UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
INSTITUTO DE BIOCIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA
ÊNFASE EM ECOLOGIA VEGETAL

Alessandro Abreu Fávero

ECOLOGIA DE COMUNIDADES DE BROMELIACEAE AO LONGO DE UM GRADIENTE DE CONTINENTALIDADE NO SUL DO BRASIL

Porto Alegre

2020

Alessandro Abreu Fávero

ECOLOGIA DE COMUNIDADES DE BROMELIACEAE AO LONGO DE UM GRADIENTE DE CONTINENTALIDADE NO SUL DO BRASIL

Tese apresentada como requisito parcial para obtenção do título de Doutor em Botânica com ênfase em Ecologia Vegetal na Universidade Federal do Rio Grande do Sul.

Orientador: Dr. Prof. Jorge Luiz Waechter

Porto Alegre
2020

Alessandro Abreu Fávero

ECOLOGIA DE COMUNIDADES DE BROMELIACEAE AO LONGO DE UM GRADIENTE DE CONTINENTALIDADE NO SUL DO BRASIL

Orientador: Dr. Prof. Jorge Luiz Waechter

Comissão Examinadora:
Prof. Dr. Luiz Menini Neto - Departamento de Ecologia, UFJF
Prof^{a}. Dr^{a}. Sandra Cristina Müller - Departamento de Ecologia, UFRGS
Prof. Dr. João André Jarenkow - Departamento de Botânica, UFRGS

Porto Alegre
2020

“We live in a nonrandom world. From the elements of the universe and the basic laws of physics emergent order has arisen. One manifestation of this nonrandomness is in the dauntingly complex ecological communities that blanket Earth.”

(Cadotte & Davies 2016, 41)

DEDICATÓRIA

Dedico esta Tese de Doutorado ao meu filho **Johann N. Fávero** que é uma fonte das minhas motivações e inspirações.

AGRADECIMENTOS

Como não conseguimos nada sozinhos nessa vida, expresso os meus sinceros agradecimentos:

ao meu querido orientador, Dr. Prof. Jorge Luiz Waechter, que possibilitou a realização deste trabalho; por ter compartilhado o seu conhecimento, entusiasmo, amizade e sinceridade; por sua dedicação ao meu aprendizado em todas as etapas do doutorado.

ao grande time do Laboratório de Fitoecologia e Fitogeografia do Instituto de Biociências - UFRGS, pela receptividade e pelas apresentações e discussões sobre as teorias ecológicas realizadas nos colóquios. Também pelo aprendizado, conversas, trocas de experiências, confraternizações, confissões, desabafos e ótimos momentos de descontração que compartilhamos.

à Universidade Federal do Rio Grande do Sul (UFRGS) por toda a infraestrutura.

ao Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) pelo apoio financeiro que permitiu a minha dedicação integral à pesquisa e suporte para a coleta de dados em expedições botânicas.

ao Instituto de Biociências - UFRGS por toda a infraestrutura e transporte para coleta de dados.

aos Programas de Pós-Graduação em Botânica e Pós-Graduação em Ecologia do Instituto de Biociências - UFRGS por todo o suporte de ensino-aprendizagem.

ao meu amigo Henrique Mallmann Büneker por ter compartilhado o seu conhecimento e entusiasmo sobre a família Bromeliaceae.

aos colegas que tive a oportunidade de conviver nas expedições botânicas: Anderson Mello (Japa), Angelo Augustinho Massing, Fernanda Silveira, Jonas Castro, Monica Buchs, Matias Kohler e Carlos Eduardo Velho Carvalho (Carlito).

à minha família, por me lembrar que “tudo na vida que tem valor inestimável envolve sacrifícios”; e que “a natureza não dá saltos”. Agradeço também a minha companheira e amada Anelise Marta Siegloch, por ter me apoiado e me fortalecido nos momentos difíceis. Aos meus filhos gatos - Ludwig (cucuíca) e Lola (lolídia) pelo amor incondicional, aconchego, brincadeiras e ronronar relaxante.

RESUMO

Gradientes ambientais estabelecem cenários ecológicos excepcionais para analisar os padrões e processos que determinam a estrutura de comunidades ecológicas. A compreensão da estrutura de comunidades ecológicas ao longo de um amplo escopo de gradientes ambientais requer pesquisas com enfoque em diferentes escalas espaciais (regional e local), incluindo aspectos taxonômicos, funcionais e filogenéticos. A busca por teorias que expliquem as causas da organização da estrutura de comunidades ecológicas tem impulsionado o surgimento de abordagens promissoras, como o arcabouço teórico de metacomunidade e de montagem de comunidades ecológicas. Considerando este contexto, a família Bromeliaceae constituí um sistema ecológico extraordinário para a compreensão de padrões e processos que determinam a estrutura de comunidades ecológicas, em razão das importantes funções e interações ecológicas que desempenham; e por se destacar na diversidade taxonômica, funcional e filogenética da vegetação neotropical (florestas e campos rupestres). Nesta tese, investigamos os determinantes que estabelecem a estrutura de comunidades ecológicas de Bromeliaceae ao longo de um gradiente de continentalidade, tendo por base uma sequência de 71 morros testemunhos distribuídos em um corredor geográfico subtropical, que se estende do Litoral Atlântico até as proximidades do Rio Uruguai, na porção central do Estado do Rio Grande do Sul, no sul do Brasil. No primeiro manuscrito, investigamos os padrões e processos metacomunitários de bromélias epifíticas. Demostramos que as comunidades de bromélias epifíticas estão ligadas a um padrão orientado por um gradiente Clementsiano de baixa rotatividade (turnover), constituído de quatro compartimentos metacomunitários. Além disso, evidenciamos que o arquétipo alocação de espécies (species sorting) melhor representou os processos de estabelecimento da estrutura metacomunitária. No segundo manuscrito, examinamos a estrutura funcional e filogenética das comunidades ecológicas de Bromeliaceae. Verificamos que as linhagens de Bromeliaceae manifestaram conservadorismo de nicho filogenético tropical ocupando ou rastreando nichos ancestrais. Além disso, descobrimos que a hipótese de dominância de estresse (SDH) gerou diferentes respostas nas estruturas funcional e filogenética. No entanto, evidenciamos que a montagem de comunidade foi predominantemente aleatória em relação ao pool de espécies. Concluímos que fatores ambientais (temperatura e umidade), espaciais (dispersão e conectividade) e estocásticos, assim como as formas de vida das Bromeliaceae, determinam o estabelecimento de diferentes estruturas taxonômicas, funcionais e filogenéticas das comunidades ecológicas, dando origem a um complexo biogeográfico constituído por diferentes compartimentos metacomunitários com dinâmicas estruturantes distintas.

PALAVRAS-CHAVE: Bromeliaceae, ecologia de metacomunidade, ecologia filogenética de comunidades, ecologia funcional de comunidades, gradiente litoral-interior.

ABSTRACT

Environmental gradients establish exceptional ecological scenarios to analyze the patterns and processes that determine the structure of ecological communities. Understanding the structure of ecological communities along a broad scope of environmental gradients requires research focusing on different spatial scales (regional and local), including taxonomic, functional, and phylogenetic aspects. The search for theories explaining the causes of the organisation of ecological community structure has driven the emergence of promising approaches, such as the theoretical framework of metacommunity and ecological community assembly. Considering this context, the Bromeliaceae family constitutes a unique ecological system for the understanding of patterns and processes that determine the structure of ecological communities; due to the functions and ecological interactions they perform and for standing out in the taxonomic, functional, and phylogenetic diversity in the Neotropical vegetation (forests and rupestrian grasslands). In this thesis, we investigated the determinants that establish the structure of ecological communities of Bromeliaceae along a continental gradient, based on a sequence of 71 testimonial hills distributed in a subtropical geographic corridor, which extends from the Atlantic Coast to the proximities of the Uruguay River, in the central portion of the State of Rio Grande do Sul, in southernmost Brazil. In the first manuscript, we investigated the patterns and metacommunity processes of epiphytic bromeliads. We demonstrated that epiphytic bromeliad communities are linked to a Clementsian pattern-oriented by the low turnover gradient, composed of four metacommunity compartments. Moreover, we evidenced that the species sorting archetype best represented the processes of establishing metacommunity structure. In the second manuscript, we examined the functional and phylogenetic structure of the ecological communities of Bromeliaceae. We verified that Bromeliaceae lineages manifested tropical phylogenetic niche conservatism occupying or tracking ancestral niches. Also, we found that the stress-dominance hypothesis (SDH) generated different functional and phylogenetic structure responses. However, community assembly was predominantly random concerning the species pool. We conclude that environmental (temperature and moisture), spatial (dispersal and connectivity), and stochastic factors, as well as the life forms of the Bromeliaceae, determine the establishment of different taxonomic, functional, and phylogenetic structures of the ecological communities, giving rise to a biogeographic complex constituted by four compartments of metacommunities with distinct structuring dynamics.

KEYWORDS: Bromeliaceae, coastal-inland gradient, functional community structure, ecological metacommunity structure, phylogenetic community structure

Sumário

LISTA DE FIGURAS

CHAPTER I

CHAPTER II

LISTA DE TABELAS

CHAPTER I

CHAPTER II

INTRODUÇÃO GERAL

A ecologia de comunidades estuda as espécies co-ocorrentes que potencialmente interagem umas com as outras e com ambiente abiótico de modo que estabelecem padrões de composição de espécies e de diversidade taxonômica, funcional e filogenética em um determinado local ou área (Webb et al. 2002, Cavender-Bares et al. 2009, Leibold & Chase 2018). Os ecólogos de comunidades buscam entender os padrões de diversidade e porque certas espécies coexistem, enquanto outras são incapazes de persistir juntas (Cadotte & Davies 2016). Inúmeros mecanismos ecológicos estão envolvidos para explicar esses padrões; estes dependem de limitações impostas pelo ambiente abiótico bem como limitações bióticas, onde as espécies excluem outras por causa de interações exploradoras ou competitivas, ou onde algumas espécies oferecem oportunidades adicionais para outras como resultado de interações benéficas (Cadotte & Davies 2016).

A compreensão da organização da estrutura de comunidades ecológicas requer pesquisas com enfoque nos padrões e processos ecológicos e evolutivos em diferentes escalas espaciais (e temporais) e que correlacione estas escalas (regional e local) com os aspectos taxonômicos, funcionais e filogenéticos (Webb et al. 2002, Cavender-Bares et al. 2009, Leibold & Chase 2018). Diante destas circunstâncias, a busca por teorias gerais que expliquem as causas da organização da estruture de comunidades ecológicas tem impulsionado o surgimento de algumas abordagens promissoras, como o arcabouço teórico de metacomunidade (Leibold et al. 2004, Holyoak et al. 2005, Leibold & Chase 2018), teoria de montagem de comunidade e a teoria de coexistência de espécies (Webb et al. 2002, Mayfield & Levine 2010, HilleRisLamber et al. 2012, Swenson 2019).

A teoria de metacomunidade busca explicar como os processos determinísticos e estocásticos que atuam em diferentes escalas espaciais (regional e local) interagem para estabelecer a distribuição e ocorrência das espécies em uma localidade (Leibold & Chase 2018). Leibold et al. (2004), definiram metacomunidade como "um conjunto de comunidades locais ligadas por dispersão de múltiplas espécies potencialmente interativas". No entanto, em razão das implicações que decorrem de três fatores fundamentais da estrutura de metacomunidade (escala espacial, heterogeneidade ambiental e dispersão de espécies), além dos aspectos taxonômicos, funcionais e filogenéticos, tornou-se mais adequado definir a ecologia de metacomunidade como um arcabouço teórico para o entendimento de padrões e processos subjacentes a organização da estrutura de comunidades ecológicas (Leibold & Chase 2018).

No tocante a teoria de montagem de comunidade ecológica, Webb et al. (2002) propuseram um modelo capaz de apontar os efeitos de filtragem abiótica e exclusão competitiva na organização da estrutura de comunidades ecológicas. Esse modelo preconiza analisar o padrão filogenético agrupado, no qual são selecionados táxons próximos filogeneticamente devido o processo de filtragem abiótica; o padrão filogenético sobredisperso, no qual táxons próximos são eliminados devido o processo de exclusão competitiva; ou o padrão filogenético aleatório, no qual ocorre a aleatoriedade na distribuição dos atributos funcionais ou interações neutras entre espécies. Segundo Mayfield & Levine (2010), a teoria de coexistência de espécies destaca que quando ocorrem diferenças nas habilidades de competição e o conservantismo filogenético nos atributos funcionais, a competição pode excluir espécies que são funcionalmente e filogeneticamente distantes levando ao padrão filogenético agrupado. Porém, nesta abordagem em estudos observacionais de comunidades ecológicas é mais laborioso diferenciar os efeitos dos processos de filtragem abiótica e exclusão competitiva.

Diante deste cenário, a família Bromeliaceae possui diversas peculiaridades ecológicas extraordinárias para investigar padrões e processos de organização da estrutura de comunidades ecológicas, em razão das importantes funções ecológicas que desempenham nos ecossistemas neotropicais; essas plantas participam nos processos de manutenção, produtividade, ciclagem de nutrientes e na capacidade de resiliência (Lugo & Scatena 1992, Oliveira 2004). Bromeliaceae compreende uma das famílias botânicas mais importantes das florestas tropicais e subtropicais nas Américas, contribuindo notavelmente para a composição de espécies e para a diversidade taxonômica, funcional e filogenética das comunidades ecológicas em que vivem (Givnish et al. 2011, 2014, Martins & Wanderley 2017). Além disso, as espécies de Bromeliaceae são reconhecidas por uma variedade de tipos de interações ecológicas e coevolutivas com um grande contingente de espécies da flora e da fauna (Filho & Machado 2006, Givnish et al. 2011, Dias et al. 2014).

Segundo Simth & Downs (1974), a família Bromeliaceae apresenta diversos atributos funcionais vegetativos que conferem diferentes formas de ocupação do substrato (epífitas, rupícolas, saxícolas e terrícolas) e formas de absorção de umidade e nutrientes (bromélias atmosférica e bromélias-tanque). Alternativamente, alguns pesquisadores (Benzing 2000, Kessler 2012, Stevens 2013, Males 2016) agrupam as bromélias em cinco tipos, conforme o modo de crescimento, estratégia de absorção de água e via fotossintética C3 e CAM. **Tipo I** – Terrestres com sistema radicular absorvente bem desenvolvido, fotossíntese C3 ou CAM. **Tipo II** – Terrestres com tanques formando-se nas bases das folhas, raízes absorventes, tricomas absorventes na base das folhas, fotossíntese CAM. **Tipo III** – Terrestre, saxícolas ou epifítica com tanque central presente, escamas absorventes, folhas grossas, raízes para suporte, a maioria da fotossíntese CAM. **Tipo IV** – Principalmente epífitas com tanques, escamas absorventes na base da folha, folhas finas, raízes para suporte, fotossíntese C3. **Tipo V** – Epífitas (ou epilíticas), epífitas do ar ou atmosférica, escamas absorventes em toda a folha, folhas grossas, fotossíntese CAM, raízes para suporte ou nenhuma.

Bromélias epifíticas (e epilíticas ou rupícolas) desenvolveram adaptações as condições extremas em consequência da heterogeneidade de habitat relacionada a disponibilidade de água e nutrientes. A ausência de raízes no solo tornou essas plantas dependentes da chuva, orvalho e nevoeiro para adquirir água e nutrientes e altamente sensíveis à umidade do ar, a fim de manter o equilíbrio osmótico (Benzing 1980, 2000). Bromélias desenvolveram adaptações como as folhas dispostas em rosetas formando uma cisterna para acumular água e nutrientes, tricomas peltados ou lanosos especializados na absorção de água e nutrientes e na reflexão da radiação solar e o metabolismo ácido crassuláceo (fotossíntese CAM) que consiste na via metabólica para síntese de carboidratos, uma adaptação as condições áridas com a abertura dos estômatos durante a noite, minimizando a perda de água. Em razão dessas características, essas plantas foram classificadas em duas principais formas de vida (Benzing 1980): bromélia atmosférica com folhas triangulares e estreitas, densamente cobertas por tricomas; bromélia-tanque com folhas longas e largas que formam um reservatório de água e nutrientes (fitotelmo) no centro da roseta.

Os padrões de distribuição de Bromeliaceae, refletem os efeitos de gradientes latitudinal, continental e altitudinal (Reitz 1983, Benzing 2000, Martinelli et al. 2008, Fontoura et al. 2012, Kessler 2012, Cach-Pérez et al. 2013), os quais são associados aos fatores climáticos, principalmente a chuva e temperatura. No Brasil, Rio de Janeiro possui maior diversidade de Bromeliaceae; no sentido norte, a partir do Espírito Santo decresce a riqueza de espécies devido, principalmente, à escassez de chuvas (Martinelli et al. 2008), em Minas Gerais as chuvas influenciam a distribuição das espécies (Versieux & Wendt 2007); no sentido sul, a partir de São Paulo decresce a riqueza de espécies devido, principalmente, à temperatura (Martinelli et al. 2008), em Santa Catarina além do gradiente latitudinal se observa a redução da riqueza de espécies no sentido de leste para oeste devido os efeitos do planalto e do gradiente de continentalidade que reduzem ainda mais a temperatura e umidade do ar, respectivamente; neste Estado muitos gêneros e espécies de Bromeliaceae encontram o limite austral de distribuição geográfica (Reitz 1983).

No Rio Grande do Sul, as comunidades ecológicas de Bromeliaceae refletem a influência de elementos florísticos das rotas de migração Atlântica, Chaquenha e Andina (Winkler 1980, 1982), bem como de endemismos nos gêneros *Tillandsia* e *Dyckia*. A partir de um centro regional de maior diversidade, nas encostas do Planalto Meridional (Serra Geral) e na Planície Costeira do extremo nordeste do Estado (Rambo 1961), ocorre uma diluição gradual de bromélias tropicais, em especial as bromélias-tanque (Waechter 1992, 2007). Por outro lado, nas regiões oeste e sul do Estado, nas províncias Pampeana e Chaquenha, há registros de um número relativamente menor de espécies (Winkler 1982, Büneker et al. 2016). Nestas províncias através da floresta subtropical dos Rios Paraná-Uruguai ocorre a dispersão de elementos florísticos (Rambo 1961), especialmente do gênero *Tillandsia* (bromélias-atmosférica), oriundos das florestas do Chaco e das montanhas dos Andes (Winkler 1982).

No centro do Rio Grande do Sul, encontramos uma sequência de morros testemunhos (por exemplo, morros isolados ou residuais, morretes e inselbergs) com diferentes geomorfologias e origens geológicas, situados ao longo de um corredor geográfico subtropical de terras de baixa altitude, que se estende do Litoral Atlântico até as proximidades do Rio Uruguai, em torno do paralelo 30º S. Esses morros testemunhos oportunizam condições propícias para investigar os efeitos da continentalidade nos processos de filtragens abióticas e interações bióticas, os quais estabelecem a estrutura de comunidades ecológicas de Bromeliaceae.

Esta tese teve o objetivo de pesquisar a estrutura metacomunitária (no primeiro manuscrito) e a estrutura funcional e filogenética (no segundo manuscrito) de comunidades ecológicas de Bromeliaceae ao longo de um gradiente de continentalidade, tendo por base uma sequência de 71 morros testemunhos, que se estende do Litoral Atlântico até as proximidades do Rio Uruguai. A pesquisa se concentrou na composição de espécies, nos padrões e processos metacomunitários e na estrutura funcional e filogenética de comunidades ecológicas. Cada capítulo, corresponde a um manuscrito científico, formatados de acordo com as normas dos periódicos selecionados para a submissão.

O Manuscrito I "**Patterns and metacommunity processes of epiphytic bromeliad assemblages along a coastal-inland gradient in a subtropical Brazilian geographic corridor**" tem o objetivo de investigar os padrões e processos que determinam a estrutura metacomunitária de bromélias epifíticas ao longo de um gradiente de continentalidade, no centro do Rio Grande do Sul, no sul do Brasil. Este manuscrito foi submetido a revista Austral Ecology.

O Manuscrito II "**Functional and phylogenetic structure of Bromeliaceae assemblages under stress-dominance hypothesis along a coastal–inland gradient in a subtropical Brazilian region**" tem o objetivo de pesquisar os fatores e os processos que estabelecem a estrutura funcional e filogenética de comunidades ecológicas de Bromeliaceae ao longo de um gradiente de continentalidade, no centro do Rio Grande do Sul, no sul do Brasil. Este manuscrito foi submetido a revista Flora.

REFERÊNCIAS

Benzing DH. 1980. *The Biology of Bromeliads*. Eureka, CA, Mad River Press.

Benzing DH. 2000. *Bromeliaceae*: *Profile of an adaptive radiation*. Cambridge University Press, New York.

Büneker HM, Witeck L. 2016. Levantamento de Bromeliaceae na região do curso médio do rio Toropi, Rio Grande do Sul, Brasil. Balduinia, 52:01-14.

Cach-Pérez MJ, Andrade JL, Chilpa-Galván, Tamayo-Chim M, Orellana R, Reyes-García C. 2013. Climatic and structural factors influencing epiphytic bromeliad Community assemblages along a gradient of water-limited environments int the Yucatan Peninsula, Mexico. Tropical Conservation Science, 6(1):283-302.

Cadotte MW, Davies TJ. 2016. *Phylogenies in Ecology: A guide to concepts and methods*. Princeton University Press, Princeton, New Jersey

Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW. 2009. The merging of community ecology and phylogenetic biology. Ecology Letters, 12:693-715.

Dias ML, Prezoto F, Abreu PF, Neto LM. 2014. Bromélias e suas principais interações com a fauna. CES Revista, Juiz de Fora, 28(1):3-16.

Filho JAS, Machado IC. 2006. *Floração e polinização das bromélias da Mata Atlântica nordestina*. In: Filho JAS, Leme EM (Eds.) *Fragmentos de Mata Atlântica do Nordeste: Biodiversidade, conservação e suas bromélias*. Andrea Jakobsson Estúdio, Rio de Janeiro.

Fontoura T, Scudeller VV, Costa AF. 2012. Floristics and environmental factors determining the geographic distribution of epiphytic bromeliads in the Brazilian Atlantic Rain Forest. Flora, 207:662-672.

Givnish TJ, Barfuss MHJ, van Ee B, Riina R, Schulte K, Horres R, Gonsiska PA, Jabaily RS, Crayn DM, Smith JAC, Winter K, Brown GK, Evans TM, Holst BK, Luther H, Till W, Zizka, G, Berry PE, Sytsma KJ. 2011. Phylogeny, adaptative radiation, and historical biogeography in Bromeliaceae: insights from an eigth-locus plastid phylogeny. American Journal of Botany, 98(5):872-895.

Givnish TJ, Barfuss MHJ, b ,Van Ee B , Riina R, Schulte K, Horres R, Gonsiska PA, Jabaily RS, Crayn DM, Smith JAC , Winter K , Brown GK , Evans TM , Holst BK, Luther H, Till W , Zizka G , Berry PE , Sytsma KJ. 2014. Adaptive radiation, correlated and contingent evolution, and net species diversification in Bromeliaceae. Molecular Phylogenetics and Evolution, 71:55-78.

HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM. 2012. Rethinking community assembly through the lens of coexistence theory. Annu. Rev. Ecol. Evol. Syst., 43:227-2248.

Holyoak M, Leibold MA, Holt RD. 2005. *Metacommunities: Spatial dynamics and ecological communities*. University of Chicago Press.

Kessler M. 2012. Environmental patterns and ecological correlates of range size among bromeliad communities of Andean forests in Bolivia. The Botanical Review, 68(1):100-127.

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters, 7:601-613.

Leibold MA, Chase JM. 2018. *Metacommunity ecology*. Monographs in population biology 59. Princeton University Press, Princeton and Oxford.

Lugo AR, Scatena FN. 1992. Epiphytes and climate change research in the caribbean: a proposal. Selbyana, 13:123-130.

Males J. 2016. Think tank: water relations of Bromeliaceae in their evolutionary context. Botanical Journal of the Linnean Society, 181:415-440.

Martinelli G, Vieira CM, Gonzalez M, Leitman P, Piratininga A, Costa AF, Forzza RC. 2008. Bromeliaceae da mata Atlântica brasileira: lista de espécies, distribuição e conservação. Rodriguésia, 59(1): 209-258.

Martins SE, Wanderley MGL. 2017. *Diversidade das bromélias da Mata Atlântica*. Editora Neotropica, São Paulo.

Mayfield MM, Levine JM. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecology Letters, 13:1085-1093.

Oliveira RR. 2004. Importância das bromélias epífitas na ciclagem de nutrientes da Floresta Atlântica. Acta Bot. Bras, 18(4):793-799.

Rambo B. 1961. Migration routes of South Brazilian Rain Forest. Pesquisa, Botânica. São Leopoldo: Instituto Anchietano de Pesquisa, 12:1-54.

Reitz R. 1983. *Bromeliáceas e a malária–bromélia endêmica*. Flora Ilustrada Catarinense.

Smith LB, Downs RJ. 1974. *Pitcairnoideae (Bromeliaceae)*. Flora Neotropica, v. 14, n.1, Hafner Press, New York.

Stevens PF. 2013. Angiosperm phylogeny website. Version 13, septemper 28. University of Missiouri, St Louis, and Missouri Botanical Garden. http://www.mobot.org/MOBOT/research/APweb/. Acessado 01 de Julho 2020.

Swenson NG. 2019. *Phylogenetic ecology. A history, critique, and remodeling*. University of Chicago Press, Chicago and London.

Versieux LM, Wendt T. 2007. Bromeliaceae diversity and conservation in Minas Gerais state, Brazil. Biodiversity and Conservation, 16:2989-3009.

Waechter JL. 1992. O epifitismo vascular na planície costeira do Rio Grande do Sul. São Paulo, UFSCAR, Curso de Pós-Graduação em Ecologia e Recursos Naturais (tese de doutorado).

Waechter JL. 2007. *Distribuição de bromeliáceas epifíticas em florestas do Rio Grande do Sul*. In: Barbosa, LM; Santos Junior NA. (Orgs.) *A Botânica no Brasil: pesquisa, ensino e políticas públicas ambientais*. Sociedade Botânica do Brasil, São Paulo.

Webb CO, Ackerly MA, McPeek, Donoghue MJ. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics, 33:475-505.

Winkler S. 1980. Die Bromeliaceae von Rio Grande do Sul (S-Brasilien). Documenta Naturae, 3:1-90.

Winkler S. 1982. Ursachen der Verbreitungsmuster einiger Bromeliaceae in Rio Grande do Sul (Südbrasilien). Flora, 170:371-393.

CHAPTER I

Patterns and metacommunity processes of epiphytic bromeliad assemblages along a coastal-inland gradient in a subtropical Brazilian geographic corridor

“The major weakness of traditional community ecology, and why it has so conspicuously failed to come up with many patterns, rules and workable contingent theory, is its overwhelming emphasis on localness. “

(Lawton 1999)

Patterns and metacommunity processes of epiphytic bromeliad assemblages along a coastal-inland gradient in a subtropical Brazilian geographic corridor

Abstract Metacommunity ecology investigates how drivers of regional and local scales cause compositional variation in a network of communities potentially linked by dispersal. We examined the metacommunity structure of epiphytic bromeliad assemblages along a coastal-inland gradient in a subtropical geographic corridor extending from the Atlantic coast to near the Uruguay River, in the central depression of Rio Grande do Sul State, in southernmost Brazil. We surveyed floristic and environmental data on a sequence of 71 testimonial hills. We used elements of metacommunity structure to identify metacommunity patterns (i.e., random, checkerboard, nested, Clementsian, Gleasonian, evenly spaced, and quasi-structured). We ran a canonical correspondence analysis to evaluate how coastal-inland gradient influenced species distribution. Finally, we employed variation partitioning to determine archetype-based metacommunity structuring processes (i.e., species sorting, neutral dynamics, patch dynamics, and mass effects). We found that temperature- and moisture-based gradients generated environmental heterogeneity that established species filtering, determining the formation of cohesive groups of epiphytic bromeliads with coincidentally occurring boundaries (i.e., quasi-Clementsian structure). As a result, we identified four metacommunity structures embedded along the coastal-inland gradient: in the eastern and east-central metacommunities, species distributions were idiosyncratic due to individual species’ responses to environmental gradients (i.e., quasi-Gleasonian structure), and in the western and west-central metacommunities, we observed Clementsian and Gleasonian structures, respectively. Habitat heterogeneity and dispersal sufficiency (i.e., species sorting archetype) were the foremost drivers establishing metacommunity structures. Ultimately, and surprisingly, in the east-central metacommunity, we detected source-sink dynamics among the testimonial hills (i.e., mass effects archetype). Our findings suggest that epiphytic bromeliad assemblages are linked to a gradient-driven pattern with moderate heterogeneity (i.e., low turnover) and identify four embedded metacommunity structures. Moreover, they indicate that the species sorting archetype best represents the processes of establishing metacommunity structures.

Keywords atmospheric bromeliads, Clementsian gradient, Gleasonian gradient, species-sorting archetype, tank bromeliads

INTRODUCTION

The family Bromeliaceae A. Juss. is considered the most conspicuous member of neotropical vascular epiphytic flora (Madison 1977; Gentry & Dodson 1987; Benzing 1990; Zotz 2016). It exhibits high biological diversity and species are abundant in mid-elevations zones where high cloud concentration ensures high levels of air humidity (500–1000m, in Ecuador, Gentry & Dodson 1987; 500–2000m, in Mexico, Wolf & Flamenco-S 2003). In their geographical range, species abundance is intensely influenced by atmospheric water availability, as they lack access to soil water (Benzing 1990; Zotz & Hietz 2001; Zotz 2005; Laube & Zotz 2006; Zotz 2013; Mendieta-Leiva *et al.* 2020). Rainfall and tropical forests are the main drivers of latitudinal biodiversity. As a result, the epiphytic bromeliad species are most evident in the tropics, particularly in cloud forests, but can also be abundant in temperate, moist forests (Benzing 2000; Zotz 2013, 2016; Taylor *et al.* 2022).

Epiphytic bromeliad assemblages have been widely studied across broad scopes of ecological or geographical gradients (Martinelli *et al.* 2008; Fontoura *et al.* 2012; Basilio *et* *al.* 2013; Leitman *et al.* 2015; Taylor *et al.* 2021), expressly encompassing floristic inventories, diversity metrics (e.g., richness, abundance, diversity indices) and causal mechanisms regulating species distribution (e.g., latitudinal, continental, and altitudinal gradients). According to Burns & Zotz (2010), Bartels & Chen (2012), Mendieta-Leiva & Zotz (2015), and Zotz (2016), to understand the ecological patterns and processes that determine the structure of vascular epiphyte assemblages, it is of fundamental importance to conduct analytical, rather than solely descriptive, studies. Therefore, to disentangle how ecological factors and processes determine or control the structure of vascular epiphyte assemblages, we require analytical studies that postulate a rigorous theoretical framework, such as the theories of community ecology (Burns & Zotz 2010; Mendieta-Leiva & Zotz 2015; Zotz 2016).

