ELIELSON LUCAS FERREIRA

COMPETIÇÃO E FATORES ABIÓTICOS INFLUENCIAM COMUNIDADES VEGETAIS NOS PÁRAMOS BRASILEIROS

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*.

Orientadora: Andreza Viana Neri

VIÇOSA - MINAS GERAIS
2022

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

T
F383c
2022

Ferreira, Elielson Lucas, 1996-
Competição e fatores abióticos influenciam comunidades vegetais nos *páramos* brasileiros / Elielson Lucas Ferreira. – Viçosa, MG, 2022.
1 dissertação eletrônica (93 f.): il. (algumas color.).

Texto em português e inglês.
Inclui apêndices.
Orientador: Andreza Viana Neri.
Dissertação (mestrado) - Universidade Federal de Viçosa, Departamento de Biologia Vegetal, 2022.
Inclui bibliografia.
DOI: https://doi.org/10.47328/ufvbbt.2022.610
Modo de acesso: World Wide Web.

1. Plantas das montanhas - Parque Estadual da Serra do Brigadeiro (MG). 2. Biodiversidade. 3. Competição (Biologia). 4. Ecologia das montanhas. I. Neri, Andreza Viana, 1977-. II. Universidade Federal de Viçosa. Departamento de Biologia Vegetal. Programa de Pós-Graduação em Botânica. III. Título.

CDD 22. ed. 581.98151

Bibliotecário(a) responsável: Bruna Silva CRB-6/2552

ELIELSON LUCAS FERREIRA

COMPETIÇÃO E FATORES ABIÓTICOS INFLUENCIAM COMUNIDADES VEGETAIS NOS PÁRAMOS BRASILEIROS

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*.

APROVADA: 07 de julho de 2022.

Assentimento:

Elielson Lucas Ferreira
Autor

Andreza Viana Neri
Orientadora

AGRADECIMENTOS

Agradeço à minha família por todo o apoio nessa jornada. Aos meus pais pela paciência, carinho e incentivo durante o tempo em que passei com eles. Ao meu irmão, que guiou os meus passos para o mestrado, sempre dando conselhos para que eu tomasse o melhor caminho em minha carreira acadêmica. Aos meus tios pelo carinho e pela recepção calorosa toda vez que retornava de Viçosa. Aos meus avós, que mesmo com sua simplicidade me despertaram o olhar para as plantas e para os padrões da natureza.

Agradeço à Bruna por me aturar durante todo o mestrado, seja nos momentos de medo pela pandemia, ou nos momentos de desmotivação, quando achava que não seria capaz de concluir minha pesquisa, por todos os percalços que enfrentei. Sou grato por me fazer acreditar que poderia seguir meu sonho, por me incentivar a me arriscar, tentar aquilo que achava ser muito além das minhas capacidades e, por fim, ter conseguido.

Gratidão também pela companhia constante dos meus amigos da Biologia, mesmo que estejamos tão distantes fisicamente. Ao Dedé, meu parceiro constante das pedaladas, que me ajudaram a superar primeiro ano de pandemia. Ao Wallace, com quem partilho o encanto pela natureza e sempre tenho conversas muito proveitosas. Ao Deão, pela companhia no momento mais crítico da pandemia. Ao Marcelo, o irmão que ganhei em Viçosa, por me ouvir nos desabafos e por me ajudar diretamente na dissertação.

Agradeço aos meus companheiros de apartamento, George, Igor e Wilson pela companhia e conversas enriquecedoras. Ao George, agradeço em especial pelas ajudas com estatística. Ao saudoso Wilson, por encher nossa casa de alegria, e que possa continuar sendo luz onde quer que esteja.

Meus agradecimentos aos amigos e colegas do LEEP, em especial ao Celso, pela companhia quase diária lá no laboratório. Não posso esquecer o Carlos, pelas conversas sobre os assuntos mais diversos possíveis. Aos colegas do grupo de pesquisa, pela companhia e por ouvirem meus desabafos.

Agradeço também ao PPG-Bot e a todos os professores que enriqueceram minha formação. À Andreza, pela oportunidade de desenvolver minha pesquisa nessa vegetação pela qual sou encantado. À Larissa por compartilhar os dados de sua tese.

Ao Instituto Estadual de Florestas (IEF), pela concessão da licença de coleta.

Meus agradecimentos ao Parque Estadual da Serra do Brigadeiro, por nos receber durante os campos. Aos funcionários que nos acolheram de formidável no período que passamos lá.

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

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

RESUMO

FERREIRA, Elielson Lucas, M.Sc., Universidade Federal de Viçosa, julho de 2022. **Competição e fatores abióticos influenciam comunidades vegetais nos *páramos* brasileiros.** Orientadora: Andreza Viana Neri.

As montanhas tropicais são grandes centros de biodiversidade no mundo, servindo como abrigos, berçários, mas também túmulos para muitas espécies. No Brasil, os campos de altitude, ou páramos brasileiros, são abrigos para diversas espécies endêmicas. Contudo, se encontram altamente ameaçados pelas mudanças climáticas, tendo em vista a sua distribuição restrita. A altitude e o solo são tidos como os principais promotores dos padrões de diversidade nesses ambientes, sendo o papel das interações bióticas negligenciado. Este estudo visa compreender como interações competitivas em associação com as variáveis topográficas determinam a estrutura e os padrões de diversidade desses ambientes, em seus aspectos taxonômico e funcional. Para tanto, estabelecemos 135 parcelas de um metro quadrado em uma montanha do Parque Estadual da Serra do Brigadeiro. Coletamos dados de composição de espécies – pelos quais calculamos índices de diversidade taxonômica –, e traços funcionais – pelos quais medimos a média e a variância de cada traço na comunidade, bem como a diversidade funcional de diversidade funcional. Este estudo foi divido em dois capítulos, que buscam responder as seguintes perguntas: 1) Como a interação entre altitude, disponibilidade de solo e densidade da cobertura vegetal influenciam na composição e na diversidade de espécies em montanhas tropicais, em nível local? 2) Como estes mesmos fatores influenciam na filtragem de estratégias funcionais entre hábitats e na coexistência de diferentes estratégias em um mesmo hábitat? No primeiro capítulo, observamos que a composição de espécies foi influenciada pelos fatores ambientais, sendo a disponibilidade de solo o fator com maior poder de explicação. Observamos também, que a diversidade aumentou com a altitude e com a escassez de solo, mas diminuiu com a densidade da cobertura vegetal. Contudo, esse padrão esteve mais associado ao aumento da equidade do que com o aumento da riqueza. Isso pode ser explicado pela redução da dominância sob condições extremas, devido à presença de espécies altamente adaptadas, que devem apresentar *fitness* similares entre elas. No segundo capítulo, vimos que a vegetação da montanha é composta primordialmente por espécies tolerantes ao estresse, mas que variaram com relação a estratégias de uso do carbono, de resistência à seca e de investimento em

crescimento. Para traços relacionados ao uso de carbono, houve um aumento da convergência funcional sob maiores altitudes e densidade de cobertura vegetal. Para traços relacionados a estratégias de resistência à seca, houve um aumento da convergência funcional em maiores altitudes e sob maior disponibilidade de solo. Nossos resultados sugerem que a altitude atua como um importante filtro abiótico nessas comunidades. Contudo, a filtragem de estratégias só acontece na presença de exclusão competitiva favorecida pelo aumento da disponibilidade de recursos e aumento da densidade de cobertura. Além disso, as médias de traços da comunidade variaram em função da interação entre os três preditores, sugerindo não haver uma única estratégia capaz de prover maior habilidade competitiva em todo o gradiente. Ao nível do habitat, a coexistência de espécies foi determinada principalmente pela disponibilidade de solo e altitude. Em alta altitude e alta disponibilidade de solo, houve maior dominância de espécies convergentes em estratégias de resistência à seca e de investimento em altura. Já em áreas de solo escasso em baixa altitude, as comunidades foram dominadas por espécies que divergem nessas estratégias, mas que apresentam alta tolerância ao estresse. Nosso estudo mostrou que os padrões de composição e diversidade taxonômica e funcional na montanha estudada são determinados pela interação entre fatores abióticos e bióticos. A predição dos impactos das mudanças climáticas nesses ambientes deve, portanto, levar em consideração as interações competitivas, que limitam a distribuição e permanência das espécies ao longo dos gradientes de altitude e solo.

Palavras-chave: Campos de altitude. Filtragem ambiental. Competição. Estratégias ecológicas. Diversidade.

ABSTRACT

FERREIRA, Elielson Lucas, M.Sc., Universidade Federal de Viçosa, July 2022. **Competition and abiotic factors influence plant communities in the Brazilian *páramos*.** Advisor: Andreza Viana Neri.

Tropical mountains are great centres of biodiversity in the world, serving as hosts, cradles, but also graves for many species. In Brazil, the *campos de altitude*, or Brazilian *páramos*, are home for several endemic species. However, they are highly threatened by climate change, given their restricted distribution. Elevation and soil are considered the main drivers of diversity patterns in these environments, with the role of biotic interactions being neglected. This study aims to understand how competitive interactions in association with topographic variables determine the structure and diversity patterns of these environments, in their taxonomic and functional aspects. In order to do that, 135 1 m^2 plots were established on a mountain in the Serra do Brigadeiro State Park. Species composition data was collected – by which taxonomic diversity indices were calculated –, and functional traits – by which community's mean, variance and functional diversity were measured. This study was divided into two chapters, which aims to answer the following questions, respectively: 1) How does the interaction between elevation, soil availability and vegetation cover density influence the composition and diversity of species in tropical mountains at a local level? 2) How do these same factors influence the filtering of functional strategies between habitats and the coexistence of different strategies in the same habitat? In the first chapter, we observed that species composition was influenced by environmental factors, with soil availability being the factor with the greatest explanatory power. We also observed that diversity increased with elevation and soil scarcity, but decreased with the density of vegetation cover. However, this pattern was more associated with an increase in evenness rather than with an increase in richness. This can be explained by the reduction in dominance under extreme conditions, due to the presence of highly adapted species, which might have similar fitness. In the second chapter, we saw that the vegetation in this mountain is primarily composed of stress-tolerant species, but that varied in terms of carbon use strategies, drought resistance strategies and investment in growth. For traits related to carbon use, there was an increase in functional convergence under higher elevations and vegetation cover density. For traits related to drought resistance strategies, there was an increase in functional convergence at higher

elevations and under greater soil availability. Our results suggest that elevation acts as an important filter abiotic filter in these communities. However, strategy filtering only occurs with the presence of competitive exclusion favoured by the increase in resource availability and plant cover density. In addition, the means of community traits varied as a function of the interaction between the three predictors, suggesting that there is no single strategy capable of providing greater competitive ability along the whole gradient. At the habitat level, species coexistence was mainly determined by soil availability and elevation. At high elevation and high soil availability, there was a greater dominance of convergent species in drought resistance strategies and in height. On the other hand, in areas of scarce soil at low elevation, communities were dominated by species that diverge in these strategies, but that present high stress-tolerance. Our study showed that the patterns of taxonomic and functional composition and diversity in the studied mountain are determined by the interaction between abiotic and biotic factors. The predictions of climate change impacts on these environments must, therefore, take into account the competitive interactions, which limit the distribution and permanence of species along the gradients of elevation and soil.

Keywords: Brazilian *Páramos*. Environmental filtering. Competition. Ecological strategies Diversity.

SUMÁRIO

INTRODUÇÃO GERAL

A divulgação do último relatório do Painel Intergovernamental sobre Mudanças Climáticas (Masson-Delmotte, V., P. Zhai, A. Pirani et al. 2021) trouxe um alerta ainda maior sobre a vulnerabilidade dos ecossistemas às mudanças globais. Dentre os impactos diretos do aquecimento do planeta, estão as mudanças na distribuição das espécies devido ao deslocamento de hábitats ao longo do espaço (Bellard et al. 2012, Assis and de Mattos 2016, Habibullah et al. 2022). O desaparecimento de alguns hábitats e limitações na dispersão das espécies podem causar uma grande perda da biodiversidade do planeta (Graae et al. 2018, Nunez et al. 2019). Somado a isso, as mudanças no clima podem favorecer a invasão de espécies, impactando as populações de espécies nativas (Elith and Leathwick 2009, Czarniecka et al. 2019). Contudo, a estabilidade dos ecossistemas pode ser mantida graças á heterogeneidade ambiental, que pode tamponar os efeitos das mudanças climáticas (Graae et al. 2018). Além disso, outros fatores ambientais, como a disponibilidade de recursos e a presença de competidores, podem ter grande contribuição para a sobrevivência e a habilidade competitiva das espécies (Chesson 2000, Mayfield and Levine 2010). Isso torna crucial a compreensão dos fatores que determinam a distribuição das espécies em nível local, como a competição por recursos e a heterogeneidade ambiental.

Por serem ambientes onde o efeito dos fatores abióticos sobre a distribuição das espécies se torna mais explícito, os ecossistemas de montanha têm sido considerados bons laboratórios para o estudo dos efeitos das mudanças no clima (López-Angulo et al. 2020a, Tito et al. 2020). A grande diversidade de micro-hábitats em uma curta escala espacial, causada pelos fortes gradientes topográficos, faz das montanhas verdadeiros “berçários” de novas espécies (Rangel et al. 2018, Rahbek et al. 2019a, 2019b). No entanto, a alta especialização também faz delas grandes “túmulos” para diversas linhagens, visto que a alta especificidade também torna as espécies que as habitam mais suscetíveis a extinções (Rangel et al. 2018, Rahbek et al. 2019a). Esse duplo carácter torna os ecossistemas de montanha extremamente vulneráveis, mas também locais cruciais para o entendimento dos efeitos do clima sobre a biodiversidade (Beniston 2003, Sanders and Rahbek 2012, Christmann and Oliveras 2020).

O aumento da radiação UV e da intensidade dos ventos, somado à diminuição da pressão atmosférica e da temperatura com a altitude, representam fatores altamente estressantes para as plantas (Sanders and Rahbek 2012, Thakur and Chawla 2019). Além

disso, a variação na topografia pode levar à formação de hábitats com solo escasso, onde a baixa retenção de umidade e a menor disponibilidade de nutrientes se tornam fatores limitantes para a maioria das plantas (Porembski 2006, 2007, Bernard-Verdier et al. 2012, Neri et al. 2016). A variação conjunta desses fatores cria um mosaico de diferentes hábitats, os quais estão associados a drásticas mudanças na composição de espécies, promovendo um aumento da beta-diversidade (Cordeiro and Neri 2019, Rahbek et al. 2019a, Campos et al. 2021). Contudo, a intensificação da severidade ambiental causada pelo aumento na altitude e na escassez de solo pode levar à perda de diversidade, pela exclusão de espécies pobremente adaptadas a essas condições extremas (Read et al. 2014, Thakur and Chawla 2019, López-Angulo et al. 2020). Esse processo, chamado filtragem ambiental, é tido como um dos principais promotores dos padrões de composição e diversidade nas montanhas tropicais (Negreiros et al. 2014, Kraft et al. 2015a).

