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ECOSYSTEMS

Determinants of anuran assemblages in Amazonian White-sand Ecosystems

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Abstract: Amazonian white-sand ecosystems have predominantly sandy soils and a high amount of endemism, and several species found within them are adapted to long periods of drought. However, little is known about the variation in the structure of anuran assemblages in these ecosystems. Considering that most species are not uniformly distributed in heterogeneous landscapes, we tested the hypothesis that anuran assemblage variation in white-sand ecosystems is related to changes in vegetation structure. Specifically, we focused on a heterogeneous patch of white-sand ecosystems of the central Amazon and evaluated whether vegetation structure and soil characteristics, including root depth, influence the richness, abundance, and composition of anuran assemblages. Our results showed that low amounts of clay in the soil play an important role in structuring vegetation in these ecosystems, and these are the main factors that organize anuran assemblages. The *Campinaranas* close to the water bodies have a high species richness, while *Campina* landscapes limit the occupation of most of species. Our findings indicate that anurans undergo environmental filtering in white-sand ecosystems and are organized into hierarchical subgroups, in which only species with specialized reproduction can successfully occupy the most water-restricted environments.

Key words: Structure, environmental filters, Campinas, Campinaranas, nestedness.

INTRODUCTION

The Amazon, although predominantly formed by tropical rainforests (Veloso et al. 1991), contains various other habitats that are distinguished by their species composition or, indirectly, by topographic, climatic (rainfall, temperature, wind velocity, air humidity, among others), and hydrological characteristics (Terborgh & Andresen 1998). Such a complex vegetation structure in the Amazon arises from variations in edaphic, biological, microclimatic factors, and/or from anthropogenic interferences taking place at different spatial scales (Ab'Saber 2002). Within this variety of forest habitat types, white-sand ecosystems are among the most distinctive (Pires & Prance 1985).

Although historically overlooked in the literature (Adeney et al. 2016), white-sand ecosystems are patchily distributed across the entire Amazon and resemble an island system of vegetation growing on sandy soils (Prance 1996). These ecosystems have a distinct vegetation structure that is adapted to long periods of drought (Anderson 1981, Prance 1996). They range from open heathlands (*Campinas*), dominated by herbaceous vegetation, to tall forests (*Campinaranas*) that are susceptible to seasonal flooding (Vicentini 2004, Damasco et al. 2013). The patterns of diversity, evolutionary processes, and ecological services of white-sand ecosystems are key elements for understanding the dynamics of the Amazon region (Anderson

1981, Fine & Bruna 2016, Adeney et al. 2016). Studies of birds and plants have shown that white-sand ecosystems have high levels of endemism, distinct species composition, and lower species richness when compared to other Amazonian habitats, such as upland forests and wetlands (Adeney 2009, Fortunel et al. 2014, Borges et al. 2015). Alonso et al. (2013) and Borges (2013) demonstrated that, in the central and western Amazon, white-sand ecosystems greatly contribute to the beta diversity of bird assemblages. However, there is little information on how environmental factors affect the structure of assemblages of other animal groups that inhabit white-sand ecosystems.

Anuran amphibians are particularly sensitive to physical changes in the environment, and some of their behavioral and ecological traits can provide information about their spatial distributions (Gardner et al. 2007, Ribeiro et al. 2012). For example, the diversity of reproductive modes among anuran species can promote distinct species distributions (Duellman 1999). Species that lay their eggs directly in water may have a more restricted spatial distribution due to greater dependence on water bodies (Haddad & Prado 2005), while species that do not depend on water for tadpole development may show wider spatial distributions (Menin et al. 2007). Some studies have shown that the spatial distribution of Amazonian anurans changes accordingly to the size of the streams, edaphic factors, and vegetation structure (see Menin et al. 2007, Condrati 2009, Rojas-Ahumada et al. 2012, Ferreira et al. 2018). However, it is not known whether these factors determine the structure of anuran assemblages in white-sand ecosystems. In this study, we evaluate some of the environmental factors influencing the distribution of anurans in a patch of white-sand ecosystems in the central Amazon and describe the structural pattern of the anuran assemblages in this unique environment.