A better understanding of the ecological patterns and processes that determine the organisation of vascular epiphyte assemblages along a broad scope of environmental gradients depends, fundamentally, on a theoretical framework that simultaneously considers regional and local spatial scales (Burns & Zotz 2010; Mendieta-Leiva & Zotz 2015). Thus, in this context, we believe that the theoretical framework of metacommunity ecology can be a powerful tool to underpin our understanding of the ecological patterns and processes that establish epiphytic bromeliad assemblages across a broad scope of a coastal-inland gradient. This can highlight patterns and provide a nexus of various regional and local ecological processes and can help to determine the roles of niche- and dispersal-based species dynamics (Leibold & Chase 2018).

Metacommunity ecology describes a regional network of local communities connected by different dispersal rates in an environment with considerable heterogeneity (Leibold *et al.* 2004; Holyoak *et al.* 2005; Leibold & Chase 2018). The cornerstone of metacommunity theory is the simultaneous consideration of multiple spatial scales, where the structure of local communities results from the interplay of stochastic and deterministic processes both locally and regionally (Brown *et al.* 2011; Logue *et al.* 2011; Heino *et al.* 2015). Notably, the metacommunity theoretical framework encompasses a set of regional-scale process theories that focus on environmental heterogeneity and dispersal rates, and a set of local-scale process theories that focus on resource use and response, and demographic stochasticity (Leibold & Chase 2018; Thompson *et al.* 2020).

This theoretical framework comprises two complementary approaches. The first seeks to identify hypothetical patterns of species distribution and different types of gradients in several idealised scenarios (Leibold & Mikkelson 2002; Presley *et al.* 2010). The includes random distribution (Hubbell 2001), checkerboard distribution (Diamond 1975), nested subset distribution (Patterson & Atmar 1986), evenly spaced gradient (Tilman 1982), Gleasonian gradient (Gleason 1926), and Clementsian gradient (Clements 1916). The second approach is supported by four theoretical frameworks, referred to as the metacommunity archetypes of species sorting, neutral dynamics, patch dynamics, and mass effects. These archetypes predict, in detail, a set of specific mechanistic processes that simultaneously control metacommunity assembly (Leibold *et al.* 2004; Leibold & Chase 2018). According to Logue *et al.* (2011), they result from the three-dimensional spatial overlap of habitat heterogeneity in terms of environmental and biotic features, dispersal rate, and equivalence between species in terms of niche and fitness. Thus, these archetypes function simultaneously and hierarchically (Leibold *et al.* 2004; Holyoak *et al.* 2005; Brown *et al.* 2017; Leibold & Chase 2018).

At the regional level, many studies agree that the topography of the neotropics provides favourable conditions for the diversity of vascular epiphytic flora (Gentry & Dodson 1987; Benzing 1990; Wolf & Flamenco-S 2003; Zotz 2005; Taylor *et al.* 2022). Mountainous environments have numerous microsites with different abiotic and biotic conditions, permitting a high diversity of vascular epiphytes due to niche partitioning (Gentry & Dodson 1987). Mountainous environments situated at mid-elevation are characteristically very moist. They consist of mist-filled valleys and intensely moist escarpments, providing favourable conditions for the establishment and growth of vascular epiphytes (Gentry & Dodson 1987; Benzing 1987, 1990). At the local level, the climatic conditions of forests vary from canopy to ground, giving rise to multiple environmental gradients that influence the structure of vascular epiphyte assemblages (Petter *et al.* 2016; Zotz 2016). Intrinsically, vascular epiphyte assemblages are influenced by two patterns of species distribution: vertical distribution, related to variations in light levels, moisture, and temperature from the canopy to the forest interior, and horizontal distribution, which is linked to differences in vegetation and the present species of phorophytes (Benzing 1990; Burns & Zotz 2010; Zotz 2016). Vascular epiphyte assemblages are strongly dependent on phorophyte growth and spatio-temporal variation of the related ecological niches in each phorophyte (Benzing 1990; Zotz & Vollrath 2003; Taylor & Burns 2015; Zotz 2016).

In Rio Grande do Sul, the southernmost subtropical State of Brazil, temperature and moisture gradients, as well as cold winter temperatures and sporadic frosts, influence the distribution of epiphytic bromeliads (Winkler 1980, 1982). Their distribution also responds to the topography, vegetation types, and migration routes of floristic elements from the tropical forest and Chacoan domain, as well as to historical biogeographic events (Rambo 1961; Winkler 1980). In the central portion of Rio Grande do Sul, the tank bromeliads *Aechmea*, *Billbergia*, *Edmundoa*, *Nidularium*, *Vriesea*, and *Wittrockia* occur mainly in the Atlantic Forest regions in the far east and, especially, the north of the coastal plain (Rambo 1950; Winkler 1980, 1982). The atmospheric bromeliads, such as *Tillandsia*, comprise two subgroups (Winkler 1980): *Tillandsia*-mesophytic, which are widely distributed and occur in moderately moist and warm environments, and *Tillandsia*-xerophytic, which are restricted to the far westernmost regions with xeric environments.

In the central portion of Rio Grande do Sul, there is an extensive low-lying region forming a depression that represents a subtropical coastal-inland corridor between the northern and southern highlands (*Serra Geral* and *Serra do Sudetes*, respectively). Along this corridor, numerous testimonial hills (i.e., residual hills or isolated hills) represent archipelago-like settings for the dispersal and colonization of epiphytic bromeliads. Unfortunately, most of the areas (forests and grasslands) around these testimonial hills are heavily affected by agriculture, timber plantations, and urbanisation. Accordingly, due to the relatively wide extension of the coastal-inland corridor and the distinctive local environments provided by each testimonial hill, we can assume that the bromeliad species undergo selective filtering, generating different ecological assemblages. Although local-scale drivers influencing the diversity and composition of bromeliad assemblages have been well studied, it remains unknown how these local drivers interact with the regional scale, determining metacommunity structure. We believe that, in this circumstance, along a coastal-inland gradient, the interrelationship between the local and regional scales should give rise to the Clementsian pattern. Likewise, the establishment of metacommunities is due to species sorting processes, including environmental heterogeneity and dispersal sufficiency, where dispersal rates are intermediate such that most species are present in most of the habitats they find suitable. Thus, species partition habitats according to their preferences and tolerance to abiotic and biotic conditions (Leibold & Chase 2018).

In this scenario, the theoretical framework of metacommunity ecology can be a powerful toolbox for unravelling the drivers that establish epiphytic bromeliad assemblages. To this end, in this article, we investigated the metacommunity structure of epiphytic bromeliad assemblages in a broad scope of a coastal-inland gradient. Our objectives were: (1) to identify the idealised metacommunity pattern; (2) to assess how coastal-inland gradient influences species distribution; and (3) to examine how archetype-based metacommunity processes establish epiphytic bromeliad assemblages. We assume that a coastal-inland climatic gradient controls the structure of epiphytic bromeliad assemblages, which leads us to expect a Clementsian idealised metacommunity structure, as epiphytic bromeliad assemblages should form discrete and cohesive subgroups (community compartments) in specific regions along the coastal-inland gradient. We predict that environmental factors, such as habitat filtering, will have greater influence than spatial factors, such as species dispersal, in metacommunity structuring processes. Thus, species sorting should be the central archetype representing the processes of metacommunity structuring because species distributions are influenced by climatic heterogeneity and dispersal sufficiency.

METHODS

Study region

We conducted this study in the central portion of Rio Grande do Sul State in southernmost Brazil, in a coastal-inland geographic corridor where the altitude approaches sea level on the coastal plain and reaches approximately 200 meters in the vicinity of the Uruguay River (Fig. 1). This corridor lies between the Atlantic Forest and Pampean grassland biomes (Graeff 2015), resulting in a floristic combination of tropical rainforest and dry subtropical grassland elements. Numerous isolated hills (i.e., testimonial hills) of differing lithology (granitic rocks, sedimentary rocks, basaltic rocks) and geomorphology (inselbergs, tabuliform hills, ruiniform hills) occur in the study area.

The study region lies entirely within the moist subtropical climate domain (Bailey 2014). According to Köppen's classification, the climate is of the Cfa type and is defined as warm-temperate with hot summers and lacking a well-defined dry season (Peel *et al*. 2006). Based on 24 meteorological stations lying within the study area (Alvares *et al*. 2013), mean annual temperatures vary only from 18ºC to 19ºC and mean annual rainfall is roughly 1500mm–1900mm. The continental climatic gradient in the central depression is manifested mainly by an increasing mean annual temperature range, starting at 10.5ºC near the coastline and ending at 12.5ºC in the westernmost region (Fig. S.1). Elevation has little effect on mean annual temperature, but in general a difference of 1°C can be observed between sea level and 200m (Fig. S.2). The increased rainfall may be related to the proximity of the southern Brazilian plateau (escarpments of the *Serra Geral*) or other moisture-capturing elevations.

Sampling epiphytic bromeliad assemblages

We performed the floristic survey on a sequence of 71 testimonial hills distributed along a coastal-inland corridor, covering approximately 600km from east to west (Fig. 1, Table A.1). Because the forests of the Atlantic coast and woodlands of the Pampa biome are medium in height (about 15m to 20m high; Graeff 2015) and epiphytic bromeliads are usually conspicuous and easy to observe, we recorded the presence-absence of species from the ground (Zotz 2016), using binoculars when necessary (Fig. 2A, B). In addition, when it was possible to access the forest canopy, we free-climbed (without a rope) for canopy-based sampling (Fig. 2C). We recorded epiphytic bromeliads with the asystematic floristic survey method, using different sampling efforts until no new species were found. To this end, we explored phorophytes in all possible environments of testimonial hills, such as bases, cliffs, slopes, tops, and inselbergs. Our photographic records enabled accurate identification of all species and allowed the confirmation of some species based on the taxonomic literature. The scientific names of species reflect the guidance of the Flora do Brasil 2020 (http://floradobrasil.jbrj.gov.br/).

Environmental variables survey

We recorded climatic, geographic, and physiographic factors in our environmental data survey for each testimonial hill. These are assumed to influence the distribution of epiphytic bromeliads (Winkler 1980) or influence directly on forest structures (Graeff 2015). Presumably, the combination of these factors generates unique environmental conditions for each testimonial hill or patch, i.e., each discrete area of habitat (Leibold *et al.* 2004). We obtained temperature and precipitation (Table A.2) from Worldclim-Global Climate Data (Fick & Hijmans 2017) at 2.5 arcminutes of resolution. We obtained the geographic variables from the Google Earth application (Appendix S1): (1) we obtained the geographic coordinates (Datum WGS 84); (2) we measured the distance from the Atlantic coast in kilometres; (3) we measured the planimetric areas (polygons) in hectares; and (4) we measured the highest elevation above sea level in meters.

We recorded physiographic features (Fig. 3) through categorical variables: (1) different types of predominant geology: granitic rocks (Plu, 22 hills), sedimentary rocks (Sed, 28 hills), and basaltic rocks (Vol, 21 hills); (2) types of physiography based on floristics and biogeographic regions: Pampean (Pam), Espinal (Esp), Paranean (Par), and Atlantic (Atl); (3) vegetational types: a mosaic of forests and grasslands (Mos), exclusively forests (For), and exclusively rocky grasslands (Roc); (4) the spatial vertical structure of the trees: no canopy or savanoid (Sav), two strata or understory and dossel (Ucc), and three strata or understory, dossel, and emergent (Uce); and (5) types of rocky outcrop: flat rocky outcrops (Fro), cliffs or inselbergs (Esc), and tremendous rounded boulders (Bou).

Statistical and ecological analyses

Elements of metacommunity structure (EMS)

We used EMS to identify the idealized metacommunity structure. We interpreted the EMS with three metrics (Leibold & Mikkelson 2002; Presley *et al.* 2010): coherence, turnover, and boundary clumping. Coherence reflected the degree to which species responded to the same latent environmental gradient; it calculated the number of embedded absences within species ranges. Turnover represented how species composition changed in sites along the latent environment gradient. Boundary clumping measured the degree to which species distribution boundaries occurred coincidentally.

We ran a reciprocal averaging analysis with a site-by-species matrix, which maximized the proximity of species with similar distributions, as well as the proximity of sites with similar species compositions (RA, Hill 1973). From the ordination of the species scores on axis 1 (RA1, i.e., the latent environmental gradient), we computed coherence, turnover, and boundary clumping (Leibold & Mikkelson 2002). For coherence and turnover, we used the Z-test (standardized effect size); for boundary clumping, we used the Morisita index (I) followed by a Chi-square test to estimate significance. We tested the probability of acceptance of the EMS null hypothesis based on 9999 permutations at a 5% significance level. We used the "r1" null model to measure coherence and turnover. It preserved the species richness of the site (row totals) and filled the species ranges (columns) based on their marginal probabilities. This model is less sensitive to type I and type II errors (Presley *et al.* 2010; Dallas *et al.* 2020). We utilized the metacom R package (version 1.5.3, Dallas 2014; Dallas *et al*. 2020).

We interpreted the EMS as follows (Leibold & Mikkelson 2002; Leibold & Chase 2018): If coherence was negative, the pattern was identified as checkerboard; if coherence was nonsignificant, the pattern was identified as random; and, if coherence was positive, a second test for turnover was conducted. If turnover was negative, the pattern was identified as nested subsets; if turnover was nonsignificant or positive, the third test was conducted for boundary clumping. $I < 1$ indicated an evenly spaced pattern, $I > 1$ indicated a Clementsian pattern, and $I = 1$ indicated a Gleasonian pattern. When a nonsignificant turnover was recorded, a quasi-structured pattern was identified. A quasi-structure results from weaker structuring forces than those operating on structures with significant turnover; they have the same characteristics as their associated idealized structure except that their range turnover is indistinguishable from random (for more details on this phenomenon, see Presley *et al.* 2010).

Analysis of species-environment relationships

We ran a canonical correspondence analysis (CCA) to determine the main environmental factors influencing species composition according to the method proposed by Thioulouse *et al*. (2018). We used two matrices, the first formed by qualitative data (i.e., sites x species presence-absence) and the second formed by quantitative (climatic and geographic) and qualitative (physiographic) variables. In the second matrix of sites x predictor variables, we standardized and centred the quantitative variables. We applied the Monte Carlo test with 999 randomizations to test the significance of the correlation values ($P < 0.05$). We adopted a correlation circle to select the foremost environmental predictors. According to Thioulouse *et al.* (2018), the correlation circle demonstrates the relationships between environmental variables by grouping positively correlated variables and placing negatively correlated variables in opposite quadrants. Those variables furthest from the origin are the most representative. We employed the R packages ade4 (version 1.7-19, Dray *et al.* 2022) and adegraphics (version 1.0-16, Dray & Siberchicot 2021).

Metacommunity structuring processes

We ran variation partitioning to determine the proportion of the metacommunity variation that could be explained by environmental or spatial predictors (Borcard *et al.* 1992). This decomposed the variation in the epiphytic bromeliad assemblages into five fractions: environment, space, space-independent environment, environment-independent space, and residual variation suggesting stochasticity influences (Leibold & Chase 2018; Leibold *et al.* 2021). To obtain the spatial and environmental fractions, we employed principal components of neighbour matrices (PCNM) and CCA analyses (Borcard *et al*. 2018) and applied the outcomes of these analyses to the variation partitioning (Peres-Neto & Legendre 2010; Dray *et al.* 2012). The PCNM generated spatial variables of the geographic coordinates of the testimonial hills (latitude and longitude) represented as a Euclidean distance matrix (Borcard & Legendre 2002). The resulting eigenvectors associated with positive eigenvalues were used as spatial components (Borcard *et al*. 2018). In the CCA for the highly correlated variables, we applied the multicollinearity test with a variance inflation factor (VIF) and removed variables with high collinearity one at a time, repeating the test until all variables were within the established limit of $VIF < 8$ (Borcard *et al*. 2018). We employed the Monte Carlo test with 999 randomizations to evaluate the significance of the correlation values ($P < 0.05$). We used the vegan R package (version 2.6-2, Oksanen *et al*. 2022).

Finally, we used the combination of the proportions of explained variation (i.e., space-independent environment, environment-independent space, and residual variation) to determine metacommunity archetypes and to predict which core environmental and spatial processes controlled compositional variation in the metacommunity (Leibold & Chase 2018). To illustrate the combination of the proportions of variation along three axes, we used the R package ggtern to generate a ternary plot (version 3.3.5, Hamilton 2021).

RESULTS

In this study, we registered 41 species in seven genera and two subfamilies (Table 1). Bromelioideae showed the highest number of genera (5), followed by Tillandsioideae (2). The number of species, however, was greater in Tillandsioideae (30 species), distantly followed by Bromelioideae (11 species). The frequency of genera by number of species was *Tillandsia* (16 species), *Vriesea* (14 species), *Aechmea* (4 species), *Nidularium* (3 species), *Billbergia* (2 species), and *Edmundoa* and *Wittrockia* (1 species each).

The EMS (Table 2) identified a quasi-Clementsian structure along the coastal-inland gradient. In this case, the number of observed embedded absences (A) was lower than the mean (M) produced by the null model for coherence. The metacommunity structure was significantly positively coherent, indicating a non-random structure and that species distribution was influenced by the same latent environmental gradient. For species turnover, the observed value of the replacement number (R) was higher than the mean (M) produced by the null model but was nonsignificant, indicating a non-nested quasi-structure. Finally, for boundary clumping, the Morisita index (I) was higher than 1 and the Chi-square test was significant, indicating that boundary clumping was significantly different from that expected in random distribution, confirming the quasi-Clementsian structure (Fig. 4).

This pattern of species distribution evinced four different regional metacommunities. According to Presley *et al.* (2010), compartment structures occur embedded within

Clementsian distributions. The eastern and east-central metacommunities (Table 2) exhibited positive, significant coherence, positive, nonsignificant turnover, and nonsignificant boundary clumping (i.e., quasi-Gleasonian structure). The west-central metacommunity presented positive, significant coherence, positive, significant turnover, and nonsignificant boundary clumping (i.e., Gleasonian structure). Finally, the western metacommunity exhibited positive, significant coherence, positive, significant turnover, and significant boundary clumping greater than 1 (i.e., Clementsian structure).

The CCA (Fig. 5) showed a variation in species composition along the coastal-inland gradient. It confirmed that environmental factors explained 70.57% of the variation in species composition; the eigenvalues for the first two axes were 0.418 and 0.194, respectively. The correlation circle (Fig. 6) indicated that the Atlantic rainforest (Atl) was negatively and strongly correlated (-0.725) with the first ordination axis; this variable determined the species distribution in the coastal plain or, essentially, the tank bromeliad distribution. At the other end of the ordination axis were the bioclimatic variables related to temperature: bio5 (0.877, very strong), bio7 (0.801, strong), and bio4 (0.784, strong), which probably determine the distribution of atmospheric bromeliads in the deciduous woodlands of the westernmost region. The variable bio2 (temperature) showed a positive, strong correlation (0.750) with the first axis and a negative, moderate correlation (-0.513) with the second axis. The distance from the coast (Dcl) showed a positive, moderate correlation (0.615) with the first axis and negative, moderate correlation (-0.645) with the second axis.

The partitioning of variation along the coastal-inland gradient indicated that most of the compositional variation in epiphytic bromeliad assemblages could be attributed to residual variation; the purely spatial and purely environmental factors explained only 2.6% and 4.6%, respectively. At the level of regional metacommunities (Fig. 7), the partitioning of variation showed that only the purely environmental factors and residual variation influenced the compositional variation of the eastern, west-central, and western metacommunities, while, in the east-central metacommunity, the purely spatial factors, purely environmental factors, and residual variation acted in concert.

DISCUSSION

Idealized metacommunity structures

Along the coastal-inland gradient, the epiphytic bromeliads exhibited Clementsian structure. This structure appears in several biological groups, such as dragonflies (McCauley *et al.* 2008), gastropods (Presley *et al.* 2011a), birds (Presley *et al.* 2011b), plants and soil organisms (Shevtsov *et al.* 2013), parasites (Dallas & Presley 2014), and fish (Erõs *et al.* 2014; Fernandes *et al.* 2014), among others.

The quasi-Clementsian structure indicates that the epiphytic bromeliads formed cohesive groups of species occupying similar ecological niches, with coincidental boundaries of occurrence. Clementsian gradients consist of discrete communities that replace each other in a group (Clements 1916). Presley *et al.* (2010) suggested that this structure occurs because species distributions may be smaller than their potential niche occupancy ranges. In a Clementsian gradient, each compartment of species composition or community group (i.e., metacommunity) can be analysed independently of the others or the broader environment into which it is embedded (Presley *et al.* 2010). Accordingly, the species composition of epiphytic bromeliad assemblages results from processes emerging from the four regional metacommunity structures embedded along the coastal-inland gradient. In addition, the quasi-structure results from weak structuring forces creating low species turnover among epiphytic bromeliad assemblages (i.e., from hill to hill). According to Erõs *et al.* (2017), when environmental heterogeneity is relatively moderate, the metacommunity will exhibit a structure with low turnover: a quasi-structure. Gradient-driven patterns with moderate heterogeneity provide lower niche occupancy opportunities for species, leading to low species turnover (Erős *et al.* 2017), i.e., low beta diversity.

Under these conditions, atmospheric and tank bromeliads requiring the same environmental conditions have similar geographic ranges, as suggested by Leibold & Mikkelson (2002), Presley *et al.* (2010), and Leibold & Chase (2018). In Clementsian structures, the species composing cohesive and discrete groups tend to coexist and share common biogeographic histories (Presley *et al.* 2010). Consequently, we postulate macroecological processes play a critical role in structuring epiphytic bromeliad assemblages; regardless of how individual species may respond, physiological and evolutionary trade-off mechanisms are associated with climatic barriers (Dahlgren & Ehrlen 2011; Meynard *et al.* 2013). As a result, species with similar biological traits occur and disappear in the same regions along the coastal-inland gradient.

Presumably, the occurrence of climatic stress zones for atmospheric and tank bromeliads leads to the establishment of regional floristic clusters or metacommunities. The coastal-inland gradient drives different climatic and vegetational conditions, giving rise to environmental heterogeneity among the testimonial hills, but also generates climatic barriers that reduce or prevent connectivity among testimonial hills. The species composition among epiphytic bromeliad assemblages is thus highly predictable as a function of a climatic gradient. In other words, the occurrence of different metacommunity structures is related to the degree of heterogeneity of the temperature range and air moisture (see the next section for more details). Studies along zones of elevational gradients have also confirmed this observation (Leibold & Mikkelson 2002; Barone *et al*. 2008; Meynard *et al*. 2013), showing that cohesive groupings of species replace each other over short distances due to the physiological constraints imposed by changing environmental factors such as temperature, amount of rainfall, air moisture, and fog. In our study, the quasi-Clementsian structure affirmed that the distribution of epiphytic bromeliads along the coastal-inland gradient comprises a biogeographic complex based on four regional metacommunity compartments with overlapping boundaries, as the assemblages share several species among themselves (i.e., they have low turnover).

Additionally, along the coastal-inland gradient, the east-central and eastern metacommunities that are mainly composed of tank bromeliads exhibited a quasi-Gleasonian structure; the quasi-structure suggested a low turnover or a gradient-driven pattern with moderate heterogeneity (He *et al.* 2020). Meanwhile, the west-central metacommunity, composed of atmospheric bromeliads, exhibited a Gleasonian structure with high turnover or a gradient-driven pattern with high heterogeneity (He *et al.* 2020). In turn, these structures predict that species distributions occur independently of each other (Presley *et al.* 2010). Epiphytic bromeliad assemblages or local communities, in this context, emerge as collections of species that occur together in a given place and time due to overlapping tolerances of environmental conditions and biotic interactions. Gleasonian gradients suggest a continuum of species composition that gradually changes without the formation of discrete assemblages (Gleason 1926). In other words, the metacommunities are composed of species that present idiosyncratic responses to environmental gradients (Gleason 1926; Leibold & Chase 2018). Finally, the western metacommunity exhibited a Clementsian structure. In the westernmost region, there is a climatic zone with a higher temperature range and lower air moisture, as well as cold winter temperatures and sporadic frosts (Graeff 2015), which gives rise to two floristic subgroups of *Tillandsia* species (Winkler 1980): *Tillandsia*-xerophytic, originating from the Chacoan domain and adapted to xeric environments, and *Tillandsia*-mesophytic, with a wide geographic distribution and adapted to moderately warm and moist regions. Clementsian structures are gradient-driven patterns with high heterogeneity (He *et al.* 2020). High turnover correlates with the size of epiphytic bromeliad rosettes, as smaller species can share heterogeneous environments more finely than larger species (Leibold & Chase 2018).

Environmental gradients that drive species distribution

The CCA showed that Atlantic coastal rainforest, temperature range, and distance from the coast were the factors that most influenced the epiphytic bromeliad distribution. These results align with the studies Martinelli *et al.* (2008) and Fontoura *et al.* (2012) performed in a broad area of the Atlantic Forest domain. In Rio Grande do Sul, the northern coastal plain, with its proximity to the southern Brazilian plateau of the *Serra Geral*, has a more maritime climate that attenuates the temperature range and increases the air moisture and the frequency of rainfall, as suggested by Rambo (1950, 1961) and Kamino *et al*. (2019). Consequently, the epiphytic bromeliad assemblages in the northern coastal plain, as in the entire Atlantic rainforest, are mainly those that thrive in maritime climates, where the sea breeze supplies consistent air moisture, as specified by Rambo (1950). According to Gentry & Dodson (1987) and Fontoura *et al*. (2012), the higher air moisture combined with elevation above sea level provides the essential conditions for a greater number of vascular epiphytic species. Moving westward into the woodlands of the Pampa biome, the epiphytic bromeliad distributions are established by continentality. We found a marked decrease in tank bromeliad species richness from the Atlantic coast westward. In contrast, the species richness of atmospheric bromeliads increased.

Along the coastal-inland gradient, only two tank bromeliads (*Aechmea recurvata* and *Vriesea friburgensis* var. *tucumanensis*) were recorded in the testimonial hills located further inland; *A. recurvata* occurred along the entire continental gradient, while *V.*

friburgensis var. *tucumanensis* was restricted to the western and west-central regions. In addition to these two species, Büneker & Witeck-Neto (2016) also recorded *V. platynema* in the deciduous seasonal forest approximately 400km from the Atlantic coast. We also registered the unexpected occurrence of *Billbergia zebrina* and *Vriesea gigantea* in Santa Maria municipality on Elephant Hills (29°40'15"S 53°43'12"W) and Lizard's Stone (29º37'38"S 53º52'25"W), respectively.

In the westernmost region, we found the essentially atmospheric bromeliads adapted to relatively dry environments. These extreme epiphytic bromeliads, as mentioned by Gomes *et al.* (2019) are *Tillandsia* species distributed from the drier Chacoan domain (Winkler 1980; Gomes *et al*. 2019), extending eastwards to Rio Grande do Sul from the parklands of Argentina across the enclosed and moister deciduous seasonal forest of the upper Paraná-Uruguay River basins (Rambo 1961; Winkler 1980). In our floristic survey, we recorded the following *Tillandsia*-xerophytic species: *T. bandensis*, *T. duratii*, *T. loliacea*, *T. pohliana*, *T. streptocarpa*, and *T. tricholepis*. In this region, Büneker *et al.* (2015) registered *T. bandensis* only as a lithophyte species. We also observed that only *T. tricholepis* extends from the westernmost to the northern coastal plain, as Winkler (1980) and Gonçalves & Waechter (2003) noted.

As discussed above, it is evident that distance from the coast regulates the spatial distribution of atmospheric and tank epiphytic bromeliads due to the attendant temperature range and air moisture, and, presumably, cold winter temperatures and sporadic frosts, in addition to vegetation types. The genera *Vriesea* and *Tillandsia* are emblematic of the area, being more diversified in coastal and inland regions, respectively, as reported by several authors (Winkler 1980; Martinelli *et al*. 2008; Fontoura *et al*. 2012; Melo & Waechter 2018).

Metacommunity structuring processes

Variation partitioning revealed that the compositional variation of epiphytic bromeliad assemblages along the coastal-inland gradient can be attributed to a relatively small proportion of purely spatial and purely environmental factors. However, the largest proportion of the compositional variation is attributed to residual variation, which is difficult to interpret as it results from a combination of unmeasured variables, sampling effects, and stochasticity (Leibold & Chase 2018). Stochasticity implies that some epiphytic bromeliads may compete equally with each other and that niche differentiation is unimportant. It assumes that dispersal limitation drives the compositional variation of the assemblages (Hubbell 2001). Along the coastal-inland gradient, the influence of purely environmental factors is considerably more relevant. These drive the compositional variation of epiphytic bromeliad assemblages through individual species' responses to habitat filtering processes and promote dispersal processes that offer each species ample opportunity to establish in any locality where positive population growth can occur. Presumably, purely spatial factors drive dispersal surplus such that some species persist in locations with suboptimal conditions, generating source-sink dynamics.

In the context of metacommunities embedded along the coastal-inland gradient, the largest proportion of compositional variation is again attributed to residual variation. Purely environmental and purely spatial factors are of relatively minor importance. Above all, the compositional variation of the metacommunities is attributed to environmental heterogeneity, except in the east-central metacommunity that is influenced by environmental heterogeneity and dispersal rates. However, purely environmental factors exert different intensities of influence on the composition of the metacommunities. Habitat filtering is more intense in the western and eastern metacommunities than in the west-central and east-central metacommunities due to the influences of continentality further inland and maritimity in the coastal plain.

Additionally, the morphologies and dispersal modes of epiphytic bromeliads influence the compositional variation in metacommunities; smaller atmospheric bromeliads partition environmental heterogeneity more finely than larger tank bromeliads, and species with weaker dispersal capabilities (i.e., shorter dispersal distances) are more subject to the influence of spatial factors (Leibold & Chase 2018). As a result, the west and west-central metacommunities composed predominantly of atmospheric bromeliads are structured by environmental factors. By contrast, the east and east-central metacommunities composed mainly of tank bromeliads are structured by spatial and environmental factors. We must note that epiphytic bromeliad species respond differently to spatial and environmental factors, i.e., they have different dispersal rates and react differently to environmental conditions. Furthermore, habitat patches such as testimonial hills are not equally connected. The most intensely connected patches in a metacommunity may experience strong spatial effects, while the more isolated ones may experience strong environmental effects (Leibold & Chase 2018).