É difícil distinguir se uma espécie não se encontra em um ambiente por ausência de características adaptativas que permitam sua sobrevivência sob as condições locais ou se ela foi excluída competitivamente por outra espécie (Mayfield and Levine 2010, Kraft et al. 2015a, Cadotte and Tucker 2019). Nesse sentido, o aumento da densidade de indivíduos em um hábitat pode levar a exclusão de espécies pouco adaptadas à alta depleção de recursos do solo por competidores e à competição por luz (de Bello et al. 2012, Kraft et al. 2015b, Czarniecka et al. 2019). Esse fator depende, no entanto, da presença de alguma característica funcional que permita maior habilidade competitiva, o que pode estar relacionado a estratégias universais (Grime 1977), ou ser relativo às condições abióticas locais (Enquist et al. 2015, Thakur and Chawla 2019). Contudo, a importância da competição na estruturação de comunidades montanas tropicais é ainda negligenciada, muito pela ideia de que em ambientes com forte estresse abiótico, o efeito da competição se torna menos importante (Wilson and Lee 2000).

Além disso, as condições bióticas e abióticas de um hábitat não só podem determinar quais espécies são filtradas para dentro ou para fora das comunidades, como também podem influenciar sua coexistência estável (Chesson 2000, Enquist et al. 2015, Pastore et al. 2021). De acordo com a teoria moderna da coexistência, a co-ocorrência de duas espécies em um mesmo ambiente acontece devido ao equilíbrio entre diferenças de *fitness* e diferenças de nicho entre elas (Chesson 2000). Em comunidades vegetais montanas, as diferenças de nicho podem estar relacionadas a diferentes estratégias de alocação de carbono e de tolerância à seca, que podem, por sua vez, implicar em diferenças de *fitness* (Porembski 2007, Matos et al.

2021, 2022). Em condições menos severas, espera-se que espécies com estratégias divergentes possam dominar os recursos, visto que reduzem a competição entre si devido a menor sobreposição de nicho (Pastore et al. 2021). Por outro lado, o aumento da severidade ambiental pode fazer com que espécies com estratégias divergentes tenham perda de *fitness*, resultando em comunidades dominadas apenas por espécies com características convergentes (Pastore et al. 2021). Por esse motivo, o aumento da altitude, da densidade de indivíduos e a diminuição da disponibilidade de solo em um hábitat pode impactar a partição de recursos entre as espécies ocorrentes, gerando comunidades com maior dominância por espécies com estratégias semelhantes (Hillebrand et al. 2008). A compreensão de como os fatores ambientais determinam as relações de dominância nessas comunidades pode servir para prever e controlar futuras invasões biológicas (Gauzere et al. 2020, Fernandes et al. 2021).

Os páramos brasileiros, mais conhecidos como campos de altitude, são ecossistemas particularmente vulneráveis às mudanças climáticas devido à sua distribuição restrita (Scarano et al. 2016, Christmann and Oliveras 2020). Estão associados a montanhas formadas por gnaisse e granito do sudeste e sul o Brasil, localizando-se em estreitas faixas altitudinais de 1500 a 2900 m de altitude (Safford 1999a, Vasconcelos 2011). Os campos de altitude estão situados em meio ao domínio da Mata Atlântica – um dos hotspots de biodiversidade global (Myers et al. 2000) – e abrigam uma grande diversidade de espécies vegetais, muitas das quais são endêmicas (Safford 2007). Sua vegetação apresenta gradientes edáficos bem marcados, havendo forte heterogeneidade na vegetação ao longo desses gradientes (Safford 1999a, Caiafa and Silva 2005, Tinti et al. 2015). Por esse motivo, são ecossistemas ideais para testar a influência das interações entre fatores abióticos e bióticos sobre os processos de montagem de comunidades (Tito et al. 2020).

No presente estudo, amostramos uma montanha no Parque Estadual do Brigadeiro, em Minas Gerais. Foram realizadas coletas de dados de composição de espécies, de traços funcionais e variáveis ambientais em 135 parcelas, distribuídas em três hábitats distintos: o topo (T), a encosta superior (US) e a encosta inferior (BS). Esses dados foram utilizados para responder duas perguntas centrais: 1) Como a interação entre altitude, disponibilidade de solo e densidade da cobertura vegetal influenciam na composição e na diversidade de espécies em montanhas tropicais, em nível local? 2) Como estes mesmos fatores influenciam na filtragem de estratégias funcionais entre hábitats e na coexistência de diferentes estratégias em um mesmo hábitat? Essas perguntas geraram hipóteses que foram testadas nos dois capítulos que seguem.

REFERÊNCIAS

Alcantara, S., R. de Mello-Silva, G. S. Teodoro, K. Drequeceler, D. D. Ackerly, and R. S. Oliveira. 2015. Carbon assimilation and habitat segregation in resurrection plants: A comparison between desiccation- and non-desiccation-tolerant species of Neotropical Velloziaceae (Pandanales). Functional Ecology 29:1499–1512.

Alves, R. J. V, and J. Kolbek. 2010. Can campo rupestre vegetation be floristically delimited based on vascular plant genera ? Plant Ecology 207:67–79.

Antonelli, A., W. D. Kissling, S. G. A. Flantua, M. A. Bermúdez, A. Mulch, A. N. Muellner-Riehl, H. Kreft, H. P. Linder, C. Badgley, J. Fjeldså, S. A. Fritz, C. Rahbek, F. Herman, H. Hooghiemstra, and C. Hoorn. 2018. Geological and climatic influences on mountain biodiversity. Nature Geoscience 11:718–725.

Assis, M. V., and E. A. de Mattos. 2016. Vulnerabilidade da vegetação de campos de altitude às mudanças climáticas. Oecologia Australis 20:24–36.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1–48.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters 15:365–377.

de Bello, F., C. Carmona, A. Dias, L. Götzenberger, M. Moretti, and M. Berg. 2021. Response Traits and the Filtering Metaphor. Pages 57–74 Handbook of Trait-Based Ecology From Theory to R Tools. Cambridge University Press, Cambridge.

de Bello, F., J. N. Price, T. Munkemuller, J. Liira, M. Zobel, W. Thuiller, P. Gerhold, L. Götzenberger, S. Lavergne, J. Lepš, K. Zobel, and M. Partel. 2012. Functional species pool framework to test for biotic effects on community assembly. Ecology 93:2263–2273.

Beniston, M. 2003. Climatic change in mountain regions: a review of possible impacts. Climatic Change 59:5–31.

Benites, V. de M., A. N. Caiafa, E. De Sá Mendonça, C. E. Schaefer, and J. C. Ker. 2003. Solos e vegetação nos complexos rupestres de altitude da Mantiqueira e do Espinhaço. Floresta e Ambiente 10:76–85.

Benites, V. M., C. E. G. R. Schaefer, E. S. Mendonça, and L. Martin Neto. 2001. Caracterização da matéria orgânica e micromorfologia de solos sob Campos de Altitude no parque estadual da Serra do Brigadeiro (MG). Revista Brasileira de Ciência do Solo

25:661–674.

Bernard-Verdier, M., M. L. Navas, M. Vellend, C. Violle, A. Fayolle, and E. Garnier. 2012. Community assembly along a soil depth gradient: Contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. Journal of Ecology 100:1422–1433.

Braun-Blanquet, J. 1979. Fitosociologia: Bases para el estudio de las comunidades vegetales. First edition. H. Blume Ediciones, Madrid, Espanha.

Breheny, P., and W. Burchett. 2017. Visualization of Regression Models Using visreg. The R Journal 9:56–71.

Bueno de Mesquita, C. P., L. S. Tillmann, C. D. Bernard, K. C. Rosemond, N. P. Molotch, and K. N. Suding. 2018. Topographic heterogeneity explains patterns of vegetation response to climate change (1972 – 2008) across a mountain landscape , Niwot. Arctic, Antarctic, and Alpine Research 50.

Cáceres, M. De, and P. Legendre. 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90:3566–3574.

Cadotte, M. W., and C. M. Tucker. 2019. Should Environmental Filtering be Abandoned ? Trends in Ecology & Evolution.

Caiafa, A. N., and A. F. da Silva. 2005. Composição florística e espectro biológico de um campo de altitude no Parque Estadual da Serra do Brigadeiro, Minas Gerais – Brasil. Rodriguésia 56:163–173.

Caiafa, A. N., and A. F. da Silva. 2007. Structural analysis of the vegetation on a highland granitic rock outcrop in Southeast Brazil 1 3:657–664.

Callaway, R. M., R. W. Brooker, P. Choler, Z. Kikvidze, C. J. Lortie, R. Michalet, L. Paolini, F. I. Pugnaire, B. Newingham, E. T. Aschehoug, C. Armas, D. Kikodze, and B. J. Cook. 2002. Positive interactions among alpine plants increase with stress. Nature 417:844–848.

Campos, P. V., P. M. Villa, C. E. G. R. Schaefer, J. A. Nunes, S. Porembski, and A. V. Neri. 2021. Community composition , beta diversity and structure of high altitude grasslands along an altitudinal gradient in southeastern Beta diversity , community composition and structure of high altitude grasslands along an altitudinal gradient in southeastern B. Revista de Biología Tropical 68:977–986.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology, Evolution, and Systematics 31:343–366.

Chesson, P. 2018. Updates on mechanisms of maintenance of species diversity. Journal of Ecology 106:1773–1794.

Christmann, T., and I. Oliveras. 2020. Nature of Alpine Ecosystems in Tropical Mountains of South America. Page Encyclopedia of the World's Biomes. Elsevier.

Colles, A., L. H. Liow, and A. Prinzing. 2009. Are specialists at risk under environmental change? Neoecological, paleoecological and phylogenetic approaches. Ecology Letters 12:849–863.

Cordeiro, A. de A. C., and A. V. Neri. 2019. Spatial patterns along an elevation gradient in high altitude grasslands, Brazil. Nordic Journal of Botany 37:1–10.

Czarniecka, M., W. Zygmunt, K. Milan, and C. Salza. 2019. Diversity loss in grasslands due to the increasing dominance of alien and native competitive herbs. Biodiversity and Conservation 28:2781–2796.

Debouk, H., F. de Bello, and M. Sebasti. 2015. Functional Trait Changes , Productivity Shifts and Vegetation Stability in Mountain Grasslands during a Short-Term Warming. PLoS ONE 10:1–17.

Elith, J., and J. R. Leathwick. 2009. Species distribution models: Ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics 40:677–697.

Enquist, B. J., J. Norberg, S. P. Bonser, C. Violle, C. T. Webb, A. Henderson, L. L. Sloat, and V. M. Savage. 2015. Scaling from Traits to Ecosystems : Developing a General Trait Driver Theory via Integrating Trait-Based and Metabolic Scaling Theories. Advances in Ecological Research 52:249–318.

Fernandes, G. W., L. B. S. Tameirão, A. R. Costa, D. G. Ribeiro, M. N. Neves, B. G. Souza E Brito, and D. Negreiros. 2021. Functional traits of three major invasive grasses in a threatened tropical mountain grassland. Anais da Academia Brasileira de Ciencias 93:1–7.

Gastauer, M., J. Thiele, S. Porembski, and A. V. Neri. 2020. How do altitude and soil properties influence the taxonomic and phylogenetic structure and diversity of Brazilian páramo vegetation? Journal of Mountain Science 17:1045–1057.

Gauzere, P., X. Morin, C. Violle, I. Caspeta, C. Ray, and B. Blonder. 2020. Vacant yet invasible niches in forest community assembly. Functional Ecology:1365-2435.13614.

Graae, B. J., V. Vandvik, W. S. Armbruster, W. L. Eiserhardt, J. Svenning, J. Ehrlén, J. D. M. Speed, K. Klanderud, K. Anne, A. Milbau, Ø. H. Opedal, I. G. Alsos, R. Ejrnæs, H.

Henrik, H. J. B. Birks, K. B. Westergaard, H. H. Birks, and J. Lenoir. 2018. Stay or go – how topographic complexity influences alpine plant population and community responses to climate change. Perspectives in Plant Ecology, Evolution and Systematics 30:41–50.

Griffiths, H., and J. Males. 2017. Succulent plants. Current Biology 27:890–896.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111:1169–1194.

Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology 86:902–910.

Grime, J. P. 2006. Trait convergence and trait divergence in herbaceous plant communities : Mechanisms and consequences. Journal of Vegetation Science 17:255–260.

Habibullah, M. S., B. H. Din, S. H. Tan, and H. Zahid. 2022. Impact of climate change on biodiversity loss: global evidence. Environmental Science and Pollution Research 29:1073–1086.

Hillebrand, H., D. M. Bennett, and M. W. Cadotte. 2008. Consequences of Dominance: A Review of Evenness Effects on Local and Regional Ecosystem Processes. Ecology 89:1510–1520.

Kassambara, A., and F. Mundt. 2020. factoextra: Extract and Visualize the Results of Multivariate Data Analyses.

Köppen, W., and R. Geiger, editors. 1936. Das geographische System der Klimate (1936). Gebrüder Borntl'aeger, Berlin.

Kraft, N. J. B., P. B. Adler, O. Godoy, E. C. James, S. Fuller, and J. M. Levine. 2015a. Community assembly, coexistence and the environmental filtering metaphor. Functional Ecology 29:592–599.

Kraft, N. J. B., O. Godoy, and J. M. Levine. 2015b. Plant functional traits and the multidimensional nature of species coexistence. Proceedings of the National Academy of Sciences of the United States of America 112:797–802.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. lmerTest Package: Tests in Linear Mixed Effects Models. Journal of Statistical Software 82:1–26.

Laliberté, E., G. Zemunik, and B. L. Turner. 2014. Environmental filtering explains variation in plant diversity along resource gradients. Science 345:1602–1605.

Lê, S., J. Josse, and F. Husson. 2008. FactoMineR: A Package for Multivariate Analysis.

Journal of Statistical Software 25:1–18.

López-Angulo, J., D. S. Pescador, A. M. Sánchez, A. L. Luzuriaga, L. A. Cavieres, and A. Escudero. 2020a. Impacts of climate, soil and biotic interactions on the interplay of the different facets of alpine plant diversity. Science of the Total Environment 698:133960.

López-Angulo, J., D. S. Pescador, A. M. Sánchez, A. L. Luzuriaga, L. A. Cavieres, and A. Escudero. 2020b. Impacts of climate, soil and biotic interactions on the interplay of the different facets of alpine plant diversity. Science of the Total Environment 698:133960.

