Universidade Federal do Rio Grande do Sul
Instituto de Biociências
Bacharelado em Ciências Biológicas

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Aninhamento funcional em comunidades de anuros de lagoas efêmeras

Porto Alegre
[2024]

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Trabalho de Conclusão de Curso apresentado como requisito parcial à obtenção do título de bacharel em Ciências Biológicas da/do Instituto de Biociências da Universidade Federal do Rio Grande do Sul.

Orientador: Adriano Sanches Melo

Porto Alegre

[2024]

CIP - Catalogação na Publicação

Salaberry, Joaquim Flesch
Aninhamento funcional em comunidades de anuros de lagoas efêmeras / Joaquim Flesch Salaberry. -- 2024.
50 f.
Orientador: Adriano Sanches Melo.

Trabalho de conclusão de curso (Graduação) -- Universidade Federal do Rio Grande do Sul, Instituto de Biociências, Bacharelado em Ciências Biológicas, Porto Alegre, BR-RS, 2024.

1. gradiente ambiental. 2. lagoas. 3. hidroperíodo. 4. diversidade funcional. 5. substituição de espécies. I. Melo, Adriano Sanches, orient. II. Título.

Elaborada pelo Sistema de Geração Automática de Ficha Catalográfica da UFRGS com os dados fornecidos pelo(a) autor(a).

FOLHA DE APROVAÇÃO

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Orientador: Adriano Sanches Melo

Aprovado em: Porto Alegre,22 de agosto de 2024.

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Dedico essa humilde obra à minha falecida cachorrinha, Pipa. Que foi a melhor companheira que uma criança sozinha poderia pedir.

AGRADECIMENTOS

Quero agradecer principalmente a minha família que me apoiou e me apoia diariamente, seja dando estrutura ou servindo de alento para os dias mais ruins. Meu pai por me ensinar a ter caráter, e minha mãe por me ensinar que posso escolher quem eu quero ser.

Quero agradecer também a minha namorada, Clara Bourscheid Del Pino Martins, que é fonte de inspiração e aconchego sempre.

Agradeço ao meu orientador, que apesar de sua função ser a de me ajudar, certamente já ajudou mais do que é sua atribuição nesses – quase - 4 anos que trabalhei no Laboratório de Metacomunidades.

Por fim, quero agradecer ao CNPq pelas bolsas de Iniciação Cientifica, que financiou esse e outros projetos. E também abriu portas a diversas experiências que moldam quem sou hoje e inspiram quem eu busco ser.

RESUMO

Padrões na diversidade dentro e entre comunidades ecológicas podem ser gerados por fatores ambientais, níveis de conectividade e dispersão, e interações bióticas. Quanto à variabilidade entre comunidades (diversidade beta), espera-se uma alta substituição de espécies quando estas estão limitadas diferencialmente a porções dos gradientes ambientais ou bióticos. Adicionalmente, comunidades podem diferir em suas composições devido a diferenças de riqueza de espécies. Neste caso, partes do gradiente permitem que muitas espécies coexistam, enquanto outras restringem apenas às espécies tolerantes. Como consequência, porções menos diversificadas do gradiente possuem um subconjunto (aninhamento) de espécies de partes mais diversificadas. Anuros que se desenvolvem em lagoas efêmeras são particularmente sensíveis a fatores locais, como interações bióticas e fatores ambientais (por exemplo, área e hidroperíodo da lagoa). Hipotetizo que mais espécies e com traços funcionais mais diversificados seriam capazes de habitar lagoas maiores e com hidroperíodos mais longos, enquanto apenas um subconjunto de espécies e traços deveria tolerar as condições adversas das lagoas pequenas e efêmeras. Avaliei se um gradiente de permanência (hidroperíodo e tamanho) das lagoas resulta em aninhamento funcional em duas metacomunidades de anuros em regiões tropicais e subtropicais do Brasil. A primeira metacomunidade incluiu 1514 anuros adultos de 23 espécies distribuídos em 11 lagoas, enquanto a segunda incluiu 10.852 girinos de 21 espécies em 38 lagoas. Estimei a diversidade funcional com base no tamanho corporal ou proporção corporal, uso do habitat e modos reprodutivos. Minha hipótese foi testada usando o treeNODF, que considera não apenas a incidência das espécies nas lagoas efêmeras, mas também sua semelhança funcional. Observei aninhamento funcional nas duas metacomunidades, tanto para área da lagoa quanto para hidroperíodo (usados como variáveis substitutas de permanência da lagoa). Portanto, as lagoas efêmeras ou aquelas com redução drástica na área incluíram não apenas uma diversidade funcional inferior, mas um subconjunto da diversidade presente em lagoas mais permanentes. A abordagem utilizada para testar aninhamento, baseada numa hipótese clara, contrasta com a tradição de estudos sobre aninhamento em que não se inclui o gradiente que gera o aninhamento no teste estatístico, e ainda traz uma dimensão a mais, funcional, sobre a diversidade nesse tipo de sistema.

Palavras-chave: gradiente ambiental; lagoas; hidroperíodo; diversidade funcional; substituição de espécies; girinos.

ABSTRACT

Diversities within or among ecological communities may vary according to environmental factors, isolation and biotic interactions. Regarding the diversity among communities (beta diversity), high turnover of species is expected when species are restricted to portions of environmental or biotic gradients. Additionally, communities may have different species compositions due to differences in species richness. In this case, portions of a gradient allow many species to coexist whereas other portions restrict the presence to tolerant species. Thus, a nested pattern may emerge where communities in diversity-poor portions of the gradient are subsets of those in the richer portions. Anurans that develop in ponds are primarily sensitive to local factors such as biotic and environmental factors (e.g pond area and hydroperiod). I hypothesized that more species and with more diversified functional traits should be able to inhabit larger ponds with longer hydroperiods, whereas only a subset of species and traits should tolerate the harsh conditions of small and ephemeral ponds. I tested whether pond permanence (pond area and hydroperiod) generates functional nestedness of two anuran metacommunities in tropical and subtropical regions of Brazil. The first metacommunity included 1514 adult anurans of 23 species distributed in 11 ponds, whereas the second one included 10,852 tadpoles of 21 species in 38 ponds. I estimated functional diversity using body size or body ratio, habitat use and reproductive modes. My hypothesis was tested using treeNODF, which uses not only the incidence of species in ponds, but also their functional resemblance. I found functional nestedness in the two metacommunities and both for pond area and hydroperiod (used as proxies for pond permanence). Thus, ephemeral ponds or those with drastic reduction in area included not only lower functional diversity, but diversity that is a subset of that present in more permanent ponds. My hypothesis-driven approach contrasts with previous work that assessed nestedness using taxonomic data and did not include explicit hypotheses in their statistical tests.