Purely environmental factors and residual variation drive the processes that control compositional variation in the eastern, west-central, and western metacommunities. This suggests the species sorting archetype, which predicts that compositional variation in metacommunities is determined by climatic and vegetational niche partitioning independent of purely spatial factors, as an accurate overall framework. This archetype posits that density-independent responses to abiotic heterogeneity are strong and that they differ between species. The species sorting archetype assumes that dispersal is sufficient for species to access favourable patches, but the dispersal rate is not so high as to homogenize the metacommunities (Thompson *et al.* 2020). Finally, compositional variation in the central-eastern metacommunity is controlled by a combination of purely environmental and purely spatial factors, in addition to residual variation. However, the purely environmental factors are substantially more influential, revealing that habitat filtering and niche partitioning processes control composition variation in this area. Purely spatial factors indicate that the testimonial hills are intensely connected and some species (e.g., *Tillandsia mallemontti*, *T. gardneri*, *Vriesea philippocoburgii*, *V. rubroviridis*, and *V. vagans*) may support source-sink dynamics. Habitat heterogeneity, dispersal sufficiency, and dispersal surplus appear to drive the emergence of an interface between species sorting and mass effects archetypes (Leibold & Chase 2018).

CONCLUSION

In this article, we have demonstrated that environmental, spatial, and stochastic factors, as well as life forms, influence the compositional variation of epiphytic bromeliad assemblages along the coastal-inland gradient, giving rise to a biogeographic complex with a quasi-Clementsian structure of moderate heterogeneity (i.e., low turnover) composed of four regional metacommunity compartments with different structuring dynamics. We infer that temperature range and air humidity are the environmental factors driving environmental filtering. This supports our assumption that environmental factors such as habitat heterogeneity predominate over spatial factors such as dispersal. The species sorting archetype describes the core processes in structuring metacommunities, largely independent of spatial effect. It predicts that compositional variation in epiphytic bromeliad assemblages results from deterministic drivers such as local resource utilization and interspecific interactions, birth and mortality rates related to local environmental conditions, competitive abilities influenced by habitat heterogeneity, and dispersal sufficiency (i.e., whether species have opportunities to establish wherever positive population growth can occur). We recommend that, for a greater understanding of metacommunity structuring processes, future research investigate the functional and phylogenetic structures of epiphytic bromeliad assemblages.

ACKNOWLEDGEMENTS

We thank the Brazilian Council for Research and Technologic Development (CNPq) for the doctoral scholarship and research funding. We appreciate the Institute of Biosciences of the Federal University of Rio Grande do Sul (UFRGS) for laboratory and field expeditions facilities. We are grateful to Daniel Dutra Saraiva, João André Jarenkow, Luiz Menini Neto, Sandra Cristina Müller, and to peer reviewers who provided valuable suggestions that led to substantial improvements in this scientific paper.

REFERENCES

Alvares C. A., Stape J. L., Sentelhas P. C., Gonçalves J. L. M. & Sparovek G. (2013) Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* 22(6), 711–728.

Bailey R. G. (2014) The Humid Temperate Ecoregions, in: Bailey (ed), Ecoregions - The ecosystem geography of the oceans and continents. 2nd edition, Springer, New York, USA. doi.org/10.1007/978-1-4939-0524-9

Barone J. A., Thomlinson J., Cordero P. A. & Zimmerman J. K. (2008) Metacommunity structure of tropical forest along an elevational gradient in Puerto Rico. *Journal of Tropical Ecology* 24, 525–534. doi:10.1017/S0266467408005208

Bartels S. F. & Chen H. Y. H. (2012) Mechanisms Regulating Epiphytic Plant Diversity. *Critical Reviews in Plant Sciences* 31:5, 391-400. doi.org/10.1080/07352689.2012.680349

Basílio G.A., Barbosa D. E. F., Furtado S. G., Silva F. R. & Menini Neto L. (2015) Community ecology of epiphytic Bromeliaceae in a remnant of Atlantic Forest in Zona da Mata, Minas Gerais State, Brazil. *Hoehnea* 42(1), 21-31. doi.org/10.1590/2236-8906-68/2013

Benzing D. H. (1987) Vascular epiphytism: Taxonomic participation and adaptive diversity. *Annals of the Missouri Botanical Garden* 74 (2), 183-204.

Benzing D. H. (1990) Vascular Epiphytes: General Biology and Related Biota. Oberlin College, Ohio: Cambridge University Press.

Benzing DH. 2000. *Bromeliaceae*: *Profile of an adaptive radiation*. Cambridge University Press, New York.

Borcard D., Legendre P. & Drapeau P. (1992) Partialling out the spatial component of ecological variation. *Ecology* 73, 1045–1055. doi.org/10.2307/1940179

Borcard D. & Legendre P. (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling* 153, 51–68. doi.org/10.1016/S0304-3800(01)00501-4

Borcard D., Gillet F. & Legendre P. (2018) Numerical ecology with R. Local: Springer.

Bried J. T. & Siepielski A. M. (2018) Opportunistic data reveal widespread species turnover in *Enallagma damselflies* at biogeographical scales. *Ecography* 41, 958–970. doi: 10.1111/ecog.03419

Brown B. L., Swan C. M., Auerbach D. A. A., Grant E. H. C., Hitt N. P., Maloney K. O. & Patrick C. (2011) Metacommunity theory as a multispecies, multiscale framework for studying the influence of river network structure on riverine communities and ecosystems. *North American Benthological Society Journal* 30(1), 310-327. doi: 10.1899/10-129.1

Brown B. L., Sokol E. R., Skelton J. & Tornwall B (2017) Making sense of metacommunities: dispelling the mythology of a metacommunity typology. Oecologia 183, 643–652. doi: 10.1007/s00442-016-3792-1

Büneker H. M., Pontes R. P. & Witeck-Neto, L. (2015) Novos registros em *Tillandsia* L. (Bromeliaceae, Tillandsioideae) para o Rio Grande do Sul, Brasil. *Rodriguésia* 66(2), 493–498. doi: 10.1590/2175-7860201566216

Büneker H. M. & Witeck-Neto, L. (2016) Levantamento de Bromeliaceae da região do curso médio do Rio Toropi, Rio Grande do Sul, Brasil. *Balduinia* 52, 01–14. doi.org/10.5902/2358198022371

Burns K. C. & Zotz G. (2010) A hierarchical framework for investigating epiphyte assemblages: networks, meta-communities, and scale. *Ecology* 91(2), 377–385. doi: 10.1890/08-2004.1

Clements F. E. (1916) Plant succession an analysis of the development of vegetation. Carnegie Institution of Washington, Washington, DC.

Dahlgren J. P. & Ehrlen J. (2011) Incorporating environmental change over succession in an integral projection model of population dynamics of a forest herb. *Oikos* 120, 1183–1190. doi.org/10.1111/j.1600-0706.2010.19063.x

Dallas T. (2014) Metacom: an R package for the analysis of metacommunity structure. *Ecography* 37, 402–405. doi.org/10.1111/j.1600-0587.2013.00695.x

Dallas T. & Presley S. J. (2014) Relative importance of host environment, transmission potential and host phylogeny to the structure of parasite metacommunities. *Oikos* 123, 866–874. doi.org/10.1111/oik.00707

Dallas T. & Pulliam T. (2020) Analysis of the elements of metacommunity structure. version 1.5.1. Available in https://cran.r-project.org/package=metacom (accessed 15 May 2020).

Diamond J.M. (1975) Assembly of species communities, in: Cody, M., Diamond J. (Eds) Ecology and evolution of communities. Harvard University Press, Cambridge, MA.

Dray S., Legendre P. & Peres-Neto P. R. (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbor matrices (PCNM). *Ecological Modelling* 196, 483–493. doi.org/10.1016/j.ecolmodel.2006.02.015

Dray S., Dufour A-B. & Thioulouse J. (2022) Package ade4: Analysis of ecological data: Exploratory and Euclidean methods in environmental sciences. http://www.R-project.org. (Accessed 10 May 2022).

Dray, S., Siberchicot, A. (2021) Package adegraphics: An S4 lattice-based package for representation of multivariate data. http://www.R-project.org. (Accessed 10 January 2022).

Erős T., Sály P., Takács P., Higgins C. L., Bíró P. & Schmera D. (2014) Quantifying temporal variability in the metacommunity structure of stream fishes: the influence of non-native species and environmental drivers. *Hydrobiologia* 722, 31–43. doi.org/10.1007/s10750-013-1673-8

Erős T., Takács P., Specziár A., Schmera, D. & Sály, P. (2017) Effect of landscape context on fish metacommunity structuring in stream networks. *Freshwater Biology* 62, 215–228. doi.org/10.1111/fwb.12857

Fernandes I. M., Henriques-Silva R., Penha J., Zuanon J. & Peres-Neto P. R. (2014) Spatiotemporal dynamics in a seasonal metacommunity structure is predictable: the case of floodplain-fish communities. *Ecography* 37, 464–475. doi.org/10.1111/j.1600-0587.2013.00527.x

Fick S. E. & Hijmans R.J. (2017) Worldclim 2: New 1-Km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*. Available in https://www.worldclim.org/ (Accessed 03 March 2019).

Flora do Brasil 2020 em construção. Jardim Botânico do Rio de Janeiro. Disponível em <http://floradobrasil.jbrj.gov.br/ >. (Accessed 03 March 2022).

Fontoura T., Scudeller V. V. & Costa A. F. (2012) Floristics and environmental factors determining the geographic distribution of epiphytic bromeliads in the Brazilian Atlantic Rain Forest. *Flora* 207, 662–672. doi.org/10.1016/j.flora.2012.05.003

Gentry A. H. & Dodson C. H. (1987) Diversity and biogeography of neotropical vascular epiphytes. *Annals Missouri Botanical Garden* 74, 205-233. doi.org/10.2307/2399395

Gleason H. A. (1926) The individualistic concept of plant association. *Bulletin of the Torrei Botanical Club* 53:7–26.

Gonçalves C. N. & Waechter J. L. (2003) Aspectos florísticos e ecológicos de epífitos vasculares sobre figueiras isoladas no norte da planície costeira do Rio Grande do Sul. *Acta Botanica Brasilica* 17, 89–100. doi.org/10.1590/S0102-33062003000100007

Gomes A. C., Ferreira B. H., Souza C. S., Arakaki L. M. M., Aoki C., Paggi G. M. & Sigrist M.R. (2019) Adaptive response of extreme epiphyte *Tillandsia* Species (Bromeliaceae) is demonstrated by different sexual reproduction strategies in the Brazilian Chaco. *Botanical Journal of the Linnean Society* XX, 1–15. doi.org/10.1093/botlinnean/boz104

Graeff O. (2015) Fitogeografia do Brasil uma atualização de bases e conceitos. Editora: Nau.

Hamilton N. E. & Ferry M. (2018) ggtern: Ternary diagrams using ggplot2. *Journal of Statistical Software, Code Snippets* 87(3), 1–17. doi: 10.18637/jss.v087.c03

He S., Chen K., Soininen J., Heino J., Ding N. & Wang B. (2020) Elements of metacommunity structure of diatoms and macroinvertebrates within stream networks differing in environmental heterogeneity. *Journal of Biogeography* 00, 1–10. doi: 10.1111/jbi.13859

Heino J., Melo A. S., Siqueira T., Soininen J., Valanko S. & Bini L. M. (2015) Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology* 60, 845–869. doi:10.1111/fwb.12533

Hill M. O. (1973) Reciprocal averaging: An eigenvector method of ordination. *Journal of Ecology* 61, 237–249. doi.org/10.2307/2258931

Holyoak M., Leibold, M. A., Mouquet N. M., Holt D. R. & Hoopes M.F. (2005) Metacommunities: A framework for large-scale community ecology, in: Holyoak M., Leibold M. A. & Holt R.D. (Eds.), Metacommunities: Spatial dynamics and ecological communities. The University of Chicago Press. Chicago and London, pp.1–33.

Hubbell S. P. (2001) The unified neutral theory of biodiversity and biography (Levin SA; Horn HS. (eds.). Princeton University Press.

Kamino L. H. Y., Rezende E. A., Santos L. J. C., Felippe F. M. & Assis L.W. (2019) Atlantic Tropical Brazil, in: Salgado A. A. R., Santos L. J. C. & Paisani J.C. (Eds), The physical geography of Brazil: environmental, vegetation and landscape. Springer, New York, USA, pp. 41–74.

Laube S. & Zotz G. (2006) Neither host-specific nor random: Vascular epiphytes on three tree species in a Panamanian lowland forest. *Annals of Botany* 97, 1103–1114. doi.org/10.1093/aob/mcl067

Leibold M. A. & Mikkelson G. M. (2002) Coherence, species turnover, and boundary clumping - elements of metacommunity structure. *Oikos* 97, 237–250. doi.org/10.1034/j.1600-0706.2002.970210.x

Leibold M. A., Holyoak M., Mouquet N., Amarasekare P., Chase J. M., Hoopes M. F., Holt R. D., Shurin J. B., Law R., Tilman D., Loreau M. & Gonzalez A. (2004) The metacommunity concept - a framework for multi-scale community ecology. *Ecology Letters* 7, 601–61. doi.org/10.1111/j.1461-0248.2004.00608.x

Leibold M. A. & Chase J. M. (2018) Metacommunity ecology. Monographs in population biology 59. Princeton University *Press*, Princeton and Oxford.

Leibold M. A., Rudolph F., Blanchet F. G., De Meester L., Gravel D., Hartig F., Peres-Neto P., Shoemaker L. & Chase J. M. (2020) The internal structure of metacommunities. *bioRxiv* preprint. doi: doi.org/10.1101/2020.07.04.187955

Legendre P. & Legendre L. (2012) Numerical ecology, Volume 24, 3rd Edition. Elsevier.

Leitman P., Amorim A. M., Sansevero J. B. B. & Forzza R. C. (2015) Floristic patterns of epiphytes in the Brazilian Atlantic Forest, a biodiversity hotspot. *Botanical Journal of the Linnean Society* 179, 587–601. doi.org/10.1111/boj.12342

Logue J. B., Mouquet N., Peter H., Hillebrand H. & The Metacommunity Working Group (2011) Empirical approaches to metacommunities: a review and comparison with theory. *Trends in Ecology & Evolution* 26, 482–491. doi:10.1016/j.tree.2011.04.009

Madison M. (1977) Vascular epiphytes: their systematic occurrence and salient features. *Selbyana*, 2(1), 1–13. http://www.jstor.org/stable/41759613

Martinelli G., Vieira C. M., Gonzalez M., Leitman P., Piratininga A., Costa A. F. & Forzza R. C. (2008) Bromeliaceae da Mata Atlântica brasileira: lista de espécies, distribuição e conservação. *Rodriguésia* 59(1), 209–258. doi.org/10.1590/2175-7860200859114

McCauley S. J., Davis C. J., Relyea R. A., Yurewicz L. K., David K Skelly D. K. & Werner E. E. (2008) Metacommunity patterns in larval odonates. *Oecologia* 158, 329–342. doi.org/10.1007/s00442-008-1141-8

Mendieta-Leiva G. & Zotz G. (2015) A conceptual framework for the analysis of vascular epiphyte assemblages. *Perspectives in Plant Ecology Evolution and Systematics* 17, 510–521. doi.org/10.1016/j.ppees.2015.09.003

Mendieta-Leiva G., Ramos F. N., Elias J. P. C., Zotz G., Acuña-Tarazona M., Alvim F. S., Barbosa D. E. F., Basílio G. A., Sven P., Batke S. P., Benavides A. M., Blum C. T., Boelter C. R., Brancalion P. H. S., Carmona M. J., Carvalho L. P., de la Rosa-Manzano E., Einzmann H. J. R., Fernández M., Furtado S. G., Gasper A. L., Guzmán-Jacob V., Hietz P., Irume M. V., Jiménez-López D. A., Kessler M., Kreft H., Krömer T., Machado G. M. O., Martínez-Meléndez N., Martins P. L. S. S., Mello R. M., Mendes A. F., Menini Neto L., Mortara S. R., Nardy C., Oliveira R. P., Pereira A. C. A., Pillaca L., Quaresma A. C., Quiel C. R., Medina E. S., Taylor A., Vega M. S., Wagner K., Werneck M. S., Werner F. A., Wolf J. H. D., Zartman C. E., Zuleta D., Jiménez-Alfaro B. (2020) EpIG-DB: A database of vascular epiphyte assemblages in the Neotropics. *Journal of Vegetation Science* 31(3), 518-528. doi: 10.1111/jvs.12867

Melo E. A. & Waechter J. L. (2018) Effect of vegetation matrix on diversity of epipetric bromeliads in a transitional region between evergreen and seasonal forest. *Flora* 249, 77–85. doi.org/10.1016/j.flora.2018.10.002

Meynard C. N., Lavergne S., Boulangeat I., Garraud L., Es V. J., Mouquet N. & Thuiller W. (2013) Disentangling the drivers of metacommunity structure across spatial scales. *Journal of Biogeography* 40(8), 1–12. doi.org/10.1111/jbi.12116

Mouquet N. & Loreau M. (2003) Community patterns in source-sink metacommunities. *The American Naturalist* 162(5), 544–577. doi.org/10.1086/378857

Oksanen J., Blanchet F. G., Friendly M., Kindt R., Legendre P., McGlinn P. R., O’Hara R. B., Simpson G. L., Solymos P., Stevens M. H. H., Szoecs E. & Wagner H. (2022) Vegan: Community ecology package. Version 2.6-2. Retrieved from https://cran.r-project.org, https://github.com/vegandevs/vegan.

Patterson B.D. & Atmar W. (1986) Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society* 28, 65–82. doi.org/10.1111/j.1095-8312.1986.tb01749.x

Peel M. C., Finlayson B. L. & McMahon T. A. (2006) Updated world map of the Köppen-Geiger climate classification. *Meteorol Zeitschrift* 15, 259–263. doi: 10.1127/0941-2948/2006/0130

Peres-Neto P. R., Legendre M. A., Dray S. & Borcard D. (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87, 2614–2625. doi.org/10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2

Peres-Neto P. R. & Legendre P. (2010) Estimating and controlling for spatial structure in ecological communities. *Global Ecology and Biogeography* 19, 174–184. doi.org/10.1111/j.1466-8238.2009.00506.x

Petter G., Wagner K., Wanek W., Sánchez E. J. D., Zotz G., Cabral J. S. & Kreft H. (2018) Functional leaf traits of vascular epiphytes: vertical trends within the forest, intra- and interspecific trait variability, and taxonomic signals. *Functional Ecology* 30, 188–198. doi: 10.1111/1365-2435.12490

Peterson M. L., Rice K. J. & Sexton J. P. (2013) Niche partitioning between close relatives suggests trade-offs between adaptation to local environments and competition. *Ecology and Evolution* 3(3), 512–522. doi: 10.1002/ece3.462

Presley S. J., Higgins C. L. & Willig M. R. (2010) A comprehensive framework for the evaluation of metacommunity structure. *Oikos* 119, 908–917. doi.org/10.1111/j.1600-0706.2010.18544.x

Presley S. J., Willig M. R., Bloch C. P., Castro-Arellano I., Higgins C. L. & Klingbeil B. T. (2011a) A complex metacommunity structure for gastropods along an elevational gradient. *Biotropica* 43, 480–488. doi.org/10.1111/j.1744-7429.2010.00727.x

Presley S. J., Cisneros L. M., Patterson B. D. & Willig M. R. (2011b) Vertebrate metacommunity structure along an extensive elevational gradient in the tropics: a comparison of bats, rodents and birds. *Global Ecology and Biogeography* 21, 968–976. doi.org/10.1111/j.1466-8238.2011.00738.x

Presley S. J., Mello J. H. F. & Willig M. R. (2019) Checkerboard metacommunity structure: an incoherent concept. *Oecologia* 190:323–331. doi.org/10.1007/s00442-019-04420-1

R Core Team (2017) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna., Austria. ISBN 3-900051-07-0, URL. The R Project for statistical computing 2017. http://www.R-project.org.

Rambo (1950) A Porta de Torres. *Anais Botânicos do Herbário Barbosa Rodrigues* 2, 9–20.

Rambo B. (1961) Migration routes of south Brazilian rain forest. *Pesquisa, Botânica*. São Leopoldo: Instituto Anchietano de Pesquisa 12, 1–54.

Shevtsov J., Wickings K. & Patten B. C. (2013) Evaluating the role of biotic interactions in structuring communities using a gradient analysis of multiple interacting guilds. *Oikos* 122, 1594–1605. doi.org/10.1111/j.1600-0706.2013.00267.x

Taylor A. & Burns K. (2015) Epiphyte community development throughout tree ontogeny: An island ontogeny framework. *Journal of Vegetation Science* 26, 902–910. doi.org/10.1111/jvs.12289

Taylor A., Zotz G., Weigelt P., Cai L., Karger D. N., König C. & Kreft H. (2022) Vascular epiphytes contribute disproportionately to global centres of plant diversity. *Global Ecology and Biogeography* 31(1), 62–74. doi.org/10.1111/geb.13411

Tilman D. (1982) Resource competition and community structure. Princeton University Press, Princeton, NJ.

Thioulouse J., Dray S., Dufour A.-B., Siberchicot A., Jombart T. & Pavoine S. (2018) Multivariate analysis of ecological data with ade4. Springer, New York, USA.

Thompson P. L., Guzman L. M., De Meester L., Horvath Z., Ptacnik R., Vanschoenwinkle B., Viana D. S. & Chase, J. M. (2019) A process-based framework for metacommunity ecology. *Ecology Letters* 9, 1314–1329. doi: 10.1111/ele.13568

Winkler S. (1980) Die Bromeliaceae von Rio Grande do Sul (S-Brasilien). *Documenta Naturae*. 3, 1–90.

Winkler S. (1982) Ursachen der Verbreitungsmuster einiger Bromeliaceae in Rio Grande do Sul (Südbrasilien). *Flora* 170, 371–393.

Wolf J. H. D. & Flamenco-S A. (2003) Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. *Journal of Biogeography* 30, 1689–1707. doi: 10.1046/j.1365-2699.2003.00902.x

Zotz G. & Hietz P. (2001) The physiological ecology of vascular epiphytes: Current knowledge, open questions. *Journal of Experimental Botany* 52, 2067–2078. doi.org/10.1093/jexbot/52.364.2067

Zotz, G., & Vollrath, B. (2003) The epiphyte vegetation of the palm *Socratea exorrhiza* - correlations with tree size, tree age and bryophytes cover. *Journal of Tropical Ecology* 19, 81–90. doi.org/10.1017/S0266467403003092

Zotz G. (2005) Vascular epiphytes in the temperate zones – a review. *Plant Ecology*, 176:173–183. doi.org/10.1007/s11258-004-0066-5

Zotz G. (2013) The systematic distribution of vascular epiphytes - a critical update. *Botanical Journal of the Linnean Society* 171, 453–481. doi.org/10.1111/boj.12010

Zotz G. (2016) Plants on plants: The biology of vascular epiphytes. Springer.

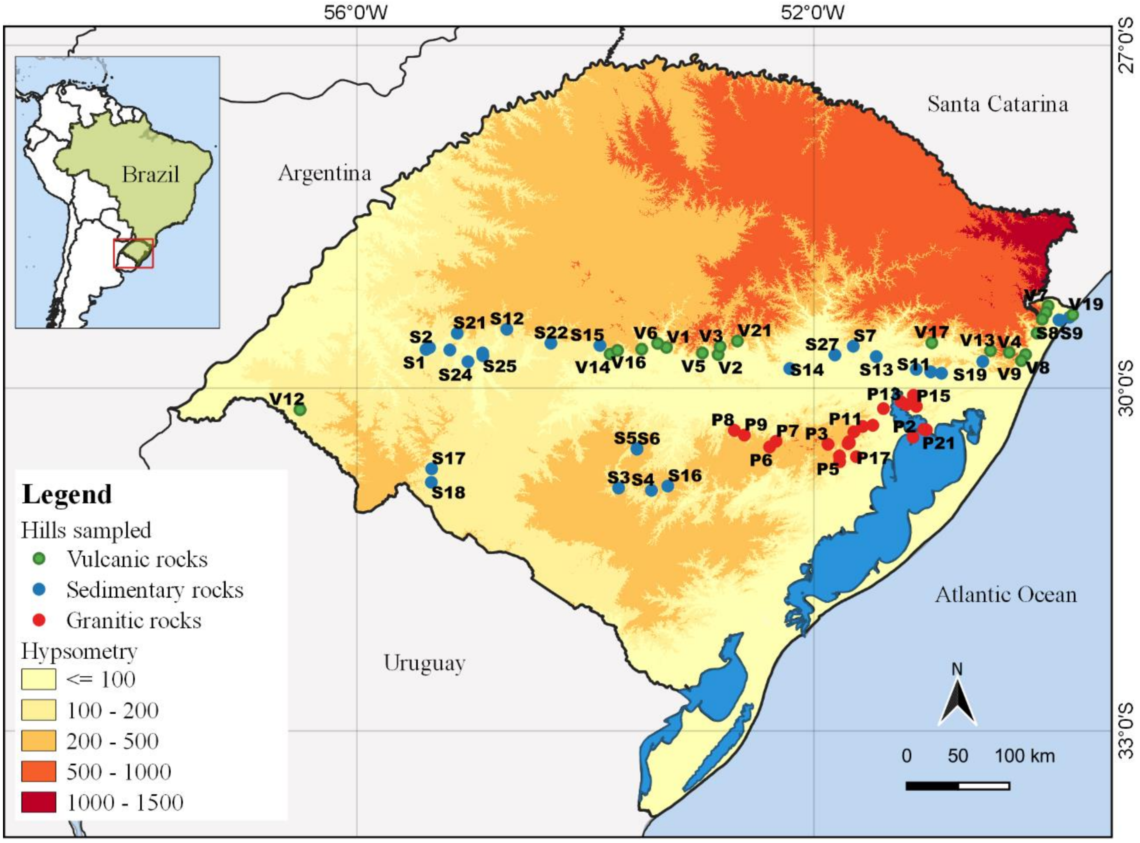


Figure 1. The hypsometric map of the Rio Grande do Sul State, southernmost Brazil. Shows the distribution of 71 testimonial hills of different lithologies along a subtropical coastal-inland corridor, extending from the Atlantic coast to near the Uruguay River.

Figure 2. Point diversity (single phorophyte) of epiphytic bromeliad assemblages in the Atlantic Forest, Morro do Forno, Morrinhos do Sul, coastal region of Rio Grande do Sul, southern Brazil. A, B - photos taken from the ground, C - photo of a phorophyte's canopy, obtained through free climbing.

Figure 3. Examples of hills with exposed rock and associated vegetation types in the central Rio Grande do Sul, southernmost Brazil. A. Volcanic hill with Atlantic rainforest (29º20'22"S, 49º58'12"W); B. Volcanic hill with deciduous seasonal forest (29º42'24"S, 52º50'21"W); C. Sedimentary hill with Atlantic rainforest (29º51'37"S, 51º00'56"W); D. Sedimentary hill with subtropical woodlands and grasslands (29º41'44"S, 54º53'47"W); E. Granitic hill with subtropical woodlands and grasslands (30°27'58"S, 52°19'57"W); F. Granitic hill with subtropical woodlands and grasslands (30°35'39"S, 51°46'38"W).

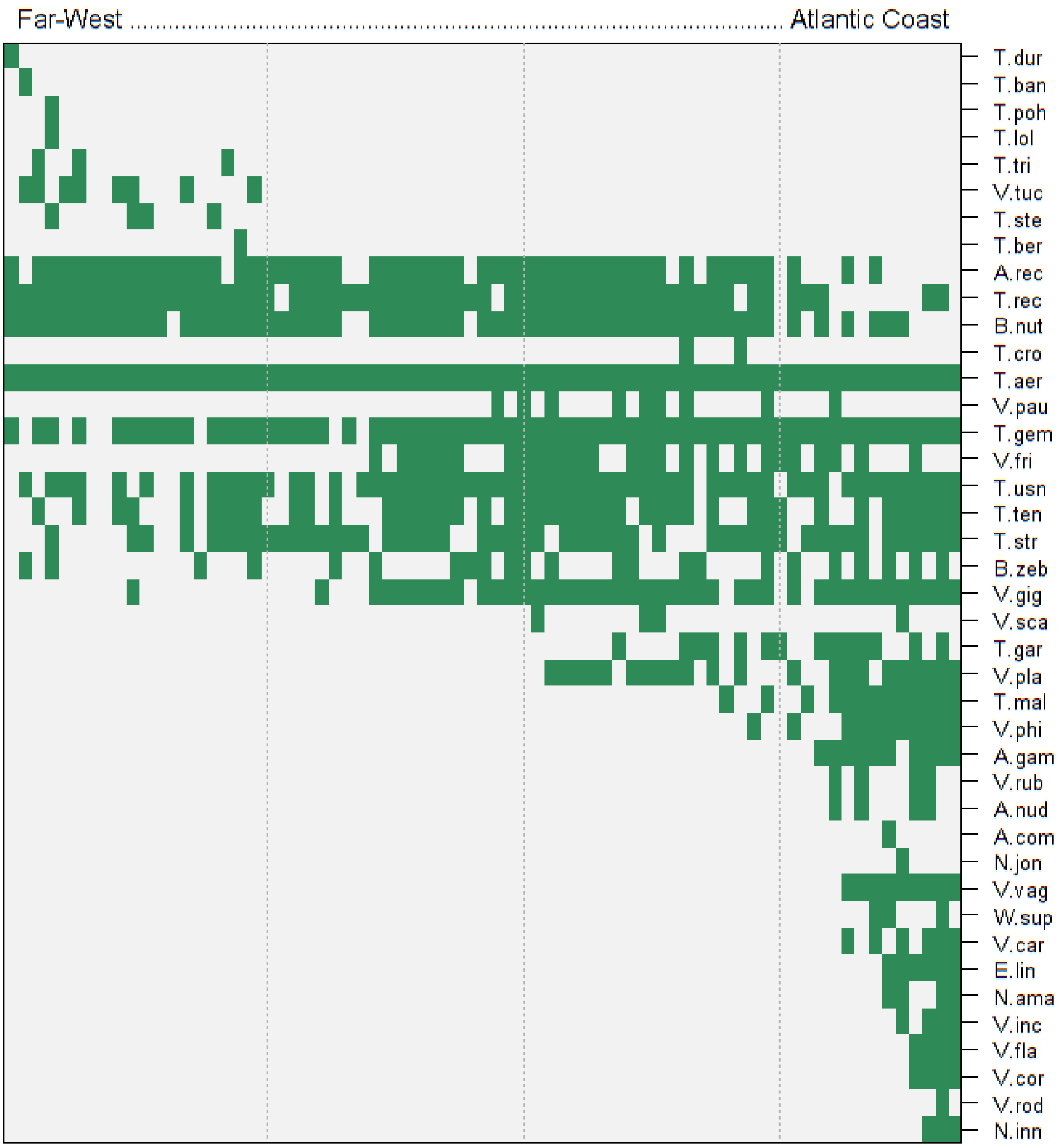


Figure 4. Diagram of the quasi-Clementsian structure of epiphytic bromeliad assemblages along the coastal-inland gradient. In the diagram, the rows and columns represent 41 species and 71 testimonial hills, respectively. Sea green rectangles indicate the occurrence of species on a sequence of testimonial hills. The left side corresponds to the region further inland and the right side to the Atlantic coast. The abbreviations of species follow in Table 1. The vertical dashed lines correspond to the boundaries between regional metacommunities.

