

Universidade Federal de São Carlos

Centro de Ciências Biológicas e da Saúde

Programa de Pós Graduação em Ecologia e Recursos Naturais

**Fatores que estruturam metacomunidades em fitotelmos de
restinga**

Bruna Golinelli Nallis

São Carlos, SP

2021

Bruna Golinelli Nallis

Fatores que estruturam metacomunidades em fitotelmos de restinga

Dissertação apresentada ao Programa de Pós Graduação do Centro de Ciências Biológicas e da Saúde como parte dos requisitos necessários para obtenção do título de Mestra em Ecologia e Recursos Naturais.

Orientador: Prof. Dr. José Salatiel Rodrigues Pires

Co-Orientador: Prof. Dr. Victor Satoru Saito

São Carlos, SP

2021



UNIVERSIDADE FEDERAL DE SÃO CARLOS
Centro de Ciências Biológicas e da Saúde
Programa de Pós-Graduação em Ecologia e Recursos Naturais

Folha de Aprovação

Defesa de Dissertação de Mestrado da candidata Bruna Golinelli Nallis, realizada em 26/11/2020.

Comissão Julgadora:

Prof. Dr. José Salatiel Rodrigues Pires (UFSCar)

Prof. Dr. Fernando Rodrigues da Silva (UFSCar)

Prof. Dr. Michel Varajão Garey (UNILA)

O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Código de Financiamento 001. O Relatório de Defesa assinado pelos membros da Comissão Julgadora encontra-se arquivado junto ao Programa de Pós-Graduação em Ecologia e Recursos Naturais

Agradecimentos

Ao Professor Dr. Salatiel pela oportunidade de realizar o mestrado, por todo apoio durante o mestrado e pelo apoio e hospitalidade que me proporcionou ao longo das coletas realizadas em Florianópolis.

Ao Professor Dr. Victor Saito por toda ajuda, conselhos, orientação e paciência ao longo destes dois anos de mestrado.

Ao CNPQ pelo apoio financeiro.

Aos professores Dr. Hugo Sarmento, Dr. Eduardo Giehl e Dr. Erika Shimabukuro pelos conselhos valiosos no trabalho de qualificação.

Ao Dr. Facundo M. Labarque e a Dra. Maria Santina de Castro Morini pela fundamental ajuda na identificação das espécies dos Aracnídeos e dos Hymenoptera.

Ao Dr. Fernando Antonio Bataghin pela ajuda na identificação das bromélias.

À Carla Mourão, aluna de doutorado da UFSC que ajudou com o cálculo de NDVI e sombreamento das áreas de coleta.

À toda equipe do Monumento Natural Lagoa do Peri pelo suporte e alojamento durante o período de coleta.

À todos meus amigos pelo apoio durante essa jornada, em especial a Paula Ribeiro pela ajuda nos campos, conselhos e por ouvir todos meus desabafos e ao Pedro Miguel por todos os conselhos e por ouvir meus desabafos.

Ao meu namorado Lincoln Borges por todo suporte, carinho e paciência comigo ao longo desses dois anos, me incentivando e me apoiando até nós momentos mais difíceis, você nunca me deixou desistir.

Aos meus irmãos por acreditarem em mim.

À minha filha Eloisa, que nesses últimos meses me fez mais forte e mais determinada do que nunca.

Por fim, aos meus pais por serem pessoas maravilhosas, me darem suporte, me ouvirem, me auxiliarem e acreditarem em mim, sem vocês nada disso seria possível.

Apresentação

Consta nas Normas Complementares do Programa de Pós-Graduação em Ecologia e Recursos Naturais (2015), no item 2 das Normas de Defesa Pública de Dissertações/Teses que: “A elaboração do trabalho final de Dissertação/Tese para defesa pública, poderá ser apresentado: no formato descritivo tradicional ou na forma de conjunto de trabalhos científicos, regidos para publicação em revista nacional ou estrangeira”.

Diante da possibilidade a presente dissertação foi elaborada na forma de um artigo científico, na qual apresento uma abordagem dos fatores capazes de estruturar metacomunidades em fitofisionomias de restinga.

Resumo

Os ecossistemas neotropicais abrigam uma imensa biodiversidade, cobrindo fitofisionomias com características únicas. As restingas são fitofisionomias características das regiões costeiras, com temperaturas quentes, solos pobres e baixa disponibilidade de água, características que dificultam a sobrevivência nessa região, contudo existem espécies vegetais que tornam a vida nesses locais mais fácil. Um exemplo é a família Bromeliaceae, que possui espécies com fitotelmos capazes de reter água e matéria orgânica, criando um ambiente oportunista para outras formas de vida. Considerando o fato de que essas plantas têm características únicas para abrigar outros organismos, cada bromélia pode ser considerada como um fragmento de habitat dentro de uma metacomunidade. Estudamos os fatores responsáveis pela estruturação da metacomunidade de macroinvertebrados em duas espécies de bromélias: *Aechmea nudicaulis* (baixa heterogeneidade de fitotelmata) e *Vriesea friburgensis* (alta heterogeneidade de fitotelmata) em uma restinga do sul do Brasil. Descobrimos que as comunidades são compostas por muitas espécies comuns e poucas de invertebrados raros. Apenas uma pequena proporção da variação da composição da comunidade (10%) foi relacionada aos fatores explicativos considerados, sendo as espécies de bromélias e o índice de cobertura vegetal (NDVI) ao redor das plantas os mais relevantes. Os resultados também mostram que, ao contrário do esperado, as bromélias com maior heterogeneidade de habitat (*V. friburgensis*) apresentaram menor riqueza de espécies. Aplicando modelos de ranqueamento de abundância, descobrimos que as comunidades individuais eram semelhantes aos modelos nulos, sem aparente estruturação por processos de nicho de espécies. No entanto, quando as comunidades foram agrupadas por espécies vegetais (somando a abundância de várias bromélias), descobrimos que os modelos de Zipf e Mandelbrot, que consideram a dinâmica de manchas de colonização e extinção por espécies generalistas e especializadas, eram os modelos mais adequados. Nossos resultados demonstram que as comunidades de bromélias não se comportam individualmente como sistemas isolados, mas como manchas de habitat dentro de uma metacomunidade, com dinâmica aleatória de manchas de colonização e extinções locais em um conjunto de

bromélias. O entendimento dessa dinâmica de metacomunidade nos ajuda a entender a importância de conservar áreas de restinga para preservar a biodiversidade neotropical.

Palavras chaves: Bromelias, Florianópolis, Macroinvertebrados, Mata Atlântica.

Abstract

Neotropical ecosystems harbour an immense biodiversity, covering phytophysiognomies with unique characteristics. The restingas are phyto-physiognomies characteristic of coastal regions, with hot temperatures, poor soils and low water availability, characteristics that make survival difficult in this region, however there are plant species that make life in these places easier. An example is the Bromeliaceae family, which has species with phytotelmos capable of retaining water and organic matter, creating an opportunistic environment for other forms of life. Considering the fact that these plants have unique characteristics to harbor other organisms, each bromeliad can be considered as a habitat patch within a metacommunity. We studied the factors responsible for the structuring of the metacommunity in two species of bromeliad: *Aechmea nudicaulis* (low phytotelmata heterogeneity) and *Vriesea friburgensis* (high phytotelmata heterogeneity) in a restinga from south Brazil. We found that communities are composed by many common and few rare invertebrate species. Only a small proportion of community composition variation (10%) was related to the explanatory factors considered, with bromeliad species and the vegetation cover index (NDVI) around the plants being the most relevant. The results also show that, contrary to expectations, bromeliads with greater habitat heterogeneity (*V. friburgensis*) had less species richness. Applying rank abundance models, we found that the individual communities were similar to null models, without apparent structuring by species niche processes. However, when the communities were grouped by plant species (summing the abundance of several bromeliads), we found that the Zipf and Mandelbrot models, which consider patch dynamics of colonization and extinction by generalist and specialist species, were the most suitable models. Our results demonstrate that the bromeliad communities do not behave individually as isolated systems, but rather as habitat patches within a metacommunity, with random patch dynamics of colonization and local extinctions in a set of bromeliads. Understanding this metacommunity dynamic helps us to understand the importance of conserving restinga areas to preserve Neotropical biodiversity.

Keyword: Bromeliads, Florianópolis, Macroinvertebrates, Atlantic Forest.

Sumário

Apresentação	6
Resumo	7
Abstract	9
Capítulo 1: Introdução geral	12
1.Introdução geral	12
2.Objetivo geral e específico.....	14
3.Referências	16
Capítulo 2: Patch dynamics drive the structure of a phytotelmata metacommunity in a Neotropical restinga	18
Abstract.....	20
1.Introdução	22
2. Material e Métodos	25
3. Resultado	31
4. Discussão	39
5.Referências	43
Considerações Finais	49
Material Suplementar	50

Capítulo 1- **Introdução Geral**

1. **Introdução Geral**

A restinga é um ecossistema encontrado próximo a áreas litorâneas formado por deposição de areia. O artigo 3 do Código Florestal 2012 refere-se as restingas como: “...depósito arenoso paralelo à linha da costa, de forma geralmente alongada, produzido por processos de sedimentação, onde se encontram diferentes comunidades que recebem influência marinha, com cobertura vegetal em mosaico, encontrada em praias, cordões arenosos, dunas e depressões, apresentando, de acordo com o estágio sucessional, estrato herbáceo, arbustivo e arbóreo, este último mais interiorizado;” (Brasil 2012).

Muitos dos organismos que se encontram nas restingas ocupam nichos específicos e exercem funções ecológicas que controlam as vegetações relacionadas. Esses organismos dependem, em algum estágio da sua vida, de estruturas criadas por outros organismos, seja ele vegetal ou animal, para conseguir sobreviver (Rocha et al. 2004). Dentre os grupos vegetacionais da restinga, a família Bromeliaceae é uma das principais representantes em criar condições favoráveis para outros organismos.

