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Can the Morphological Variation of Amazonian Bufonidae (Amphibia, Anura) Be Predicted by Their Habits and Habitats?

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Abstract

The species of the Bufonidae family exhibit a great diversity of habitats, diurnal or nocturnal habits, a complex evolutionary history, and a wide distribution, which makes this group suitable for morphological studies. In this work, we aimed to identify the existence of morphological patterns related to the habitat use and diurnal or nocturnal habits of Bufonidae in the Brazilian Amazon. To achieve this, we studied the morphological measurements of 210 specimens from three zoological collections and characterized the type of habitat and diurnality/nocturnality of the species. The morphological patterns and habitat use were investigated through principal component analysis (PCA) and multiple correspondence analysis (MCA), respectively. The evaluation of the relationships between morphological variation, habitat use, and diurnality/nocturnality was performed via redundancy analysis (RDA). Accordingly, Amazonian bufonids were divided into three morphological groups associated with different vegetation types and environments, demonstrating that body size is closely linked to diurnal or nocturnal life habits and habitat. Species with large body sizes are associated to anthropized areas, while intermediate and smaller species are associated with primary forests.

Keywords: Amazon; ecomorphology; environmental variation

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1. Introduction

Ecomorphology can be defined as the relationship between the morphological characteristics of organisms and their respective life habits [1]. Thus, we can associate ecological processes with the evolutionary history of organisms and understand patterns of habitat occupation and community composition [2,3]. As a matter of fact, the idea that the environment can model the life history of individuals was introduced by the "habitat templets" concept, which predicts the distribution of species in habitats as a trade-off between the genetic and environmental constrains and life-history traits [4]. For example, studies using tadpoles observed that species with depressed bodies tend to occupy micro-habitats closer

to the substrate, compressing the water columns [5–9]. These morphological adaptations alter biotic and abiotic interactions, avoiding (or decreasing) the overlapping of niches and consequently, increasing species diversity [10] in different environments.

The Bufonidae family, known as that containing "true toads", is widely distributed worldwide and is native to temperate and tropical regions except for Australia, New Zealand, and Madagascar [11]. Brazil is home to eight genera and 100 species [12], of which five genera are present in the Amazon area, comprising 34 species, with *Amazophrynella bilinguis* (Kaefer et al., 2019), *Amazophrynella gardai* (Mângia et al., 2020), *Rhinella exostosica* (Ferrão et al., 2020), and *Rhinella parecis* (Ávila et al., 2020) recently discovered [12]. Species of this family display a high diversity of life habits and habitat use, showing a long and complex evolutionary history, despite having a morphology that is seemingly conservative [5,6]. In addition, within this family there are species with a wide distribution that exhibit great phenotypic plasticity, which makes this group highly suitable for ecomorphological studies. Thus, the aim of our study is to identify the existence of morphological patterns in the habitat use and diurnality/nocturnality of Bufonidae species in the Brazilian Amazon.

Due to their morphology, permeable skin, and water loss through evapotranspiration, anurans are highly affected by water balance issues [13] To cope with these challenges, anurans have developed ecological strategies, such as selecting microhabitats and specific times of activity, which help regulate their body temperature [14] and ensure proximity to water sources. Body size plays a significant role in enabling longer movements, as larger species experience reduced water loss [15]. Based on these patterns, we hypothesize that larger species of Amazonian bufonids may tend to explore more open environments, farther from water bodies, during the daytime (expanding their activity period). The hypothesis is that larger species of Amazonian bufonids may tend to explore more open environments (habitats) [16,17]. In contrast, smaller species are likely to remain closer to water bodies within areas with denser vegetation and exhibit nocturnal activity to avoid desiccation [18–20].

2. Materials and Methods

2.1. Selection of Species and Morphological Trait Measurements

The specimens used in this study come from the following zoological collections: the Zoological Collection of the Faculty of Biological Sciences of Federal University of Pará (UFPA), Altamira Campus; the Herpetology Collection of the Emílio Goeldi Museum (MPEG), and the Collection of Herpetology of the National Institute of Amazonian Research (INPA). For morphometric measurements, we followed the methods of refs. [1,21] and selected 33 morphological variables (Table S1). Only species with at least three available adult individuals were selected. We included 210 specimens belonging to four genera and 15 large- (average SVL of 95.4 mm), medium- (average SVL of 51.56 mm), and small-sized species (average SVL of 22.40 mm) in the analyses.