Keywords: environmental gradient, pond area, hydroperiod, functional diversity, species turnover, tadpole.

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1 INTRODUÇÃO

A Ecologia estuda os organismos vivos na ótica de agentes de um ‘todo’, entendendo que esta totalidade irá regrá-lo e será modificada pelo organismo (TOWNSEND; BEGON; HARPER, 2009). Emergindo destas inúmeras interações entre organismos e agentes desse ‘todo’ (ex. outros organismos ou entidades físicas) identificam-se padrões, os quais são estudados pela Ecologia. Estes agentes estão dispostos fisicamente no espaço e no tempo, portanto parte do que é o estudo em Ecologia consiste em identificar a distribuição espacial e temporal destes agentes e a escala de seus padrões. Por fim, estudar Ecologia sem uma escala bem definida de análise pode ser um confundidor à interpretação dos padrões e da própria Ecologia (WU; LOUCKS, 1995).

Estudos ecológicos podem ser na escala (biológica) de populações, na escala de comunidades (diferentes espécies interagindo/competindo), e na de ecossistemas inteiros (ciclos de matéria e energia) (TOWNSEND; BEGON; HARPER, 2009). Podem levar apenas alguns dias, ou compreenderem décadas, enquanto que a escala espacial pode ser de um fragmento de um habitat, ou o planeta inteiro. E para somar, qualitativamente estas escalas são dependentes do organismo/sistema em questão (WU; LOUCKS, 1995). Por exemplo, uma lagoa temporária pode ser representativa de toda a extensão da história de vida de um organismo (bactérias e algas), ou pode ser um fragmento dentro de uma paisagem campestre mais ampla (macroinvertebrados aquáticos com adultos terrestres e anuros) (HEINO et al., 2013; WARREN et al., 2015), ou apenas um recurso do hábitat (aves e mamíferos) (BUTTERWORTH; BENBOW; BARTON, 2023).

Em última análise, sistemas ecológicos são caracterizados por relações dialéticas (bidirecionais), não lineares e complexas (muitos agentes), e suas propriedades são dependentes de escala com considerável especificidade (WU; LOUCKS, 1995). E cabe ao cientista tentar identificar e predizer quais são os padrões de cada sistema ecológico, e os limites (biológicos, espaciais e temporais) de implicação do mesmo.

Este trabalho se enquadra no campo da Ecologia de Comunidades, e portanto está interessado em entender como os organismos estão interagindo entre si e com

seu ambiente, a partir de diferenças na diversidade biológica encontrada em cada comunidade. Como a escala espacial é no nível de paisagem, o arcabouço teórico de Metacomunidades foi empregado, e com isso questões sobre disposição espacial das comunidades foram levadas em consideração para inferir sobre a dispersão dos organismos (LEIBOLD et al., 2004). Por questões históricas e de disponibilidade de dados (mais detalhes na seção de Métodos do artigo), não foi possível acessar a extensão temporal de anos dos padrões analisados no estudo. Portanto é um trabalho focado em descrever padrões espaciais na diversidade de anuros (Amphibia: Anura) que coexistem em lagoas efêmeras (duram estações ou dias) e podem competir por recurso (WELLBORN; SKELLY; WERNER, 1996; WERNER et al., 2007; HEINO et al., 2013).

Uma das grandes dificuldades em Ecologia é a definição, na prática, do que é diversidade. Isso pois 1) a diversidade pode ser quantificada de diversas maneiras, 2) existem diferentes tipos de diversidade biológica, e 3) podem ter diferentes escalas de mensuração (MAGURRAN, 2021). Podemos focar unicamente na diversidade local (diversidade ‘alfa’), ou focar na diversidade numa região (diversidade ‘gama’; todas espécies nas comunidades locais), e também na diferenciação entre comunidades (diversidade ‘beta’). Além disso, é possível quantificar a diversidade das espécies (diversidade taxonômica) e também a diversidade de características funcionais dos organismos (diversidade funcional), ou então sua variação em parentesco (diversidade filogenética). Cada combinação de tipos de diversidade (ex. diversidade beta funcional) são quantificacas com diferentes métodos. Diferentes dimensões da diversidade possuem padrões distintos (BOTH et al., 2011), e descrevem atributos diferentes do sistema. Portanto, tentar entender cada um deles é de interesse na Ecologia.

Meu trabalho se enquadra em entender a estrutura da diferenciação de atributos funcionais de Anuros em sistemas de lagoas efêmeras, partindo do pressuposto que essas comunidades diferenciam-se de maneira correlata com atributos de suas lagoas. Esta diferenciação biológica, ou diversidade beta, é avaliada por meio de comparações entre duas ou mais comunidades , e podemos encontrar diferentes maneiras cpelas quais essas comunidades podem se diferenciar (BASELGA, 2010). Duas aqui nos interessam, o aninhamento e a substituição de espécies. Aninhamento é quando a diversidade de uma comunidade

esta contida em outra (é um subconjunto da outra comunidade), e a substituição, num cenário de substituição total, ambas comunidades possuem diversidades totalmente diferentes (ex. nenhuma espécie em comum) (ULRICH; ALMEIDA-NETO; GOTELLI, 2009). Neste contexto, busquei identificar se a característica das lagoas efêmeras geraria um padrão aninhado na diversidade funcional das comunidades de anuros.

2 OBJETIVO

Entender se o gradiente de permanência de lagoas efêmeras geraria um padrão aninhado na diversidade funcional e taxonômica de comunidades de anuros, tanto para a fase adulta como para a fase larval (girino).

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3 ARTIGO DA PESQUISA

Algumas considerações antes do manuscrito em si. O artigo completo será submetido na categoria de '*Research Article*' à revista *Austral Ecology* (ISSN 1442-9993/1442-9985). Figuras e Material Suplementar estão disponíveis nos Apêndices A e B respectivamente. Foi seguido as diretrizes para submissão pelo método "*Free Format*", descrito no sítio online da revista (https://onlinelibrary.wiley.com/page/journal/14429993/homepage/forauthors.html), mas também já aproximando boa parte do estilo empregado na revista quando possível (como recomendado pelos editores). Um manuscrito submetido como '*Research Article*' precisa conter os itens a seguir listados em ordem: Página de título, Resumo (contendo o título também), Introdução, Métodos, Resultados, Discussão e Referências.

Functional nestedness of anuran metacommunities along gradients of pond permanence

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Data availability: Some extra information can be found in the Supplemental Materials. The R scripts used to perform those analysis, and all data used in the analysis, are in a github repository at: https://github.com/JoaquimFS/Functional-nestedness-anuran-metacommunity-along-gradient/tree/main

Acknowledgments: JFS received an undergraduate fellowship (Iniciação Científica, PIBIC Program, CNPq-UFRGS) and ASM a research fellowship from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (proc. 313954/2021-6).

