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EFEITOS DO AMBIENTE E DE CARACTERÍSTICAS FUNCIONAIS NA DIVERSIDADE E COMPOSIÇÃO DE ANUROS

Santa Maria, RS

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Sâmia Letícia Reolon da Cruz

EFEITOS DO AMBIENTE E DE CARACTERÍSTICAS FUNCIONAIS NA DIVERSIDADE E COMPOSIÇÃO DE ANUROS

Dissertação apresentada ao Curso de Pós-Graduação em Biodiversidade Animal, da Universidade Federal de Santa Maria (UFSM, RS), como requisito parcial para obtenção do título de **Mestre em Biodiversidade Animal.**

Orientador: Profº. Drº. Cristian de Sales Dambros

Santa Maria, RS

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RESUMO

EFEITOS DO AMBIENTE E DE CARACTERÍSTICAS FUNCIONAIS NA DIVERSIDADE E COMPOSIÇÃO DE ANUROS

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As espécies que compõe as comunidades diferem entre locais e ambientes, entretanto quais características e quais variáveis ambientais estão associados a estas mudanças não estão bem estabelecidas, especialmente em animais com ciclos de vida complexos, como os sapos. Aqui demonstramos como as características dos sapos, associadas aos fatores ambientais, determinam a mudança da composição e a diversidade de espécies de forma a responder: (i) há um turnover de espécies e funções entre as comunidades? (ii) Como os estágios de desenvolvimento pode estar influenciando nestas mudanças entre as comunidades? e (iii) Como as variáveis ambientais influenciam a diversidade e distribuição destas espécies? Para responder a estas questões, 31 sítios de coleta foram amostrados em um parque Estadual do Rio Grande do Sul. Além disso, dados morfológicos e do ciclo de vida das espécies foram obtidos de literaturas. Para relacionar as características funcionais das espécies com características ambientais, utilizamos análises de diversidade e composição funcional, assim como regressões múltiplas. Nós encontramos que a profundidade, abertura de dossel e hidroperíodo são as principais variáveis correlacionadas com a riqueza taxonômica e funcional das espécies, assim como com a troca de espécies e funcões nas determinadas comunidades. Ambas as fases (girinos e adultos) tiveram características correlacionadas com essas e outras variáveis ambientais (temperatura, oxigênio dissolvido (OD), condutividade, vegetação e área). No entanto, as características dos girinos são as que mais se correlacionam com a profundidade, abertura de dossel e hidroperíodo.

Palavras-chave: Diversidade de espécies. Características. Variáveis ambientais. Riqueza.

ABSTRACT

EFFECTS OF THE ENVIRONMENT AND FUNCTIONAL CHARACTERISTICS ON THE DIVERSITY AND COMPOSITION OF FROGS

AUTHOR: Sâmia Letícia Reolon da Cruz
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The species that compose the communities differ between environments, however which characteristics and which environmental variables are associated with these changes are not well established, especially in animals with complex life cycles, such as frogs. Here we demonstrate how frog characteristics, associated with environmental factors, determine changes in species composition and diversity to respond: (i) Is there a species turnover and characteristics between communities? (ii) How might development stages be influencing these changes across communities? and (iii) How environmental variables influence species diversity and distribution? To answer these questions, we sampled 31 sites in Turvo State Park, Rio Grande do Sul, Brazil. In addition, we obtained species morphological and life cycle data from scientific literature. To relate species functional characteristics to environmental variables, we performed taxonomic and functional composition analysis, and then multiple regressions. We found that depth, canopy openness and hydroperiod are the main variables related to taxonomic and functional richness, as well as with species and characteristics turnover in between communities. Moreover, both development stages (i.e. tadpoles and adults) had characteristics related to these main variables and temperature, dissolved oxygen (OD), conductivity, vegetation and area. However, tadpole characteristics are mainly related to depth, canopy openness, and hydroperiod.

Key-words: Species diversity. Characteristics. Environmental variables. Richness.

SUMÁRIO

INTRODUÇÃO

Diversos processos ecológicos influenciam diretamente a forma como as espécies se distribuem ao longo dos ambientes (KRAFT et al., 2015; MITTELBACH; SCHEMSKE, 2015). Estes processos podem ser bióticos (competição) e abióticos (variáveis ambientais) (CHASE; MYERS, 2011; KNAUTH et al., 2019). Estes fatores podem ter uma forte influência nas diferentes espécies e nas características das mesmas, podendo atuar como um filtro, principalmente regionalmente e localmente (LEIBOLD et al., 2004). Além disso, podem influenciar de forma diferente espécies que tem ciclo de vida dividido em diferentes fases ao longo de seu desenvolvimento (ALBECKER; MCCOY, 2017; SHI et al., 2018). Compreender como o ambiente pode influenciar a forma como as espécies estão compostas e distribuídas nas diferentes comunidades pode nos ajudar a entender como estas fases podem estar sendo afetadas por mudanças localmente.

Os filtros ambientais (e.g. profundidade de lagoas, abertura de dossel) podem selecionar as espécies ou suas características dependendo da capacidade dos mesmos de sobreviver e se reproduzir sob determinado filtro (RAMALHO et al., 2021). Espécies com ciclos de vida complexos, i.e. dividido por fases, podem ser influenciados de diferentes maneiras ao longo de seu desenvolvimento (CARLO et al., 2018). Por exemplo, organismos que vivem na água no início do seu desenvolvimento podem ser afetados diretamente pelas condições físico-químicas da mesma (PROVETE et al., 2014). No entanto, na fase adulta podem ser influenciados por outros filtros como a abertura de dossel (SCHIESARI, 2006). A forma como estas espécies são influenciadas pode determinar como estas espécies estão distribuídas no ambiente e também que fase pode influenciar como as comunidades estão compostas.

Um dos grupos mais ameaçados de extinção nas últimas décadas são os anfíbios (STUART et al., 2004; WAKE; VREDENBURG, 2008). Dentro do grupo dos anfíbios, os sapos possuem um ciclo de vida dividido em duas fases, sendo girino e adulto. São organismos que possuem respiração cutânea, ou seja, sua respiração se dá através de trocas gasosas através da pele, apesar de ainda terem pulmões (CARLO et al., 2018; WELLS, 2010). Os sapos também são animais ectotérmicos, ou seja, dependem das condições do ambiente para regular a sua temperatura corporal (ZUG; VITT (J.); CALDWELL, 2001). Sendo assim, acabam se tornando muito sensíveis a qualquer mudança no ambiente, tanto no presente quanto em mudanças ambientais futuras (VASCONCELOS; NASCIMENTO; PRADO, 2018).

Com isso, o objetivo deste estudo é entender como as características dos sapos, associadas aos fatores ambientais, determinam a mudança da composição e a diversidade de espécies de forma a responder: (i) há um turnover de espécies e funções entre as comunidades? (ii) Como os estágios de desenvolvimento pode estar influenciando nestas mudanças entre as comunidades? e (iii) Como as variáveis ambientais influenciam a diversidade e distribuição destas espécies? Entender como funciona a dinâmica destes organismos e como eles estão distribuídos nos determinados ambientes pode nos ajudar a compreender a melhor maneira de mitigar e questões que ameaçam a conservação destes organismos.

Estrutura da dissertação

Esta dissertação é apresentada em um capítulo único, estruturado em formato de "*Research papers*", conforme as normas da revista *Oikos*.

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Effects of the environment and functional characteristics on the diversity and composition of frogs

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Abstract

The species that compose the communities differ between environments, however which characteristics and which environmental variables are associated with these changes are not well established, especially in animals with complex life cycles, such as frogs. Here we demonstrate how frog characteristics, associated with environmental factors, determine changes in species composition and diversity to respond: (i) Is there a species turnover and characteristics between communities? (ii) How might development stages be influencing these changes across communities? and (iii) How environmental variables influence species diversity and distribution? To answer these questions, we sampled 31 sites in Turvo State Park, Rio Grande do Sul, Brazil. In addition, we obtained species morphological and life cycle data from scientific literature. To relate species functional characteristics to environmental variables, we performed taxonomic and functional composition analysis, and then multiple regressions. We found that depth, canopy openness and hydroperiod are the main variables related to taxonomic and functional richness, as well as with species and characteristics turnover in between communities. Moreover, both development stages (i.e. tadpoles and adults) had characteristics related to these main variables and temperature, OD, conductivity, vegetation and area. However, tadpole characteristics are mainly related to depth, canopy openness, and hydroperiod.