The formation of hierarchical subgroups is a common structural pattern in both island systems and environments characterized by some degree of spatial isolation or strong resource limitation, such as the white-sand ecosystems, mainly *Campinas* that form islands within a forested matrix (Capurucho et al. 2013). In such environments, assemblages in resource-constrained environments have lower species richness and are formed by subsets of more species-rich assemblages (Patterson & Atmar 1986, Worthen 1996, Wright et al. 1998, Fleishman & Nally 2002). Forest structure on sandy soils ranges from shrubs to trees over 20 meters tall (Anderson 1981). Therefore, we expect that the anuran assemblages in these ecosystems should vary according to the forest gradient and that the species composition would differ between the main types of white-sand ecosystems. Because few anuran species have adaptations for living in water-restricted environments, we also predict that the anuran assemblage found in *Campina* environments will consist of a subgroup of species from the typical assemblage of *campinarana* environments.

MATERIALS AND METHODS

Study area

The study was carried out in a research module of the Biodiversity Research Program (PPBio) in the Rio Negro Sustainable Development Reserve (RDS Rio Negro) in the state of Amazonas, Brazil. The RDS is located on the right bank of the lower Negro River and is part of the central ecological corridor of the Amazon and the mosaic of protected areas of the lower Negro River (03° 04’ 14.5” S; 60° 44’ 27.2” W).

The reserve is classified as Dense Ombrophylous Forest; the module crosses two forest formations that are typical of white-sand ecosystems and is mainly surrounded by non-flooded upland forests: white-sand scrub and woodland (*Campina* and *Campinarana*, respectively). The *Campina* in our study is formed by stunted herbaceous-shrub vegetation, which is mainly made up of sclerophyllous species (Fig. 1a). Dry *Campinarana* is a forested habitat with a 15 to 20 m high canopy and a high density of shrubs and trees with canopies of low stature (Fig. 1b), while wet *Campinarana* has temporary ponds, resulting in high humidity levels (Fig 1c) (Vicentini 2016, Adeney et al. 2016). The white-sand types of vegetation (*Campinas* and *Campinaranas*) are distributed in small patches within the Reserve and, together, correspond to 1.8% of the total area of the conservation unit.

According to Köppen's classification, the predominant local climate is the Afi (Tropical Rainy type), with an average annual temperature of 25.6 ºC and average annual rainfall of 2,300 mm (INMET 2014). The driest period occurs between July and October, and the wettest between December and May (Silva 2018).

Sampling design

The configuration of the sampling module follows the long-term-ecological survey and rapid assessment (RAPELD) method for inventories of biodiversity (Magnusson et al. 2013). We sampled 20 plots of 250 m in length, which were organized in two parallel 5 km long transects and three connecting trails of 1 km each. The plots were separated by 200 m to 1 km (Figure 2). The plots in yellow and green followed a contour line of local topography to reduce internal heterogeneity in soil, drainage properties and, consequently, vegetation composition. The variation in altitude within each plot is minimum (Magnusson et al. 2013). The plots encompassed three white-sand vegetation types: riparian *Campinarana*, non-riparian *Campinarana*, and *Campina*. However, this system does not allow for stratified sampling of less common or scattered environmental features. In the RDS Rio Negro, the *Campina* and riparian *Campinarana* occur in small patches within the landscape; therefore, the distance between plots varied (minimum distance = 200 m) to allow for the inclusion of sampling units covering these vegetation types (Fig. 2). The riparian *Campinarana* plots in blue (Fig. 2) were established where streams cross the trails since regularly spaced plots did not occur frequently in this important habitat. Riparian plots follow the margin of the stream at 1.5 m from the water (Magnusson et al. 2013).

Sampling of anuran species

Anurans were sampled using time-limited and space-limited auditory and visual searches along the 250 m of each plot. These are

Figure 1. Examples of types of white-sand vegetation: a) *Campina*, b) Riparian *Campinarana*, c) Non-riparian *Campinarana*.

complementary methods, suitable for surveying distribution and abundance of anurans in short- and long-term studies (Zimmerman 1991, Tocher 1998, Menin 2005). Surveys were undertaken between 16:30 and 18:30 to detect predominantly diurnal and crepuscular species (e.g., *Allobates femoralis* and *Adenomera* spp.), and between 19:30 and 20:30 to detect predominantly nocturnal species. Each plot was surveyed four times by a researcher and a field assistant, who were ten meters apart from each other while walking through the plot scanning leaf litter, fallen trunks, and branches, as well as trunks and their branches up to 5 m height, with the aid of spotlights. The length of the sampling period varied between 30 min (diurnal), and 50 min (nocturnal). Auditory sampling consisted of recording the vocalizations of acoustically active individuals within a radius of 50 m.