Functional nestedness of anuran metacommunities along gradients of pond permanence

Abstract

Diversities of ecological communities may vary according to environmental factors, isolation and biotic interactions. High turnover of species is expected when species are restricted to portions of environmental or biotic gradients. In contrast, if portions of a gradient allow many species to coexist whereas other portions restrict the presence to tolerant species, a nested pattern may emerge where communities in diversity-poor portions of the gradient are subsets of those in the richer portions. Anurans that develop in ponds are affected by both biotic and environmental factors (mainly pond area and hydroperiod). We hypothesized that more species and those with more diversified functional traits should be able to inhabit larger ponds with longer hydroperiods, whereas only a reduced set of species and traits should tolerate the harsh conditions of small and ephemeral ponds. We tested whether pond permanence generates functional nestedness of two anuran metacommunities in tropical and subtropical regions of Brazil. The first metacommunity included 1514 adult anurans of 23 species distributed in 11 ponds, whereas the second one included 10,852 tadpoles of 21 species in 38 ponds. We estimated functional diversity using body size or body ratio, habitat use and reproductive modes and tested our hypothesis using treeNODF, which uses not only the incidence of species in ponds, but also their functional resemblance. We found functional nestedness in the two metacommunities and both for pond area and hydroperiod (used as proxies for pond permanence). Thus, ephemeral ponds or those with drastic reduction in area included not only lower functional diversity, but diversity that is a subset of that

present in more permanent ponds. Our hypothesis-driven approach contrasts with previous work that assessed nestedness using taxonomic data and did not include explicit hypotheses in their statistical tests.

Keywords: environmental gradient, pond area, hydroperiod, functional diversity, species turnover, tadpole.

Introduction

Small and isolated islands tend to harbor less species compared to larger islands that are closer to the source of colonizers (MacArthur & Wilson, 1967). More than a theory to explain the species richness on islands, the Theory of Island Biogeography predicts that there is a dynamic equilibrium, with species richness depending on colonization rates and local extinctions. Although initially developed for oceanic islands, the theory has been generalized to a range of island-like ecosystems, such as caves (Snowman et al., 2010), invertebrates associated with rocks in streams (Douglas & Lake, 1994) and lakes (isolated by land) (Warren et al., 2015; Itescu, 2019). In addition to the dynamic equilibrium of species richness, there are several extensions of the theory in relation to the life histories of the species present on the islands. For example, isolated islands are expected to harbor biotas composed of species with good dispersal ability, whereas these good dispersers may or may not be present on closer islands depending on their interactions with stronger competitors (MacArthur & Wilson, 1963, 1967; Tilman, 1994; Amarasekare, 2003).

The degree of isolation, competition pressure, and the availability of resources of the ecosystems may restrict the establishment of the species. Sites with few resources and/or inadequate conditions for most species in the region might select restricted groups of tolerant species (Wellborn et al., 1996; Leibold et al., 2004). Those tolerant species may or may not occur in sites with adequate conditions and/or plenty of resources. On one hand, tolerant species may not be able to colonize more favorable sites, for example due to intense competition or predation, which results in high beta diversity (or turnover) between communities. On the other hand, when these tolerant species do establish along all the gradient of resources and/or conditions, a nested pattern among the communities should result. Therefore, in the

case of nestedness, some species (e.g., generalists) would be found at most of the sites, independent of the resources and/or conditions, while others (e.g., specialists) would be restricted to sites with more resources and/or better conditions. For example, Almeida-Gomes et al. (2019) found that anurans with more specialized reproductive modes were restricted to continuous forest and large fragments while more generalist species in terms of reproductive strategies were widespread in the landscape.

A nested pattern exists when a species-rich community includes most of the species found in species poor communities. Thus, species compositions of poorer communities will mostly be a subset of those present in the richer communities (Almeida-Neto et al., 2008; Ulrich et al., 2009). Previous research has mostly studied nestedness in the context of taxonomic diversity (species richness) (Machado et al., 2012; Moreira & Maltchik, 2012; Almeida-Gomes et al., 2016), although this concept can be applied to other diversities, such as functional (traits) (Melo et al., 2014; Matthews et al., 2015; Almeida-Gomes et al., 2019) and phylogenetic diversity (evolutionary lineages) (Melo et al., 2014; Both & Melo, 2015). For functional and phylogenetic diversities, nestedness will be present when the diversities of traits or evolutionary lineages of the species in the diversity-poor sites are a subset of the functional or phylogenetic diversity of richer ones, respectively.

Most anurans need a water body for the development of their tadpoles (Werner et al., 2007; Cayuela et al., 2012, 2020). Among those species that develop in lentic habitats, one of the most important factors is pond permanence, the time interval when the pond retains water (hydroperiod) or the proportion of pond area/volume that retain water during dry periods (Both et al., 2011a, 2011b). Small ponds and/or with short hydroperiods and/or that suffer drastic reduction in wet area

are restrictive for some species because those who need a prolonged period to develop from a tadpole into an adult can die by desiccation. In contrast, large ponds (usually associated with long hydroperiods and that does not suffer severe area reduction) can include predatory fish that can prevent or significantly reduce the reproduction of many species (Wellborn et al., 2007; Werner et al., 2007; Almeida-Gomes et al., 2016). This gradient of restrictions in terms of pond permanence can cause either species turnover (beta diversity) or nestedness. Turnover occurs when most species are restricted to particular portions of the pond permanence gradient, whereas nestedness occurs if species that have short development times and are present in less permanent ponds would also be capable of tolerating predation and competition in more permanent ponds.

Some studies have found taxonomic nestedness in anuran metacommunities (Werner et al., 2007; Moreira & Maltchik, 2012), although others have not (Almeida-Gomes et al., 2016), indicating context-dependent responses to the hydroperiod gradient. Functional and phylogenetic nestedness have rarely been studied in the context of anuran metacommunities. Both & Melo (2015) evaluated whether an invasive species (*Lithobates catesbeianus*) could drive invaded communities to be phylogenetically nested into non-invaded counterparts but did not find support for their hypothesis. Almeida-Gomes et al. (2019) evaluated whether habitat amount affects the functional diversity of anurans in a fragmented landscape and found that fragments with less habitat included less functional diversity and that most of their functional diversities were nested into those with more habitat.

We studied nestedness of two anuran metacommunities along gradients of pond permanence, one with the adults and the other with juveniles (tadpoles). We hypothesized that small ponds and/or those with short hydroperiods and/or with

drastic area reduction during the dry period restrict the development of juveniles of many species and result in a nested pattern of the functional diversity in both life stages. One of the metacommunity was studied by Almeida-Gomes et al. (2016), who assessed taxonomic nestedness of adult anurans among pond communities. Taxonomic nestedness considers species as independent units and thus ignores their differences in morphological characteristics and their consequent roles in the community. A more refined approach should consider the morphological and behavioral similarities between the species since those with similar characteristics tend to respond similarly to an environmental gradient. Also, in contrast to the previous study, here we explicitly incorporated environmental variables related to pond permanence into tests, allowing us to not only test for a nested pattern, but also interpret the factors that generate nestedness (Ulrich et al., 2009; Melo et al., 2014). The other metacommunity was studied by Both et al. (2011a, b), who assessed local diversity and co-occurrence of tadpoles and guilds, but did not analyze nestedness.