2.2. Habitat and Habit Characteristics

To assign habitats to the species, we searched the following the digital databases: (i) Amphibian Species of the World (https://amphibiansoftheworld.amnh.org/ (accessed on 19 November 2024)), (ii) the IUCN Red List (https://www.iucnredlist.org/ (accessed on 19 November 2024)), (iii) the Instituto Frog-Bugio (http://www.ra-bugio.org.br/ (accessed on 20 November 2024)), along with the work of (iv) Wells (2007) [22]. We defined habitat as the forest formation where the species occurs (primary forest, secondary forest, and anthropized area), the type of environment (dry land, flooded forest, area close to water, open area, litter, and understory), and spawning site (temporary pond, phytotelmata, and

stream) that the species uses. Habit was characterized as the period in which the species is more active (diurnal or nocturnal) (Table 1).

Table 1. Characteristics of habit and habitat of the Amazonian Bufonidae (Amphibia, Anura) included in the research.

Ecological Variable	Acronym	Description
Type of vegetation where the species is found		
Primary Forest	PF	Undisturbed forest, or with little disturbance
Secondary Forest	SF	Forest in regeneration
Anthropized Area	AA	Areas whose original features (in soil, vegetation, relief) have been changed
Type of environment		
Terra Firme Forest	TF	Unflooded/non-flooded forest/dry forest
Flooded Forest	FF	Flooded areas and wetlands
Next to the Water	NW	Margins of rivers, lagoons, and dams
Open Area	AO	Pasture areas, plantations, gardens, or urban areas
Litter	LT	Aboveground layer covered by decomposing organic remains
Understory	US	Subshrub vegetation found within the forest
Spawning site		
Temporary Pond	TP	Formed in the rainy season
Plant Structure	OS	Nut capsules, hollow trunks and roots, etc.
Stream	S	Streams
Activity period		
Diurnal	D	Active during the day
Nocturnal	N	Active during the night

2.3. Statistical Analysis

To identify and describe the existence of morphological patterns, we performed a principal component analysis of covariance (PCA), with the variables as mean values of the traits measured in the individuals of each species. Patterns regarding habitat use and habit were investigated using multiple correspondence analysis (MCA); for this analysis, it was necessary to create combinations of diurnality/nocturnality and habitats (Table 2). The group formations in the PCA and in the MCA were observed and visually interpreted using, respectively, the rda and mca functions available in the vegan (rda) [23] and MASS (mca) [24] packages in the R environment [25].

To explore the association between the morphological variation and habitats and diurnality/nocturnality, we calculated the following five distance matrices: (i) Euclidean distance using species morphological variables (continuous values); (ii) Gower distance using forest formation (categorical values); (iii) Gower distance using the type of environment (categorical values); (iv) Gower distance using species spawning sites (categorical values); (v) Gower distance using activity period (categorical values). For all matrices, we performed a non-metric multidimensional scaling (NMDS) analysis, and the first five factors were used as variables to perform the Procrustes analysis, aiming to identify the relationship and significance between morphology and the other matrices. Thus, the factors of the NMDS, using morphological variables, were compared separately, with the factors of the NMDS models using data for habitat and diurnality/nocturnality, hence identifying which ecological aspect is more associated with morphology.

Finally, to identify whether there was any relationship between the morphological traits and ecological aspects, we performed a redundancy analysis (RDA) using the morphological variable matrix as a response variable and the ecological aspect matrix as an explanatory variable. We perform RDA only for the ecological aspects that had significant correlation in the Procrustes analysis. For the RDA and the NMDS, the habitat and habit

matrices were set to reveal the values of the presence and absence of the ecological aspect of each species. The RDA was useful to explore the relationships between the response variables and the explanatory variables. It combines features of multiple regression and principal component analysis (PCA), constraining the variation in the response variables to what can be explained by the predictors. Distance matrices were calculated using the vegdist function in the vegan package [23]. The NMDS was run using the nmds function, where the best model (the one with the lowest stress value) was selected using the nmds.min function. Both functions are found in the ecodist package [26]. All analyses were performed in the R environment [25].

Table 2. Combinations of the ecological characteristics of Bufonidae used in the multiple correspondence analysis (MCA). Variable acronyms are listed in Table 1.