As a recording criterion, we used the detection of a single individual per species, in each 10 m long segment of the 250 m plot, which meant that the maximum number of records per species in a given survey in each plot was 25. This standardization was necessary due to the large variation in the abundance of individuals of different species, especially between small-sized and highly abundant species (e.g., *Adenomera* spp., *Phyzelaphryne* spp., *Pristimantis* spp.).

Sampling was performed during the rainy season (December 2020 to March 2021). Rainy periods are best for anuran sampling due to

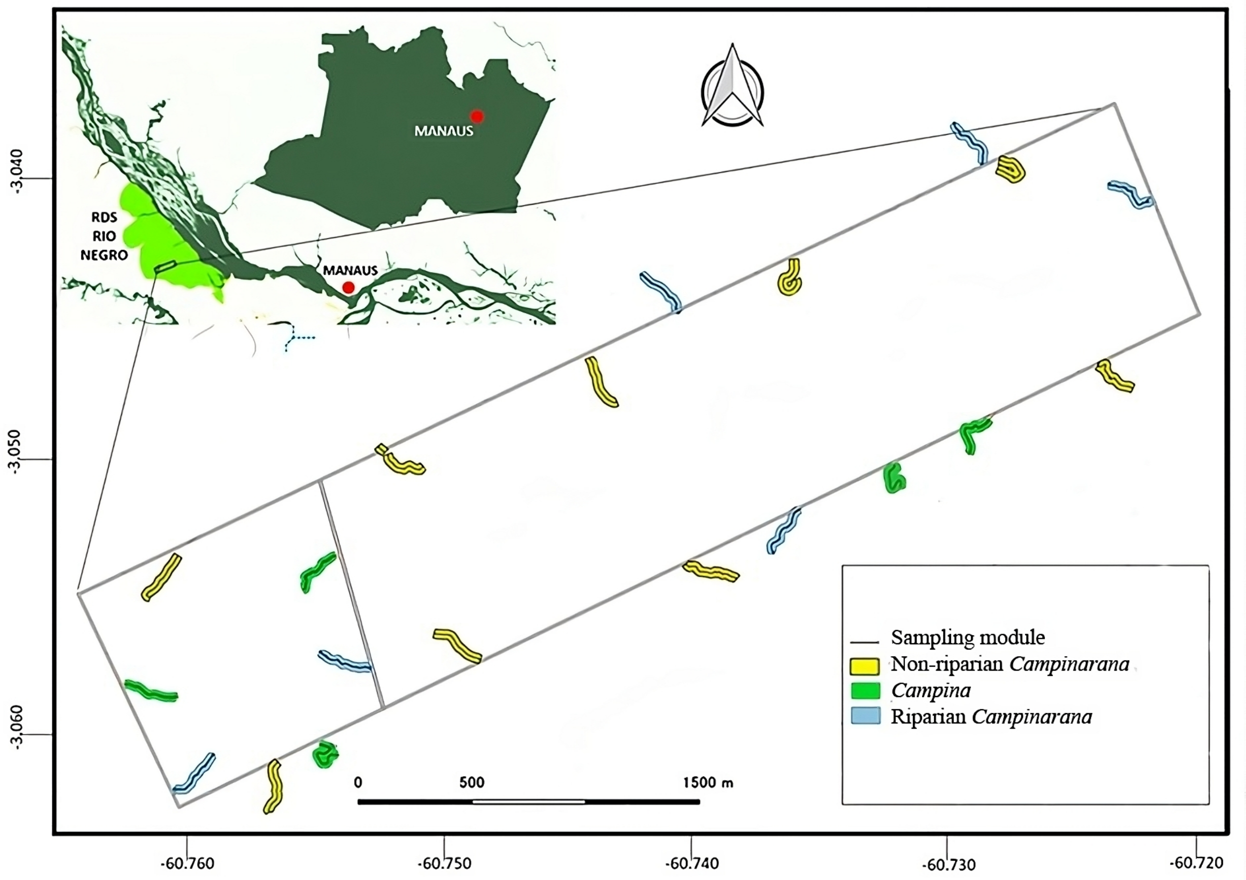

Figure 2. Location of the PPBio module in the Rio Negro Sustainable Development Reserve, Amazonas, Brazil. Sampling configuration and distribution of the 20 sampling plots.

increased availability of water bodies and high humidity in terrestrial sites (Lima et al. 2012). The abundance value for each species in each plot used in analyses was the maximum number of individuals recorded for each species among the four sampling iterations.