Marengo, J. A., L. M. Alves, C. Inpe, R. Dutra, C. Paulista, and S. Paulo. 2005. Tendências Hidrológicas da Bacia do Rio Paraíba do Sul. CPTEC/INPE 1:1–31.

Masson-Delmotte, V., P. Zhai, A. Pirani, S. L., J. B. R. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, and and B. Z. (eds. . Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu. 2021. IPCC, 2021: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press:F0003–F0003.

Matos, I. S., O. Binks, C. B. Eller, B. B. Zorger, P. Meir, T. E. Dawson, and B. H. P. Rosado. 2022. Revisiting plant hydrological niches: the importance of atmospheric resources for ground-rooted plants. Journal of Ecology n/a.

Matos, I. S., C. B. Eller, I. Oliveras, D. Mantuano, and B. H. P. Rosado. 2021. Three eco-physiological strategies of response to drought maintain the form and function of a tropical montane grassland. Journal of Ecology 109:327–341.

Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecology Letters 13:1085–1093.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Negreiros, D., S. Le Stradic, G. W. Fernandes, and H. C. Rennó. 2014. CSR analysis of plant functional types in highly diverse tropical grasslands of harsh environments. Plant Ecology 215:379–388.

Neri, A. V., G. R. A. Borges, J. A. A. Meira-Neto, L. F. S. Magnago, I. M. Trotter, C. E. G. R. Schaefer, and S. Porembski. 2016. Soil and altitude drive diversity and functioning of Brazilian Páramos (campo de altitude). Journal of Plant Ecology 10:771–779.

Nunez, S., E. Arets, R. Alkemade, C. Verwer, and R. Leemans. 2019. Assessing the impacts of climate change on biodiversity: is below 2 °C enough? Climatic Change 154:351–365.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, E. Szoecs, and H. Wagner. 2019. vegan: Community Ecology Package.

Passy, S. I., M. Bottin, J. Soininen, and H. Hillebrand. 2017. Environmental filtering and taxonomic relatedness underlie the species richness-evenness relationship Environmental filtering and taxonomic relatedness underlie the species richness – evenness relationship. Hydrobiologia.

Pastore, A. I., G. Barabás, M. D. Bimler, M. M. Mayfield, and T. E. Miller. 2021. The evolution of niche overlap and competitive differences. Nature Ecology and Evolution 5:330–337.

de Paula, L. F. A., D. Negreiros, L. O. Azevedo, R. L. Fernandes, J. R. Stehmann, and F. A. O. Silveira. 2015. Functional ecology as a missing link for conservation of a resource-limited flora in the Atlantic forest. Biodiversity and Conservation 24:2239–2253.

Pistón, N., F. de Bello, L. Götzenberger, B. H. P. Rosado, E. A. De Mattos, R. S. Gómez, and C. P. Carmona. 2019. Multidimensional ecological analyses demonstrate how interactions between functional traits shape fitness and life history strategies. Journal of Ecology 107:2317–2328.

Porembski, S. 2006. Vegatative Architecture of Desiccation-tolerant Arborescent Monocotyledons. Aliso: A Journal of Systematic and Evolutionary Botany 22:129–134.

Porembski, S. 2007. Tropical inselbergs: Habitat types, adaptive strategies and diversity patterns. Revista Brasileira de Botanica 30:579–586.

Porembski, S., J. Rexroth, K. Weising, L. Bondi, R. Mello-silva, D. C. Centeno, M. N. Datar, A. Watve, A. Thiombano, M. N. Rabarimanarivo, and L. F. A. de Paula. 2021. An overview on desiccation-tolerant mat-forming monocotyledons on tropical inselbergs. Flora 285.

Rahbek, C., M. K. Borregaard, A. Antonelli, R. K. Colwell, B. G. Holt, D. Nogues-Bravo, C. M. Ø. Rasmussen, K. Richardson, M. T. Rosing, R. J. Whittaker, and J. Fjeldså. 2019a. Building mountain biodiversity: Geological and evolutionary processes. Science 365:1114–1119.

Rahbek, C., M. K. Borregaard, R. K. Colwell, B. Dalsgaard, B. G. Holt, N. Morueta-holme, D. Nogues-bravo, R. J. Whittaker, and J. Fjeldså. 2019b. Humboldt's enigma: What causes global patterns of mountain biodiversity? Science 365:1108–1113.

Rangel, T. F., N. R. Edwards, P. B. Holden, J. A. F. Diniz-Filho, W. D. Gosling, M. T. P.

Coelho, F. A. S. Cassemiro, C. Rahbek, and R. K. Colwell. 2018. Modeling the ecology and evolution of biodiversity: Biogeographical cradles, museums, and graves. Science 361.

Read, Q. D., L. C. Moorhead, N. G. Swenson, J. K. Bailey, and N. J. Sanders. 2014. Convergent effects of elevation on functional leaf traits within and among species. Functional Ecology 28:37–45.

Roberts, D. W. 2019. Ordination and Multivariate Analysis for Ecology.

Rosado, B. H. P., and E. A. de Mattos. 2017. On the relative importance of CSR ecological strategies and integrative traits to explain species dominance at local scales. Functional Ecology 31:1969–1974.

Safford, H. D. 1999a. Brazilian Páramos I. An introduction to the physical environment and vegetation of the campos de altitude. Journal of Biogeography 26:693–712.

Safford, H. D. 1999b. Brazilian Páramos II . Macro- and mesoclimate of the *campos de altitude* and affinities with high mountain climates of the tropical Andes and Costa Rica. Journal of Biogeography:713–737.

Safford, H. D. 2007. Brazilian Páramos IV. Phytogeography of the campos de altitude. Journal of Biogeography 34:1701–1722.

Sanders, N. J., and C. Rahbek. 2012. The patterns and causes of elevational diversity gradients. Ecography 35:1–3.

Scarano, F. R., P. Ceotto, and G. Martinelli. 2016. Climate change and "campos de altitude": forecasts, knowledge and action gaps in Brazil. Oecologia Australis 20:139–144.

Thakur, D., and A. Chawla. 2019. Functional diversity along elevational gradients in the high altitude vegetation of the western Himalaya. Biodiversity and Conservation 28:1977–1996.

Tinti, B. V., C. E. R. G. Schaefer, J. A. Nunes, A. C. Rodrigues, I. F. Fialho, and A. V. Neri. 2015. Plant diversity on granite/gneiss rock outcrop at Pedra do Pato, Serra do Brigadeiro State Park, Brazil. Check List 11.

Tito, R., H. L. Vasconcelos, and K. J. Feeley. 2020. Mountain Ecosystems as Natural Laboratories for Climate Change Experiments. Frontiers in Forests and Global Change 3:1–8.

Vasconcelos, M. F. 2011. O que são campos rupestres e campos de altitude nos topos de montanha do Leste do Brasil? Brazilian Journal of Botany 34:241–246.

Wilson, J. B., and W. G. Lee. 2000. C-S-R triangle theory: Community-level predictions,

tests, evaluation of criticisms, and relation to other theories. Oikos 91:77–96.

COMPETIÇÃO E TOPOGRAFIA INFLUENCIAM NA DIVERSIDADE E A COMPOSIÇÃO DE ESPÉCIES NOS PÁRAMOS BRASILEIROS

RESUMO

FERREIRA, Elielson Lucas, M.Sc., Universidade Federal de Viçosa, julho de 2022. **Competição e topografia determinam a diversidade e a composição de espécies nos Páramos Brasileiros.** Orientadora: Andreza Viana Neri.

Os campos de altitude são um ambiente montano ainda particularmente desconhecido, principalmente com relação a sua ecologia. Por suas condições abióticas extremas, a importância da competição nesses ambientes é negligenciada, não havendo estudos que considerem como a interação entre fatores bióticos e abióticos moldam a diversidade nesses ecossistemas. Neste estudo, amostramos 135 parcelas de um m^2 em diferentes hábitats de uma montanha no Parque Estadual da Serra do Brigadeiro, Minas Gerais, Brasil. As parcelas foram distribuídas em três hábitats (i.e., topo, encosta superior e encosta inferior), de modo a testar as seguintes hipóteses: (1) Os hábitats diferem quanto à composição de espécies devido a variações nas condições bióticas e abióticas, havendo forte associação entre espécies e hábitat; (2) a diversidade taxonômica diminui em função do aumento da altitude, escassez de solo e da competição por recursos, devido ao aumento da filtragem abiótica e biótica. Medimos a composição de espécies, a diversidade de Shannon, a riqueza e a equidade de Pielou. A inclinação, a porcentagem de rocha exposta e a profundidade do solo foram medidas como *proxies* da disponibilidade de solo e a densidade de cobertura vegetal como *proxy* para a depleção de recursos por competidores. Também medimos a altitude da parcela. Utilizamos uma PERMANOVA, uma análise de espécies indicadoras (IndVal) e uma análise de redundância baseada em transformação (tb-RDA) para testar a primeira hipótese. Para testar a segunda hipótese, construímos modelos lineares mistos tendo a riqueza e os índices de diversidade como variáveis resposta e altitude, a densidade de cobertura e a escassez de solo (derivada de uma ordenação com variáveis topográficas) como preditoras. . Os três ambientes diferiram quanto à composição, sendo que cerca de 50% das espécies foram indicadoras exclusivas de um ambiente. O topo apresentou maior dissimilaridade, compreendendo 42% das espécies indicadoras. A disponibilidade de solo explicou 22,2% da variação na composição de espécies, a altitude 9,6% e a densidade de cobertura vegetal apenas 1,3%. A

riqueza respondeu positivamente à altitude e negativamente à densidade de cobertura (R^2 = 0.22). A diversidade de Shannon e equidade de Pielou foram maiores em altitudes elevadas e em baixas altitudes esses valores tenderam a diminuir sob alta densidade de cobertura e maior disponibilidade de solo (R^2 = 0,45 e R^2 = 0,42, respectivamente). A disponibilidade de solo foi o principal causador de mudanças de composição de espécies ao longo dos gradientes estudados. A menor diversidade observada sobre solos mais profundos e maior densidade de cobertura pode estar relacionada à dominância de espécies aquisitivas. Contudo, em maior altitude, possivelmente a maior partição de recursos, devido a filtragem de espécies mais especializadas para dentro da comunidade, permitiu a maior riqueza e equidade observadas. Nossos resultados reforçam o papel da heterogeneidade de hábitats na estruturação da vegetação dos campos de altitude. No entanto, a competição por recursos também é um importante fator que precisa ser melhor compreendida. A compreensão dos atributos relacionados à melhor habilidade competitiva nesses ambientes deve ser um importante passo para compreender a dinâmica desses ecossistemas e como eles podem responder às mudanças climáticas.

Palavras-chave: Campos de altitude. Páramos brasileiros. Competição. Filtragem ambiental. Diversidade.

ABSTRACT

FERREIRA, Elielson Lucas, M.Sc., Universidade Federal de Viçosa, July 2022. **Competition and topography drives diversity and composition of species in the Brazilian Páramos.** Advisor: Andreza Viana Neri.

The *Brazilian Páramos* are still a particularly unknown mountainous environment, regarding their ecology. Due to their extreme abiotic conditions, the importance of competition in these environments is neglected, and there are no studies that consider how the interaction between biotic and abiotic factors shapes the diversity in these ecosystems. In this study, 135 1 m^2 plots were sampled in different habitats in a mountain inside Serra do Brigadeiro State Park, Minas Gerais, Brazil. The plots were distributed in three habitats (i.e. the top, the upper slope and the bottom slope), in order to test the following hypotheses: (1) The habitats differ in species composition due to variations in biotic and abiotic conditions, with a strong species-habitat association; (2) taxonomic diversity decreases with increasing elevation, soil scarcity and resource depletion, due to increased abiotic and biotic filtering. We measured dissimilarity in species composition, Shannon diversity, species richness and Pielou's evenness. We measured the plot slope, percentage of exposed rock and soil depth as proxies for soil availability and we also calculated the vegetation cover density as a proxy for resource depletion by competitors. We also measured plot's elevation. We used a PERMANOVA, an indicator species analysis (IndVal) and a tb-RDA to test the first hypothesis. In order to test the second hypothesis we used a mixed linear model with richness and the diversity indexes as response variables and elevation, cover density and soil scarcity (derived from an ordination analysis) as predictors. The three environments differed in composition, with about 50% of the species being significantly associated to a single environment. The top showed the greatest dissimilarity, also comprising 42% of the indicator species. Soil availability explained 22.2% of the variation in species composition, altitude 9.6% and vegetation cover density only 1.3%. H' and J' increased with elevation and decreased with vegetation cover density, the last one with a greater effect at low elevation. This may be caused by the presence of strategies that confer greater competitive ability in these conditions, increasing its dominance, while at high elevation, the selection of highly specialized species allows for a more equal partition of resources. Contrary to our expectations, S increased with altitude, but also decreased with density, which is an indication that the increase in richness

may be an effect of decreasing dominance at higher elevations. H' and J' increased with soil scarcity at low elevation, while no effect of soil was observed for S. This may be an effect of increased productivity with greater soil availability, and the presence of several strategies that allow survival in rock outcrops, keeping richness constant along soil gradients. Our results demonstrate that topography plays a crucial role in the variation in species composition in *Brazilian Páramo*, which can delay the effects of species loss by microclimate changes. Diversity in these environments is hold by the interaction between abiotic factors and competition for resources. The presence of species with traits that allow higher dominance may cause the loss of less competitive species, making the biodiversity of high altitude grasslands strongly threatened by biological invasions with climate change. Species richness positively responded to elevation and negatively to cover density (R^2 = 0.22). Shannon diversity and Pielou's evenness were higher at higher elevation and at lower elevation, this values tended to decrease with higher cover density and higher soil avaliability (R^2 = 0,45 e R^2 = 0,42, respectively). Soil availability was the main driver of shifts in composition along the studied gradients. The lowest diversity was observed on deeper soils and with higher cover density, which can be related to the dominance of more acquisitive species. However, at higher altitude, possibly the higher resource partitioning due to the filtering of more specialized species into the community allowed the higher richness and evenness observed. Our results reinforce the role of habitat heterogeneity in structuring the *campos de altitude* vegetation. Nonetheless, competition for resources is also an importat fator that needs to be better understood. The comprehension of the traits related to better competitive ability in this environment should be an important step towards the comprehension of these ecosystems' dynamics and how they could react to climate change.

Keywords: *Campos de altitude*. Brazilian *Páramos*. Competition. Environmental filtering.