As bromélias são plantas típicas das regiões neotropicais que categorizam grupos epifíticos, rupícolas e terrícolas, onde algumas espécies possuem uma estrutura foliar espiralada do tipo roseta que formam cisternas capazes de acumular água da chuva e material orgânico, além de manterem umidade e temperatura relativamente constantes comparadas ao ambiente exterior, e possuem espinhos laterais nas folhas que garante um ambiente protegido de predadores (Rocha et al. 2004, Cogliatti-Carvalho et al. 2010). As chamadas bromélias fitotelmatas, servem de refúgio, local para forrageamento, ou reprodução para muitos organismos, incluindo vertebrados, invertebrados e protozoários, além de terem um papel importante na ciclagem de nutrientes (Tardivo & Cervi 1997, Oliveira 2004).

O estudo de bromélias fitotelmatas como microcosmos naturais têm se tornado amplamente utilizado por ecólogos e pesquisadores da área para testar teorias ecológicas

em comunidades devido suas particularidades que fazem com que as bromélias possam ser consideradas manchas de habitat que formam uma metacomunidade, onde a relação de dispersão se dá por processos espaciais e controle ambiental (Junior 2014, Leibold et al. 2004).

A dispersão é um processo que facilita a adição de novas espécies em comunidades biológicas, bem como a distribuição dos organismos no espaço e o fluxo genético entre populações interligadas (Leibold, 2004). Existem atualmente diferentes teorias que consideram a dispersão como uma das causas principais para a distribuição de espécies que constituem uma comunidade. A maioria destas teorias convergem na indicação de que este processo atua em conjunto com os processos de seleção, especiação e deriva para poder explicar os padrões de distribuição de espécies entre comunidades (Vellend 2010).

A teoria pioneira e mais conhecida que aborda a dispersão é a teoria de biogeografia de ilha descrita por MacArthur e Wilson (1967) que considera os fatores que influenciam na riqueza e distribuição de habitats, sendo o fator mais importante a relação espécie-área. A relação espécie-área é um dos padrões mais consistentes em ecologia, predizendo que áreas maiores estão diretamente relacionadas a uma maior riqueza de espécies (Harper et al 2009). Grandes áreas possuem maior heterogeneidade, disponibilidade de recursos e maior espaço disponível para a colonização, garantindo que uma maior quantidade de espécies com nichos distintos sejam capazes de colonizar e habitar esses ambientes sem que haja extinções locais (MacArthur e Wilson 1967, Jabiol et al. 2009). A principal contribuição da dispersão nesta teoria é considerar que existe uma relação da distância das ilhas com o continente modulando a influência da área da ilha na riqueza de espécies. Ilhas mais distantes possuem menores chances de receberem espécies por dispersão, indicando, portanto, que a riqueza de espécies é afetada tanto pela área da ilha, como pela distância para o continente.

Mais recentemente a teoria mais utilizada para abordar a dispersão é a teoria de metacomunidades, muito estudada atualmente como uma abordagem que estuda como a dispersão de organismos no espaço-tempo afeta a estruturação de comunidades locais. Essa teoria foi sintetizada em 2004 por Leibold e colaboradores e explica a montagem

das comunidades em escalas locais e regionais, com o propósito de elucidar os padrões de abundância encontrados nas comunidades naturais (Logue et al. 2011).

As comunidades são compostas por espécies raras e comuns que interagem entre si e são afetadas tanto pela dinâmica de dispersão como por fatores ambientais (Siqueira et al. 2012). Essas comunidades são complexas e não estão relacionadas com apenas um processo de dispersão, suas interações e composição são definidas geralmente por dois ou mais processos relacionados entre si (Logue et al. 2011). O uso da abordagem de metacomunidades é crescente, apesar de ser um conceito relativamente novo que ainda está sendo moldado e discutido, seus efeitos são significativos e as pesquisas envolvendo essa temática vem crescendo.

2. Objetivo geral e específico

O presente estudo teve como objetivo avaliar, através de trabalho em campo, metacomunidades presentes em bromélias fitotelmatas e quais os fatores bióticos e abióticos que estruturam estas metacomunidades na restinga. Investigamos a diversidade biológica que compõem os fitotelmos, os fatores abióticos das restingas e as características das bromélias encontradas ao longo dos pontos de coleta que estão relacionadas com a metacomunidade da região, avaliando como a colonização das bromélias e relação de riqueza e abundância de espécies é moldada por esses recursos. Nós predizemos que a estrutura das comunidades de bromélias está relacionada com o ambiente ao redor, esperando assim que a luminosidade, a composição do solo, a cobertura vegetal e a distância entre os pontos de coleta interfiram diretamente na composição das metacomunidades. Predizemos também que os fatores biológicos como a identidade das bromélias, o peso e estrutura foliar e a heterogeneidade de habitat em espécies com maior número de fitotelmos abriguem uma metacomunidade com riqueza e diversidade divergentes.

Neste trabalho abordamos as seguintes questões: (1) Quais fatores abióticos da restinga atuam como filtros ambientais para colonização das bromélias? (2) As características morfológicas das bromélias interferem no processo de composição das

metacomunidades? (3) Quais os modelos de ranqueamento de abundância que melhor descrevem as metacomunidades?

3. REFERÊNCIAS

- BRASIL. 2012. LEI No 12.651, DE 25 DE MAIO DE 2012. AVAILABLE AT: [HTTP://WWW.PLANALTO.GOV.BR/CCIVIL_03/_ATO2011-2014/2012/LEI/L12651.HTM](http://www.planalto.gov.br/ccivil_03/_ato2011-2014/2012/lei/L12651.htm) [ACCESSED JUNE 23, 2020].
- ROCHA, C.F.D., COGLIATTI-CARVALHO, L., NUNES-FREITAS, A.F.N., THEREZA CHRISTINA ROCHA-PESSÔA, C.R., DIAS, A.S., ARIANI, C.V. AND NUNES MORGADO, L.N. 2004. CONSERVANDO UMA LARGA PORÇÃO DA DIVERSIDADE BIOLÓGICA ATRAVÉS DA CONSERVAÇÃO DE BROMELIACEAE. *VIDALIA* 2: 52–72.
- COGLIATTI-CARVALHO, L., T. C. ROCHA-PESSÔA, A. F. NUNES-FREITAS, AND C. F. D. ROCHA. 2010. VOLUME DE ÁGUA ARMAZENADO NO TANQUE DE BROMÉLIAS, EM RESTINGAS DA COSTA BRASILEIRA. *ACTA BOT. BRAS.* 24: 84–95.
- HARPER, C. R. T. | M. B. | J. L. 2009. FUNDAMENTOS EM ECOLOGIA. ARTMED EDITORA.
- JABIOL, J., B. CORBARA, A. DEJEAN, AND R. CÉRÉGHINO. 2009. STRUCTURE OF AQUATIC INSECT COMMUNITIES IN TANK-BROMELIADS IN A EAST-AMAZONIAN RAINFOREST IN FRENCH GUIANA. *FOREST ECOLOGY AND MANAGEMENT* 257: 351–360.
- JUNIOR, A.T.P. 2014. INVERTEBRADOS DE FITOTELMA BROMELÍCOLA EM REMANESCENTES DE MATA ATLÂNTICA (MINAS GEAIS, BRASIL). DISSERTAÇÃO. UNIVERSIDADE FEDERAL DE JUIZ DE FORA, JUIZ DE FORA.
- LEIBOLD, M. A., M. HOLYOAK, N. MOUQUET, P. AMARASEKARE, J. M. CHASE, M. F. HOOPES, R. D. HOLT, J. B. SHURIN, R. LAW, D. TILMAN, M. LOREAU, AND A. GONZALEZ. 2004. THE METACOMMUNITY CONCEPT: A FRAMEWORK FOR MULTI-SCALE COMMUNITY ECOLOGY. *ECOLOGY LETTERS* 7: 601–613.
- LOGUE, J. B., N. MOUQUET, H. PETER, AND HILLEBRAND. 2011. EMPIRICAL APPROACHES TO METACOMMUNITIES: A REVIEW AND COMPARISON WITH THEORY. *TRENDS IN ECOLOGY & EVOLUTION* 26: 482–491.
- MACARTHUR, R. H., AND WILSON, E. O. 1967. THE THEORY OF ISLAND BIOGEOGRAPHY. PRINCETON UNIVERSITY PRESS.
- OLIVEIRA, N. D., C. FREDERICO, AND D. ROCHA. 2004. THE ANIMAL COMMUNITY ASSOCIATED WITH THE TANK BROMELIAD *NEOREGELIA CRUENTA* (R. GRAHAM) L. R. SMITH. 10.
- SIQUEIRA, T., L. M. BINI, F. O. ROQUE, S. R. M. COUCEIRO, S. TRIVINHO-STRIXINO, AND K. COTTENIE. 2012. COMMON AND RARE SPECIES RESPOND TO SIMILAR NICHE PROCESSES IN MACROINVERTEBRATE METACOMMUNITIES. *ECOGRAPHY* 35: 183–192
- TARDIVO, R. C., AND A. C. CERVI. 1997. O GÊNERO *CANISTRUM* E. MORREN

(BROMELIACEAE) NO ESTADO DO PARANÁ. ACTA BOT. BRAS. 11: 259–271.

VELLEND, M. 2010. CONCEPTUAL SYNTHESIS IN COMMUNITY ECOLOGY. THE QUARTERLY REVIEW OF BIOLOGY, 85(2), 183-206.