A maximum of three voucher specimens of each species were collected. The specimens were killed with a lidocaine-based anesthetic, fixed in 10% formalin, and preserved in 70% ethanol. Voucher specimens were deposited in the INPA Herpetological Collection (INPA-H) in Manaus, Amazonas, Brazil. Individuals were identified at species level based on morphological and acoustic characteristics described in the identification guides and species' descriptions. The scientific nomenclature of amphibian species follows Segalla et al. (2021). All individuals were collected under license No. 72434-1 from IBAMA/SISBio (Brazilian Ministry of the Environment). This license was subject to the approval of all ethical procedures for capturing and collecting species and specimens. We followed the guidelines of the Resolution No. 08/12/2012 of the Federal Council of Biology (CFBIO), which specifies the procedures for the capture, containment, release, and collection of vertebrates.

Environmental variables

Three environmental predictors were measured in each plot to assess their influence on anuran assemblage structure: the vegetation structure (height, canopy opening, and understory density) and root depth were also measured. These variables can influence both richness and composition of arboreal and terrestrial anurans (Pearman 1997). The proportion of clay, which is related to soil drainage, was measured because edaphic variables affect primary production and also influence trophic networks (Menin et al. 2007, Cintra et al. 2013). Clay and sand contents soil are good proxies for distance to the nearest stream (Menin et al. 2007), and clay content is associated with water bodies and the availability of breeding sites for anurans (Rojas-Ahumada et al. 2012).

Soil structure and root depth were measured every 50 m along the center line of each plot. In order to measure depth of root, a graduated ruler was inserted into the ground until it touched a root, and the mean of the measurements for each plot was used in the analyses. Composite soil-structure samples were collected with a drill at six points along each plot, to a depth of 10 cm, following the PPBio soil collection protocol (available at http: //ppbio.inpa.gov.br). Soil particle size analysis was done at the Soil Laboratory of the Department of Agronomy, INPA, and followed the total dispersion protocol adapted from EMBRAPA (Teixeira et al. 2017).

Vegetation structure was quantified using LiDAR (light detection and ranging) technology, a remote sensing system used to measure distances to structures as a function of the time elapsed between the emission and return of a laser beam (Lefsky et al. 2002). In this study, we used TML (terrestrial mobile LiDAR). Fourteen metrics describing vegetation height, canopy opening, and understory density were recorded using the TML.

Statistical analyses

We used sample-based rarefaction (interpolation) and extrapolation curves with 95% unconditional confidence intervals to compare total frog richness between flooding stages richness and interpolation (rarefaction) and extrapolated curves of non-riparian *Campinarana* (n = 09 plots), riparian *Campinarana* (n = 06) and *Campina* (n =05) were generated using the "iNEXT" package (Hsieh et al. 2016).

To evaluate the structure of the anuran assemblages in a two-dimensional space in relation to vegetation types (*Campina*, riparian *Campinarana*, and non-riparian *Campinarana*), we used principal coordinate analysis (PCoA) ordinations based on the Bray-Curtis dissimilarity index for relative-abundance data. The first two axes captured 64% (PCoA 1 = 52%; PCoA 2 = 12%) of the original species variance. PCoA analyses were conducted in R (R Core Team 2021) using the *adonis function* from the vegan package version 2.5-7 (Oksanen et al. 2020). To test whether the species composition differs between *Campina*, riparian *Campinarana*, and non-riparian *Campinarana*, pairwise comparisons between the vegetation types were made using the *anova.manyglm function*.

