Primates
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ORIGINAL ARTICLE

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 km^2) 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 km^2. 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.

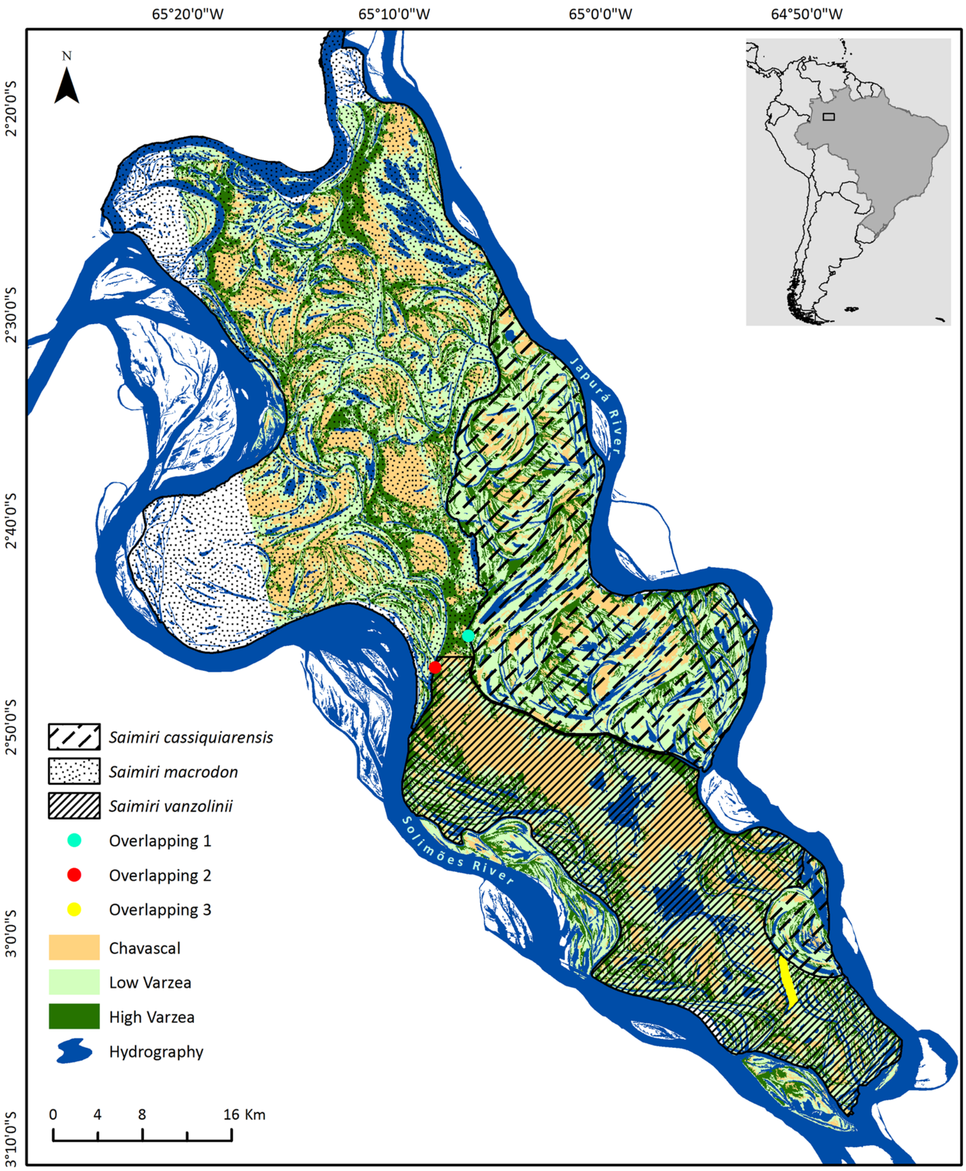

Fig. 1 Study area showing areas inhabited by the three *Saimiri* species and their habitat types associated. Overlapping 1 = mixed groups of *S. cassiquiarensis* and *S. macrodon* observed; overlapping 2 = mixed groups of *S. macrodon* and *S. vanzolinii* observed; overlapping 3 = mixed groups of *S. 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-km^2 area in the southern portion of RDSM (03º08′-02º36′S, 65º45′-67º13′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