Variable	Combinations	Group
FvA	PF	Vegetation Type
Fobs	SF	
FvC	AA	
FvD	PF × SF	
FvE	PF × AA	
FvF	SF × AA	
FvG	PF × SF × AA	
DnA	D	Activity Period
DnB	N	
HbA	FF × NW × LT	Environment where the species occurs
HbB	TF × NW × LT	
HbC	TF × FF × OA	
HbD	TF × FF × LT	
HbE	TF × FF × NW × US	
HbF	TF × FF × NW × LT	
HbG	TF × FF × NW × LT × US	
HbH	TF × FF × NW × OA	
HbI	TF × FF × NW × OA × US	
DeA	TP	Spawning site
DeB	OS	
DeC	S	
DeD	TP × PS	
DeE	TP × S	
DeF	PS × S	
DeG	TP × PS × S	

3. Results

In the analyses, we included 210 specimens belonging to four genera and 15 species. *Rhinella* was the richest genus, with 11 species, and *Rhaebo* was included with a single taxon. The PCA performed with morphological data (Figure 1) explained 96.3% of cumulative variation in its first axis (see Table S2). The variable with the highest correlation was snout-vent length (SVL), followed by head length, third-finger length, thumb length, and interorbital distance. All variables were positively associated with the first axis, thus segregating large species from smaller ones. The second axis of the PCA (Figure 1) explained 2.18% of the cumulative variation (see Table S2) and showed a positive correlation between CRC and species of the genus *Rhinella* (Figure 1). As a general pattern, we observed that *Rhinella marina* (Linnaeus, 1758), *Rhinella diptycha* (Cope, 1862), and *Rhaebo guttatus* (Schneider, 1799) were clustered on the right side of the multidimensional space, representing species with a larger body size with an average SVL of 95.4 mm and greater limb strength (Figure 1). *Rhinella granulosa* (Spix, 1824), *Rhinella major* (Müller and Hellmich, 1936), *Rhinella margaritifera* (Laurenti, 1768), *Rhinella proboscidea* (Spix, 1824), *Rhinella castaneotica* (Caldwell, 1991),

Rhinella martyi (Fouquet et al., 2007), and *Rhinella magnussoni* (Lima et al., 2007) formed an intermediate group of medium-sized species (averaging an SVL of 51.56 mm). On the left side of the graph, we recovered *Amazophrynella bokermani* (Izecksohn, 1994), *Amazophrynella minuta* (Melin, 1941), *Amazophrynella manaos* (Rojas et al., 2014), *Amazophrynella vote* (Avila et al., 2012), *Atelopus spumarius* (Cope, 1871), and *Atelopus hoogmoedi* (Lescure, 1974), the small-sized species, with an average SVL of 22.40 mm (Figure 1).