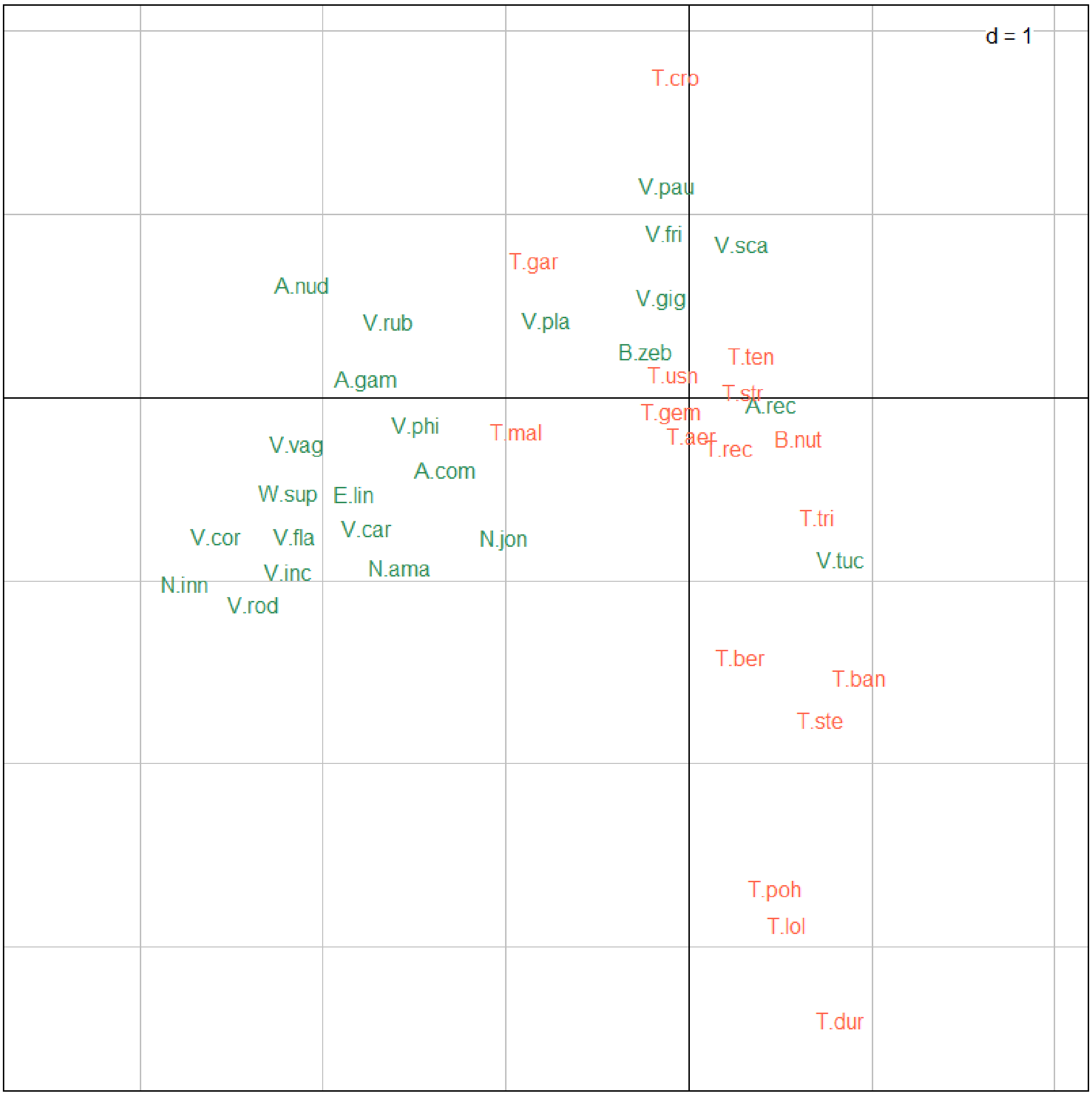


Figure 5. Canonical correspondence analysis (CCA) plot shows the ordination of epiphytic bromeliads along the first two axes. Species scores as a linear combination of environmental factors (Fig. 6). Tank bromeliads are in sea green and atmospheric bromeliads in red. The plot shows on the left side the Atlantic coast and the right side to the most continental region. Species abbreviations follow Table 1.

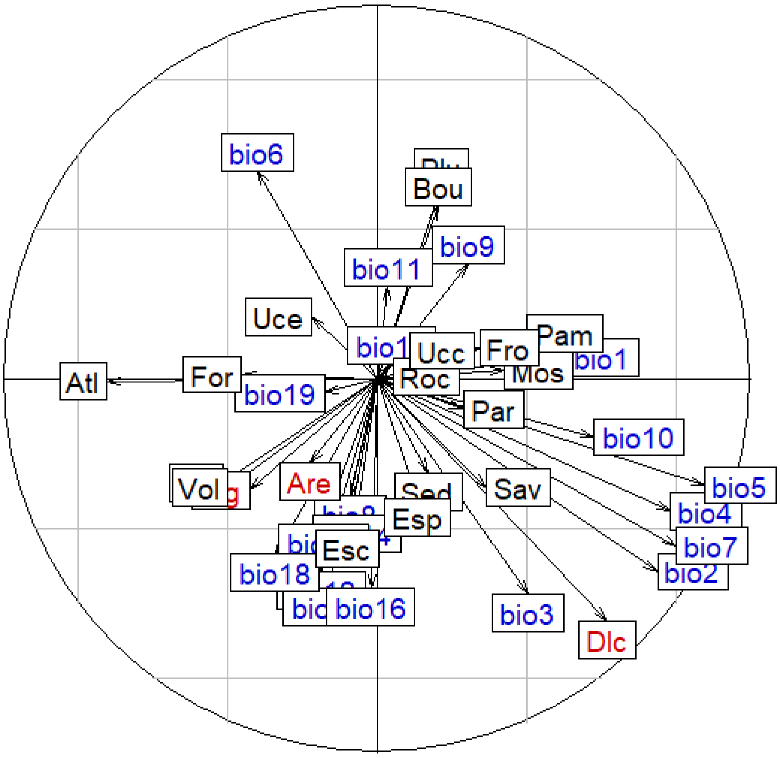


Figure 6. Correlation circle plot from the canonical correspondence analysis (CCA) based on climatic, geographic and physiographic factors surveyed on a sequence of 71 testimonial hills. Abbreviations for geographic (in red) and physiographic (in black) factors are in the text, and climate factors (in blue) follow Appendix S2. The plot shows on the left side the Atlantic coast and the right side to the most continental region.

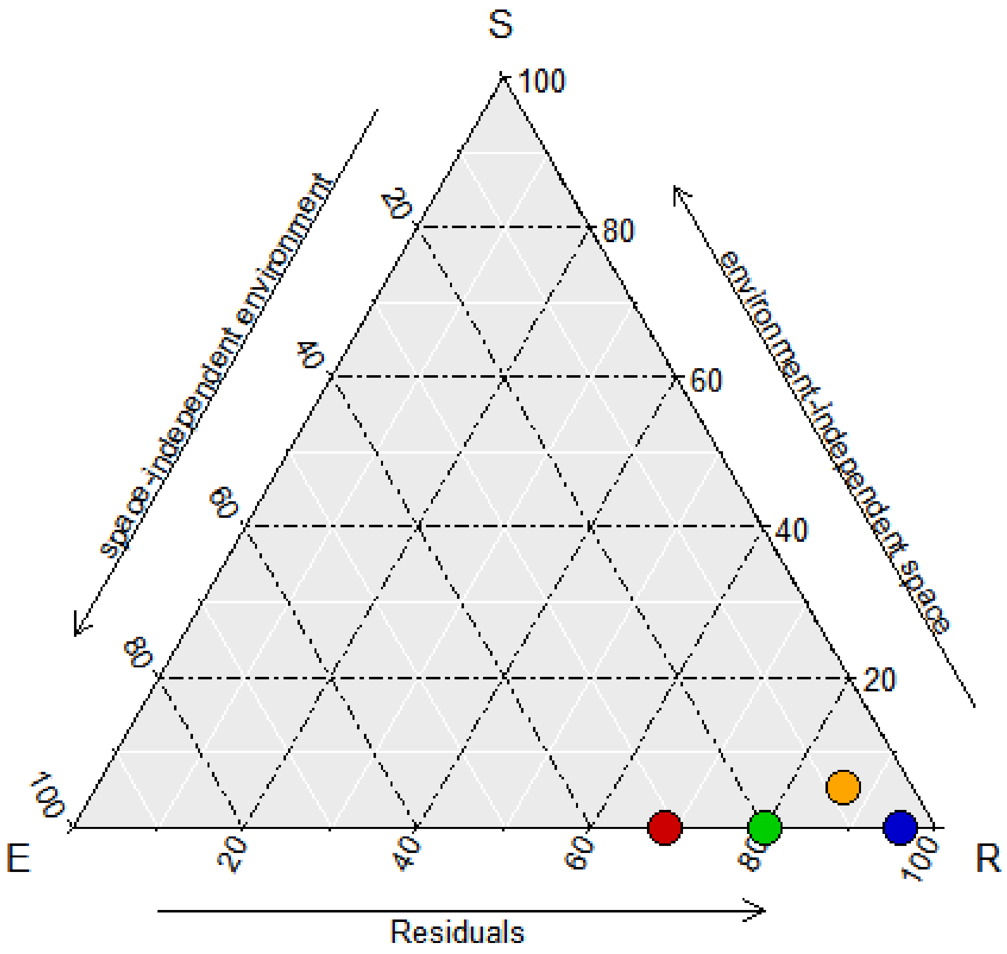


Figure 7. The ternary plot shows the variation partitioning in species composition of four metacommunities decomposed into the environment-independent space, space-independent environment, and residual variation. The large dots correspond to the metacommunities of the eastern (green), east-central (orange), west-central (blue), and western (red).

Table 1. Systematic composition, species code, ecological type based on water and nutrient absorption, and frequency of epiphytic bromeliads in four metacommunities. Frequency corresponds to the number of hills where each species occurred. Ecological types: atmospheric (A) and tank (T) bromeliads. Metacommunities: Eastern (Ea), East-Central (Ec), West-Central (Wc), and Western (We). Species names follow Flora do Brasil 2020. The name *Vriesea tucumanensis* corresponds to *Vriesea friburgensis* var. *tucumanensis*.

			Frequency				
Subfamily and Species	**Code**	**Eco-type**	**Ea**	**Ec**	**Wc**	**We**	**∑**
Bromelioideae							
Aechmea comata	*A.com*	T	1	0	0	0	1
Aechmea gamosepala	*A.gam*	T	10	0	0	0	10
Aechmea nudicaulis	*A.nud*	T	4	0	0	0	4
Aechmea recurvata	*A.rec*	T	3	23	16	11	53
Billbergia nutans	*B.nut*	A	6	25	17	11	59
Billbergia zebrina	*B.zeb*	T	6	10	5	2	23
Edmundoa lindenii	*E.lin*	T	6	0	0	0	6
Nidularium amazonicum	*N.ama*	T	4	0	0	0	4
Nidularium innocentii	*N.inn*	T	3	0	0	0	3
Nidularium jonesianum	*N.jon*	T	1	0	0	0	1
Wittrockia superba	*W.sup*	T	3	0	0	0	3
Tillandsioideae							
Tillandsia aeranthos	*T.aer*	A	13	25	20	13	71
Tillandsia bandensis	*T.ban*	A	0	0	0	1	1
Tillandsia bergeri	*T.ber*	A	0	0	1	0	1
Tillandsia crocata	*T.cro*	A	0	2	0	0	2
Tillandsia duratii	*T.dur*	A	0	0	0	2	2
Tillandsia gardneri	*T.gar*	A	8	0	0	0	8
Tillandsia geminiflora	*T.gem*	A	13	25	17	0	55
Tillandsia loliacea	*T.lol*	A	0	0	1	1	2
Tillandsia mallemontii	*T.mal*	A	10	1	2	0	13
Tillandsia pohliana	*T.poh*	A	0	0	1	1	2
Tillandsia recurvata	*T.rec*	A	4	23	20	12	59
Tillandsia streptocarpa	*T.ste*	A	0	0	4	1	5
Tillandsia stricta	*T.str*	A	11	18	17	4	50
Tillandsia tenuifolia	*T.ten*	A	9	19	12	3	43
Tillandsia tricholepsis	*T.tri*	A	0	0	2	1	3
Tillandsia usneoides	*T.usn*	A	11	23	17	6	57

Vriesea carinata	*V.car*	T	6	0	0	0	6
Vriesea corcovadensis	*V.cor*	T	4	0	0	0	4
Vriesea flammea	*V.fla*	T	4	0	0	0	4
Vriesea friburgensis	*V.fri*	T	6	17	3	0	26
Vriesea tucumanensis	*V.tuc*	T	0	0	2	5	7
Vriesea gigantea	*V.gig*	T	12	25	5	0	42
Vriesea incurvata	*V.inc*	T	4	0	0	0	4
Vriesea pauperrima	*V.pau*	T	1	8	0	0	9
Vriesea philippocoburgii	*V.phi*	T	10	1	0	0	11
Vriesea platynema	*V.pla*	T	10	12	0	0	22
Vriesea rodigasiana	*V.rod*	T	1	0	0	0	1
Vriesea rubroviridis	*V.pro*	T	4	0	0	0	4
Vriesea scalaris	*V.sca*	T	1	3	0	0	4
Vriesea vagans	*V.vag*	T	9	0	0	0	9

Table 2. Elements of metacommunity structure (EMS) of epiphytic bromeliad metacommunities. The table shows a Z-test for coherence and turnover, Morisita index (I) for boundary clumping, and metacommunity structure. The significant values ($p < 0.05$) are given in bold. A = number of absences embedded; R = number of species replacement; M = mean produced by null model; Q = quasi-structure.

	Coherence			**Turnover**			**Boundary clumping**		**Metacommunity structure**
	A	P	M	R	P	M	I	P	
First axis									
East-to-West	487	**0.05**	2079	32359	0.08	27366	3.31	**0.05**	Q-Clementsian
Eastern	92	**0.05**	205	1521	0.07	1087	0.96	0.47	Q-Gleasonian
East Central	60	**0.05**	180	348	0.08	206	2.09	0.06	Q-Gleasonian
West Central	76	**0.05**	188	703	**0.05**	398	1.54	0.10	Gleasonian
Western	31	**0.05**	104	192	**0.05**	121	2.93	**0.05**	Clementsian

Supporting information (appendices)

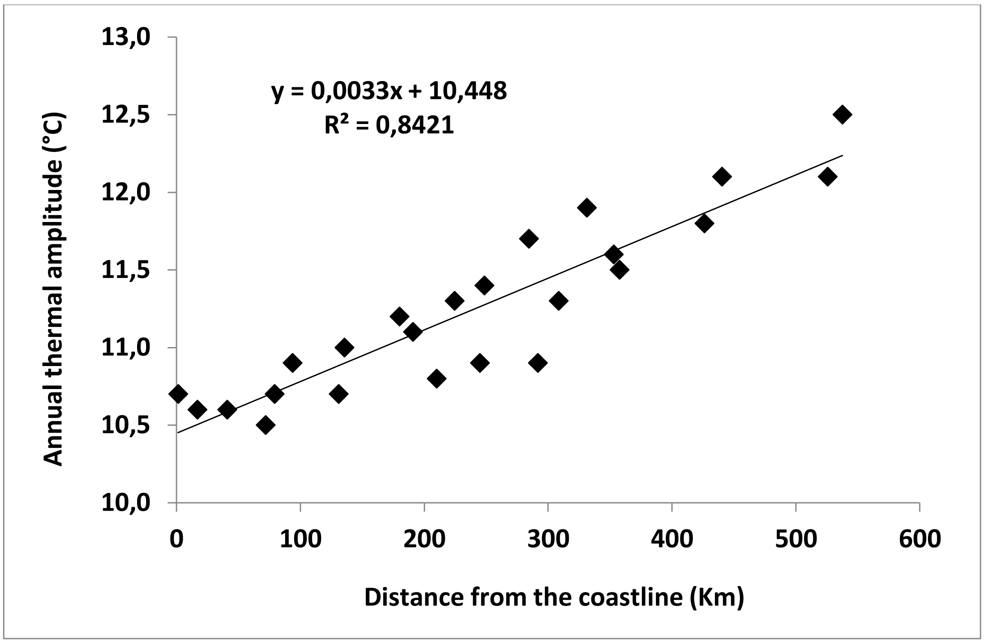


Fig. S1. This graph shows the positive correlation and linear regression between the distance from the coastline and the annual thermal amplitude, in central region of Rio Grande do Sul state, Brazil. Based on 24 meteorological stations lying within the study area (Alvares *et al*. 2013).

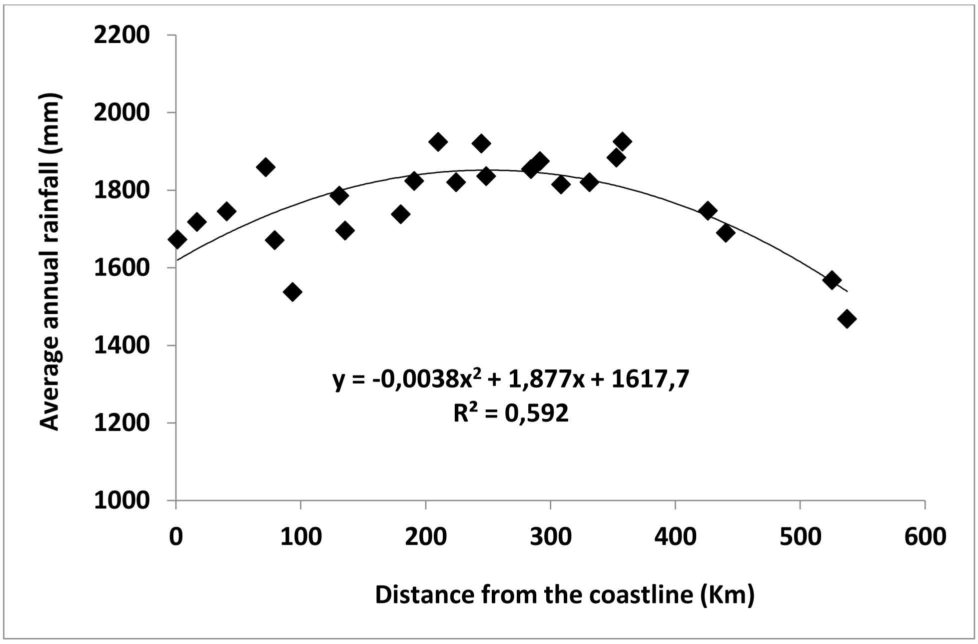


Fig. S2. This graph shows that the correlation is not linear between the distance from the coast and the average annual rainfall, in central region of Rio Grande do Sul state, Brazil. A polynomial equation was required, based on 24 weather stations located in the study area (Alvares *et al*. 2013).

Table S.1. List of the 71 hills sampled along a continental gradient, in the central Rio Grande do Sul state, southern Brazil, with data on geopolitical localization, geologic substrate [plutonic igneous rocks (P), sedimentary rocks (S), volcanic igneous rocks (V)], geographic coordinates (Datum–WGS 84), distance from coastline (DCL), highest elevation above sea level (HES), and planimetric area (Area).

Municipality	Code	Latitude S	Longitude w	DCL km	HES m	Area ha
Barra do Ribeiro	P1	30°19'33"	51°29'07"	120	350	230
Barra do Ribeiro	P2	30°25'48"	51°08'00"	80	100	170
Barão do Triunfo	P3	30°29'33"	51°52'38"	148	487	345
Cerro Grande do Sul	P4	30°38'41"	51°46'30"	125	520	82
Cerro Grande do Sul	P5	30°35'39"	51°46'38"	130	335	100
Dom Feliciano	P6	30°30'57"	52°23'18"	195	426	325
Dom Feliciano	P7	30°27'58"	52°19'57"	190	479	180
Encruzilhada do Sul	P8	30°22'14"	52°41'50"	230	315	350
Encruzilhada do Sul	P9	30°24'43"	52°36'35"	225	425	700
Guaiba	P10	30°10'47"	51°23'33"	115	200	160
Mariana Pimentel	P11	30°20'11"	51°34'28"	125	289	130
Mariana Pimentel	P12	30º23'01"	51°39'03"	130	326	3
Porto Alegre	P13	30°07'10"	51°14'22"	100	145	170
Porto Alegre	P14	30º03'48"	51°07'47"	95	200	750
Porto Alegre	P15	30°09'38"	51°06'15"	85	290	1260
Porto Alegre	P16	30°08'46"	51°11'27"	100	220	175
Sentinela do Sul	P17	30°36'03"	51°37'44"	119	295	35
Sertão Santana	P18	30°29'13"	51°42'05"	131	321	18
Sertão Santana	P19	30°28'14"	51°41'43"	139	326	31
Sertão Santana	P20	30°28'47"	51°41'25"	130	192	9
Viamão	P21	30°21'59"	51°01'00"	70	260	240
Viamão	P22	30°21'38"	51°02'19"	70	170	285
Alegrete	S1	29°39'43"	55°23'46"	530	180	35
Alegrete	S2	29°39'43"	55°21'56"	520	105	10
Bagé	S3	30°52'30"	53°42'36"	297	304	990
Caçapava do Sul	S4	30°53'43"	53°25'22"	265	208	36
Caçapava do Sul	S5	30°31'45"	53°33'01"	305	268	6
Caçapava do Sul	S6	30°32'04"	53°32'57"	305	335	770
Catupi	S7	29°38'02"	51°39'23"	165	195	10
Dom Pedro de Alcântara	S8	29°24'15"	49°51'22"	8	105	48
Dom Pedro de Alcântara	S9	29°24'15"	49°51'22"	5	20	46

Gravataí	S10	29°52'15"	50°53'03"	207	78	21
Gravataí	S11	29°51'31"	50°58'40"	90	345	485
Jaguari	S12	29°29'09"	54°41'14"	470	265	65
Montenegro	S13	29°43'29"	51°27'18"	141	207	73
Passo do Sobrado	S14	29°49'47"	52°12'44"	215	180	10
Santa Maria	S15	29º37'38"	53º52'25"	380	240	5
Santana da Boa Vista	S16	30°51'29"	53°16'48"	255	323	205
Santana do Livramento	S17	30°42'25"	55°20'48"	465	315	30
Santana do Livramento	S18	30°49'30"	55°20'59"	455	310	45
Santo Antonio da Patrulha	S19	29°46'05"	50°31'22"	49	146	30
São Francisco de Assis	S20	29°40'01"	55°11'15"	496	185	12
São Francisco de Assis	S21	29°31'13"	55°7'23"	517	204	99
São Pedro do Sul	S22	29°36'27"	54°18'11"	420	225	5
São Vicente do Sul	S23	29°43'04"	54°53'52"	473	252	170
São Vicente do Sul	S24	29°46'10"	55°01'44"	471	260	83
São Vicente do Sul	S25	29°41'36"	54°54'02"	475	310	365
Sapucaia do Sul	S26	29°50'12"	51°06'18"	102	283	29
Taquari	S27	29°42'37"	51°49'02"	177	260	74
Torres	S28	29°22'50"	49°45'49"	0,9	65	24
Agudo	V1	29°38'39"	53°17'29"	330	385	95
Candelária	V2	29º42'25"	52º50'21"	275	535	150
Candelária	V3	29°38'12"	52°49'18"	278	496	2233
Cará	V4	29º41'18"	50º17'39"	30	886	4300
Cerro Branco	V5	29°41'37"	52°58'36"	290	530	550
Dona Francisca	V6	29°36'33"	53°22'08"	330	398	25
Mampituba	V7	29°16'50"	49°57'04"	25	685	750
Maquiné	V8	29°42'24"	50°08'53"	16	343	566
Maquiné	V9	29°45'39"	50°11'06"	15	465	575
Morrinhos do Sul	V10	29º20'22"	49º58'12"	25	610	195
Quaraí	V11	30°11'21"	56°29'56"	610	235	90
Quaraí	V12	30°11'25"	56°29'58"	610	285	185
Riozinho	V13	29º40'22"	50º27'19"	45	780	90
Santa Maria	V14	29°42'10"	53°47'03"	368	237	63
Santa Maria	V15	29°40'15"	53°43'12"	435	363	245
São João do Polêsine	V16	29°39'36"	53°30'29"	342	445	1406
Sapiranga	V17	29°36'14"	50°58'08"	100	580	915
Tajuva	V18	29°23'51"	50°00'07"	25	860	465
Torres	V19	29°21'29"	49°44'07"	0	10	2
Três Forquilhas	V20	29°31'11"	50°02'50"	20	420	60
Vale do Sol	V21	29°35'19"	52°40'14"	265	362	50

Table S.2. Bioclimatic variables are derived from the monthly temperature and rainfall values, representing annual trends (e.g., mean annual temperature, annual precipitation) seasonality (e.g., annual range in temperature and precipitation) and extreme or limiting environmental factors (e.g., temperature of the coldest and warmest month, and precipitation of the wet and dry quarters). A quarter is a period of three months (1/4 of the year).

They are coded as follows:

BIO1 = Annual Mean Temperature

BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp))

BIO3 = Isothermality (BIO2/BIO7) (×100)

BIO4 = Temperature Seasonality (standard deviation ×100)

BIO5 = Max Temperature of Warmest Month

BIO6 = Min Temperature of Coldest Month

BIO7 = Temperature Annual Range (BIO5-BIO6)

BIO8 = Mean Temperature of Wettest Quarter

BIO9 = Mean Temperature of Driest Quarter

BIO10 = Mean Temperature of Warmest Quarter

BIO11 = Mean Temperature of Coldest Quarter

BIO12 = Annual Precipitation

BIO13 = Precipitation of Wettest Month

BIO14 = Precipitation of Driest Month

BIO15 = Precipitation Seasonality (Coefficient of Variation)

BIO16 = Precipitation of Wettest Quarter

BIO17 = Precipitation of Driest Quarter

BIO18 = Precipitation of Warmest Quarter

BIO19 = Precipitation of Coldest Quarter

CHAPTER II

Functional and phylogenetic structure of Bromeliaceae assemblages along a coastal-inland gradient in a subtropical Brazilian region

“As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera.”

(Charles Darwin 1859, 127)

Functional and phylogenetic structure of Bromeliaceae assemblages under stress-dominance hypothesis along a coastal-inland gradient in a subtropical Brazilian region

Abstract In community assembly, habitat filtering processes drive trait convergence (i.e., phylogenetic underdispersion). Or otherwise, competitive exclusion processes or limiting similarity drive trait divergence (i.e., phylogenetic overdispersion). The stress-dominance hypothesis (SDH) conjectures that the relative importance of habitat filtering increases while the competitive exclusion decreases along a gradient of increasing environmental stress. Aiming to study Bromeliaceae assemblages under the SDH on a broad scope of coastal-inland gradient, we investigated the functional and phylogenetic structure on a sequence of testimonial hills distributed along a subtropical geographic corridor extending from the Atlantic coast to near the Uruguay River in southernmost Brazil. We scrutinized four functional traits: life forms, rosette size, light requirement, and photosynthetic pathways. We computed RLQ techniques for analyzing the associations among environment, space, species, traits, and phylogeny. We evaluated the phylogenetic signal and computed the phylogenetic distances for analyzing the functional and phylogenetic structure. Our results affirmed that functional traits exhibited a phylogenetic signal, suggesting that phylogenetic niche conservatism controls the distribution of tropical species along the coastal-inland gradient. Overall, the phylogenetic distances did not differ from the null expectation, meaning that the community assembly processes were random concerning the species pool. However, the functional and phylogenetic structure showed a paradox regarding SDH prediction. Habitat filtering influenced functional traits while limiting similarity operated on species phylogeny. This study highlights those lineages manifesting phylogenetic niche conservatism occupy or track ancestral ecological niches. The SDH generates different functional and phylogenetic structure responses. Nevertheless, community assembly is predominantly random concerning the species pool.

Keywords

abiotic filtering, bromeliads, environmental gradient, phylogenetic community ecology, species coexistence, trait-based ecology

1. Introduction

The theoretical framework of community ecology based on functional and phylogenetic structure enables a mutual understanding of the ecological and evolutionary processes that control community assembly and species coexistence (Cadotte and Davies, 2016; Swenson, 2019; de Bello et al., 2021). In this framework, species phylogeny is used as a proxy to examine the degree of biological similarity and phylogenetic relatedness among species in a given ecological community (Webb, 2000; Webb et al., 2002). Thus, in an ecological community in which species have evolutionarily conserved functional traits (i.e., synapomorphies), it is possible to use a phylogenetic tree (i.e., species phylogeny) to compute and identify two hypothetical patterns in order to reveal the processes of phylogenetic structuring: phylogenetic underdispersion and phylogenetic overdispersion (Webb et al., 2002; Cavender-Bares et al., 2009; Swenson and Enquist, 2009). Community structure that exhibits phylogenetic overdispersion (or trait divergence) has greater functional and phylogenetic diversity than expected based on a random sample of the regional species pool. The structuring processes are fundamentally based on competitive exclusion within clades, niche partitioning, and limiting similarity (Webb et al., 2002; Cavender-Bares et al., 2009; Mayfield and Levine, 2010; Cadotte and Davies, 2016; Swenson, 2019; de Bello et al., 2021). On the other hand, community structure that exhibits phylogenetic underdispersion (or trait convergence), or phylogenetic clustering, has lower functional and phylogenetic diversity than predicted by random sampling. The structuring processes are fundamentally based on competition between clades and habitat filtering (Webb et al., 2002; Cavender-Bares et al., 2009; Mayfield and Levine, 2010; Cadotte and Davies, 2016; Swenson, 2019; de Bello et al., 2021). In addition, competitive exclusion may cause phylogenetic underdispersion because species with similar fitness need only slight niche differences and differences in the competitive ability to coexist (Mayfield and Levine, 2010).

Given this background, several studies have been conducted to examine how the relative importance of habitat filtering and competitive exclusion vary along different environmental gradients (Graham et al., 2012; Coyle et al., 2014; Miazaki et al., 2015; Lhotsky et al., 2016; Gastauer et al., 2017; Ramm et al., 2018; Ács et al., 2019). These studies are based on the stress-dominance hypothesis (SDH, Swenson and Enquist, 2007), which postulates that along an ecological or geographical gradient in a harsh environment, habitat filtering is the dominant driver of functional and phylogenetic diversity. While the limiting similarity, i.e., competitive exclusion, is more influential in less stressful habitats (Grime 2006; Swenson and Enquist 2007; Coyle et al. 2014). In short, under the gradient of SDH, habitat filtering constricts the presence of organisms within a community to individuals that possess similar morphological, physiological, and phenological traits. In contrast, competitive exclusion limits the coexistence of ecologically similar species with niche overlap (Grime, 2006; Mayfield and Levine, 2010; HilleRisLambers et al., 2012; Coyle et al., 2014).