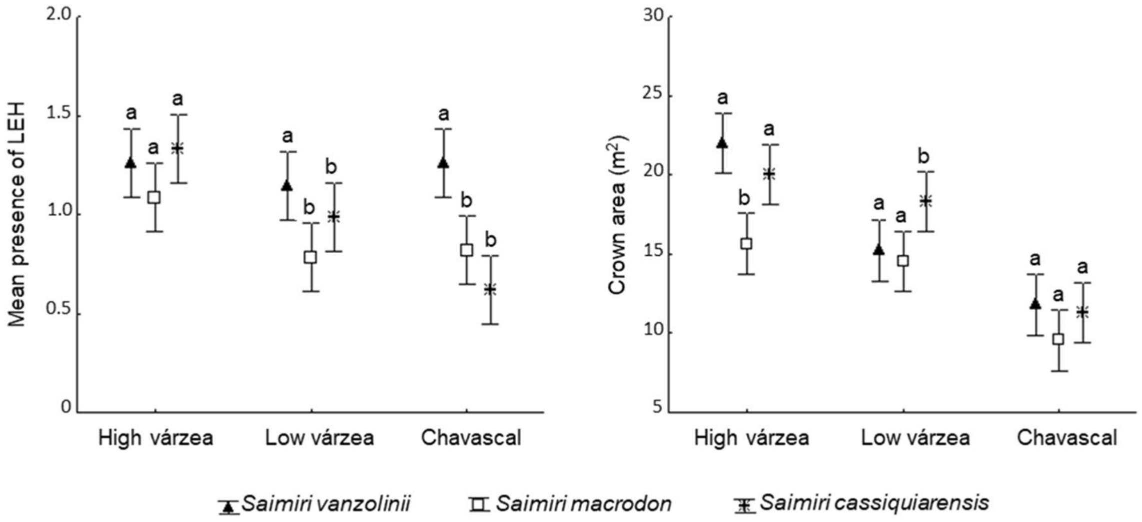

Fig. 2 Mean (± confidence interval) presence of lianas, epiphytes and hemi-epiphytes (LEH), and mean (± confidence interval) crown area (m^2) for trees and palms in three habitats in areas inhabited by *Saimiri vanzolinii*, *S. cassiquiarensis* and *S. macrodon*. For the same independent variable, a 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 callophylla* (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).

