NATHÁLIA SILVA

CHANGES IN THE GROWTH-SURVIVAL TRADE-OFF IN A BRAZILIAN TROPICAL BASIN

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Botânica, para obtenção do título de *Magister Scientiae*.

Orientador: João Augusto Alves Meira Neto

VIÇOSA – MINAS GERAIS
2021

Ficha catalográfica elaborada pela Biblioteca Central da Universidade Federal de Viçosa - Campus Viçosa

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Silva, Nathália, 1995-

S586c Changes in the pattern of the growth-survival trade-off in a
2021 brazilian tropical basin / Nathália Silva. – Viçosa, MG, 2021.
68 f. : il. (algumas color.) ; 29 cm.

Inclui apêndice.
Orientador: João Augusto Alves Meira Neto.
Dissertação (mestrado) - Universidade Federal de Viçosa.
Inclui bibliografia.

1. Comunidades vegetais. 2. Ecologia de paisagens.
3. Filogenia. 4. Montagem de comunidades. 5. Mata atlântica.
I. Universidade Federal de Viçosa. Departamento de Biologia
Vegetal. Programa de Pós-Graduação em Botânica. II. Título.

CDD 22. ed. 577.82

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APROVADA: 22 de abril de 2021.

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AGRADECIMENTOS

Agradeço imensamente a toda a minha família por apoiarem integralmente os meus sonhos e meus passos.

Aos meus amigos, obrigada por todos os momentos compartilhados, risadas, surtos, desabafos e amparos. A vida em Viçosa é adorável na companhia de vocês! E certamente a quarentena também foi mais confortável podendo contar com vocês mesmo à distância.

Ao meu orientador João, por acreditar e investir no meu potencial desde a iniciação científica. Por partilhar comigo seu conhecimento, pela paciência e pelos conselhos que levarei para vida; afinal, resolvendo ‘uma crise por vez’ iremos longe!

Ao Celso e meus colegas do LEEP pelo carinho e excelente convivência durante esses incríveis 4 anos no laboratório. Os papos com cafezinho, as experiências divididas, reuniões e seminários enriqueceram meu dia a dia.

A todos os envolvidos direta ou indiretamente neste trabalho, na minha vivência na UFV e em Viçosa.

Ao Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), pela concessão da bolsa de estudos e apoio.

O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Código de Financiamento 001.

Obrigada!

“Só quem toma um sonho como sua forma de viver pode desvendar o segredo de ser feliz...”

(Ricardo Feghali, Roupa Nova)

“*Be brave, be curious, be determined, overcome the odds. It can be done*.”

(Stephen Hawking, Brief answers to the big questions)

RESUMO

SILVA, Nathália, M.Sc., Universidade Federal de Viçosa, abril de 2021. **Alterações no padrão do *trade-off* crescimento-sobrevivência uma bacia tropical brasileira**. Orientador: João Augusto Alves Meira Neto.

Os traços funcionais relacionados a estratégias ecológicas da aquisição e conservação de recursos refletem um *trade-off* entre crescimento e sobrevivência e o estudo destas relações lançam luz sobre como as plantas captam recursos e como respondem ao ambiente físico. Há uma necessidade crescente de se conhecer a ecologia funcional de determinadas floras, para apoiar medidas de restauração e conservação, principalmente em regiões tropicais. O objetivo do primeiro capítulo deste trabalho foi compreender a relevância da altura máxima das plantas como um proxy de crescimento e dos traços funcionais associados como explicativos do *trade-off* crescimento-sobrevivência. O segundo capítulo buscou responder se o padrão do *trade-off* crescimento-sobrevivência varia ao longo de gradientes climáticos e físicos no nível regional na Mata Atlântica, e se os traços funcionais têm seus nichos conservados filogeneticamente. Com estes objetivos, o estudo foi desenvolvido com a flora lenhosa da Bacia do Rio Doce (BRD), região de larga escala representativa da biodiversidade da mata atlântica do sudeste brasileiro, totalizando 1.912 espécies em 79 pontos amostrais da bacia. Os traços funcionais coletados foram a altura máxima, o comprimento e a largura das folhas, dos pecíolos, dos frutos e da semente, além da síndrome de dispersão das espécies. As análises envolveram modelos lineares generalizados e suas extensões mistas, com posterior seleção de modelos significativos e o cálculo de sinal filogenético, todas realizadas no ambiente estatístico R. Os resultados do capítulo 1 demonstram que a variável altura máxima provou ser um *proxy* confiável do crescimento das plantas lenhosas, e que o *trade-off* crescimento-sobrevivência exibe um padrão considerável através dos traços funcionais utilizados, apresentando como características aquisitivas árvores maiores com folhas e pecíolos maiores e como característica conservativa sementes mais largas. O segundo capítulo indicou processos de filtragem ambiental atuando em larga escala nas comunidades vegetais da bacia, interferindo nos valores dos traços funcionais e no padrão do *trade-off* crescimento-sobrevivência, que varia ao longo dos gradientes hídrico, térmico e altitudinal. O gradiente hídrico apresenta padrão vegetativo conservativo, com folhas e pecíolos menores, enquanto o padrão reprodutivo é aquisitivo, com frutos e sementes pequenos a medida em que a precipitação horizontal aumenta. Ao contrário, o gradiente térmico indica um padrão vegetativo aquisitivo, com folhas e pecíolos maiores, e um padrão reprodutivo conservativo, com frutos e sementes grandes. O gradiente altitudinal seguiu o padrão de umidade. Os estresses crônicos relacionados com as mudanças hídricas e térmicas com a variação da altitude podem influenciar os intervalos de estabelecimento das plantas, tornando a estratégia reprodutiva aquisitiva e a conservação de água pelas folhas mais favoráveis nessas condições. A temperatura mais elevada pode favorecer a estratégia fotossintética aquisitiva devido à área maior disponível para trocas de calor e à competitividade e tolerância em ambientes sombreados, com assistência de suporte mecânico de pecíolos maiores. Este estudo confirma que o *trade-off* entre a rápida aquisição e conservação de recursos em florestas tropicais governa a coexistência entre diversas estratégias ecológicas que operam independentemente nos diferentes níveis da planta, representados aqui pelo tamanho dos órgãos relacionados à fotossíntese, suporte hidráulico e reprodução, promovendo a diferenciação de nicho nessas comunidades. O estudo da flora lenhosa completa da BRD é uma importante adição à compreensão da ecologia funcional da região, promovendo uma base para abordagens mais precisas para entender as funções e serviços ecossistêmicos da mata atlântica.

Palavras-chave: *Trade-off* ecológico. Filtragem ambiental. Regras de montagem. Estratégias ecológicas. Mata atlântica.

ABSTRACT

SILVA, Nathália, M.Sc., Universidade Federal de Viçosa, April, 2021. **Changes in the pattern of the growth-survival trade-off in a brazilian tropical basin**. Advisor: João Augusto Alves Meira Neto.

The functional traits related to ecological strategies for the acquisition and conservation of resources reflect a trade-off between growth and survival and the study of these relationships highlights how plants capture resources and how they respond to the physical environment. There is a rising need to know the functional ecology of certain floras, to support restoration and conservation measures, especially in tropical regions. The objective of the first chapter of this study was to understand the relevance of the maximum height of the plants as a growth proxy and the associated functional traits as explanations of the growth-survival trade-off. The second chapter attempted to answer whether the pattern of the growth-survival trade-off varies across climatic and physical gradients at the regional level in the Atlantic Forest, and whether the functional traits have their niches conserved phylogenetically. To these purposes, the study was carried out with the woody flora of the Rio Doce Basin (RDB), a large-scale region representative of the Atlantic Forest biodiversity of southeastern Brazil, totaling 1.912 species in 79 sampling points in the basin. The functional traits collected were the maximum height, the length and width of the leaves, petioles, fruits and seeds, in addition to the species dispersion syndrome. The analyzes involved generalized linear models and their mixed extensions, with subsequent selection of significant models and the calculation of the phylogenetic signal, all performed in the R statistical environment. The results of the first chapter demonstrate that the maximum height variable proved to be a reliable proxy for the growth of woody plants, and that the growth-survival trade-off exhibits a considerable pattern through the functional traits used, presenting larger trees with larger leaves and petioles as acquisitive characteristics and larger seeds as a conservative characteristic. The second chapter indicated environmental filtering processes operating on a large scale in the basin's plant communities, interfering with the values of the functional traits and the pattern of the growth-survival trade-off, which varies along the hydric, thermal and altitudinal gradients. The hydric gradient presents a conservative vegetative pattern, with smaller leaves and petioles, while the reproductive pattern is acquisitive, with small fruits and seeds as the horizontal precipitation increases. On the contrary, the thermal gradient indicates an acquisitive vegetative pattern, with larger leaves and petioles, and a conservative reproductive pattern, with large fruits and seeds. The altitudinal gradient followed the humidity pattern. Chronic stresses related to water and thermal changes with altitude variation can influence plant establishment intervals, making the reproductive acquisition strategy and leaf water conservation more favorable in these conditions. The higher temperature can favor the acquisitive photosynthetic strategy due to the larger area available for heat exchanges and the competitiveness and tolerance in shaded environments, with assistance from mechanical support of larger petioles. This study confirms that the trade-off between the rapid acquisition and conservation of resources in tropical forests governs the coexistence between several ecological strategies that operate independently at different levels of the plant, represented here by the size of the organs related to photosynthesis, hydraulic support and reproduction, promoting niche differentiation in these communities. The study of the complete woody flora of RDB is an important addition to the functional ecology knowledge of the region, promoting a basis for more accurate approaches to understand the ecosystem functions and services of the Atlantic forest.

Keywords: Ecological trade-off. Environmental filtration. Assembly rules. Ecological strategies. Atlantic forest.

SUMÁRIO

INTRODUÇÃO GERAL

A teoria de nicho prediz que as diferenças de traços funcionais entre espécies norteiam as especializações em diferentes nichos, permitindo a coexistência das plantas (BLUNDO; MALIZIA; GONZÁLEZ-ESPINOSA, 2015; MARACAHIPES et al., 2018; MEIRA-NETO et al., 2019; NEGREIROS et al., 2016; STERCK et al., 2011). Uma forma de compreender melhor como as espécies coexistem e lidam com pressões ambientais é através do estudo das estratégias ecológicas ligadas a traços funcionais relacionados ao uso de recursos pelas plantas (MARACAHIPES et al., 2018; MCGILL et al., 2006; STERCK et al., 2011). Nesse contexto, os traços funcionais são definidos como as características mensuráveis morfológicas ou fisiológicas que governam a performance de um organismo (MCGILL et al., 2006; STERCK et al., 2011).

Existe um consenso crescente de que a abordagem que foca na diversidade de traços funcionais, em vez do número de espécies em si, determina fortemente a montagem de comunidades e o funcionamento do ecossistema, pois concentra-se nas características que definem como os organismos interagem com seus ambientes físicos, químicos e biológicos circundantes (DÍAZ; CABIDO, 2001; NOCK; VOGT; BEISNER, 2016). Ainda existem lacunas no entendimento das relações entre traços, mecanismos de coexistência, crescimento e sobrevivência das plantas, por isso, a junção dessas abordagens é uma maneira promissora de obter uma visão abrangente e completa dos vínculos entra a diversidade de plantas e os processos do ecossistema e de contribuir para o gerenciamento prático da conservação da diversidade e dos serviços ecossistêmicos (DÍAZ; CABIDO, 2001; STERCK et al., 2011). Além disso, a recente possibilidade de construção de extensos bancos de dados sobre os traços funcionais de floras regionais completas, incluindo a disponibilidade de informações precisas sobre o meio abiótico, permite a exploração de amplos padrões, em escalas cada vez maiores, fornecendo novas perspectivas para a ecologia funcional (DIAZ; CABIDO; CASANOVES, 1998; LEUSCHNER; MEIER, 2018; NOCK; VOGT; BEISNER, 2016).

Através da premissa de que as espécies usam diferentes estratégias ecológicas ao adquirir e conservar recursos (MONTEIRO et al., 2017), o gradiente entre uma estratégia ecológica e outra origina diferentes arranjos funcionais que podem indicar um *trade-off* entre crescimento e sobrevivência das plantas (MARACAHIPES et al., 2018; MEIRA-NETO et al., 2019, p.; STERCK et al., 2011). O *trade-off* crescimento-sobrevivência (‘*growth-survival* *trade-off*) é importante e considerado onipresente, e pode ajudar a explicar grande parte da variação ecológica entre as espécies (ATKINSON, 2008). Há evidências consistentes de que características vegetativas e reprodutivas contribuem para o *trade-off* crescimento-sobrevivência à nível de comunidade (HAN et al., 2019; MEIRA-NETO et al., 2019, p.), mas se faz necessário compreender esse fenômeno em escalas espaciais maiores em nível interespecífico, com um maior número amostral e utilizando uma variedade maior traços funcionais chave (MARACAHIPES et al., 2018). Em escalas maiores de investigação é possível analisar a paisagem ao longo de variações ambientais, ajudando a compreender mais facilmente como as espécies mudam e são afetadas pelo ambiente (DÍAZ; CABIDO, 2001; MCGILL et al., 2006). Além disso, a grande escala espacial ultrapassa possíveis interferências de mecanismos de diferenciação de nicho que operam em escalas menores, como a exclusão competitiva, a imigração e as flutuações locais de abundância (D’ANDREA et al., 2020).

Associações consistentes e previsíveis entre traços funcionais e condições abióticas que podem levar a uma filtragem ambiental remetem a muito tempo no estudo ecológico e se mantém um direcionamento de pesquisa importante (DIAZ; CABIDO; CASANOVES, 1998; LEUSCHNER; MEIER, 2018; MAO et al., 2020; OLIVEIRA-FILHO; FONTES, 2000). Quando um fator ambiental variável afeta uma característica mais que outra, a correlação entre dois traços funcionais também tende a mudar entre os ambientes e alterar o gradiente de seleção, visto que os *trade-offs* são oriundos da história evolutiva das espécies (STEARNS, 1989). Gradientes de altitude podem ser úteis na exploração de padrões de biodiversidade, pois representam uma mudança ambiental considerável ao longo de distâncias geográficas passíveis de serem analisadas, e funcionam como filtros ambientais indiretos, limitando a ocorrência das espécies por fatores associados (e.g. temperatura, pluviosidade, radiação solar, condições edáficas) (KÖRNER, 2007; NERI et al., 2017).

As interações entre estratégias ecológicas e processos evolutivos também devem ser levadas em consideração para entender os padrões encontrados naturalmente ao longo de gradientes ambientais (DAKOS et al., 2019). Os fatores abióticos podem funcionar como filtros ambientais causadores de agrupamento filogenético nas comunidades em caso de conservantismo de nicho, ou seja, quando caracteres funcionais determinantes de nicho são predominantemente conservados nas linhagens filogenéticas (GASTAUER; MEIRA-NETO, 2014; SOBRAL; CIANCIARUSO, 2012). O sinal filogenético é útil para explorar a evolução de traços funcionais ao longo de gradientes ambientais e pode sugerir que alguns processos ecológicos são mais plausíveis do que outros, ajudando a prever o funcionamento ecossistêmico e mudanças em resposta a alterações ambientais (HELMUS et al., 2010; KNAPP et al., 2008; PERES, 2016; XU et al., 2017). Os traços funcionais vegetativos e reprodutivos, como características ecológicas hereditárias, podem ser predominantemente conservados ou predominantemente convergentes nas linhagens filogenéticas de comunidades.

Tendo em vista a importância da Mata Atlântica na biodiversidade altamente heterogênea e endêmica que abriga e a falta de estudos que levem em consideração a diversidade funcional de traços foliares e reprodutivos em conjunto, principalmente em áreas tropicais e em escalas espaciais maiores (DÍAZ; CABIDO, 2001; ESPINDOLA et al., 2016; MYERS et al., 2000; OLIVEIRA-FILHO; FONTES, 2000; STERCK et al., 2011), esse trabalho pode contribuir significantemente com dados empíricos que apoiem as medidas regionais de recuperação e conservação das florestas atlânticas.