Methods

Study areas and sampling

The first metacommunity was inventoried in a pasture matrix near to Reserva Ecológica de Guapiaçu (22º24'S, 42º44'W), in the municipality of Cachoeiras de Macacu, Rio de Janeiro, Brazil. The area is composed of a fragmented landscape, with small forest fragments (Atlantic Rain Forest) surrounded by pasture. The samples were carried in 2013 during the wet period of the region (November–March) (Almeida-Gomes et al., 2016). Eleven temporary ponds were inventoried for adults during 22 days in the summer (15 days in February and 7 days in March 2013). Pond permanence was estimated using pond area and hydroperiod (permanence of water,

in days, during the sampling period). Pond area varied between 41.4 and 820.6 m² (mean = 238 m²) and the hydroperiod varied from 5 to 22 days (mean = 15 days). Despite of the brief period studied, most ponds presented hydroperiods shorter than 22 days. Also, most species show explosive breeding following intense rains and are active only during the days water is available. Additional information can be found in Almeida-Gomes et al. (2016).

The second metacommunity was assessed in a rural landscape in South Brazil and included natural grasslands, forest patches and pasture (Pampa region; between 30° 57’ and 31°03’ S, 53° 25’ and 53° 89’ W). The inventories of tadpoles were conducted during the end of the Spring season (November 2007) in 38 ponds and throughout 7 days. Pond permanence was estimated as pond area in the Spring and proportion of the pond area that retained water until a subsequent visit in the next summer (January 2008). Pond area in the Spring varied between 2.6 and 1294.7 m² (mean = 187.5 m²) and proportion pond wetted area in Summer from 0 (pond dried completely) to 0.99 (mean = 0.23). Additional information can be found in Both et al. (2011a, b).

Functional traits

A functional trait can be defined as a measurable aspect of an organism that somehow determines its interaction with the environment where it lives (Flynn et al., 2009). Five functional traits were used to perform the analyses on functional diversity in the adults dataset; i) body size (mm; snout-vent length, SVL), ii) habit (arboreal or terrestrial) and three traits related to reproductive mode, iii) egg deposition (aquatic or terrestrial or arboreal), iv) foam nest formation (presence or absence) and v) flooding trigger (presence or absence). Body size ranged from 21.4 to 180 mm. The

habit and reproductive traits of frogs were obtained from Haddad & Prado (2005).

The frog species found presented five reproductive modes according to the classification of Haddad & Prado (2005) (numbers 1, 4, 11, 24, and 30; see Tables S1 and S2 in the Supporting Materials). Body size is associated with several life history strategies and habit indicates the preferred location of the species to carry out its activities, whereas reproductive traits summarize a number of life history strategies and how much the environment provides the conditions and resources for the species to complete its development (Haddad & Prado, 2005; Oliveira et al., 2017).

Eight categorical traits were used to estimate functional similarity among tadpoles. Five traits assessed tadpole morphology regarding position of body structures: i) eye (lateral or dorsal), ii) mouth (ventral or terminal or subterminal), iii) spiracle (ventral or terminal or lateral), and the height of iv) ventral and v) dorsal tail fins (higher or lower of the tail musculature at the body-tail juncture). Traits also included vi) body ratio (height/width; equal to or greater than one, or less than one) and two characteristics related to species behavior, vii) clutch deposition (directly in water, in trees or with foam nests) and vii) tadpole schooling (presence or absence). The traits capture different dimensions of how tadpoles use resources and the environment as well as life histories strategies to survive.

Data Analyzes

We used the Gower dissimilarity index, which handles categorical and quantitative data, to build functional trees for the two datasets. The resulting dissimilarity matrices were used in UPGMA (Unweighted Pair-Group Method using Arithmetic Averages)

classifications to generate dendrograms that synthetized the functional resemblance among species.

The nestedness assessment was done using the treeNODF method, derived from the NODF, which compares two communities and assesses, in a first step, if the species richness in the supposedly species-poor community actually has fewer species (Almeida-Neto et al., 2008). If the statement is not met, NODF is zero. If it is met, nestedness is estimated as the proportion of the species richness in the species-poor community that is present in the species-rich community. The procedure is repeated for all pairs of communities and the average is recorded. The NODF procedure requires communities to be ordered and the most frequent use of NODF orders communities in terms of decreasing species richness, which maximizes nestedness (most of the nestedness values are non-zero) (e.g., Almeida-Gomes et al., 2016). However, once a hypothesis generating nestedness is available, it can be used to order communities, from the hypothesized species-richest to the hypothesized species-poorest (Melo et al., 2014). Thus, if nestedness is important, its generating mechanism may be inferred.

The treeNODF method employs the same logic of NODF but uses diversities that consider the relationship between species expressed in a tree. Thus, species with distinct functional traits should contribute more to functional diversity of a community than species functionally similar to other species in the tree. Thus, treeNODF evaluates not only the composition of species, but the resemblance among them. The method operates as the NODF, comparing hypothesized diversity-richer communities to diversity-poorer communities. Also, the determination of which community in the pair should present the highest diversity can be derived from an external (e.g., environmental) variable. In our study we hypothesized that pond

permanence generates nestedness and implemented two tests for each dataset using the proxies pond area (both datasets) and hydroperiod (adult dataset) or proportion of remaining wetted area in a subsequent visit (tadpole dataset).

The treeNODF can be partitioned into two components, one due to the composition of species (S.fraction), similar (but not identical) to the NODF index, and the other exclusively due to the resemblance among species (topo.NODF). The relative importance of the components allows assessments of whether nestedness is mostly due to diversity-rich communities harboring more species (S.fraction) or distinctiveness of their species (topo.NODF).

One additional vantage of using explicitly a hypothesis to order communities is that the significance of the observed nestedness can be assessed using a permutation test, instead of the use null models that may produce contrasting results depending on the mostly subjective chosen way the data matrix is shuffled (e.g. Both et al. 2011b). The test is done by permuting values of the variable used to order communities, which in this study were pond area (both datasets) and hydroperiod (adults) or proportion of remaining wetted area (tadpoles), and recalculating the statistics (treeNODF, S.fraction and topo.NODF). This is equivalent to permutating matrix lines (communities) randomly. Different of null models, however, the procedure does not shuffle cell values. The statistics were recalculated, and the procedure repeated 9999 times to generate a distribution of null values. Finally, the observed values of the statistics were compared with their respective null distribution obtained with the permutations and p-values estimated as the proportion of values that were greater or equal to the observed ones (Melo et al., 2014).