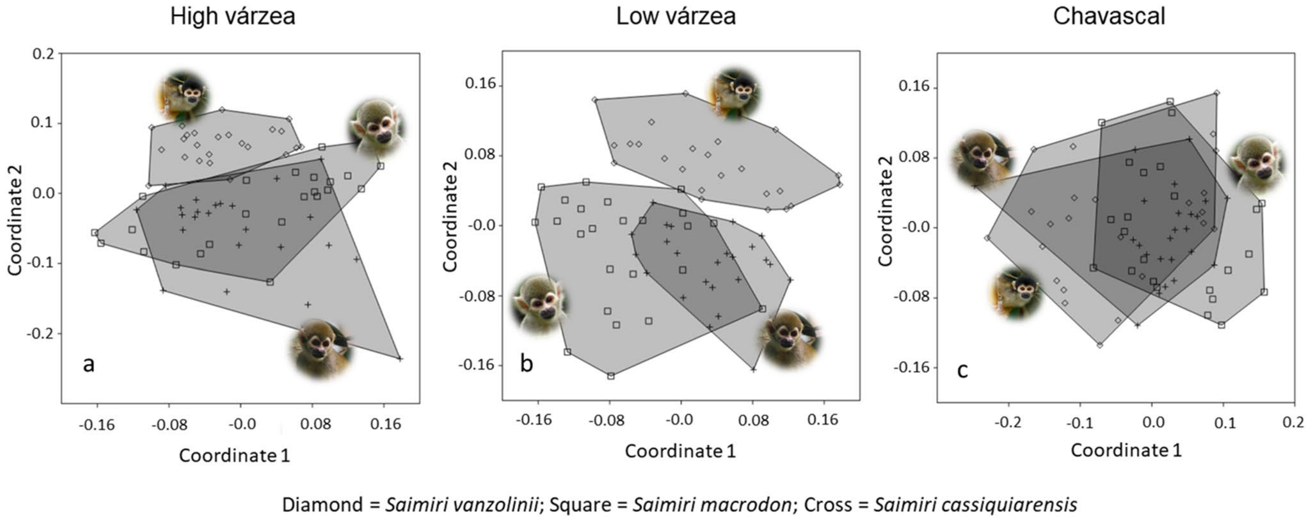

Fig. 3 Two-dimensional NMDS plots of similarity among arboreal community in three types of habitats in three *Saimiri* ranges. Each sampled plot in each habitat is indicated by a different symbol. Diamond = *Saimiri vanzolinii*; square = *Saimiri macrodon*; cross = *Saimiri cassiquiarensis*

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		
Habitat	SV×SM	SV×SC	SM×SC	SV×SM	SV×SC	SM×SC	SV×SM	SV×SC	SM×SC
R	0.364	0.394	0.115	0.382	0.407	0.370	0.181	0.236	0.122
P	< 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°	*Attalea phalerata* (3.96%)	*Xylopia calophylla* (2.84%)	*Attalea phalerata* (3.42%)
2°	*Leonia glycycarpa* (2.71%)	*Guatteria olivaceae* (2.31%)	*Xylopia calophylla* (3.06%)
3°	*Oxandra riedeliana* (2.43%)	*Pseudolmedia laevigata* (2.16%)	*Leonia glycycarpa* (2.29%)
4°	*Guatteria olivaceae* (2.36%)	*Eschweilera albiflora* (2.12%)	*Eschweilera albiflora* (2.20%)
5°	*Inga splendens* (2.31%)	*Oxandra riedeliana* (2.11%)	*Guatteria olivaceae* (2.14%)
6°	*Pseudolmedia laevigata* (2.30%)	*Molouetia tamaquarina* (2.06%)	*Virola surinamensis* (2.03%)
7°	*Eschweilera parvifolia* (2.24%)	*Ocotea cymbarum* (2.02%)	*Cecropia membranaceae* (1.98%)
8°	*Ocotea cymbarum* (2.18%)	*Attalea phalerata* (1.97%)	*Gustavia poeppigiana* (1.93%)
9°	*Theobroma cacau* (2.02%)	*Garcinia madruno* (1.88%)	*Molouetia tamaquarina* (1.79%)
10°	*Molouetia tamaquarina* (2.01%)	*Eschweilera parvifolia* (1.81%)	*Sapium glandulosum* (1.78%)
Low Várzea			
1°	*Licania apetala* (9.22%)	*Licania apetala* (7.45%)	*Mabea nitida* (3.50%)
2°	*Inga splendens* (4.15%)	*Micropholis trunciflora* (6.13%)	*Neea spruceana* (3.13%)
3°	*Maquira coriaceae* (3.94%)	*Micropholis egensis* (5.81%)	*Eschweilera albiflora* (3.30%)
4°	*Licaria armeniaca* (3.49%)	*Aniba terminalis* (4.21%)	*Minquartia guianensis* (2.82%)
5°	*Micropholis egensis* (3.21%)	*Annona tenuipes* (4.15%)	*Pouteria procera* (2.62%)
6°	*Micropholis trunciflora* (3.20%)	*Calycolpus goetheanus* (3.67%)	*Annona tenuipes* (2.49%)
7°	*Cratylia* sp. (3.08)	*Maquira coriaceae* (3.62%)	*Virola calophylla* (2.48%)
8°	*Annona tenuipes* (2.99%)	*Cratylia sp.* (3.41%)	*Xylopia calophylla* (2.34%)
9°	*Aniba terminalis* (2.56%)	*Allophylus amazonicus* (2.99%)	*Drypetes variabilis* (2.20%)
10°	*Lacistma aggregatum* (2.16%)	*Hura crepitans* (2.15%)	*Leonia glycycarpa* (1.99%)
Chavascal			
1°	*Pseudobombax munguba* (9.22%)	*Pseudobombax munguba* (7.45%)	*Pseudobombax munguba* (9.47%)
2°	*Paramachaerium ormosioides* (4.15%)	*Triplaris weigeltiana* (6.14%)	*Triplaris weigeltiana* (6.11%)
3°	*Symmeria paniculata* (3.94%)	*Triplaris dugandii* (5.81%)	*Triplaris dugandii* (4.79%)
4°	*Sickingia tinctoria* (3.49%)	*Astrocaryum jauari* (4.21%)	*Buchenavia oxycarpa* (4.51%)
5°	*Triplaris dugandii* (3.21%)	*Buchenavia oxycarpa* (4.15%)	*Paramachaerium ormosioides* (3.61%)
6°	*Triplaris weigeltiana* (3.20%)	*Cecropia latiloba* (3.67%)	*Sickingia tinctoria* (3.57%)
7°	*Eugenia florida* (3.08%)	*Symmeria paniculata* (3.62%)	*Astrocaryum jauari* (3.51%)
8°	*Buchenavia oxycarpa* (2.99%)	*Eugenia florida* (3.41%)	*Cecropia latiloba* (3.50%)
9°	*Astrocaryum jauari* (2.56%)	*Aniba affinis* (2.99%)	*Ficus americana* (3.44%)
10°	*Piranhea trifoliata* (2.16%)	*Ficus americana* (2.15%)	*Aniba affinis* (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 conservativism (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. cassiquiarenis* 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 an\ ~ 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 (Irion 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.