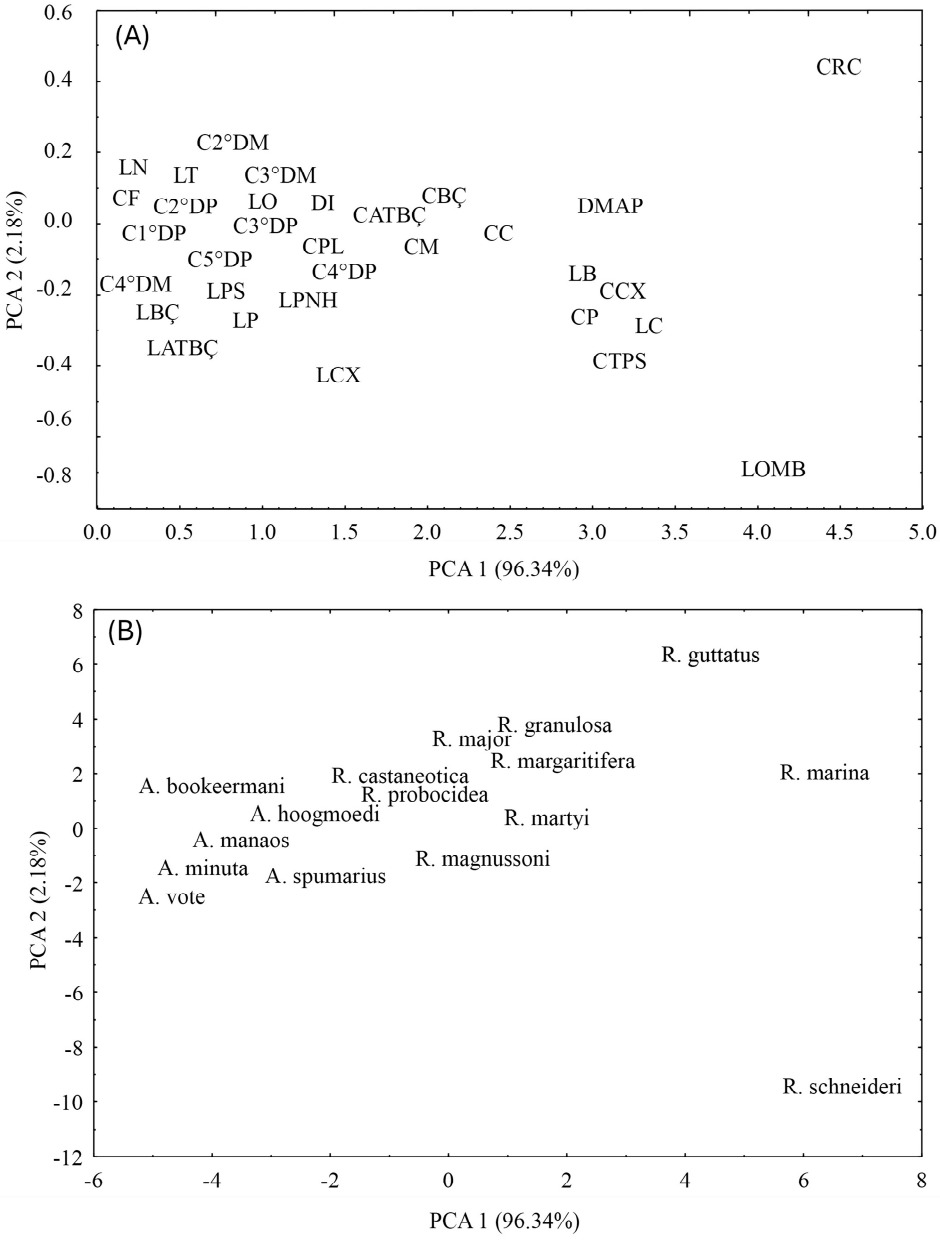

Figure 1. Principal component analysis (PCA) of morphological characteristics (**A**) of Amazonian Bufonidae (**B**). The acronyms are listed in Table S1.

The MCA, performed with ecological data (Figure 2), showed an 86.8% correlation among the variables, with 28.9% of cumulative explanation with the first axis (Table S3). The variable with the highest correlation in the first axis was HbH (combination of dry land forest, flooded forest, area next to the water, and open area), followed by FvF (secondary forest and anthropized area). The variable most related to the second axis was DeF (temporary pond and stream), followed by FvD (primary and secondary forest). As a pattern, we observed that *R. diptycha* and *R. marina* are more associated with secondary

forests and anthropized areas, nocturnal habits, and open areas with dry land forest or flooded forests, close to water bodies. The species *R. magnussoni*, *R. major*, *R. castaneotica* e *R. proboscidea*, and *R. margaritifera* prefer primary and secondary forests, occurring in litter habitats and exhibiting both diurnal and nocturnal habits. The species *A. bookermani*, *A. manaos*, *A. minuta*, *A. vote*, *A. hoogmoedi*, and *A. spumarius* were associated with primary forests, occupying litter habitats in understories of dry land forest (Figure 2).