1. INTRODUÇÃO

As montanhas dos trópicos são importantes guardiãs da biodiversidade no mundo (Rangel et al. 2018, Rahbek et al. 2019a, 2019b). A maior heterogeneidade climática ao longo do gradiente altitudinal quando comparadas a montanhas temperadas e subtropicais são fatores determinantes para a alta diversidade das montanhas tropicais (Rahbek et al. 2019b). Somado a isso, a variação na disponibilidade de recursos devido à topografia extremamente irregular torna ainda maior a complexidade de seus hábitats, resultando na presença de mosaicos de diferentes fitofisionomias, que marcam as comunidades vegetais presentes nas montanhas tropicais (Safford 1999a, Antonelli et al. 2018, Bueno de Mesquita et al. 2018, Rahbek et al. 2019a). Devido às suas condições extremas, as espécies ocorrentes nesses ambientes são altamente especializadas, algumas tendo sua distribuição restrita a um único tipo de hábitat (Porembski 2007, Neri et al. 2016, Cordeiro and Neri 2019, Thakur and Chawla 2019). Isso torna as comunidades de altitude particularmente vulneráveis aos efeitos das mudanças climáticas, que podem ocasionar perda de hábitat e a entrada de espécies invasoras (Assis and de Mattos 2016, Scarano et al. 2016, Rahbek et al. 2019a). Portanto, é crucial compreender como a complexidade topográfica e as interações competitivas determinam os padrões de distribuição e diversidade de espécies nas montanhas dos trópicos (Graae et al. 2018, Tito et al. 2020).

Com o aumento da severidade ambiental, a intensificação das pressões seletivas faz com que as comunidades vegetais sejam compostas por grupos de espécies cada vez mais adaptadas às condições locais (Kraft et al. 2015, Cadotte and Tucker 2019, de Bello et al. 2021). Este processo, chamado de filtragem ambiental, pode levar à perda de diversidade, devido à exclusão de espécies pouco adaptadas (Laliberté et al. 2014, Passy et al. 2017). Em ecossistemas de montanha, o aumento da radiação UV e da intensidade dos ventos, somado à diminuição da pressão atmosférica e da temperatura com a altitude, representam importantes filtros abióticos para a distribuição de plantas (Neri et al. 2016, Gastauer et al. 2020). Além disso, a diminuição na disponibilidade de solo devido às variações topográficas também pode gerar uma forte pressão seletiva (Bernard-Verdier et al. 2012, Neri et al. 2016). A menor disponibilidade e o menor acúmulo de água e nutrientes em áreas de afloramento rochoso tornam as plantas que ocorrem nesses ambientes mais susceptíveis à desnutrição e à seca (Porembski 2006, 2007).

Não só fatores abióticos podem levar à diminuição da diversidade (Kraft et al. 2015). Em ambientes onde há alta competição por recursos, plantas com características funcionais que conferem uma maior habilidade competitiva podem dominar os recursos, levando a uma maior abundância, ou mesmo levar as demais espécies à exclusão (Grime 1977, 2006, Chesson 2000, Mayfield and Levine 2010). Como efeito, as comunidades podem se tornar dominadas por uma ou poucas espécies que possuem tais características (Grime 2006, Mayfield and Levine 2010). Apesar de que para alguns autores, os fatores abióticos extremos podem sobrepujar o efeito de interações bióticas, como a competição (Grime 1977, Wilson and Lee 2000), a avaliação do impacto desses fatores sobre os padrões de diversidade é um campo ainda pouco explorado em montanhas tropicais.

No Brasil, os campos de altitude, também chamados de Páramos brasileiros, ainda são ecossistemas particularmente pouco estudados, havendo pouca informação sobre como fatores bióticos e abióticos estruturam essa vegetação (Safford 1999a, Caiafa and da Silva 2007, Vasconcelos 2011, Campos et al. 2021). Esses ecossistemas, que cobrem as montanhas próximas ao centro econômico do país, tem grande importância no abastecimento dos rios que correm pelas regiões Sudeste e Sul (Marengo et al. 2005). Os campos de altitude abrigam uma grande diversidade de espécies vegetais, dentre as quais diversas são endêmicas de uma única montanha (Safford 2007, Alves and Kolbek 2010, Assis and de Mattos 2016). No entanto, diferente de outras vegetações associadas à altitude nos neotrópicos, como os Páramos Andinos, os campos de altitude se situam ao longo de uma estreita faixa de 1700 até 2890, o que torna as espécies que nele ocorrem extremamente vulneráveis às mudanças no clima (Safford 1999b, 1999a, Rahbek et al. 2019b). Isso torna urgente a compreensão de como os fatores bióticos e abióticos moldam a biodiversidade nos campos de altitude.

De modo a compreender o efeito da interação entre a altitude, a disponibilidade de solo e a competição sobre a distribuição das espécies e a diversidade nos campos de altitude, nós amostramos três hábitats distintos em uma montanha no Sudeste do Brasil. Testamos, então, as seguintes hipóteses: (1) Os hábitats diferem quanto à composição de espécies devido a variações nas condições bióticas e abióticas, havendo forte associação entre espécies e hábitat; (2) A diversidade taxonômica diminui em função do aumento da altitude, da escassez de solo e da maior densidade de cobertura vegetal, devido ao aumento da filtragem abiótica e biótica.

2. MATERIAIS E MÉTODOS

2.1. Área de estudo

O presente estudo foi realizado no Parque Estadual da Serra do Brigadeiro (PESB), situado no extremo norte da Serra da Mantiqueira, Minas Gerais, Brasil, entre os meridianos 42º 40’ e 40º 20’ Oeste e os paralelos 20º 33’ e 21º 00’ Sul (Benites et al. 2003). A Serra do Brigadeiro é formada por rochas ígneas e metamórficas, principalmente granito, gnaisse e magmatitos (Benites et al. 2001), havendo também a presença de quartzo. O clima da região é do tipo tropical de altitude (Köppen and Geiger 1936), apresentando temperatura média anual de 18º C e precipitação média anual de 1300 mm (Benites et al. 2001, Caiafa and Silva 2005). O parque está situado no domínio da Mata Atlântica, com vegetação composta por fragmentos secundários de floresta ombrófila densa e campos de altitude, sendo estes presentes a partir de 1600 m de altitude (Caiafa and Silva 2005). Um dos picos mais altos do Parque Estadual da Serra do Brigadeiro é a Pedra do Pato, erguendo-se a 1980 m acima do nível do mar. Neste pico há uma grande variedade de ambientes, como platôs, áreas de alta declividade, escarpas, vales e terrenos mal drenados. A vegetação em cada um desses ambientes apresenta diferenciações florísticas e fitofisionômicas (Tinti et al. 2015).

Figura 1. Pedra do Pato, Parque Estadual da Serra do Brigadeiro, MG, Brasil. (Foto: Braz Cosenza).

2.2. Amostragem e análises estatísticas

Lançamos 15 parcelas de nove metros quadrados, cada uma subdividida em nove subparcelas de um metro quadrado, totalizando 135 unidades amostrais. Para abranger ao máximo os gradientes ambientais do pico, as parcelas foram lançadas em três ambientes diferentes, chamados de topo, encosta superior e encosta inferior. Em cada subparcela, realizamos o levantamento florístico de todas as plantas vasculares presentes e medida a porcentagem de cobertura de cada espécie (Braun-Blanquet 1979).

Medimos em campo quatro variáveis abióticas: a inclinação, profundidade do solo, porcentagem de rocha exposta em cada subparcela (variáveis topográficas) e altitude. A inclinação foi medida utilizando um clinômetro e a profundidade do solo utilizando uma ponteira centimetrada, ambas as medidas tendo sido feitas em nível de subparcela. Devido à variação mínima de altitude entre subparcelas dentro da mesma parcela, esta variável foi medida em nível de parcela utilizando um GPS.

Estimamos visualmente a cobertura absoluta das espécies dentro de cada subparcela para estimar sua cobertura e frequência relativas das mesmas. Estes dois parâmetros foram utilizados para calcular o valor de importância (VI) das espécies nos hábitats, uma medida que representa a dominância de cada espécie. Estes três parâmetros permitem analisar a estrutura das comunidades. A associação de espécies aos ambientes foi medida utilizando a análise de espécies indicadoras (IndVal) (Cáceres and Legendre 2009). Este valor é calculado com base em dois parâmetros: a especificidade, que mede o grau de limitação na ocorrência de uma espécie a uma área; e a fidelidade, está maior quanto mais frequente é a espécie dentro do ambiente. Para o cálculo desta métrica, foi utilizado o pacote *labdsv* (Roberts 2019).

Para avaliar a diferença de composição das espécies entre os ambientes, foi realizado um escalonamento multidimensional não métrico (NMDS) baseado na dissimilaridade de Bray-Curtis. A significância da diferença de composição foi acessada usando uma análise de variância permutacional multivariada (PERMANOVA). A influência das variáveis bióticas e abióticas sobre a vegetação foi testada usando uma análise de redundância canônica baseada em transformação (tb-RDA) utilizando-se a função *rda.* Foi utilizada a transformação de Hellinger na tabela de espécies, que representa as distâncias entre parcelas sendo menos influenciada por zeros duplos. Para acessar a variância explicada pela altitude, as variáveis topográficas e a densidade de cobertura foi utilizada a função *varpart* do mesmo pacote. O valor de significância marginal de cada grupo de variáveis foi acessado utilizando a função

anova.cca. Todas estas análises foram conduzidas utilizando-se o pacote *vegan* (Oksanen et al. 2019).

Visto que a diversidade taxonômica pode ser decomposta em dois componentes, a riqueza e a equabilidade, foi medido o índice de diversidade de Shannon para cada parcela, influenciado por variações em ambos os componentes. Além disso, foram calculadas a riqueza de espécies em cada parcela (S) e a Equabilidade de Pielou (J'), de forma a acessar a contribuição de cada componente na diversidade das comunidades vegetais. A relação das métricas de diversidade com os fatores ambientais foi testada utilizando modelos lineares mistos (lmm) através do pacote *lme4* (Bates et al. 2015). Utilizamos o efeito somado e da interação entre as variáveis preditoras de efeito fixo e a parcela como variável de efeito aleatório, devido ao desenho aninhado da amostragem. Para sintetizar os dados de topografia, realizamos uma Análise de Componentes Principais (PCA) e retivemos o eixo de maior variação (PC1) para utilização no modelo (Fig. S1). A PCA foi feita por meio dos pacotes *factoextra* e *FactoMineR* (Lê et al. 2008, Kassambara and Mundt 2020). Os modelos foram validados por inspeção da distribuição dos resíduos e a significância do efeito de cada preditor foi calculada utilizando o pacote *lmerTest* (Kuznetsova et al. 2017). Os resultados dos modelos foram plotados utilizando resíduos parciais com o pacote *visreg* (Breheny and Burchett 2017), sendo o efeito da altitude representado de forma categórica apenas para facilitar a compreensão.

3. RESULTADOS

Ao todo amostramos 44 espécies nos três locais coletados na Pedra do Pato (Tabela 1). Não foi possível identificar três destas ao nível de família, por não apresentarem floração no período da coleta. As demais espécies estão distribuídas em 20 famílias, das quais Orchidaceae foi a família com mais espécies (cinco), seguida de Asteraceae, Bromeliaceae e Poaceae (todas com quatro espécies coletadas). A encosta inferior foi o local com o menor número de espécies coletadas, somando 17 espécies em 12 famílias. O topo e a encosta superior tiveram ambos um total de 21 espécies em 11 famílias, sendo três espécies indeterminadas restritas ao topo.

Tabela 1: Lista de famílias e espécies amostradas na Pedra do Pato, Parque Estadual da Serra do Brigadeiro, MG, e os respectivos ambientes em que ocorreram. BS = encosta inferior, US = encosta superior, T = topo.

Famílias	**Espécies**	**Hábitats**
Amaryllidaceae	*Hippeastrum glaucescens* (Mart. ex Schult. & Schult. f.) Herb.	BS, US
Anemiaceae	*Anemia* sp.	BS
Apocynaceae	*Mandevilla tenuifolia* (J.C. Mikan) Woodson	BS
Asteraceae	*Asteraceae* sp.	BS, US
	Baccharis platypoda DC.	T
	Baccharis sp.	T
	Lepidaploa decumbens (Gardner) H. Rob.	US
Bromeliaceae	*Alcantarea* sp.	US
	Bromeliaceae sp.	US
	Dyckia cinerea Mez	BS, US
	Pitcairnia cf. *carinata*	BS, US
Cyperaceae	*Bulbostylis scabra* (J. Presl & C. Presl) C.B. Clarke	BS, US
	Cryptangium comatum Boeckeler	US
	Trilepis lhotzkiana Nees ex Arn.	BS, US
Ericaceae	*Gaultheria serrata* (Vell.) Sleumer ex Kin.-Gouv.	T
	Gaylussacia densa Cham.	T
Eriocaulaceae	*Paepalanthus sp*	US
Euphorbiaceae	*Croton splendidus* Mart. ex Colla	T
Fabaceae	*Crotalaria micans* Link	T
Lamiaceae	*Hesperozygis nitida* (Benth.) Epling	T
Lycopodiaceae	*Lycopodiaceae sp*	BS
	Lycopodium clavatum L.	T
	Lycopodium sp	T
Melastomataceae	*Behuria comosa* R. Tavares, Baumgratz & R. Goldenb.	BS
	Pleroma echinatum Gardner	T
	Pleroma manicatum (Cogn.) P.J.F. Guim. &	BS, US

	Michelang.	
Orchidaceae	*Acianthera prolifera* (Herb. ex Lindl.) Pridgeon &	
	M.W. Chase	US
	Acianthera teres (Lindl.) Borba	BS, US
	Epidendrum secundum Jacq.	US, T
	Gomesa ramosa (Lindl.) M.W. Chase & N.H.	
	Williams	US, T
	Zygopetalum maculatum (Kunth) Garay	BS, US
Piperaceae	*Peperomia galioides* Kunth	US
Poaceae	*Poacea sp1*	T
	Poacea sp2	T
	Poacea sp3	T
	Poaceae sp4	BS, US, T
Pteridaceae	*Lytoneuron columbinum*	BS, US
Salicaceae	*Abatia americana* (Gardner) Eichler	T
Smilacaceae	*Smilax* sp.	T
Velloziaceae	*Vellozia candida* J.C. Mikan	BS
Velloziaceae	*Vellozia variegata* Goethart & Henrard	BS, US
Intederminada	*Indet1*	T
	Indet2	T
	Indet3	T

No topo, assim como na encosta superior, quatro espécies tiveram valor de importância (VI) superior a 10%, sendo elas *Hesperozygis nitida* (22,27%), *Baccharis platypoda* (13,00%), *Lycopodium* sp. (13,59%) e *Croton splendidus* (12,31%) (Fig. S2A). As dominantes do topo foram as espécies com as porcentagens de cobertura e de frequência mais altas na comunidade (Fig. S3A, S4A). Contudo, a espécie *Gaultheria serrata* esteve também entre as mais frequentes, apesar da baixa cobertura. A maior parte das espécies teve baixos VI, porém as frequências foram mais proporcionalmente divididas entre elas do que a cobertura. *Dyckia cinerea*, foi a mais dominante na encosta superior (Fig S2B), devido a seu alto valor de cobertura (Fig. S3B), porém, assim como na comunidade BS, não esteve entre as mais frequentes (Fig. S4B). Poaceae sp4, *Trilepis lhotzkiana* e *Pitcairnia* cf. *carinata* tiveram também alto VI (maior que 10%), possuindo alta cobertura e frequência. Na encosta inferior,

a espécie dominante foi *Vellozia variegata* Goethart & Henrard com VI de 32,50% (Fig. S2C), sendo a mais frequente e com a maior cobertura. A espécie *Dyckia cinerea* Mez (13,12%) foi a segunda mais dominante (Fig. S3C), devido ao seu alto valor de cobertura, contudo não estando entre as três mais frequentes (Fig. S4C). *Trilepis lhotzkiana* Nees ex Arn. foi a terceira mais dominante (VI = 12,90%), sendo a segunda mais frequente. As demais espécies apresentaram valores de importância menores que 8,00%.