To investigate whether environmental variables influence the structure of the anuran assemblages, the *manyglm multivariate function*, extension of generalized linear models (Warton et al. 2012) in the mvabund package version 4.1.3 was used (Wang et al. 2012). The effect of environmental variables was evaluated using the *anova.manyglm function*, which re-samples abundance data while accounting for correlations among species. The p-value was calculated from 999 bootstraps. A multivariate generalized linear model was fitted using the mvabund package version 4.1.3, in which the vegetation types were entered as the predictor variable and the species-abundance data as the response variable, which was modeled using a negative binomial distribution and a log link function. Therefore, we have:

$$\text{Assemblages Structure} = \text{vegetation structure} + \text{root depth} + \text{clay proportion}$$

Vegetation structure variables were tested for multicollinearity using Pearson's multiple correlation (Supplementary Material - Table SI). LiDAR metrics were summarized in a principal component analysis (PCA) (Table SII). Pearson's correlation values were also used to assess the independence between environmental variables (PCA of vegetation structure, root depth, and proportion of clay). These variables were included in the model and maintained in subsequent analyses (Table SIII) because they were not correlated. The summary of vegetation structure, root depth and clay proportion data used in statistical tests are presented in Table SIV.

Histograms of species distributions (Dambros 2014) throughout the environmental gradients were generated to describe the responses of each species to the environmental variables. All statistical analyses were undertaken using the statistical software R version 3.6.1 (R Core Team 2021).

RESULTS

Species sampling

We found 19 anuran species, which were distributed in six families (Table I). The families with the highest number of species recorded were Hylidae and Leptodactylidae (six species each), followed by Bufonidae (two species), and Aromobatidae, Centrolenidae, Eleutherodactylidae, Microhylidae and Pipidae (one species each).

The number of species recorded per sampling plot varied from 2 to 13. The mean abundance of each species, recorded per sample plot, is presented in the Supplementary material (Table SV). The most widely distributed species in the sampled area were *Adenomera* aff. *andreae*, *Osteocephalus vilarsi*, and *Trachycephalus cunauaru*, all of which were recorded in at least 75% of the plots. Eight species were recorded in 25-60% of the plots, seven species were found in only 20% of the plots, and four species were recorded only in

Table I. List of anuran species recorded in the Rio Negro Sustainable Development Reserve and sum of occurrences in the different sampled habitats.

Taxon	***Campina*** **(n = 5)**	**Non-riparian *Campinarana* (n = 9)**	**Riparian *Campinarana* (n = 6)**
Arombatidae			
Allobates femoralis (Boulenger, 1884)	0	3	3
Bufonidae			
Rhinella sp.	0	8	11
Rhinella marina (Linnaeus, 1758)	2	3	5
Centrolenidae			
Vitreorana ritae (Lutz, 1952)	0	0	14
Eleutherodactylidae			
Phyzelaphryne miriamae (Heyer, 1977)	0	30	39
Hylidae			
Boana boans (Linnaeus, 1758)	0	3	3
Boana lanciformis (Cope, 1871)	0	0	6
Osteocephalus vilarsi (Melin, 1941)	2	27	7
Scinax albertinae (Ferrão, Moravec, Ferreira, Moraes & Hanken, 2022)	2	10	0
Trachycephalus cunauaru (Gordo, Toledo, Suárez, Kawashita-Ribeiro, Ávila, Morais & Nunes, 2013)	22	15	4
Leptodactylidae			
Adenomera aff. gridipappi (Müller, 1923)	6	123	67
Adenomera sp.	0	37	27
Leptodactylus pentadactylus (Laurenti, 1768)	0	4	7
Leptodactylus petersii (Steindachner, 1864)	0	1	4
Leptodactylus rhodomystax (Boulenger, 1884)	0	16	4
Leptodactylus riveroi (Heyer & Pyburn, 1983)	0	0	3
Microhylidae			
Chiasmocleis hudsoni (Parker, 1940)	0	5	0
Phyllomedusidae			
Phyllomedusa vaillantii (Boulenger, 1882)	0	0	3
Pipidae			
Pipa pipa (Linnaeus, 1758)	0	1	0

the riparian *Campinarana* (*Vitreorana ritae*, *Phyllomedusa vailantii*, *Leptodactylus riveroi*, and *Boana lanciformis*). There were no species unique to the non-riparian *Campinarana*, nor to the *Campina* (Table I). *Pipa pipa* was excluded from the analyses because it an exclusively aquatic species and only one individual within a non-riparian *Campinarana* plot recorded. The specimen was inhabiting a shallow, clean water pool located approximately two meters distant from a water body.