Capítulo 2

Patch dynamics drive the structure of a phytotelmata metacommunity in a Neotropical restinga

**Patch dynamics drive the structure of a phytotelmata metacommunity in a
Neotropical restinga**

Bruna Golinelli Nallis¹, Victor Satoru Saito^{2*}, José Salatiel Rodrigues Pires³

¹ Graduate Program in Ecology and Natural Resources, Federal University of São Carlos (UFSCar), Rod. Washington Luís km 235 - SP-310, São Carlos/SP, Brasil. E-mail: bruna.gnallis@hotmail.com

² Environmental Sciences Department, Federal University of São Carlos (UFSCar), Rod. Washington Luís km 235 - SP-310, São Carlos/SP, Brasil. E-mail: victor.saito@gmail.com

– Corresponding author*

³ Ecology and Zoology Department, Federal University of Santa Catarina (UFSC), Campus Universitário, Trindade, Florianópolis/SC, Brasil. E-mail: salatiel.pires@ufsc.br

Abstract

Neotropical ecosystems are home to a proportionately high global biodiversity. The restingas, have challenging abiotic characteristics for the survival of some species, however there are species that have structures that facilitate the survival of organisms in this region, such as the Bromeliacea family, which has species with phytothomes capable of retaining water and organic matter, creating opportunistic environments for other forms of life. Considering the fact that these plants have unique characteristics to house other organisms, each bromeliad can be considered a habitat fragment within a metacommunity. We studied the factors responsible for the structure and dynamics of the metacommunity in *Aechmea nudicaulis* and *Vriesea friburgensis* in a sandbank in southern Brazil. We found that communities are made up of many common and few rare species. Only 10% of the variation in the composition of the community was related to the explanatory factors considered. The results also show that, bromeliads with greater habitat heterogeneity showed less species richness, contrary to what is expected to be found in nature. Applying abundance rating models, we found that individual communities were similar to null models. However, when grouping communities by species, we found that the Zipf and Mandelbrot models were the most suitable models. Our results demonstrate that the bromeliad communities do not behave individually as isolated systems, but as habitat patches within a metacommunity, with random colonization dynamics and local extinctions in a set of bromeliads. Understanding this metacommunity dynamics helps us to

understand the importance of conserving sandbank areas to preserve neotropical biodiversity.

Keywords: Bromeliad, Phytotelmata, Macroinvertebrates, Atlantic Forest.

4. INTRODUCTION

Neotropical ecosystems are capable of harboring a high biodiversity in comparison to its area (Rull 2011). The restingas are phytophysiognomies present in the neotropics, characteristic of coastal regions that have a varied extension along sandbanks. Some of characteristics by restingas are the high exposure to the sun light, high temperatures, poor and sandy soil and high salinity capable of acting directly in filtering the organisms that inhabit these regions and in the patterns of species distribution (Franco et al. 1984, Henriques et al. 1984, Ormond 1960). The state of Santa Catarina includes the largest Brazilian restinga with a unique biodiversity composed by many endemic species (Gonçalves-Santos et al. 2015).

Given the harsh conditions of high temperatures, low resources like nutrients and water availability, the species inhabiting restingas commonly depend, at some stage in their life, on structures created by another individual, whether it is a plant or animal, in order to survive (Rocha et al. 2004). Among these groups, the Bromeliaceae family has epiphytic, rupicolous and terrestrial species, with groups with phytotelmatous characteristics, that is, they present a leaf structure in the form of a rosette capable of storing water and organic matter in its interior, in addition to maintaining relatively constant humidity and temperature in relation to the external environment. In addition, several species have thorns on their leaves, guaranteeing an environment protected from predators, being important for several animal species making them an important group for the maintenance of restinga biodiversity (Lopez 1995, Rocha et al. 2004, Cogliatti-Carvalho 2010, Morales & Najara 2013).

The bromeliads tanks have a complex architecture, and can be divided into two types: (i) a central channel consisting of spiraled leaves capable of storing water, such as the *Billbergia* and *Aechmea* genera. (ii) Alternating leaves capable of forming several water accumulating compartments that separate through the leaf base, increasing the supply of micro-habitats, such as the *Vriesea* and *Neoregelia* genera (Zotz 1999). In this way, different species of bromeliads can present communities with different abundance given that they provide habitats with distinct heterogeneity (Jocque & Field 2014).

Phytothelon bromeliads harbor communities of associated insects and some vertebrate species that make this system a peculiar microcosm, in which its structure affects the dynamics of colonization and extinction of other species (Shmida & Wilson 1985). Conceptually, they can be considered habitat patches that form a metacommunity, where geographic distances, size and characteristics of habitats and regional abundance of individuals potentially influence the composition of the community through dispersion processes and species niche (Leibold et al. 2004, Migliorini et al. 2018, Malfatti and Utz 2019). The use of metacommunities for ecosystem studies is growing and is a promising framework for understanding natural communities in fragmented landscapes (Heino et al. 2015). The use of bromeliads is also common for studies related to the effects of climate change, studying food networks and observing the resistance and resilience of communities through disturbances.

In the context of metacommunities, the abundance of species results from the sum of ecological conditions and resources available to a community, as well as immigration and emigration rates, and the influences of competitors, predators and diseases, which will determine the birth and death rates of species (Townsend et al. 2010). One way of

characterizing the abundance of communities is by applying species abundance distribution models, also known as SAD (SAD - Species Abundance Distribution plots, McGill et al. 2007). More precisely, SADs can be described as vectors of ranked abundance for all species in the community, where the shape of these vectors describes the abundance relationships among species (McGill et al. 2007). There are numerous models that help to classify and describe SADs arranged in five groups: purely statistical models, branching models, population dynamics models, niche partition models and individual spatial distribution models (Fávero et al. 2015). These ecological models help us to identify patterns of dominance, rarity and uniformity, in addition to testing hypotheses regarding the organization of species in metacommunities in relation to local processes, such as immigrations and extinctions (Magurran 1988, McGill 2007).

In this study we aimed to describe the structure of bromeliad macroinvertebrate metacommunity and to identify biotic and abiotic factors influencing it. We investigated 1) the biological diversity that compose phytohelminth communities, 2) which are the abiotic factors of restingas and which are the bromeliad characteristics that explain metacommunity variation, 3) the rank-abundance relationships that describe them. We predicted that the richness and abundance of bromeliad communities are related to the surrounding environment, expecting that sun exposure, vegetation cover and the distance between bromeliads would explain metacommunity structure. We also predict that larger and more heterogeneous habitats, described by biological factors such as the identity of bromeliads, weight and leaf structure would harbor greater diversity of inhabiting species.

5. MATERIAL E METHODS

2.1. Study Area

The field sampling was carried out in March 2019, end of the rainy season. The bromeliads were sampled in a restinga fragment at the the Natural Monument Lagoa do Peri - MONA da Lagoa do Peri, Florianópolis, Santa Catarina, localized in south of Brazil, an integral protection conservation unit located at $27^{\circ}42'41''$ S and $48^{\circ}30'06''$ O and $27^{\circ}46'29''$ S and $48^{\circ}33'34''$ O (Figure 1) (Floram 2019). The MONA have two types of terrestrial ecosystems, first is the rainforest represented by rainforest located in the hillside areas of Morro do Ribeirão da Ilha, one of the last remaining rainforests in the region; second is the restinga, located in a area who separate the lagoon from the sea (Floram 2019).

2.2. Community sampling

We collected bromeliad macroinvertebrate communities using active pursuit within a 270 m transect going from the edge of Lagoa do Peri to the beginning of the beach. The transect was determined by drone pictures, totaling six sampling points with a distance of 54 m from each other (Figure 1). We chose to collect 10 m inside the restinga transect trail to reduce anthropogenic impact noise. We made, with the aid of a compass a 2, 5 m X 2, 5 m quadrant and choosed the bromeliads would be collected by the destructive method and non-destructive method. For sampling, we measured the shortest distance from the center of the quadrant to the nearest bromeliad, posteriorly made a cut in the plant base and put the plants in plastic bags. The bromeliads were weighty using a portable digital scale and

taken to the research base to be cleaned and to start the screening process. The bromeliads identification were realized by a botanic professional by photos (see acknowledgment).

To collect the phytotelm material we used two methods, one destructive, where the rosettes of bromeliads were ripped out and cleaned in water and other method less invasive, where the bromeliads were cleaned without damaging rosettes. The bromeliads submitted to the non destructive method were returned near the original sampling site after the screening.

The material collected from the bromeliads was placed in trays and the macroinvertebrates were screened and fixed in flasks containing 70% alcohol. In the laboratory, the specimens were identified with the aid of an electronic stereomicroscope and identification keys. Aquatic macroinvertebrates were identified to the lowest possible taxonomic level (Hamada et al. 2018). The ants and spiders samples were identified with help of specialists to the lowest possible taxonomic level and preserved in a 70% solution alcohol. Anurans found in bromeliads during the collection period were identified by means of photos, being released after identification.

We calculated five community predictors for the subsequent data analyses namely geographical distance between points, identity of the sampling site, weight of the bromeliad, species of bromeliad and the Normalized Vegetation Difference Index (NDVI) (table S1 of the Supplementary Material).

For the NDVI calculation we use satellite pictures by the United States Geological Survey (USGS) Earth Explorer, corresponding to the month of April 2020 (USGS 2020). The pictures were captured by the Sentinel-2 Satellite, which has 13 spectral bands, with spatial resolutions of 10, 20 or 60 m, depending on the band. All the pictures process and

analysis were realized on QGIS 3.4.15 software enabling get the NDVI. We used red bands (Red) and near infrared (NIR), both with a resolution of 10 m. We made the calculation with a raster calculator, one software functionalities using the index:

$$NDVI = (NIR - Red) / (NIR + Red)$$

From this command, QGIS make calculation and after show the new picture gered with NDVI information. With the medium values given for each pictures were possible have a value index for each demarcated point.