References

Ayres JM (1985) On a new species of squirrel monkey, genus Saimiri, from Brazilian Amazonia (Primates, Cebidae). Pap Avulsos Zool 36(14):47–164

Assis RL, Wittmann F (2011) Forest structure and tree species composition of the understory of two central Amazonian várzea forests of contrasting flood heights. Flora 206:251–260. https://doi.org/10.1016/j.flora.2010.11.002

Ayres JM (1993) As matas de várzea do Mamirauá: médio rio Solimões. Sociedade Civil Mamirauá/CNPq, Brasília

Ayres JM, Clutton-Brock TH (1992) River boundaries and species range size in Amazonian primates. Am Nat 40:531–537

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. Ecol Lett 15:365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Boubli JP, Rylands AB (2008) *Saimiri vanzolinii*. The IUCN Red List of Threatened Species 2008. http://www.iucnredlist.org/details/19839/0. Accessed 5 Sep 2017

Boubli JP, Rylands AB, de la Torre S, Stevenson P (2008) *Saimiri sciureus*. The IUCN Red List of Threatened Species 2008. http://www.iucnredlist.org/details/41537/0. Accessed 5 Sep 2017

Boyle B, Hopkins N, Lu Z, Garay JAR, Mozzherin D, Rees T, Matasci N, Narro ML, Piel WH, Mckay SJ, Lowry S, Freeland C, Peet RK, Enquist BJ (2013) The taxonomic name resolution service: an online tool for automated standardization of plant names. BMC Bioinform 14:16. https://doi.org/10.1186/1471-2105-14-16

Cadotte MW, Davies TJ, Regetz J, Kembel SW, Cleland E, Oakley TH (2010) Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. Ecol Lett 13:96–105. https://doi.org/10.1111/j.1461-0248.2009.01405.x

Chapman CA, Chapman LJ, Wrangham R, Gebo KHD, Gardner L (1992) Estimators of fruit abundance of tropical trees. Biotropica 24:527–531

Chiou KL, Pozzi L, Lynch-Alfaro JW, Di Fiore A (2011) Pleistocene diversification of living squirrel monkeys (*Saimiri* spp.) inferred from complete mitochondrial genome sequences. Mol Phylogen Evol 59:736–745. https://doi.org/10.1016/j.ympev.2011.03.025

Clarke KR (1993) Nonparametric multivariate analysis of changes in community structure. Aust J Ecol 18:117–143

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. Prymer-E Ltd, Plymouth

Connell JH (1980) Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35:131–138

Cunha AA, Vieira MV (2004) Two bodies cannot occupy the same place at the same time, or the importance of space in the ecological niche. Bull Ecol Soc Am 85:25–26

Ferreira-Ferreira J, Silva TFS, Streher AS, Affonso AG, Furtado LFA, Forsberg BR, Valsecchi J, Queiroz HL, Novo EMLM (2014) Combining ALOS/PALSAR derived vegetation structure and inundation patterns to characterize major vegetation types in the Mamirauá Susteinable Development Reserve, Central Amazon floodplain, Brazil. Wet Ecol Manag 23:41–59. https://doi.org/10.1007/s11273-014-9359-1