Esta dissertação foi dividida em dois capítulos com o objetivo de entender a relevância dos traços vegetativos e reprodutivos na separação de nichos e na estruturação de comunidades Atlânticas e nas variações do *trade-off* crescimento-sobrevivência ao longo dos gradientes ambientais de uma bacia geográfica atlântica, gerando avanços teóricos e práticos na abordagem da ecologia funcional. O primeiro capítulo teve como hipótese de que a altura máxima é explicada pelos tamanhos das folhas, pecíolos, frutos e sementes e, assim, pode ser usada como *proxy* (uma variável representante) do crescimento das plantas em nível regional na Mata Atlântica. O segundo capítulo tem como hipóteses que (1) à medida que as condições climáticas se tornam mais severas com o aumento da altitude, a estratégia conservativa de recursos é favorecida, enquanto que, com a redução da altitude, aumento da temperatura e outras condições associadas, a estratégia de aquisição é favorecida; e que (2) diferentes posições do gradiente ambiental geram comunidades filogeneticamente agrupadas devido ao conservantismo filogenético de nicho de características funcionais na Mata Atlântica. Os dois capítulos foram escritos em inglês e estruturados em padrão de artigo científico, com o objetivo de facilitar posteriores submissões a publicações.

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CHAPTER 1: THE GROWTH-SURVIVAL TRADE-OFF IN A BRAZILIAN TROPICAL BASIN

RESUMO – Publicado no 40° ERBOT[1].

A procura por traços funcionais relevantes ao *trade-off* crescimento-sobrevivência (CS) é essencial para a compreensão dos processos de montagem das comunidades de plantas. O objetivo deste trabalho foi identificar os principais traços funcionais determinantes das estratégias ecológicas desse *trade-off* entre a aquisição e conservação de recursos em nível regional nas comunidades tropicais atlânticas da Bacia do Rio Doce (BRD), bacia que enfrenta severos e recentes desastres ambientais, a fim de gerar informação sobre ecologia funcional para fins de conservação e restauração na região. Os traços funcionais de plantas lenhosas – altura máxima (Hmax), comprimento e largura da folha (FLC e FLL), do pecíolo (PC e PL), do fruto (FC e FL) e da semente (SC e SL) – foram coletados em literatura especializada e herbários virtuais (REFLORA, SpeciesLink). Foram realizados dois modelos lineares generalizados mistos (GLMM) (o 1° com 895 espécies com todos os dados completos e o 2° com 1.912 espécies, apenas com traços foliares completos) e posterior seleção de modelos, usando Hmax como variável resposta e os outros traços funcionais como variáveis explanatórias. No GLMM 1, PC e SL foram significativos e positivamente correlacionados com Hmax. No GLMM 2, FLC, PC e PL foram significativos, com FLC e PC positivamente e PL negativamente correlacionado com Hmax. Os principais determinantes do *trade-off* CS na BRD foram PC, PL, FLC e SL, resultado que é congruente com a literatura da Mata Atlântica em escalas menores. Hmax provou ser um proxy confiável de crescimento das plantas em ambos os modelos. PC foi a única variável significativa em ambos os modelos globais, apresentando-se como um traço altamente explicativo para o crescimento de plantas na Mata Atlântica, um resultado inesperado, visto que esse traço funcional é raramente medido de maneira isolada. Plantas mais altas foram associadas a folhas maiores e pecíolos mais longos e estreitos, sugerindo estratégia aquisitiva, e com sementes mais largas, característica de estratégia conservativa, sugerindo evoluções independentes de caracteres, permitindo a coexistência e diversificação de estratégias ecológicas governadas pelo *trade-off* CS. Estudos futuros devem focar no contexto abiótico, nas relações filogenéticas e nas variações intraespecíficas dos traços funcionais, a fim de complementar o conhecimento sobre a diversidade funcional regional.

Palavras-chave: estratégias ecológicas, ecologia funcional, regras de montagem, traços funcionais.

[1]SILVA, Nathália; NETO, João A. A. Meira. DETERMINANTES DO TRADE-OFF CRESCIMENTO-SOBREVIVÊNCIA EM UMA BACIA TROPICAL BRASILEIRA. In: Anais do 40º Encontro Regional de Botânicos - Regional MG, BA, ES. Anais (ISBN: 978-65-5941-087-3). Vitória (ES) Universidade Federal do Espírito Santo, 2020. Disponível em: <www.even3.com.br/anais/40ERBOT/300844-DETERMINANTES-DO-TRADE-OFF-CRESCIMENTO-SOBREVIVENCIA-EM-UMA-BACIA-TROPICAL-BRASILEIRA>.

ABSTRACT

The search for functional traits relevant to the growth-survival (GS) trade-off is essential for understanding the assembly processes of plant communities. The objective of this study was to identify the main functional traits that determine the ecological strategies of this trade-off between the acquisition and conservation of resources at the regional level in the Atlantic tropical communities of the Rio Doce Basin (RDB), a basin that faces severe and recent environmental disasters, in order to generate information on functional ecology for conservation and restoration purposes in the region. The functional traits of woody plants - maximum height (Hmx), leaf length and width (LL and LW), petiole (PL and PW), fruit (FL and FW) and seed (SL and SW) - were collected in specialized literature and virtual herbariums (REFLORA, SpeciesLink). Two generalized linear mixed models (GLMM) were performed (the 1st with 895 species with all complete data and the 2nd with 1.912 species, only with complete leaf traits) and subsequent model selection, using Hmx as the response variable and the other functional traits as explanatory variables. In GLMM 1, PL and SW were significant and positively correlated with Hmx. In GLMM 2, LL, PL and PW were significant, with LL and PL positively and PW negatively correlated with Hmx. The main determinants of the GS trade-off at RDB were PL, PW, LL and SW, a result that is congruent with the Atlantic Forest literature on smaller scales. Hmx proved to be a reliable proxy for plant growth in both models. PL was the only significant variable in both global models, presenting as a highly explanatory trait for plant growth in the Atlantic Forest, an unexpected result, since this functional isolated trait is rarely measured. Taller plants were associated with larger leaves and longer and narrower petioles, suggesting an acquisitive strategy, and with larger seeds, characteristic of a conservative strategy, suggesting independent evolution of characters, allowing the coexistence and diversification of ecological strategies governed by the GS trade-off. Future studies should focus on the abiotic context, on phylogenetic relationships and on intraspecific variations of functional traits, in order to complement knowledge about regional functional diversity.

Keywords: ecological strategies, functional ecology, assembly rules, functional traits.

1 INTRODUCTION

Understanding how species coexist through different ecological strategies remains a challenge in ecology. Inherent differences and correlations in a variety of functional traits, within certain limits, represent these strategies and determine the specializations of species in different niches (Stearns 1989; Sterck et al. 2006; Muller-Landau 2010; Sterck et al. 2011; Díaz et al. 2016). The study of ecological strategies linked to functional traits related to the use of resources by plants has proved to be promising (Mcgill et al. 2006; Sterck et al. 2011; Maracahipes et al. 2018), since the combination of these traits expresses the plant balance between the challenges of growth, survival and reproduction (Díaz et al. 2016).

Two strategies that have been investigated are the acquisitive species that have fast acquisition of resources and consequently fast growth; and conservative species with high resource conservation rates, survival, and stress tolerance (Diaz et al. 2004; Atkinson 2008; Sterck et al. 2011). Given that environments vary in quantity of resources and a combination of favorable traits in one environment doesn’t necessarily lead to success in another (Garnier et al. 2016), the different functional designs of the ‘fast-slow continuum’ may reflect trade-offs in resource allocation, between plant growth and survival (Sterck et al. 2006; Atkinson 2008; Sterck et al. 2011; Garnier et al. 2016).

The growth-survival trade-off can explain much of the ecological variation and the coexistence between species (Giacomini 2007; Atkinson 2008; Muller-Landau 2010), as it is likely to be widely applied to different floras, environments, and forms of life, and it is also independent of geographic location (Diaz et al. 2004). Due to the possibility of compiling large databases, collecting different and numerous functional traits and analyzing them with the most diverse statistical methods, the discussion around this concept and the confirmation of this ecological conflict have raised in the ecological literature in recent decades in the most diverse ways (Garnier et al. 2016), from the study of tree species in tropical forests (Sterck et al. 2006; Wright et al. 2010; Sterck et al. 2011; Meira-Neto et al. 2019), subtropical forests (Han et al. 2019), cerrados (savannah ecosystem) (Maracahipes et al. 2018), shrub species in campos rupestres (Negreiros et al. 2016), monocarpic species (Metcalf et al. 2006), to the level of comparisons between continents (Diaz et al. 2004) and globally (Díaz et al. 2016).

There is evidence that vegetative and reproductive characteristics of plants contribute to the growth-survival trade-off, presenting relatively constant general patterns. Tall plants, large leaves and small diaspores are generally related to the acquisitive strategy, while smaller plants, small leaves, and large diaspores tend to be associated with the conservative strategy (Diaz et al. 2004; Muller-Landau 2010; Sterck et al. 2011; Adler et al. 2014; Díaz et al. 2016; Maracahipes et al. 2018; Han et al. 2019; Meira-Neto et al. 2019). However, in studies with different life forms, habitats and spatial scales, the wide range of traits that can be measured have different degrees of relevance. Thus, it is necessary to understand the relationships between the functional traits, in order to understand the variations in the expressions and patterns of the ecological strategies of the growth-survival trade-off in new environments and spatial scales (Giacomini 2007; Maracahipes et al. 2018).

There are three dimensions of key functional traits that capture the essence of the shape and function of the plant, contributing to the growth-survival trade-off at different scales: a dimension of fertility, indicating the allocation of resources for reproduction; a dimension of competitive ability, indicating the allocation of resources for the growth, and a dimension of resources acquisition, indicating the allocation for the construction of photosynthetic structures for interception of light (Westoby et al. 2002; Garnier et al. 2016; Díaz et al. 2016). Within these dimensions, there are useful morphological traits, which vary considerably between species, are easily measured on continuous scales, and can predict the links between functional traits and ecological strategies, enabling their use in a wide range of ecological research (Diaz et al. 2004; Mcgill et al. 2006; Adler et al. 2014).

Pertinent examples of functional traits applicable to the growth-survival ecological strategies are the measures of plant height, leaf size, fruit size, and seed size (Diaz et al. 2004; Adler et al. 2014). The maximum height is a key quantitative trait used as a proxy for the variation of the general size of the plant, and corresponds to the organisms ability to capture light resources and disperse diaspores, indicating competitive ability and carbon acquisition, in addition to being correlated with attributes involved in the most diverse functions of the plant (Westoby et al. 2002; Garnier et al. 2016; Díaz et al. 2016; Hodgson et al. 2017). The leaf size is a basic leaf trait that can be divided between the dimensions of the leaf blade and the petiole (Pasini & Mirjalili 2006; Niinemets et al. 2006; Garnier et al. 2016). These traits are related to the acquisition and efficiency in the use of energy and the hydraulic balance of the plant, and contribute strongly to differences in the performance and carbon economy of the organisms (Westoby et al. 2002; Navarro et al. 2010; Pérez-Harguindeguy et al. 2013; Garnier et al. 2016). Fruit size is a trait consistently related to seed size and both traits are associated with fertility, dispersion, reproductive success, and tolerance to plant stress (Almeida-Neto et al. 2008; Muller-Landau 2010; Lönnberg & Eriksson 2013).

In general, taller plants are related to large leaves, with greater leaf area available for photosynthetic processes, presenting higher growth rates (Sterck et al. 2011; Price et al. 2014; Díaz et al. 2016; Meira-Neto et al. 2019). Higher plants also positively correlate with large seeds, a design that allows quick acquisition of resources on the one hand, and conservation of resources within protected tissues on the other (Diaz et al. 2004; Prado Júnior 2016). This apparent lack of coordination of plant traits suggests that the trade-offs relative to ecological strategies operate independently on different plant organs (Wright et al. 2004; Baraloto et al. 2010; Silva et al. 2015). Despite this, there is no consensus on the interaction of strategies for the acquisition and conservation of resources at the level of the entire plant, and few studies have investigated this relationship (Wright et al. 2004; Nascimento 2016). Baraloto et al. (2010), Silva et al. (2015) and Meira-Neto et al. (2019) found independent strategies in different stem, leaf and reproductive organs of Amazon and Atlantic plants, while De la Riva et al. (2016) found a high degree of functional coordination between leaf, stem and root traits of Mediterranean species at the community level, making it necessary to analyze the relationship between the different traits on larger scales, to obtain solid conclusions about how the trade-off in the continuum of acquisitive-conservative traits works.

The search for which traits of the Atlantic Forest species – a large global hotspot – contribute to the growth-survival trade-off, the relationships and the mechanisms involved, is essential to expand the knowledge of the processes that drive the separation of niches and the assembly of communities of this biome, since the acquisition of resources and the growth of plants are essential factors for crucial functions of the ecosystem, and can contribute to the practical management of the conservation of diversity more accurately (Sterck et al. 2011; Maracahipes et al. 2018; Meira-Neto et al. 2019; Vitória et al. 2019).

In view of the importance of the Atlantic Forest in the highly heterogeneous and endemic biodiversity that it has and the lack of studies that analyze the diversity of vegetative and reproductive traits together, especially in tropical areas and at larger spatial scales (Myers et al. 2000; Díaz & Cabido 2001; Sterck et al. 2011; Espindola et al. 2016), this study aimed to understand the relevance of vegetative and reproductive traits in the separation of niches and in the assemblage of Atlantic communities in a hydrographic basin, generating theoretical and practical advances in the approach of functional ecology. This chapter had the hypothesis that the maximum height is explained by the sizes of leaves, petioles, fruits and seeds and, thus, can be used as a proxy for the growth of plants at the regional level in the Atlantic Forest.

2 MATERIALS AND METHODS

a. Study area

The Rio Doce Basin (RDB) (Figure 1) is in southeastern Brazil, covering an area of 86,715 km² in the states of Minas Gerais (86%) and Espírito Santo (14%), thus being a basin of the federal domain (Coelho 2009; IGAM 2010; ANA 2016). The RDB is inserted minimally in the Cerrado biome (2%) in the extreme west while its almost totality (98%) is within the limits of a large global hotspot, the Atlantic Forest (Myers et al. 2000; IGAM 2010; Pires et al. 2017), with a considerable species richness of this domain. Over centuries of degradation, deforestation, and urbanization, the RDB has lost more than 71% of the coverage of its native vegetation and, recently, was the main victim of the worst environmental disaster in the history of Brazil (Oliveira-Filho & Fontes 2000; ANA 2016; Meira et al. 2016; Espindola et al. 2016; Pires et al. 2017). The landscape in the basin is a mosaic with a high altitudinal variation witch results in several geomorphological patterns (Figure 1) (ANA 2016). The climate is tropical with average temperatures between 18 and 24.6°C. Two fluviometric periods are well marked, with precipitation ranging from 800 to 1,300 mm in the rainy season, and from 150 to 250 mm in the dry season (IGAM 2010).

b. Floristic data set

Floristic data were obtained from the NeoTropTree database, which has lists of tree species from the Neotropics (Oliveira-Filho 2017). The correct names and synonyms were verified on the Flora do Brasil 2020 website (BFG 2018). Species without exsiccates available for conference at online herbariums or at the Herbarium of the Federal University of Viçosa (VIC), as well as species of Cactaceae with cladodes, were removed from the database. The final species list contains 1.912 woody species from different physiognomies of the Atlantic forest, belonging to 106 families of angiosperms, gymnosperms and arborescent pteridophytes, distributed in 79 sampling points in the RDB (Figure 1).

c. *Functional traits*

The RDB plant species had the following traits collected at the interspecific level: maximum plant height (Hmax, in meters), seed length (SL), seed width (SW), fruit length (FL), fruit width (FW), leaf blade length (LL), leaf blade width (LW), petiole length (PL) and petiole width (PW), all in millimeters.