Key-words: Species diversity. Characteristics. Environmental variables. Richness.

1. Introduction

The species distribution varies from one local to another (Leibold et al. 2004). This difference reflects the numerous adaptative characteristics of the species, that determine their relationship between the abiotic environment and biotic interactions in the communities (Chase and Myers 2011, Knauth et al. 2019). Understanding how these characteristics are associated with their distribution helps us to figure out the distribution patterns and their causes (Ricklefs 1987, Leibold et al. 2004, Pyron and Wiens 2013). Some taxonomic groups present different life stages, and in each phase, the organisms present characteristics could be more sensitive to the environment and define how the species are distributed in the environment gradient (Santos and Conte 2014, Albecker and McCoy 2017, Shi et al. 2018). However, it is necessary to understand the association of these species' characteristics with their response to the environment to determine how the communities are assembled throughout the environments.

In this context, it is known that frogs are animals extremely sensitive to environmental variations because they have cutaneous respiration (i.e., they carry out their gas exchange through the skin, although they also have lungs) (Wells 2010). They are ectothermic animals, i.e., they need the environment to regulate their body temperature (Zug et al. 2001). Moreover, they have a complex life cycle, divided in two phases: (i) tadpole and (ii) adult, and this cycle can be a determining factor in the choice of their habitats (Carlo et al. 2018). As a result, this great physiological and behavioral sensitivity to environment changes makes them the most endangered vertebrate taxa and may suffer even more from future climate changes (Vasconcelos et al. 2018). Thus, understanding how life cycle and species characteristics will be related to some environmental factors are important determinants of the species distribution across different environments (Blaustein and Belden 2003, Schiesari 2006, Vasconcelos et al. 2009, Provete et al. 2014, Franco-Belussi et al. 2016).

Due to the low ability of amphibians to disperse over long distances (Alex Smith and M. Green 2005), the regional and local environmental factors could strongly impact their distribution along the environments (Percino-Daniel et al., 2021). Some environmental factors, as canopy opening, depth, or vegetation around the ponds could have different influences on frogs, for example, selecting some species or characteristics (Ramalho et al. 2021). Adults and tadpoles responses to the same environmental factor can cause opposite effects on their diversity, reducing the impact of the environment on their distribution or even amplifying these impact on species diversity (i.e, with synergistic effect) (Borges Junior and Rocha 2013, Valério et al. 2016, Riemann et al. 2017). Then, understanding how these characteristics are determinant together can help in understanding the distribution of species.

In this study, we aim to understand how characteristics of frogs, associated with environmental factors, determine the change in species diversity and local composition, in order to answer: (i) Is there taxonomic and functional turnover between communities? (ii) How the development stages could be determinants for these changes between communities? and (iii) – What are the main environmental factors associated with taxonomic and functional turnover? Answering these questions helps us understand the ecological patterns of these organisms, as well as mitigate or protect these groups of animals from threats, helping to conserve the species.

2. **Methods**

2.1. Study area

We conducted the study at Turvo State Park (27°07’S–27°16’S; 53°48’W–54°04’W, covering an area of 17492 ha), located in the municipality of Derrubadas, state of Rio Grande do Sul, southern Brazil (Figure 1). The Park is an integral protection conservation composed in most of its extension by Deciduous Seasonal Forest type vegetation (SEMA, 2005). The climate of the region is characterized as subtropical, sub-humid, with the temperature of the hottest month (January) being above 22 °C and that of the coldest month ranging from -3 °C to 28 °C (MALUF, 2000). The average annual rainfall is 1665 millimeters with rainfall distributed throughout the year, with no defined dry season (SEMA, 2005).

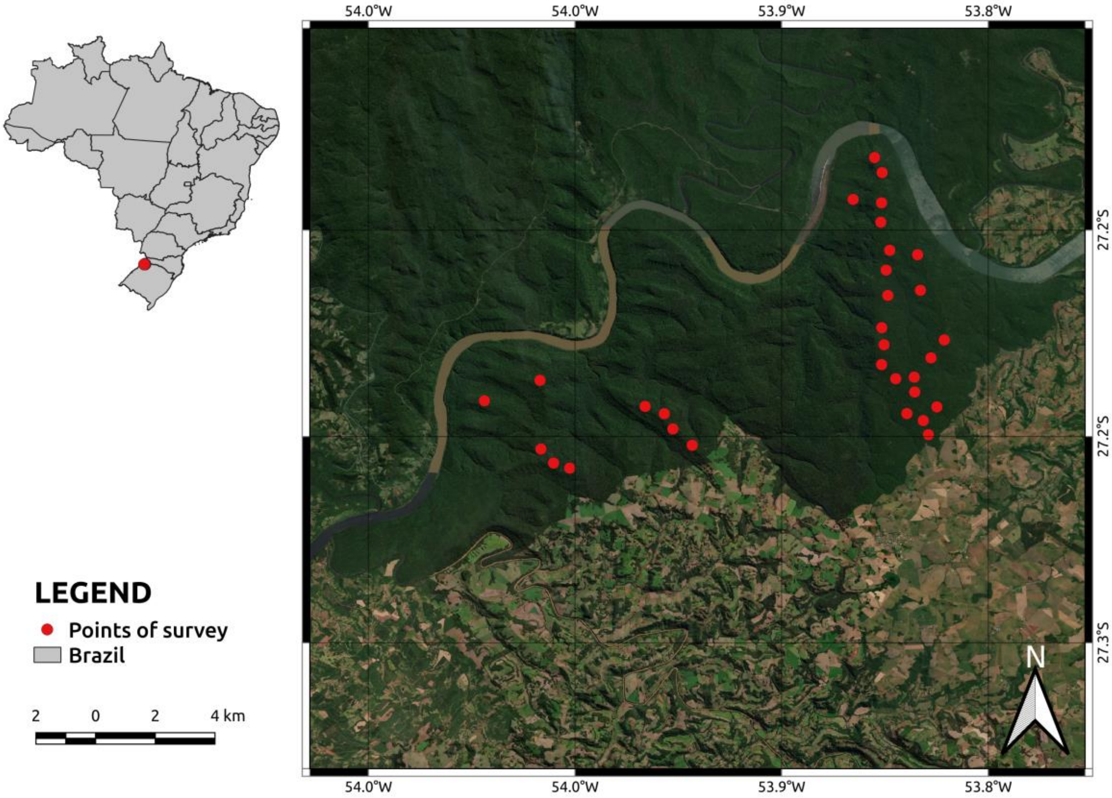

Figure 1. Map of the study area at the Turvo State Park. Red dots represent the 31 sampling sites.

2.2. Sampling data

We conducted three field campaigns from October 2020 to February 2021. We choose these months (from spring to summer) because they have the highest reproduction peak and the frogs are more active (Gerhardt 1994). As the Park is contoured by areas of agriculture, so it does not have a buffer zone, e.g. transition between the forest gradient and plantations, we delimited a distance of the edge of 500 meters for the surveys. We also delimited a distance of 500 meters from one pond to another to had statistic independence in the analysis.

To choose the ponds that were sampled, we obtained satellite images from the National Institute for Space Research (INPE) of the last rainy season with high rainfall (05/19/2017). From these images we applied an infrared layer that highlighted points where there was water. From these demarcations on the map and using the main roads of the park, we were able to choose randomly 31 ponds throughout the Park.