During the sample-based rarefaction curves, richness estimates detected by no-riparian *Campinarana* and riparian *Campinarana* were higher than the richness detected by *Campina*. However, extrapolation to 11 plots indicates that the 95% confidence intervals converge, so white sand types of vegetation richness differ in the total number of species they support, but the curves demonstrate that we have reached the asymptote, and that the data is representative (Supplementary Material - Figure S1).

Species composition

Two PCoA axes were used to visualize how the compositions of anuran assemblages differ across the main vegetation types sampled. The ordination evidenced two major clusters, which corresponded significantly to the most distinct vegetation types (*Campina* and *Campinarana*). Tendencies for compositional divergences were also evident when comparing riparian and non-riparian *Campinarana* assemblages, but their clusters overlapped in the ordination space (Figure 3).

The species composition of anuran assemblages was influenced by vegetation structure ($p \leq 0.01$) and clay proportion ($p \leq 0.01$), but not by root depth ($p = 0.12$) (Table II). The soil from the riparian *Campinarana* had a higher proportion of clay than the other vegetation types. Pairwise comparisons showed differences in the species composition between all the analyzed vegetation types ($p \leq 0.005$ in all cases) (Table II).

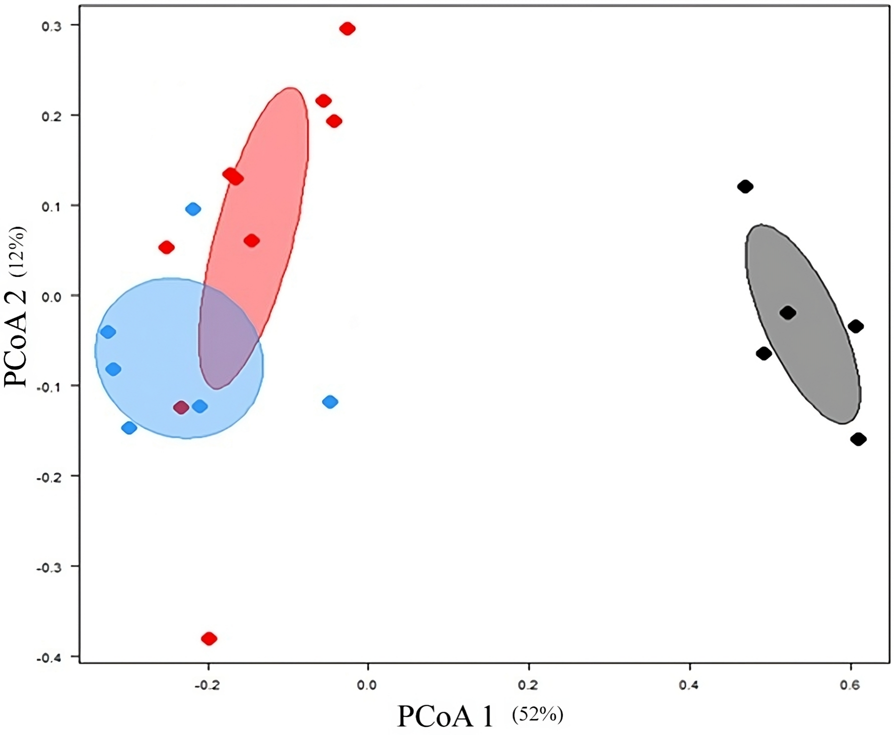

Figure 3. The first two axes of a principal coordinate analysis (PCoA) based on the relative abundance of anuran species, showing the 95% confidence ellipses of the plot samples in relation to the types of white-sand vegetation in the RDS Rio Negro. Black = *Campina*, red = non-riparian *Campinarana*, blue = riparian *Campinarana*.

All species found in the *Campina* were also recorded in the other vegetation types; while 86% of the species found in the non-riparian *Campinarana* were also recorded in the riparian *Campinarana*. The anuran assemblage of the *Campina* generally consisted of a subgroup of the non-riparian *Campinarana* assemblage, and both these assemblages were mainly subgroups of the riparian *Campinarana* assemblage (Figure 4). The species ordination according to clay proportion and vegetation structure followed a similar pattern of distribution (Figures S2 and S3).

DISCUSSION

Our results clearly show that the structure of anuran assemblages differs between the two main types of white-sand vegetation analyzed (*Campina* and *Campinarana*), which is a pattern that has also been reported for plant and bird assemblages (Adeney 2009, Borges et al. 2015). Such differences in plant, bird and anuran assemblages in white-sand ecosystems are mainly attributed to variations of edaphic factors (Borges 2013, Damasco et al. 2013).

