerca</i> (2.62%)
6°	<i>Micropholis trunciflora</i> (3.20%)	<i>Calycolpus goetheanus</i> (3.67%)	<i>Annona tenuipes</i> (2.49%)
7°	<i>Cratylia</i> sp. (3.08)	<i>Maquira coriaceae</i> (3.62%)	<i>Virola calophylla</i> (2.48%)
8°	<i>Annona tenuipes</i> (2.99%)	<i>Cratylia</i> sp. (3.41%)	<i>Xylopia calophylla</i> (2.34%)
9°	<i>Aniba terminalis</i> (2.56%)	<i>Allophylus amazonicus</i> (2.99%)	<i>Drypetes variabilis</i> (2.20%)
10°	<i>Lacistema aggregatum</i> (2.16%)	<i>Hura crepitans</i> (2.15%)	<i>Leonia glycyarpa</i> (1.99%)
Chavascal			
1°	<i>Pseudobombax munguba</i> (9.22%)	<i>Pseudobombax munguba</i> (7.45%)	<i>Pseudobombax munguba</i> (9.47%)
2°	<i>Paramachaerium ormosioides</i> (4.15%)	<i>Triplaris weigeltiana</i> (6.14%)	<i>Triplaris weigeltiana</i> (6.11%)
3°	<i>Symmeria paniculata</i> (3.94%)	<i>Triplaris dugandii</i> (5.81%)	<i>Triplaris dugandii</i> (4.79%)
4°	<i>Sickingia tinctoria</i> (3.49%)	<i>Astrocaryum jauari</i> (4.21%)	<i>Buchenavia oxycarpa</i> (4.51%)
5°	<i>Triplaris dugandii</i> (3.21%)	<i>Buchenavia oxycarpa</i> (4.15%)	<i>Paramachaerium ormosioides</i> (3.61%)
6°	<i>Triplaris weigeltiana</i> (3.20%)	<i>Cecropia latiloba</i> (3.67%)	<i>Sickingia tinctoria</i> (3.57%)
7°	<i>Eugenia florida</i> (3.08%)	<i>Symmeria paniculata</i> (3.62%)	<i>Astrocaryum jauari</i> (3.51%)
8°	<i>Buchenavia oxycarpa</i> (2.99%)	<i>Eugenia florida</i> (3.41%)	<i>Cecropia latiloba</i> (3.50%)
9°	<i>Astrocaryum jauari</i> (2.56%)	<i>Aniba affinis</i> (2.99%)	<i>Ficus americana</i> (3.44%)
10°	<i>Piranhea trifoliata</i> (2.16%)	<i>Ficus americana</i> (2.15%)	<i>Aniba affinis</i> (2.79%)

Discussion

Understanding how ecological factors drive niche specialization and geographical distribution of species is complex

since many variables can be involved. Our results show that differences among habitats are associated with differences in habitat use by three species of *Saimiri*. Tree and palm species diversity differs between high- and low-várzea areas

(Wittmann et al. 2006; Assis and Wittmann 2011), thus it could promote squirrel monkey species segregation.

We also found differences among the habitats used by the different species of *Saimiri* with respect to crown area and presence of LEH. High várzeas did not show differences among the *Saimiri* species' distributions with respect to LEH, but in both low várzea and chavascal, areas inhabited by *S. vanzolinii* had the highest presence of LEH when compared to areas inhabited by the other two species. While we lack data on the diet of *S. macrodon* and *S. cassiquiarensis*, *S. vanzolinii* consume a high proportion of LEH (Paim et al. 2017). Presence of LEH might be an important factor restricting the distribution of *S. vanzolinii*, which may contribute to its segregation. Finally, crown area in the high várzeas was largest in the *S. vanzolinii* and *S. cassiquiarensis* distributions. In addition, low várzeas inhabited by *S. cassiquiarensis* had the largest crown area. Chavascal had the smallest crown area in all squirrel monkey distributions, with no differences among them. Mean crown areas is positively related to food resource availability and may influence diet supplements for primates (Chapman et al. 1992). Thus, our results suggest that the areas occupied by *S. cassiquiarensis* in both high and low várzea potentially contain the greatest food. This finding suggests why *S. cassiquiarensis* prefer low várzeas (Paim 2008).

We found a clear separation of *S. vanzolinii* in the low- and high-várzea areas, meaning that the similarity between these habitats inhabited by *S. macrodon* and *S. cassiquiarensis* is high. In contrast, we observed a less distinct separation in the chavascal areas, meaning that this habitat is similar across the areas inhabited by the three *Saimiri* species. However, in this habitat, we registered one outlier for areas occupied by *S. cassiquiarensis*, which might influence the results (Fig. 3). In addition, we registered differences in the tree communities in all paired combinations for the three habitats, as demonstrated by the ANOSIM. *R* values demonstrated differences among habitats occupied by the three species of *Saimiri*. For the high várzeas, we observed the greater difference between two pairs: *S. vanzolinii* and *S. macrodon*, and *S. vanzolinii* and *S. cassiquiarensis*. We detected lower difference between high várzeas occupied by *S. macrodon* and *S. cassiquiarensis* (Table 1). Low várzeas presented similar *R* values, following the same pattern observed for the high várzeas, with the lower difference observed between areas occupied by *S. macrodon* and *S. cassiquiarensis* (Table 1). In general, chavascal presented the lower differences among all comparisons, with areas inhabited by *S. vanzolinii* and *S. cassiquiarensis* exhibiting the greater difference (Table 1). Such findings suggest that there are ecological differences between habitat types, where habitats occupied by *S. vanzolinii* differed greatly from those occupied by the two congeneric species. The strong overlap