Each field campaign had an average duration of 16 days, with an interval of approximately 30 days from one campaign to another. On each day, we aimed to sample three points per day. In order to record the richness of species present in the places, during the day, one to two recorders were arranged in the ponds, depending on the size of it, and when a recorder was placed, it was located in the middle of the pond, or, two recorders being placed one in each side, to obtain the highest possible sing from the species. These recorders remained in place for 24 hours being collected and checked the next day.

2.3. Environmental variables survey

To understand how the environmental variables could influence the richness and functional diversity of tadpoles and adults, we measured 13 environmental predictors. Pond morphology was categorized into: (i) the amount of vegetation covering the water surface (dividing water coverage in quadrants and acquiring the percentage of coverage), (ii) hydroperiod (ephemeral – drying during sampling, and permanent – never drying during the entire sampling), pond area (m²), total area (m²) and depth (m) according to (Iop et al. 2012, Provete et al. 2014, Vasconcelos et al. 2018). We also collected altitude from google earth.

Canopy opening was quantified through photographs of quadrants, with the camera positioned with the upper part facing North, 30 cm from the ground, adapted from (Paletto and Tosi 2009, Buskirk 2011). These photos were analyzed in the R software, and canopy opening at each point was quantified as the percentage of pixels with at least 10% of green in the RGB color scale. Then we could quantify the percentage of canopy opening in each pond.

We obtained water pH, conductivity, dissolved oxygen, turbidity and temperature with a Horiba U-10 multiparameter. These variables were measured in all campaigns and were carried out at the same time as the other equipment was placed in ponds. The same consisted of placing the equipment with the sensors immersed in the water, being normally done on the surface, with the sensors at a maximum of 20 cm deep. After two minutes, when the device reached stability, the characteristics were collected. These data may have an influence on the richness of tadpoles within the ponds, as it is related to the development and time of the tadpole's metamorphosis, in addition to influencing the choice of breeding sites by adults (Provete et al. 2014).

In addition to the mentioned variables, to collected UVA radiation data that can affect survival and other aspects of the life cycle (Lipinski et al. 2016), we allocated radiometers in the ponds, which were placed in the same places every time. Locations closest to possible wetlands were selected, taking into account that many species use these areas for reproduction. This equipment was available during the 24 hours that the recorders remained, but they collect data primarily during the day, as that is when there is sunlight.

To identify the species observed through field recording, we selected 75 species with occurrence near Turvo State Park. These represent all frog species known from northern Argentina and southern Brazil (Vaira 2002, Lucas and Marocco 2011, Agostini et al. 2016). Then, we consulted the Fonoteca Neotropical Jacques Vielliard – FNJV (FNJV, 2022) which contains vocalizations of the 75 species selected. The requested calls from the FNJV were deposited in the Arbimon software, which was used to identify the species (Aide et al. 2013). In this software, we could visualize the sonogram (i.e. the image from a certain soundscape in which we can see the frequencies and duration of the sounds). In it, we manually selected the vocalization of each specie in a window a window that we called as a template (Figure 2). This template was made only in the call of the species, choosing the correct frequency and duration of it, and then having an example vocalization for each species.

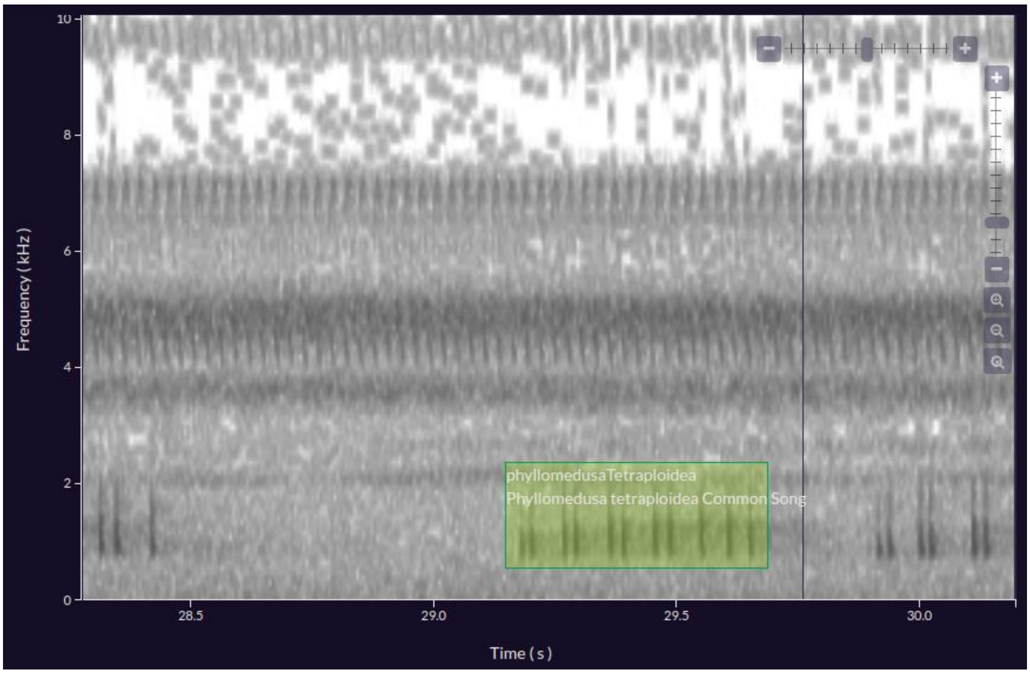

Figure 2. Sonogram showing the template (in yellow) the vocalization of a *Phyllomedusa tetraploidea.* In the x axis is duration and in y axis is the frequency of the vocalization.

To analyze all recorded audios, we used the 'Pattern matching' tool in the Arbimon Software. With this tool, all recordings made during the field campaign are researched and those vocalizations that show frequency and duration similar to the template songs (i.e., species) are selected. For the identification accuracy, we used a threshold of 0.2, where values closer to 0 capture any similar noise to the frequencies and duration provided, and values closer to 1 are more similar to templates of certain species. After running the analysis, the species present in the points were manually validated.

2.4. Functional morphological and ecological characteristics

After species identification, we classified all tadpoles and adults recorded in the ponds according to 4 functional characteristics for tadpoles and 4 for adults, respectively. We selected these functional characteristics from bibliographies (Duellman and Trueb 1994, Toledo et al. 2007, Hadad et al. 2013, de Souza Queiroz et al. 2015, Mello et al. 2018, Brodeur et al. 2020, Hocking and Babbitt., 2014), but mainly from the AmphiBIO database (Oliveira et al. 2017). In relation to the tadpoles, their ecological guilds (e.g., nektonic and benthic) are determined in according to morphological aspects, as height of the tail, relative width of the caudal musculature and relative length of the tail (in Gosner stages 34 to 38) (Gosner 1960, Both et al. 2011a). For adults, the functional characteristics selected were: (i) body size (mm), (ii) habitat (open or closed), (iii) habit (arboreal, terrestrial or aquatic), and (iv) period of activity (night or day). These variables were chosen because they are directly associated with ecological aspects, thus being influenced by the structure of the ecosystem and also acting in defense against predation (Strauß et al. 2010, Both et al. 2011b; Mcdiarmid and Altig, 1999). Moreover, some of these characteristics (e.g., guilds for tadpoles and habitat for adults) are linked to some environmental variables such as hydroperiod and morphology of ponds, as well as the presence or absence of vegetation in water bodies (Haddad and Prado 2005).

2.5. Statistical analysis

To understand how the environmental variables affect the taxonomic diversity and the mean species characteristics, we associated these variables with species richness, functional richness (FRic), and the community weight mean (CWM). At each sampling point, frog diversity was quantified by the number of identified species (species richness). The functional richness of each community was measured by the multidimensional volume delimited by the species characteristics presents in the community (Laliberté and Legendre 2010). The community weight mean of frogs characteristics (CWM; Lavorel et al. 2008) was measured as the mean of the values of each characteristic for all species present in each community. Therefore, CWM was measured separately for each one of those 8 characteristics belonging to adults and tadpoles, and we performed separated models.