The hypothetically-focused nature of our statistical analyses requires the availability of a gradient to order communities. The two datasets studied included

ponds with the same value of hydroperiod (adults dataset) or proportion of remaining wetted area (tadpoles). For example, several ponds in the tadpole dataset dried completely and it is not possible to order them. The removal of ponds with repeated permanence scores would cause loss of information at portions of the gradient. Thus, we obtained all treeNODF values between pairs of ponds and later removed the pairs with repeated scores in the pond permanence gradient. These remaining values were then used to obtain mean statistics and p-values.

The Gower dissimilarity was obtained through the *daisy* function in the package *cluster* (Maechler et al., 2022). The functional dendrogram was obtained using the *hclust* function in the package *stats* (R Core Team, 2020), which in turn was transformed into a *tree* object through the function *as.phylo* in the package *ape* (Paradis and Schliep, 2019). The *treeNODF* and its components as well as the permutation tests were obtained using an edited version of the function *treeNODFtest* from the package *CommEcol* (Melo, 2021) to deal with multiple sites presenting the same value of pond permanence.

Results

The inventory of adults included 1514 individuals of 23 species in 11 ponds. Species richness in ponds varied from 3 to 14, with a mean of 8.54 species for pond. Eight species occurred in only one pond (*Rhinella icterica*, *Dendropsophus anceps*, *Dendropsophus berthalutzae*, *Phyllomedusa burmeisteri*, *Pithecopus rohdei*, *Boana semilineata*, *Scinax alter* and *Trachycephalus nigromaculatus*), and *Dendropsophus bipunctatus* is the only specie present in 11 ponds (average species occurrence = 4.09). *Leptodactylus latrans*, *Scinax aff. x-signatus* and *Dendropsophus seniculus* were present in, respectively, 10, 9 and 8 ponds. Pond hydroperiod and pond area

were uncorrelated (r = 0.126, p = 0.712) in adults dataset.

The inventory of tadpoles in spring obtained 18 species in 38 ponds. Tadpole richness in ponds varied from 1 (8 ponds) to 8 (1 pond) with a mean of 3.03 species. Two species were present in a single pond, *Leptodactylus mystacinus* and *Leptodactylus fuscus*. The most frequent species were *Physalaemus gracilis* (23 ponds), *Boana pulchella* (13), *Scinax fuscovarius* (11) and *Boana albopunctata* (10). Average species presence in ponds was 6.39. Pond area and proportion of remaining wetted area in the dry season were partially correlated (r = 0.370, p = 0.022)

Functional diversities of adults in small ponds were subsets of the diversities present in larger ones (treeNODF = 63.077, p = 0.051). Similarly, functional diversity in ponds with shorter hydroperiods were functionally nested in the diversity of ponds with extended hydroperiods (treeNODF = 67.587, p = 0.025). Regarding the components of treeNODF, the one related to species composition was important for both pond area (S.Fraction = 55.037, p = 0.028) and hydroperiod (S.Fraction = 54.745, p = 0.038). The tree topology component was not important for pond area (topoNODF = 8.041, p = 0.516), but it was for hydroperiod (topoNODF = 12.842, p = 0.042). Thus, for adults, the hypothesis of functional nestedness was supported and the component that most contributed to this result was the one due to species composition (S.Fraction).

Similar to the results with adults, functional diversities of tadpoles in small ponds were subsets of the diversities in larger ponds (treeNODF = 50.732, p = 0.004). The proportion of pond wetted area in the subsequent dry period, however, did not cause nestedness in functional diversity (treeNODF = 47.944, p = 0.067). Regarding the components of treeNODF, the one related to species composition of

tadpoles was important for pond area ((S.Fraction = 22.774, p = 0.003) , but not for the proportion of remaining wetted area (S.Fraction = 17.789, p = 0.309). The topology of the tree component was important for tadpole functional nestedness both for pond area (topoNODF = 27.958, p = 0.028) and proportion of remaining wetted pond area (topoNODF = 30.155, P = 0.019) (Fig. 1).

Discussion

The high treeNODF values for both proxies of pond permanence and datasets indicate that the studied metacommunities are structured by environmental gradients that generate nestedness of functional diversity. Thus, small ponds and those with short hydroperiods or that suffered reduction on wetted area have a subset of the functional diversity present in larger ponds and those with longer hydroperiods or that maintained similar wetted area in the subsequent dry period. The relative importance of the two treeNODF components varied with the pond permanence proxy used and dataset. For adults, the component due to species composition (S.Fraction) was more important (area) or similar (hydroperiod) than that due to tree functional topology (topoNODF). For tadpoles, the component due to species composition was more important than that due to tree functional topology for the proxy pond area, but the reverse occurred with the proxy proportion of remaining wetted area in the subsequent dry period.

Our finding of a nested pattern for adults contrasts with the results of Almeida-Gomes et al. (2016) who employed the same data set and did not detect nestedness. The current study contributes to a growing recognition of the importance of an integrative approach of diversity in community ecology studies that uses taxonomic and, depending on the context of the objectives, functional or phylogenetic diversities

(Petchey & Gaston, 2006; Cianciaruso et al., 2009). Functional diversity has been associated with the capability of biological systems to maintain stability against disturbances (resistance) and quickly return to a steady state (resilience) (Folke et al., 2004). Thus, our results show that tree-diversity, such as the functional diversity used, may not only detect nestedness in datasets that did not show taxonomic nestedness, but that functional traits may be structured in a gradient of environmental condition.

A second difference between this work and that of Almeida-Gomes et al. (2016) is that we ordered sites accordingly to a hypothesized environmental gradient that should generate nestedness, whereas in the previous work they ordered sites, as has been done in many previous studies, by decreasing species richness in communities (Melo et al., 2014; Almeida-Gomes et al., 2019). The use of plausible causes is preferable (Ulrich et al., 2009) as interpretation of a nestedness hypothesis is straightforward (Melo et al., 2014). A third difference in relation to Almeida-Gomes et al. (2016) is the use of permutation tests, which maintain the original data intact. Previous tests of nestedness that ordered sites according to decreasing species richness have used null models that randomize the elements of the data matrix and change its original structure. Even if some of these null models are intended to maintain aspects of the original data structure, they produce different results (e.g., Both et al., 2011b), likely due to differences in Type I errors (Gotelli, 2000; Ulrich & Gotelli, 2007), and it is not always easy to choose the most adequate one. Thus, the explicit use of a hypothesized causal factor of nestedness and its associated permutation test not only makes interpretations straightforward but avoids the difficult decision for an adequate null model.