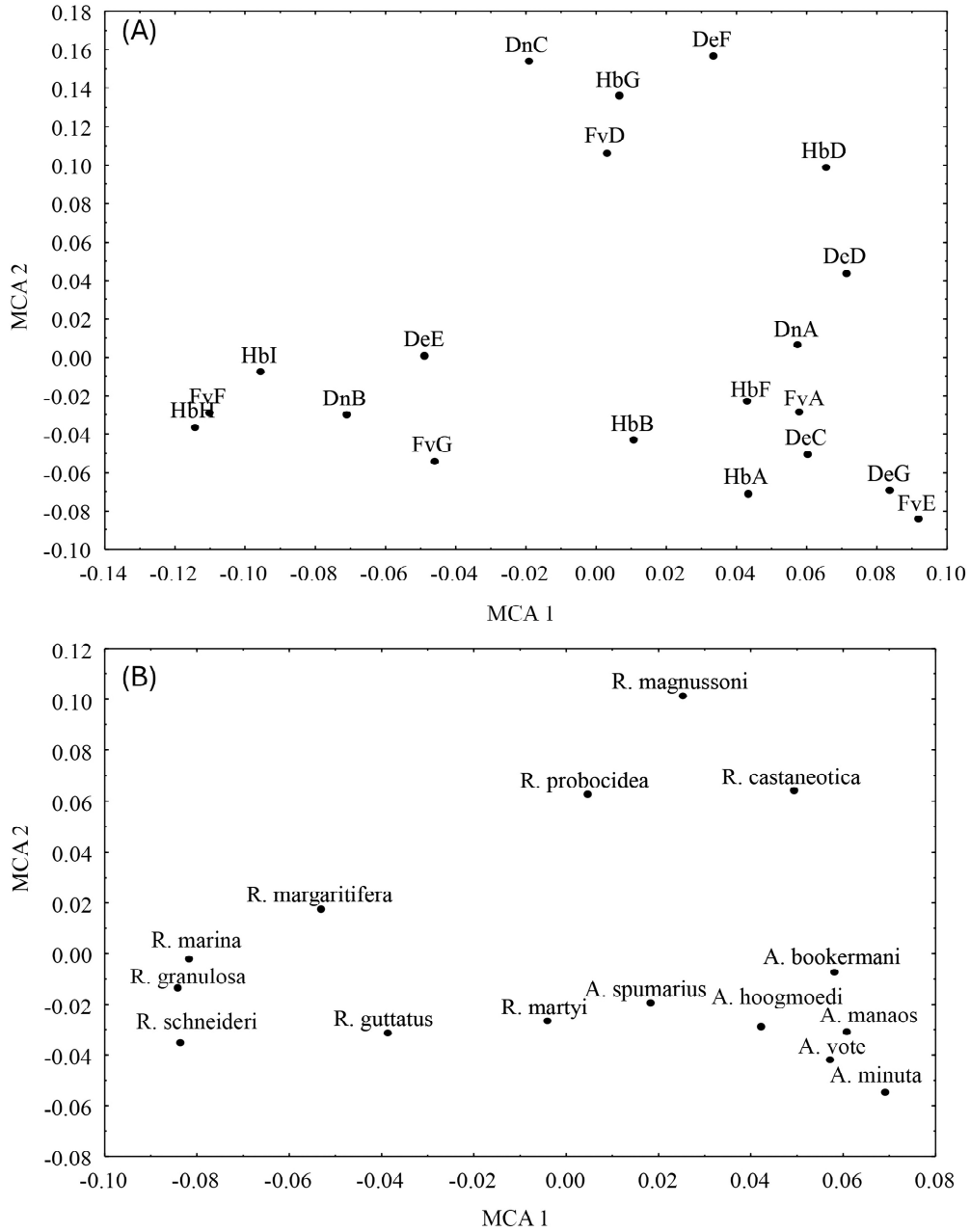

Figure 2. Multiple correspondence analysis (MCA) of habit characteristics (**A**) of Amazonian Bufonidae species (**B**). The acronyms are listed in Table 1.

All NMDS models exhibited a stress level of less than 0.001, for which we use five dimensions. The Procrustes analysis showed a significant correlation between the morphological characteristics and the types of vegetation where the species is found, with a 63% correlation ($m^2 = 0.638$; $p = 0.002$), type of environment, with a 48% correlation ($m^2 = 0.487$; $p = 0.033$), and activity period, with a 49% correlation ($m^2 = 0.493$; $p = 0.040$). The spawning sites showed no relationship with the morphological traits ($m^2 = 0.087$; $p = 0.852$).

The RDA (Figure 3 and see Table S4), performed using the morphological traits, vegetation, environment, and activity period, explained 88.2% of the accumulated variation in the first axis (Figure 3). Among the morphological variables, the measurement with the highest correlation with the first axis was the rostrum cloacal length, followed by total foot length and the distance between the fore and hindlimbs, mouth size, head length, and arm length (Figure 3 and Table S4). In general, we observed species with larger body size, i.e., CRC larger them 60 mm (e.g., *R. guttatus*, *R. marina* and *R. diptycha*), associated with anthropized areas, open areas, and dry land forests (Figure 3). Species with smaller size, i.e., CRC less of them 30 mm (*Amazoprhynella* and *Atelopus* genus), were associated with primary forests, inhabiting leaf litter, and with diurnal habits. Finally, species with intermediate size, i.e., CRC between 30 and 60 mm (*R. castaneotica* and *R. proboscidea*), occurred in primary forests (*R. castaneotica* and *R. proboscidea*), anthropized areas, and secondary forests (*R. margaritifera* and *R. martyi*) (Figure 3).