To find the taxonomic and functional beta diversity (species composition) in each location, we quantified the taxonomic and functional Jaccard pairwise dissimilarity index (Legendre and Legendre 2012). The difference in general composition of species can be divided in two ways, being in the species substitution model (turnover) or in the nesting model (nestedness) (Legendre and Legendre 2012). The turnover model is related to the replacement of species and functions in the sampled environments, almost always due to ecological processes such as environmental filtering or limitation in dispersion (Ricotta and Pavoine 2015, Hill et al. 2017). The nesting model, on the other hand, happens when we have communities with a lower richness that are poorer subsets of larger and richer communities, thus representing a factor of species loss along the sampled sites (Baselga 2010). In addition, it can represent a more functionally similar community, as it is a subset of another location (Villéger et al. 2011).

In order to understand which environmental variables are influencing the species and functional richness we performed a multiple regression model and used stepAIC from the package MASS to simplify the model. The stepAIC choose the best combination of environmental variables without impacting much on the performance. For the taxonomic and functional composition of the species, the sampled locations were ordered based on the pairs obtained in the Jaccard dissimilarity matrix, both for the taxonomic and functional parts. The ordering of each matrix was performed using a Principal Coordinate Analysis (PCoA) and the first ordering axes were used as a response variable in multiple regression models also using the stepAIC to summarize the variables. These regressions were made from the environmental variables (predictors) in relation to the ordering axes of the PCoA (response). All the response and predictors variables were standardized before the analysis. In addition to confirm that the models with better performance were chosen with stepAIC, we applied other automated model selection that generates a model selection table with best combinations of fixed effect terms (table S2 to S5).

To extract functional diversity (FRic), we used the function dbFD of the package FD (Laliberté and Legendre 2010). To standardize the data, we used the function decostand from the package vegan (Oksanen *et al*, 2016). To perform the multiple regression model we used the function stepAIC from the package MASS (Venables WN, Ripley BD, 2002). To generate the table with the best environmental variables selected, we used the function dredge from the package (MuMIn) (Barton, 2009). All the data was obtained, prepared, and analyzed in the R program (R Core Team 2022).

3. Results

We registered seventeen species from four families (Table S6). The species number per pond varied from one to fifteen. Species richness increased with pond depth (Table 1) and canopy opening (Table 1; Figure 3ab). When testing for the effects of these variables individually, pond depth explained up to 47% of the variation in species richness, whereas canopy opening explained up to 25% of this variation. When controlling for the effect of other variables (altitude, vegetation, and dissolved oxygen), depth and canopy opening still explained 8% and 11% of the variation in species richness (Figures 4 and 5; Table S7). Also, we observed a similar increase of functional richness (FRic) with pond depth (Table 1; Figure 3c).

Table 1. Table representing how the variables influenced species richness, functional richness (FRic), the species taxonomic (Tax. Comp. turnover) and functional (Func. Comp. Turnover) composition. Numbers in bold represent the analysis that presented $p < 0.05$.

	Richness	FRic	Tax. Comp. (Turnover)	Func. Comp. (Turnover)
Altitude	0.16	-	-	-
Area	-	-	-0.91	-
Depth	**0.38***	**0.57****	**1.01*****	-
Vegetation	0.18	-	0.74	-
pH	-	-	-	-
Conductivity	-	-	0.26	-0.29.
OD	0.28.	-	-	0.28
Turbidity	-	-	-	-
Temperature	-	-	-	-0.34.
Can. Open.	**0.35****	-	-	**0.47***
Pond Area	-	-	-	-
Radiation	-	-	-	-
Hydroperiod (permanent vs. ephemeral)	-	-0.3	-0.22	**-0.33***
f	11.52	5.06	5.27	5.03
DF	24	26	24	23
R^2	0.64	0.21	0.42	0.41
p-value	**<0.001*****	**0.01****	**0.002****	**0.002****

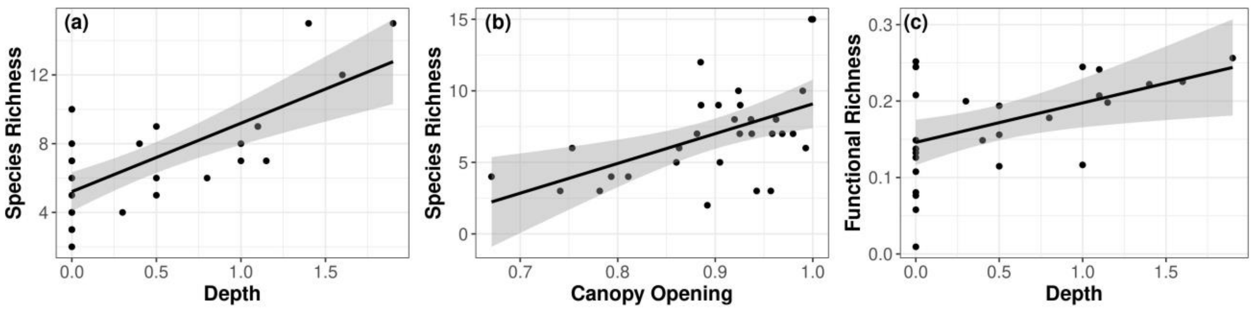

Figure 3. Relationship between (a) depth, (b) canopy opening and species richness of frogs and the relationship between (c) depth and functional richness of frogs.

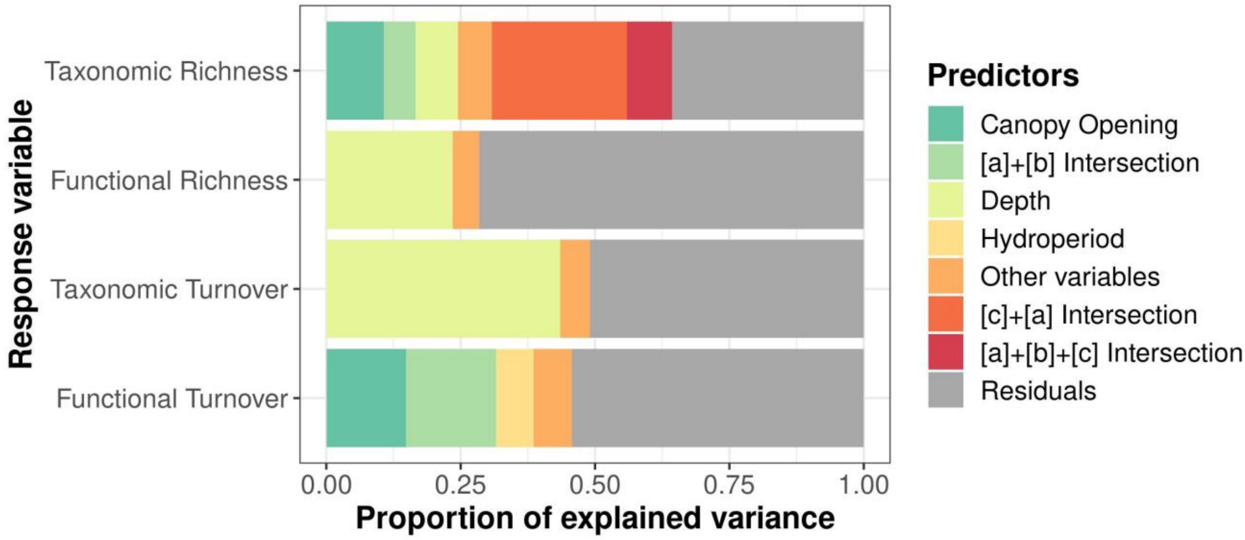

Figure 4. Variance partitioning showing the proportion of explained variance (%) of how depth (A), canopy opening (B) and hydroperiod (ephemeral and permanent ponds) (predictors) influence taxonomic richness, functional richness, taxonomic and functional turnover (responsible).