Our results indicated that overall functional nestedness as well as its two

components tended to be important, despite a few exceptions depending on the dataset and proxy of pond permanence used (Fig. 1). The component due to species composition was important for both proxies of pond permanence in adults, but only for pond area in the tadpole dataset. Thus, ponds with short permanence tended to have species compositions that are subsets of larger and lasting ponds. Our results agree with previous studies highlighting that large habitat islands (e.g., forest fragments, ponds) may support more species than small ones because of their higher habitat heterogeneity and stability and the higher probability of receiving individuals from the regional species pool (Almeida-Gomes et al., 2022).

The functional tree topology indicated that the two proxies of pond permanence were important for tadpoles, but only hydroperiod resulted in nestedness for adults (Fig. 1). Thus, ponds with short permanence tended to included subsets of the trait diversities found in more permanent ponds. In fact, desiccation due to short water permanence is among the major restriction factors for the development of amphibian clutches and tadpoles in ephemeral ponds (Laurila & Kujasalo, 1999; Neckel-Oliveira, 2004; Gervasi & Foufopoulos, 2008). As clutch viability and tadpole survival are strongly affected by pond hydroperiod, only species with traits able to perform adjustments in time of oviposition and metamorphosis should be able to colonize these habitats (Hartel et al., 2011; Da Silva et al., 2012; Goméz-Rodríguez et al., 2012; Trumbo et al., 2012). Indeed, phenotypic plasticity may allow some species to thrive in ephemeral ponds due to the reduction of their developmental periods, minimizing desiccation risks (Richter-Boix et al., 2011).

We estimated pond permanence using two proxy variables in the two datasets studied. Thus, we could expect nestedness results to be similar for both proxies. However, results slightly differed according to the pond permanence proxy used. In

fact, proxies were only weakly correlated (adults: r = 0.126; tadpoles: r = 0.370), indicating we assessed two partially independent gradients causing overall nestedness and its two components. It can be argued that hydroperiod (adults) or remaining pond wetted area to more accurately estimate the stress gradients caused by potential desiccation, selecting for species with short development time. In contrast, pond area may include not only a component associated (negatively) to pond permanence, but an ecological component related to habitat size. Thus, the effect of area per se, independent of pond permanence, should have resulted in important effects on nestedness in species composition, with larger ponds harboring more adults and tadpoles. Area was also important for nestedness due to functional tree topology for tadpoles. Larger habitat islands usually have greater habitat heterogeneity compared to smaller islands. For example, Almeida-Gomes et al. (2016) recorded more individuals and species in large ponds with isolated trees on their edges than in small ponds without trees. Moreover, larger ponds may receive more individuals and species by chance because of the target effect (Almeida-Gomes et al., 2022). In addition to species richness, large ponds may also allow the coexistence of species with distinct traits.

Our results indicate that the conservation of frog species in disturbed habitats relies on the maintenance of larger and lasting ponds in the landscape. These ponds include diversity (species and traits) not present in small or ephemeral pods. Thus, they can act as sources of colonizers for small and more ephemeral ponds in their metacommunity. Our study illustrates how comprehensive approaches to diversity of anurans in ponds reveal patterns overlooked by traditional aspects of taxonomic diversity.