Os três locais tiveram diferenças significativas na composição de espécies (Figura 2). As parcelas do topo foram as mais agrupadas entre si e mais distantes das demais áreas. As parcelas de encosta apresentaram maior dissimilaridade entre si, mas formação de grupos separados entre a encosta superior e inferior. 31 espécies foram selecionadas como indicadoras (70% do total de espécies), sendo 23 (52%) de apenas um hábitat (Tabela 2). A encosta inferior e a encosta superior apresentaram cinco espécies indicadoras de cada uma e sete indicadoras de ambas (22% das indicadoras), a maioria destas apresentando alta especificidade e baixa fidelidade. O topo foi o local com o maior número de espécies indicadoras, totalizando 13 espécies (42% das indicadoras), estas, no geral, apresentaram valores de fidelidade mais altos que as demais áreas. Apenas uma espécie foi selecionada como indicadora do topo e da encosta superior e nenhuma do topo e da encosta inferior.

A tb-RDA mostrou haver relação significativa entre os preditores e a composição de espécies, com explicação de 47,6% da variação entre as três comunidades (Fig. 2B). O topo associado a maiores altitudes, maior profundidade de solo e maior densidade na cobertura de espécies, conforme o eixo RDA1 (variação explicada de 38,33%). Houve separação entre a encosta superior e inferior no eixo RDA2 (variação explicada de 7,45%), estando a encosta superior associada a maiores altitudes, maior inclinação e exposição de rocha. A partição do efeito das variáveis revelou uma maior influência da topografia na composição de espécies (R^2 = 22,2%), seguida da altitude (R^2 = 9,6%) (Fig. 2C). Apesar de o efeito parcial da densidade ter sido significativo, sua contribuição foi muito baixa (R^2 = 1,3%).

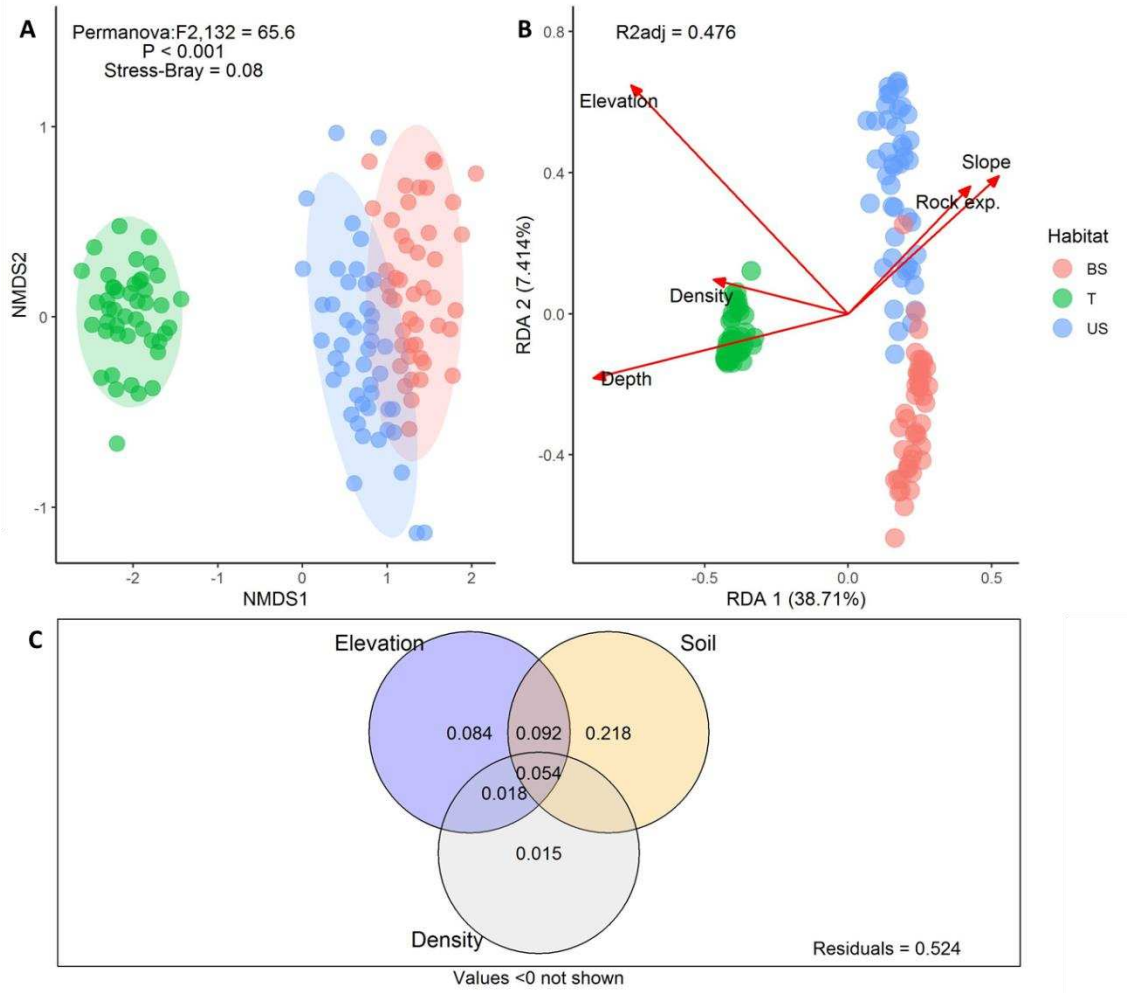

Figura 2. Dissimilaridade entre hábitats e relação com o ambiente. (A) NMDS mostrando padrões de dissimilaridade florística entre hábitats e valor de significância da PERMANOVA. (B) tb-RDA mostrando relação da composição com as variáveis ambientais. (C) Partição da variância explicada pela altitude, pelas variáveis relacionadas à disponibilidade de solo e pela densidade de cobertura vegetal. BS = encosta inferior, US = encosta superior, T = topo.

Tabela 2. Espécies indicadoras dos hábitats na Pedra do Pato. S = especificidade, F = fidelidade, IndVal = valor indicador, P = valor de p. BS = encosta inferior, US = encosta superior, T = topo.

Hábitat	Espécie	S	F	IndVal	P
BS	*Vellozia variegata*	0.82	0.98	0.90	0.001
	Acianthera teres	0.92	0.6	0.74	0.001
	Mandevilla tenuifolia	1.00	0.36	0.60	0.001
	Behuria comosa	1.00	0.22	0.47	0.001
	Vellozia candida	1.00	0.16	0.39	0.002

US	*Poaceae sp4*	0.78	0.71	0.75	0.001
	Asteraceae sp	0.94	0.22	0.46	0.001
	Cryptangium comatum	1.00	0.20	0.45	0.001
	Lepidaploa decumbens	1.00	0.16	0.39	0.003
	Paepalanthus sp	1.00	0.11	0.33	0.008
T	*Croton splendidus*	1.00	1.00	1	0.001
	Hesperozygis nitida	1.00	0.98	0.99	0.001
	Lycopodium sp	1.00	0.98	0.99	0.001
	Baccharis platypoda	1.00	0.93	0.97	0.001
	Gaultheria serrata	1.00	0.91	0.96	0.001
	Lycopodium clavatum	1.00	0.60	0.78	0.001
	Gomesa ramosa	0.96	0.42	0.64	0.001
	Gaylussacia densa	1.00	0.29	0.54	0.001
	Poacea sp1	1.00	0.29	0.54	0.001
	Indet2	1.00	0.18	0.42	0.001
	Crotalaria micans	1.00	0.18	0.42	0.002
	Pleroma echinatum	1.00	0.16	0.39	0.004
	Poacea sp3	1.00	0.11	0.33	0.009
BS + US	*Trilepis lhotzkiana*	1.00	0.90	0.95	0.001
	Hippeastrum glaucescens	1.00	0.74	0.86	0.001
	Lytoneuron columbinum	1.00	0.64	0.80	0.001
	Pitcairnia cf. carinata	1.00	0.63	0.80	0.001
	Dyckia cinerea	1.00	0.61	0.78	0.001
	Pleroma manicatum	1.00	0.38	0.62	0.001
	Zygopetalum maculatum	1.00	0.32	0.57	0.001
US + T	*Epidendrum secundum*	1.00	0.38	0.62	0.001

A diversidade de espécies foi significativamente influenciada pelos preditores (Tabela 3). A diversidade de Shannon e a equidade de Pielou apresentaram efeitos significativos da interação entre altitude e PC1 e entre altitude e densidade de cobertura (Fig. 3A-D). Essas duas métricas tenderam a aumentar com a maior escassez de solo (valores positivos de PC1) e a diminuir com o aumento da densidade de cobertura. Entretanto, em maiores altitudes os índices de Shannon e Pielou apresentaram os mais altos valores, sendo o efeito de PC1 e da

densidade de cobertura quase nulos. A riqueza de espécies sofreu um efeito positivo da altitude e negativo da densidade de cobertura, não havendo efeito significativo de PC1 e nem das interações entre preditores (Fig. 3E).

Tabela 3: Coeficientes e nível de significância dos modelos lineares mistos para as métricas de diversidade. R^2 marginal = variação explicada pelos preditores de efeito fixo; R^2 condicional = variação explicada pelo modelo incluindo efeitos aleatórios. Níveis de significância = *p ≤ 0,05, **p ≤ 0,01, ***p ≤ 0,001.

PREDICTORS	S	H'	J'
(Intercept)	**6.81** ***	**1.26** ***	**0.66** ***
PC1	-0.15	0.04	**0.04** ***
Elevation	**0.69** **	**0.29** ***	**0.13** ***
Density	**-0.86** *	**-0.36** ***	**-0.16** ***
PC1*Elevation	-0.23	**-0.13** ***	**-0.06** ***
PC1*Density	-0.19	-0.03	0.01
Elevation*Density	-0.03	**0.18** **	**0.10** ***
PC1*Elevation *Density	0.24	-0.02	-0.03
Marginal R^2 / Conditional R^2	0.218 / 0.277	0.452 / 0.556	0.423 / 0.653

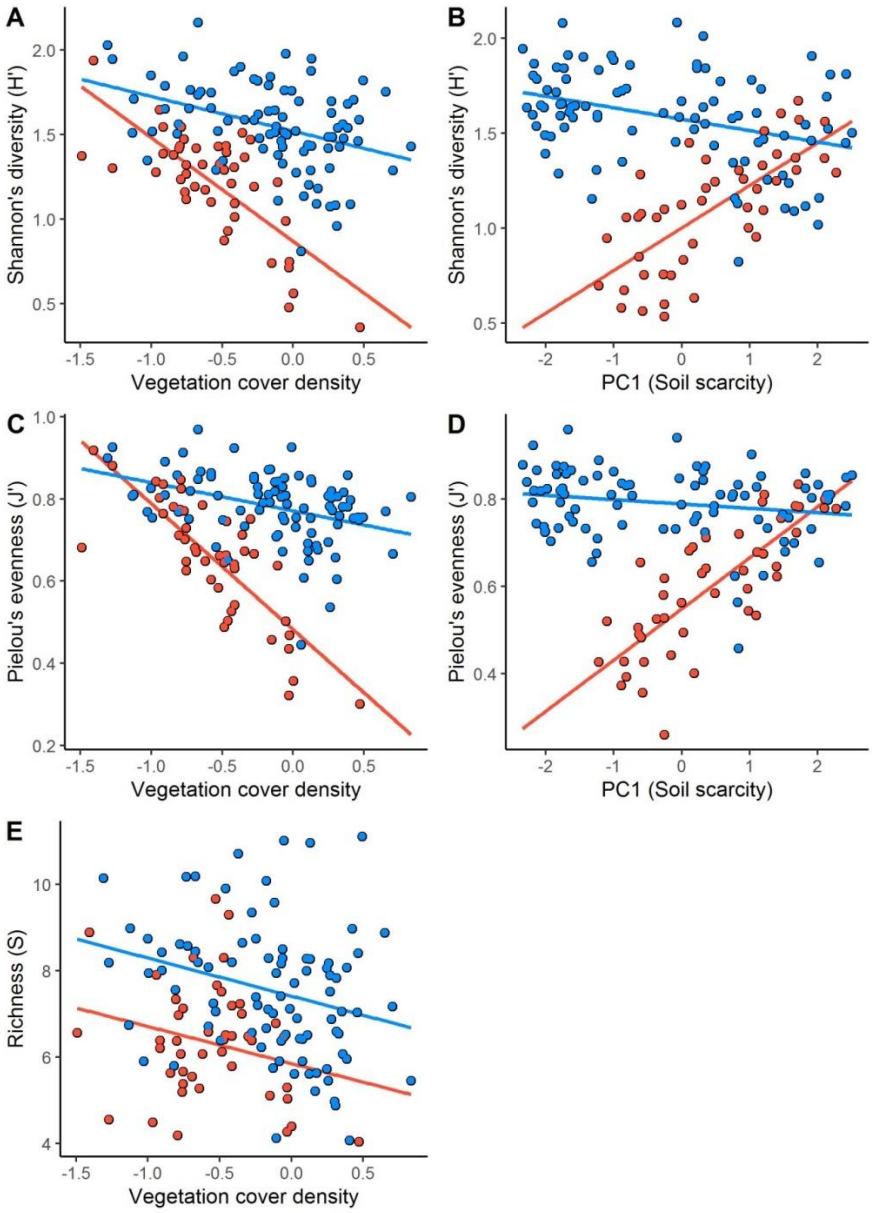

Figura 3: Gráficos dos resíduos parciais das métricas de diversidade em função da densidade de cobertura vegetal e da escassez de solo, condicionados a baixa altitudes (vermelho) e altas altitudes (azul). (A, B) efeito da densidade, da escassez de solo e da interação com a altitude sobre H'; (C,D) efeito da densidade, da escassez de solo e da interação com a altitude sobre J'; (E) efeito da altitude e da altitude sobre S. A escassez de solo (em A, C e E) e a densidade (em B e D) foram igualadas à mediana.