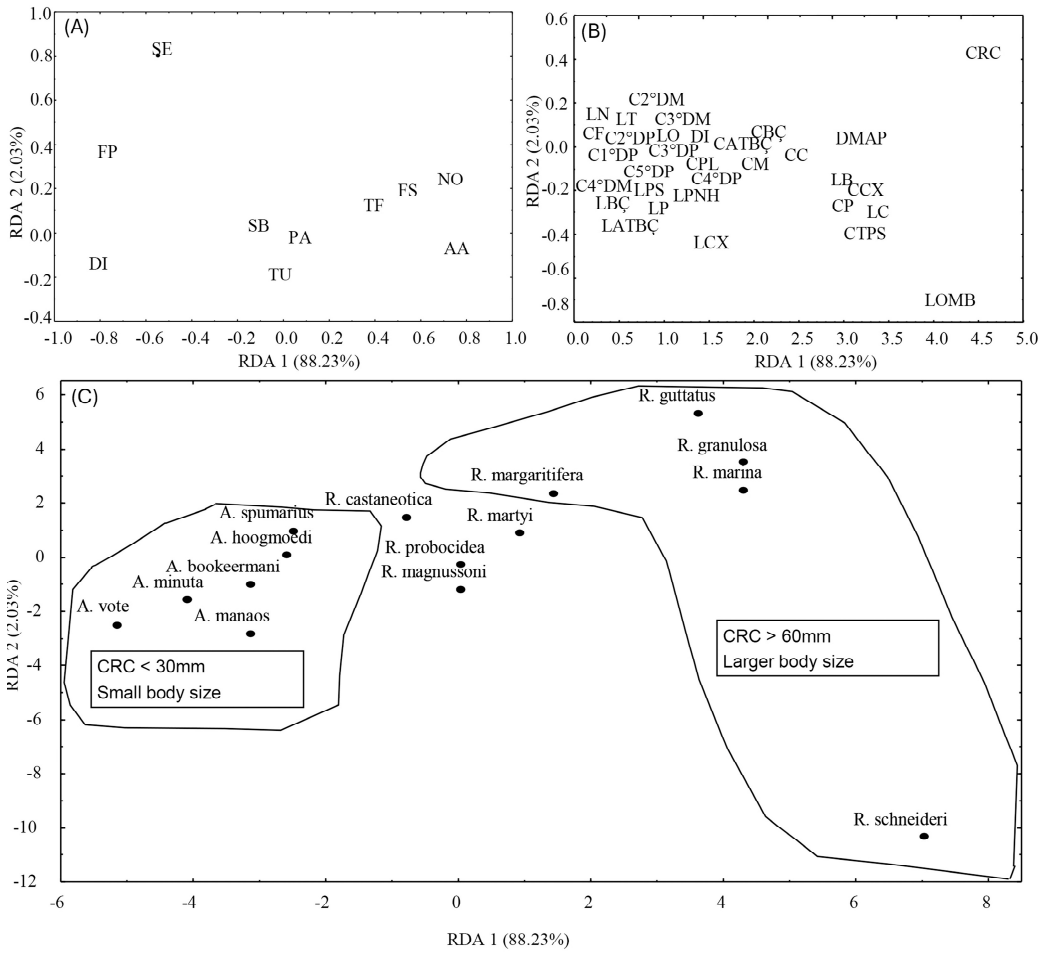

Figure 3. Redundancy analysis (RDA) between habitat and habit (**A**) and morphological characteristics (**B**) of the Amazonian Bufonidae (Amphibia, Anura) species (**C**). The acronyms for habitat and habit are listed in Table 1, and those for morphological characteristics are found in Table S1.

4. Discussion

We found three general morphological traits in the large- (average SVL of 95.4 mm), medium- (average SVL of 51.56 mm), and small-sized (average SVL of 22.40 mm) species analyzed. Larger and more robust taxa were represented by the species *Rhinella marina* and *R. diptycha*. Medium-sized taxa were represented by the *Rhinella granulosa* and *R. margaritifera* species groups. The first comprises *R. major* and *R. granulosa*, while the later includes *R. margaritifera*, *R. proboscidea*, *R. castaneotica*, *R. martyi*, and *R. magnussoni*. Smaller

species were represented by *Amazophrynella bookermani*, *A. minuta*, *A. manaos*, and *A. vote*, plus *Atelopus spumarius* and *A. hoogmoedi*.