Although SDH is widely accepted and proven by several studies (e.g., Coyle et al., 2014; Miazaki et al., 2015), controversies still exist about the direction and causes of changes (Coyle et al., 2014). For example, the relative importance of habitat filtering and competitive exclusion may change along gradients of productivity conditions to stress, contradicting the SDH prediction (Grime, 2006). According to this example, Mason et al. (2012) and Carboni et al. (2014) reported the transition from the relative importance of competitive exclusion to habitat filtering with increasing productivity along an environmental gradient. This issue is in line with the study by Mayfield and Levine (2010), which postulates that higher productivity should lead to phylogenetic underdispersion, as increased competition excludes species with traits associated with lower competitive ability. However, as Navas and Violle (2009) have documented, the most significant influence of habitat filtering is expected at both ends of the average productivity gradient.

The family Bromeliaceae represents a model system for developing and testing predictions about habitat filtering and competitive exclusion processes based on a broad-scope environmental gradient related to SDH. This botanical family occurs throughout the Neotropics, contributing remarkably to the species composition and taxonomic, functional, and phylogenetic diversity of ecological communities (Benzing, 2000; Givnish et al., 2011; Ladino et al., 2019). In addition, Bromeliaceae contains several ecological types that live on different substrates: terrestrial, saxicolous, lithophytic, and epiphytic (Benzing, 2000). They also stand out for adaptations such as the leaves being arranged in rosettes to form water-impounding structures (i.e., phytotelma storage tanks), leaves consisting of scales or trichomes specialized in absorbing water and nutrients and reflecting solar radiation, and crassulacean acid metabolism (CAM), the metabolic pathway for carbohydrate synthesis adapted to the water supply in arid environments (Benzing, 2000; Givnish et al., 2007; 2011; 2014). According to Kessler (2002a; b), the autecological traits of Bromeliaceae species are associated with different abiotic (e.g., temperature and rainfall) and biotic factors (e.g., pollinators and dispersers). In general, latitudinal, continental, and altitudinal gradients control the distribution of Bromeliaceae (Benzing, 2000; Kessler 2002a; Martinelli et al. 2008; Fontoura et al. 2012).

In the extreme south of Brazil, in the central part of Rio Grande do Sul State, between the northern and southern plateaus, we can observe an extensive low-altitude geographic corridor extending from the Atlantic coast to near the Uruguay River. Along this subtropical corridor, there is a continental climatic gradient that is believed to control the distribution of Bromeliaceae (Winkler, 1980). The genus *Dyckia* occurs along the coastal–inland gradient in dry, water-deficient environments on rocky outcrops or inselbergs. The genera *Aechmea*, *Billbergia*, *Edmundoa*, *Nidularium*, *Vriesea*, and *Wittrockia* are concentrated in moist climate regions, such as the deciduous forests east and, especially, north of the coastal plain in the Atlantic Forest. The genus *Tillandsia* has a wide geographic distribution (Winkler, 1980; 1982). In other words, tank bromeliads and mesophytic atmospheric bromeliads (i.e., tropical species) occurring in the easternmost region are constrained especially by maritimity. Whereas xerophytic atmospheric bromeliads (e.g., Chacoan species) occurring in the westernmost region are constrained mainly by continentality. Under these circumstances, the life forms and C_3 and CAM metabolism of Bromeliaceae species generally condition their occupation of mesic or xeric habitats (Winkler, 1980).

Furthermore, in this geographic corridor, we find numerous testimonial hills with different lithologies and geomorphologies surrounded by subtropical grasslands and forests that have been affected by agriculture, timber plantations, and urbanization. These testimonial hills represent ideal sites for testing theories of community assembly and species coexistence along with a broad scope of the environmental gradient under the SDH; since they are delimited in space (i.e., they form a scenery of geographical islands) and undergo influence by climatic and vegetational factors. In these testimonial hills, species richness of Bromeliaceae from the coastal toward inland shows a monotonous decrease with increasing continentality (Winkler, 1980). Therefore, it is likely that the relative importance of habitat filtering may intensify with increasing distance from the coast (i.e., continentality).

To the best of our knowledge, no study has yet investigated the functional and phylogenetic structure of Bromeliaceae assemblages under the SDH. From this perspective, understanding the factors and processes that drive community assembly and species coexistence is critical to preserving Bromeliaceae biodiversity. We intended, in this article, to investigate the functional and phylogenetic structure of Bromeliaceae assemblages under the SDH on a sequence of testimonial hills distributed along with a broad scope of a coastal–inland gradient. Our main objectives were (i) to assess the distribution of Bromeliaceae according to functional traits by considering four key traits that influence the ecological performance of Bromeliaceae species: life form, rosette size, light requirement, and photosynthetic pathway and (ii) to determine patterns, underdispersion or overdispersion, of functional and phylogenetic structure in order to identify the processes that control community assembly and species coexistence. For this, we consider the SDH prediction. We hypothesize that functional and phylogenetic diversity and the relative importance of competitive exclusion will decrease. In contrast, the habitat filtering will intensify along the coastal-inland gradient because tropical Bromeliaceae species will not be adapted to occupy the subtropical climatic niches further inland.

2. Methods

2.1 Study region

We conducted this study in the central part of Rio Grande do Sul State in southernmost Brazil, in a subtropical geographic corridor extending from the Atlantic coastal plain to near the Uruguay River in which altitude approaches sea level on the easternmost region and reaches approximately 200 meters on the westernmost region (Fig. 1). Along this geographic corridor, an extensive continental gradient intersects different environments such as rainforests, deciduous forests, rupestrian grasslands, and woodlands (Graeff, 2015). In addition, there are numerous testimonial or residual hills (sensu Rossato et al., 2008) with different altitudes, lithologies, and geomorphologies.

According to the Köppen system, the regional climate is a temperate zone, Cfa type, characterized by rainfall every month, with temperatures ranging from no less than 3°C to more than 22°C. In summer, temperatures close to 40°C are sporadically recorded. In winter, the temperatures slightly above 0°C are typically recorded, with frosts and occasional negative temperatures (Nimer, 1990). The least rainy region, with rainfall isohyets of 1200mm and 1300mm, is located on the Atlantic coastal plain and to the south of Rio Grande do Sul, on the border with the Oriental Republic of Uruguay. In the central region of Rio Grande do Sul, rainfall is approximately 1750mm (Nimer, 1990).

2.2 Survey of Bromeliaceae species and functional traits

Our sampling was conducted on 71 testimonial hills distributed over an expanse of approximately 600km (Fig. 1, Table 1). In these testimonial hills, the floristic survey of Bromeliaceae consisted of non-systematic records with different sampling efforts. The distinct localities or habitats (bases, sides, rocky outcrops or inselbergs, and tops) were explored until new species were no longer found. As Bromeliaceae species are generally conspicuous and relatively easy to observe, we recorded them from the ground by direct observation, using high-resolution binoculars when necessary. In addition, to sample epiphytic Bromeliaceae when the forest canopy was accessible, we free-climbed (i.e., without a rope). To sample lithophytic Bromeliaceae, on rocky walls in most cases, we walked and free-climbed to reach the tops of hills or inselbergs to approximate the species. Photographic records allowed further identification, and some species were confirmed based on taxonomic literature. We used Flora do Brasil 2020 (http://floradobrasil.jbrj.gov.br/) to confirm species names (i.e., the taxon names).

Additionally, we recorded the following functional traits (adapted from Benzing, 2000): (a) Substrate occupation and water and nutrient absorption (atmospheric epiphyte [AT/EP], tank-epiphyte [TA/EP], atmospheric lithophyte [AT/LI], tank-lithophyte [TA/LI], root lithophyte [RO/LI], root geophyte [RO/GE]); (b) Average estimated rosette size (small [RS] < 20cm, medium [RM] 20 to ≤ 40cm, and large [RL] > 40cm); (c) Light requirement (heliophytes [HE] observed on rocky outcrops or rocky walls in full sun; in open fields; forest edges or in the forest canopy in full sun, sciophytes [SC] observed growing in the forest lower strata or on rocks within forests; on rocky walls in full shade, and indifferent [IN] nonselective species found in both categories; (d) Photosynthetic pathway (3-carbonic acid [C_3] or crassulacean acid metabolism [CAM]). For this classification, we used the works of Griffiths and Smith (1983), Benzing (1990, 2000), Craig (1994), Crayn et al. (2004, 2015), Males (2016), Males and Griffiths (2017), among others. In addition, we consider the relationship between phylogenetic relatedness and trait similarity to support this classification (de Bello et al., 2021).

2.3 Survey of environmental factors

For each testimonial hill, 19 bioclimatic variables, rasterized at 2.5-minute resolution, were obtained from WorldClim 2.1 (Fick and Hijmans, 2017) and associated with geographic coordinates. For this, we used the R packages: raster (ver. 3.5-15, Hijmans et al. 2022) and maptools (ver. 1.1-3, Bivand et al. 2022). The following geographic variables were obtained from the Google Earth application: (a) geographical coordinates referenced in the WGS 84 system. (b) Distance from the coastline (Dlc), in kilometers. (c) Planimetric area (Are), in hectares. In addition, was obtained maximum altitude above sea level (Hel), in meters, using the global positioning system (GPS) digital device.

The registered physiographic features were (a) Predominant lithology: granitic (Plu, 22 hills), sedimentary (Sed, 28 hills), and volcanic (Vol, 21 hills); (b) Physiography, primarily based on floristics and biogeographic province: Pampean (Pam), Espinal (Esp), Paranean (Par), and Atlantic (Atl); (c) Vegetation: a mosaic of forest and grassland (Mos), exclusively forest (For), and exclusively rocky grassland (Roc); (d) Vertical spatial structure (forest canopy layers): no canopy (savanoid, Sav), two layers (understory and canopy, Unc), and three layers (understory, canopy, and overstory, Uce); (e) Types of rocky outcrops: flat outcrops (Fro), rocky walls or inselbergs (Esc), and tremendous rounded boulders (Bou).

2.4 Phylogenetic tree

We used the GBOTB.extend.tre mega-tree proposed by Smith and Brow (2018) to construct an ultrametric phylogenetic tree (Fig. 2). We designated the closest relatedness for species not reported in the GenBank and Tree of Life Project, especially for the genera *Dyckia* and *Tillandsia*, based on reproductive and vegetative morphological traits. In addition, we conducted a taxonomic review of the Bromeliaceae family. We considered the major phylogeny-based works, such as Barfuss et al. (2016), who performed taxonomic studies of the Bromeliaceae subfamily Tillandsioiedeae based on multilocus DNA sequence phylogeny and morphology; Givinish et al. (2011), who considered eight-locus plastid phylogeny; among others. In the R package V.PhyloMaker (ver. 0.1.0, Jin and Qian, 2019), the function “nodes.info.1” extracted the information from the root and basal node of the largest grouping at the genus level of the mega-tree and “scenario 3,” a more conservative function, provided a dated phylogenetic tree according to phylogenetic calibration. We used the bifurcatr algorithm of the R package PDcalc (ver. 0.4.4.9000, Nipperess and Wilson, 2021) to break the polytomies. It is a modification described by Rangel et al. (2015). It works as follows: (a) Randomly choose two edges from a polytomy. (b) Join the edges with a new node. (c) Generate a new edge. (d) Link polytomy node to new node via new edge. (e) Generate a new branch length (from a random uniform distribution) for a new edge. (f) Adjust lengths of descendent edges (to preserve ultrametricity). We randomized the algorithm 999 times to generate several equally plausible trees. For the graphic representations of the phylogenetic tree, we used the R packages picante (ver. 1.8.2, Kembel et al. 2020) and phytools (ver. 1.0-3, Revell, 2022).

2.5 Statistical and ecological analysis

2.5.1 Associations among species, traits, phylogeny, environment, and space

We used the RLQ technique (Dolédec et al., 1996) intending to relate a plot-by-environmental-variable table (R) to a species-by-traits table (Q), with a plot-by-species table (L) serving as a link between R and Q (Choler, 2005; Thioulouse et al., 2018). We assumed that the L table measures the intensity of the associations between R and Q tables (Choler, 2005). This technique is a co-inertia analysis and is robust to collinearity (see more details in Dray et al., 2003 and ter Braak et al., 2018). The reader should consult

Dolédec et al. (1996), Dray et al. (2014), and Thioulouse et al. (2018) for more details about the mathematical approach.

We used RLQ techniques for the following reasons: First, we run the fourth-corner analysis to provide global pictures of functional trait-environment relationships (Dray et al., 2014; Thioulouse et al., 2018). Second, we computed RLQ ordination to identify the main co-structure between functional traits and environmental variations mediated by species presence-absence (Dray et al., 2014; Thioulouse et al., 2018). Lastly, we used an extension of the RLQ approach (Pavoine et al., 2011) to examine the relationships of environmental filters and functional traits in an explicitly phylogenetic and geographic context.

The fourth-corner analysis allowed evaluating the significance of bivariate associations, i.e., one single trait and one single environmental variable at a time (Dray et al., 2014). For this analysis, we used model 6 (Dray et al., 2014), which combines model 2 (permutation of L lines) and model 4 (permutation of L columns), to generate the maximum P-values ($P \leq 0.05$) produced by permutation tests (999 randomizations). We displayed the results of the fourth-corner tests (positive, negative, and nonsignificant associations) in a plotting matrix. For more details on the mathematical model, see Legendre et al. (1997), Dray and Legendre (2008), and Thioulouse et al. (2018).

Next, after selecting only the associated variables between the R and Q tables, we performed RLQ ordination. For this, we computed three separate analyses: correspondence analysis (CA) for L table and principal correspondence analysis (PCA) for R and Q tables (weighted according to CA). RLQ ordination maximizes the covariance between the scores of sites (sampling units) constrained by the environmental variables in R table and the scores of species constrained by the functional traits in Q table (Choler, 2005; Thioulouse et al., 2018). The fourth corner table was computed containing the covariance between sites and species. For the first ordination axis, RLQ computed coefficients for the environmental variables and species traits. These coefficients measured the contributions of individual variables and were used to compute site and species scores; they maximized the first eigenvalue. The analysis proceeded in the same way for the successive orthogonal ordination axes. We applied the Monte-Carlo test (999 randomizations) to evaluate the significance ($P \leq 0.05$) of the co-structure between R and Q for the first two axes. For these analyses, we utilized the R packages ade4 (ver. 1.7-18, Dray et al., 2021) and adegraphic (ver. 1.0-16, Dray and Siberchicot, 2021).

Lastly, by employing the extended RLQ approach (Pavoine et al., 2011), we examined the relationships between the E (environmental) and S (spatial, i.e., geographic coordinates of the hills) tables and between the T (traits) and P (phylogeny) tables. We retained the Cartesian coordinates of sites in the factorial analysis related to environmental variables (XE) and geographic space (XS) analysis, and the coordinates of species in the factorial analyses of functional traits (XT) and species phylogeny (XP). Subsequently, we standardized each table (XE*, XS*, XT*, and XP*) using the square root of the first eigenvalue to ensure that each table, or matrix, is comparable at the same scale. We then used multifactorial analysis to combine the XE* and XS* tables and the XT* and XP* tables to form the R and Q tables, respectively (for more details, see Pavoine et al., 2011). Next, we treated the L table (species presence-absence) by correspondence analysis (CA), R table by principal component analysis (PCA), and Q table by principal coordinate analysis (PCoA). Finally, we run RLQ ordination. We used the following R packages: phylobase (ver.0.8.10, Hackathon et al., 2020), ade4 (ver. 1.7-18, Dray et al., 2021), adiv (ver. 2.1.1, Pavoine 2021), fastmap (ver. 1.1.0, Chang 2021), and ape (ver.5.6-1, Paradis et al., 2022).

2.5.2 Phylogenetic signal

We detected the phylogenetic signal of binary traits using the D-statistic (Cadotte and Davies, 2016). We standardized the effect of phylogeny size and prevalence by two null models (Fritz and Purvis, 2010): phylogenetic randomness and Brownian motion. We interpreted the D-statistic as follows (Fritz and Purvis, 2010): (a) D equal to 1 if the distribution of the binary trait is random concerning phylogeny, (b) D greater than 1 if the distribution of the trait is more overdispersed than the random expectation, (c) D equal to 0 if the binary trait is distributed as expected under the Brownian motion model of evolution, (d) D less than 0 if the binary trait is more phylogenetically conserved than the Brownian expectation. We used 999 permutations to assign P-values ($P \leq 0.05$). See more details about the mathematical model in Fritz and Purvis (2010). For this analysis, we used the R package caper (ver. 1.0.1, Orme et al., 2018).

2.5.3 Phylogenetic distances

We determined the functional and phylogenetic structure of Bromeliaceae assemblages employing the net relatedness index (NRI) and the nearest taxon index (NTI). NRI estimated the average phylogenetic relatedness between all possible pairs of taxa in an assemblage, thus emphasizing deeper branches of the phylogenetic tree (Webb et al., 2002; Swenson, 2019). In contrast, NTI estimated the average nearest phylogenetic neighbor between the individuals in an assemblage, thus emphasizing compositional patterns at the tips of the phylogenetic tree (Webb et al., 2002; Swenson, 2019). Due to the lack of complete independence between functional and phylogenetic structure (Cadotte et al., 2019; de Bello et al., 2017, 2021), we used the methodological approach of decoupling traits and phylogeny described by de Bello et al. (2017), providing the following dissimilarity distances: functional dissimilarity (Fdist, non-decoupled traits), phylogenetic dissimilarity (Pdist, non-decoupled phylogeny), decoupled functional dissimilarity (dcFdist, decoupled traits), and decoupled phylogenetic dissimilarity (dcPdist, decoupled phylogeny). Here, we used the R packages geiger (ver. 2.0.7, Harmon, 2020), phylolm (ver. 2.6.2, Ho et al., 2020), ape (ver. 5.6-2, Paradis et al., 2022), and phytools (ver. 1.0-1, Revell, 2022).

With these distances, we calculated NRI and NTI for each Bromeliaceae assemblage using species pools defined from four metacommunities (easternmost, east-central, west-central, westernmost) as verified by Fávero et al. (2022) along the coastal-inland gradient (in pre-publication phase). For this, we used species presence-absence. We obtained NRI and NTI by multiplying the standardized effect size mean phylogenetic (pairwise) distances (SES.MPD and SES.MNTD) by -1 (Kembel et al., 2020). We used the null model (999 randomizations) without constriction, in which the species richness of each assemblage was kept constant but the species were randomized from the species pool (Kembel and Hubbell, 2006). We evaluated whether the NRI and NTI differed significantly from zero (i.e., expected) with a two-tailed test and a significance level of 5% (Cadotte and Davies, 2016). Significantly positive NRI or NTI values indicate phylogenetic underdispersion, i.e., co-occurring taxa are more closely related than expected by a null model. While significantly negative NRI or NTI values indicate phylogenetic overdispersion, i.e., co-occurring taxa are less closely related than expected by a given null model. NRI or NTI values that do not differ from the null expectation of phylogenetic structure are interpreted as being phylogenetically random relative to the species pool. Here, we employed the R package picante (ver. 1.8.2, Kembel et al., 2020).

To verify the functional and phylogenetic structure, under the SDH, we plotted NRI and NTI versus distance from the coast on a scatter plot with a smoothing line within a 95% confidence interval (Field et al., 2012). We fitted this smoothing line to the data to explore the relationships between variables without an appropriate specific model (e.g., regression line, Field et al., 2012). We calculated using the lowess smoothing method (Cleveland, 1979). In this analysis, we utilized the R package ggplot2 (ver. 3.3.5, Wickham et al., 2021).

3. Results

We registered the occurrence of 65 species in 10 genera and three subfamilies. Bromelioideae represented the greatest number of genera (7), followed distantly by Tillandsioideae (2) and Pitcairnioideae (1). The number of species, however, was higher in Tillandsioideae (36), distantly followed by Pitcairnioideae (15) and Bromelioideae (14). The genera ordered by the number of species represented were *Tillandsia* (22), *Dyckia* (15), *Vriesea* (14), *Aechmea* (4), *Nidularium* (3), *Billbergia* and *Bromelia* (2), and *Ananas, Edmundoa,* and *Wittrockia* (1). The list of species and their recorded functional traits is shown in Table 2. Figure 3 displays photographs of the ecological types in different habitats on the testimonial hills.

The fourth-corner tests (Fig. 4) revealed that functional traits were associated with at least one of the environmental variables, except for status epiphytic, rooting, and sunlight indifference. However, they were not significantly associated with most of the environmental variables. The RLQ ordination (Fig. 5) showed that a coastal–inland gradient constrained the distribution of species' functional traits. Along the ordination axes, the spatially closest species showed similar functional traits and occupied similar ecological niches. The first two ordination axes contributed 86.6% ($P < 0.001$) and 9.8% ($P = 0.006$) in the total variation in the distribution of species, respectively.

However, extension of the RLQ approach demonstrated a discrepancy between the trait- and phylogeny-based information coefficient points (Fig. 6). The distribution of

Bromeliaceae along the first axis of RLQ ordination, especially the genus *Dyckia*, has been influenced by other ecological and evolutionary aspects not considered in our study. The associations (fourth-corner test) of environmental and spatial variables with functional traits and phylogeny were significant ($P < 0.001$). Also, relationships between environment and functional traits; environment and phylogeny; space and functional traits; and space and phylogeny were significant ($P < 0.005$). The first axis of the RLQ ordination explained 75.5% ($P < 0.001$) of the total variation. Pearson correlations (Fig. 7) between the environmental variables and the coordinates of the testimonial hills evidenced that the positive side of the ordination axis was strongly correlated with the maximum temperature of warmest month (bio5) and the annual temperature variation (bio7). Denoting that in the westernmost region, atmospheric bromeliads with smaller rosettes and CAM predominated (Fig. 7). In contrast, the negative side of the ordination correlated weakly with the minimum temperature of coldest month (bio6) and moderately strongly with Atlantic Forest (Atl). Denoting that in the easternmost region, tank bromeliads with large rosettes, sciophytes, and C3 predominated (Fig. 7).

The D-statistic (Table 3) identified phylogenetic signals in rosette size and light requirement, indicating that these functional traits are conserved. The phylogenetic signals for the other functional traits were strong, indicating that species with these functional traits depend on the occupation of conserved niches, i.e., they tend to conserve ancestral ecological traits. Below a significance level of 0.01, almost all functional traits differed significantly from random distributions throughout phylogeny and did not differ significantly from the Brownian motion model. Lithophyte status differed significantly from both the Brownian motion and random distribution models.

According to the dissimilarity distances (Fig. 8, Table 4 and 5), we evidenced that the functional and phylogenetic structures exhibited an incongruent response along the coastal-inland gradient. Environmental filtering regulated the functional structure (NRI and NTI, dcFdist) while limiting similarity controlled the phylogenetic structure (NRI and NTI, dcPdist). But when we analyzed the combined functional and phylogenetic structures (Fig. 9, Table 4 and 5), i.e., the combination of the trait dissimilarity distance and the phylogeny dissimilarity distance decoupled from the trait information (Fdist + dcPdist), the NRI revealed that limiting similarity controlled the structure of Bromeliaceae assemblages in the easternmost region. However, with increasing continentality, approximately 200km from the coast, the preponderance of environmental filtering began to control the structure of the Bromeliaceae assemblages. This circumstance is in agreement with the SDH prediction. Yet, the NTI suggested that limiting similarity controlled the Bromeliaceae assemblages.

4. Discussion

Our results suggested that the functional and phylogenetic structure of Bromeliaceae assemblages along the coastal-inland gradient was governed by a paradox of the stress-dominance hypothesis (SDH) due to the differential fitness of atmospheric and tank bromeliads to temperature and moisture variation, as predicted by Winkler (1980). We found that the distribution of functional traits was associated with distance from the coast, a proxy for temperature range and variation in air moisture. On the Atlantic Coastal Plain, the maritime climate favored tank bromeliads with C3 photosynthesis and medium to large rosettes. Whereas in the far western region, the continental climate favored atmospheric bromeliads with CAM photosynthesis and smaller rosettes. Based on Ramm et al. (2018), we hypothesized that rosettes with high surface-to-volume ratios were more adapted to thermally stressful environments (i.e., lower moisture, higher insolation, and higher evapotranspiration) because they allow greater thermoregulation compared with rosettes with lower surface-to-volume ratios. However, Schlesinger and Marks (1977) proposed that species with higher surface-to-volume ratios (e.g., *T. usneoides*) are more effective at capturing aerosolized minerals than conserving water. C3 and CAM species in the coastal plain share the same habitats and are subject to the same thermal and solar radiation stress. According to Waechter (2002), moist forests represent a barrier for xerophytic floras (i.e., CAM species); however, rocky outcrops or inselbergs reduce the moisture available, enabling the broad colonization of xerophytic genera, e.g., *Dyckia* and *Tillandsia*. Alternatively, Reinert (1988) proposed that the CAM may be a salt exposure strategy in the maritime climate. Additionally, as Winkler (1980) noted, in the westernmost region, the continental climate favors CAM species.

We found that most functional traits have a strong phylogenetic signal. This indicates that climatic niche occupancy along the coastal–inland gradient is influenced by tropical niche conservatism (Wiens and Donoghue, 2004). Thus, we assume that tropical niche conservatism may be crucial in explaining the distribution of tank bromeliad lineages since fundamental niche occupancy is determined by the intrinsic functional traits of Bromeliaceae lineages. Tropical tank bromeliad lineages that have not developed ecophysiological adaptations to migrate to the subtropical continental climate (i.e., temperate climate) remain confined to the subtropical maritime climate north of the Atlantic Coastal Plain. We postulate that habitat tracking processes dictate the distributions of functional traits through stabilizing selection (Ackerly, 2003). Tank bromeliad lineages preferentially occupy habitats closer to tropical climate conditions, exhibiting tropical niche conservatism. They track habitats similar to the tropical ancestral niche rather than adapting to new climatic niches (Harvey and Pagel, 1991; Ackerly, 2003). *Vriesea friburguensis* var. *tucumanensis* is the only tank bromeliad lineage restricted to the westernmost end of the coastal–inland gradient. We presume that the distribution of this lineage is the result of niche evolution (Wiens and Donoghue, 2004), i.e., it evolved ecophysiological adjustments to invade the temperate climatic niche and thus lost the ability to colonize and persist in the maritime climatic niche (i.e., the ancestral tropical climatic niche). Furthermore, few tank bromeliad lineages (*A. recurvata*, *B. zebrina*, *V. gigantea*, and *V. platynema*) have overcome the barriers of a subtropical continental climate and dispersed westward into the deciduous forests of the midwestern region of Rio Grande do Sul. These lineages likely have ecophysiological plasticity to be able to occupy a wide range of climatic regimes in the transitional zone from maritime to continental climate. As Gobara (2015) documented, *V. gigantea* is a C_3 species; nevertheless, seasonal water stress (i.e., water scarcity) induces CAM.

As Winkler (1980) reported, two groups of *Tillandsia* occur along the coastal–inland gradient: mesophytes of widespread occurrence or restricted to the easternmost region, and xerophytes restricted to the westernmost region. The xerophytic lineages *T. bandensis*, *T. duratii*, *T. loliacea*, *T. pohliana*, *T. streptocarpa*, and *T. uruguayensis* are unable to migrate eastward due to the maritime climate. They originate from the drier Chacoan domain (Winkler, 1980; Gomes et al., 2019) and generally extend into Rio Grande do Sul through the parks of Argentina (Winkler, 1980); *T. uruguayensis* expands from Uruguay (Rossado et al., 2018). We conjecture that these lineages, well as those of *Dyckia*, occupy remnant niches of a past climate. During the Holocene, about 10.000 years BP, in a dry climate in Rio Grande do Sul, xerophytic lineages predominated. After the last glacial maximum between 10.000- and 5.000-years BP, the climate became warm and moist, favoring the expansion of subtropical forests (Rambo, 1961; Behling, 1998; Behling et al., 2005) and forming barriers that prevent the distribution of xerophytic lineages found on rocky outcrops or inselbergs. These remnant niches are drivers of local endemism, e.g., *T. polzii*, *T. jonesii*, and *T. bella*, in addition to *D. agudensis*, *D. alba*, *D. hebdingii*, *D. ibicuiensis*, *D. myriostachya*, *D. nigrospinulata*, *D. retardata*, *D. rigida*, *D. tomentosa*, and *D. vicentensis*. In contrast, the xerophytic lineages *T. xiphioides*, *T. mallemontii*, *T. gardneri*, and *T. crocata* are adapted to the moist tropical forest and lack the ecophysiological adjustments necessary to occupy the temperate climatic niche at the western end, exhibiting phylogenetic niche conservatism.

Wiens and Donoghue (2004) and Wiens and Graham (2005) mentioned that climatic niche specialization appears to be important in many groups that occur in tropical regions, such as crocodiles, caecilians, and trogonoid birds, but are absent in geographically adjacent temperate regions. We thus suggest that niche conservatism determines the distribution of functional traits in Bromeliaceae lineages along the coastal–inland gradient. Lineages that manifest phylogenetic niche conservatism tend to occupy or trace ancestral ecological niches throughout biogeographic history. When niche conservatism is not present, the ecophysiological adjustments to environmental heterogeneity exhibit greater flexibility.

In general, in Bromeliaceae assemblages along the coastal-inland gradient, community assembly processes were random with respect to the species pool. Thus, we cannot independently infer the processes of habitat filtering and limiting similarity (i.e., competitive exclusion), although the functional and phylogenetic structure is dictated by a paradox of the SDH. In the coastal plain, the Bromeliaceae assemblages are regulated mainly by competitive exclusion processes, but the distribution of some atmospheric bromeliads is regulated by maritimity, a habitat filtering process. In the west, the continental climate regulates the distribution of tank bromeliads (habitat filtering), while atmospheric bromeliads are regulated mainly by limiting similarity.

As Swenson (2019) suggested, the abiotic environment likely plays a role in selecting phenotypes that competitively dominate the system. Along the coastal–inland gradient, congeneric lineages (e.g., *Tillandsia*) tend to possess similar biological traits and therefore tend to compete more intensely than lineages of distinct genera (Darwin, 1859). Darwin's niche occupancy paradox probably occurs, that is, phylogenetically close lineages tend to occupy similar ecological niches, but such lineages should also experience strong competitive interactions due to niche overlap, which limits species coexistence (Webb et al., 2002; Cavender-Bares et al., 2009). However, species coexistence can occur when subtle niche differences overcome slight differences in competitive ability or strong niche differences overcome large differences in competitive ability (Mayfield and Levine, 2010). Alternatively, the high similarity of functional traits between some Bromeliaceae lineages must also lead to stochasticity (Hubbell, 2001), thus regulating the functional and phylogenetic structure of Bromeliaceae assemblages.