It is observed that the variation of anuran assemblages across the white-sand ecosystems was mainly influenced by both vegetation structure and the proportion of clay in the soil. Changes in vegetation affect demographic patterns in animal assemblages (de Vasconcelos et al. 2013), which is an influence that has been reported for various taxonomic groups (Franklin et al. 2005, Bobrowiec et al. 2014, Fiorillo 2020, Peixoto et al. 2020). Previous research has suggested that vegetation structure is not a good predictor of spatial distribution of species of Amazonian Ombrophylous Forest anuran assemblages, as other variables predictors, such as distance from water bodies, terrain slope, clay content and soil moisture (Menin et al. 2007, Condrati 2009, Ribeiro et al. 2012).

However, our study showed that variations in the species composition of anuran assemblages of Amazonian white-sand ecosystems were closely related to changes in the vegetation structure. Among the three vegetation types studied, the forested environments (riparian and non-riparian *Campinarana*) likely harbored all the species recorded. This higher species richness is because these environments have

Table II. Results of the manyglm analysis performed to test the relationship between the structure of the anuran assemblage and the environmental variables, and pairwise comparisons between the C*ampina*, non-riparian and riparian *Campinarana* in the RDS Rio Negro. Results show the deviation table with test values (Wald) and frequentist probability values (p) based on 999 bootstrap interactions with PIT trap re-sampling. LR stands for logarithmic odds ratio statistic.

Environmental variables	**Wald**	**p**
Vegetation structure	18.755	0.001
Root depth	15.302	0.123
Clay proportion	16.387	0.013
Post hoc pairwise comparisons	**Sum-of-LR statistic**	**p**
Campina vs. riparian C*ampinarana*	80.05	0.001
Campina vs. non-riparian C*ampinarana*	52.36	0.001
Non-riparian C*ampinarana* vs. riparian C*ampinarana*	38.29	0.005

greater availability of reproductive sites and micro-habitats with adequate humidity and temperature ranges, thus increasing survival rates in the driest periods (Lieberman 1986, Keller et al. 2009, Lima et al. 2012). Despite the predominance of sandy soils in the vegetation types studied (more than 84%), we found that the presence of clay in the soil influenced the composition of anuran assemblages. The soil in the *Campinarana* has a higher proportion of clay and a higher availability of nutrients (Damasco et al. 2013) than the other vegetation types, which also may explain the higher species richness recorded for. Furthermore, the positive correlation between amphibian diversity and abundance and clay soils can be explained by considering that other studies have found a relationship between this type of soils and the availability of water bodies. (Woinarski et al. 1999, Menin et al. 2007, Ferreira et al. 2018) that some anurans use for reproduction (Menin et al. 2011).

A pattern of hierarchical subgroups in the structure of assemblages may occur in areas with environmental limitations (Kodric-Brown & Brown 1993). In Amazonian floodplain forests, only the species that are resistant to seasonal floods occur throughout the entire flooding gradient (Alvarenga et al. 2018, Ramalho et al. 2018). This pattern, however, contrasts with the conclusions of Worthen (1996), who asserted that high environmental variability in small environments is responsible for harboring different, specialized species, thus creating strong species-area relationships without necessarily forming a hierarchical-subset structure. We suggest that the main factor underlying the hierarchical pattern of anuran assemblage in white-sand ecosystems is the high interspecific variation in habitat requirements, given that