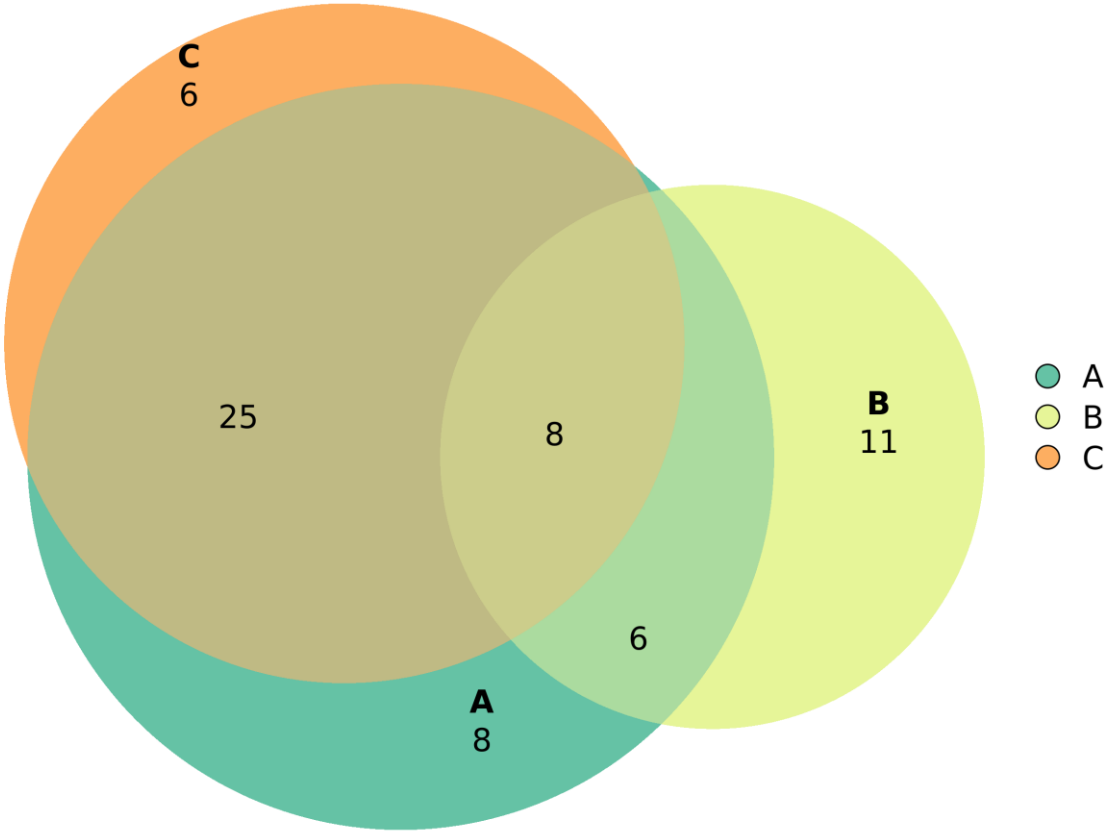

Figure 5. Variance partitioning diagram showing the fractions of explained variance (%) of how depth (A), canopy opening (B) and other variables, such as altitude, vegetation, and dissolved oxygen (C) influence species richness.

The first PCoA axis, representing changes in species composition, was associated with pond depth (Table 1; Figure 4). In contrast, the first PCoA axis, representing changes in functional composition, was associated with canopy opening and hydroperiod (Table 1; Figure 4). Ponds with open canopies had benthic tadpoles with higher caudal musculature (width) and tail length, and adults with aquatic habits and smaller bodies (CWM results in Table S1; Figure 5a,c). Compared with permanent ponds, ephemeral ponds (Hydroperiod) had tadpoles with larger tail lengths, and adults with primarily arboreal and nocturnal habits (CWM results in Table S1; Figure 5b,d). Other environmental variables, especially pond depth, were associated with changes in community CWM, but not with changes in functional composition at the community level (Table S1).

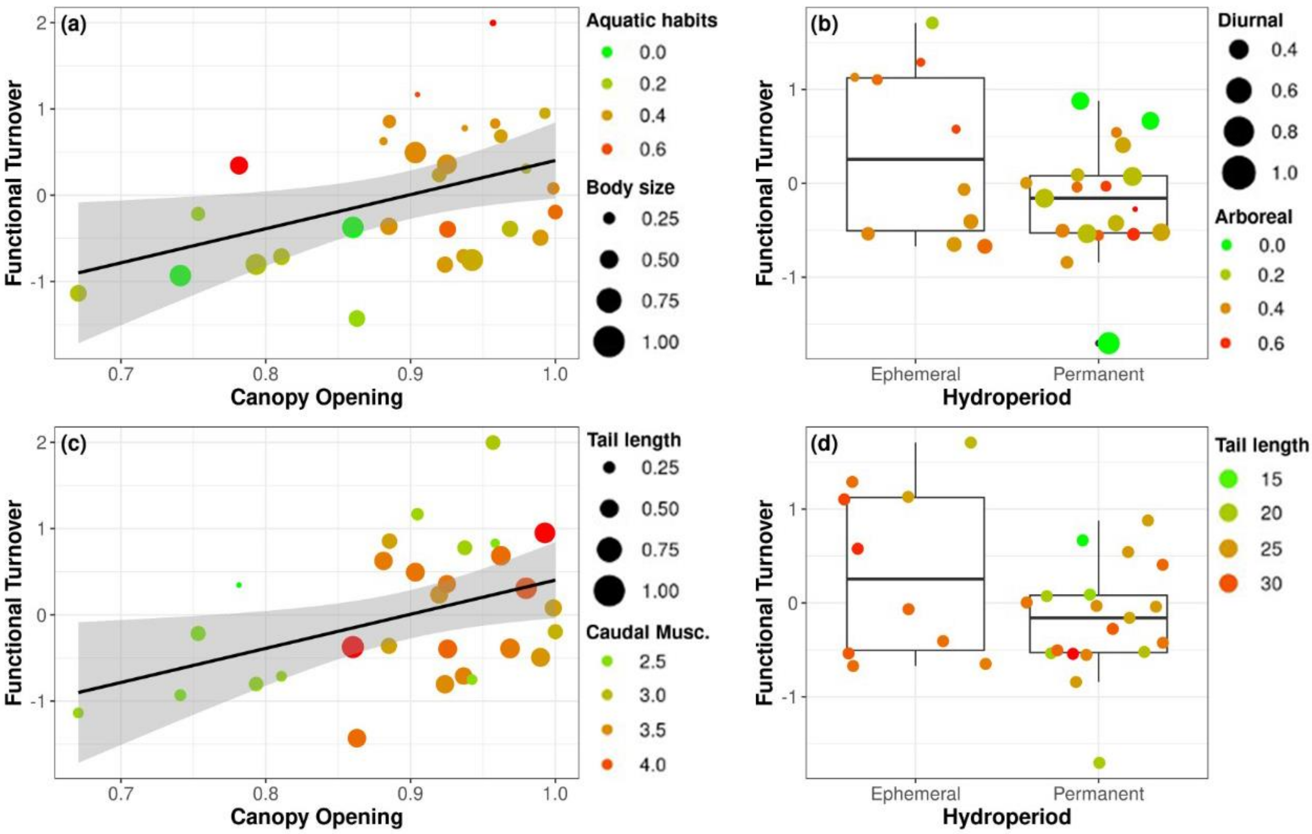

Figure 6. Relationship of how (a, c) canopy opening and (b, d) hydroperiod influences adults and tadpoles characteristics (CWM) of frog species. In (a) the gradient of color represents the mean of aquatic habit of each community and the size of the circles represents the mean body size for each community. In (b) the color gradient represents the mean of arboreal species of each community and the size of the circles represents the mean of diurnal species for each community. In (c) the color gradient represents the mean caudal musculature size of tadpoles in each community and the size of the circles represents the mean tail length of tadpoles for each community. In (d) the color gradient represents the mean tail length size of tadpoles in each community and the size of the circles represents the mean body size for each community.