5. Conclusion

In this study, we have shown that the functional traits of tropical Bromeliaceae experience influenced by phylogenetic niche conservatism, which prevents certain species from occurring in continental zones. Lineages that manifest phylogenetic niche conservatism tend to occupy or track ancestral ecological niches. The functional and phylogenetic structure of Bromeliaceae assemblages exhibits a paradox of the stress-dominance hypothesis (SDH). Habitat filtering and competitive exclusion, concomitantly, influence community assembly and species coexistence due to the differential fitness of atmospheric and tank bromeliads to the effects of coastal and continental climate. Yet, community assembly is predominantly random concerning the species pool. We recommend that for a greater understanding of the structuring processes of Bromeliaceae assemblages along the coastal-inland gradient, future research should investigate the internal structure of metacommunities based on functional and phylogenetic aspects.

6. References

Ackerly, D.D., 2003. Community assembly, niche conservatism, and adaptive evolution in changes environments. International Journal of Plant Sciences 164(3):S165–S184. doi:10.1086/368401

Ács, É., Földi, A., Vad, C.F., Trábert, Z., Kiss, K.T., Duleba, M., Borics, G., Grigorszky, I., Botta-Dukát, Z., 2019. Trait-based community assembly of epiphytic diatoms in saline astatic ponds: a test of the stress-dominance hypothesis. Scientific Reports 9:15749. doi.org/10.1038/s41598-019-52304-4

Barfuss, M.H.J., Till, W., Le, E.M.C., Pinzón, J.P., Manzanares, J.M., Halbritter, H., Samuel, R., Brown, G., 2016. Taxonomic revision of Bromeliaceae subfam. Tillandsioideae based on a multi-locus DNA sequence phylogeny and morphology. Phytotaxa 279(1):001–097. doi.org/10.11646/phytotaxa.279.1.1

Behling, H., 1998. Late Quaternary vegetational and climatic changes in Brazil. Review of Palaeobotany and Palynology 99(2): 143–156. doi:10.1016/S0034-6667(97)00044-4

Behling, H., Pillar V.D., Bauermann, S.G., 2005. Late Quaternary grassland (Campos), gallery forest, fire and climate dynamics, studied by pollen, charcoal and multivariate analysis of the São Francisco de Assis core in western Rio Grande do Sul (southern Brazil). Review of Palaeobotany and Palynology 133(3–4), 235–248. doi:10.1016/j.revpalbo.2004.10.004

Benzing, D.H., 1990. Vascular Epiphytes: General Biology and Related Biota. Cambridge Tropical Biology Series.

Benzing, D.H., 2000. Bromeliaceae: Profile of An Adaptive Radiation. Cambridge Press.

Bivand, R., Lewin-Koh, N., Pebesma, E., Archer, E., Baddeley, A., Bearman, N., Bibiko, H-J., Brey, S., Callahan, J., Carrillo, G., Dray, S., Forrest, D., Friendly, M., Giraudoux, P., Golicher, D., Rubio, V.G., Hausmann, P., Hufthammer, K.O., Jagger, T., Johnson, K., Lewis, M., Luque, S., MacQueen, D., Niccolai, A., Pebesma, E., Lamigueiro, O.P., Plunkett, E., Rubak, E., Short, T., Snow, G., Stabler, B., Stokely, M., Turner, R., 2022. Package maptools: Tools for Handling Spatial Objects. Version 1.1-3. https://cran.r-project.org/web/packages/maptools/index.html. (Accessed 14 March 2022).

Cadotte, M.W., Davies, T.J., 2016. Phylogenies in ecology: A guide to concepts and methods. Princeton. NJ: Princeton University Press.

Carboni, M., de Bello, F., Štepán J., Jí, D., Horník, J., Lepš, J., Reitalu, T., Klimešová, J., 2014. Changes in trait divergence and convergence along a productivity gradient in wet meadows. Agriculture, Ecosystems and Environment 182:96-105. doi.org/10.1016/j.agee.2013.12.014

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A., Kembel, S.W., 2009. The merging of community ecology and phylogenetic biology. Ecology Letters 12:693–715. doi:10.1111/j.1461-0248.2009.01314.x

Chang, W., RStudio, Tessil, 2021. Package fastmap: Fast Data Structures. Version: 1.1.0. https://cran.r-project.org/web/packages/fastmap/index.html. (Accessed 10 March 2022).

Choler, P., 2005. Consistent Shifts in Alpine Plant Traits along a Mesotopographical Gradient. Arctic, Antarctic, and Alpine Research 37(4):444-453,.DOI: 10.1657/1523-0430(2005)037[0444:CSIAPT]2.0.CO;2

Cleveland, W.S., 1979. Robust Locally Weighted Regression and Smoothing Scatterplots. Journal of the American Statistical Association 74(368):829–836.

Coyle, J.R., Halliday, F.W., Lopez, B.E., Palmquist, K.A., Wilfahrt, P.A., Hurlbert, A.H., 2014. Using trait and phylogenetic diversity to evaluate the generality of the stress-dominance hypothesis in Eastern North American tree communities. Ecography 37:814–826. doi: 10.1111/ecog.00473

Craig, E.M., 1994. Physiological ecology of the Bromeliaceae. Botanical Review 60(1):1–82. https://www.jstor.org/stable/4354220

Crayn, D.M., Winter, K., Smith, J.A.C., 2004. Multiple origins of crassulacean acid metabolism and the epiphytic habit in the Neotropical family Bromeliaceae. PNAS 101(10):3703–3708. https://doi.org/10.1073/pnas.0400366101

Crayn, D.M., Winter, K., Schulte, K., Smith, J.A.C., 2015. Photosynthetic pathways in Bromeliaceae: phylogenetic and ecological significance of CAM and C3 based on carbon isotope ratios for 1893 species. Botanical Journal of the Linnean Society 178(2):169–221. doi.org/10.1111/boj.12275

Darwin, C., 1859. The Origin of Species. Modern Library, New York.

de Bello, F., Šmilauer, P., Diniz-Filho, J.A.F., Carmona, C.P., Lososová, Z., Herben, T., Götzenberger, L., 2017. Decoupling phylogenetic and functional diversity to reveal hidden signals in community assembly. Methods in Ecology and Evolution 8(10):1200-1211. doi.org/10.1111/2041-210X.12735

de Bello, F., Carmona, C.P., Dias A.T.C., Götzenberger L., Moretti, M., Berg, M.P., 2021. Handbook of trait-based ecology. Cambridge, UK: New York, NY: Cambridge University Press.

Dolédec, S., Chessel, D., ter Braak C.J.F., Champely, S., 1996. Matching species traits to environmental variables: a new three-table ordination method. Environmental and Ecological Statistics 3:143–166. doi:10.1007/BF02427859

Dray S., Chessel, D., Thioulouse, J., 2003. Co-inertia analysis and the linking of ecological data tables. Ecology 84(11):3078-3089. doi.org/10.1890/03-0178.

Dray, S., Legendre, P., 2008. Testing the species traits-environment relationships: the fourth-corner problem revisited. Ecology 89(12):3400-3412. doi.org/10.1890/08-0349.1

Dray, S., Dufour, A.-B., Thioulouse, J., 2021. Package ade4: Analysis of ecological data: Exploratory and Euclidean methods in environmental sciences. Version 1.7-18. http://www.R-project.org. (Accessed 10 January 2022).

Dray, S., Siberchicot, A., 2021. Package adegraphics: An S4 lattice-based package for representation of multivariate data. Version 1.0-16. http://www.R-project.org. (Accessed 10 January 2022).

Fick, S.E., Hijmans, R.J., 2017. Worldclim 2: New 1-Km spatial resolution climate surfaces for global land areas. International Journal of Climatology. https://www.worldclim.org. (Accessed 03 January 2020).

Field, A., Miles, J., Field, Z., 2012. Discovering statistics using R. Sage. Los Angeles, London, New Delhi, Singapore, Washington DC.

Flora do Brasil 2020. Jardim Botânico do Rio de Janeiro. Disponível em: <http://floradobrasil.jbrj.gov.br/>. (Accessed 21 March 2021).

Fritz, S. A., Purvis, A., 2010. Selectivity in mammalian extinction risk and threat types: A new measure of phylogenetic signal strength in binary traits. Conservation Biology 24:1042-1051. doi:10.1111/j.1523-1739.2010.01455.x

Gastauer, M., Saporetti-Junior, A.W., Valladares, F., Meira-Neto, J.A.A., 2017. Phylogenetic community structure reveals differences in plant community assembly of an oligotrophic white-sand ecosystem from the Brazilian Atlantic Forest. Acta Botanica Brasilica 31(4):531–538. doi: 10.1590/0102-33062016abb0442

Givnish, T.J., Millam, K.C., Berry, P.E., Sytsma, K.J., 2007. Phylogeny, adaptive radiation, and historical biogeography of Bromeliaceae inferred from ndhF sequence data. In Columbus, J.T., Friar, E.A., Porter, J.M., Prince, L.M., Simpson, M.G. [eds.], Monocots: Comparative biology and evolution – Poales, 3 – 26. Rancho Santa Ana Botanic Garden, Claremont, California, USA.

Givnish, T.J., Barfuss M.H.J., Van Ee, B., Riina, R., Schulte, K., Horres, R., Gonsiska, P.A., Jabaily, R.S., Crayn, D.M., Smith J.A.C., Winter, K., Brown, G.K., Evans, T.M., Holst, B.K., Luther, H., Till, W., Zizka, G., Berry, P.E., Sytsma, K.J., 2011. Phylogeny, adaptive radiation, and historical biogeography in Bromeliaceae: insights from an eight-locus plastid phylogeny. American Journal of Botany 98(5): 872–895. doi:10.3732/ajb.1000059

Givnish, T.J., Barfuss, M.H.J., Van Ee, B., Riina, R., Schulte, K., Horres, R., Gonsiska, P.A., Jabaily, R.S., Crayn, D.M., Smith, A.C., Winter, K., Brown, G.K., Evans, T.M., Holstm, B.K., Luther, H., Till, W., Zizka, G., Berry, P.E., Sytsma, K.J., 2014. Adaptive radiation correlated and contingent evolution, and net species diversification in Bromeliaceae. Molecular Phylogenetics and Evolution 71:55–78. doi:10.1016/j.ympev.2013.10.010

Gobara, B.N.K., 2015. Caracterização da capacidade de indução ao CAM em plantas de *Vriesea gigantea* (Bromeliaceae) sob déficit hídrico. Dissertação - Ciências Biológicas (Botânica), Universidade de São Paulo, Brazil.

Gomes, A.C., Ferreira, B.H., Souza, C.S., Arakaki, L.M.M., Aoki, C., Paggi, G.M., Sigrist, M.R., 2019. Adaptive response of extreme epiphyte *Tillandsia* Species (Bromeliaceae) is demonstrated by different sexual reproduction strategies in the Brazilian Chaco. Botanical Journal of the Linnean Society. XX:1–15. doi:10.1093/botlinnean/boz104

Graeff, O., 2015. Fitogeografia do Brasil uma atualização de bases e conceitos. Editora: Nau.

Graham, C.H., Parra, J.L., Tinoco, B.A., Stiles F.G., McGuire, J.A., 2012. Untangling the influence of ecological and evolutionary factors on trait variation across hummingbird assemblages. Ecology 93(8):99–111. doi.org/10.1890/11-0493.1

Griffiths, H., Smith, J.A.C., 1983. Photosynthetic pathways in the Bromeliaceae of Trinidad: relations between life-forms, habitat preference and the occurrence of CAM. Oecologia 60:176–184. doi.org/10.1007/BF00379519

Grime, J.P., 2006. Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. Journal of Vegetation Science 17(2):255-260. doi.org/10.1111/j.1654-1103.2006.tb02444.x

Fontoura, T., Scudeller V.V., Costa, A.F., 2012. Floristics and environmental factors determining the geographic distribution of epiphytic bromeliads in the Brazilian Atlantic Rain Forest. Flora 207:662–672. doi.org/10.1016/j.flora.2012.05.003

Hackathon, R., Bolker, B., Butler, M., Cowan, P., de Vienne, D., Eddelbuettel, D., Holder, M., Jombart, T., Kembel, S., Michonneau, F., Orme, D., O'Meara, B., Paradis, E., Regetz, J., Zwickl, D., 2020. Package phylobase: Base Package for Phylogenetic Structures and Comparative Data. Version 0.8.10. https://cran.r-project.org/web/packages/phylobase/index.html. (Accessed 10 March 2022).

Harmon, L., Pennell, M., Brock, C., Brown, J., Challenger, W., Eastman, J., FitzJohn, R., Glor, R., Hunt, G., Revell, L., Slater, G., Uyeda, J., Weir, J., 2020. Package geiger: Analysis of Evolutionary Diversification. Version 2.0.7. https://cran.r-project.org/web/packages/geiger/. (Accessed 15 March 2022).

Harvey, P.H., Pagel, M.D., 1991. The comparative method in evolutionary biology. Oxford: Oxford University Press.

Hijmans, R.J., van Etten, J. Sumner, M., Cheng, J., Baston, D., Bevan, A., Bivand, R., Busetto, L., Canty, M., Fasoli, B., Forrest, D., Ghosh, A., Golicher, D., Gray, J., Greenberg, J.A., Hiemstra, P., Hingee, K., Ilich, A., Institute for Mathematics Applied Geosciences, Karney, C., Mattiuzzi, M., Mosher, S., Naimi, B., Nowosad, J., Pebesma, E., Lamigueiro, O.P., Racine, E.B., Rowlingson, B., Shortridge, A., Venables, B., Wueest, R., 2022. Package raster: Geographic Data Analysis and Modeling. Version 3.5-15. https://cran.r-project.org/web/packages/raster/index.html (Accessed 14 March 2022).

HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M., Mayfield, M.M., 2012. Rethinking community assembly through the lens of coexistence theory. Annual Review of Ecology, Evolution, and Systematics 43:227–248. doi.org/10.1146/annurev-ecolsys-110411-160411

Ho, L.S., Ane, C., Lachlan, R., Tarpinian, K., Feldman, R., Yu, Q., van der Bijl, W., Maspons, J., Vos, R., 2020. Package phylolm: Phylogenetic Linear Regression. Version 2.6.2. https://cran.r-project.org/web/packages/phylolm/index.html. (Accessed 15 March 2022).

Hubbell, S.P., 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Oxford.

Jin, Y., Qian, H., 2019. V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants. Ecography 42:1353–1359. doi:10.1111/ecog.04434

Kembel, S.W., Hubbell, S.P., 2006. The phylogenetic structure of a neotropical tree community. Ecology – Ecological Society of America 87:S86:S99. doi:10.1890/0012-9658(2006)87[86:TPSOAN]2.0.CO;2

Kembel, S.W., Ackerly, D.D., Blomberg, S.P., Cornwell, W.K., Cowan, P.D., Helmus, M.R., Morlon, H., Webb, C.O., 2020. Package picante: Integrating Phylogenies and Ecology. Version 1.8.2. http://www.R-project.org. (Accessed 15 March 2022).

Kessler, M., 2002a. Environmental patterns and ecological correlates of range size among bromeliad communities of Andean forest in Bolivia. The Botanical Review 68(1):100–127. doi:10.1663/0006-8101/(2002)068 [0100:EPAECO]2.0.CO.2

Kessler, M., 2002b. Species richness and ecophysiological types among Bolivian bromeliad communities. Biodiversity and Conservation 11:987–1010. doi:10.1023/A:1015875807613

Ladino, G., Ospina-Bautista, F., Varón, J.E., Jerabkova, L. Kratina, P., 2019. Ecosystem services provided by bromeliad plants: A systematic review. Ecology and Evolution 9(12):7360–7372. doi.org/10.1002/ece3.5296

Legendre, P., Galzin, R., Harmelin-Vivien, M.L., 1997. Relating behavior to habitat: solutions to the fourth-corner problem. Ecology - Ecological Society of America 78:547–562. doi:10.1890/0012-9658(1997)078[0547:RBTHST]2.0.CO;2

Lhotsky, B., Kovács, B., Ónodi, G., Csecserits, A., Rédei, T., Lengyel, A., Kertész, M., Botta-Dukát, Z., 2016. Changes in assembly rules along a stress gradient from open dry grasslands to wetlands. Journal of Ecology 104:507–517. doi: 10.1111/1365-2745.12532

Males, J., 2016. Think tank: water relations of Bromeliaceae in their evolutionary context. Botanical Journal of the Linnean Society 181(3):415–440. doi.org/10.1111/boj.12423

Males, J., Griffiths, H., 2017. Functional types in the Bromeliaceae: relationships with drought-resistance traits and bioclimatic distributions. Functional Ecology 31:1868–1880. doi: 10.1111/1365-2435.12900

Martinelli G., Vieira C.M., Gonzalez M., Leitman P., Piratininga A., Costa A.F., Forzza R.C., 2008. Bromeliaceae da Mata Atlântica brasileira: lista de espécies, distribuição e conservação. Rodriguésia 59(1):209–258. doi.org/10.1590/2175-7860200859114

Mason, N.W.H., Richardson, S.J., Peltzer, D.A., de Bello, F., Wardle, D.A., Allen, R.B., 2012. Changes in coexistence mechanisms along a long-term soil chronosequence revealed by functional trait diversity. Journal of Ecology 100(3):678-689. doi.org/10.1111/j.1365-2745.2012.01965.x

Mayfield, M.M., Levine, J.M., 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecology Letters 13:1085–1093. doi.org/10.1111/j.1461-0248.2010.01509.x

Miazaki, A.S., Gastauer, M., Meira-Neto, J.A.A., 2015. Environmental severity promotes phylogenetic clustering in campo rupestre vegetation. Acta Botanica Brasilica 29(4):561–566. doi: 10.1590/0102-33062015abb0136

Navas, M., Violle, C., 2009. Plant traits related to competition: how do they shape the functional diversity of communities? Community Ecology 10(1):131–137. https://www.jstor.org/stable/24113559

Nimer, E., 1990. Clima. In: Geografia do Brasil – Região Sul. Rio de Janeiro, IBGE. V2.

Nipperess, D., Wilson, P., 2021. An r package for Phylogenetic Diversity (PD) calculations in ecology, biogeography and conservation biology. Version 0.4.4.9000. https://github.com/davidnipperess/PDcalc. (Accessed 15 March 2022).

Ormer, D., 2018. The caper package: comparative analysis of phylogenetics and evolution in R. Version 1.0.1. http://www.R-project.org. (Accessed at: 15 February 2020).

Paradis, E., Blomberg, S., Bolker, B., Brown, J., Claramunt, S., Claude, J., Cuong, H.S., Desper, R., Didier, G., Durand, B., Dutheil, J., Ewing, R.J., Gascuel, O., Guillerme, T., Heibl, C., Ives, A., Jones, B., Krah, F., Lawson, D., Lefort, V., Legendre, P., Lemon, J., Louvel, G., Marcon, E., McCloskey, R., Nylander, J., Opgen-Rhein, R., Popescu, A-A., Royer-Carenzi, M., Schliep, K., Strimmer, K., de Vienne, D., 2022. Package ape: Analyses of Phylogenetics and Evolution. Version 5.6-2. https://cran.r-project.org/web/packages/ape/index.html. (Accessed 10 March 2022).

Pavoine, S., Vela, E., Gachet, S., de Bélair, G., Bonsall, M.B., 2011. Linking patterns in phylogeny, traits, abiotic variables and space: a novel approach to linking environmental filtering and plant community assembly. Journal of Ecology 99:165–175. doi: 10.1111/j.1365-2745.2010.01743.x

Pavoine, S., 2021. Package adiv: Analysis of Diversity. Version 2.1.1. https://cran.r-project.org/web/packages/adiv/index.html. (Accessed 10 March 2022).

R Development Core Team R, 2017. R: A language and environment for statistical computing R. Foundation for statistical computing, Vienna, Austria. ISBN 3-900051-07-0, URL. The R Project for statistical computing 2017. http://www.R-project.org

Rambo, B., 1961, Migration routes of South Brazilian Rain Forest. Pesquisa, Botânica. São Leopoldo: Instituto Anchietano de Pesquisa 12:1–54.

Ramm, T., Cantalapiedra, J.L., Wagner, P., Penner, J., Rödel, M.-O., Müller J., 2018. Divergent trends in functional and phylogenetic structure in reptile communities across Africa. Natural Communications 9(4697):1–10. doi:10.1038/s41467-018-07107-y

Rangel, T.F., Colwell, R.K., Graves, G.R., Fučíková, K., Rahbek, C., Diniz-Filho. J.A.F., 2015. Phylogenetic uncertainty revisited: Implications for ecological analyses. Evolution 69:1301-1312. doi:10.1111/evo.12644

Reinert, F., 1998. Epiphytes: photosynthesis, water balance and nutrients. In Scarano, F.R., Franco, A.C. (eds.). Ecophysiological strategies of xerophytic and amphibious plants in the neotropics. Serie Oecologia Brasiliensis. Rio de Janeiro, Brazil 4:87–10.

Revell, L.J., 2022. Package phytools: Phylogenetic tools for comparative biology (and other things). Version 1.0.3. http://www.R-project.org. (Accessed 08 April 2022).

Rossado, A. J., Donadío, S., JOSÉ M. Bonifacino, J. M., 2018. Tillandsia uruguayensis (Tillandsioideae, Bromeliaceae), a new epilithic species from Uruguay. Phytotaxa 345 (2): 133–142. doi.org/10.11646/phytotaxa.345.2.4

Rossato, M.S., Bellanca, E.T., Fachinello, A., Cândido, L.A., Silva, C.R., Suertegaray, D.M., 2008. Terra: feições ilustradas / organizado por Dirce Maria Antunes Suertegaray. 3ª Edição – Porto Alegre: Editora da UFRGS.

Schlesinger, W.H., Marks, P. L., 1977. Mineral cycling and the niche of Spanish moss, *Tillandsia usneoides* L. American Journal of Botany, 64(10), 1254–1262. doi:10.1002/j.1537-2197.1977.tb10819.x

Swenson, N.G., Enquist, B.J., 2007. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. American Journal of Botany 91:451–459. doi.org/10.3732/ajb.94.3.451

Swenson, N.G., Enquist, B.J., 2009. Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. Ecology 90:2161–2170. doi.org/10.1890/08-1025.1

Swenson, N.G., 2019. Phylogenetic ecology: A history, critique, and remodeling. University of Chicago Press, Chicago and London.

ter Braak, C.J.F., Šmilauer, P., Dray. S., 2018. Algorithms and biplots for double constrained correspondence analysis. Environmental and Ecological Statistics 25:171–197. doi.org/10.1007/s10651-017-0395-x

Thioulouse J., Dray, S., Dufour, A.-B., Siberchicot, A., Jombart, T., Pavoine, S., 2018. Multivariate analysis of ecological data with ade4. Springer, New York, USA.

Waechter, J.L., 2002. Padrões geográficos na flora atual do Rio Grande do Sul. Ciências & Ambiente – Fitogeografia do Sul da América, Santa Maria 1(24): 93–108.

Webb, C.O., 2000. Exploring the phylogenetic structure of ecological communities an example for rain forest trees. American Naturalist, 156:145–155. doi: 10.1086/303378

Webb, C.O., Ackerly, M.A., McPeek, Donoghue, M.J., 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33:475–505. doi:10.1146/annurev.ecolsys.33.010802.150448

Wickham, H., Chang, W., Henry, L., Pedersen, T.L., Takahashi, K., Wilke, C., Woo, K., Yutani, H., Dunnington, D., RStudio, 2020. Create Elegant Data Visualisations Using the Grammar of Graphics. http://www.R-project.org. (Accessed 20 March 2022).

Wiens, J.J., Donoghue, M.J., 2004. Historical biogeography, ecology and species richness. Trend in Ecology and Evolution 19:639–644. doi:10.1016/j.tree.2004.09.011

Wiens, J.J., Graham, C.H., 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review Ecology and Systematics 36:519–539. doi.org/10.1146/annurev.ecolsys.36.102803.095431

Winkler, S., 1980. Ursachen der Verbreitungsmuster einiger Bromeliaceae in Rio Grande do Sul (Südbrasilien). Flora 170:371–393.

Winkler S., 1982. Die Bromeliaceae von Rio Grande do Sul (S-Brasilien). Documenta Naturae. 3:1–90.

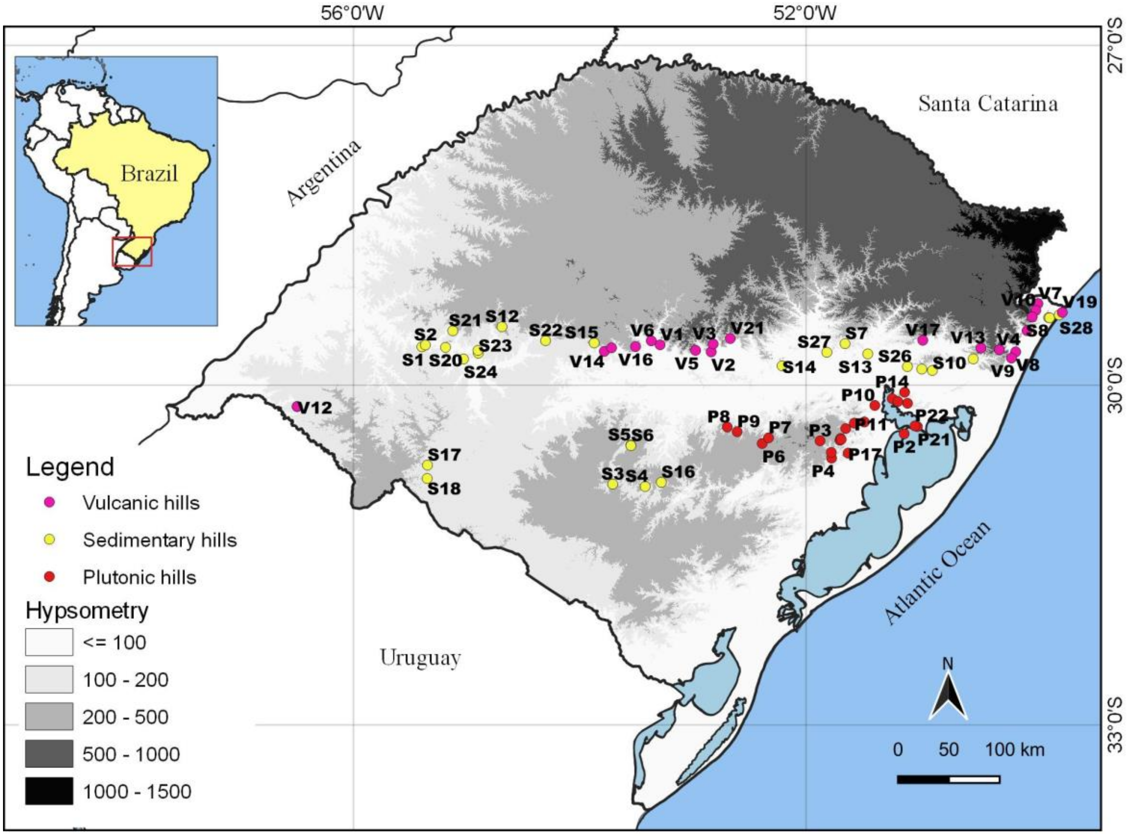


Fig. 1. Hypsometric map of Rio Grande do Sul State showing the location and lithology of the 71 studied testimonial hills distributed along a coastal-inland geographic corridor formed by Central Depression.

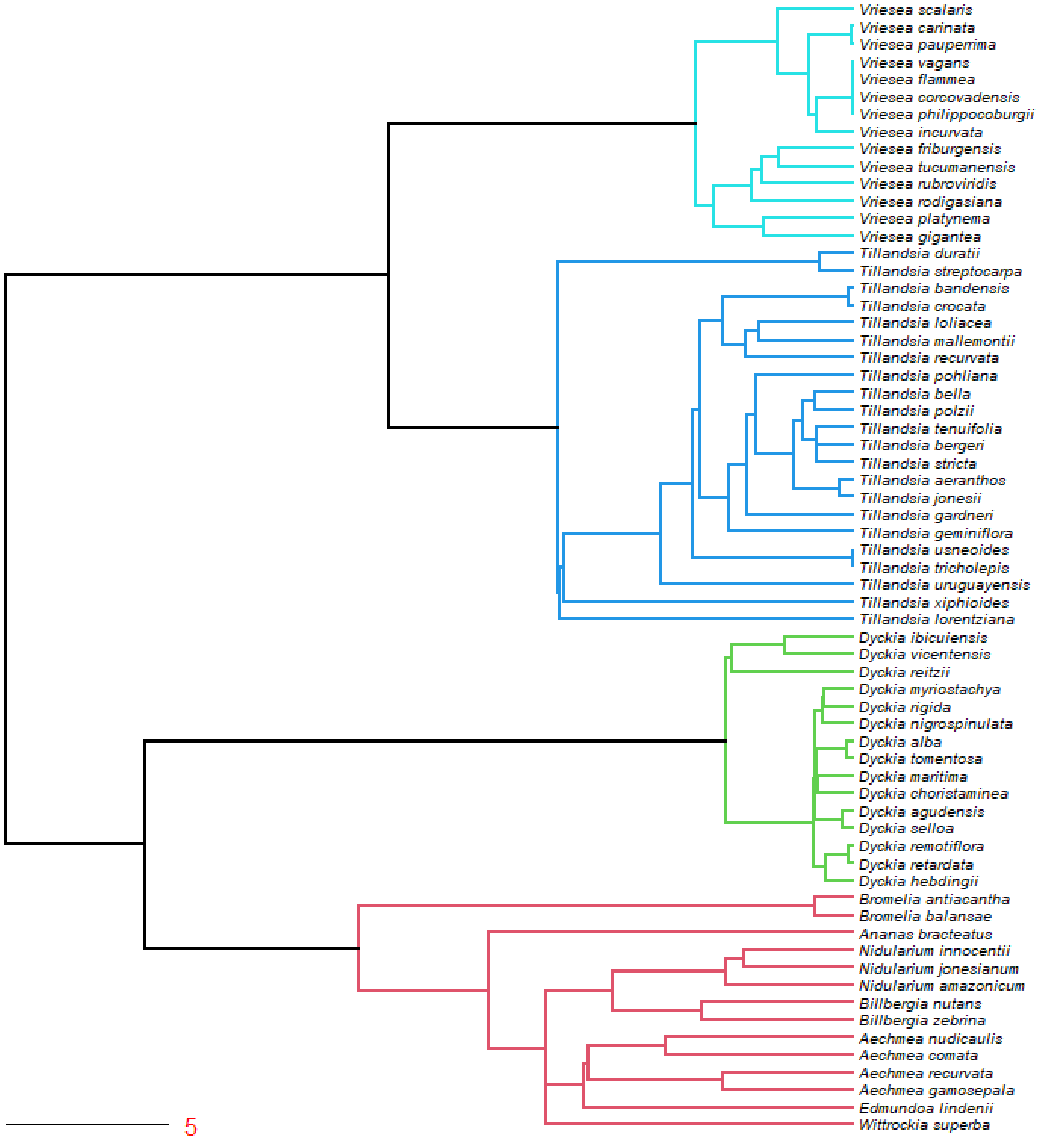
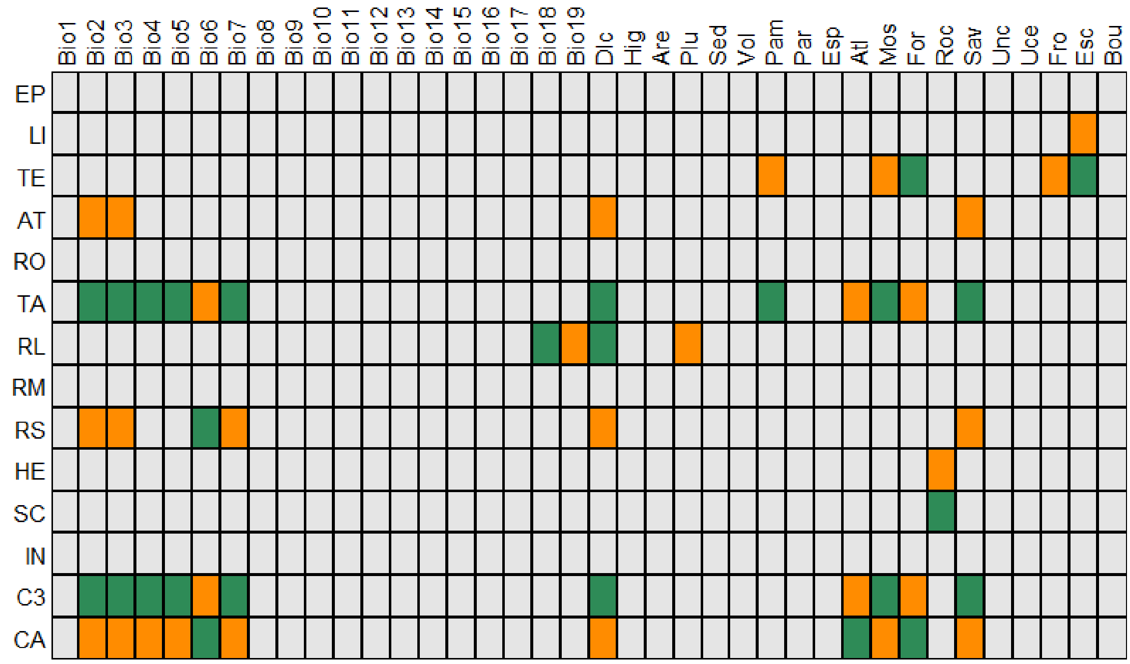


Fig. 2. Phylogenetic tree of the Bromeliaceae species pool (65 species). It was based on the mega-tree GBOTB.extended.tre (Smith and Brown, 2018) and the designation of the closest relative based on morphological and phylogenetic aspects. The scale left below indicates five million years.