4. DISCUSSÃO

Os resultados da RDA mostraram que a disponibilidade de solo foi o principal fator responsável pela variação na composição de espécies no pico. A presença de afloramentos

rochosos com baixa disponibilidade de solo leva a escassez de recursos, além da barreira física que a falta de substrato impõe para a fixação das raízes (Porembski 2007). Isso impõe um obstáculo para o estabelecimento de plantas adaptadas aos platôs, que possuem maior disponibilidade de solo (de Paula et al. 2015). Por outro lado, as plantas adaptadas aos afloramentos devem apresentar desvantagem competitiva ao se estabelecer nos platôs, dado o metabolismo de carbono lento, que leva a menor taxa de crescimento (Alcantara et al. 2015). A força dessa barreira adaptativa também se mostra pelo elevado número de espécies indicadoras com 100% de especificidade ao topo e também aos dois ambientes de encosta juntos. Apenas uma espécie foi indicadora das duas áreas de maior altitude (topo e encosta superior), mostrando que, apesar da contiguidade geográfica entre essas duas áreas, o que representaria uma maior probabilidade de dispersão, o filtro do solo é suficiente para impedir a troca de espécies entre esses ambientes.

A escassez de solo também contribuiu para a diversidade, levando à formação de comunidades mais equitativas, mas não necessariamente mais ricas. Esse efeito pode ser explicado pela presença de múltiplas estratégias que permitem a sobrevivência em áreas de afloramento rochoso, contribuindo para a formação de comunidades diversas com espécies igualmente capazes de utilizar os recursos (Alcantara et al. 2015, Matos et al. 2021, 2022). Algumas espécies apresentam tolerância à seca, sendo capazes de recuperar a turgidez após a seca completa dos tecidos (Porembski et al. 2021). Além disso, outras espécies apresentam diversas adaptações anatômicas e metabólicas que permitem se manterem com alto potencial hídrico mesmo sob baixa disponibilidade hídrica (Griffiths and Males 2017, Matos et al. 2021). Há também aquelas espécies que completam seu ciclo de vida antes da chegada da seca, mantendo-se como banco de sementes até que as condições favoreçam novamente sua germinação (Matos et al. 2021). Por outro lado, em áreas de maior disponibilidade de solo, a ausência da filtragem causada pela falta de recursos permitiria que mais espécies fossem capazes de se estabelecer nesse ambiente (Debouk et al. 2015). Desta forma, tanto a ausência de filtro ambiental em ambientes com maior disponibilidade de solo, quanto a diversidade de estratégias adaptadas aos afloramentos rochosos causariam a resposta contínua da riqueza a esse gradiente.

A altitude é apontada como uma importante causadora das mudanças na composição de espécies em campos de altitude (Neri et al. 2016, Cordeiro and Neri 2019, Gastauer et al. 2020). Contudo, seu efeito neste trabalho foi mais baixo em comparação com o efeito somado das variáveis topográficas. O curto gradiente altitudinal amostrado, de apenas 200 m de

desnível, pode ter sido o causador da baixa explicação desta variável para as mudanças na composição de espécies. Além disso, apesar de haver espécies específicas de cada ambiente quando consideramos apenas as áreas de encosta, que divergem primordialmente em altitude, vemos que a diferença de composição entre elas se deve muito mais a uma mudança nas abundâncias do que por substituição de espécies. Esse efeito pode estar relacionado a pequenas diferenças de fitness entre essas espécies em resposta aos microclimas causados pela variação na altitude (Chesson 2000, 2018). Assim, as pequenas diferenças de temperatura, umidade, exposição a ventos, pressão atmosférica e radiação UV leva a alterações nos padrões de abundância das espécies (Pistón et al. 2019).

Apesar do efeito da altitude ter sido baixo sobre a variação na composição de espécies, seu efeito sobre a diversidade foi bastante acentuado. Contudo, seu efeito foi diferente do esperado, sendo as parcelas em maior altitude aquelas com maior diversidade. Esse padrão pode ter sido causado pela presença unicamente de espécies fortemente especializadas (Cordeiro and Neri 2019), com pequenas diferenças de fitness entre elas (Mayfield and Levine 2010, Pastore et al. 2021), o que se apoia na alta associação entre espécies e hábitat observada. A baixa dominância causada pela igualdade de fitness entre as espécies pode permitir que mais espécies pudessem colonizar as áreas mais elevadas (Hillebrand et al. 2008). Já em menores altitudes, a presença de espécies mais dominantes pode excluir espécies menos competitivas, reduzindo a riqueza (Grime 1998, Czarniecka et al. 2019). Mudanças no microclima ao longo do gradiente altitudinal podem, portanto, levar à perda de diversidade nos campos de altitude, levando não só à perda de espécies com nichos restritos (Colles et al. 2009, Rahbek et al. 2019a), como também aumentando a discrepância nas abundâncias entre espécies coocorrentes.

A densidade de cobertura teve um baixíssimo efeito sobre a composição de espécies. No entanto, seu efeito sobre a diversidade foi fortemente significativo, tendo impacto sobre as três métricas de diversidade utilizadas. O aumento da densidade de cobertura levou à perda de diversidade tanto com relação à riqueza quanto à equidade. Com o aumento da competição por recursos, a presença de estratégias adaptativas que levam a otimização do uso dos recursos pode permitir a dominância sobre as demais estratégias coocorrentes (Grime 2006, Mayfield and Levine 2010, Kraft et al. 2015). Classicamente, esse tipo de dominância é atribuído a estratégias mais aquisitivas (Bernard-Verdier et al. 2012, Debouk et al. 2015), o que já foi observado em campo de altitude (Matos et al. 2021). Entretanto, uma vez que as condições ambientais nos campos de altitude são tão variáveis de um hábitat para o outro, é

difícil assumir que estratégias aquisitivas necessariamente determinarão a dominância em todos os diferentes hábitats (Rosado and de Mattos 2017, Matos et al. 2021). Portanto, é ainda necessário compreender a relação da dominância com as estratégias funcionais para esclarecer mais afundo os processos que governam a montagem de comunidades nesses ambientes.

5. CONCLUSÃO

O presente estudo mostra que a altitude, a disponibilidade de solo modulada pela topografia e a densidade de competidores são importantes determinantes da diversidade nos campos de altitude. Apesar da maior explicação da variação na composição ter sido causada pela disponibilidade de solo, a altitude foi um importante fator para a diversidade, permitindo uma distribuição mais homogênea das abundâncias. Com o aumento das temperaturas causado pelas mudanças globais, as comunidades em alta altitude podem se tornar menos diversas, devido à maior dominância de algumas espécies. Somado a esse resultado, a perda de diversidade observada com o aumento da densidade de cobertura reforça a ideia de que não só a adaptação às condições extremas dos campos de altitude é determinante para a sobrevivência das espécies que ali habitam. A competição por recursos é também um fator determinante para a coexistência das espécies e tem seu efeito mediado pela interação com fatores abióticos. Sendo assim, as previsões dos impactos das mudanças climáticas nesse ambiente devem considerar não só o impacto da perda de microclimas, mas também de como as espécies responderão a isso sob diferentes níveis de recurso e sob diferentes densidades de competidores.

6. REFERÊNCIAS

Alcantara, S., R. de Mello-Silva, G. S. Teodoro, K. Drequeceler, D. D. Ackerly, and R. S. Oliveira. 2015. Carbon assimilation and habitat segregation in resurrection plants: A comparison between desiccation- and non-desiccation-tolerant species of Neotropical Velloziaceae (Pandanales). Functional Ecology 29:1499–1512.

Alves, R. J. V, and J. Kolbek. 2010. Can campo rupestre vegetation be floristically delimited based on vascular plant genera ? Plant Ecology 207:67–79.

Antonelli, A., W. D. Kissling, S. G. A. Flantua, M. A. Bermúdez, A. Mulch, A. N. Muellner-Riehl, H. Kreft, H. P. Linder, C. Badgley, J. Fjeldså, S. A. Fritz, C. Rahbek, F. Herman,

H. Hooghiemstra, and C. Hoorn. 2018. Geological and climatic influences on mountain biodiversity. Nature Geoscience 11:718–725.

Assis, M. V., and E. A. de Mattos. 2016. Vulnerabilidade da vegetação de campos de altitude às mudanças climáticas. Oecologia Australis 20:24–36.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1–48.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters 15:365–377.

de Bello, F., C. Carmona, A. Dias, L. Götzenberger, M. Moretti, and M. Berg. 2021. Response Traits and the Filtering Metaphor. Pages 57–74 Handbook of Trait-Based Ecology From Theory to R Tools. Cambridge University Press, Cambridge.

de Bello, F., J. N. Price, T. Munkemuller, J. Liira, M. Zobel, W. Thuiller, P. Gerhold, L. Götzenberger, S. Lavergne, J. Lepš, K. Zobel, and M. Partel. 2012. Functional species pool framework to test for biotic effects on community assembly. Ecology 93:2263–2273.

Beniston, M. 2003. Climatic change in mountain regions: a review of possible impacts. Climatic Change 59:5–31.

Benites, V. de M., A. N. Caiafa, E. De Sá Mendonça, C. E. Schaefer, and J. C. Ker. 2003. Solos e vegetação nos complexos rupestres de altitude da Mantiqueira e do Espinhaço. Floresta e Ambiente 10:76–85.

Benites, V. M., C. E. G. R. Schaefer, E. S. Mendonça, and L. Martin Neto. 2001. Caracterização da matéria orgânica e micromorfologia de solos sob Campos de Altitude no parque estadual da Serra do Brigadeiro (MG). Revista Brasileira de Ciência do Solo 25:661–674.

Bernard-Verdier, M., M. L. Navas, M. Vellend, C. Violle, A. Fayolle, and E. Garnier. 2012. Community assembly along a soil depth gradient: Contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. Journal of Ecology 100:1422–1433.

Braun-Blanquet, J. 1979. Fitosociologia: Bases para el estudio de las comunidades vegetales. First edition. H. Blume Ediciones, Madrid, Espanha.

Breheny, P., and W. Burchett. 2017. Visualization of Regression Models Using visreg. The R Journal 9:56–71.

Bueno de Mesquita, C. P., L. S. Tillmann, C. D. Bernard, K. C. Rosemond, N. P. Molotch,

and K. N. Suding. 2018. Topographic heterogeneity explains patterns of vegetation response to climate change (1972 – 2008) across a mountain landscape , Niwot. Arctic, Antarctic, and Alpine Research 50.

Cáceres, M. De, and P. Legendre. 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90:3566–3574.

Cadotte, M. W., and C. M. Tucker. 2019. Should Environmental Filtering be Abandoned ? Trends in Ecology & Evolution.

Caiafa, A. N., and A. F. da Silva. 2005. Composição florística e espectro biológico de um campo de altitude no Parque Estadual da Serra do Brigadeiro, Minas Gerais – Brasil. Rodriguésia 56:163–173.

Caiafa, A. N., and A. F. da Silva. 2007. Structural analysis of the vegetation on a highland granitic rock outcrop in Southeast Brazil 1 3:657–664.

Callaway, R. M., R. W. Brooker, P. Choler, Z. Kikvidze, C. J. Lortie, R. Michalet, L. Paolini, F. I. Pugnaire, B. Newingham, E. T. Aschehoug, C. Armas, D. Kikodze, and B. J. Cook. 2002. Positive interactions among alpine plants increase with stress. Nature 417:844–848.

Campos, P. V., P. M. Villa, C. E. G. R. Schaefer, J. A. Nunes, S. Porembski, and A. V. Neri. 2021. Community composition , beta diversity and structure of high altitude grasslands along an altitudinal gradient in southeastern Beta diversity , community composition and structure of high altitude grasslands along an altitudinal gradient in southeastern B. Revista de Biología Tropical 68:977–986.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology, Evolution, and Systematics 31:343–366.

Chesson, P. 2018. Updates on mechanisms of maintenance of species diversity. Journal of Ecology 106:1773–1794.

Christmann, T., and I. Oliveras. 2020. Nature of Alpine Ecosystems in Tropical Mountains of South America. Page Encyclopedia of the World's Biomes. Elsevier.

Colles, A., L. H. Liow, and A. Prinzing. 2009. Are specialists at risk under environmental change? Neoecological, paleoecological and phylogenetic approaches. Ecology Letters 12:849–863.

Cordeiro, A. de A. C., and A. V. Neri. 2019. Spatial patterns along an elevation gradient in high altitude grasslands, Brazil. Nordic Journal of Botany 37:1–10.

Czarniecka, M., W. Zygmunt, K. Milan, and C. Salza. 2019. Diversity loss in grasslands due

to the increasing dominance of alien and native competitive herbs. Biodiversity and Conservation 28:2781–2796.

Debouk, H., F. de Bello, and M. Sebasti. 2015. Functional Trait Changes , Productivity Shifts and Vegetation Stability in Mountain Grasslands during a Short-Term Warming. PLoS ONE 10:1–17.

Elith, J., and J. R. Leathwick. 2009. Species distribution models: Ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics 40:677–697.

Enquist, B. J., J. Norberg, S. P. Bonser, C. Violle, C. T. Webb, A. Henderson, L. L. Sloat, and V. M. Savage. 2015. Scaling from Traits to Ecosystems : Developing a General Trait Driver Theory via Integrating Trait-Based and Metabolic Scaling Theories. Advances in Ecological Research 52:249–318.

Fernandes, G. W., L. B. S. Tameirão, A. R. Costa, D. G. Ribeiro, M. N. Neves, B. G. Souza E Brito, and D. Negreiros. 2021. Functional traits of three major invasive grasses in a threatened tropical mountain grassland. Anais da Academia Brasileira de Ciencias 93:1–7.

Gastauer, M., J. Thiele, S. Porembski, and A. V. Neri. 2020. How do altitude and soil properties influence the taxonomic and phylogenetic structure and diversity of Brazilian páramo vegetation? Journal of Mountain Science 17:1045–1057.

Gauzere, P., X. Morin, C. Violle, I. Caspeta, C. Ray, and B. Blonder. 2020. Vacant yet invasible niches in forest community assembly. Functional Ecology:1365-2435.13614.