4. Discussion

Although frogs have a wide distribution across the planet (Duellman and Trueb 1994), they are also one of the most fragile and threatened group of animals (Stuart et al. 2004, Wake and Vredenburg 2008). An explanation for this threat is how their functional characteristics could interact with the environmental variables (Kopp and Eterovick 2006, Menin et al. 2011, Marques and Nomura 2018). Thus, in this study we asked: “what are the effects of the environment and characteristics in the diversity and composition of frogs species?”. We found that deeper ponds with larger canopy opening shelter more frog’s species. In addition, we observed higher functional richness in deeper ponds. Therefore, environmental variables as depth and canopy opening can be associated with the survival and development of tadpoles, suggesting a strong influence on community structure (Provete et al. 2014).

Depth seems to follow, in this case, the same species-area pattern (Lomolino and Weiser 2001) as other taxonomic groups (e.g., more area shelter more species), as deeper ponds could shelter more frog species (Provete et al. 2014, de Souza Queiroz et al. 2015). Besides that, deeper ponds could retain water in dry seasons, allowing species with different development times to reproduce and achieve breeding success, especially those that develop slower. Species with slow development tends to develop larger bodies (Valenzuela-Sánchez et al. 2015). In fact, we found that these environments shelter larger body-size species of tadpoles and adults. Also, deeper ponds provide more space for nektonic and benthic tadpoles and, then, they could coexist without competition (Eterovick and Fernandes 2001). Nektonics have the mouth ahead of their bodies and usually feed on the top of the water bodies, while benthic tadpoles have their mouth below their bodies, because they feed more often at the bottom of water bodies (Mcdiarmid and Altig 1999). Therefore, the increase of functional richness observed in deeper ponds justified the pattern where different layers of depths could have tadpoles with different nektonic and benthic species, since they feed using different resources (Annibale et al. 2018).

The difference in the type of environment preferred by species is also corroborated when we saw that species composition change with more depth. Frogs are highly dependent on water for development, especially when they are in the tadpole phase, mostly due their reproductive modes (Haddad and Prado 2005). Shallow ponds had a different composition of species when compared with deep ponds. In contrast, shallow and deep ponds tend to share the same set of characteristics. This could provide an inside that these changes in species composition with pond depth represent that they contributed to providing more space for species reproduction and different microhabitats for adults and tadpoles (Chesson 2000). Therefore, differences in pond depths add more species, but they did not alter the functional components in the communities, demonstrating some resilience to this environmental variable (Strauß et al. 2010, Both et al. 2011b).

In contrast, ponds with open canopy increased the number of species and change the functional composition. These environments present more food availability (Schiesari 2006, Rowland et al. 2016). Canopy opening ponds allow the entering of more light and also have greater amounts of dissolved oxygen (Werner and Glennemeier 1999, Stoler and Relyea 2011), helping the increase of primary productivity (i.e., organic matter synthesis that promotes more food and nutritional quality to tadpoles in these locals) (Schiesari 2006, Rowland et al. 2016). However, despite functional composition change from open to close canopies, the functional richness did not increase in sites with greater canopy opening. This may indicate that despite having a greater number of species, open canopy ponds were occupied by species with similar characteristics. For example, in these places, there is commonly observe species with smaller body sizes and greater aquatic habits. In fact, in open canopy ponds, species with fast development and smaller body sizes, as *Physalaemus cuvieri* were observed (Barreto and Andrade 1995). However, some studies show that most frogs tolerate open environments, possibly due to their greater availability of food, while few species specialize in more closed environments, leading to these differences in species characteristics (Werner and Glennemeier 1999, Provete et al. 2014).

Meanwhile, canopy opening and hydroperiod seem to promote change in the functional composition of ponds. Throughout the time, frogs have developed many strategies to reach reproductive and development success (Haddad and Prado 2005). These strategies were mainly used to avoid dryness until their life cycle was completed (Prado et al. 2005). Open canopy ponds tend to receive more quantity of solar radiation, and consequently have more chances to dry. In these locals, frogs with a slower development may not reach success in finishing their life cycle (Acosta et al. 2017). Therefore, locals that dry more often and present open canopy tend to have species with distinct characteristics. For example, tadpoles with large caudal structures and benthic tadpoles are observed in ponds with opening canopy. Meanwhile, in locals that dry more often, tadpoles had smaller caudal lengths and had adults with smaller bodies. This could happen because with more solar incidence, the water tends to be warmer and the tadpoles developing faster (Laugen et al. 2003), and leading to adults with smaller bodies (Denver et al. 1998, Burraco et al. 2017). In addition, frogs evolve strategies to deal with dry environments (Pechmann et al. 1989, Otto et al. 2007, Thompson and Popescu 2021), as to put their eggs in foam nests that could protect the tadpole from dryness and direct solar radiation (Méndez-Narváez et al. 2015).

Many authors argue about how the environment could influence the characteristics of frogs (Rojas-Ahumada et al. 2012, Figueiredo et al. 2019, Ramalho et al. 2021). Nonetheless, these studies are conducted with adults or with tadpoles, becoming difficult to understand how these different phases can be influenced together. In addition, studies with other taxonomic groups (e.g., plants) that also have life cycles divided into phases, demonstrate that understanding how the characteristics of these phases are influenced by the environment is essential to understanding whether they will be successful in their development (Bosch et al. 2014, Li et al. 2020). Frogs are extremely influenced by environmental filters, especially in a local scale (Leão-Pires et al. 2018). However, tadpoles seem to have the highest sensitivity, as the most influential filters primarily impact this initial phase. This demonstrates that in addition to the low dispersion reported in adult individuals (Alex Smith and M. Green 2005, Cayuela et al. 2020), their reproductive success also depends a lot on the place where these tadpoles are deposited. In addition, the type of environment seems to significantly affect the body shape and habits of these species. Also, these characteristics being filtered mainly by differences between open and closed canopies, ponds depth and whether they dry up or not. These results can provide us with insights into how these communities are influenced and how they should be managed in forest environments.

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Supplementary Material

Table 1. Table representing how the variables influenced the community weight mean of frogs characteristics (CWM). It was measured as the mean of the values of each characteristic (Width Caudal Musculature (WCM), Tail length (TL), Tail Height (TH), Benthic, Nektonic, Foam Nest, Eggs in water, Terrestrial Habit (HT), Aquatical Habit (HAq), Arboreal Habit (Harb), activity period (Day), activity period (Night), Body size (Body)) for all species present in each community. Numbers in bold represent the analysis that presented $p < 0.05$.

	WCM	TL	TH	Benthic	Nektonic	FoamNest	EggsInWater	HT	HAq	Harb	Day	Night	Body
Altitude	-0.28	-0.18	**-0.46****	-	-	-	-	-	-	-	-0.33	0.34.	**-0.44***
Area	-1	-	-	-	-	-	-	2.61.	-	-3.11.	**3.67***	**-1.31***	**4.57****
Depth	**0.53***	**0.76****	**0.58****	**-0.38***	**0.38***	-0.76	0.29	**-0.59***	-0.55.	**0.66***	-0.39	0.45.	**0.53***
Vegetation	0.8	-	-	-	-	-	-	-1.76	-	**2.42***	**-2.98***	1.19.	**-3.94****
pH	0.25	0.25	-	-	-	-	-	-	0.37	0.24	**-0.46***	0.27	**-0.61****
Conductivity	-	-	0.28	-	-	-0.34.	-	-0.24	**-0.61****	-	-	-	**0.48***
OD	-	-	-0.37.	-	-	-	-	-0.27	-	-	-	0.26	-
Turbidity	-	-	-	-	-	-	-	-	-	-	-	-	-
Temperature	-	-0.21	-	-	-	-	-	-	-	-	-	-	-
Can. Open.	**0.40***	**0.33***	**-**	**0.48****	**-0.48****	0.34.	-	-	**0.64****	-	-0.27	0.33.	**-0.54****
Pond Area	-	**-0.38***		-	-	-	-	-0.95	-	0.86	-0.98.	-	**-1.22***
Radiation	-	**-**	-	-	-	-	-	-	-	-	-	-	-
Hydroperiod (permanent vs. ephemeral)	-0.44	**-0.54****	-0.32.	-	-	0.38.	-	**0.46***	0.40.	**-0.52****	**0.40***	-0.29	-
f	5.64	5.97	4.19	5.17	5.17	3.06	2.64	3.53	3.58	3.51	3.69	4.61	4.35
DF	22	22	24	27	27	25	28	22	24	23	21	21	21
R^2	0.52	0.54	0.35	0.22	0.22	0.22	0.05	0.37	0.3	0.34	0.42	0.49	0.48
pvalue	<0.001***	0.003***	0.007**	0.01**	0.01**	0.03**	0.11	0.01**	0.01**	0.01**	0.007**	0.002**	0.003**

Table 2. Table representing the automated model selection generated a model selection table with best combinations of fixed effect terms (altitude (alt), area, canopy opening (Canop.), conductivity (cond.), depth, hydroperiod (hidro), Radiation (UVA), dissolved oxigen (OD), pH, pond area (P.Area), temperature (temp.), turbidity (turb.), water vegetation (W.Veg), that influenced species richness. This model is based on the AIC value, in which the best model will be the one that is the smallest distance from the probabilistic process that generated the data. Here we observe only models with delta < 4.