Fig. 3. These photographs illustrate the life forms of Bromeliaceae species in different habitats on the testimonial hills. A. *Vriesea friburgensis*. B. *V. incurvata*. C. *V. platynema*. D. *V. philippocoburgii*. E. *V. scalaris*. F. *Tillandsia aeranthos*. G. *T. geminiflora*. H. *T. pohliana*. I. *T. uruguayensis*. J. *T. bella* and *Dyckia alba*. K. *D. vicentensis*. L. *D. ibicuiensis*. M. *D. maritima*. N. *Bromelia antiacantha*. O. *Billbergia zebrina*. P. *Edmundoa lindenii*. Q. *Nidularium amazonicum*. A-E, G-M and P - Habit. F, N, O, and Q - Inflorescence detail.



	Bio1	Bio2	Bio3	Bio4	Bio5	Bio6	Bio7	Bio8	Bio9	Bio10	Bio11	Bio12	Bio13	Bio14	Bio15	Bio16	Bio17	Bio18	Bio19	Dlc	Hig	Are	Plu	Sed	Vol	Pam	Par	Esp	Atl	Mos	For	Roc	Sav	Unc	Uce	Fro	Esc	Bou
EP	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜
LI	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟧	⬜
TE	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟧	⬜	⬜	⬜	🟧	🟩	⬜	⬜	⬜	⬜	🟧	🟩	⬜
AT	⬜	🟧	🟧	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟧	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟧	⬜	⬜	⬜	⬜	⬜
RO	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜
TA	⬜	🟩	🟩	🟩	🟩	🟧	🟩	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟩	⬜	⬜	⬜	⬜	⬜	🟩	⬜	⬜	🟧	🟩	🟧	⬜	🟩	⬜	⬜	⬜	⬜	⬜
RL	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟩	🟧	🟩	⬜	⬜	🟧	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜
RM	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜
RS	⬜	🟧	🟧	⬜	⬜	🟩	🟧	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟧	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟧	⬜	⬜	⬜	⬜	⬜
HE	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟧	⬜	⬜	⬜	⬜	⬜	⬜
SC	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟩	⬜	⬜	⬜	⬜	⬜	⬜
IN	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜
C3	⬜	🟩	🟩	🟩	🟩	🟧	🟩	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟩	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟧	🟩	🟧	⬜	🟩	⬜	⬜	⬜	⬜	⬜
CA	⬜	🟧	🟧	🟧	🟧	🟩	🟧	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟧	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟩	🟧	🟩	⬜	🟧	⬜	⬜	⬜	⬜	⬜

Fig. 4. Associations between functional traits and environmental variables resulting from fourth-corner tests. Dark orange cells correspond to positive significant associations, while sea green cells correspond to negative significant associations. Nonsignificant associations are in gray. Codes for functional traits and environmental variables can be seen in the methods.

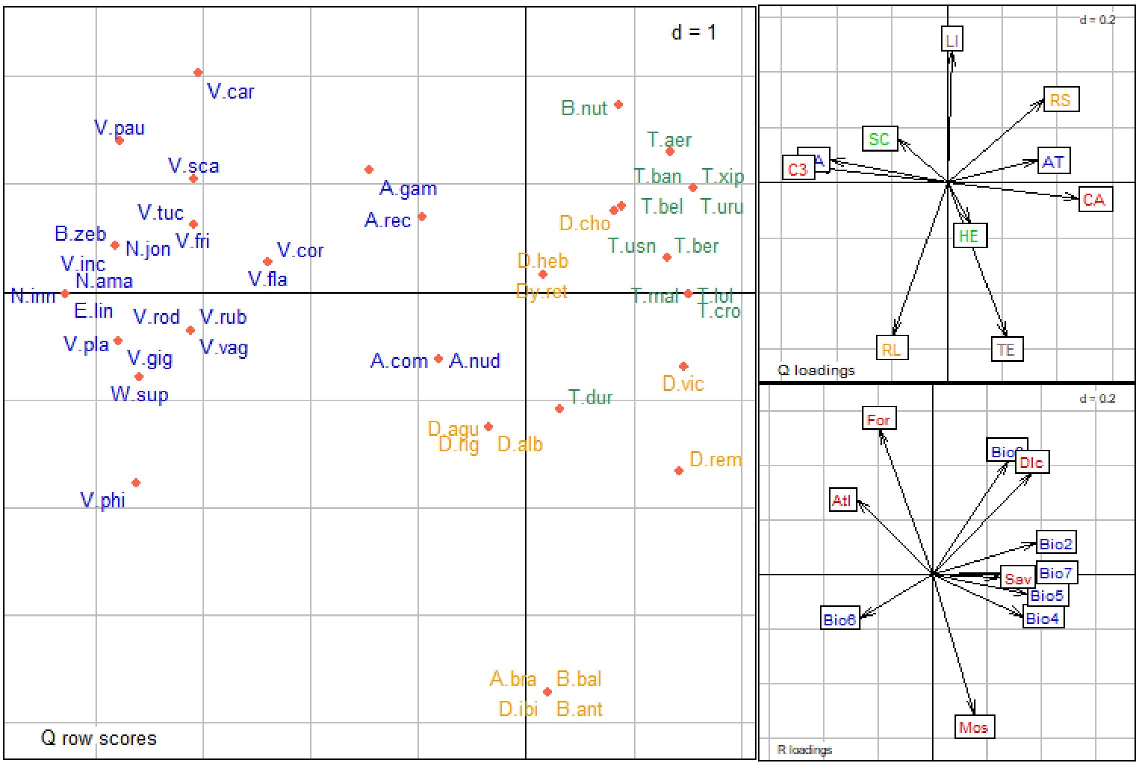


Fig. 5. Results of the first two axes of RLQ ordination. At the left, scores of species (Q row scores), above right, coefficients for functional traits (Q loadings), and below right, coefficients for environmental variables (R loadings). The codes for species names, environmental variables and functional traits can be seen in the methods and in Table 2. The values of d give the grid size. In blue, tank bromeliads; in sea green, atmospheric bromeliads; in dark orange, root bromeliads.

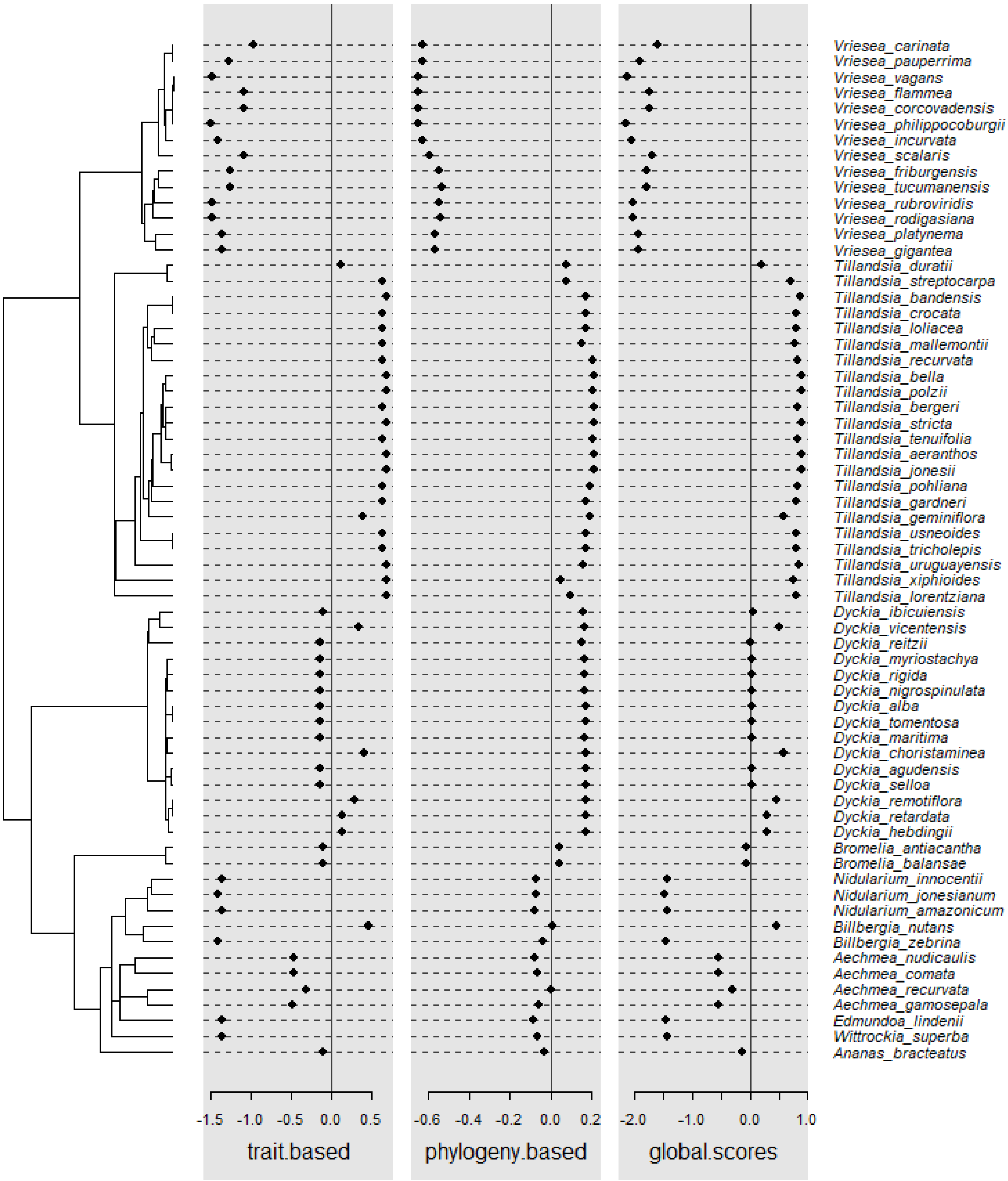


Fig. 6. Dot plot of coefficients of trait- and phylogeny-based information, and global scores, on the first axis of RLQ ordination, next to the phylogenetic tree.

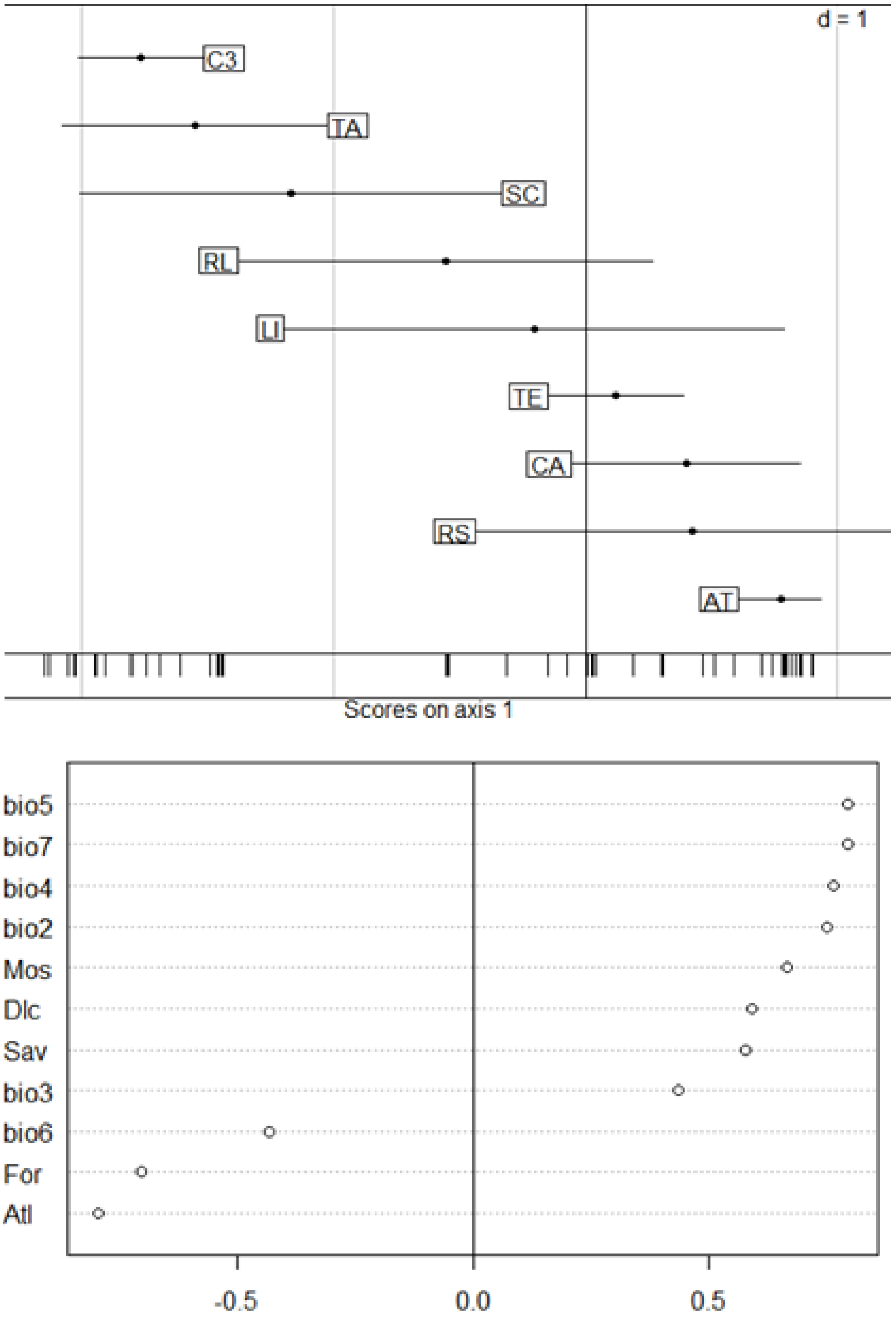


Fig. 7. Correlations of functional traits and environmental variables to the first axis of the RLQ ordination. Above, functional traits are located at the average coordinates of the species that possess them. Below are Pearson correlations (based on raw data) between the environmental variables and the coordinates of the testimonial hills.

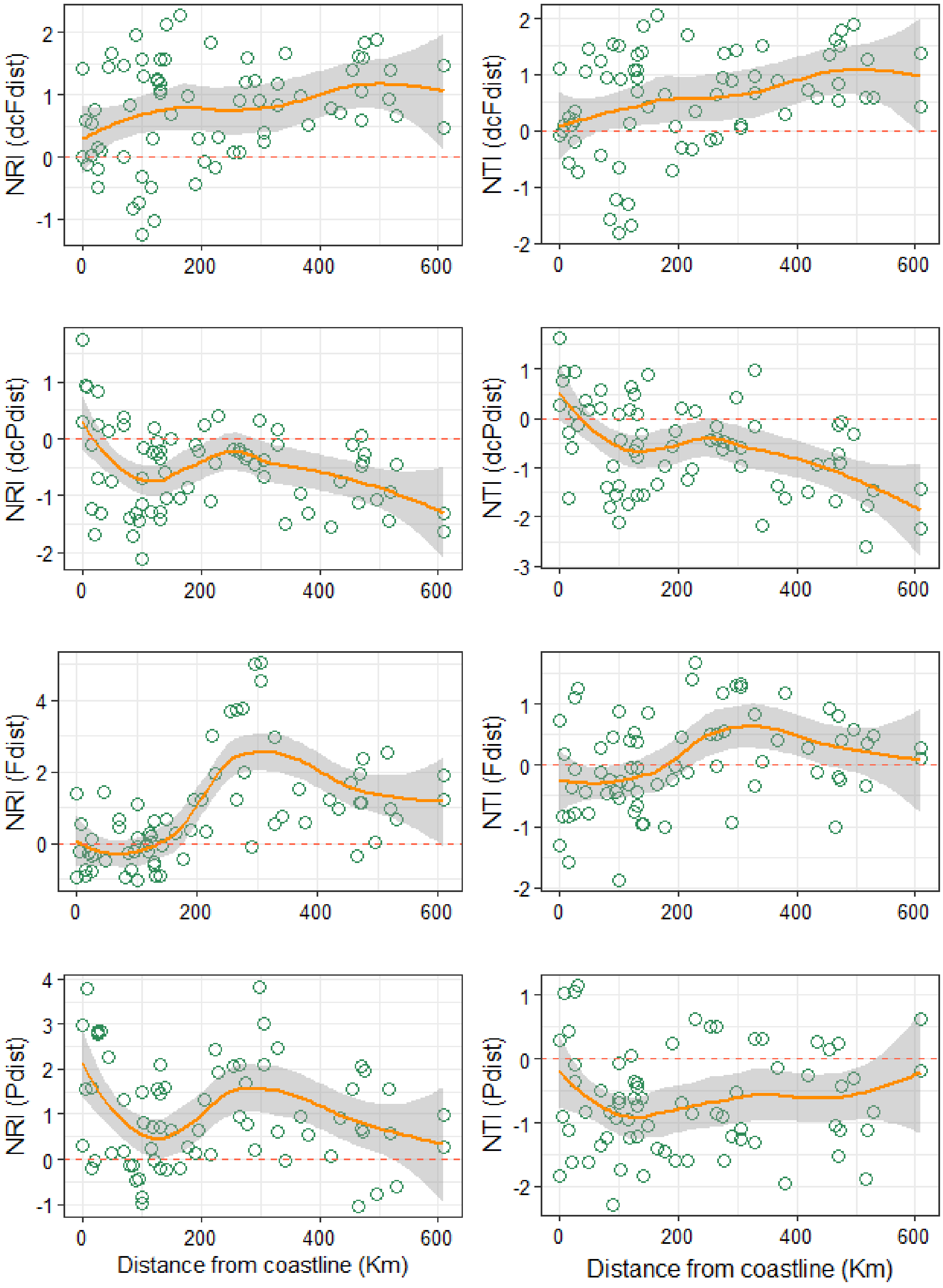


Fig. 8. Scatterplots show variations of net relatedness index (NRI) and nearest taxon index (NTI) along with the distance from the coastline (kilometers), using various dissimilarity measured, either decoupled (dcFdist, decoupled functional dissimilarity; dcPdist,

decoupled phylogenetic dissimilarity) or not (Fdist, functional dissimilarity; Pdist, phylogenetic dissimilarity). Scatterplots have a smoothing line (dark orange) summarizing the relationship of phylogenetic metrics to the distance from the coastline. The shaded area (gray) around the dark orange line is the 95% confidence interval.

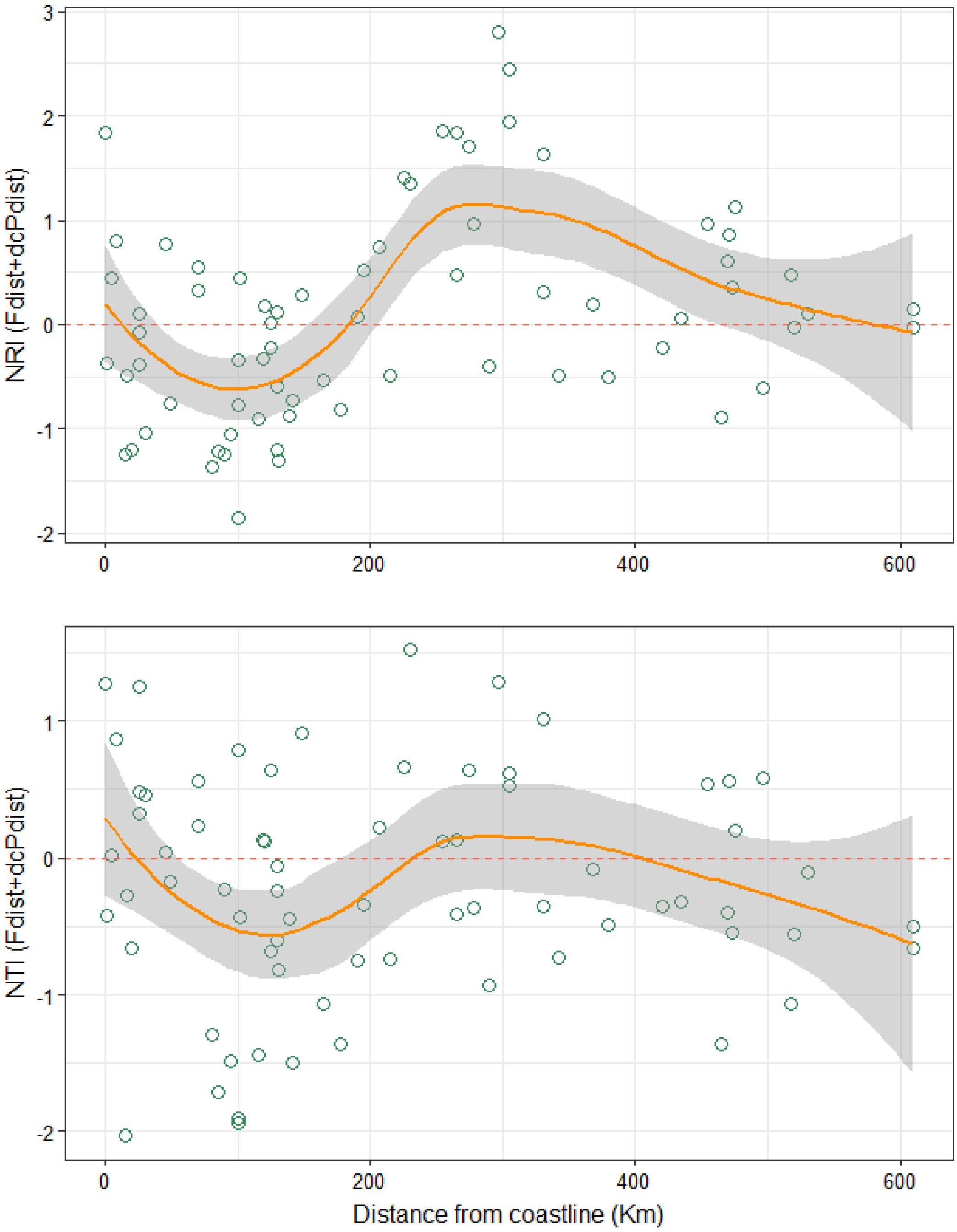


Fig. 9. Scatterplots show variations of net relatedness index (NRI) and nearest taxon index (NTI) along with the distance from the coastline (kilometers), using dissimilarity distance of combined traits and phylogeny without their overlap (Fdist + dcPdist). Scatterplots have a smoothing line (dark orange) summarizing the relationship of phylogenetic metrics to the distance from the coastline. The shaded area (gray) around the dark orange line is the 95% confidence interval.

Tab. 1. List of the 71 testimonial hills sampled along the coastal-inland gradient, with an expanse the approximately 600km, in the central Rio Grande do Sul State, in southernmost Brazil, with data on geopolitical localization, geologic substrate code [granitic rocks (P), sedimentary rocks (S), volcanic rocks (V)], geographic coordinates (Datum–WGS 84), distance from the coastline (DLC), highest elevation above sea level (HEL), and planimetric area (Area). We organized the data according to distance from the coast.

Municipality	Code	Latitude S	Longitude W	DLC Km	HEL m	Area Ha
Torres	V19	29°21'29"	49°44'07"	0	10	2
Torres	S28	29°22'50"	49°45'49"	0.9	65	24
Dom Pedro de Alcântara	S9	29°24'15"	49°51'22"	5	20	46
Dom Pedro de Alcântara	S8	29°24'15"	49°51'22"	8	105	48
Maquiné	V9	29°45'39"	50°11'06"	15	465	575
Maquiné	V8	29°42'24"	50°08'53"	16	343	566
Três Forquilhas	V20	29°31'11"	50°02'50"	20	420	60
Mampituba	V7	29°16'50"	49°57'04"	25	685	750
Morrinhos do Sul	V10	29º20'22"	49º58'12"	25	610	195
Tajuva	V18	29°23'51"	50°00'07"	25	860	465
Cará	V4	29º41'18"	50º17'39"	30	886	4300
Riozinho	V13	29º40'22"	50º27'19"	45	780	90
Santo Antonio da Patrulha	S19	29°46'05"	50°31'22"	49	146	30
Viamão	P21	30°21'59"	51°01'00"	70	260	240
Viamão	P22	30°21'38"	51°02'19"	70	170	285
Barra do Ribeiro	P2	30°25'48"	51°08'00"	80	100	170
Gravataí	S10	29°52'15"	50°53'03"	80	78	21
Porto Alegre	P15	30°09'38"	51°06'15"	85	290	1260
Gravataí	S11	29°51'31"	50°58'40"	90	345	485
Porto Alegre	P14	30º03'48"	51°07'47"	95	200	750
Porto Alegre	P13	30°07'10"	51°14'22"	100	145	170
Porto Alegre	P16	30°08'46"	51°11'27"	100	220	175
Sapiranga	V17	29°36'14"	50°58'08"	100	580	915
Sapucaia do Sul	S26	29°50'12"	51°06'18"	102	283	29
Guaiba	P10	30°10'47"	51°23'33"	115	200	160
Sentinela do Sul	P17	30°36'03"	51°37'44"	119	295	35
Barra do Ribeiro	P1	30°19'33"	51°29'07"	120	350	230
Cerro Grande do Sul	P4	30°38'41"	51°46'30"	125	520	82
Mariana Pimentel	P11	30°20'11"	51°34'28"	125	289	130
Cerro Grande do Sul	P5	30°35'39"	51°46'38"	130	335	100
Mariana Pimentel	P12	30º23'01"	51°39'03"	130	326	3

Sertão Santana	P20	30°28'47"	51°41'25"	130	192	9
Sertão Santana	P18	30°29'13"	51°42'05"	131	321	18
Sertão Santana	P19	30°28'14"	51°41'43"	139	326	31
Montenegro	S13	29°43'29"	51°27'18"	141	207	73
Barão do Triunfo	P3	30°29'33"	51°52'38"	148	487	345
Catupi	S7	29°38'02"	51°39'23"	165	195	10
Taquari	S27	29°42'37"	51°49'02"	177	260	74
Dom Feliciano	P7	30°27'58"	52°19'57"	190	479	180
Dom Feliciano	P6	30°30'57"	52°23'18"	195	426	325
Passo do Sobrado	S14	29°49'47"	52°12'44"	215	180	10
Encruzilhada do Sul	P9	30°24'43"	52°36'35"	225	425	700
Encruzilhada do Sul	P8	30°22'14"	52°41'50"	230	315	350
Santana da Boa Vista	S16	30°51'29"	53°16'48"	255	323	205
Caçapava do Sul	S4	30°53'43"	53°25'22"	265	208	36
Vale do Sol	V21	29°35'19"	52°40'14"	265	362	50
Candelária	V2	29º42'25"	52º50'21"	275	535	150
Candelária	V3	29°38'12"	52°49'18"	278	496	2233
Cerro Branco	V5	29°41'37"	52°58'36"	290	530	550
Bagé	S3	30°52'30"	53°42'36"	297	304	990
Caçapava do Sul	S5	30°31'45"	53°33'01"	305	268	6
Caçapava do Sul	S6	30°32'04"	53°32'57"	305	335	770
Agudo	V1	29°38'39"	53°17'29"	330	385	95
Dona Francisca	V6	29°36'33"	53°22'08"	330	398	25
São João do Polêsine	V16	29°39'36"	53°30'29"	342	445	1406
Santa Maria	V15	29°40'15"	53°43'12"	366	363	245
Santa Maria	V14	29°42'10"	53°47'03"	368	237	63
Santa Maria	S15	29º37'38"	53º52'25"	380	240	5
São Pedro do Sul	S22	29°36'27"	54°18'11"	430	225	5
Santana do Livramento	S18	30°49'30"	55°20'59"	455	310	45
Santana do Livramento	S17	30°42'25"	55°20'48"	465	315	30
Jaguari	S12	29°29'09"	54°41'14"	470	265	65
São Vicente do Sul	S24	29°46'10"	55°01'44"	471	260	83
São Vicente do Sul	S23	29°43'04"	54°53'52"	473	252	170
São Vicente do Sul	S25	29°41'36"	54°54'02"	475	310	365
São Francisco de Assis	S20	29°40'01"	55°11'15"	496	185	12
São Francisco de Assis	S21	29°31'13"	55°7'23"	517	204	99
Alegrete	S2	29°39'43"	55°21'56"	520	105	10
Alegrete	S1	29°39'43"	55°23'46"	530	180	35
Quaraí	V11	30°11'21"	56°29'56"	610	235	90
Quaraí	V12	30°11'25"	56°29'58"	610	285	185

Tab. 2. List and code of Bromeliaceae species observed along the coastal-inland gradient with their functional traits. The scientific names of the species follow Flora of Brazil 2020. The name *Vriesea tucumanensis* corresponds to *Vriesea friburgensis* var. *tucumanensis*.