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APÊNDICE A – FIGURA 1

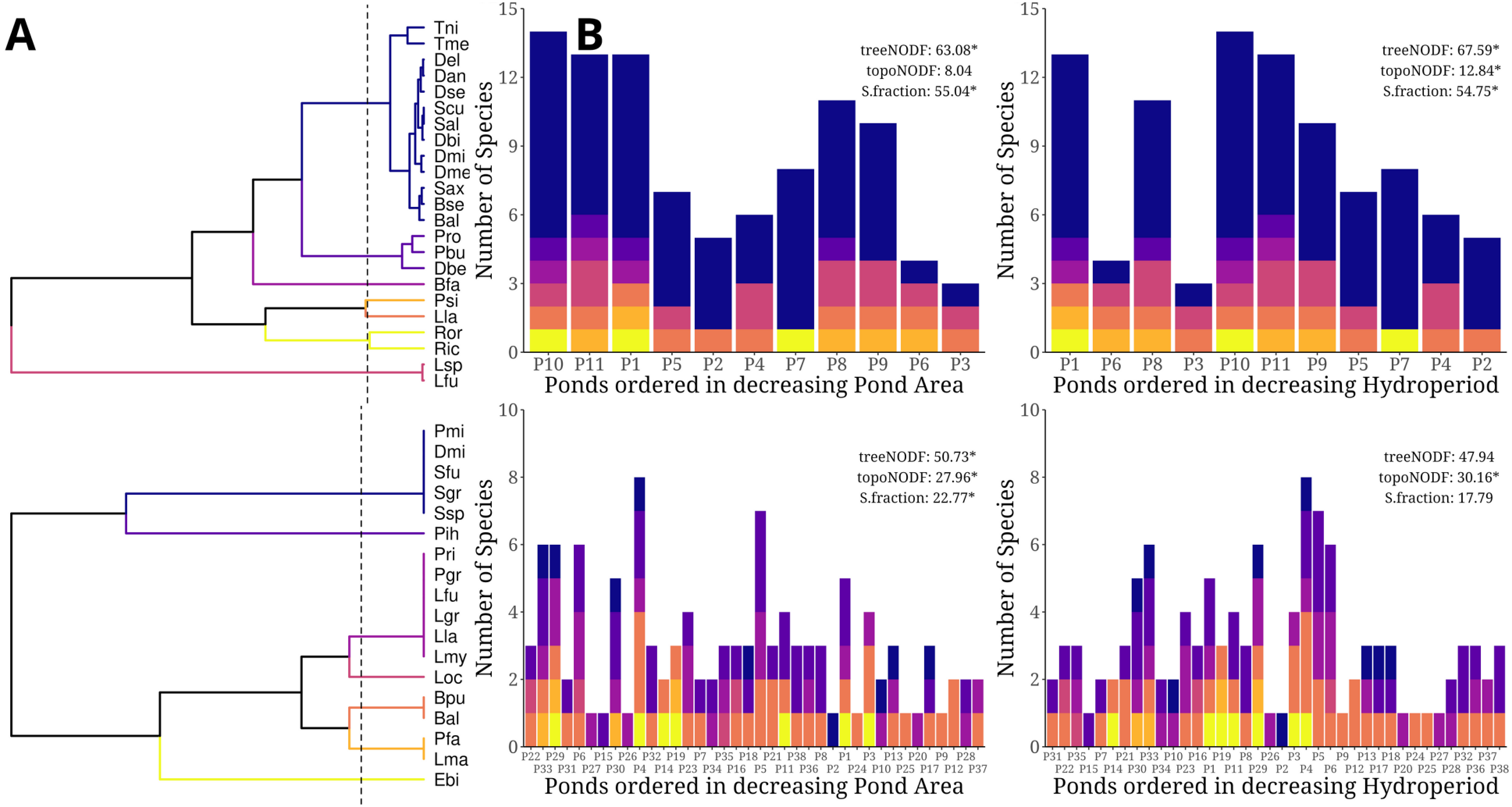


Figure 1. Functional nestedness analysis figure of each Anuran metacommunity. Adults metacommunity in the top and tadpoles in the botton. A) Trait dendogram for each metacomunity, generated by a Gower dissimilarity index. Colors refer to seven groups generated by a clustering technique of cutting the three branches in 0.105 of the length (dashed gray line), where each color represents a non-analytical group (clusters were not used for the treeNODF analysis) present in the B side. B) Number of species per pond ordered decreasingly with the gradient. In each graph are present the treeNODF analysis components for data + nestedness hypothesis combination. Where '*' is present means that the value was significant ($P < 0.05$). Name abbreviations at top side of portion A: *Boana albomarginata* = Bal, *Boana faber* = Bfa, *Boana semilineata* = Bse, *Dendropsophus anceps* = Dan, *Dendropsophus berthalutzae* = Dbe, *Dendropsophus bipunctatus* = Dbi, *Dendropsophus elegans* = Del, *Dendropsophus meridianus* = Dme, *Dendropsophus minutus* = Dmi, *Dendropsophus seniculus* = Dse, *Leptodactylus fuscus* = Lfu, *Leptodactylus latrans* = Lla, *Leptodactylus spixi* = Lsp, *Phyllomedusa burmeisteri* = Pbu, *Pithecopus rohdei* = Pro, *Physalaemus signifer* = Psi, *Rhinella icterica* = Ric, *Rhinella ornata* = Ror, *Scinax alter* = Sal, *Scinax aff. x-signatus* = Sax, *Scinax cuspidatus* = Scu, *Trachycephalus mesophaeus* = Tme, *Trachycephalus nigromaculatus* = Tni. Name abbreviations at bottom side of portion A: Dendropsophus minutus = Dmi, Boana albopunctata = Bal, Boana pulchella = Bpu, Scinax fuscovarius = Sfu, Scinax granulatus = Sgr, Scinax sp. = Ssp, Pseudis minuta = Pmi, Phyllomedusa iheringii = Pih, Physalaemus biligonigerus = Pbi, Physalaemus gracilis = Pgr, Physalaemus riograndensis = Pri, Pseudopaludicola falcipes = Pfa, Leptodactylus macrosternum = Lem, Leptodactylus fuscus = Lfu, Leptodactylus gracilis = Lgr, Leptodactylus latinasus = Lla, Leptodactylus mystacinus = Lmy, Leptodactylus ocellatus = Loc, Limnomedusa macroglossa = Lma, Elachistocleis bicolor = Ebi.

APÊNDICE B – MATERIAL SUPLEMENTAR

Austral Ecology

Supplementary Materials

Functional nestedness of an anuran metacommunity in a gradient of pond permanence

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Table S1: Table of species and their respective traits for adults data. SVL: Snout-vent length(mm), used as body size proxy. Habit: ARB - Arboreal, TER - Terrestrial. RMn: reproductive mode number which their means are showed in the Table S2. Abreviations after each species name are the same showed in Figure 1.

Specie	SVL	Habit	RMn	Egg Deposition	Foam Nest	Flooding Trigger
Boana albomarginata	58	ARB	1	Aquatic	0	0
Boana faber	110	ARB	4	Aquatic	0	1
Boana semilineata	50	ARB	1	Aquatic	0	0
Dendropsophus anceps	39	ARB	1	Aquatic	0	0
Dendropsophus berthalutzae	24.5	ARB	24	Arborial	0	0
Dendropsophus bipunctatus	33	ARB	1	Aquatic	0	0
Dendropsophus elegans	38	ARB	1	Aquatic	0	0
Dendropsophus meridianus	21.4	ARB	1	Aquatic	0	0
Dendropsophus minutus	25	ARB	1	Aquatic	0	0
Dendropsophus seniculus	43	ARB	1	Aquatic	0	0
Leptodactylus fuscus	45	TER	30	Terrestrial	1	1
Leptodactylus latrans	115	TER	11	Aquatic	1	0
Leptodactylus spixi	47	TER	30	Terrestrial	1	1
Phyllomedusa burmeisteri	65	ARB	24	Arborial	0	0
Pithecopus rohdei	48	ARB	24	Arborial	0	0
Physalaemus signifer	29	TER	11	Aquatic	1	0
Rhinella icterica	180	TER	1	Aquatic	0	0
Rhinella ornata	100	TER	1	Aquatic	0	0
Scinax alter	31	ARB	1	Aquatic	0	0
Scinax aff. x-signatus	53	ARB	1	Aquatic	0	0
Scinax cuspidatus	31	ARB	1	Aquatic	0	0
Trachycephalus mesophaeus	76	ARB	1	Aquatic	0	0
Trachycephalus nigromaculatus	100	ARB	1	Aquatic	0	0

Table S2: Reproductive modes for the adults data (sensu Haddad & Prado 2005) of the frogs found near to Reserva Ecológica de Guapiaçu (Cachoeiras de Macacu, Rio de Janeiro, Brazil).

Reproductive modes/Traits
Aquatic eggs
Eggs deposited in water
Mode 1 Eggs and exotrophic tadpoles in lentic water.
Mode 4 Eggs and early larval stages in natural or constructed basins; subsequent to flooding, exotrophic tadpoles in ponds or streams.
Eggs in foam nests
Mode 11 Foam nest floating on pond; exotrophic tadpoles in ponds.
Terrestrial or arboreal eggs (not in water)
Arboreal eggs
Mode 24 Eggs hatching into exotrophic tadpoles that drop in lentic water.
Eggs in foam nest (terrestrial or arboreal)
Mode 30 Foam nest with eggs and early larval stages in subterranean constructed nests; subsequent to flooding, exotrophic tadpoles in ponds.

Table S3: Species richness, abundance, hydroperiod (days) and pond area (m^2) found in each pond of adults data (P1-P11).

Pond	richness	abundances	hydroperiod	area
P1	13	460	22	272.3
P2	5	47	5	232.3
P3	3	28	21	41.38
P4	6	15	6	193.3
P5	7	60	9	268.1
P6	4	23	22	48.2
P7	8	39	9	167.1
P8	11	210	22	164.7
P9	10	61	10	89.1
P10	14	442	20	820.6
P11	13	156	19	320.1

Table S4: Adult community data matrix with the abundance of each specie found in each pond.