(Intercept)	alt	area	Canop.	cond.	depth	hidro	UVA	OD	pH	P.Area	temp.	turb.	W.Veg	df	logLik	AICc	delta	weight
0			0.38		0.39			0.32						5	-25.38	63.25	0	0.03
0			0.4		0.48			0.31				-0.17		6	-24.32	64.29	1.04	0.02
0			0.35		0.45			0.36	-0.15					6	-24.64	64.94	1.69	0.01
0		0.13	0.38		0.36			0.3						6	-24.69	65.04	1.78	0.01
0			0.38		0.39			0.3					0.12	6	-24.72	65.09	1.83	0.01
0			0.31		0.47	-0.14		0.32						6	-24.83	65.31	2.06	0.01
0			0.37		0.32			0.3		0.14				6	-24.84	65.33	2.08	0.01
0			0.38	-0.11	0.35			0.32						6	-24.85	65.35	2.1	0.01
0			0.36		0.6									4	-27.92	65.44	2.19	0.01
0	0.09		0.36		0.39			0.32						6	-25.01	65.67	2.42	0.01
0			0.36		0.34			0.29			0.12			6	-25.04	65.74	2.48	0.01
0			0.41					0.43		0.27				5	-26.82	66.14	2.88	0.01
0			0.32		0.38		0.08	0.32						6	-25.26	66.18	2.93	0.01
0			0.38		0.69							-0.19		5	-26.88	66.26	3	0.01
0		0.17	0.36		0.54									5	-26.92	66.35	3.09	0.01
0			0.37		0.57								0.16	5	-26.96	66.42	3.16	0.01
0					0.38		0.33	0.31						5	-26.97	66.45	3.19	0.01
0	0.16		0.35		0.38			0.28					0.18	7	-23.7	66.49	3.24	0.01
0			0.33		0.48						0.2			5	-27.02	66.53	3.28	0.01
0			0.35		0.48					0.2				5	-27.04	66.57	3.32	0.01
0			0.34		0.55	-0.13		0.31				-0.17		7	-23.83	66.75	3.49	0.01
0			0.38		0.43			0.28			0.13	-0.18		7	-23.92	66.94	3.68	0
0	0.13	0.16	0.34		0.35			0.29						7	-23.97	67.02	3.77	0
0			0.4		0.46			0.29				-0.15	0.09	7	-24	67.09	3.84	0
0			0.39					0.42			0.25			5	-27.35	67.19	3.94	0
0		0.08	0.39		0.44			0.3				-0.14		7	-24.07	67.23	3.98	0
0			0.46					0.56						4	-28.82	67.25	3.99	0

Table 03. Table representing the automated model selection generated a model selection table with best combinations of fixed effect terms that influenced functional richness. This model is based on the AIC value, in which the best model will be the one that is the smallest distance from the probabilistic process that generated the data. Here we observe only models with delta < 4.

(Intercept)	depth	hidro	df	logLik	AICc	delta	weight
0	0.57	-0.3	4	-35.87	81.41	0	0.5
0	0.45		3	-37.38	81.72	0.3	0.43
0			2	-40.64	85.74	4.33	0.06

Table 4. Table representing the automated model selection generated a model selection table with best combinations of fixed effect terms (altitude (alt), area, canopy opening (Canop.), conductivity (cond.), depth, hydroperiod (hidro), Radiation (UVA), dissolved oxigen (OD), pH, pond area (P.Area), temperature (temp.), turbidity (turb.), water vegetation (W.Veg) that influenced species composition (turnover). This model is based on the AIC value, in which the best model will be the one that is the smallest distance from the probabilistic process that generated the data. Here we observe only models with delta < 4.

(Intercept)	alt	area	Canop.	cond.	depth	hidro	UVA	OD	pH	P.Area	temp.	turb.	W.Veg	df	logLik	AICc	delta	weight
0				0.25	0.71									4	-33.5	76.6	0	0.02
0					0.62									3	-34.9	76.72	0.12	0.02
0					0.79					-0.28				4	-33.78	77.15	0.55	0.02
0				0.22	0.85					-0.23				5	-32.64	77.77	1.17	0.01
0		-0.18			0.68									4	-34.18	77.96	1.35	0.01
0					0.52							0.2		4	-34.18	77.96	1.36	0.01
0				0.29	0.8	-0.18								5	-32.75	78.01	1.41	0.01
0		-0.16		0.24	0.76									5	-32.93	78.35	1.75	0.01
0				0.27	0.59						0.19			5	-32.97	78.44	1.84	0.01
0	-0.13				0.63									4	-34.48	78.57	1.96	0.01
0					0.67	-0.13								4	-34.54	78.69	2.08	0.01
0					0.55				0.14					4	-34.56	78.72	2.12	0.01
0					0.63								-0.12	4	-34.58	78.76	2.16	0.01
0					0.52						0.15			4	-34.59	78.78	2.18	0.01
0			0.1		0.59									4	-34.67	78.93	2.33	0.01
0			0.11	0.26	0.68									5	-33.22	78.93	2.33	0.01
0					0.69					-0.3	0.19			5	-33.26	79.01	2.41	0.01
0				0.24	0.72								-0.1	5	-33.26	79.02	2.42	0.01
0					0.87	-0.15				-0.29				5	-33.26	79.02	2.42	0.01
0		-0.89			0.82								0.69	5	-33.28	79.05	2.45	0.01
0				0.26	0.95	-0.2				-0.25				6	-31.73	79.12	2.52	0.01
0					0.67			-0.08						4	-34.8	79.2	2.59	0.01
0				0.21	0.65							0.09		5	-33.36	79.22	2.62	0.01
0				0.25	0.76			-0.08						5	-33.39	79.28	2.68	0.01
0	-0.18	-0.22			0.71									5	-33.39	79.29	2.68	0.01
0	-0.06			0.23	0.71									5	-33.4	79.31	2.71	0.01