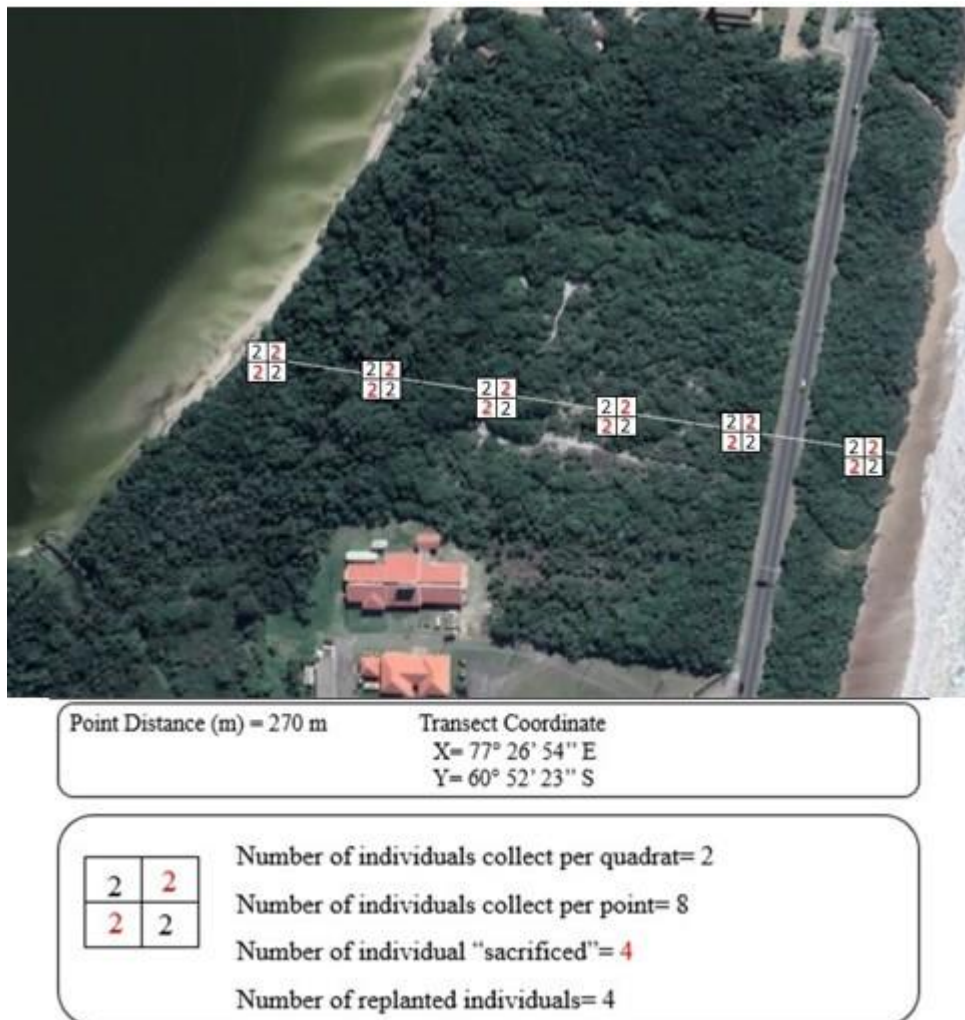


Figure 1. Sampling design and location of bromeliad samples. In the left side is Lagoa do Peri and in the right side is Armação beach, Saanta Catarina, south of Brazil.

2.3. Data analysis

2.3.1 Relationship among predictive variables

In order to verify the relationship among the predictor variables, we applied Pearson correlations among quantitative variables (weight of plants and NDVI) and box plots among quantitative and qualitative variables (identity of plants and sampling sites in relation to the quantitative variables indicated above).

2.3.2 Explaining richness, total abundance and diversity

We applied multiple regressions to relate species richness to the weight of bromeliads and species identity. Our prediction was that higher richness would be found in larger plants and bromeliads with greater heterogeneity in phytotelm. The same analysis was performed using total community abundance and Shannon's diversity as response variables.

2.3.3 Describing and explaining the structure of metacommunities

We used a non-metric multidimensional scaling analysis (NMDS) to visualize the similarity in community composition in relation to the selected factors. For that, the ordinations were structured in relation to the distance in meters from sampling points, plant weight, plant identity and NDVI. The dissimilarity between communities was calculated using Bray-Curtis metric.

Complementarily, we used multiple regressions in distance matrices (MRM), using data of community dissimilarity as response matrix and the Euclidean distance of each predictor variable (based on NMDS graphs), as explanatory matrices (Lichstein 2007). This analysis aimed to understand which were the environmental variables most correlated with the differences in the composition of the communities. That is, properly testing the

relationships visually estimated by NMDS. The individually significant variables in the MRM were used in a variation partition approach, where the individual explanatory power is extracted (Peres-Neto et al. 2006).

We applied species abundance distribution models (SAD) to each individual community (each bromeliad community) and also summing the abundance of all communities of each bromeliad species, in order to identify patterns of abundance that occur in the different species. The model fitting were adjusted according to different models (see description below) of SADs, which are the (1) null model, (2) niche preemption model, (3) lognormal, (4) Zipf and Mandelbrot. These models represent large groups of SADs that uncover patterns of dominance, rarity and uniformity and enable the application of hypotheses about the organization of species in communities (Magurran 1988, Magurran et al. 2011).

- 1- The null model uses a brockenstick branching model where individuals are randomly distributed among species and between communities. This model assumes that individuals in the pool have the same chance of colonization and death (Hubbell 2001). According to these assumptions, communities are maintained by the processes of immigration and emigration of species, these processes being dependent on the regional abundance of species (species more common in the region are more likely to migrate to communities). In essence, this model does not consider the species' niches as fundamental to the patterns found.
- 2- The niche preemption model fits a classic model from the Motomura geometric series, which predicts that each species has a local abundance estimated from a

single dominance parameter that decays according to a constant (Odum 1986).

This model fits a straight line on an abundance ranking plot and considers that communities are colonized by only a few dominant species (He & Tang 2008).

- 3- The log-normal model assumes that the ranking of abundances on a logarithmic scale has a normal distribution. One consequence of this is that, according to the central limit theorem, ecological communities will have many species with intermediate abundance and few rare or common species (Ricklefs 1993).

Although initially developed based on the ecological niche theory, recently, neutral models were able to reproduce the same patterns (Magurran et al. 2011).

- 4- The Zipf and the Zipf-Mandelbrot models fit a model with one or two parameters, respectively, on the proportion of the most abundant species and on the decay abundance of the rarest species. This model assumes that, in succession processes, late colonizing species are those that need specific characteristics in the habitat, that is, they have a specialized niche and thus are more difficult to find. While early colonizing species are more generalist and dominate in abundance regardless of the time of succession (Magurran 2013). This model assumes that colonization is initially stochastic depending on the regional abundance of generalist species, but that mature communities are determined according to the niche of late species.

The models fit were compared use Akaike information criteria (AIC). All analyses were performed using the R software with the *vegan* package (Oksanen et al. 2018).

6. RESULTS

3.1. Overall results

We collected a total of 39 plant individuals from two different species of bromeliads (*Aechmea nudicaulis* and *Vriesea friburgensis*), being 16 from *A. nudicaulis* and 23 from *V. friburgensis*. We found in general, many common species and few rare species of organisms that inhabit the restingas tank bromeliads, with higher abundance of the groups Hymenoptera, Collembola, Annelida and Coleoptera. We identified 1,211 invertebrate individuals (Table S2 to Supplementary Information). From the total number, we used 1,076 individuals in the subsequent analyses, as very rare species were removed from the metacommunity ($n > 12$) (aiming a better adjustment of the data in the comparative analyses, Siqueira et al. 2012). This was done due to the high number of empty cells, which prevented some multivariate statistical analyses from being performed. With this reduction in species, there was a reduction in the number of bromeliads analyzed, which went from 39 to 37 bromeliads.

3.2 Relationships among predictive variables

The correlation between the abiotic quantitative variables indicated that the weight of the plants was correlated with the NDVI ($r = -0.56$). In addition, the box plots indicated that plant species occupy locations with different shading and tend to have different sizes (Figure 2). *A. nudicaulis* occurs in more shaded places and are lighter. The weight of the plants also showed an apparent quadratic relationship with the sampling sites, with the largest individuals at the central sites of the transect.

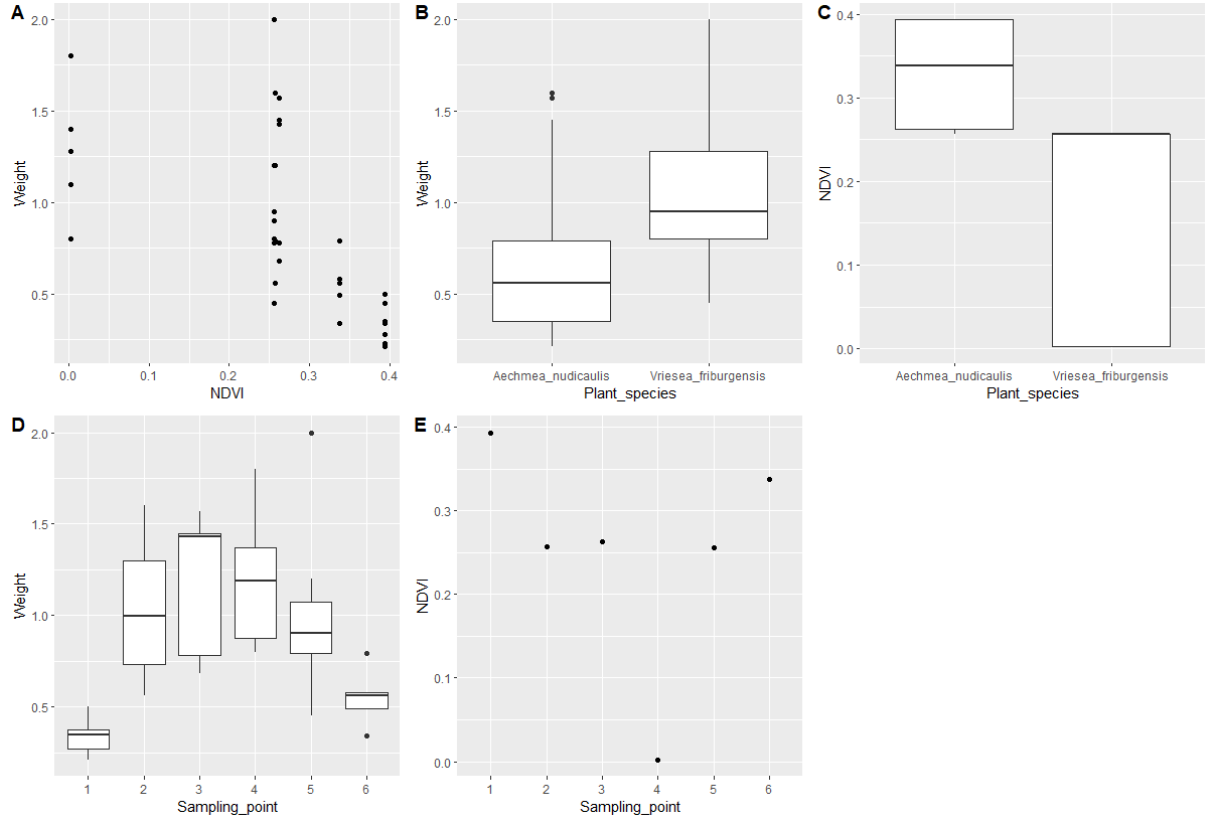


Figure 2. Interrelationship between the predictor variables. Relationship of quantitative variables with the different species of bromeliad and the sampling sites, A) relationship of NDVI with the weight of bromeliads. B) relationship between the weight of bromeliads and plant species *A. nudicaulis* and *V. friburgensis*, C) relationship of the NDVI and the plant species *A. nudicaulis* and *V. friburgensis*, D) relationship of the weight of the bromeliads to the sampling sites, E) relationship of NDVI with the sampling sites.