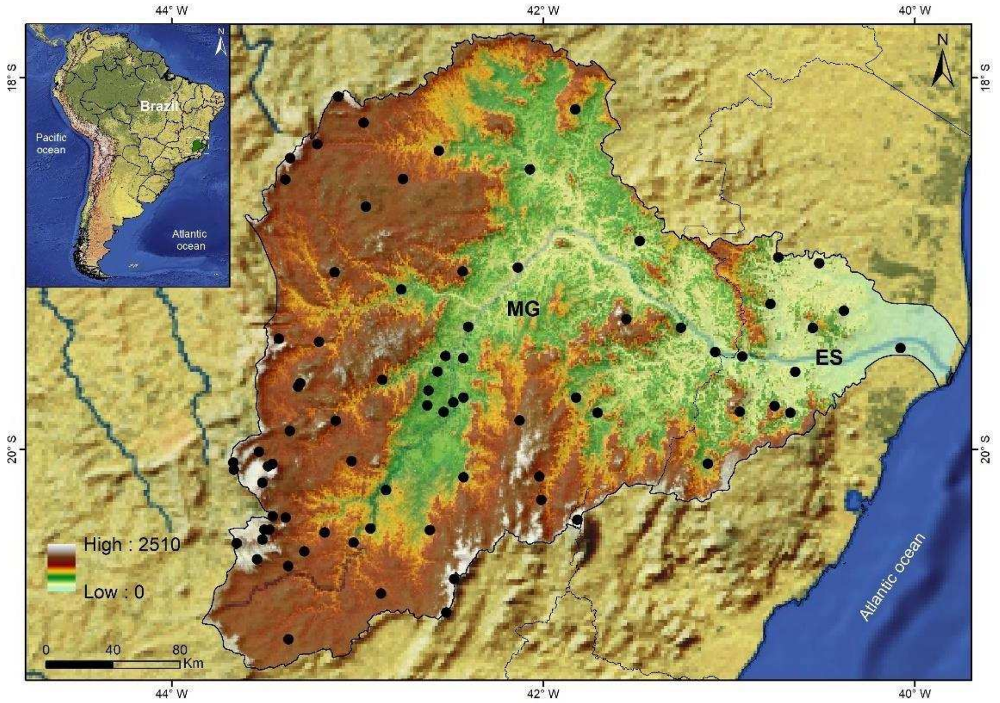

Figure 1. Altimetry and location of the 79 points studied in the Rio Doce Basin. MG – Minas gerais; ES – Espírito Santo. Data: WGS 84 (Adapted from Oliveira-Junior et al. 2020).

The maximum height of all the 1.912 species was obtained through description data and observations in the reports generated by consulting the Reflora virtual herbarium (BFG 2018). The leaves also had the traits collected for all 1.912 species. The values were obtained and their average calculated by consulting a minimum of two herbarium specimens (measurement of five fully expanded leaves in each exsiccata, (totaling 10 samples, according to the protocol for minimum repetition of leaf traits by Cornelissen et al. (2003), with some exceptions for rare species that only the type exsiccata was found (with less than 10 suitable leaves). In these cases, the average was calculated based on the maximum possible number of suitable leaves of the exsiccate. The consultation was carried out using the SpeciesLink System, using the exsiccatae tool with calibration and Reflora virtual herbarium, with refined searches for the locations of Minas Gerais and Espírito Santo (BFG 2018; INCT 2020).

Information about fruits and seeds was obtained for 895 species, in several specialized sources, such as books (Lorenzi 1992; Lorenzi 1998; Lorenzi 2011), specialized websites (Flora Brasiliensis - http://florabrasiliensis.cria.org.br/, Userful Tropical Plants database - http://tropical.theferns.info/, CNCFlora - http://cncflora.jbrj.gov.br/portal and others), herbariums (e.g. Herbário VIC, SpeciesLink, Reflora), scientific papers on taxonomic treatment, thesis, and dissertations (e.g. Pereira et al. 2006; Silva & Paoli 2006; Pirani 2006; Martins et al. 2009; Santos 2013; Reginato & Goldenberg 2018).

d. Generalized linear mixed models

Generalized mixed linear models (GLMM) were performed in the statistical environment R (R Core Team 2020), using the lme4 package with the 'lmer' function to fit a mixed effect model to the data, using the variable 'family' (fam) as random effect, since leaf size and its parts have a phylogenetic background, which can be exemplified by the leaf size of plants of the Arecaceae family (palm trees). This procedure minimizes a possible effect on the response variables (i.e. phylogenetic dependence; Herrera 2002; Kleiman & Aarssen 2007). The MuMIn package with the 'dredge' function was used to select models using maximum height combinations with the terms of the global models. All variables had their values log-transformed to reduce the effect of outliers.

Global model 1 was calculated using all the 8 functional traits measured for 895 species as fixed effects, while global model 2 was calculated using only the 4 leaf functional traits for 1912 species as fixed effects.

Global model 1 lmer(Hmax ~ LL + LW + PL + PW + SL + SW + FL + FW + (1 | fam))
Global model 2 lmer(Hmax ~ LL + LW + PL + PW + (1 | fam))

To select the model that best explained the variation in maximum height, the second-order Akaike information criterion (AICc) was used, and all models with $\triangle$AICc less or equal to 2 were considered parsimonious. When more than one model was selected, the average parameters of the models and standard errors were calculated using the 'model.avg' function of the *MuMIn* package, showing the significance values for each explanatory variable. There was no need to limit the number of explanatory variables to avoid overfitting because of the large number of species, but for the construction of global models only explanatory variables with a correlation less than 0.6 between them were used (https://github.com/rojaff/dredge_mc).

3 RESULTS

In the analysis of the global model 1, with 895 species, using Hmax as the response variable, five models (△AICc ≤ 2) were selected with all functional traits as explaining variables, but fruit width, with weights between 0.045 and 0.094 (Table 1). In this test where all functional characteristics were used as explanatory variables, only two were significant: the petiole length (PL) and the seed width (SW), positively correlated with the maximum height of the plant (Table 1; figure 2).

In the analysis of the global model 2, with 1.912 species, using Hmax as the response variable, two GLMM (△AICc ≤ 2) were found, with weights of 0.716 and 0.283 (Table 1). In this test with the four leaf functional characteristics as explanatory variables, three were significant: leaf length (LL), petiole length (PL) and petiole width (PW), which, unlike the other variables, was correlated negatively with the maximum height. Only the leaf width (LW) was not significant (Table 1; figure 3).

Table 1. Generalized linear mixed models.

Model code	**(Intrc)**	**FL**	**FW**	**LL**	**LW**	**PL**	**PW**	**SL**	**SW**	**df**	**logLik**	**AICc**	**delta**	**weight**
Model 1														
181	0.6630			0.11140		0.09987	-0.11710		0.1616	7	-79.838	173.8	0.00	0.094
189	0.6667			0.15040	-0.061660	0.11630	-0.10740		0.1630	8	-79.384	174.9	1.13	0.054
245	0.6570			0.10730		0.10110	-0.11680	0.04365	0.1239	8	-79.419	175.0	1.20	0.052
177	0.8460					0.12720	-0.06497		0.1685	6	-81.563	175.2	1.42	0.046
145	0.8548					0.10910			0.1645	5	-82.608	175.3	1.48	0.045
p	**< 2e-16**	0.98242		0.29637	0.74544	**0.00072**	0.16805		**< 2e-16**					
Model 2														
14	0.4700			0.2321		0.10430	-0.15370			6	-324.354	660.8	0.00	0.716
16	0.4723			0.2441	-0.01923	0.10870	-0.14990			7	-324.276	662.6	1.86	0.283
p	**< 2e-16**			**6.00e-07**	0.841	**3.57e-05**	**8.18e-05**							

Note: Log-transformed explanatory variables: FL, fruit length; FW, fruit width; LL, leaf length; LW, leaf width; PL, petiole length; PW, petiole width; SL, seed length; SW, seed width; *df*, degrees of freedom; logLik, log-likelihood; AICc, Akaike's information criterion; △ (stepping scale for model selection ≤ 2); weight, the proportion of the explained variance; and *p*, the significance of the best global model (bold results are significant).

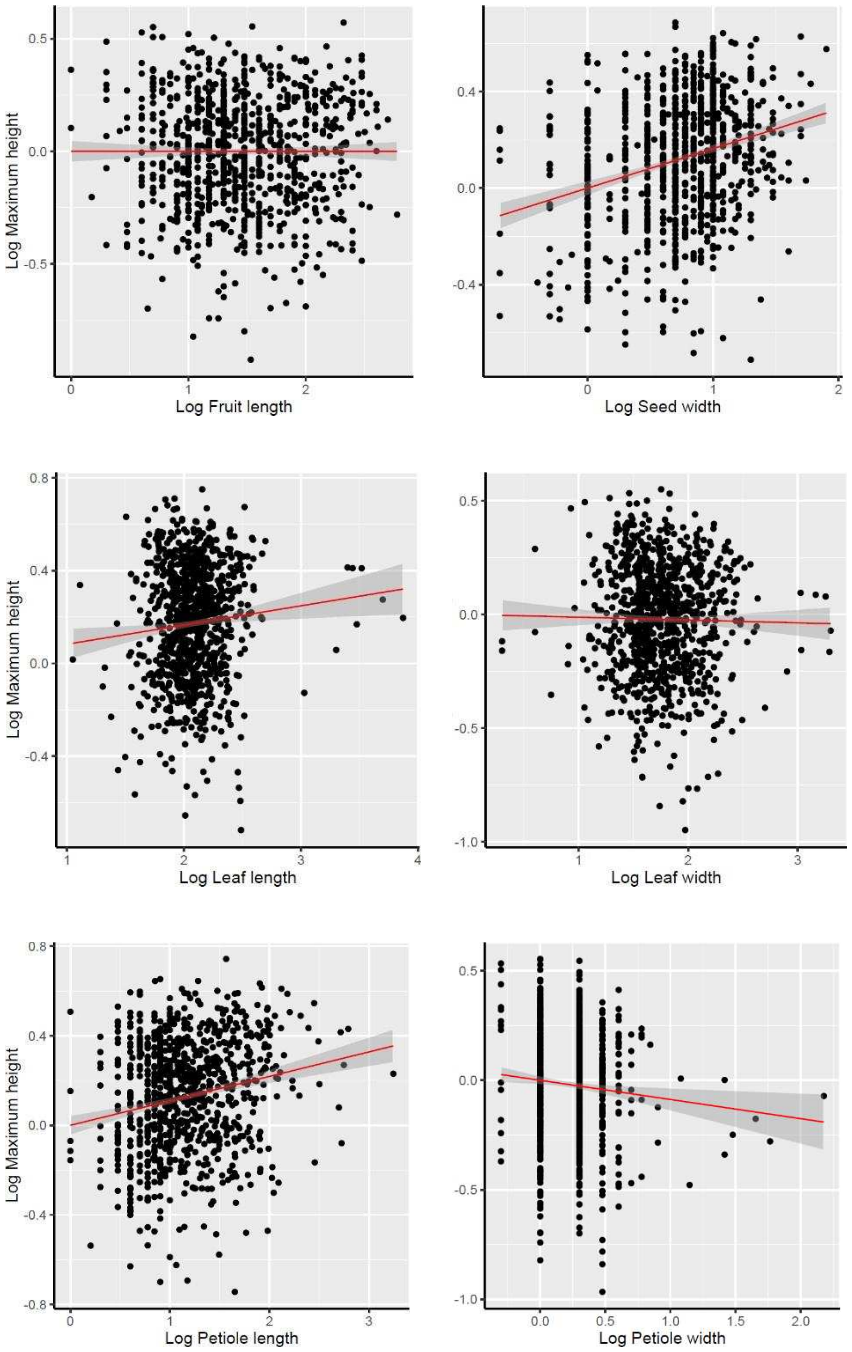

Figure 2. Global model 1 - Maximum height as a response variable and vegetative and reproductive characteristics as explanatory variables: fruit length (FL), p = 0.98242; seed width (SW), p <0.00001; leaf length (LL), p = 0.29637; leaf width (LW), p = 0.74544; petiole length (PL), p = 0.00072; and petiole width (PW), p = 0.16805 (table 1).

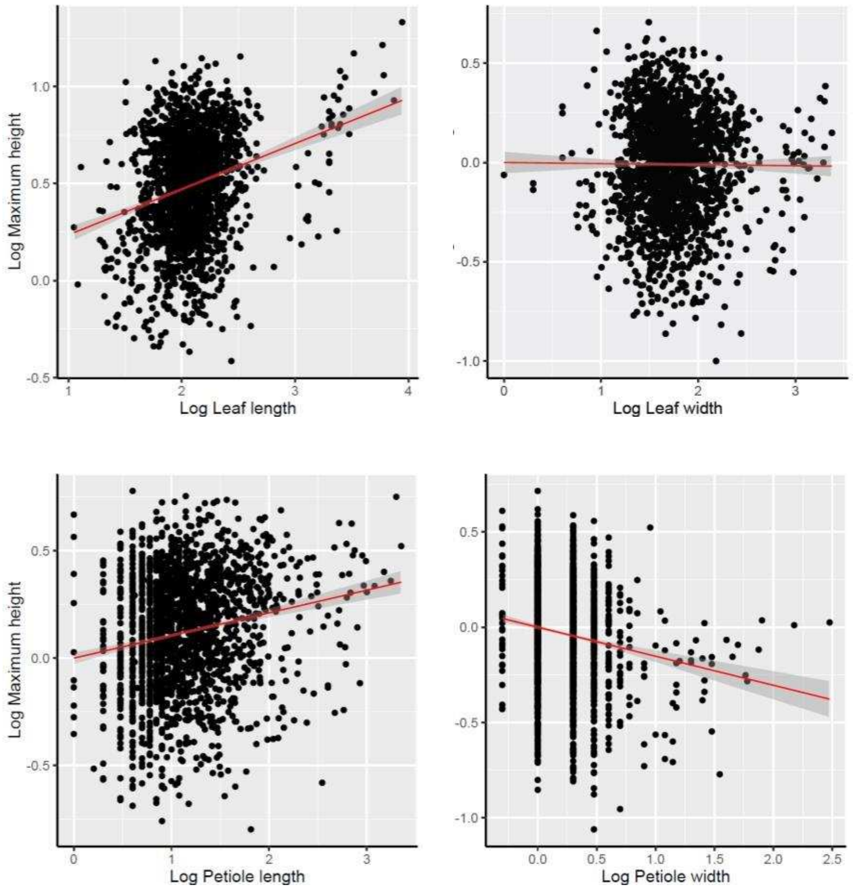

Figure 3. Global model 2 - Maximum height as a response variable and vegetative characteristics as explanatory variables: leaf length (LL), p <0.00001; leaf width (LW), p = 0.841; petiole length (PL), p <0.00001; and petiole width (PW), p <0.00001 (table 1).

4 DISCUSSION

The maximum height was a reliable and significant response variable as a proxy for the growth of species in both models, evidencing its importance as one of the three dimensions inherent to the spectrum of plant form and function (Díaz et al. 2016). In general, leaf traits (LL, PL and PW) were good explaining variables of height in the RDB, while the only significant reproductive trait was seed width.

The leaf blade length was positively correlated with Hmax in the global model 2 with 1.912 species. This is congruent with results of other studies which indicate that large leaves are associated with tall plants, suggesting that large leaf is mostly part of an acquisitive strategy of resource (Cornelissen 1999; Diaz et al. 2004; Navarro et al. 2010; Price et al. 2014; Garnier et al. 2016; Díaz et al. 2016; Hodgson et al. 2017; Meira-Neto et al. 2019) while small leaf is associated with short plants, suggesting that small leaf is mostly part of conservative strategy of resources. The leaf size directly impacts the capture of photosynthetic resources because, the larger the leaf, the larger the area available for the light interception, and the higher the rate of resource acquisition (Hodgson et al. 2017). Also, small woody plants may not support external branches thick enough to support large leaves, making this design allometrically unlikely, but not impossible (Navarro et al. 2010). Also, Kleiman & Aarssen (2007) suggested a trade-off between leaf size and quantity (leaf size/number trade-off), in which the selection would favor an intense foliation of small leaves or the production of large leaves.