Francis AP, Currie DJ (2003) A globally consistent richness-climate relationship for angiosperms. Am Nat 161:523–536

Furch K (1984) Water chemistry of the Amazon basin: the distribution of chemical elements among freshwaters. In: Sioli H (ed) The Amazon: limnology and landscape ecology of a mighty tropical river and its basin. Junk Publishers, Dordrecht, pp 167–199

Gaston KJ, Blackburn TM, Lawton JH (1997) Interspecific abundance range size relationships: an appraisal of mechanisms. J Anim Ecol 66:579–601

Haffer J (1969) Speciation in Amazonian forest birds. Science 165:131–137

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. Paleontol Electr 4:1–9

Haugaasen T, Peres CA (2005) Mammal assemblage structure in Amazonian flooded and unflooded forests. J Trop Ecol 21:133–145. https://doi.org/10.1111/j.1744-7429.2005.00079.x

SPSS (2013) SPSS Base 22.0 for Windows user's guide. SPSS Inc, Chicago

IPCC (2014) Climate Change 2014: Synthesis Report. In: Pachauri RK, Meyer LA (eds) Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change. IPCC, Geneva, pp 2–26

Irion G, Mello JASN, Morais J, Piedade MTF, Junk WJ, Garming L (2010) Development of the Amazon valley during the middle to late quaternary: sedimentological and climatological observations. In: Junk HJ, Wittmann F, Parolin P, Piedade MTF, Schöngart J (eds) Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Dordrecht, pp 27–42

Jenkins DG, Ricklefs RE (2011) Biogeography and ecology: two reviews of one world. Phil Trans 366:2331–2335. https://doi.org/10.1098/rstb.2011.0064

Junk WJ, Piedade MTF (1997) Plant life in the floodplain with special reference to herbaceous plants. In: Junk WJ (ed) The central Amazon floodplain: ecology of a pulsing system. Springer, Berlin, pp 147–185

Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in river-floodplain systems. In: Dodge DP (ed) Proceedings of international large river symposium (LARS). Canadian special publication of fisheries and aquatic sciences, Toronto, pp 110–127

Junk WJ, Piedade MTF, Schöngart J, Wittmann F (2012) A classification of major natural habitats of Amazonian white-water river floodplains (várzeas). Wetl Ecol Manag 20:461–475. https://doi.org/10.1007/s11273-012-9268-0

Kirkpatrick M, Barton NH (1997) Evolution of a species' range. Am Nat 150(1):1–23

Klammer G (1984) The relief of the extra-Andean Amazon basin. In: Sioli H (ed) The Amazon: limnology and landscape ecology of a might tropical river and its basin. Junk Publishers, Dordrecht, pp 47–83

Lavergne A, Ruiz-García M, Catzeflis F, Lacote S, Contamin H, Mercereau-Puijalon O, Lacoste V, de Thoisy B (2010) Phylogeny and phylogeography of squirrel monkeys (genus *Saimiri*) based on cytochrome b genetic analysis. Am J Primatol 72:242–253. https://doi.org/10.1002/ajp.20773

Leal SAZ, Defler TR (2013) Sympatric distribution of two species of *Alouatta* (*A. seniculus* and *A. palliata*: Primates) in Chocó, Colombia. Neotrop Primates 20(1):1–11

Legendre P, Legendre L (1998) Numerical ecology, 2nd edn. Elsevier, Amsterdam

Lynch-Alfaro J, Boubli JP, Paim FP, Ribas CC, Silva MN, Messias MR, Röhe F, Mercês MP, Silva Júnior JS, Silva CR, Pinho GM, Koshkarian G, Nguyen MTT, Harada ML, Rabelo RM, Queiroz HL, Alfaro ME, Farias IP (2015) Biogeography of squirrel monkeys (genus *Saimiri*): south-central Amazon origin and rapid pan-Amazonian diversification of a lowland primate. Mol Phylogenet Evol 82:436–454. https://doi.org/10.1016/j.ympev.2014.09.004

McNamara JM, Fawcett TW, Houston AI (2013) An adaptive response to uncertainty generates positive and negative contrast effects. Science 340:1084–1086. https://doi.org/10.1126/science.1230599