3.3 Explaining richness, total abundance and diversity

The richness and diversity of the communities were related to the bromeliad identity, with higher richness and diversity found in *A. nudicaulis*, going against our prediction of higher diversity in the species with the greatest heterogeneity of phytothelmata (Table 1).

Contrary to our prediction, we found no relationship between the weight of plants and richness and diversity. It is interesting to note that, despite not being a significant factor in the analyses, *A. nudicaulis* individuals are lighter, but with greater richness and diversity (Figure 2B). Community abundance was not explained by any of used variables.

Table 1. Multiple linear regression between species richness, total abundance and Shannon diversity in restinga phytotelmos communities in relation to the weight and taxonomic identity of bromeliads. In bold, significant relationships for alpha = 0.05.

Response		Degrees of		
Variables	Predictor variables	freedom	F value	P value
Species richness	Weight	1	0.95	0.33
	Species	1	16.68	<0.01
	Weight: species	1	0.71	0.40
	Residuals	31		
Total Abundance	Weight	1	0.03	0.86
	Species	1	2.33	0.13
	Weight: species	1	1.41	0.24
	Residuals	31		
Shannon Diversity	Weight	1	0.32	0.57
	Species	1	9.22	<0.01
	Weight: species	1	0.90	0.34
	Residuals	31		

3.4 Describing and explaining the metacommunity structure

The NMDS (Figure 3) showed that the variables potentially related to the structure of communities are the identity of the colonized plants, NDVI and plant weight (linear adjustment between two-dimensional and calculated distances = 0.83). It is possible to observe that the communities of *V. friburgensis*, (heavier and in less shaded places) are

closer to each other, forming a more homogeneous group and that the communities of *A. nudicaulis* are more heterogeneous. The geographical distance among sampling sites did not present a clear relationship with the dissimilarity among communities.

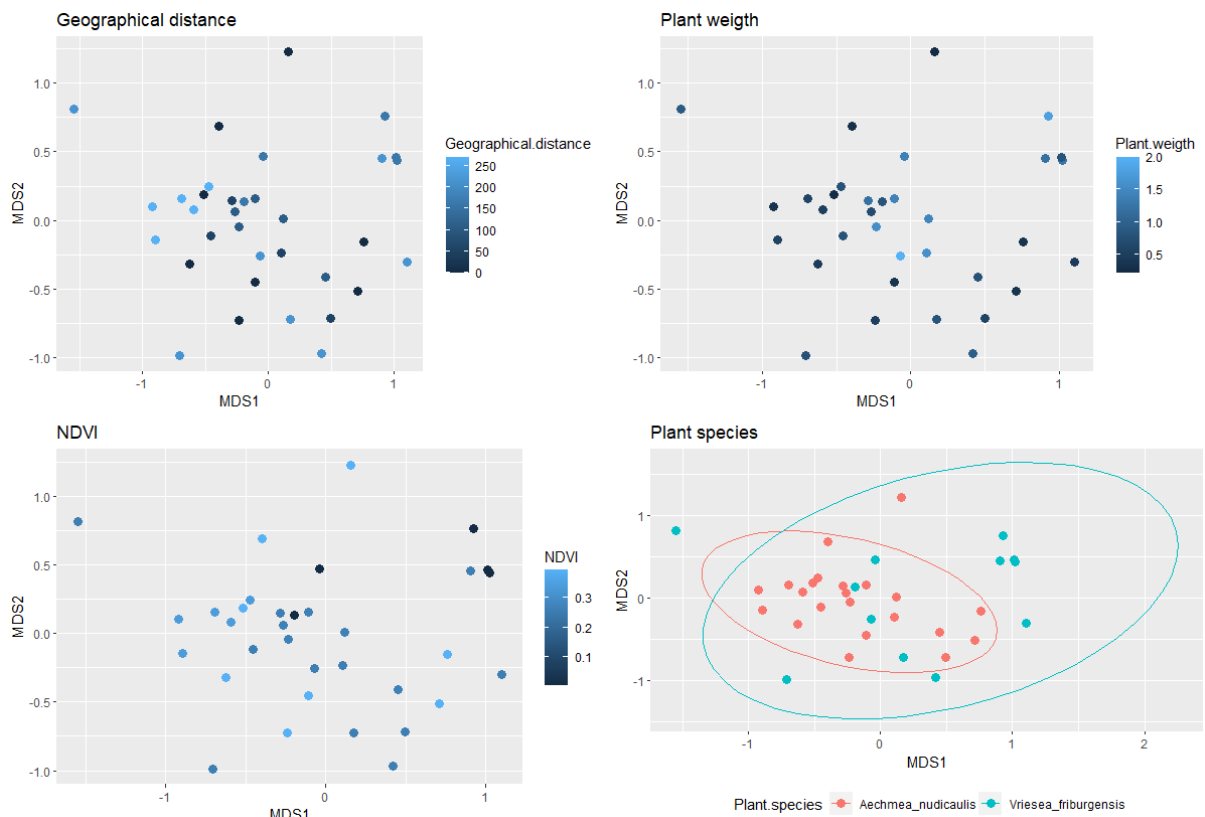


Figure 3. Community ordination (NMDS) in relation to different explanatory variables. Quantitative variables (geographical coordinate, weight, NDVI) were stratified in color gradients, a) ordination according to the geographic distance among points, b) ordination of the weight of plants, c) ordination of the NDVI, d) ordination of the plant species in different colors with probabilistic ellipses.

The multiple regression of distance matrices (MRM) showed that there is no relationship between most of the predictor variables and the composition of the communities. Only the plant species ($F = 13.99$, $p = 0.004$) and NDVI ($F = 19.76$, $p =$

0.024) were significant, supporting what was observed in the NMDS. In addition, the variance partition indicated that the two significant variables (species and NDVI) explained together only a small proportion of the variation (10%), with 4% shared and 6% purely of the NDVI, without a individual part explained solely by species identity.

3.5 SADs models

The modeling of the SAD indicated that many communities in *V. friburgensis* were better fitted (according to AIC) by the null model (10 out of 13 communities) (Figure 4). In *A. nudicaulis* the pattern was similar, with 10 out of 21 communities being better adjusted by the null model, followed by the Zipf and Mandelbrot models (similar models, adding up to 6 out of 21 communities) (Figure 5). When we merged the communities (summing abundances) of each plant species, the Zipf and Mandelbrot models were the ones that best fit in *V. friburgensis* (AIC Zipf = 105.9656 and AIC Mandelbrot = 107.9656) and also in *A. nudicaulis* (AIC Zipf = 137.903 and AIC Mandelbrot = 139.903) (Figure 6) (Table S3 of Supplementary Information).

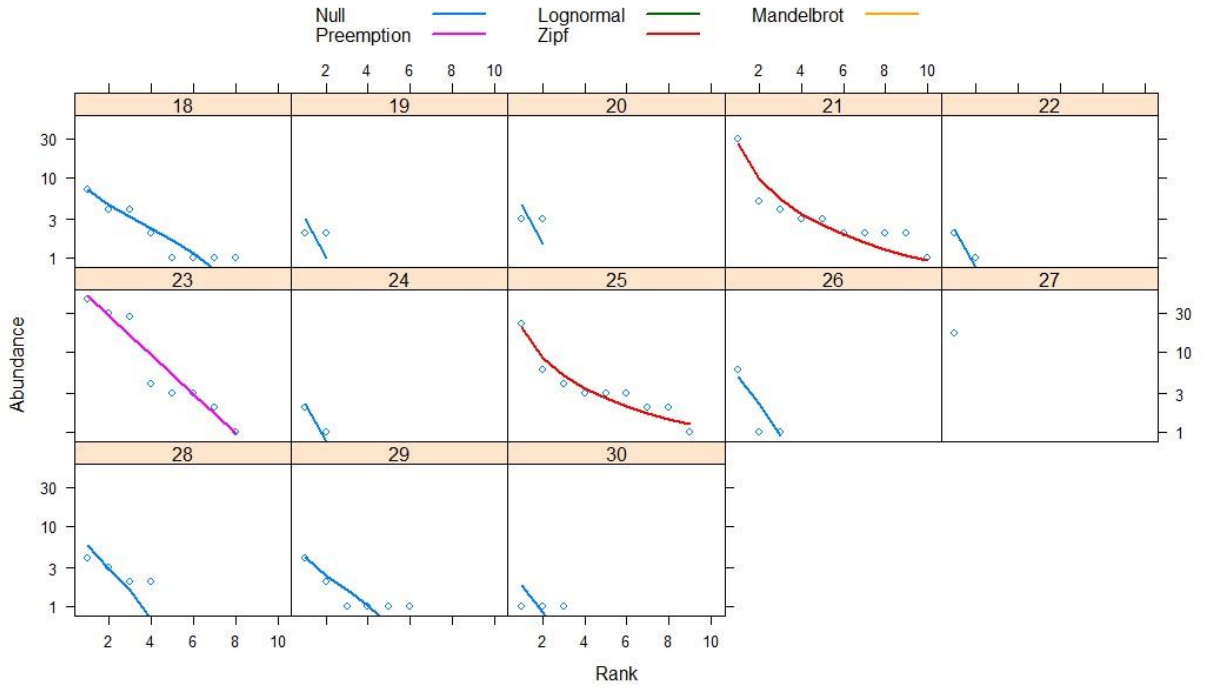


Figure 4. SADs of *Vriesea friburgensis* analyzing each bromeliad separately. The graphs indicate the most plausible model according to AIC criteria and show how random (null model) the patterns are when we try to analyze them individually.