LW was not selected in any global model, a result that differs from that found for another Atlantic Forest (Meira-Neto et al. 2019), whose height was explained mainly by the variation in leaf width. Navarro et al. (2010) also found the variation in leaf width more relevant than the variations in leaf length for Mediterranean species. However, differences of sites and methods using a broader database and with a selection of non-correlated explanatory characters, the leaf width was replaced in the models by other explanatory variables in the RDB Atlantic Forests.

The petiole length was the only significant characteristic in both models and proved to be a highly explanatory trait of tree growth in the Atlantic Forest, an unexpected result since it is less used than other leaf variables such as length and width of leaves. In the RDB, taller plants were related to longer petioles. The petiole is a structural component of the leaf whose main functions are the support of the leaf blade weight, the spatial positioning, and the vascularization of the leaf (Pasini & Mirjalili 2006; Garnier et al. 2016). The size and shape of the petiole are optimized on different length scales in order to facilitate its functions (Pasini & Mirjalili 2006). An increase in length of petiole can increase the efficiency of the light interception, since the leaf blade is farther from the stem/branch and other leaves and the probability of being shaded decreases (Pearcy et al. 2005; Brites & Valladares 2005; Niinemets et al. 2006). Thus, this structural feature adds an additional dimension to the interpretations of patterns of variation in leaf size (Niinemets et al. 2007). Large leaves require greater investment in support to ensure adequate mechanical structure and to avoid self-shading and wind damage (Niinemets et al. 2006; Kleiman & Aarssen 2007; Garnier et al. 2016). In view of these characteristics, long petioles are presented as functional traits of the acquisition strategy, while short petioles, of the conservative resource strategy.

Hmax was positively correlated with SW, indicating that taller plants have wider seeds, a result that is congruent with other studies that found the same relationship between tall species and large diaspores and small species with small diaspores (Whitman & Aarssen 2010; Lönnberg & Eriksson 2013; Díaz et al. 2016; Han et al. 2019; Candido et al. 2020). Larger seeds are associated with tolerance to greater stress in a shaded environment of taller forests (Muller-Landau 2010; Meira-Neto et al. 2019), being part of the conservative strategy, while smaller seeds have more advantage in fertility and have additional adaptations for fast growth (Muller-Landau 2010; Metz et al. 2010; Turnbull et al. 2012), suggesting an acquisition strategy. The trees height increases as the seed size increases and the conservative strategy of large seeds is associated with acquisitive strategy of greater growth of trees in these forests, congruently with the results of greater fruits explaining greater heights in Atlantic Rainforests (Meira-Neto et al. 2019). This also shows that conservative characters in trees can be associated with different acquisitive traits to assemble plants strategies, revealing independent character evolution, and allowing the coexistence of complex plant strategies in complex environments such as tropical forests (Baraloto et al. 2010; Meira-Neto et al. 2019).

Differently from the work of Meira-Neto et al. (2019), who found a significant relationship between Hmax and fruit variables (FL and FW) in an Atlantic Rainforest community, the global models in RDB replaced fruit by seed. As the model’s selection used only significant explanatory variables with less than 0.6 correlation and as the size of seeds is positively correlated to the seeds size, it replaced the fruits size in the found models.

The main drivers of the growth-survival trade-off found for RDB were the length of the petiole, the width of the petiole, the length of the leaf, and the width of the seed. These drivers differ from the main drivers found for another single Atlantic Forest (Meira-Neto et al. 2019), which were the width of the leaf and fruit. However, the results are not so different as fruit size and seed size are positively related, and that leaf width and leaf length are positively related.

5 CONCLUSION

As hypothesized, the maximum height was adequately explained by the functional traits measured and involved in the growth-survival trade-off, and represented, in a significant way, the maximum potential growth of BRD's Atlantic Forest species. This study supports the coexistence of different strategies among tree species for leaf, petioles, and seeds sizes, driven by a trade-off between fast acquisition and conservation of resources in tropical forests, which can promote the differentiation of niches in these communities. Finally, since the plants are not ecologically isolated, but inserted in a complex environmental context, susceptible to environmental filters, biotic interactions, and phylogenetic effects (Herrera 2002; Kleiman & Aarssen 2007; Navarro et al. 2010; Vitória et al. 2019), the next steps are related to the study of the functional traits integrated to the abiotic factors, phylogenetic histories and possible multiple interactions between the traits, in order to expand and complement the knowledge about the functional diversity of the plants in the tropical forest environment.

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CHAPTER 2: ENVIRONMENTAL FILTERS CHANGE THE PATTERNS OF TRAITS RELATED TO THE GROWTH-SURVIVAL TRADE-OFF IN A NEOTROPICAL REGION

RESUMO

Uma maneira de entender as regras de montagem que governam as assembleias de plantas é através da abordagem de traços funcionais e suas relações com o ambiente. É esperado que haja uma modificação das estratégias ecológicas relacionadas ao *trade-off* crescimento-sobrevivência com a variação dos gradientes ambientais. Investigar estas relações tem impacto no manejo e conservação da biodiversidade vegetal. Traços funcionais comumente utilizados em estudos de larga escala são os relacionados ao tamanho da planta, incluindo o tamanho da planta inteira, das estruturas fotossintéticas e reprodutivas. A relação entre os traços funcionais das espécies com a filogenia também deve ser levada em consideração, pois esta relação não é independente da relação taxonômica. O objetivo deste estudo foi investigar a relação entre os padrões de traços funcionais e o ambiente em uma bacia hidrográfica inserida na Mata Atlântica, na tentativa de responder à algumas perguntas como: quais são os principais fatores ambientais envolvidos na montagem de comunidades da região? Como as estratégias ecológicas funcionais e o *trade-off* crescimento-sobrevivência se modificam através dos gradientes ambientais? Os traços funcionais são conservados ou sobredispersos na filogenia? O estudo foi feito na Bacia do Rio Doce (BRD), bacia de importância federal que tem sofrido severos e recentes impactos ambientais. Os dados florísticos e ambientais foram coletados no banco de dados NeoTropTree. Foram coletadas informações sobre 10 traços funcionais vegetativos e reprodutivos de 1.912 espécies (altura máxima, comprimento e largura da lâmina foliar, do pecíolo, do fruto e da semente e síndromes de dispersão), e suas médias calculadas para 79 pontos da BRD. Para quantificar as relações entre traços funcionais e variáveis ambientais, foram feitos modelos lineares generalizados (GLM), com posterior seleção de modelos e separação dos modelos parcimoniosos através do △AICc. O sinal filogenético de cada traço funcional foi calculado através de dois métodos a fim de observar se havia a conservação filogenética de nicho em algum deles. Todas as análises foram realizadas no programa R. Todos os traços funcionais tiveram suas variâncias explicadas por um total de doze variáveis ambientais relacionadas ao gradiente térmico, hídrico e altitudinal. Foi observado sinal filogenético significativo em três traços funcionais (SW, FW e LW), sugerindo agrupamento filogenético de nicho nas partes mais altas da bacia. Este trabalho demonstra que existem processos de filtragem ambiental atuando nas comunidades de plantas da BRD, interferindo nos tamanhos dos órgãos vegetais e consequentemente influenciando o padrão do *trade-off* crescimento-sobrevivência observado, além de ser uma explicação plausível para o padrão de conservantismo filogenético de nicho encontrado para as larguras do fruto, da semente e da folha. As estratégias ecológicas mudam através dos gradientes hídrico, térmico e altitudinal da BRD. Este estudo confirma e destaca a influência de múltiplos fatores ambientais na montagem de comunidades da BRD e pela primeira vez demonstra sua importância na estruturação dos traços funcionais e estratégias ecológicas para a captura e uso de recursos pelas espécies lenhosas na bacia. O gradiente hídrico apresenta padrão vegetativo conservativo, com folhas e pecíolos menores, enquanto o padrão reprodutivo é aquisitivo, com frutos e sementes pequenos a medida em que a precipitação horizontal aumenta. Ao contrário, o gradiente térmico indica um padrão vegetativo aquisitivo, com folhas e pecíolos maiores, e um padrão reprodutivo conservativo, com frutos e sementes grandes. O gradiente altitudinal seguiu o padrão de umidade. Os estresses crônicos relacionados com as mudanças hídricas e térmicas com a variação da altitude podem influenciar os intervalos de estabelecimento das plantas, tornando a estratégia reprodutiva aquisitiva e a conservação de água pelas folhas mais favoráveis nessas condições. A temperatura mais elevada pode favorecer a estratégia fotossintética aquisitiva devido à área maior disponível para trocas de calor e à competitividade e tolerância em ambientes sombreados, com assistência de suporte mecânico de pecíolos maiores. Os traços funcionais vegetativos responderam consistentemente ao gradiente térmico, indicando que as restrições térmicas são mais importantes à estratégia de aquisição de energia luminosa e uso da água. Os traços funcionais reprodutivos responderam mais fortemente ao gradiente hídrico, sugerindo que os custos da reprodução são influenciados pela estabilidade do ambiente e disponibilidade hídrica. Este estudo confirma que o *trade-off* crescimento-sobrevivência opera independentemente nos diferentes níveis da planta e organiza diferentes estratégias relacionadas à fotossíntese e reprodução. Essa é uma importante adição à compreensão da ecologia funcional da região, promovendo uma base para o conhecimento das funções e serviços ecossistêmicos presentes na Mata Atlântica.

Palavras-chave: filtragem ambiental, traços funcionais, estratégias ecológicas.

ABSTRACT

One approach to understand the assembly rules that govern plant communities is by centering functional traits and their relationship with the environment. It is expected that there will be a modification of ecological strategies related to the growth-survival trade-off with the variation of environmental gradients. Investigating these relationships has an impact on the management and conservation of plant biodiversity. Functional traits commonly used in large-scale studies are those related to plant size, such as the size of the entire plant, and of photosynthetic and reproductive structures. The relationship between the functional traits with phylogeny must also be considered, as this relationship is not independent from the taxonomic relationship. The aim of this study was to investigate the relationship between the patterns of functional traits and the environment in a hydrographic basin inserted in the Atlantic Forest, to answer some questions such as: which are the main environmental factors involved in the assembly of communities in the region? How do functional ecological strategies and the growth-survival trade-off change through environmental gradients? Are functional traits conserved or overdispersed in phylogeny? The study was carried out in the Rio Doce Basin (RDB), an important basin that has suffered severe and recent environmental impacts. Floristic and environmental data were collected in the NeoTropTree database. Information was collected on 10 vegetative and reproductive functional traits of 1.912 species (maximum height, length and width of the leaf blade, petiole, fruit and seed and dispersion syndromes), and their averages calculated for 79 RDB points. To quantify the relationships between functional traits and environmental variables, generalized linear models (GLM) were calculated, with subsequent selection of models and separation of the parsimonious models through △AICc. The phylogenetic signal of each functional trait was calculated using two methods in order to observe whether there was a phylogenetic conservation of niche in any of them. All analyzes were performed in the R program. All functional traits had their variances explained by a total of twelve environmental variables related to the thermal, hydric and altitudinal gradient. A significant phylogenetic signal was observed in three functional traits (SW, FW and LW), suggesting a niche phylogenetic clustering in the upper part of the basin. This work demonstrates that there are environmental filtering processes acting in the RDB plant communities, interfering in the sizes of plant organs and consequently influencing the observed growth-survival trade-off pattern, in addition to being a plausible explanation for the phylogenetic conservatism pattern of niche found for fruit, seed and leaf widths. Ecological strategies change through RDB's hydric, thermal and altitudinal gradients. This study confirms and highlights the influence of multiple environmental factors in the assembly of BRD communities and for the first time demonstrates its importance in structuring the functional traits and ecological strategies for the capture and use of resources by woody species in the basin. The hydric gradient presents a conservative vegetative pattern, with smaller leaves and petioles, while the reproductive pattern is acquisitive, with small fruits and seeds as the horizontal precipitation increases. On the contrary, the thermal gradient indicates an acquisitive vegetative pattern, with larger leaves and petioles, and a conservative reproductive pattern, with large fruits and seeds. The altitudinal gradient followed the humidity pattern. Chronic stresses related to water and thermal changes with altitude variation can influence the plant establishment intervals, making the reproductive strategy and the conservation of water by the leaves more favorable in these conditions. The higher temperature can favor the acquisitive photosynthetic strategy due to the larger available area for heat exchanges and the competitiveness and tolerance in shaded environments, with assistance from mechanical support of larger petioles. The vegetative functional traits consistently responded to the thermal gradient, indicating that thermal restrictions are more important to the strategies of acquisition of light energy and use of water. The reproductive functional traits responded more strongly to the water regime, suggesting that the costs of reproduction are influenced by the stability of the environment and water availability. This study confirms that the growth-survival trade-off operates independently at different levels of the plant and organizes different strategies related to photosynthesis and reproduction. This is an important addition to the understanding of the functional ecology of the region, providing a basis for understanding the ecosystem functions and services present in the Atlantic Forest.

Keywords: environmental filtering, functional traits, ecological strategies.

1 INTRODUCTION

The search for assembly rules remains a central theme in ecology. There is a thriving understanding that the approach based on functional traits and their relationship with the physical environment is a promising path to provide insights into these processes, with direct implications for the conservation and management of ecosystems (Maharjan et al. 2011; Nock et al. 2016; Masarovičová et al. 2018). The use of plant functional traits related to the acquisition and conservation of resources reflects a trade-off between growth and survival, and represent ecological strategies that determine how plants respond to environmental factors (Díaz & Cabido 2001; Blundo et al. 2015; Sobral 2020). Identifying the patterns of ecological strategies along abiotic gradients helps to understand the structure of communities and predict which species will be able to escape environmental filters in different habitats (Díaz & Cabido 2001; Mcgill et al. 2006; Blundo et al. 2015) which is extremely relevant in the face of changes in vegetation cover and global climate (Diaz et al. 1998; Gallagher & Leishman 2012).

The attempt to systematize ecological strategies with environmental conditions serving as environmental filters is old (Box 2019), and has been made at several spatial scales. A number of studies demonstrate that the extrapolation of results based on environmental gradients must be analyzed case-by-case, as they strongly depend on the local conditions of the study area (Garnier et al. 2016). As the scale increases, the strength of environmental filtering seems to increase, while the importance of biotic interactions and disturbances seems to decrease (Diaz et al. 1998; Garnier et al. 2016). At the global level, however, Moles et al. (2014) found a weak association between functional traits and environmental variables. It has been suggested that the effect of environmental factors on functional traits can be spatially variable at different scales, demonstrating that environmental filtering is a fundamental process in communities assemblage, even in complex systems like tropical forests (Reich et al. 2003; Lebrija-Trejos et al. 2010; Echeverría-Londoño et al. 2018; Bu et al. 2019). Recent studies have focused on intermediary spatial scales, given the relative importance of processes acting on a regional scale and the effects of climatic factors on well-defined portions of ecosystems (Diaz et al. 1998; Kneitel & Chase 2004). Considering that in many cases it is of interest to know the response of a certain flora, researchers have suggested exploring the interrelation of functional traits involved in trade-offs and how they vary along environmental gradients in complete regional floras, especially in richer places, such as in the tropics (Diaz et al. 1998; Kneitel & Chase 2004; Leuschner & Meier 2018) and, as far as we know, except for the study by Almeida-Neto et al. (2008), which demonstrated large-scale trends in the relative frequency of characteristics of fruits along climatic and geographic gradients in the Atlantic Forest, the relationship of multiple functional traits and environmental gradients at greater magnitudes in this biome is unknown, so this study is likely to offer new insights to the knowledge of functional ecology in this global hotspot.