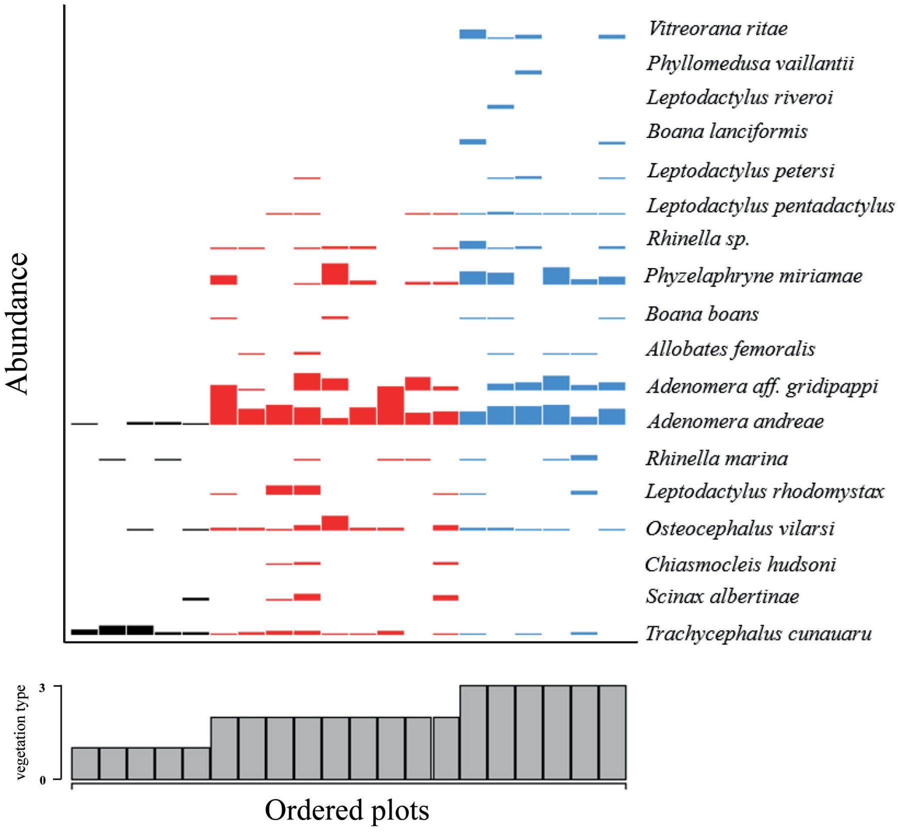

Figure 4. Distribution of records by abundance of anuran species in relation to types of white-sand vegetation. Black = *Campina*, red = non-riparian *Campinarana*, blue = riparian *Campinarana*.

more generalist species can be found in most environments, while more specialized species occur only in a subgroup of sites that suit the narrower habitat requirements of these species (Loo et al. 2002). Our understanding about how environmental variation shapes diversity patterns within landscapes can be widened by exploring species-habitat questions. The types of white-sand vegetation form fragile landscapes that extend naturally as small islands within the Amazon biome (Adeney et al. 2016, Vicentini 2016). These unique habitats are highly relevant for species diversity, and harbor both endemic and rare species (Farroñay et al. 2019, Ferrão et al. 2019, Capurucho et al. 2013).

The reduction in both species' richness and abundance of individuals, in relation to the proportion of clay in the soil, is a proxy of distance from riparian areas in environments with tall forests (Menin et al. 2007, Rojas-Ahumada et al. 2012), and indicates that the availability of water is a limiting factor for distribution of anuran species. This is similar to the white-sand ecosystems in the Amazon, where the highest richness and abundance was found in the riparian *Campinaranas*, which are 1.5 m from the streams. We believe we have discovered which habitat requirements are key for structuring anuran assemblages in white-sand ecosystems; however, it is necessary to increase our knowledge regarding the dynamics of white-sand ecosystems and the species that inhabit them so as to better assess the threats that these fragile habitats may suffer. This is especially that case for the patch of white sand near Manaus, the largest city in the Amazon, which is growing rapidly and uses this sand for construction.

CONCLUSIONS

Our understanding about how environmental variation shapes diversity patterns within landscapes can be widened by exploring species-habitat questions. The different types of white-sand vegetation form fragile landscapes that extend naturally as small islands within the Amazon biome (Adeney et al. 2016, Vicentini 2016). These unique habitats are highly relevant for species diversity, and harbor both endemic and rare species (Farroñay et al. 2019, Ferrão et al. 2019). In this study, we have explored the relationships between anuran spatial distribution and soil and vegetation characteristics in three types of white-sand vegetation in the Amazon. The pattern of hierarchical subsets of species found for the white-sand anuran assemblages was explained by both vegetation structure and proportion of clay in the soil. The reduction in both species' richness and abundance of individuals, relative to the distance from riparian areas, indicates that the availability of water is a limiting factor for anuran species distribution in white-sand landscapes in the Amazon.

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SUPPLEMENTARY MATERIAL

Figures S1, S2 and S3.
Tables SI, SII, SIII, SIV and SV.

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