This morphological pattern reflects a good correspondence with taxonomy, clustering morphologically similar taxa [27–29]. Species from the same genus, family, or even a common evolutionary lineage tend to exhibit very similar physical characteristics [30,31]. Our results suggest that ecomorphological patterns can be explained by the tendency of organisms to avoid competition, either intraspecific or interspecific [32]. Occupancy of different habitats and differential resource exploitation would allow species to coexist in a region [33,34].

We observed that large species are tolerant to anthropized areas, being abundant in open habitats. A similar pattern was observed in previous studies for Amazonian anurans, in which this group expressed higher diversity in open areas and secondary forests, with a wide occurrence in pasture and urban areas [35,36].

Species from the *R. granulosa* and *R. margaritifera* groups (with intermediate size), occupied mainly secondary forests. However, there is a great tendency of the *R. granulosa* group to occupy open areas, and the *R. margaritifera* group is more common in primary forests [37]. These organisms differ in the sequential use of the habitat, with species from the *R. granulosa* group being nocturnal [38] and *R. gr. Margaritifera* being diurnal [30]. The possible structuring process of this pattern might be the plasticity (tolerance) some groups of anuran amphibians exhibit in response to environmental conditions, especially water loss [39,40].

The species *R. marina* and *R. granulosa* display a nocturnal foraging behavior; at dusk they usually search of food and arrive at breeding sites [41,42]. In addition, the behavior of hiding during the day, between fallen logs and in small cavities in the ground, allows them to avoid sun exposure [38,43] and contributes to the use of open areas by this group. However, species of the genera *Atelopus* and *Amazophrynella* display diurnal habits, and due to their small body size, they are more susceptible to dehydration [44]. These organisms mainly occupy the litter of forested habitats, i.e., sites/microhabitats where they usually hide from predators, seek food, and avoid sun exposure and consequently, dehydration [5,7,44,45].

Another factor that may favor the use of open and anthropized areas by species of the *Rhinella marina* group is its generalist feeding habit [34,46,47]. Its species usually forage at night, feeding on the orders Coleoptera, Hymenoptera, Gastropoda, and Orthoptera, among others [38,43,46]. Species of the genus *Atelopus*, e.g., *A. cruciger* (Venezuela) and *A. varius* (Panama and Costa Rica), prefer to feed on ants and bedbugs found in forest litter [48,49], indicating that these species, because they occupy different environments, exhibit high food plasticity. That is, with the use of the same areas at different times of the day, species do not meet and therefore, do not compete for space. Thus, habitat and habit selection in this group can reduce competition pressure [50]. The same scenario occurs in the *R. granulosa* and *R. margaritifera* species groups, species that occupy the same habitat but differ in the circadian time of resource use, so it is possible that they present high niche tolerance values when in syntopy.

In general, species of the *R. marina* group were associated with open areas, *R. granulosa* and *R. margaritifera* with secondary forests, *Rhaebo guttatus* occurred in all habitats, and the genera *Atelopus* and *Amazophrynella* occupied primary forests. A possible explanation for this pattern would be the evolutionary pressure that molded the basal groups [46].

Precipitation influences amphibian populations [51,52], not only by increasing reproductive activity, but also in their daily activity. During dry periods, amphibians tend to remain sheltered and inactive, since the low relative humidity of the air favors the loss of body water [52].

However, due to the constant degradation that natural ecosystems have been suffering mainly via anthropic actions, several microhabitats exploited by anurans have been altered or completely eliminated, with natural ecosystem degradation considered to be the main factor causing the population declines [53,54] observed in several species on a global scale. Concomitantly, information on the association of species with their habitats allows for the recognition of local distribution patterns that constitute important information for territorial management and biological conservation.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/jzbg6040050/s1, Table S1: Morphological variables used to assess morphological and ecomorphological patterns in Amazonian Bufonidae; Table S2: Principal component analysis (PCA) performed using the morphological measurements of Amazonian Bufonidae. Acronyms are listed in Table S1; Table S3: Multiple correspondence analysis (MCA) performed using the characteristics of habit and habitat of Amazonian Bufonidae. Acronyms are listed in Table 1; Table S4: Redundancy analysis (RDA) performed between habitat and habit and ecomorphological characteristics of the Amazonian Bufonidae (Amphibia, Anura) species. Acronyms of morphological variables are listed in Table S1.

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