Graae, B. J., V. Vandvik, W. S. Armbruster, W. L. Eiserhardt, J. Svenning, J. Ehrlén, J. D. M. Speed, K. Klanderud, K. Anne, A. Milbau, Ø. H. Opedal, I. G. Alsos, R. Ejrnæs, H. Henrik, H. J. B. Birks, K. B. Westergaard, H. H. Birks, and J. Lenoir. 2018. Stay or go – how topographic complexity influences alpine plant population and community responses to climate change. Perspectives in Plant Ecology, Evolution and Systematics 30:41–50.

Griffiths, H., and J. Males. 2017. Succulent plants. Current Biology 27:890–896.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111:1169–1194.

Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology 86:902–910.

Grime, J. P. 2006. Trait convergence and trait divergence in herbaceous plant communities : Mechanisms and consequences. Journal of Vegetation Science 17:255–260.

Habibullah, M. S., B. H. Din, S. H. Tan, and H. Zahid. 2022. Impact of climate change on biodiversity loss: global evidence. Environmental Science and Pollution Research 29:1073–1086.

Hillebrand, H., D. M. Bennett, and M. W. Cadotte. 2008. Consequences of Dominance: A Review of Evenness Effects on Local and Regional Ecosystem Processes. Ecology 89:1510–1520.

Kassambara, A., and F. Mundt. 2020. factoextra: Extract and Visualize the Results of Multivariate Data Analyses.

Köppen, W., and R. Geiger, editors. 1936. Das geographische System der Klimate (1936). Gebrüder Borntl'aeger, Berlin.

Kraft, N. J. B., P. B. Adler, O. Godoy, E. C. James, S. Fuller, and J. M. Levine. 2015a. Community assembly, coexistence and the environmental filtering metaphor. Functional Ecology 29:592–599.

Kraft, N. J. B., O. Godoy, and J. M. Levine. 2015b. Plant functional traits and the multidimensional nature of species coexistence. Proceedings of the National Academy of Sciences of the United States of America 112:797–802.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. lmerTest Package: Tests in Linear Mixed Effects Models. Journal of Statistical Software 82:1–26.

Laliberté, E., G. Zemunik, and B. L. Turner. 2014. Environmental filtering explains variation in plant diversity along resource gradients. Science 345:1602–1605.

Lê, S., J. Josse, and F. Husson. 2008. FactoMineR: A Package for Multivariate Analysis. Journal of Statistical Software 25:1–18.

López-Angulo, J., D. S. Pescador, A. M. Sánchez, A. L. Luzuriaga, L. A. Cavieres, and A. Escudero. 2020a. Impacts of climate, soil and biotic interactions on the interplay of the different facets of alpine plant diversity. Science of the Total Environment 698:133960.

López-Angulo, J., D. S. Pescador, A. M. Sánchez, A. L. Luzuriaga, L. A. Cavieres, and A. Escudero. 2020b. Impacts of climate, soil and biotic interactions on the interplay of the different facets of alpine plant diversity. Science of the Total Environment 698:133960.

Marengo, J. A., L. M. Alves, C. Inpe, R. Dutra, C. Paulista, and S. Paulo. 2005. Tendências Hidrológicas da Bacia do Rio Paraíba do Sul. CPTEC/INPE 1:1–31.

Masson-Delmotte, V., P. Zhai, A. Pirani, S. L., J. B. R. Connors, C. Péan, S. Berger, N. Caud,

Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, and and B. Z. (eds. . Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu. 2021. IPCC, 2021: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press:F0003–F0003.

Matos, I. S., O. Binks, C. B. Eller, B. B. Zorger, P. Meir, T. E. Dawson, and B. H. P. Rosado. 2022. Revisiting plant hydrological niches: the importance of atmospheric resources for ground-rooted plants. Journal of Ecology n/a.

Matos, I. S., C. B. Eller, I. Oliveras, D. Mantuano, and B. H. P. Rosado. 2021. Three eco-physiological strategies of response to drought maintain the form and function of a tropical montane grassland. Journal of Ecology 109:327–341.

Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecology Letters 13:1085–1093.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Negreiros, D., S. Le Stradic, G. W. Fernandes, and H. C. Rennó. 2014. CSR analysis of plant functional types in highly diverse tropical grasslands of harsh environments. Plant Ecology 215:379–388.

Neri, A. V., G. R. A. Borges, J. A. A. Meira-Neto, L. F. S. Magnago, I. M. Trotter, C. E. G. R. Schaefer, and S. Porembski. 2016. Soil and altitude drive diversity and functioning of Brazilian Páramos (campo de altitude). Journal of Plant Ecology 10:771–779.

Nunez, S., E. Arets, R. Alkemade, C. Verwer, and R. Leemans. 2019. Assessing the impacts of climate change on biodiversity: is below 2 °C enough? Climatic Change 154:351–365.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, E. Szoecs, and H. Wagner. 2019. vegan: Community Ecology Package.

Passy, S. I., M. Bottin, J. Soininen, and H. Hillebrand. 2017. Environmental filtering and taxonomic relatedness underlie the species richness-evenness relationship Environmental filtering and taxonomic relatedness underlie the species richness – evenness relationship. Hydrobiologia.

Pastore, A. I., G. Barabás, M. D. Bimler, M. M. Mayfield, and T. E. Miller. 2021. The evolution of niche overlap and competitive differences. Nature Ecology and Evolution 5:330–337.

de Paula, L. F. A., D. Negreiros, L. O. Azevedo, R. L. Fernandes, J. R. Stehmann, and F. A. O. Silveira. 2015. Functional ecology as a missing link for conservation of a resource-limited flora in the Atlantic forest. Biodiversity and Conservation 24:2239–2253.

Pistón, N., F. de Bello, L. Götzenberger, B. H. P. Rosado, E. A. De Mattos, R. S. Gómez, and C. P. Carmona. 2019. Multidimensional ecological analyses demonstrate how interactions between functional traits shape fitness and life history strategies. Journal of Ecology 107:2317–2328.

Porembski, S. 2006. Vegatative Architecture of Desiccation-tolerant Arborescent Monocotyledons. Aliso: A Journal of Systematic and Evolutionary Botany 22:129–134.

Porembski, S. 2007. Tropical inselbergs: Habitat types, adaptive strategies and diversity patterns. Revista Brasileira de Botanica 30:579–586.

Porembski, S., J. Rexroth, K. Weising, L. Bondi, R. Mello-silva, D. C. Centeno, M. N. Datar, A. Watve, A. Thiombano, M. N. Rabarimanarivo, and L. F. A. de Paula. 2021. An overview on desiccation-tolerant mat-forming monocotyledons on tropical inselbergs. Flora 285.

Rahbek, C., M. K. Borregaard, A. Antonelli, R. K. Colwell, B. G. Holt, D. Nogues-Bravo, C. M. Ø. Rasmussen, K. Richardson, M. T. Rosing, R. J. Whittaker, and J. Fjeldså. 2019a. Building mountain biodiversity: Geological and evolutionary processes. Science 365:1114–1119.

Rahbek, C., M. K. Borregaard, R. K. Colwell, B. Dalsgaard, B. G. Holt, N. Morueta-holme, D. Nogues-bravo, R. J. Whittaker, and J. Fjeldså. 2019b. Humboldt's enigma: What causes global patterns of mountain biodiversity? Science 365:1108–1113.

Rangel, T. F., N. R. Edwards, P. B. Holden, J. A. F. Diniz-Filho, W. D. Gosling, M. T. P. Coelho, F. A. S. Cassemiro, C. Rahbek, and R. K. Colwell. 2018. Modeling the ecology and evolution of biodiversity: Biogeographical cradles, museums, and graves. Science 361.

Read, Q. D., L. C. Moorhead, N. G. Swenson, J. K. Bailey, and N. J. Sanders. 2014. Convergent effects of elevation on functional leaf traits within and among species. Functional Ecology 28:37–45.

Roberts, D. W. 2019. Ordination and Multivariate Analysis for Ecology.

Rosado, B. H. P., and E. A. de Mattos. 2017. On the relative importance of CSR ecological strategies and integrative traits to explain species dominance at local scales. Functional Ecology 31:1969–1974.

Safford, H. D. 1999a. Brazilian Páramos I. An introduction to the physical environment and vegetation of the campos de altitude. Journal of Biogeography 26:693–712.

Safford, H. D. 1999b. Brazilian Páramos II . Macro- and mesoclimate of the *campos de altitude* and affinities with high mountain climates of the tropical Andes and Costa Rica. Journal of Biogeography:713–737.

Safford, H. D. 2007. Brazilian Páramos IV. Phytogeography of the campos de altitude. Journal of Biogeography 34:1701–1722.

Sanders, N. J., and C. Rahbek. 2012. The patterns and causes of elevational diversity gradients. Ecography 35:1–3.

Scarano, F. R., P. Ceotto, and G. Martinelli. 2016. Climate change and "campos de altitude": forecasts, knowledge and action gaps in Brazil. Oecologia Australis 20:139–144.

Thakur, D., and A. Chawla. 2019. Functional diversity along elevational gradients in the high altitude vegetation of the western Himalaya. Biodiversity and Conservation 28:1977–1996.

Tinti, B. V., C. E. R. G. Schaefer, J. A. Nunes, A. C. Rodrigues, I. F. Fialho, and A. V. Neri. 2015. Plant diversity on granite/gneiss rock outcrop at Pedra do Pato, Serra do Brigadeiro State Park, Brazil. Check List 11.

Tito, R., H. L. Vasconcelos, and K. J. Feeley. 2020. Mountain Ecosystems as Natural Laboratories for Climate Change Experiments. Frontiers in Forests and Global Change 3:1–8.

Vasconcelos, M. F. 2011. O que são campos rupestres e campos de altitude nos topos de montanha do Leste do Brasil? Brazilian Journal of Botany 34:241–246.

Wilson, J. B., and W. G. Lee. 2000. C-S-R triangle theory: Community-level predictions, tests, evaluation of criticisms, and relation to other theories. Oikos 91:77–96.

APÊNDICE A: MATERIAIS SUPLEMENTARES

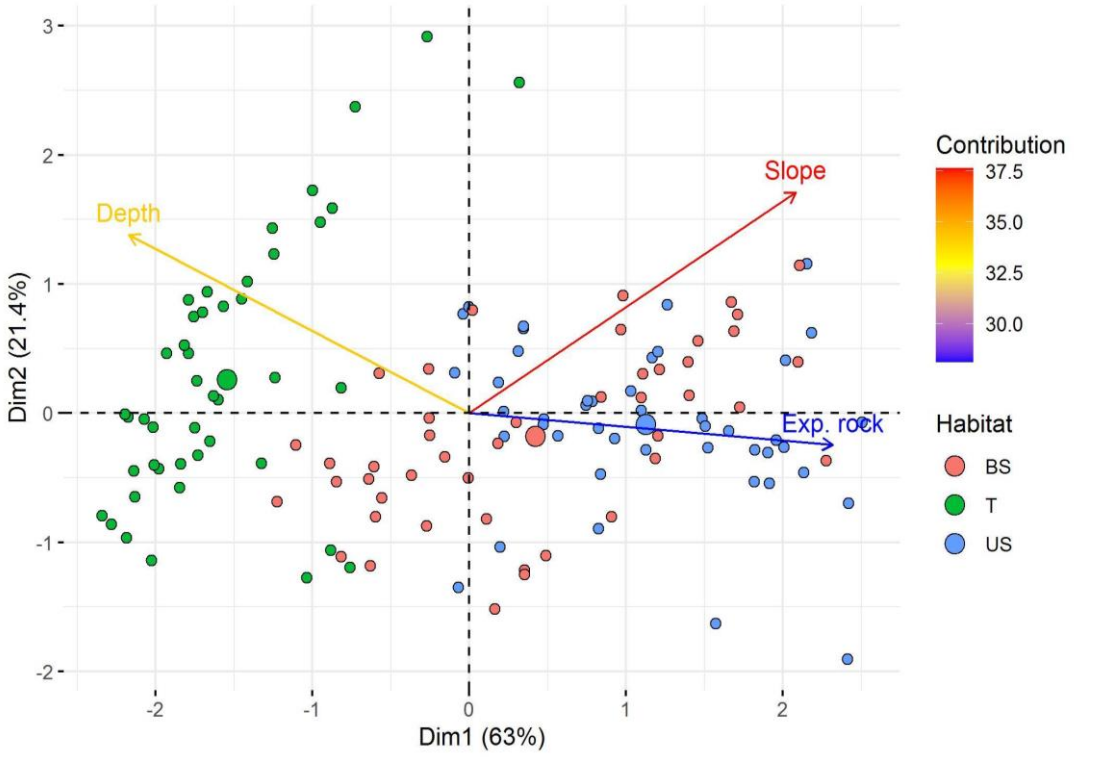

Figura S1: Disponibilidade de solo mediada por topografia na Pedra do Pato. Os pontos indicam as parcelas e as cores indicam os diferentes habitats encontrados: BS, encosta inferior; T, topo; US, encosta superior. As setas indicam os vetores das variáveis ambientais e a contribuição de cada uma para a variação explicada pelas duas primeiras dimensões (Contrib.).