Subfamily/Species	Code	EP	LI	TE	AT	RO	TA	RL	RM	RS	HE	SC	IN	C3	CA
Bromelioideae															
Aechmea comata	*A.com*	1	0	0	0	0	1	0	1	0	1	0	0	0	1
Aechmea gamosepala	*A.gam*	1	1	0	0	0	1	0	1	0	0	1	0	0	1
Aechmea nudicaulis	*A.nud*	1	0	0	0	0	1	0	1	0	1	0	0	0	1
Aechmea recurvata	*A.rec*	1	1	0	0	0	1	0	1	0	0	0	1	0	1
Ananas bracteatus	*A.bra*	0	0	1	0	1	0	1	0	0	1	0	0	0	1
Billbergia nutans	*B.nut*	1	1	0	1	0	0	0	0	1	0	1	0	0	1
Billbergia zebrina	*B.zeb*	1	0	0	0	0	1	0	1	0	0	1	0	1	0
Bromelia antiacantha	*B.ant*	0	0	1	0	1	0	1	0	0	1	0	0	0	1
Bromelia balansae	*B.bal*	0	0	1	0	1	0	1	0	0	1	0	0	0	1
Edmundoa lindenii	*E.lin*	1	1	0	0	0	1	1	0	0	0	1	0	1	0
Nidularium amazonicum	*N.ama*	1	1	0	0	0	1	1	0	0	0	1	0	1	0
Nidularium innocentii	*N.inn*	1	1	0	0	0	1	1	0	0	0	1	0	1	0
Nidularium jonesianum	*N.jon*	1	0	0	0	0	1	0	1	0	0	1	0	1	0
Wittrockia superba	*W.sup*	1	1	0	0	0	1	1	0	0	1	0	0	1	0
Pitcairnioideae															
Dyckia agudensis	*D.agu*	0	1	0	0	1	0	1	0	0	1	0	0	0	1
Dyckia alba	*D.alb*	0	1	0	0	1	0	1	0	0	1	0	0	0	1
Dyckia choristaminea	*D.cho*	0	1	0	0	1	0	0	0	1	1	0	0	0	1
Dyckia hebdingii	*D.heb*	0	1	0	0	1	0	0	1	0	1	0	0	0	1
Dyckia ibicuiensis	*D.ibi*	0	0	1	0	1	0	1	0	0	1	0	0	0	1
Dyckia maritima	*D.mar*	0	1	0	0	1	0	1	0	0	1	0	0	0	1
Dyckia myriostachya	*D.myr*	0	1	0	0	1	0	1	0	0	1	0	0	0	1
Dyckia nigrospinulata	*D.nig*	0	1	0	0	1	0	1	0	0	1	0	0	0	1
Dyckia reitzii	*D.rei*	0	1	0	0	1	0	1	0	0	1	0	0	0	1
Dyckia remotiflora	*D.rem*	0	0	1	0	1	0	0	0	1	1	0	0	0	1
Dyckia retardata	*Dy.ret*	0	1	0	0	1	0	0	1	0	1	0	0	0	1
Dyckia rigida	*D.rig*	0	1	0	0	1	0	1	0	0	1	0	0	0	1
Dyckia selloa	*D.sel*	0	1	0	0	1	0	1	0	0	1	0	0	0	1
Dyckia tomentosa	*D.tom*	0	1	0	0	1	0	1	0	0	1	0	0	0	1
Dyckia vicentensis	*D.vic*	0	1	1	0	1	0	0	0	1	1	0	0	0	1
Tillandsioideae															
Tillandsia aeranthos	*T.aer*	1	1	0	1	0	0	0	0	1	0	0	1	0	1
Tillandsia bandensis	*T.ban*	1	1	0	1	0	0	0	0	1	1	0	0	0	1
Tillandsia bella	*T.bel*	0	1	0	1	0	0	0	0	1	1	0	0	0	1
Tillandsia bergeri	*T.ber*	1	0	0	1	0	0	0	0	1	0	0	1	0	1
Tillandsia crocata	*T.cro*	1	0	0	1	0	0	0	0	1	1	0	0	0	1
Tillandsia duratii	*T.dur*	1	1	0	1	0	0	1	0	0	1	0	0	0	1
Tillandsia gardneri	*T.gar*	1	0	0	1	0	0	0	0	1	1	0	0	0	1

Tillandsia geminiflora	*T.gem*	1	0	0	1	0	0	0	0	1	0	1	0	0	1
Tillandsia jonesii	*T.jon*	0	1	0	1	0	0	0	0	1	1	0	0	0	1
Tillandsia loliacea	*T.lol*	1	0	0	1	0	0	0	0	1	1	0	0	0	1
Tillandsia lorentziana	*T.lor*	0	1	0	1	0	0	0	0	1	1	0	0	0	1
Tillandsia mallemontii	*T.mal*	1	0	0	1	0	0	0	0	1	1	0	0	0	1
Tillandsia pohliana	*T.poh*	1	0	0	1	0	0	0	0	1	1	0	0	0	1
Tillandsia polzii	*T.pol*	0	1	0	1	0	0	0	0	1	1	0	0	0	1
Tillandsia recurvata	*T.rec*	1	0	0	1	0	0	0	0	1	1	0	0	0	1
Tillandsia streptocarpa	*T.ste*	1	0	0	1	0	0	0	0	1	1	0	0	0	1
Tillandsia stricta	*T.str*	1	1	0	1	0	0	0	0	1	1	0	0	0	1
Tillandsia tenuifolia	*T.ten*	1	0	0	1	0	0	0	0	1	1	0	0	0	1
Tillandsia tricholepis	*T.tri*	1	0	0	1	0	0	0	0	1	1	0	0	0	1
Tillandsia uruguayensis	*T.uru*	0	1	0	1	0	0	0	0	1	1	0	0	0	1
Tillandsia usneoides	*T.usn*	1	0	0	1	0	0	0	0	1	0	0	1	0	1
Tillandsia xiphioides	*T.xip*	0	1	0	1	0	0	0	0	1	1	0	0	0	1
Vriesea carinata	*V.car*	1	1	0	0	0	1	0	0	1	0	1	0	1	0
Vriesea corcovadensis	*V.cor*	1	0	0	0	0	1	0	0	1	1	0	0	1	0
Vriesea flammea	*V.fla*	1	0	0	0	0	1	0	0	1	1	0	0	1	0
Vriesea friburgensis	*V.fri*	1	1	0	0	0	1	0	1	0	1	0	0	1	0
Vriesea tucumanensis	*V.tuc*	1	1	0	0	0	1	0	1	0	1	0	0	1	0
Vriesea gigantea	*V.gig*	1	1	0	0	0	1	1	0	0	0	0	1	1	0
Vriesea incurvata	*V.inc*	1	0	0	0	0	1	0	1	0	0	1	0	1	0
Vriesea pauperrima	*V.pau*	1	1	0	0	0	1	0	1	0	0	1	0	1	0
Vriesea philippocoburgii	*V.phi*	1	0	0	0	0	1	1	0	0	1	0	0	1	0
Vriesea platynema	*V.pla*	1	1	0	0	0	1	1	0	0	0	0	1	1	0
Vriesea rodigasiana	*V.rod*	1	0	0	0	0	1	0	1	0	1	0	0	1	0
Vriesea rubroviridis	*V.rub*	1	0	0	0	0	1	0	1	0	1	0	0	1	0
Vriesea scalaris	*V.sca*	1	0	0	0	0	1	0	0	1	0	1	0	1	0
Vriesea vagans	*V.vag*	1	0	0	0	0	1	0	1	0	1	0	0	1	0

Life-forms: epiphytic (EP), lithophytic (LI), terrestrial (TE); atmospheric (AT), root (RO), tank (TA). **Average rosette size**: small < 20cm (RS), medium 20 ≥ 40cm (RM), large > 40cm (RL). **Relation to sun exposure**: heliophyte (HE), sciophyte (SC), indifferent (IN). **Photosynthetic pathways**: 3-carbon acid (C3), crassulacean acid metabolism (CAM).

Tab. 3. Phylogenetic signal of the functional traits of Bromeliaceae species. In the D-statistic, the P (Brownian) and P (random) indicate significant levels of departure from the Brownian motion and phylogenetic randomness models, respectively ($P < 0.05$).

Functional traits	**Statistic D**	**P (Brownian)**	**P(random)**
Substrate occupation			
Epiphyte (EP)	-0,125	0,656	0,000
Lithophyte (LI)	0,599	0,013	0,004
Terrestrial (TE)	-0,371	0,799	0,001
Life form			
Atmospheric (AT)	-0,601	0,993	0,000
Tank (WA)	-0,891	0,992	0,000
Root (RO)	-0,892	0,975	0,000
Rosette size			
Large (RL)	0,252	0,207	0,000
Medium (RM)	0,357	0,163	0,001
Small (RS)	0,222	0,217	0,000
Light requirement			
Heliophyte (HE)	0,249	0,198	0,000
Indifferent (IN)	0,392	0,220	0,030
Sciophyte (SC)	0,381	0,103	0,000
Photosynthetic pathways			
Crassulacean acid metabolism (CA)	-0,441	0,935	0,000
3-carbon acid (C_3)	-0,404	0,932	0,000

Tab. 4. Values of the net relatedness index (NRI) along with the distance from the coastline (Dlc), using various dissimilarities measured, either decoupled (dcFdist, decoupled functional dissimilarity; dcPdist, decoupled phylogenetic dissimilarity) or not (Fdist, functional dissimilarity; Pdist, phylogenetic dissimilarity), and dissimilarity distance of combined traits and phylogeny without their overlap (Fdist + dcPdist). As computed with species presence-absence.

Dlc	**dcFdist**		**dcPdist**		**Fdist**		**Pdist**		**Fdist + dcPdist**	
	NRI	**P-value**	**NRI**	**P-value**	**NRI**	**P-value**	**NRI**	**P-value**	**NRI**	**P-value**
0	0.011	0.513	1.757	0.034	1.393	0.086	2.994	**0.021**	1.846	**0.040**
0.9	1.414	0.072	0.308	0.387	-0.980	0.846	0.318	0.299	-0.373	0.633
5	0.590	0.293	0.942	0.182	-0.214	0.542	1.544	0.075	0.451	0.320
8	-0.110	0.531	0.909	0.183	0.544	0.270	3.789	**0.006**	0.793	0.207
15	0.527	0.293	-1.232	0.888	-0.938	0.823	-0.198	0.504	-1.241	0.894
16	0.015	0.490	-0.115	0.55	-0.742	0.738	1.584	0.062	-0.495	0.675
20	0.752	0.239	-1.695	0.959	-0.262	0.561	-0.036	0.450	-1.198	0.882
25	0.153	0.444	-0.684	0.753	0.115	0.423	2.790	**0.016**	-0.392	0.628
25	-0.190	0.572	0.841	0.201	-0.777	0.768	2.833	**0.014**	0.096	0.454
25	-0.485	0.670	0.253	0.396	-0.364	0.614	2.794	**0.018**	-0.079	0.513
30	0.106	0.455	-1.317	0.904	-0.327	0.586	2.839	**0.016**	-1.033	0.844
45	1.446	0.075	0.149	0.437	1.431	0.084	2.270	**0.036**	0.778	0.199
49	1.657	**0.055**	-0.746	0.758	-0.510	0.678	0.134	0.376	-0.754	0.767
70	0.004	0.521	0.250	0.411	0.448	0.293	0.172	0.350	0.329	0.376
70	1.466	0.074	0.368	0.373	0.678	0.229	1.325	0.100	0.548	0.278
80	0.821	0.206	-1.405	0.927	-0.959	0.835	-0.139	0.494	-1.367	0.921
85	-0.825	0.777	-1.704	0.964	-0.288	0.573	-0.137	0.480	-1.219	0.899
90	1.947	**0.026**	-1.311	0.900	-0.753	0.759	-0.478	0.609	-1.251	0.899
95	-0.735	0.763	-1.456	0.931	-0.221	0.554	-0.455	0.633	-1.050	0.841
100	-0.326	0.631	-2.109	0.982	-1.059	0.882	-0.992	0.881	-1.860	0.981
100	-1.253	0.884	-1.157	0.877	-0.086	0.480	-0.832	0.800	-0.775	0.760
100	1.571	0.062	-0.684	0.763	0.145	0.388	1.490	0.076	-0.344	0.617
102	1.288	0.096	-0.161	0.575	1.074	0.137	0.819	0.170	0.443	0.324
115	-0.481	0.678	-1.287	0.900	-0.082	0.503	0.242	0.350	-0.901	0.810
119	0.293	0.394	-0.234	0.600	-0.224	0.551	0.714	0.204	-0.330	0.623
120	-1.025	0.843	0.200	0.451	0.272	0.360	-0.024	0.433	0.176	0.407
125	1.235	0.117	-0.039	0.528	0.210	0.369	1.545	0.083	0.007	0.461
125	1.255	0.115	-0.277	0.611	0.021	0.448	1.549	0.074	-0.227	0.569
130	1.088	0.150	-0.217	0.590	0.605	0.249	1.467	0.081	0.112	0.435
130	1.183	0.122	-1.419	0.921	-0.538	0.674	-0.187	0.501	-1.203	0.902
130	1.038	0.151	-0.336	0.620	-0.613	0.709	2.099	**0.038**	-0.595	0.720
131	1.571	**0.054**	-1.287	0.898	-0.900	0.813	0.716	0.196	-1.302	0.915
139	1.575	0.056	-0.577	0.711	-0.914	0.822	1.576	0.074	-0.883	0.797
141	2.139	**0.013**	-1.044	0.848	-0.062	0.472	-0.228	0.504	-0.722	0.751
148	0.686	0.260	-0.007	0.514	0.674	0.228	0.635	0.219	0.287	0.377
165	2.274	**0.004**	-1.037	0.851	0.264	0.343	-0.217	0.505	-0.532	0.685
177	0.976	0.174	-0.847	0.809	-0.445	0.631	0.287	0.316	-0.824	0.791
190	-0.448	0.664	-0.114	0.541	0.367	0.325	0.150	0.367	0.066	0.462
195	0.295	0.395	-0.200	0.579	1.226	0.118	0.639	0.235	0.514	0.301
207	-0.071	0.542	0.239	0.408	1.201	0.116	1.337	0.096	0.736	0.241

215	1.846	**0.032**	-1.084	0.845	0.320	0.313	0.117	0.364	-0.492	0.679
225	-0.160	0.582	-0.414	0.660	3.020	**0.012**	2.453	**0.031**	1.405	0.085
230	0.322	0.404	0.399	0.367	1.922	**0.052**	1.945	0.060	1.348	0.097
255	0.065	0.483	-0.176	0.580	3.706	**0.003**	2.079	**0.043**	1.848	**0.038**
265	0.083	0.470	-0.184	0.576	3.722	**0.004**	2.095	**0.037**	1.838	**0.038**
265	0.905	0.189	-0.246	0.583	1.223	0.114	0.955	0.132	0.480	0.300
275	1.191	0.128	-0.353	0.633	3.763	**0.006**	1.705	0.063	1.710	**0.052**
278	1.601	**0.048**	-0.290	0.610	1.971	**0.048**	0.789	0.176	0.968	0.162
290	1.233	0.114	-0.447	0.673	-0.088	0.488	0.220	0.344	-0.408	0.635
297	0.903	0.194	0.333	0.392	5.026	**0.001**	3.843	**0.004**	2.811	**0.006**
305	0.385	0.380	-0.664	0.749	4.542	**0.002**	2.105	**0.040**	1.946	**0.042**
305	0.247	0.419	-0.372	0.645	5.062	**0.002**	3.010	**0.009**	2.441	**0.018**
330	0.834	0.217	-0.110	0.547	2.953	**0.010**	2.476	**0.026**	1.627	0.059
330	1.182	0.121	0.150	0.454	0.538	0.258	0.626	0.224	0.315	0.356
342	1.660	**0.015**	-1.507	0.923	0.731	0.2075	-0.018	0.415	-0.498	0.669
368	0.981	0.169	-0.969	0.840	1.503	0.084	0.946	0.147	0.199	0.379
380	0.510	0.313	-1.323	0.913	0.575	0.263	0.537	0.250	-0.501	0.688
420	0.775	0.245	-1.559	0.942	1.202	0.123	0.083	0.370	-0.220	0.570
435	0.705	0.259	-0.756	0.769	0.981	0.160	0.900	0.167	0.052	0.457
455	1.392	**0.027**	-0.117	0.558	1.704	0.0685	1.553	0.078	0.966	0.165
465	1.602	**0.037**	-1.123	0.871	-0.378	0.618	-1.041	0.925	-0.893	0.804
470	1.043	0.144	0.058	0.492	1.121	0.132	0.669	0.218	0.610	0.273
471	0.582	0.308	-0.484	0.677	1.945	**0.042**	2.082	**0.041**	0.866	0.204
473	1.584	0.060	-0.409	0.673	1.141	0.119	0.626	0.228	0.349	0.336
475	1.838	**0.026**	-0.254	0.616	2.354	**0.024**	1.959	**0.047**	1.124	0.135
496	1.879	**0.013**	-1.065	0.853	0.036	0.433	-0.775	0.781	-0.604	0.712
517	0.932	0.180	-1.452	0.925	2.550	**0.017**	1.572	0.073	0.468	0.295
520	1.388	0.072	-0.928	0.815	0.952	0.159	0.566	0.232	-0.028	0.493
530	0.669	0.265	-0.463	0.694	0.680	0.230	-0.625	0.688	0.096	0.450
610	1.463	**0.029**	-1.300	0.896	1.216	0.115	0.280	0.345	-0.025	0.477
610	0.472	0.348	-1.636	0.946	1.896	**0.044**	0.992	0.164	0.145	0.415

Tab. 5. Values of the nearest taxon index (NTI) along with the distance from the coastline (Dlc), using various dissimilarities measured, either decoupled (dcFdist, decoupled functional dissimilarity; dcPdist, decoupled phylogenetic dissimilarity) or not (Fdist, functional dissimilarity; Pdist, phylogenetic dissimilarity), and dissimilarity distance of combined traits and phylogeny without their overlap (Fdist + dcPdist). As computed with species presence-absence.

Dlc	**dcFdist**		**dcPdist**		**Fdist**		**Pdist**		**Fdist + dcPdist**	
	NTI	**P-value**	**NTI**	**P-value**	**NTI**	**P-value**	**NTI**	**P-value**	**NTI**	**P-value**
0	-0.077	0.574	1.613	0.060	0.729	0.243	0.299	0.357	1.846	**0.040**
0.9	1.107	0.146	0.271	0.392	-1.313	0.912	-1.835	0.969	-0.373	0.633
5	0.003	0.511	0.758	0.220	-0.846	0.812	-0.908	0.807	0.451	0.320
8	0.113	0.461	0.961	0.163	0.186	0.403	1.022	0.164	0.793	0.207
15	0.229	0.421	-1.603	0.951	-1.579	0.946	-1.113	0.865	-1.241	0.894
16	-0.586	0.721	-0.286	0.605	-0.828	0.793	0.441	0.345	-0.495	0.675
20	0.097	0.453	-0.599	0.715	-0.356	0.628	-1.613	0.951	-1.198	0.882
25	0.355	0.377	0.118	0.464	1.119	0.130	-0.097	0.537	-0.392	0.628
25	0.183	0.430	0.963	0.164	-0.797	0.771	-0.364	0.646	0.096	0.454
25	-0.189	0.572	0.951	0.170	-0.066	0.524	1.057	0.150	-0.079	0.513
30	-0.736	0.760	-0.133	0.540	1.249	0.102	1.140	0.131	-1.033	0.844
45	1.060	0.141	0.376	0.357	-0.430	0.663	-0.833	0.815	0.778	0.199
49	1.463	0.071	0.185	0.421	-0.784	0.777	-1.620	0.941	-0.754	0.767
70	-0.442	0.683	0.210	0.419	-0.121	0.524	-0.497	0.704	0.329	0.376
70	1.231	0.109	0.574	0.282	0.281	0.400	-1.350	0.920	0.548	0.278
80	0.932	0.183	-1.396	0.923	-0.474	0.683	-1.239	0.893	-1.367	0.921
85	-1.580	0.939	-1.787	0.969	-0.234	0.593	-0.823	0.792	-1.219	0.899
90	1.550	0.058	-0.980	0.843	0.467	0.312	-2.285	0.983	-1.251	0.899
95	-1.232	0.888	-1.542	0.946	-0.441	0.672	-0.916	0.819	-1.050	0.841
100	-0.669	0.748	-2.110	0.986	-0.538	0.707	-0.682	0.756	-1.860	0.981
100	-1.831	0.960	-1.369	0.922	-1.892	0.969	-0.610	0.741	-0.775	0.760
100	1.520	0.056	0.092	0.457	0.884	0.190	-0.057	0.528	-0.344	0.617
102	0.928	0.178	-0.426	0.656	-0.271	0.608	-1.737	0.945	0.443	0.324
115	-1.297	0.893	-1.743	0.960	-0.312	0.601	-0.950	0.819	-0.901	0.810
119	0.118	0.454	0.162	0.438	0.414	0.341	-1.245	0.905	-0.330	0.623
120	-1.688	0.957	0.632	0.259	-0.049	0.518	0.041	0.495	0.176	0.407
125	1.066	0.140	0.482	0.319	0.532	0.292	-0.353	0.657	0.007	0.461
125	1.067	0.146	-0.655	0.736	-0.774	0.780	-0.615	0.741	-0.227	0.569
130	0.930	0.178	-0.524	0.675	-0.045	0.535	-0.370	0.671	0.112	0.435
130	1.089	0.160	-1.548	0.949	0.383	0.351	-1.217	0.886	-1.203	0.902
130	0.709	0.257	0.093	0.467	-0.442	0.673	-0.450	0.698	-0.595	0.720
131	1.338	0.085	-0.767	0.760	-0.666	0.735	-0.730	0.775	-1.302	0.915
139	1.407	0.071	-0.333	0.621	-0.955	0.831	-0.626	0.747	-0.883	0.797
141	1.863	**0.020**	-1.545	0.938	-0.968	0.832	-1.846	0.959	-0.722	0.751
148	0.429	0.340	0.880	0.207	0.851	0.193	-1.041	0.857	0.287	0.377
165	2.055	**0.010**	-1.330	0.917	-0.315	0.637	-1.403	0.918	-0.532	0.685
177	0.645	0.267	-0.966	0.825	-1.010	0.841	-1.454	0.928	-0.824	0.791
190	-0.711	0.756	-0.571	0.704	-0.239	0.614	0.236	0.408	0.066	0.462
195	0.086	0.476	-0.271	0.598	-0.023	0.508	-1.606	0.943	0.514	0.301
207	-0.298	0.622	0.192	0.427	0.452	0.315	-0.691	0.757	0.736	0.241
215	1.699	**0.040**	-1.246	0.900	-0.116	0.527	-1.602	0.939	-0.492	0.679

225	-0.322	0.636	-1.039	0.855	1.400	0.083	-0.861	0.799	1.405	0.085
230	0.350	0.397	0.150	0.449	1.682	0.065	0.629	0.267	1.348	0.097
255	-0.156	0.581	-0.427	0.629	0.501	0.313	0.512	0.294	1.848	**0.038**
265	-0.149	0.593	-0.399	0.613	0.509	0.297	0.501	0.290	1.838	**0.038**
265	0.632	0.289	-0.168	0.562	-0.014	0.494	-0.867	0.828	0.480	0.300
275	0.940	0.187	-0.634	0.720	1.189	0.124	-0.893	0.825	1.710	**0.052**
278	1.378	0.067	-0.468	0.688	0.553	0.288	-1.600	0.938	0.968	0.162
290	0.901	0.189	-0.548	0.694	-0.947	0.820	-1.210	0.882	-0.408	0.635
297	1.432	0.073	0.409	0.347	1.317	0.089	-0.513	0.704	2.811	**0.006**
305	0.115	0.473	-0.973	0.844	1.291	0.101	-1.272	0.895	1.946	**0.042**
305	0.041	0.520	-0.602	0.725	1.339	0.092	-1.099	0.862	2.441	**0.018**
330	0.678	0.262	0.964	0.178	0.834	0.211	0.313	0.391	1.627	0.059
330	0.964	0.167	-0.174	0.543	-0.337	0.634	-1.306	0.902	0.315	0.356
342	1.511	**0.016**	-2.160	0.982	0.071	0.482	0.313	0.361	-0.498	0.669
368	0.901	0.196	-1.355	0.908	0.404	0.337	-0.149	0.564	0.199	0.379
380	0.287	0.396	-1.603	0.951	1.178	0.126	-1.951	0.983	-0.501	0.688
420	0.721	0.265	-1.477	0.934	0.273	0.379	-0.251	0.587	-0.220	0.570
435	0.584	0.289	-0.943	0.830	-0.123	0.558	0.261	0.393	0.052	0.457
455	1.359	**0.026**	-0.930	0.833	0.924	0.183	0.150	0.403	0.966	0.165
465	1.631	**0.027**	-1.679	0.952	-1.023	0.826	-1.037	0.844	-0.893	0.804
470	0.832	0.210	-0.137	0.536	-0.182	0.574	-1.529	0.930	0.610	0.273
471	0.542	0.328	-0.709	0.767	0.803	0.209	0.248	0.385	0.866	0.204
473	1.522	0.065	-0.908	0.829	-0.233	0.597	-1.116	0.879	0.349	0.336
475	1.773	**0.030**	-0.086	0.502	0.410	0.336	-0.429	0.663	1.124	0.135
496	1.890	**0.011**	-0.332	0.625	0.586	0.274	-0.318	0.625	-0.604	0.712
517	0.592	0.293	-2.610	0.998	-0.350	0.644	-1.873	0.963	0.468	0.295
520	1.264	0.081	-1.759	0.968	0.370	0.365	-1.122	0.863	-0.028	0.493
530	0.586	0.288	-1.459	0.937	0.493	0.322	-0.842	0.800	0.096	0.450
610	1.387	**0.021**	-1.424	0.925	0.117	0.463	0.622	0.263	-0.025	0.477
610	0.421	0.359	-2.223	0.992	0.275	0.381	-0.175	0.576	0.145	0.415

CONSIDERAÇÕES FINAIS

Nesta tese buscamos avançar alguns pontos elementares para compreender a conexão de padrões e processos que estabelecem a estrutura de comunidades ecológicas de Bromeliaceae ao longo de um gradiente de continentalidade. Tentamos ligar a estrutura metacomunitária de bromélias epifíticas com a distância da costa do litoral Atlântico, a fim de investigar os principais fatores ambientais que determinam os padrões de distribuição de espécies e os processos de estruturação da diversidade em diferentes escalas espaciais (regional e local). Buscamos, também, evidenciar as influências do gradiente de continentalidade na distribuição de Bromeliaceae com base nos atributos funcionais, bem como nas estruturas funcional e filogenética de comunidades ecológicas, tendo por base os padrões e processos de montagem de comunidades ecológicas.

Constatamos que a organização da estrutura de comunidades ecológicas de Bromeliaceae sofre influências do gradiente de continentalidade, que gera uma heterogeneidade ambiental de filtros abióticos (temperatura e umidade) e bióticos, que por sua vez impulsionam uma diversificação de nichos ecológicos. Neste gradiente, devido ao fato de algumas espécies de Bromeliaceae serem possivelmente adaptadas às mesmas condições ambientais, as comunidades ecológicas foram distribuídas na forma de unidades distintas, mas com baixa rotatividade de espécies (turnover). Esta condição, retrata um gradiente quase-Clementsiano, onde as comunidades ecológicas circunscritas formam grupos coesos, caracterizados por limites de distribuição causados por filtros ambientais.

No primeiro manuscrito, demonstramos que o gradiente de continentalidade ocasiona a formação de diferentes nichos climáticos que aumentam a heterogeneidade ambiental entre os morros testemunhos, e desse modo, possibilita a diferenciação de nichos ecológicos, mas, por outro lado, estabelece barreiras climáticas que reduzem ou impedem a conectividade entre as comunidades ecológicas (ou morros testemunhos). Algumas espécies de bromélias epifíticas colonizam os habitats mais adequados; e os morros testemunhos suportam diferentes espécies devido possivelmente a partição de nicho; pois fornecem qualidades ambientais suficientes para reter as populações locais de certas bromélias epifíticas. No entanto, o processo de dispersão limitada provavelmente diminui a dissimilaridade da composição de espécies entre as comunidades ecológicas, ao longo do gradiente de continentalidade devido a ação do processo de efeito de massa. Este processo sugere que as espécies de bromélias epifíticas com dispersão excedente podem superar as barreiras climáticas; e assim, essas espécies interferem na estrutura de comunidades ecológicas que não possuem recursos ecológicos suficientes ou condições ambientais adequadas para algumas populações, gerando a dinâmica fonte-sumidouro.

No segundo manuscrito, verificamos que a distribuição de espécies de Bromeliaceae ao longo do gradiente de continentalidade foi condicionada por atributos funcionais, que foram relacionados principalmente a fatores climáticos (temperatura e umidade). A maioria dos atributos funcionais analisados apresentaram sinal filogenético. Os atributos funcionais filogeneticamente conservados provavelmente impõem restrições ecológicas históricas e contemporâneas, que influenciam a distribuição das espécies. A estruturação das comunidades ecológicas de Bromeliaceae são essencialmente relacionadas ao padrão filogenético aleatório. No entanto, ao nível de metacomunidades as estruturas funcional e filogenética sofrem influências principalmente do processo de filtragem abiótica, mas no extremo leste do gradiente de continentalidade, na região litorânea, a metacomunidade também sofre influência do processo de exclusão competitiva entre as espécies congêneres. Ao nível dos morros testemunhos, a montagem das comunidades e a coexistência de espécies são influenciadas principalmente pela filtragem abiótica e por processos estocásticos.

Como perspectiva de continuidade de futuras pesquisas, presumimos que estudos com uma extensão mais detalhada (grão mais fino ou escala de vizinhança) poderão elucidar outros mecanismos que influenciam a organização da estrutura de comunidades ecológicas de Bromeliaceae, ao longo do gradiente de continentalidade. Novas abordagens poderão se concentrar em aspectos da partição de nichos ecológicos, nos efeitos dependentes da densidade e nas interações biológicas ou ecológicas, fornecendo informações mais precisas sobre ecologia metacomuntária, montagem de comunidades e coexistência de espécies. Além disso, encorajamos a realização de pesquisas focadas nas estruturas funcional e filogenética relacionadas com a estrutura horizontal e estratificação vertical de florestas, arquitetura e ontogenia de forófitos, ao longo do gradiente de continentalidade, as quais deverão contribuir para o desenvolvimento de novas hipóteses e elucidações de outros padrões e processos da estrutura comunitária de Bromeliaceae não abordadas nesta tese.