Two climatic environmental filters appear as the main ones in numerous studies that document the dynamics between functional and environmental patterns at different scales: precipitation and temperature, which alternate in importance (Oliveira-Filho & Fontes 2000; Diaz et al. 2004; Maharjan et al. 2011; Blundo et al. 2015; Wright et al. 2017; Rezende et al. 2017; Bruelheide et al. 2018; Caruso et al. 2020). In addition, the use of altitude as an abiotic variable has been shown to be useful, but it should be analyzed with caution, as this variable is considered an indirect influence through associated physical factors, such as atmospheric temperature and pressure, wind, radiation and soil depth, as well as regionally influencing the water regime, seasonality and humidity (Körner 2007; Almeida-Neto et al. 2008; Garnier et al. 2016). Due to the complexity of these parameters, there is no way to define large specific trends, since the gradient of humidity can go in any direction, both at high and low altitudes (Körner 2007) so, therefore, other variables that relates to humidity besides precipitation are important and should be added to studies of environmental gradients.

The interspecific variation of key functional traits has been used to define ecological strategies for the acquisition and conservation of resources (Reich et al. 2003; Blundo et al. 2015), focusing on traits that can be interpreted as proxies that capture important ecological dimensions that influence species performance, such as competitive vigor, fertility, productivity, dispersion, and regeneration (Westoby 1998; Cornelissen et al. 2003; Díaz et al. 2016; Monteiro et al. 2017; Leuschner & Meier 2018). Since several important metabolic processes operate largely through size, attributes related to it demonstrate ecological significance and should be studied (Box 2019), including the size of the whole plant, the size of photosynthetic surfaces, and the size of support and reproductive structures.

Several studies using the sizes of plant, leaf, fruit, and seed have found significant results in relation to the environment. In general, the wet to dry gradient is expected to favor conservative traits, with plants exhibiting small stature (Blundo et al. 2015; Moreira 2017; Box 2019; Dantas & Pausas 2020), narrow leaves (Herrera 2002; Maharjan et al. 2011; Meng et al. 2015; Hodgson et al. 2017; Asefa et al. 2017; Zhang & Li 2019) and short petioles (Niinemets et al. 2006). These characteristics related to survival have also been observed in sunnier, highest and colder habitats (Körner 2007; Gallagher & Leishman 2012; Zhang & Li 2019), in poor nutrient soils (Garnier et al. 2016; Hodgson et al. 2017; Dantas & Pausas 2020) and locations with higher disturbance frequency and intensity (Stevenson 2015; Monteiro et al. 2017). On the other hand, these same environmental factors tend to be related to small fruits and seeds (Almeida-Neto et al. 2008; Duivenvoorden & Cuello A 2012; Asefa et al. 2017; Liu et al. 2017), typical traits of an acquisition strategy of resource use, demonstrating that different plant organs may present independent ecological strategies (Wright et al. 2004; Silva et al. 2015).

At the other extremity of the growth-survival trade-off are the acquisitive traits, represented by taller plants, with larger and wider leaves and longer petioles which, together with conservative reproductive traits, such as larger and wider fruits and seeds, are observed in more humid and warmer forests (Almeida-Neto et al. 2008; Lebrija-Trejos et al. 2010; Maharjan et al. 2011; Jensen & Zwieniecki 2013; Blundo et al. 2015; Madani et al. 2018), at low altitudes (Duivenvoorden & Cuello A 2012) and habitats rich in nutrients (Asefa et al. 2017). These characteristics are strongly related to shade tolerance, in environments with vertical competition for light (Niinemets et al. 2006; Monteiro et al. 2017; Hodgson et al. 2017; Dantas & Pausas 2020).

However, there are variations in these patterns. Almeida (2015) found larger leaves at higher altitudes in the Brazilian semiarid region. The effects of temperature are even less consistent than those of altitude, as both the increase and decrease in the size of several organs have been documented. Stark et al. (2017) found smaller alpine and montane plants in temperate meadows in regions with higher average temperatures, while higher temperatures were related to taller plants in neotropical montane forests (Blundo et al. 2015) and at the global level (Madani et al. 2018). Small leaves were related to higher temperatures in a North American temperate environment (Stark et al. 2017) and in an Australian xeric environment (Xu et al. 2020), while Gallagher & Leishman (2012) found smaller leaves in colder environments in temperate Australia. Large seeds have been linked to higher temperatures at the global level (Madani et al. 2018), but Liu et al. (2017) suggests that the most common pattern is for smaller seeds to be found in warmer environments. These findings show that new analysis in different environments are still required, since these patterns vary depending on the scale, the vegetation analyzed and the local and regional geographic peculiarities (Körner 2007; Garnier et al. 2016).

It is also necessary to consider the pertinence of phylogenetic information in the interpretation of trait-environment relations (Asefa et al. 2017), since the climatic and environmental conditions in which species evolved have a long-standing influence on functional traits through niche phylogenetic conservatism, which is the persistence of ancestral traits in existing species, which underlie the assembly of communities (Cavender-Bares et al. 2016). The phylogenetic clustering resulting from evolutionary conservatism has been documented along precipitation gradients, indicating that initial adaptations to specific climatic conditions tend to be well maintained within certain lineages (Baraloto et al. 2012). Since combinations of sizes of different plant organs can identify ecological specializations of the present, but can also reflect ancestry (Herrera 2002; Hodgson et al. 2017), functional ecology studies can benefit from a phylogenetic dimension for a more accurate interpretation of the found patterns (Hodgson et al. 2017).

To understand the importance of environmental filtering in the assembly of communities, this study aimed to assess how different physical and climatic factors lead to the variation of functional traits of woody plants related to the growth-survival trade-off in a set of tropical communities in the Atlantic Forest, with the hypotheses that (1) as climatic conditions become more severe with the increase in altitude, the conservative strategy is favored, while, with the reduction of altitude, increase in temperature and other associated conditions, the acquisitive strategy is favored; and that (2) different positions of the environmental gradient generate communities phylogenetically clustered because of the niche conservatism of functional traits in the Atlantic Forest.

2 MATERIALS AND METHODS

a. Study area

The Rio Doce Basin (RDB) (Figure 1) is located in the hydrographic region of the Southeast Atlantic, in the Southeast of Brasil, covering an area of 86,715 km² in the states of Minas Gerais (86%) and Espírito Santo (14%), thus being a basin of the federal domain (Coelho 2009; IGAM 2010; ANA 2016). The RDB is inserted almost totally (98%) within the limits of a large global hotspot, the Atlantic forest (Myers et al. 2000; IGAM 2010; Pires et al. 2017). Over centuries of degradation, deforestation, urbanization and economic growth centered on the exploitation of commodities, putting pressure on the natural resources, the RDB has lost more than 71% of the coverage of its native vegetation and, recently, was the main victim of one of the worst environmental disasters in the history of Brasil (Oliveira-Filho & Fontes 2000; ANA 2016; Meira et al. 2016; Espindola et al. 2016; Pires et al. 2017).

The region possesses a considerable species richness of the Atlantic forest domain and have biogeographic and climatic processes that delimited the basin in a precise way, making it a suitable study area for analysis on a regional scale. The landscape in the basin is a mosaic with high altitudinal variation witch results in several geomorphological patterns (Figure 1) and accentuates the characteristics of air masses involved in the dynamics of its atmospheric circulation, giving the region great climatic variation (IGAM 2010; ANA 2016). The climate, following Köppen classification, is tropical humid, with average temperatures between 18 and 24.6°C (Coelho 2009; IGAM 2010). Two fluviometric periods are well marked, with precipitation ranging from 800 to 1.300 mm in the rainy season, and from 150 to 250 mm in the dry season (IGAM 2010).

b. Floristic and environmental data set

Floristic and environment data were obtained from NeoTropTree database, which has lists of tree species from Neotropics (Oliveira-Filho 2017). The matrix was composed of subregion codes distributed in 79 sampling points in the RDB (Figure 1). The correct names and synonyms were verified on the Flora do Brasil 2020 website (BFG 2018). Species without exsiccates available for conference at online herbariums or at the Herbarium of the Federal University of Viçosa (VIC), as well as species of Cactaceae with cladodes, were removed from the database. The final species list contains 1.912 woody species from different physiognomies of the Atlantic forest, belonging to 106 families of angiosperms, gymnosperms and arborescent pteridophytes.

25 quantitative environmental variables were taken for each site, presented in Table 1. After previous analysis in GLM, showing that certain variables did not interact with any functional trait, these were eliminated, resulting in 14 explanatory variables in the global models (*http://www.neotroptree.info/projectdetails/database/sites* for details).

c. Functional traits

The RDB woody plant species had 10 functional traits collected at the interspecific level, related to light interception, leaf economics and reproductive ability (Table 2).

The leaves had the traits collected for all 1.912 species. The values were obtained and their average calculated by consulting a minimum of two herbarium specimens (measurement of five fully expanded leaves in each exsiccata, (totaling 10 samples, according to the protocol for minimum repetition of leaf traits by (Cornelissen et al. 2003), with some exceptions for rare species that only the type exsiccate was found (with less than 10 suitable leaves). In these cases, the average was calculated based on the maximum possible number of suitable leaves of the exsiccate. The consultation was carried out using the SpeciesLink System, using the exsiccatae tool with calibration and Reflora virtual herbarium, with refined searches for the locations of Minas Gerais and Espírito Santo whenever possible (BFG 2018; INCT 2020).

Table 1. Environmental variables for each locality in the Rio Doce Basin, with their abbreviations and units when relevant (variables in bold were used in the analyses).

Environmental Variables	***Abbreviation***	***Unit***
Altitude at site center	Alt	m
Annual mean temperature	TempAnn	°C
Mean diurnal range	TempDayRng	°C
Isothermality	Isotherm	%
Temperature seasonality	TempSeas	°C
Maximum temperature of warmest month	TempMax	°C
Minimum temperature of coldest month	TempMin	°C
Temperature annual range	TempAnn	°C
Annual precipitation	PrecAnn	mm
Precipitation of wettest month	PrecWetP	mm
Precipitation of driest month	PrecDryP	mm
Precipitation seasonality	PrecSeas	%
Duration of the water deficit period	WDD	Days
Severity of the water deficit period	WDS	mm
Duration of the water excess period	WED	Days
Severity of the water excess period	WES	mm
Hyperseasonality	HyperSeas	%
Number of days with frost	DaysFrost	Days
Cloud interception or horizontal precipitation	CloudItcp	mm
Grassy cover	GrassyCover	%
Surface rockyness	RankedRockiness	%
Soil texture class	RankedSand	%
Soil drainage class	RankedDrainage	-
Soil water storage	SoilWaterStorage	-
Soil fertility based on average TBS	RankedTBS	%
Soil salinity	SoilSalinity	-

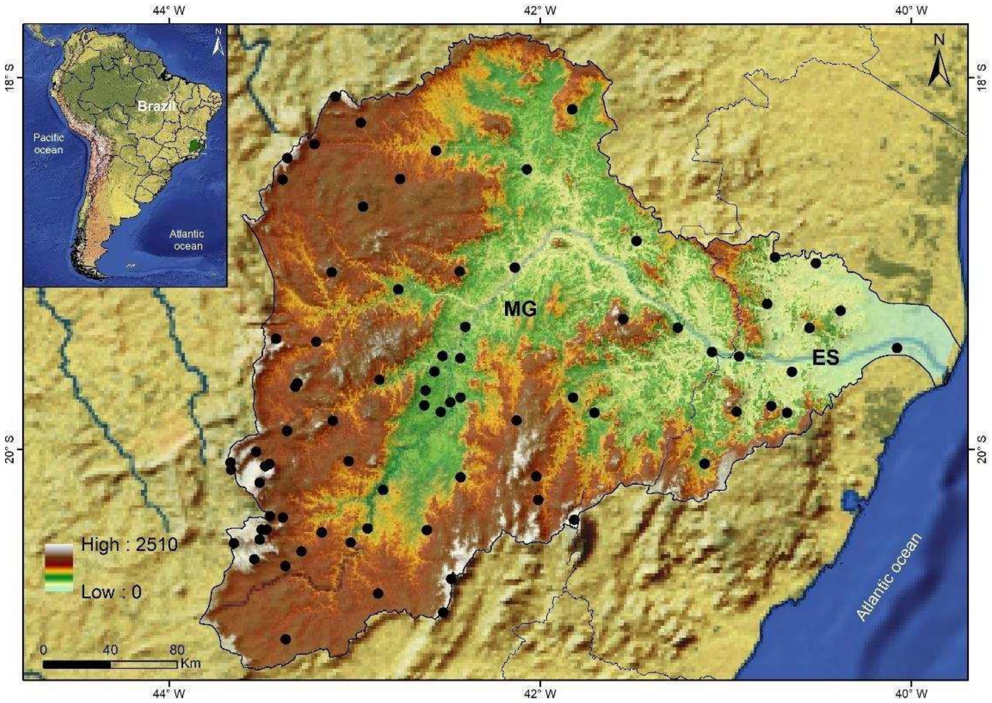

Figure 1. Altimetry and location of the 79 points studied in the Rio Doce Basin. MG – Minas gerais; ES – Espírito Santo. Data: WGS 84 (Adapted from Oliveira-Junior et al. 2020).

The maximum height and the dispersal syndromes were obtained for all 1.912 species, fruit variables for 1.295 species and seed variables had their measurements obtained for 895 species. The information about these traits were obtained through measurement in exsiccate, description data and observations in the reports generated by consulting the Reflora virtual herbarium (BFG 2018) and in several specialized sources, such as books (Lorenzi 1992; Lorenzi 1998; Lorenzi 2011), specialized websites (Flora Brasiliensis - http://florabrasiliensis.cria.org.br/, Userful Tropical Plants database - http://tropical.theferns.info/, CNCFlora - http://cncflora.jbrj.gov.br/portal and others), herbariums (e.g. Herbário VIC and exsiccatae tool of SpeciesLink), scientific papers on taxonomic treatment, thesis, and dissertations (Pereira et al. 2006; Silva & Paoli 2006; Pirani 2006; Martins et al. 2009; Santos 2013; Reginato & Goldenberg 2018).

Based on the species list for each location, all traits had their averages calculated for each of the 79 points in the basin, in millimeters for the quantitative traits, and the proportion in percentage for the dispersion syndromes.

Table 2. Functional traits quantified in this study, with their abbreviations and units when relevant.

Functional traits	***Abbreviation***	***Unit***	***Leading function***	***Number of species***
Plant Maximum Height	Hmx	m	Light interception (Competitive strength)	1.912
Leaf blade length	LL	mm	Plant economics (light capture versus overheating, fixation of carbon)	1.912
Leaf blade width	LW	mm		
Petiole length	PL	mm		
Petiole width	PW	mm		
Fruit length	FL	mm	Reproductive ability (potential for dispersion, colonization and resistance)	1.295
Fruit width	FW	mm		
Seed length	SL	mm		898
Seed width	SW	mm		
Dispersal syndromes	ZOO ANEMO AUTO	-		1.912

d. Generalized linear models

Generalized linear models (GLM) using a Gaussian distribution were used to quantify the relationships between traits values and physical and climatic variables. The 'dredge' function was used to select models using the functional traits combinations with the terms of the global models. All variables had their values scale-transformed to the standardization of the data.

Global model glm(scale(*'functional trait'*) ~ scale(Alt) + scale(TempAnn) + scale(TempDayRng) + scale(Isotherm) + scale(TempSeas) + scale(TempMax) + scale(PrecAnn) + scale(PrecDryP) + scale(WaterDefDur) + scale(WaterDefSev) + scale(WaterExcDur) + scale(WaterExcSev) + scale(DaysFrost) + scale(CloudItcp)).

To select the model that best explained the variation in each trait, second-order Akaike information criterion (AICc) was used, and all models with △AICc less or equal to 2 were considered parsimonious. When more than one model was selected, the average parameters of the models and standard errors were calculated using the 'model.avg' function of the *MuMIn* package, showing the significance values for each explanatory variable. To avoid overfitting, the number of explanatory variables in a single model was limited to a maximum of five, and only explanatory variables with a correlation of less than 0.6 between them were used (*https://github.com/rojaff/dredge_mc*). After the average of the models, the coefficients of the conditional averages, which averages only over the models where the parameter appears, were considered (Barton 2020).