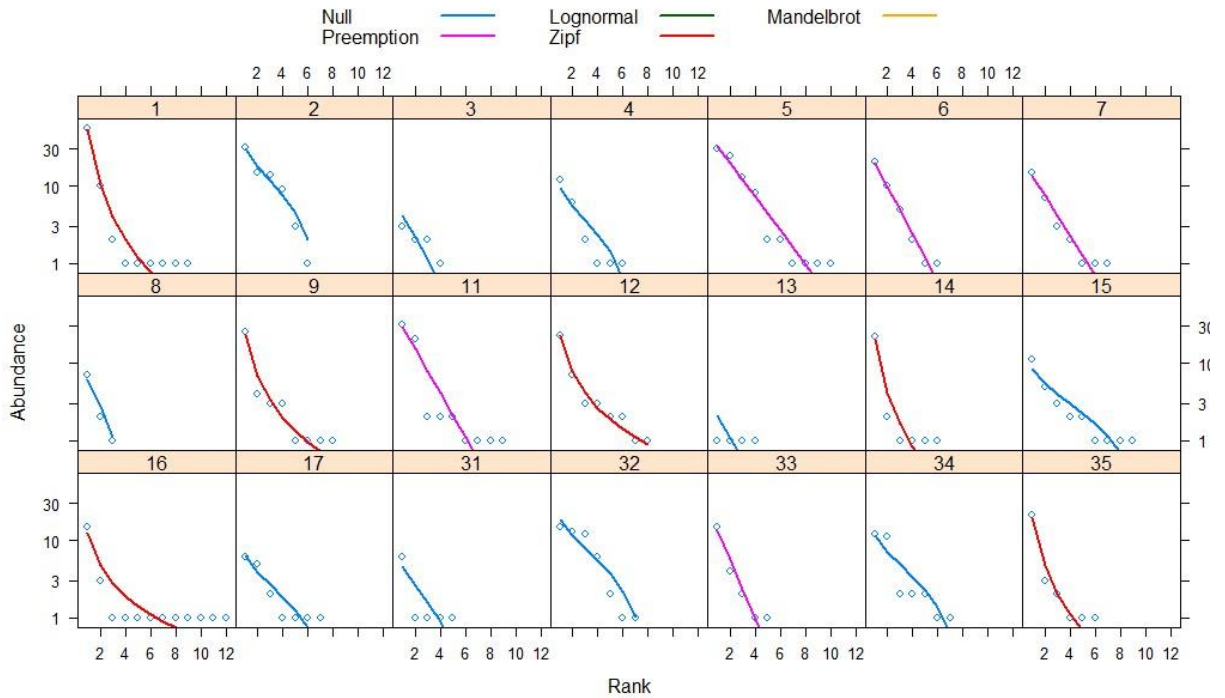


Figure 5. SADs of *Aechmea nudicaulis* analyzing each bromeliad separately. The graphs indicate the most plausible model according to AIC criteria and show how random (null model) the patterns are when we try to analyze them individually.

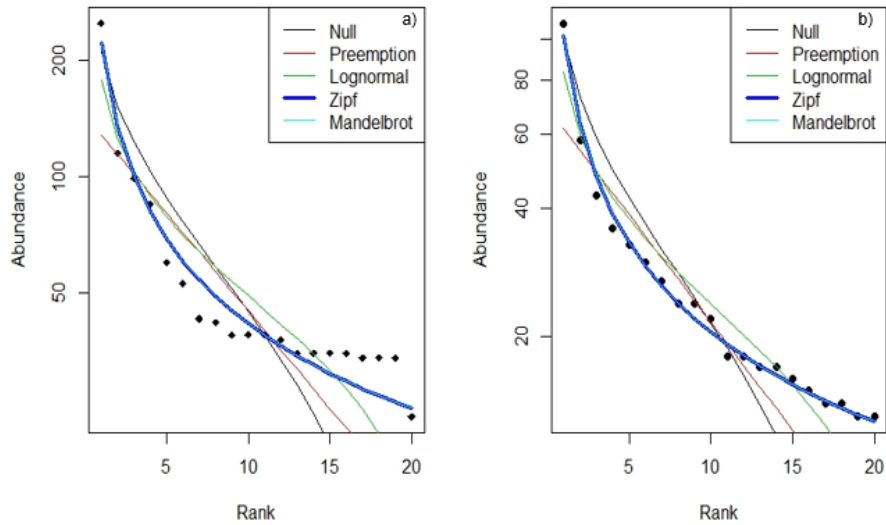


Figure 6. Rank abundance models for the sum of the abundances in the two bromeliads found in restinga. The graph shows that the best models are the Zipf and the Mandelbrot which fits models with a parameter on the proportion of the most abundant species and a decline in the abundance of the rarest species. a) on the left side the graph corresponds to the sum of the communities of *Vriesea friburgensis*, b) on the right side of *Aechmea nudicaulis*.

7. DISCUSSION

We found that the different species of bromeliad and the amount of vegetation cover had some relationship with the composition of studied communities, but most of the variation remained unexplained. Contrary to our expectations, we found no relationship between the habitat size (weight of plants) and richness and composition of communities. However, communities in species with central phytotelma (*A. nudicaulis*) contained greater richness and diversity of species. Furthermore, the fact that bromeliads are considered as whole ecosystems (they have different trophic levels, nutrient cycling internally, Migliorini et al. 2018), did not guarantee that the species that live in them form an internally regulated community, showing themselves as habitat patches that together structure a dynamic metacommunity (results from SADs) (Lopez 1995, Malfatti & Utz 2019). Our results indicate that restinga phytotelmata communities have immigration and extinction flows that are dynamic and partially random, these being the possible mechanisms structuring the metacommunity.

As expected, the variables related to shading and canopy coverage were associated with different species of bromeliads, suggesting that the sandbank gradient affects the macrofauna. A study by Bussel et al 2018 showed strong but varied impacts on the bromeliad macrofauna according to the vegetation cover. Areas with low vegetation cover are more exposed to the sun, the more shaded areas have a greater number of resources due to the input of milder leaves and temperatures (Farjalla et. Al 2016). Fluctuations in water temperature tend to be less with the increase in vegetation cover, thus influencing species richness (Kratina et al. 2017). Such explanation must be valid for our studied

metacommunity, especially considering the common high temperatures of restingas in the neotropics.

It is also known that species of tank bromeliad vary widely in size and form of life, encompassing different environmental gradients on a large scale (Jabiol et al 2009). Bromeliads of different species have phytotelma with varied structures that could influence the species-area relationships. The species-area relationship is well known in bromeliad ecology and studies indicate that this is one of the strongest relationships for determining the communities of aquatic invertebrates, as they consider that there is likely little connectivity between multiple-bromeliad tanks. The difference in species richness found in plants with different structures may be related to the daily fluctuations in temperature within phytotelmos. Bussel et al. 2018 show in their studies that the daily temperature fluctuation is more recurrent in species exposed to the sun, and these fluctuations may be responsible for a loss in species richness, which can cause a trophic cascade. Bromeliad species like *Vriesea*, despite being more heterogeneous, were the species that were most exposed to sunlight. On the other hand, the weight of bromeliads was not a significant factor, potentially due to the common rains during the month of May, which occurred throughout the sampled period, causing floods that can be very harmful in bromeliads, since they leach important nutrients, basal resources and even smaller macroinvertebrates (Sirivastava et al. 2020). The rains can also dismantle the previously formed community and remove the possible signatures that the size and heterogeneity of bromeliads have in the structuring of communities.

Supporting the idea above, the individual SAD analyzes of the bromeliad communities were not enough to reproduce a strongly structured deterministic pattern

within each community, since the null pattern of occupation of the bromeliads was the most commonly supported model (Figure 4 and Figure 5). This null model simulate a random colonization from the regional pool, with any internal local process influencing it. However, when we summed the communities' abundances by species of bromeliad (Figure 6), we found that the models that best explain the pattern of abundances are the Zipf and the Mandelbrot types. These models relate the type of habitat to the capacity of local colonization. This suggests that each bromeliad is a habitat patch with a flow of extinction and colonization determined by the quality of the environment in which they are found, level of maturity of the ecosystem and flow of disturbances, where the set of these bromeliads would be a metacommunity under succession process. Thus, the data studied were adjusted in the Zipf-Mandelbrot model potentially due to the presence of many bromeliads in the early stages of colonization, characterizing pioneer environments, which can be present in most areas of the community mosaic, especially in rainy periods that overflow the phytotelmata. These potential overflows should remove the organisms from the tanks and force a restart of colonization, enhancing the neutral and unstructured pattern of analysis at individual bromeliad scale.

We conclude that the most important factors that shape the metacommunity in the present study are the identity of the bromeliad and the vegetation cover in the places where the bromeliads are found. We also showed that the identity of the plant is related to the species richness in the communities, with *A. nudicaulis* being the species with the highest richness, probably because it has a deeper phytotelma which decreases the percentage of overflow and are able to retain water for a longer time.