0			0.12		0.77					-0.29				5	-33.42	79.34	2.74	0.01
0					0.6		0.04							4	-34.87	79.34	2.74	0.01
0				0.24	0.73					-0.26	0.21			6	-31.9	79.44	2.84	0.01
0				0.25	0.7		0.03							5	-33.47	79.45	2.85	0.01
0				0.27	0.73				-0.03					5	-33.49	79.48	2.88	0.01
0	-0.1				0.79					-0.26				5	-33.51	79.51	2.91	0.01
0					0.73				0.11	-0.26				5	-33.53	79.56	2.96	0
0					0.71					-0.22		0.1		5	-33.61	79.73	3.13	0
0		-0.16		0.27	0.85	-0.19								6	-32.09	79.82	3.22	0
0		-0.8		0.22	0.88								0.63	6	-32.12	79.89	3.29	0
0	-0.2				0.66								-0.19	5	-33.72	79.93	3.33	0
0					0.78		0.05			-0.28				5	-33.72	79.95	3.34	0
0		-0.19			0.74	-0.14								5	-33.73	79.96	3.36	0
0					0.81			-0.04		-0.27				5	-33.75	80.01	3.4	0
0		-0.03			0.79					-0.25				5	-33.76	80.03	3.42	0
0					0.79					-0.28			0	5	-33.78	80.05	3.45	0
0		-0.19			0.58						0.16			5	-33.81	80.12	3.52	0
0					0.57	-0.13						0.2		5	-33.82	80.13	3.53	0
0			0.12	0.22	0.82					-0.25				6	-32.24	80.13	3.53	0
0		-0.13			0.59							0.14		5	-33.83	80.16	3.56	0
0	-0.11				0.54							0.18		5	-33.86	80.21	3.61	0
0					0.43						0.14	0.19		5	-33.89	80.29	3.69	0
0		-0.19	0.11		0.65									5	-33.9	80.31	3.71	0
0	-0.16				0.7	-0.17								5	-33.91	80.31	3.71	0
0		-0.16		0.25	0.64						0.19			6	-32.34	80.34	3.74	0
0		-0.17			0.62				0.11					5	-33.95	80.4	3.8	0
0				0.3	0.69	-0.16					0.15			6	-32.39	80.43	3.82	0
0					0.6	-0.16			0.17					5	-34.02	80.53	3.93	0
0			0.08		0.5							0.19		5	-34.03	80.56	3.95	0
0	-0.16		0.14		0.59									5	-34.05	80.61	4	0

Table 5. Table representing the automated model selection generated a model selection table with best combinations of fixed effect terms (altitude (alt), area, canopy opening (Canop.), conductivity (cond.), depth, hydroperiod (hidro), Radiation (UVA), dissolved oxigen (OD), pH, pond area (P.Area), temperature (temp.), turbidity (turb.), water vegetation (W.Veg) that influenced functional composition (turnover). This model is based on the AIC value, in which the best model will be the one that is the smallest distance from the probabilistic process that generated the data. Here we observe only models with delta < 4.

(Intercept)	alt	area	Canop.	cond.	depth	hidro	UVA	OD	pH	P.Area	temp.	turb.	W.Veg	df	logLik	AICc	delta	weight
0			0.38	-0.25		-0.35								5	-31.97	76.55	0	0.02
0			0.41			-0.35								4	-33.47	76.61	0.06	0.02
0						-0.4	0.36							4	-34.15	77.97	1.43	0.01
0				-0.24		-0.4	0.32							5	-32.77	78.15	1.6	0.01
0			0.37			-0.4		0.16						5	-32.89	78.4	1.85	0.01
0			0.46	-0.3		-0.3					-0.18			6	-31.31	78.45	1.9	0.01
0			0.53											3	-35.85	78.65	2.1	0.01
0	0.14		0.38			-0.35								5	-33.04	78.69	2.15	0.01
0		-0.15	0.4	-0.28		-0.34								6	-31.44	78.7	2.15	0.01
0			0.59	-0.33							-0.28			5	-33.12	78.85	2.31	0.01
0			0.5	-0.24										4	-34.62	78.9	2.35	0.01
0			0.42	-0.29		-0.31				-0.14				6	-31.59	79	2.45	0.01
0			0.38	-0.26		-0.35							-0.12	6	-31.59	79	2.45	0.01
0			0.41			-0.35							-0.09	5	-33.27	79.16	2.61	0.01
0			0.36	-0.22		-0.39		0.11						6	-31.67	79.17	2.62	0.01
0			0.47	-0.29		-0.33		0.28			-0.34			7	-29.92	79.18	2.63	0.01
0		-0.09	0.42			-0.34								5	-33.29	79.18	2.64	0.01
0			0.37	-0.28		-0.39			0.11					6	-31.69	79.2	2.65	0.01
0			0.32			-0.35	0.12							5	-33.35	79.31	2.76	0.01
0			0.45			-0.33					-0.08			5	-33.35	79.32	2.77	0.01
0			0.56	-0.33	-0.26									5	-33.38	79.36	2.81	0.01
0			0.38		0.06	-0.38								5	-33.42	79.44	2.89	0.01
0			0.42			-0.34				-0.03				5	-33.45	79.51	2.96	0
0			0.35	-0.26		-0.38						0.07		6	-31.85	79.52	2.97	0
0			0.41			-0.36			0.02					5	-33.46	79.53	2.99	0
0			0.41			-0.35						0.01		5	-33.47	79.55	3	0

0				-0.29		-0.48								4	-34.95	79.57	3.02	0
0	0.17					-0.39	0.33							5	-33.49	79.58	3.03	0
0	0.06		0.37	-0.23		-0.35								6	-31.89	79.6	3.05	0
0			0.41	-0.27	-0.07	-0.31								6	-31.89	79.6	3.06	0
0			0.31	-0.24		-0.36	0.08							6	-31.9	79.62	3.08	0
0			0.55	-0.32						-0.24				5	-33.53	79.66	3.11	0
0			0.49	-0.41		-0.34			0.24		-0.3			7	-30.23	79.8	3.25	0
0			0.46			-0.36		0.29			-0.25			6	-32.02	79.85	3.31	0
0						-0.45	0.31	0.14						5	-33.75	80.1	3.56	0
0			0.64	-0.51	-0.5				0.33					6	-32.18	80.18	3.63	0
0		-0.16		-0.27		-0.38	0.35							6	-32.19	80.19	3.65	0
0			0.59								-0.18			4	-35.26	80.19	3.65	0
0						-0.49								3	-36.63	80.21	3.67	0
0				-0.29		-0.36	0.4				-0.17			6	-32.24	80.3	3.75	0
0						-0.4	0.37						-0.11	5	-33.86	80.33	3.78	0
0				-0.26		-0.4	0.33						-0.14	6	-32.28	80.37	3.83	0
0			0.61	-0.32				0.23			-0.43			6	-32.29	80.41	3.86	0
0		-0.18	0.52	-0.28										5	-33.9	80.42	3.87	0
0		-0.1				-0.39	0.38							5	-33.92	80.44	3.9	0
0	0.15		0.49											4	-35.42	80.51	3.96	0
0			0.57		-0.14									4	-35.46	80.59	4.04	0

Table 6. Table showing the species and their respective families that were founded in Turvo State Park.

Species	Family
Boana faber	Hylidae
Dendropsophus microps	Hylidae
Dendropsophus minutus	Hylidae
Leptodactylus latrans	Leptodactylidae
Leptodactylus mystacinus	Leptodactylidae
Leptodactylus plaumanni	Leptodactylidae
Lithobates catesbeianus	Ranidae
Phyllomedusa tetraploidea	Hylidae
Physalaemus albonotatus	Leptodactylidae
Physalaemus biligonigerus	Leptodactylidae
Physalaemus cuvieri	Leptodactylidae
Physalaemus gracilis	Leptodactylidae
Rhinella icterica	Bufonidae
Scinax aromothyella	Hylidae
Scinax fuscovarius	Hylidae
Scinax granulatus	Hylidae
Scinax perereca	Hylidae

Table 7. Table explaining shared proportions (i.e., Adjusted R²) as returned by the variance partitioning in figure 4 representing how canopy opening, depth, hydroperiod and other variables influenced species richness, functional richness (FRic), the species taxonomic (Tax. Comp. turnover) and functional (Func. Comp. Turnover) composition. Bold values represent explained proportion very difficult to be observed at random (i.e., $p < 0.05$; as returned by the analysis of variance of the redundancy analysis).

	Adjusted R^2			
	Rich	FRic	Turn Tax.	Turn. Func
[a] Canopy	**0.10669**	-	-	**0.15886**
[b] Depth	**0.07903**	**0.25468**	**0.49942**	-
[c] Hydro	-	0.05292	-	**0.07476**
Other variables	0.06312	-	0.06409	0.07543
[a]+[b]	0.05819	-	-	0.17967
[a]+[c]	0.24976	-	-	-0.02934
[a]+[b]+[c]	0.08354	-	-	-0.05421
Residuals	0.35533	0.77515	0.58456	0.58133