and similarity observed in NMDS and ANOSIM between *S. cassiquiarensis* and *S. macrodon* areas indicate that other factors beyond what we have considered here (e.g. dynamic of flooded forests formation, divergence and speciation of these two species, and ability to disperse) could influence the spatial segregation of these species.

We found the richness for the most common tree species were dissimilar among different habitats. Despite the fact that many species are common in both the high- and low-várzea areas (Wittmann et al. 2006; Assis and Wittmann 2011), the difference in their abundances among areas may explain this result. For example, *Attalea phalerata* (a palm tree) contributed 3.11% of the dissimilarity of the high várzea occupied by each species. To our knowledge, studies focusing on chavascal diversity have never been conducted.

Current geographic distributions of species may be constrained by dispersal limitation or niche conservatism (Wiens and Donoghue 2004), though it is likely that niche breadth and geographic distribution are positively correlated. Our findings, coupled with the lack of evidence for dispersal limitation in these three species, suggest that habitat differences between *Saimiri* species result from niche specialization and subsequent spatial segregation. It is theorized that spatially restricted species are constrained by niche specialization and local conditions (e.g. food availability and habitat selection; Kirkpatrick and Barton 1997). On the other hand, widespread species might owe their geographic distribution to larger niche breadth, since they are able to occupy a greater variety of habitats (Gaston et al. 1997). Our results are supported by both theories, since *S. vanzolinii* occurs in a very restricted distribution and the areas in which it is found are quantitatively and qualitatively different from those inhabited by congeners. Additionally, *S. macrodon* and *S. cassiquiarensis* are both widespread species and their habitats are very similar, at least with respect to the variables analyzed here.

Conditions experienced by species in the recent past will influence their response to current conditions (McNamara et al. 2013). *Saimiri vanzolinii* diversified in Mamirauá ~ 260 kya, which is the most recent radiation among all squirrel monkeys. *Saimiri cassiquiarensis* and *S. macrodon* diversified earlier (~ 300 and ~ 420 kya, respectively) in other centers of endemism (Lynch-Alfaro et al. 2015). The current floodplain forests observed at the study site are of Holocene origin, only around 11 thousand years old (Irión et al. 2010). This type of environment experiences short and long-term modification based on destruction and reconstruction of channels, small rivers and islands, and dramatically affects the region's vegetation and landscape (Klammer 1984; Wittmann et al. 2010). It is likely that divergence and speciation of *S. vanzolinii* could have occurred in areas close to the region currently protected by Mamirauá Reserve. This

suggests that constraints imposed by *S. cassiquiarensis* and *S. macrodon* could have forced *S. vanzolinii* to its current limited distribution. Although there is presently no evidence to support this claim, past competition (Connell 1980) and long-term modification in the flooded forests (Klammer 1984; Wittmann et al. 2010) may partly explain the current geographical distribution of *S. vanzolinii*. In the study area, small channels limit the distribution of all *Saimiri* species (Paim et al. 2013). *Saimiri* can swim (F.P. Paim personal observation), but it appears that when the squirrel monkeys cross the channel, they do not establish populations on the other side or have not done so thus far. Further, in at least two areas, there are no geographic barriers between *S. vanzolinii* and *S. cassiquiarensis* or between *S. vanzolinii* and *S. macrodon* (Paim et al. 2013), and mixed-species groups have been observed (Paim and Rabelo 2015). Studies focusing on ecological phylogeography, historical biogeography, and genetic characterization of individuals in mixed groups must be conducted to relate the floodplain forest formation with the current geographical distribution of *Saimiri* and its radiation in Central Amazon.

Species inhabiting small geographical areas are at higher risk of extinction from stochastic events and climate change (Bellard et al. 2012). The current habitat of *S. vanzolinii* is very sensitive to changes occurring in the floodplain forests. According to the International Union for Conservation of Nature (IUCN Red List), *Saimiri vanzolinii* is considered to be vulnerable to extinction (Boubli and Rylands 2008; Paim et al. 2015), while *S. cassiquiarensis* and *S. macrodon* are considered as of least concern (Boubli et al. 2008). Based on the limited geographical distribution of *S. vanzolinii* and our results, we are concerned that any habitat loss due to anthropogenic disturbance (e.g. selective logging) or habitat modification caused by global climate change (IPCC 2014) could lead *S. vanzolinii* to extinction. Thus, there is an urgent need for a detailed conservation plan for *S. vanzolinii* and continue monitoring should be a priority.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Statement on the welfare of animals This article does not contain any studies with human participants or animals performed by any of the authors.

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