All analysis were performed in the statistical environment R (R Core Team 2020), using the following packages: vegan, lme4, MuMIn, ggplot2, AICcmodavg, lattice, ggcorrplot, corrplot and car (Sarkar 2008; Wickham 2016; Wei & Simko 2017; Fox & Weisberg 2019; Kassambara 2019; Barton 2020; Mazerolle 2020; Oksanen & et al 2020; Bates et al. p. 4).

e. Phylogenetic signal

In order to observe the presence or absence of phylogenetic niche conservatism in functional traits, the phylogenetic signal was calculated, which corresponds to a statistical sample in which evolutionarily related species that contain values of traits closer to each other than randomly expected will present a significant sign (Garnier et al. 2016). This method has been considered useful to explore the evolution of functional traits along environmental gradients (Xu et al. 2017).

For this analysis, three phylogenetic trees were generated using the Phylomatic tool in Phylocom 4.2, based on the megatree R20160415.new and supported by the APG VI classification system (Webb et al. 2002; Gastauer & Meira-Neto 2016; The Angiosperm Phylogeny Group 2016). The first tree had a total of 1.892 species, excluding pteridophytes and gymnosperms, due to their strong effect on phylogenetic metrics (by having very deep branches); the second tree had 1.295 species that contained filled fruit data (FL and FW); and the third tree had 895 species that contained filled seed data (SL and SW), except gymnosperms, excluded for the reasons stated above. The resulting phylogenetic trees were visualized and converted to the 'newick' format in the Figtree v1.4.3 program (Rambaut 2010).

The phylogenetic signal was tested by two approaches, for comparative purposes: the Pagel’s λ (Pagel 1999) and Blomberg’s K (Blomberg et al. 2003). These methods assume that the evolution of functional traits follows the Brownian movement (BM) model. Pagel’s λ is estimated by maximum likelihood and considers the length of the branches of the phylogenetic tree to measure the phylogenetic dependence of the observed trait data (Pagel 1999; Peres 2016). Blomberg’s K is a ratio of mean square errors (MSE0/MSE), expressing the strength of the phylogenetic signal through the ratio between the observed and expected mean square error. For both, a value close to 0 indicates phylogenetic independence or a slight convergence in the trait. Generally, the upper limit of Pagel’s λ is close to 1, while Blomberg’s K can reach values above 1, in both, indicating greater similarity between close species than randomly expected, while $K=1$ indicates what would be randomly expected and $K<1$ indicates that the traits are more different than expected, suggesting overdispersion (Münkemüller et al. 2012; Satdichanh et al. 2015).

Blomberg’s K and Pagel’s λ were estimated with the ‘phylosig’ function from the Phytools package (Revell 2012). To obtain the statistical significance of K, 10.000 randomizations were performed using the 'nsim' argument.

3 RESULTS

In the GLM analysis and model selection, all functional traits had their variances explained by a total of twelve environmental variables (Altitude, Daysfrost, Isotherm, TempMax, TempSeas, TempAnn, CloudItcp, PrecDryP, WaterDefDur, WaterDefSev, WaterExcDur and WaterExcSev), which were related in a specific positive or negative pattern with the different traits. Only TempDayRng and PrecAnn were not significantly related to any functional trait. Table 3 in appendix I show the details.

The FL global model resulted in 8 GLM with weights between 0.154 and 0.063. For FL, Altitude and CloudItcp were negatively correlated. For FW, the global model resulted in 11 GLM with significant values, with weights between 0.120 and 0.045 and, similarly to FL, Altitude and CloudItcp were negatively correlated. In the global model for SL, 3 GLM were found with weights between 0.238 and 0.102, being positively correlated with Daysfrost and negatively correlated with Altitude and CloudItcp. SW had 5 significant GLM with weights between 0.182 and 0.069 and was negatively correlated with Altitude and CloudItcp (Figure 2; table 3 for details).

LL obtained 10 GLM with weights between 0.078 and 0.029 in the selection, and was negatively related to CloudItcp and Altitude, and positively correlated with DaysFrost, Isotherm, TempMax and WaterExcDur. The global model for LW resulted in 8 GLM with weights between 0.142 and 0.052, being negatively correlated with CloudItcp and Altitude, and positively correlated with Daysfrost, Isotherm and TempMax. PL obtained 15 GLM with weights between 0.060 and 0.023, showing a negative relationship with CloudItcp and a positive relationship with Daysfrost. The PW global model resulted in 12 GLM with weights between 0.049 and 0.018 in the selection, being negatively related with Altitude and TempSeas, and positively correlated with Isotherm and TempAnn (Figure 3; table 3 for details).

In the analysis of the Hmx global model, 4 significant GLMs were found, with weights between 0.189 and 0.080. Hmx was positively correlated with Daysfrost and negatively correlated with Altitude and CloudItcp. Among the dispersion syndromes, ZOO had only 1 GLM supplied after selection, with a weight of 0.505, being negatively related with PrecDryP, WaterDefDur and WaterExcSev. ANEMO had 2 GLM selected with weights between 0.614 and 0.297 and was negatively related to WaterDefSev and positively related to PrecDryP, WaterDefDur and WaterExcSev. And AUTO had 1 GLM supplied, with a weight of 0.649, showing a negative relationship with WaterDefSev and WaterExcDur and a positive relationship with CloudItcp, TempAnn and WaterExcSev (Figure 4; table 3 for details).

The phylogenetic signal (Table 3) by Pagel's λ method resulted in significant values close to 1 for almost all functional traits, indicating a proximity of these traits in the phylogeny, except PW and SL, which presented λ equal to 1, suggesting phylogenetic structure as expected by the Brownian movement. By Blomberg's K method, FW, LW and weakly SW presented values higher than 1, which indicates a higher similarity of functional traits between the lineages than expected by the Brownian movement, suggesting a conservation of these characteristics throughout the phylogeny. The other functional traits showed values lower than 1, indicating that these traits are more different than expected by the Brownian movement, and would be overdispersed in the phylogeny.

4 DISCUSSION

The results of this study demonstrate that there are environmental filtering processes acting on a large scale in the assembly of RDB plant communities, interfering in the values of functional traits along the gradients and in the observed growth-survival trade-off pattern. Three gradients influence the functional traits of the BRD woody species: a thermal gradient, a hydric gradient and an altitudinal gradient. These main environmental gradients found here related to the functional ecology of plants were already known and involved in other aspects of the region's vegetation. Oliveira-Filho & Fontes (2000) indicate the seasonality of precipitation and temperature as the main environmental variables that influence the evolution and speciation of plants in southeastern Brazil, and the subsequent study by Eisenlohr & de Oliveira-Filho (2015) confirms both spatial and environmental factors influencing floristic patterns in the Atlantic Forest. Saiter et al. (2015) found the thermal gradient and the seasonality of precipitation as the main determinants of RDB's phytogeographic patterns. Meira-Neto et al. (2020) demonstrate that water and thermal variables influence the richness of species, dispersal syndromes, phylogenetic structure and diversity of plants of RDB. Therefore, this study is congruent with previous findings, highlights the influence of multiple environmental factors in the assemblage of RDB communities and unprecedented demonstrates their importance in structuring the functional profiles and ecological strategies for the capture and use of resources by the woody species in communities of the landscape's basin.

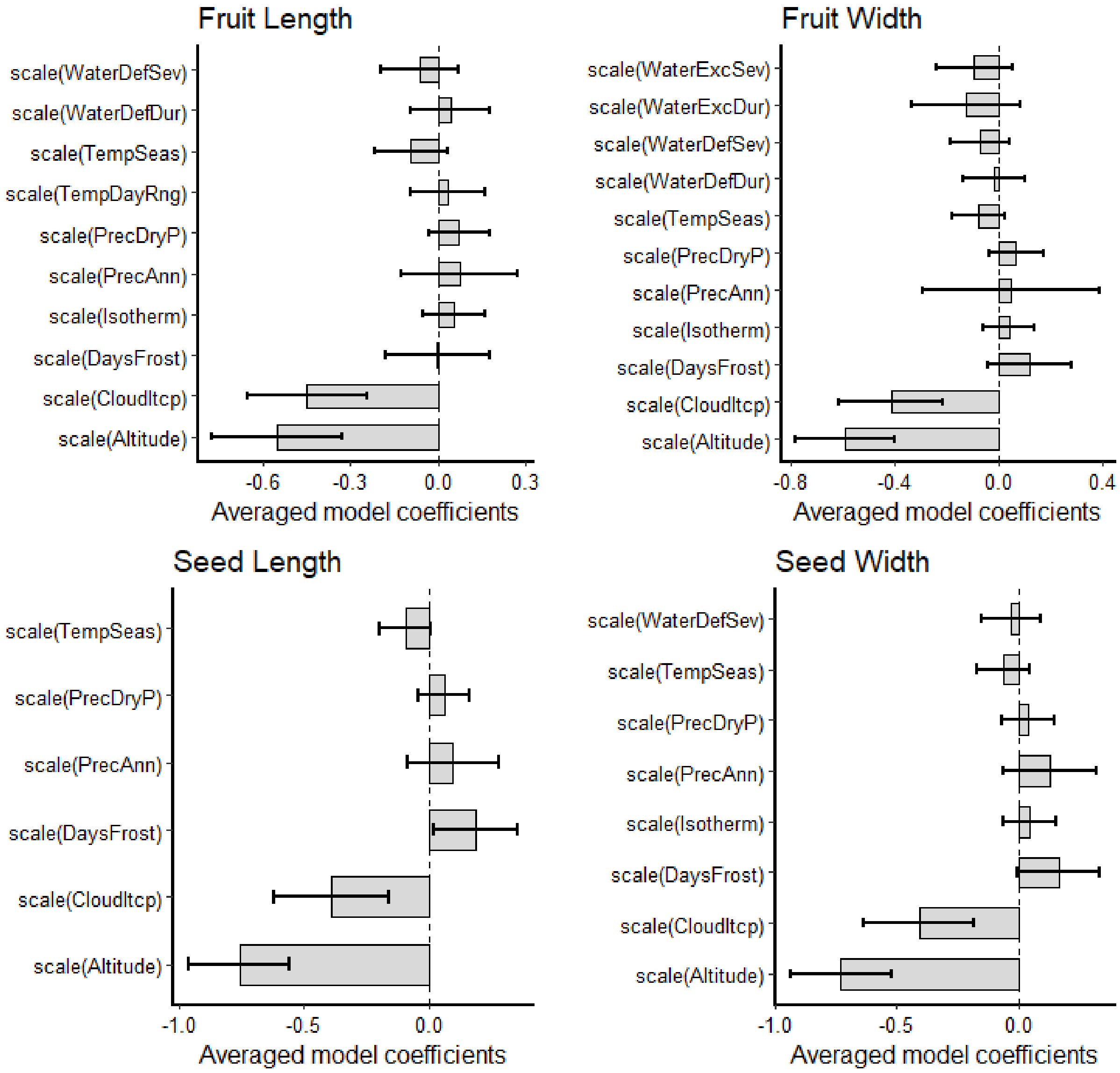

Figure 2. Averaged model coefficients for fruit length (FL), fruit width (FW), seed length (SL) and seed width (SW) general linear models (Appendix I for details).

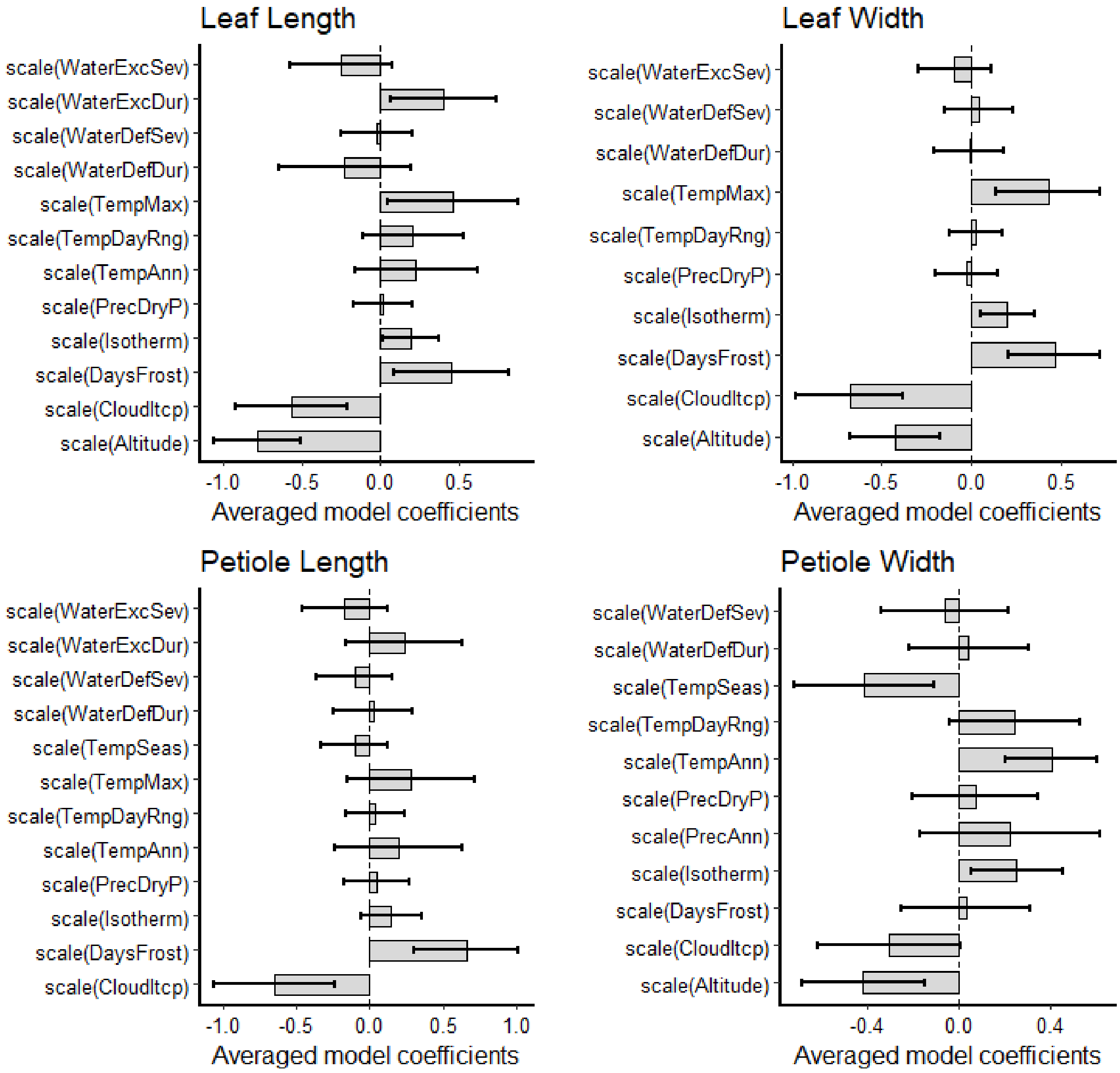

Figure 3. Averaged model coefficients for leaf length (LL), leaf width (LW), petiole length (PL) and petiole width (PW) general linear models (Appendix I for details).