Studies with bromeliads are good models for understanding larger communities. Understanding its dynamics through metacommunity lenses provided ways to understand patterns that would be quite unpredictable when looking only at local factors. The study also shows us the importance of rain dynamics, which together with other works can provide a foundation for understanding how these communities behave in extreme situations.

8. REFERENCES

- ARMBRUSTER, P., R. HUTCHINSON, and P. COTGREAVE. 2002. Factors influencing community structure in a South American tank bromeliad fauna. *Oikos* 96: 225–234.
- BUSSE, A., ANTIQUEIRA, P.A.P., NEUTZLING, A.S., WOLF, A.M., ROMERO, G.Q., PETERMANN, J.S. 2018. Different in the dark: The effect of habitat characteristics on community composition and beta diversity in bromeliad microfauna.
- FRANCO, A.C., VALERIANO, D.M., DOS SANTOS, F.M., HAY, J.D., HENRIQUES, R.P.B. and DE MEDEIROS, R A. 1984. Os climas das zonas de vegetação da praia da restinga de barra de Maricá, Rio de Janeiro.
- FARJALLA V.F., GONZÁLEZ A.L., CÉREGHINO R., DÉZERALD O., MARINO N.A.C., PICCOLI G.C.O. ET AL. TERRESTRIAL SUPPORT OF AQUATIC FOOD WEBS DEPENDS ON LIGHT INPUTS: A GEOGRAPHICALLY-REPLICATED TEST USING TANK BROMELIADS. *ECOLOGY* 2016; 97(8):2147–56.
- SANTOS, B.G., FREY, G., FRIGERI, E. and GARCIA, S. 2011. Heterogeneidade espacial e riqueza de espécies em comunidades bromelícolas. *In* Livro do curso de campo “Ecologia da Mata Atlântica.” p. 4, G. Machado & P.I.K.L. Prado, Universidade Federal de São Paulo.
- ROCHA C. F. D. D., COGLIATTI-CARVALHO, L., DE ALMEIDA, FREITAS, A. F. N. D., ROCHA-PESSÔA, T.C., DIAS, A.S., ARIANI, C.V. and MORGADO, L.N. 2004. Conservando

uma larga porção da diversidade biológica através da conservação de Bromeliaceae.
Vidalia 2: 52–72.

ROCHA C. F. D. D., COGLIATTI-CARVALHO, L., DE ALMEIDA, D. R. and FREITAS, A. F. N.
D. 2000. Bromeliads: biodiversity amplifiers. *Jornal of the Bromeliad Society* 50:
81–83.

COGLIATTI-CARVALHO, L., FREITAS, A. F. N. D., ROCHA, C. F. D. D. and VAN SLUYS, M.
2001. Variation in structure and composition of Bromeliaceae at five zones of
“restinga” in Jurubatiba National Park, Macaé, RJ. *Brazilian Journal of Botany* 24:
01–09.

COGLIATTI-CARVALHO, L., T. C. ROCHA-PESSÔA, A. F. NUNES-FREITAS, and C. F. D.
ROCHA. 2010. Volume de água armazenado no tanque de bromélias, em restingas
da costa brasileira. *Acta Bot. Bras.* 24: 84–95.

FÁVERO, A., M. DO PRADO COSTA, M. FIGUEIRA, D. ANDRIOLLO, and S. LONGHI. 2015.
Distribuição de abundância de espécies da comunidade arbórea do topo de um
morro na floresta estacional subtropical. *Ciência Rural* 45: 806–813.

FLORAM - FUNDAÇÃO MUNICIPAL DO MEIO AMBIENTE. AVAILABLE AT:

[HTTP://WWW.PMF.SC.GOV.BR/ENTIDADES/FLORAM/](http://www.pmf.sc.gov.br/entidades/floram/) [ACCESSED JUNE 22, 2020].

FRANK, J. H., S. SREENIVASAN, P. J. BENSHOFF, M. A. DEYRUP, G. B. EDWARDS, S. E.

HALBERT, A. B. HAMON, M. D. LOWMAN, E. L. MOCKFORD, R. H. SCHEFFRAHN, G. J.

STECK, M. C. THOMAS, T. J. WALKER, AND W. C. WELBOURN. 2004. INVERTEBRATE

ANIMALS EXTRACTED FROM NATIVE TILLANDSIA (BROMELIALES: BROMELIACEAE) IN

SARASOTA COUNTY, FLORIDA. *FLORIDA ENTOMOLOGIST* 176–185.

GONÇALVES-SOUZA, T., SANTOS, A.J., ROMERO, G.Q. ET AL. 2015. CONSERVATION ALONG

A HOTSPOT RIM: SPIDERS IN BRAZILIAN COASTAL RESTINGAS. *BIODIVERS CONSERV*
24, 1131–1146

HAMADA, N., J. H. THORP, and D. C. ROGERS. 2018. Thorp and covich's freshwater
invertebrates: keys to Neotropical hexapoda. 4th ed. ELSEVIER ACADEMIC
Press.

HE, F., and D. TANG. 2008. Estimating the niche preemption parameter of the geometric
series. *Acta Oecologica* 33: 105–107.

HEINO, J., A. S. MELO, T. SIQUEIRA, J. SOININEN, S. VALANKO, and L. M. BINI. 2015.
Metacommunity organisation, spatial extent and dispersal in aquatic systems:
patterns, processes and prospects. *Freshwater Biology* 60: 845–869.

HUBBELL, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*
(MPB-32). Princeton University Press.

JABIOL, J., B. CORBARA, A. DEJEAN, and R. CÉRÉGHINO. 2009. Structure of aquatic insect
communities in tank-bromeliads in a East-Amazonian rainforest in French Guiana.
Forest Ecology and Management 257: 351–360.

JOCQUE, M., and R. FIELD. 2014. Aquatic invertebrate communities in tank bromeliads:
how well do classic ecological patterns apply? *Hydrobiologia* 730: 153–166.

KRATINA P, PETERMANN JS, MARINO NAC, MACDONALD AAM, SRIVASTAVA DS.
ENVIRONMENTAL CONTROL OF THE
MICROFAUNAL COMMUNITY STRUCTURE IN TROPICAL BROMELIADS. *ECOLOGY AND*
EVOLUTION 2017; 7(5):1627–34.

KITCHING, R. L. 2000. *Food Webs and Container Habitats: The Natural History and*
Ecology of Phytotelmata. Cambridge University Press, Cambridge.

- LEIBOLD, M. A., M. HOLYOAK, N. MOUQUET, P. AMARASEKARE, J. M. CHASE, M. F. HOOPES, R. D. HOLT, J. B. SHURIN, R. LAW, D. TILMAN, M. LOREAU, and A. GONZALEZ. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7: 601–613.
- LICHSTEIN, J. W. 2007. Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecol* 188: 117–131.
- Ligeiro, R., Melo, A.S., Callisto, M., 2010. Spatial scale and the diversity of Macroinvertebrates in a Neotropical catchment. *Freshw. Biol.* 55, 424–435.
- LOPEZ, L. C. S., and R. I. RIOS. 2001. Phytotelmata Faunal Communities in Sun-Exposed Versus Shaded Terrestrial Bromeliads from Southeastern Brazil. *Selbyana* 22: 219–224.
- LOPEZ, L.C.S., MADEIRA, J.A, RIBEIRO, K.T., and RIOS, R.I. 1995. Comunidades associadas aos tanques de duas bromélias de restinga da barra de maricá e seus processos de recolonização. *Bromélia* V.2: 18–31.
- MACDONALD, A. A. M. 2016. Abiotic and biotic factors creating variation among bromeliad communities. University of British Columbia. Available at: <https://open.library.ubc.ca/cIRcle/collections/ubctheses/24/items/1.0308741> [Accessed June 22, 2020].
- MAGURRAN, A. E. 1988. *Ecological Diversity and Its Measurement*. Princeton University Press.
- MAGURRAN, A. E. 2013. *Measuring Biological Diversity*. John Wiley & Sons.
- MAGURRAN, A. E., and B. J. MCGILL eds. 2011. *Biological diversity: frontiers in measurement and assessment*. Oxford University Press, Oxford ; New York.

- MALFATTI, E. 2019. VARIACÃO ALTITUDINAL DA COMUNIDADE DE INVERTEBRADOS. 54.
- MCGILL, B. J., R. S. ETIENNE, J. S. GRAY, D. ALONSO, M. J. ANDERSON, H. K. BENECHA, M. DORNELAS, B. J. ENQUIST, J. L. GREEN, F. HE, A. H. HURLBERT, A. E. MAGURRAN, P. A. MARQUET, B. A. MAURER, A. OSTLING, C. U. SOYKAN, K. I. UGLAND, AND E. P. WHITE. 2007. SPECIES ABUNDANCE DISTRIBUTIONS: MOVING BEYOND SINGLE PREDICTION THEORIES TO INTEGRATION WITHIN AN ECOLOGICAL FRAMEWORK. *ECOL LETTERS* 10: 995–1015.
- MIGLIORINI, G. H., D. S. SRIVASTAVA, and G. Q. ROMERO. 2018. Leaf litter traits drive community structure and functioning in a natural aquatic microcosm. *Freshwater Biology* 63: 341–352.
- MORALES, C. O., and J. MONGE NÁJERA. 2013. Centenario de la publicación de “*Las bromeliáceas epífitas consideradas como medio biológico*” (1913) Clodomiro Picado Twight, pionero de la ecología de las bromeliáceas. RBT 61. Available at: <http://revistas.ucr.ac.cr/index.php/rbt/article/view/12787> [Accessed June 22, 2020].
- ODUM, E. P., and C. J. TRIBE. 1986. *Ecologia*. Guanabara, Rio de Janeiro.
- OLIVEIRA, N. D., C. FREDERICO, and D. ROCHA. The animal community associated with the tank bromeliad *Neoregelia cruenta* (R. Graham) L. R. Smith. 10.
- OKSANEN, J., F. G. BLANCHET, R. KINDT, and P. R. MINCHIN. 2018. *veganCommunityEcologyPackageversion2.5-3October2018.pdf*.
- PERES-NETO, P. R., P. LEGENDRE, S. DRAY, and D. BORCARD. 2006. Variation Partitioning Of Species Data Matrices: Estimation And Comparison Of Fractions. *Ecology* 87: 2614–2625.