Paim FP (2008) Estudo comparativo das espécies de *Saimiri* Voigt, 1831 (Primates, Cebidae) na Reserva Mamirauá, Amazonas. Dissertation, Museu Paraense Emílio Goeldi

Paim FP, Rabelo RM (2015) Methods for capturing wild squirrel monkeys in a floodplain forest: a comparison of two techniques and two species. Neotrop Primates 22:7–11

Paim FP, Silva Júnior JS, Valsecchi J, Harada ML, Queiroz HL (2013) Diversity, geographic distribution and conservation of squirrel monkeys, *Saimiri* (primates, Cebidae) in the floodplain forests of central Amazonia. Int J Primatol 34:1055–1076. https://doi.org/10.1007/s10764-013-9714-8

Paim FP, Silva Júnior JS, Queiroz HL (2015) Avaliação do risco de extinção de *Saimiri vanzolinii* Ayres, 1985 no Brasil. http://www.icmbio.gov.br/portal/biodiversidade/fauna-brasileira/estado-de-conservação/7268-mamiferos-saimiri-vanzolinii-macaco-de-cheiro-de-cabeça-preta.html. Accessed 5 Sep 2017

Paim FP, Chapman CA, Queiroz HL, Paglia AP (2017) Does resource availability affect the diet and behaviour of the Vulnerable squirrel monkey, *Saimiri vanzolinii*? Int J Primatol 38:572–587. https://doi.org/10.1007/s10764-017-9968-7

Parolin P, Wittmann F, Schöngart J (2011) Tree phenology in Amazonian floodplain forests. In: Junk WJ, Piedade MTF, Wittmann F, Schöngart J, Parolin P (eds) Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Dordrecht, pp 105–126

Peres CA (1997) Effects of habitat quality and hunting pressure on arboreal folivore densities in neotropical forests: a case study of howler monkeys (*Alouatta* spp.). Folia Primatol 68:199–222

Prance GT (1979) Notes on the vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. Brittonia 31:26–38

Ramalho EE, Macedo J, Vieira TM, Valsecchi J, Calvimontes J, Marmontel M, Queiroz HL (2009) Ciclo hidrológico nos ambientes de várzea da Reserva de Desenvolvimento Sustentável Mamirauá—médio Rio Solimões, período de 1990 a 2008. Uakari 5:61–87

Ribas CC, Aleixo A, Nogueira ACR, Miyaki CY, Cracraft J (2012) A paleobiogeographic model for biotic diversification within Amazonia over the past three million years. Proc R Soc 279:681–689. https://doi.org/10.1098/rspb.2011.1120

Rylands AB, Mittermeier RA, Bezerra BM, Paim FP, Queiroz HL (2013) Species accounts of Cebidae. In: Mittermeier RA, Rylands AB, Wilson DE (eds) Handbook of the mammals of the world – Primates. Lynx Edicions, Barcelona, pp 390–413

Schöngart J, Piedade MTF, Ludwigshausen S, Horna V, Worbes M (2002) Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. J Trop Ecol 18:581–597

Wallace AR (1852) On the monkeys of the Amazon. Proc R Soc 20:107–110

Wiens JJ (2011) The niche, biogeography and species interactions. Philos Trans R Soc 366:2336–2350. https://doi.org/10.1098/rstb.2011.0059

Wiens JJ, Donoghue MJ (2004) Historical biogeography, ecology and species richness. Trends Ecol Evol 19:639–644. https://doi.org/10.1016/j.tree.2004.09.011

Wittmann F, Schöngart J, Montero JC, Motzer T, Junk WJ, Piedade MTF, Queiroz HL, Worbes M (2006) Tree species composition and diversity gradients in white-water forests across the Amazon basin. J Biogeogr 33:1334–1347. https://doi.org/10.1111/j.1365-2699.2006.01495.x

Wittmann F, Junk WJ, Schongart J (2010) Phytogeography, species diversity, community structure and dynamics of central Amazonian floodplain forests. In: Junk WJ, Wittmann F, Parolin P, Piedade MTF, Schöngart J (eds) Amazonian floodplain forests: ecophysiology, biodiversity and sustainable management. Springer, Dordrecht, pp 61–102

Zar JH (2010) Biostatistical analysis. Prentice-Hall, Upper Saddle River