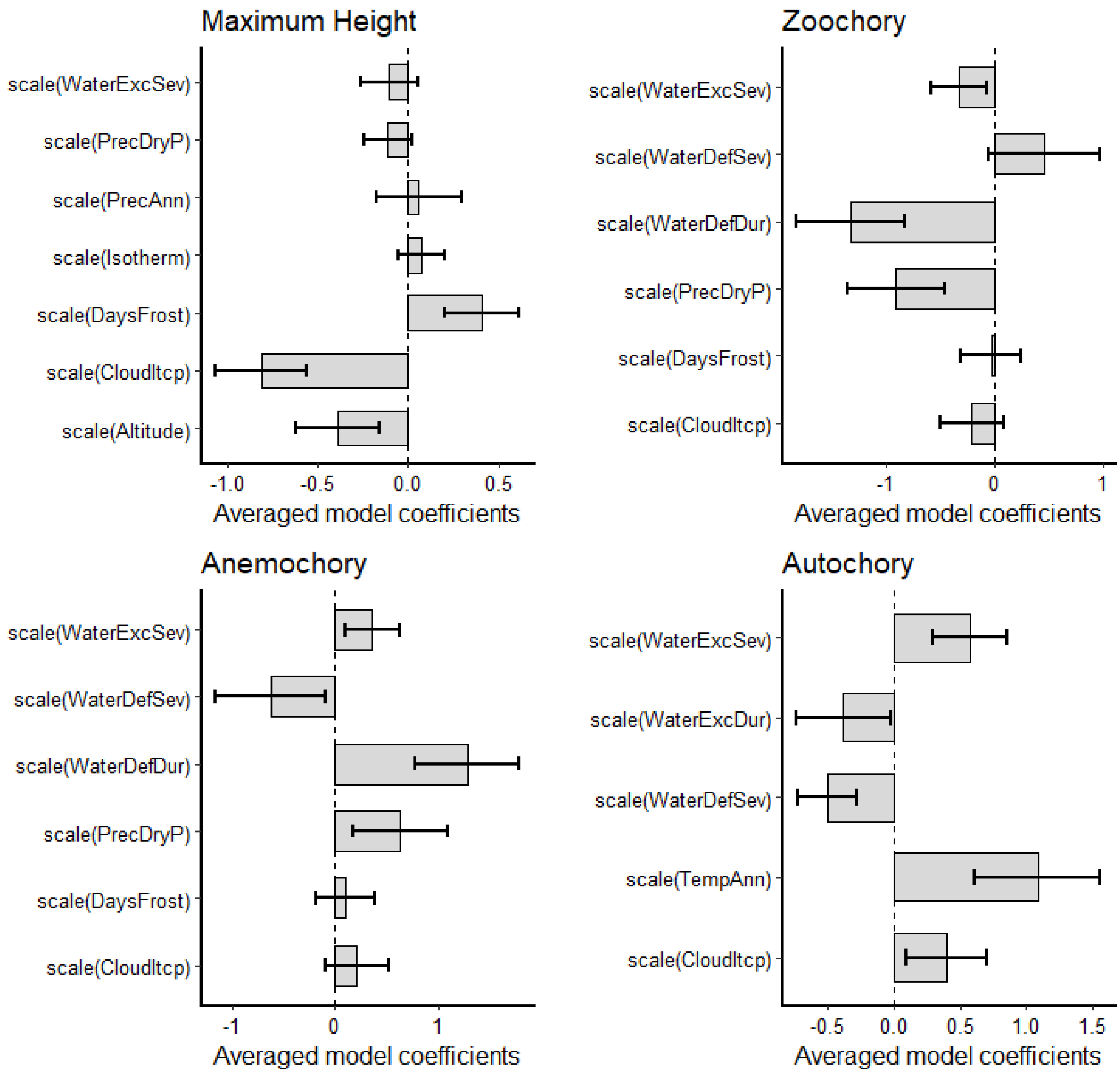

Figure 4. Averaged model coefficients for maximum height (HMX), zoochory (ZOO), anemochory (ANEMO) and autochory (AUTO) general linear models (Appendix I for details).

Table 3. Phylogenetic signal by two methods: Pagel’s Lambda and Blomberg’s K (10.000 randomizations).

Trait	***λ***	***p***	***K***	***p***
Hmx	0.9999459	*0*	0.9566531	*0,0001*
LL	0.9999515	*0*	0.8510101	*0,0001*
LW	0.999942	*0*	**1.161973**	*0,0001*
PL	0.9999688	*0*	0.9550456	*0,0001*
PW	1.000041	*0*	0.7920057	*0,0001*
FL[1]	0.9999355	*0*	0.8052719	*0,0001*
FL[2]	0.9992517	*0*	0.7730529	*0,0001*
FW[1]	0.9999405	*0*	0.6545251	*0,0001*
FW[2]	0.9999663	*0*	**1.166487**	*0,0001*
SL[1]	0.9998036	*0*	0.957341	*0,0001*
SL[3]	1.000036	*2.275887e-276*	0.7583714	*0,0001*
SW[1]	0.9996134	*0*	**1.075391**	*0,0001*
SW[3]	0.9993255	*2.620273e-298*	0.7520232	*0,0001*
Dispersal	0.9998222	*0*	0.9253056	*0,0001*

[1] Complete phylogenetic tree, with 1.892 species, except pteridophytes and gymnosperms.
[2] Phylogenetic tree with 1.295 species containing fruit data.
[3] Phylogenetic tree with 895 species containing seed data, except gymnosperms.

The conservative vegetative strategy and the acquisitive reproductive strategy predominated simultaneously in environments with a higher incidence of horizontal precipitation (cloud interception), that had a significant relationship with nine functional traits. Horizontal precipitation can be an important source of humidity in certain environments, such as in cloudy nanoforests, common on the western limit of RDB, as it represents an additional supply of water through the fogs and the atmospheric interception of water by the canopy, with subsequent drainage (Moreira 2017; Domínguez et al. 2017). These environments are typically under chronic and variable environmental stresses (Moreira 2017), which can decrease the intervals of opportunity for plant establishment, making the reproductive strategy of rapid germination and growth more favorable (Liu et al. 2017; Chen et al. 2020).

The vegetative traits showed an opposite, conservative pattern, along the same hydric gradient. Smaller trees and leaves are advantageous characteristics in environments less favorable to growth (Hodgson et al. 2017), such as sites with low water retention or poor nutrients soils (Niinemets et al. 2006; Kleiman & Aarssen 2007). A plausible explanation would be that, despite the increase of available water in the atmosphere, potentially available for canopy interception, possibly it is not equally available in the soil, which, by not adequately supplying water for transpiration and cooling, favors conservative strategies with greater water use efficiency and with greater light capture (Chapin et al. 1993; Körner 2007; Jensen & Zwieniecki 2013; Moles et al. 2014; Meng et al. 2015; Garnier et al. 2016; Asefa et al. 2017; Pérez-Ramos et al. 2019; Xu et al. 2020). This may be the case in RDB, as the sites with the highest levels of horizontal precipitation are found in nebular nanoforests and rocky fields (*campos rupestres*), ecosystems of great environmental complexity, often under water and soil extremes (Moreira 2017; Neri et al. 2017; Vitória et al. 2019). The variables related to the soil (e.g. rockiness, texture, drainage) present in the NeoTropTree database were not significantly related to the functional traits in previous analysis (data not shown). The study of more specific functional traits, such as hydraulic, physiological and root traits, together with data on the edaphic gradient, with its nutritional and water variables, can help to capture other aspects and factors involved in the pattern found here for this hydric gradient variable.

The thermal gradient exhibited an inverse pattern. Plants located in places with more frost days showed, on average, more conservative reproductive traits, and more acquisitive vegetative traits. This result was not expected, since, according to the literature, the greater the length and width of leaves, the more susceptible to frost damage, and the more the vegetation tends to present conservative traits in general (Augspurger 2009; Cavender-Bares et al. 2016; Leuschner & Meier 2018). Despite this, the occurrence of damage depends on several factors, such as the moment, the frequency, the distribution and the magnitude of the frosts, which may or may not affect the plant, depending on the sensitivity of the different stages of development (Augspurger 2009; Garnier et al. 2016). Studies that take frost into account in functional ecology are focused on temperate regions, with harsh winters and many days of frost. For example, Augspurger (2009) counted 8 days of frost in a spring month in Illinois, USA, against a maximum of 9 days of frost in an entire year at one of the RDB points. It is possible that the few days of frost in the basin, located in a tropical region, are not capable of causing damage to the plant organs and, on the contrary, other favorable conditions of these places, such as greater humidity, favor vegetative acquisitive characteristics (Mao et al. 2020).

Other authors suggest the deciduous habit as an escape strategy from low temperatures and freezing in woody plants (Cavender-Bares et al. 2016; Box 2019). In addition, Liu et al. (2018) suggests that the variable 'number of days with frost' may not be suitable for complex analysis of vegetation responses and possible frost damage, as susceptibility varies with the specific growth stage. Although frost already appears as an important factor that limits the distribution of species in southeastern Brasil (Oliveira-Filho & Fontes 2000), this phenomenon does not seem to impact the vegetative traits related to capture and use of resource strategies of woody plants in RDB. The conservative pattern of reproductive functional traits found on this gradient, on the other hand, may be linked to the fast acquisition of resources by larger leaves, because the more photosynthetic gains, the more energy can be allocated for reproduction (Liu et al. 2017).

The vegetative acquisitive pattern was also maintained in three other variables of the thermal gradient, presenting expected results. Larger leaves were observed in places with higher maximum temperatures, and wider petioles in places with higher annual temperatures. These acquisitive traits were also more frequent in environments with lower thermal amplitudes. High temperatures and isothermality are characteristic of places with more suitable and stable conditions for growth, such as equatorial, fluvial, tropical, wet, evergreen forests (Oliveira-Filho 2017). Fast growth plants are characteristic of humid, warm regions with vertical luminous gradients (Lebrija-Trejos et al. 2010; Jensen & Zwieniecki 2013; Blundo et al. 2015; Vilà-Cabrera et al. 2015; Mao et al. 2020), and the greater height allows the plant to properly capture and control larger leaf resources (Box 2019), which may have benefits derived from a larger area for heat exchange, maximizing photosynthetic gains in hot, humid and shaded environments, with the assistance of mechanical and water support of larger petioles (Kleiman & Aarssen 2007; Niinemets et al. 2007; Lebrija-Trejos et al. 2010; Vilà-Cabrera et al. 2015; Wright et al. 2017; Hodgson et al. 2017). On the contrary, a conservative pattern was negatively related to the temperature seasonality, demonstrating that the greater the temperature variation throughout the year, the narrower the petiole, suggesting a predominance of a conservative use of water in these sites (Blundo et al. 2015; Pérez-Ramos et al. 2019).

In the altitudinal gradient the predominant vegetative strategy was the conservation of resources and the predominant reproductive strategy was that of rapid acquisition of resources with increasing altitude. This pattern is well documented in studies of altitudinal variations (Körner 2007; Almeida-Neto et al. 2008; Duivenvoorden & Cuello A 2012; Xu et al. 2017;

Zhang & Li 2019; Vitória et al. 2019; Mao et al. 2020). The altitudinal gradient is considered an aggregating gradient, as it has several and complex climatic and geological influences considered more stressful for plants, such as the increasing solar radiation, decreasing temperatures, acceleration of air masses, promotion of cloudiness, shallower soils and with low availability of nutrients and water (Oliveira-Filho & Fontes 2000; Körner 2007; Schöb et al. 2013; Neri et al. 2017). Thus, plant responses must reflect a combination of multiple gradients, mainly with the influence of the humidity gradient (Körner 2007), as was found here, the same trade-off pattern for these two gradients. In addition, the dispersion of small fruits and the high capacity for colonization of small seeds may be related to the greater capacity to germinate in open environments and to migrate in the landscape, which may have great influence in the upper RDB. The highest places in the basin have greater grass cover, characteristic of rocky environments in the region (high altitude grasslands; Neri et al. 2017) and have a higher percentage of zoochoric species dispersed by birds (data not shown), so plants with small, zoochoric fruits and small seeds, which can tolerate exposure to the sun and germinate quickly under favorable conditions can benefit (Chen et al. 2020).

The reproductive traits related to dispersion were strongly influenced by the water regime in the model's selection. Sites with longer periods without rain (WDD), but with intense rains in the dry period (WES, PrecDryP), present a higher proportion of anemochoric and autochoric species, also showing a lower proportion of zoochoric species. This pattern of higher proportion of species with abiotic dispersion is associated with the middle and lower portion of the basin, where there is a strong maritime influence on humidity in the dry season, but still has, on average, less annual precipitation (Cupolillo et al. 2008; IGAM 2010). This region is characterized by the presence of deciduous and mainly semi-deciduous forests (NeoTropTree database; data not shown), where there is enough canopy opening to release the propagules in the absence or decrease of foliage (Almeida-Neto et al. 2008; Blundo et al. 2015; Chen et al. 2017). On the other hand, sites with long periods of rain or with severe water deficit (WED and WDS, respectively) show a decrease in the proportion of abiotically dispersed species, suggesting that, if very intense, seasonal droughts or even summer droughts (*veranicos*), characterized by short periods of water deficit in the middle of the rainy season (Cupolillo et al. 2008), do not favor this type of dispersion. In addition, despite the lower proportion between species (7% on average; data not shown), the autochory was the only one to respond positively to the annual temperature, congruent with the points with semideciduous seasonal forests at the middle/lower portion of the basin; and to the interception of clouds, greater at the highest points of the basin, with more shrubby vegetation, which characteristically has a higher proportion of abiotically dispersed species (Blundo et al. 2015).

Three functional traits were preserved along the phylogeny, all related to the width of vegetative and reproductive organs (FW, SW, LW). These traits are strongly linked to organ's length and plant size (Hodgson et al. 2017; Sobral 2020) and are more likely to be conserved in phylogenetic trees, since they are directly connected with other traits involved in the same functions related to the growth-survival trade-off (Webb et al. 2002). In niche conservatism, closest species explore similar environments where there are suitable conditions for development (Wiens et al. 2010). Since the presence of the phylogenetic signal suggests that some ecological processes are more plausible than others (Sobral & Cianciaruso 2012), and these three traits were related to environmental variables present in the hydric, thermal and altitudinal gradients, environmental filtering is one of the possible explanations for the niche conservation of these functional traits (Webb et al. 2002; Lososová et al. 2016; Carrión et al. 2017). However, different processes can generate the same phylogenetic signal value and estimating it is not the same as knowing the responsible processes (Baraloto et al. 2012). In addition, the phylogenetic signal was calculated for the regional species pool as a whole. Xu et al. (2017) calculated the phylogenetic signal for each community and more precisely detected the relationship between phylogeny and the altitudinal gradient. So, new phylogenetic signal measures for each of the RDB communities and related environmental variables can elucidate these results.

The thermal gradient markedly influenced the vegetative functional traits, which related to five significant thermal variables (DaysFrost, Isotherm, TempMax, TempAnn and TempSeas), against only two significant water variables (CloudItcp and WED). The hydric gradient assertively influenced the reproductive functional traits, which showed a significant relationship with six water variables (CloudItcp, PrecDryP, WDD, WDS, WED, WES) and with only two thermal variables (DaysFrost and TempAnn). Precipitation impacts the production and maintenance costs of fleshy fruits, usually associated with larger seeds. Therefore, larger fruits and seeds are found in more humid environments and with stable temperatures (Chen et al. 2017; Madani et al. 2018). On the other hand, although hydric limitation is a factor that can limit growth, photosynthetic organs size and activity (Wright et al. 2017; Vitória et al. 2019; Mao et al. 2020), thermal restrictions seem to be more important in the assembly of vegetative functional traits in BRD. The temperature of the leaf is an essential control of the rates of metabolic processes, and the size of the leaf directly affected its temperature, so, in the absence of sufficient water in the soil for efficient transpiration, the thermal restriction becomes relevant (Meng et al. 2015; Wright et al. 2017), and the positive response of the leaf size to the duration of the hydric excess and negative response to the interception of clouds which, as already mentioned, may be linked to edaphic variations, it seems to endorse this relationship. The altitudinal gradient proved to be a broadly aggregating and complex gradient, generating a response in eight functional, vegetative and reproductive traits, what was expected, since the functional variations follow the thermal and water gradients linked to elevation.