- RAIMUNDO P.B. HENRIQUES, M.L.MEIRELLES, and JOHN D. HAY. 1984. Ordenação e distribuição de espécies das comunidades vegetais na praia da restinga de Barra de Maricá, Rio de Janeiro.
- RICHARDSON, B. A. 1999. The Bromeliad Microcosm and the Assessment of Faunal Diversity in a Neotropical Forest1. *Biotropica* 31: 321–336.
- RICKLEFS, R. E., and D. SCHLUTER eds. 1993. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago.
- MONTEZUMA, R.C.M. and ARAUJO, D.S.D. 2007. Estrutura da vegetação de uma restinga arbustiva inundável no parque nacional da restinga de jurubatiba, rio de janeiro.
- RULL, V. 2011. NEOTROPICAL BIODIVERSITY: TIMING AND POTENTIAL DRIVERS. *TRENDS IN ECOLOGY & EVOLUTION*, 26(10), 508-513
- SANTOS, B.G.; G. FREI, E. FRIGERI & S. GARCIA. 2011. HETEROGENEIDADE ESPACIAL E RIQUEZA DE ESPÉCIES EM COMUNIDADES BROMELÍCULAS. EM: LIVRO DO CURSO DE CAMPO “ECOLOGIA DA MATA ATLÂNTICA” (G. MACHADO & P.I.K.L. PRADO, EDS.). UNIVERSIDADE DE SÃO PAULO, SÃO PAULO.
- SIQUEIRA, T., L. M. BINI, F. O. ROQUE, S. R. M. COUCEIRO, S. TRIVINHO-STRIXINO, and K. COTTENIE. 2012. Common and rare species respond to similar niche processes in macroinvertebrate metacommunities. *Ecography* 35: 183–192.
- SRIVASTAVA, D. ET AL. ECOLOGICAL RESPONSE TO ALTERED RAINFALL DIFFERS ACROSS THE NEOTROPICS. *ECOLOGY*
- SHMIDA, A., and M. V. WILSON. 1985. Biological Determinants of Species Diversity. *Journal of Biogeography* 12: 1.

TOWNSEND, C.R.; BEGON, M. & HARPER, J.L. 2010. FUNDAMENTALS IN ECOLOGY. 3. ED.

PORTO ALEGRE: ARTMED, 576P

USGS. EarthExplorer. Science for a Change World. Available at:

<https://earthexplorer.usgs.gov/> [Accessed June 23, 2020].

WARD, J. V. 1992. Aquatic insect ecology. Wiley, New York.

ZOTZ, G. 1999. How Much Water is in the Tank? Model Calculations for Two Epiphytic

Bromeliads. *Annals of Botany* 83: 183–192.

Considerações Finais

A área de estudo está localizada em um fragmento de restinga com uma cobertura vegetal capaz de alterar o local onde se encontram as diferentes espécies de bromélias, podendo também alterar a composição de macroinvertebrados aquáticos que habitam essas bromélias. Os componentes de heterogeneidade de habitat e peso (tamanho) das plantas não foram fatores determinantes para a riqueza e diversidade, ao contrário do esperado e previsto em literatura os ambientes com menor heterogeneidade espacial foram os que apresentaram maior riqueza.

O fato dessas bromélias não serem comunidades isoladas e sim comunidades onde ocorrem interações entre espécies e fluxo de migração, colonização e extinção nos mostra a importância de estudá-las para aprendemos sobre a dinâmica dos organismos que compõem a fauna local e a importância destes para a estrutura do ecossistema, podendo este ser um trabalho base para estudos de preservação em áreas de restinga.

Apesar do estudo mostrar alguns dos fatores capazes de estruturar as metacomunidades de bromélias, possivelmente existem outros fatores responsáveis por essa estruturação que não foram analisados nesse estudo, deixando para estudos posteriores uma proposta de análises mais aprofundadas que abranja outros fatores bióticos e abióticos locais, como a composição do solo, decomposição do material orgânico dentro das bromélias, influencia da salinidade nas áreas próximas a praia e rede de interação da comunidade.

Informações Suplementares

SI 1. Tabela 1. Variáveis explanatórias avaliadas nas comunidades de bromélias.

Distance	ID_point	collection_mode	NDVI	mean_shading	sd_shading	Weight_kg	Bromeliad_specie
0	1	ND	0.393484	98692	73612	0.35	Aechmea_nudicaulis
0	1	D	0.393484	98692	73612	0.34	Aechmea_nudicaulis
0	1	D	0.393484	98692	73612	0.35	Aechmea_nudicaulis
0	1	ND	0.393484	98692	73612	0.5	Aechmea_nudicaulis
0	1	D	0.393484	98692	73612	0.45	Aechmea_nudicaulis
0	1	ND	0.393484	98692	73612	0.28	Aechmea_nudicaulis
0	1	D	0.393484	98692	73612	0.23	Aechmea_nudicaulis
0	1	ND	0.393484	98692	73612	0.21	Aechmea_nudicaulis
54	2	ND	0.256637	100510	76092	1.2	Aechmea_nudicaulis
54	2	D	0.256637	100510	76092	1.2	Aechmea_nudicaulis
54	2	ND	0.256637	100510	76092	0.79	Aechmea_nudicaulis
54	2	D	0.256637	100510	76092	1.6	Aechmea_nudicaulis
54	2	ND	0.256637	100510	76092	0.56	Aechmea_nudicaulis
108	3	ND	0.262639	105585	67763	0.68	Aechmea_nudicaulis
108	3	D	0.262639	105585	67763	1.43	Aechmea_nudicaulis
108	3	ND	0.262639	105585	67763	1.57	Aechmea_nudicaulis
108	3	ND	0.262639	105585	67763	0.78	Aechmea_nudicaulis
108	3	D	0.262639	105585	67763	1.45	Aechmea_nudicaulis
162	4	ND	0.002141	131350	38100	1.8	Vriesea_friburgensis
162	4	D	0.002141	131350	38100	1.28	Vriesea_friburgensis
162	4	D	0.002141	131350	38100	0.8	Vriesea_friburgensis
162	4	ND	0.002141	131350	38100	1.1	Vriesea_friburgensis
162	4	ND	0.002141	131350	38100	1.4	Vriesea_friburgensis
162	4	D	0.002141	131350	38100	0.8	Vriesea_friburgensis

216	5	D	0.255847	105709	47066	2.0	<i>Vriesea_friburgensis</i>
216	5	ND	0.255847	105709	47066	1.2	<i>Vriesea_friburgensis</i>
216	5	ND	0.255847	105709	47066	0.9	<i>Vriesea_friburgensis</i>
216	5	D	0.255847	105709	47066	0.45	<i>Vriesea_friburgensis</i>
216	5	D	0.255847	105709	47066	0.8	<i>Vriesea_friburgensis</i>
216	5	ND	0.255847	105709	47066	0.78	<i>Vriesea_friburgensis</i>
216	5	D	0.255847	105709	47066	0.95	<i>Vriesea_friburgensis</i>
270	6	ND	0.337638	115893	66472	0.56	<i>Aechmea_nudicaulis</i>
270	6	D	0.337638	115893	66472	0.34	<i>Aechmea_nudicaulis</i>
270	6	D	0.337638	115893	66472	0.49	<i>Aechmea_nudicaulis</i>
270	6	ND	0.337638	115893	66472	0.58	<i>Aechmea_nudicaulis</i>
270	6	ND	0.337638	115893	66472	0.79	<i>Aechmea_nudicaulis</i>

SI 2. Tabela 2. Numero de indivíduos amostrados em duas especies de bromélias.

Species plant	<i>Camponotus novogranade nsis</i>	<i>Linepithe ma iniquum</i>	<i>Nylanderia docilis</i>	Tinanoac ea immatur e	Diptera_ sp immatur e	Scirtida e immatu re	Collembol a sp	Lepidopt era sp1	Blattaria	Polyzonii da sp
<i>Aechmea</i>										
<i>nudicaulis</i>	13	63	13	17	20	84	248	29	41	12
<i>Vriesea</i>										
<i>friburgensis</i>	45	30	2	5	0	11	96	1	22	1
Species plant	<i>Eurydice pulchra</i>	Tabenida e	Ceratopogoni dae	<i>Argia</i> sp.	Annelid a	Simulid ae pulpa	Chironomi dae	Cuculidae	<i>Scinax catharinae</i> tadpole	Psychodi dae
<i>Aechmea</i>										
<i>nudicaulis</i>	21	14	18	26	92	25	13	6	20	11
<i>Vriesea</i>										
<i>friburgensis</i>	3	3	3	16	15	15	10	7	0	5

SI 3. Tabela 3. AIC dos moldelos estatísticos adaptados as bromélias no sul do Brazil.

Ranking	Part1	Part2	Part3	Standard	AIC	BIC
<i>Vriesea</i>				Standard deviations		
Null model				103.6129	203.6037	203.6037
Pre-emption model	0.10996			50.3854	152.3762	153.3719
Lognormal	3.1319	0.66171		21.0391	125.0299	127.0213
Zipf	0.1819	-0.69685		1.9748	105.9656	110.9528
Mandelbrot	0.1819	-0.69685	1.3351e-06	1.9748	107.9656	110.9528
Ranking	Part1	Part2	Part3	Standard	AIC	BIC
<i>Aechmea</i>				Standard deviations		
Null model				278.011	392.320	392.320
Pre-emption model	0.11006			170.178	286.488	287.483
Lognormal	3.8553	0.678		88.628	206.937	208.929
Zipf	0.19086	-0.72823		19.594	137.903	139.895
Mandelbrot	0.19086	-0.72823	3.2306e-07	19.594	139.903	142.890