Species	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11
Rhinella icterica	0	0	0	0	0	0	1	0	0	0	0
Rhinella ornata	3	0	0	0	0	0	0	0	0	1	0
Dendropsophus anceps	0	0	0	0	0	0	0	0	0	1	0
Dendropsophus berthalutzae	0	0	0	0	0	0	0	0	0	1	0
Dendropsophus bipunctatus	111	32	9	5	10	1	12	83	6	174	22
Dendropsophus elegans	219	2	0	0	16	0	4	31	0	155	3
Dendropsophus meridianus	1	0	0	0	0	0	3	0	0	0	4
Dendropsophus minutus	21	0	0	0	3	0	0	0	1	25	0
Dendropsophus seniculus	0	1	0	1	15	0	3	14	22	7	11
Boana albomarginata	2	0	0	0	0	0	2	8	0	4	0
Boana faber	56	0	0	0	0	0	0	1	0	4	1
Boana semilineata	2	0	0	0	0	0	0	0	0	0	0
Phyllomedusa burmeisteri	1	0	0	0	0	0	0	0	0	0	0
Pithecopus rohdei	0	0	0	0	0	0	0	0	0	0	7
Scinax alter	0	0	0	0	0	0	0	0	0	0	5
Scinax cuspidatus	19	0	0	0	0	0	1	0	3	1	0
Scinax aff. x-signatus	6	9	0	3	8	0	10	34	12	37	18
Trachycephalus mesophaeus	0	0	0	0	0	0	0	0	3	10	2
Trachycephalus nigromaculatus	0	0	0	0	0	0	0	1	0	0	0
Leptodactylus fuscus	0	0	13	1	2	4	0	14	1	0	15
Leptodactylus latrans	11	1	6	3	5	10	0	12	7	13	62
Leptodactylus spixi	0	0	0	2	0	0	0	1	5	2	4
Physalaemus signifer	1	0	0	0	0	6	0	6	1	0	2

Table S5: Pond permanence variables, latitude and longitude for each community in the tadpole metacomunity. Area I is the area (m^2) in the Spring, and Area II is in the summer. Permanency degree is the fraction of the initial area (Area I) that least during Summer (Area II).

Pond	Latitude	Longitude	Area I	Area II	Permanency degree
P1	30.79	53.25	23.3	12.9	0.6
P2	30.76	53.27	29.4	0	0.0
P3	30.83	53.48	14.8	0	0.0
P4	30.87	53.30	109.3	0	0.0
P5	31.00	53.39	42.1	0	0.0
P6	30.87	53.40	216.3	0	0.0
P7	31.01	53.50	72.3	63.5	0.9
P8	30.61	53.65	30.7	6.1	0.2
P9	30.77	53.62	6.8	0	0.0
P10	30.57	53.64	11.8	8.6	0.7
P11	30.63	53.66	37.6	13.5	0.4
P12	30.72	53.70	3.1	0	0.0
P13	30.57	53.73	10.7	0	0.0
P14	30.68	53.75	95.4	80.9	0.8
P15	30.65	53.52	117.3	104.6	0.9
P16	30.66	53.57	50.7	28.1	0.6
P17	30.83	53.38	7.0	0	0.0
P18	30.86	53.58	49.1	0	0.0
P19	30.76	53.47	88.6	32.5	0.4
P20	30.71	53.48	8.6	0	0.6
P21	30.83	53.46	37.8	31.2	0.8
P22	30.85	53.52	1294.0	1213.7	0.9
P23	30.91	53.55	76.9	47.6	0.6
P24	30.64	53.78	19.4	0	0.0
P25	30.66	53.74	10.2	0	0.8
P26	30.77	53.72	115.1	4.6	0.0
P27	30.85	53.75	168.8	0	0.7
P28	30.68	53.89	2.8	0	0.0
P29	30.97	53.67	249.7	37.1	0.1
P30	30.96	53.75	116.6	90.8	0.8
P31	30.90	53.53	227.5	226.7	1.0
P32	31.02	53.67	100.4	0	0.0
P33	31.03	53.74	441.0	337.6	0.8
P34	30.90	53.54	66.4	49.4	0.7
P35	30.89	53.52	51.4	47.4	0.9
P36	30.77	53.68	36.6	0	0.0
P37	30.94	53.50	2.5	0	0.0
P38	30.68	53.67	36.7	0	0.0

Table S6: Trait values for each species present in the tadpole metacommunity. Not all species present in this table is present in the Table S7.

Species	Eye position	Oral position	Dorsal fin	Ventral fin	Spiracle position	Body ratio	School behavior	Clutch behavior
Limnomedusa macroglossa	1	3	0	0	1	2	0	1
Dendropsophus minutus	0	2	1	1	1	1	0	1
Boana albopunctata	0	3	0	0	1	2	0	1
Boana pulchella	0	3	0	0	1	2	0	1
Phyllomedusa iheringii	0	1	0	1	2	1	0	2
Pseudis minuta	0	2	1	1	1	1	0	1
Scinax fuscovarius	0	2	1	1	1	1	0	1
Scinax granulatus	0	2	1	1	1	1	0	1
Scinax sp.	0	2	1	1	1	1	0	1
Physalaemus biligonigerus	1	3	0	0	1	2	0	3
Physalaemus cuvieri	1	3	0	0	1	2	0	3
Physalaemus gracilis	1	3	0	0	1	2	0	3
Physalaemus riograndensis	1	3	0	0	1	2	0	3
Pseudopaludicola falcipes	1	3	0	0	1	2	0	1
Leptodactylus chaquensis	1	3	0	0	1	2	1	3
Leptodactylus fuscus	1	3	0	0	1	2	0	3
Leptodactylus gracilis	1	3	0	0	1	2	0	3
Leptodactylus latinasus	1	3	0	0	1	2	0	3
Leptodactylus mystacinus	1	3	0	0	1	2	0	3
Leptodactylus ocellatus	1	3	0	0	1	2	1	3
Elachistocleis bicolor	0	1	0	0	3	2	0	1

Table S7: Tadpoles community data matrix with the presence of each specie found in each pond.

Species	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	P16	P17	P18	P19	P20	P21	P22	P23	P24	P25	P26	P27	P28	P29	P30	P31	P32	P33	P34	P35	P36	P37	P38
Limnomedusa macroglossa	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dendropsophus minutus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Boana albopunctata	0	0	1	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0
Boana pulchella	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	1	1	1	1	1	0
Phyllomedusa iheringii	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Pseudis minuta	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Scinax fuscovarius	1	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1
Scinax granulatus	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Scinax sp.	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0
Physalaemus gracilis	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	1	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	1	1	0	0	1	1	1
Physalaemus riograndensis	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Pseudopaludicola falcipes	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0
Leptodactylus fuscus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptodactylus gracilis	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptodactylus latinasus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Leptodactylus mystacinus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptodactylus ocellatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0
Elachistocleis bicolor	1	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0