Caruso et al. (2020) suggest that, in general, water availability is a selection agent that leads to adaptation to the abiotic environment more important than temperature. But this evident difference in environmental filters during the vegetative and reproductive phases found here opens a question about the different pressures that acts as agents of adaptation to the abiotic environment in different stages of plant life. Consequently, this results also supports the repeated observation that the growth-survival trade-off operates independently at different levels of the plant in order to assemble a set of plant strategies promoted by the traits related to photosynthesis and reproduction (Diaz et al. 1998; Wright et al. 2004; Baraloto et al. 2010; Silva et al. 2015; Bruelheide et al. 2018). Selective pressures act on the individual, so functional traits cannot be filtered independently at individual level (Diaz et al. 1998) but functional traits can be selected independently at population and species levels (Meira-Neto et al. 2019). However, different characteristics occupy different positions in the spectrum between slow and fast use of resources (Silva et al. 2015), since the pressures during the different phases - vegetative and reproductive - can be vastly different, and the same conditions can be favorable or unfavorable, depending on the moment in the plant's life history (Lavorel & Garnier 2002; Garnier et al. 2016).

5 CONCLUSION

This study confirms the two suggested hypotheses. Regarding the first hypothesis, the ecological strategies based on the growth-survival trade-off change over BRD's hydric, thermal and altitudinal gradients. Conservative vegetative and acquisitive reproductive strategies prevail in the higher portions of the basin, which are also the places with greatest horizontal precipitation. On the other hand, acquisitive vegetative and conservative reproductive strategies prevail in sites with increasing temperatures and isothermality. In addition, the dispersion syndromes were influenced by the duration and severity of the hydric gradient. About the second hypothesis, niche conservatism and phylogenetic clustering was observed for fruit, seed and leaf widths, and environmental filtering is a plausible explanation for this phenomenon.

The water gradient influenced the dispersion-related functional traits more assertively, and not those linked to the growth-survival trade-off, while the temperature gradient significantly influenced the trade-off-related functional traits. Dispersion may not be directly related to the growth-survival trade-off, but it is an important variable to understand the functional dynamics of the Atlantic forest, as well as other aspects of the reproductive phase of plants.

There are many recent works demonstrating the necessity to recover ecological interactions and functions, protect natural resources and provide ecosystem services in RDB (Neves et al. 2016; Garcia et al. 2017; Meira-Neto & Neri 2017; Oliveira-Junior et al. 2020), but the lack of data on functional traits of species in the region is a barrier to large-scale restoration based on functional ecology (Carlucci et al. 2020). So, this study is an important addition to the understanding of the functional ecology of the region and promoting the basis for knowledge of the ecosystem functions and services present in the basin, necessary for functional restoration (Sobral 2020; Carlucci et al. 2020).

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7 APPENDIX I

Table 3. Generalized linear models.

Model Code	(Int)	scl(Alt)	scl(Cli)	scl(DyF)	scl(PDP)	scl(WES)	scl(Ist)	scl(PrA)	scl(WDD)	scl(WDS)	scl(TmS)	scl(TmM)	scl(TDR)	scl(TmA)	scl(WED)	df	logLik	AIC	delta	weight
FL																				
532	-5,59E-17	-0.5454	-0.4638					0.07305			-0.089710					6	-43.067	98.1	0.00	0.154
52	-1,07E-16	-0.5853	-0.4317		0.070850			0.07895								6	-43.435	98.9	0.74	0.106
40	-1,36E-16	-0.5320	-0.3998	-0.016780	0.074520											6	-43.752	99.5	1.37	0.077
2580	-7,31E-17	-0.5666	-0.4633					0.06352		-0.052700	-0.061580					7	-42.754	99.5	1.37	0.077
2064	-6,43E-17	-0.5515	-0.4128	-0.020560			0.055900			-0.074000						7	-42.823	99.6	1.51	0.072
1556	-4,32E-17	-0.5277	-0.4654					0.08173	0.0419900		-0.111400					7	-42.867	99.7	1.60	0.069
660	-3,16E-17	-0.5551	-0.4604					0.08583			-0.109700		0.035580			7	-42.899	99.8	1.66	0.067
536	-2,17E-17	-0.5459	-0.4946	0.036540				0.07492			-0.091640					7	-42.964	99.9	1.79	0.063
p	1	**1.00e-06**	**2.01e-05**	0.980	0.176		0.311	0.457	0.550	0.354	0.155		0.583							
FW																				
40	2,55E-16	-0.6200	-0.4304	0.117600	0.07433											6	-35.768	83.5	0.00	0.120
10248	2,74E-16	-0.6034	-0.4249	0.111100		-8,23E-02				-0.061490						7	-34.779	83.6	0.02	0.118
8232	2,71E-16	-0.5708	-0.4193	0.106000	0.05428	-8,22E-02										7	-34.829	83.7	0.12	0.113
12308	2,29E-16	-0.5560	-0.3838			-1,63E-01		0.23460							-0.15660	7	-35.243	84.5	0.95	0.075
14340	1,61E-16	-0.5445	-0.3512			-5,76E-02				-0.091810					-0.09074	7	-35.309	84.6	1.08	0.070
2064	3,13E-16	-0.6449	-0.4408	0.120100			0.041800			-0.066940						7	-35.343	84.7	1.15	0.067
9224	2,84E-16	-0.5898	-0.4136	0.119300		-9,67E-02			-0.018710							7	-35.378	84.8	1.22	0.065
48	3,07E-16	-0.6103	-0.4344	0.115100	0.05880		0.040180									7	-35.424	84.8	1.31	0.062
56	2,46E-16	-0.5918	-0.4180	0.115600	0.07490			-0.04302								7	-35.647	85.3	1.76	0.050
536	3,32E-16	-0.5676	-0.4781	0.164300				-0.04515			-0.0767100					7	-35.660	85.3	1.78	0.049
52	1,43E-16	-0.5738	-0.3355		0.09805			-0.04977								6	-36.749	85.5	1.96	0.045
p	1	**<2e-16**	**5.08e-05**	0.152	0.193	0.207	0.418	0.775	0.757	0.225	0.139				0.241					
SL																				
536	-3,10E-16	-0.7561	-0.4370	0.212800				0.09780			-0.0920100					7	-37.022	88.0	0.00	0.238
40	-4,25E-16	-0.7328	-0.3349	0.163900	0.06423											6	-38.507	89.0	0.97	0.147
56	-4,03E-16	-0.7994	-0.3641	0.168600	0.06290			0.10150								7	-37.872	89.7	1.70	0.102
p	1	**<2e-16**	**0.00086**	**0.02624**	0.21887			0.29419			0.08109									
SW																				
536	-5,36E-17	-0.7480	-0.4570	0.187000				0.12880			-0.061720					7	-39.543	93.1	0.00	0.182
56	-1,16E-16	-0.7778	-0.4081	0.158100	0.04081			0.13130								7	-39.926	93.9	0.77	0.124
40	-1,44E-16	-0.6917	-0.3703	0.152000	0.04253											6	-40.929	93.9	0.77	0.123
2064	-8,43E-17	-0.6957	-0.3782	0.149700			4,61E-02			-0.032890						7	-40.459	94.9	1.83	0.073
48	-8,33E-17	-0.6803	-0.3751	0.149200	0.02440		4,69E-02									7	-40.517	95.0	1.95	0.069
p	1	**<2e-16**	**0.000401**	0.057881	0.488142		0.389091	0.181833		0.594510	0.257000									

LL																			
271	9,95E-17		-0.58320	0.517200			0.2031				0.4445				6	-84.412	180.8	0.00	0.078
12551	-1,27E-16		-0.50010	0.493300		-0.2854					0.6525			0.37600	7	-83.632	181.3	0.44	0.063
8463	1,30E-16		-0.57330	0.458700		-0.1414	0.1927				0.3166				7	-83.664	181.3	0.50	0.061
12422	-3,34E-16	-0.7791		0.140500		-0.4157						0.209700		0.43540	7	-84.029	182.1	1.23	0.042
1154	-4,57E-16	-0.7859						-0.4065000				0.378700			5	-86.314	182.6	1.80	0.032
1295	5,16E-17		-0.57170	0.495000			0.1897	-0.0495800			0.4679				7	-84.314	182.6	1.80	0.032
399	1,08E-16		-0.56580	0.507500			0.2037				0.4478	0.032460			7	-84.336	182.7	1.85	0.031
2319	7,98E-17		-0.58070	0.513500			0.1962		2,04E-02		0.4566				7	-84.395	182.8	1.97	0.029
303	8,26E-17		-0.57970	0.509900	0.016770		0.1966				0.4432				7	-84.396	182.8	1.97	0.029
8271	2,60E-16		-0.62230	0.438300		-0.1697	0.1904						0.2252		7	-84.403	182.8	1.98	0.029
p	1	**<2e-16**	**0.00173**	**0.01525**	0.86377	0.12727	**0.03125**	0.28658	0.86012		**0.02883**	0.19937	0.25762	**0.02082**					
LW																			
271	5,74E-16		-0.6932	0.492400			0.19620				0.4454				6	-70.866	153.7	0.00	0.142
2064	6,55E-16	-0.4098	-0.6496	0.433300			0.21900		0.067150						7	-70.087	154.2	0.44	0.114
48	6,49E-16	-0.4395	-0.6559	0.432000	-0.044350		0.21550								7	-70.241	154.5	0.75	0.097
8463	5,94E-16		-0.6867	0.453900		-0.09310	0.18930				0.3611				7	-70.410	154.8	1.09	0.082
399	5,82E-16		-0.6794	0.484700			0.19670				0.4479	0.02570			7	-70.798	155.6	1.87	0.056
1295	5,62E-16		-0.6904	0.486900			0.19290	-0.012160			0.4511				7	-70.857	155.7	1.98	0.053
303	5,65E-16		-0.6914	0.488700	0.008372		0.19290				0.4447				7	-70.860	155.7	1.99	0.052
2319	5,72E-16		-0.6929	0.492000			0.19540		-0.002220		0.4467				7	-70.865	155.7	2.00	0.052
p	1	**0.000896**	**8.7e-06**	**0.000351**	0.765989	0.365580	**0.010048**	0.903032	0.642963		**0.003699**	0.728879							
PL																			
271	5,38E-16		-0.65120	0.66080			0.15150				0.269200				6	-96.368	204.7	0.00	0.060
263	3,49E-16		-0.63310	0.71490							0.347300				5	-97.547	205.1	0.36	0.050
79	6,48E-16		-0.69550	0.65400			0.15040						0.21290		6	-96.779	205.6	0.82	0.040
8463	5,64E-16		-0.64120	0.60160		-0.1432	0.14090				0.139600				7	-95.802	205.6	0.87	0.039
8455	3,50E-16		-0.62310	0.64330		-0.1628					0.193900				6	-96.829	205.7	0.92	0.038
71	4,80E-16		-0.66920	0.71270									0.30700		5	-97.873	205.7	1.01	0.036
2311	2,98E-16		-0.62260	0.67580					-0.129700		0.401600				6	-96.940	205.9	1.14	0.034
8271	6,57E-16		-0.68020	0.57600		-0.1737	0.14580						0.05084		7	-95.985	206.0	1.24	0.033
12551	3,95E-16		-0.59290	0.62930		-0.2358					0.356700			0.234000	7	-96.078	206.2	1.42	0.030
2319	4,21E-16		-0.64290	0.64860			0.12830		-0.068060		0.309600				7	-96.224	206.4	1.71	0.026
295	3,14E-16		-0.62020	0.67010							0.325500			0.078360	6	-97.242	206.5	1.75	0.025
399	5,61E-16		-0.63020	0.64910			0.15220				0.273100			0.03906	7	-96.286	206.6	1.84	0.024
303	5,14E-16		-0.64660	0.65140			0.14300				0.267500			0.021710	7	-96.347	206.7	1.96	0.023
1295	5,62E-16		-0.65710	0.67220			0.15840	0.0254900			0.257200				7	-96.349	206.7	1.96	0.023
8967	4,95E-16		-0.70520	0.65510		-0.1303				-0.104900	0.138500				7	-96.358	206.7	1.98	0.022
p	1		**0.00194**	**0.00030**	0.64784	0.25860	0.16831	0.85326	0.43283	0.35759	0.21253	0.70282	0.37882	0.24461					

PW																			
674	2,07E-16	-0.3877			0.0885400						-0.3572	0.2886000			6	-96.352	204.7	0.00	0.049
10	2,88E-16	-0.4240					0.2613								4	-98.359	204.7	0.01	0.049
643	5,17E-16		-0.3673000								-0.5031	0.2438000			5	-97.367	204.7	0.03	0.048
660	3,70E-16	-0.4229	-0.1893000					0.2274000			-0.4442	0.2796000			7	-95.533	205.1	0.36	0.041
514	1,44E-17	-0.4214									-0.2414				4	-98.921	205.8	1.14	0.028
73	3,26E-16						0.2521						0.4069		4	-99.210	206.4	1.72	0.021
42	2,52E-16	-0.4219			0.0485200		0.2405								5	-98.253	206.5	1.80	0.020
2694	2,16E-16	-0.4564		0.032330						-0.086610	-0.3661	0.2869000			7	-96.270	206.5	1.84	0.020
675	5,12E-16		-0.3638000		0.0602500						-0.4728	0.2646000			6	-97.278	206.6	1.85	0.019
2058	2,63E-16	-0.4427					0.2484			-0.036930					5	-98.307	206.6	1.91	0.019
1667	5,02E-16		-0.3484000						0.043800		-0.5115	0.2304000			6	-97.308	206.6	1.91	0.019
138	3,02E-16	-0.4239					0.2613					0.0199900			5	-98.337	206.7	1.97	0.018
1034	2,80E-16	-0.4309					0.2570		-0.013280						5	-98.352	206.7	2.00	0.018
p	1	**0.00225**	0.05523	0.82266	0.60543		**0.01417**	0.26044	0.74387	0.66566	**0.00823**	0.09256	**6.2e-05**						
HMX																			
40	3,52E-16	-0.4057	-0.8142	0.416700	-0.098120										6	-55.867	123.7	0.00	0.189
8232	3,72E-16	-0.3430	-0.8000	0.401900	-0.123700	-0.10470									7	-54.951	123.9	0.17	0.174
48	4,49E-16	-0.3876	-0.8217	0.412100	-0.126900		0.0743200								7	-55.155	124.3	0.58	0.142
56	3,65E-16	-0.4453	-0.8315	0.419400	-0.098920			0.060470							7	-55.723	125.4	1.71	0.080
p	1	**0.0009**	**<2e-16**	**9,00E-05**	0.0966	0.1981	0.2570	0.6115											
ZOO																			
11299	1,59E-15		-0.205600		-0.93690	-0.317300			-1,337	0.42520					7	-94.764	203.5	0.00	0.505
p			0.1716	0.8433	**6.63e-05**	**0.0107**			**2.00e-07**	0.0806									
ANEMO																			
11299	-7,19E-17		0.213800		0.66440	0.3533			1,283	-0.5891000					7	-97.581	209.2	0.00	0.614
11301	1,08E-16			0.1090000	0.57540	0.3872			1,282	-0.7040000					7	-98.308	210.6	1.45	0.297
p	1		0.17015	0.45462	**0.00583**	**0.00596**			**8,00E-07**	**0.02040**									
AUTO																			
14403	-8,48E-16		0.396000			0.574600				-0.489700			1,1100	-0.3719	7	-86.118	186.2	0.00	0.649
p	1		**0.0104**			**6.53e-05**				**1.47e-05**			**7.70e-06**	**0.0362**					

Note: Scaled explanatory variables: Alt, altitude; ClI, Cloud interception; DyF, days with frost; PDP, precipitation of dry period; WES, water excess severity; Ist, isothermality; PrA, annual precipitation; WDD, water deficit duration; WDS, water deficit severity; TmS, temperature seasonality; TmM, maximum temperature; TDR, temperature day range; TmA, annual temperature; WED, water excess duration; *df*, degrees of freedom; logLik, log-likelihood; AICc, Akaike's information criterion; △ (stepping scale for model selection ≤ 2); weight, the proportion of the explained variance; and *p*, the significance of the best global model (bold results are significant).