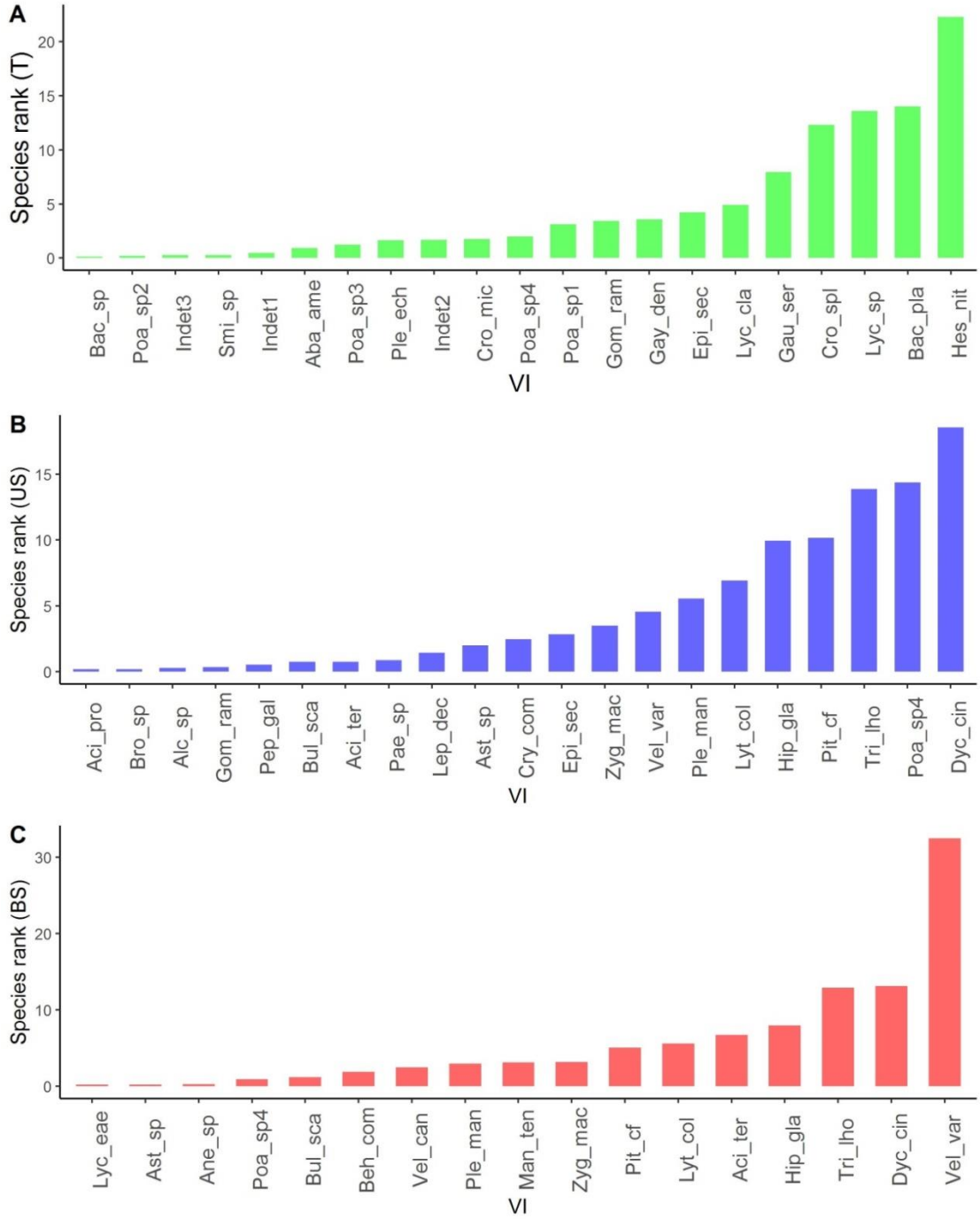

Figura S2: Valor de importância das espécies em cada hábitat: (A) topo (T); (B) encosta superior (US); (C) encosta inferior (BS). As espécies foram ranqueadas de acordo com o valor indicador.

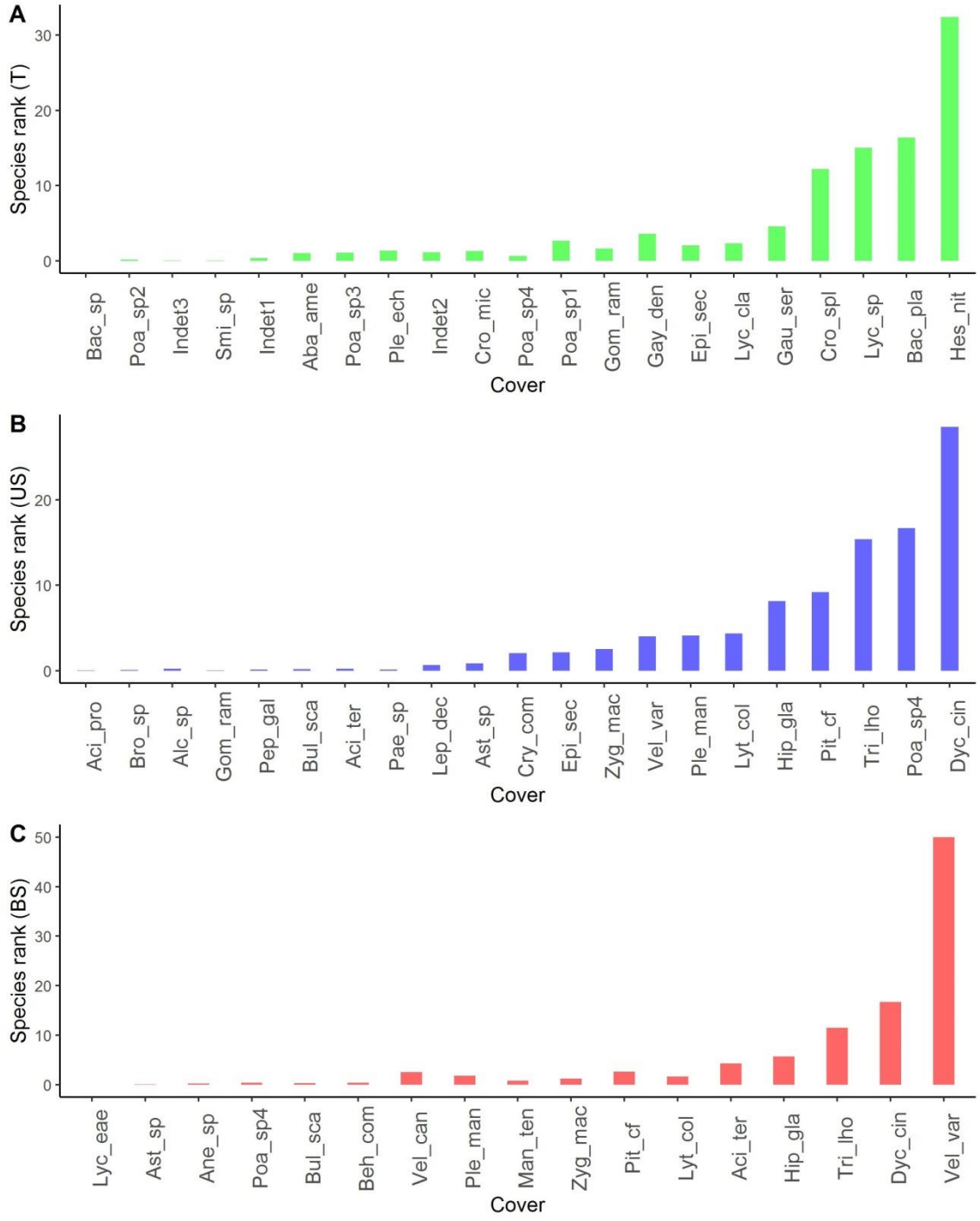

Figura S3: Distribuição da cobertura das espécies por hábitat: (A) topo (T); (B) encosta superior (US); (C) encosta inferior (BS). As espécies foram ranqueadas de acordo com o valor indicador.

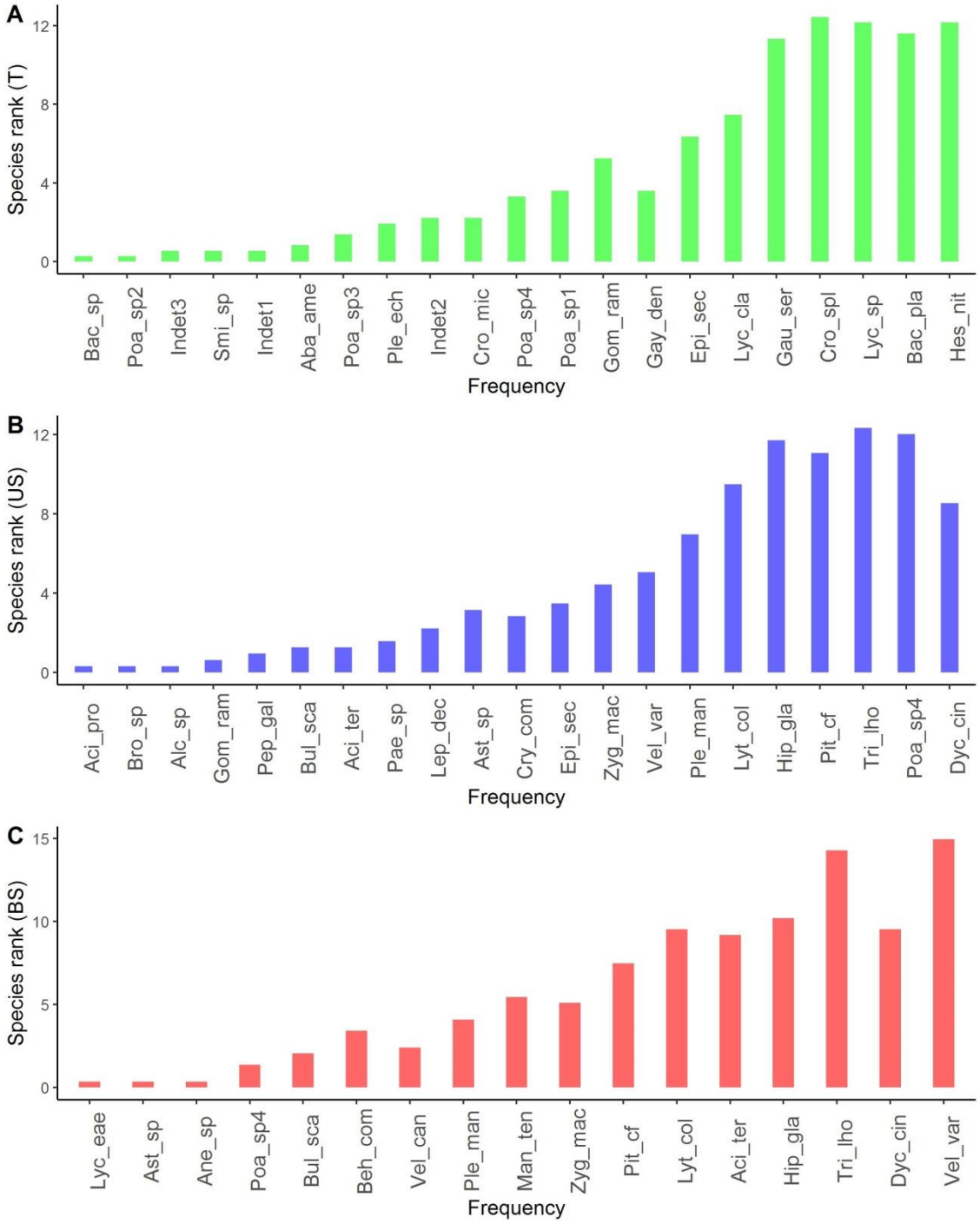

Figura S4: Distribuição da frequência das espécies por hábitat: (A) topo (T); (B) encosta superior (US); (C) encosta inferior (BS). As espécies foram ranqueadas de acordo com o valor indicador.

CAPÍTULO 2: ABIOTIC AND BIOTIC FACTORS DRIVE COEXISTENCE OF DIFFERENT STRATEGIES IN MOUNTAIN COMMUNITIES

RESUMO

FERREIRA, Elielson Lucas, M.Sc., Universidade Federal de Viçosa, julho de 2022. **Fatores bióticos e abióticos determinam a coexistência de diferentes estratégias em comunidades de montanha.** Orientadora: Andreza Viana Neri.

A compreensão dos fatores relacionados à filtragem e a coocorrência das espécies nas montanhas tropicais é de grande importância para prever o efeito das mudanças globais nesses ambientes. Este estudo visa compreender o papel da interação entre a altitude, a disponibilidade de solo e a densidade da cobertura vegetal sobre a montagem das comunidades em uma área de campo de altitude no Sudeste do Brasil. Para tal, exploramos as diferentes estratégias funcionais presentes na montanha e testamos as seguintes hipóteses: (1) a montagem das comunidades se dá por filtragem de atributos que permitem as espécies sobreviverem às condições do hábitat e a competir por recursos; (2) a dominância nos hábitats se dá por presença de atributos convergentes, sob maiores pressões bióticas e abióticas, e divergentes, sob menores pressões, devido à melhora de fitness quando há menor sobreposição de nicho. Utilizamos uma PCA e a classificação de estratégias CSR para visualizar o espaço funcional ocupado pelas espécies. Calculamos a diversidade funcional e a variância e média dos atributos funcionais da comunidade considerando apenas a ocorrência das espécies para a primeira hipótese (FRic, variância e média), e ponderando pela cobertura relativa das espécies na comunidade para a segunda hipótese (FDis, CWV e CWM). Utilizamos modelos lineares mistos para calcular o efeito das variáveis ambientais sobre as medidas de tamanho do efeito dos processos de montagem da comunidade – calculados usando modelos nulos específicos para cada hipótese. Três eixos de variação nas estratégias das espécies foram observados: o primeiro relacionado a atributos de resistência à seca e à estratégia C; o segundo relacionado à economia de recursos e às estratégias S e R; e o terceiro relacionado ao crescimento vertical. Uma redução da riqueza funcional e da variância de atributos associados ao segundo eixo ocorreu em função da altitude e da densidade de cobertura. Tamanhos de efeito negativos (que indicam filtragem) só foram observados em maior altitude. Houve também uma redução na variância de atributos associados ao primeiro

eixo em função do aumento da altitude e da diminuição da disponibilidade de solo. Tamanhos de efeito negativos só foram observados com altitude e disponibilidade de solo elevadas. As espécies dominantes divergiram mais em todo o espaço funcional e em atributos de resistência à seca com menor altitude e disponibilidade de solo. Respostas idiossincráticas foram observadas para os valores médios de atributo (média e CWM) em função da interação entre os preditores. A altitude atuou reduzindo o espaço funcional da comunidade, contudo, esse filtro só foi forte o suficiente para excluir espécies da comunidade quando a disponibilidade de solo e a densidade de cobertura foram altas. Isso demonstra a existência de atributos que permitem maior habilidade competitiva, mas também que estes variam em função das condições ambientais. Os hábitats com menores altitude e disponibilidade de solo foram os que apresentaram maior riqueza e dispersão funcional, associada à alta variância e CWV em atributos de resistência à seca. Isso sugere que existe forte partição no uso da água, favorecendo espécies distantes funcionalmente e permitindo sua coexistência.

Palavras-chave: Páramos brasileiros. Montagem de comunidades. Filtragem ambiental. Competição. Coexistência.

ABSTRACT

FERREIRA, Elielson Lucas, M.Sc., Universidade Federal de Viçosa, July 2022. **Abiotic and biotic factors drive coexistence of different strategies in mountain communities.** Orientadora: Andreza Viana Neri.

Tropical mountains are highly threatened environments by climate change. Understanding the environmental factors and traits related to filtering and species co-occurrence is of great importance to predict the effects of global change on these environments. This study aims to understand the role of the interaction between altitude, soil availability and vegetation cover density on community assembly in an altitude grassland (*campos de altitude*) on a mountaintop in Southeast Brazil. To this end, we explored the different functional strategies present in the mountain and tested the following hypotheses: (1) communities are assembled by the filtering of traits that allow species to survive under the habitat conditions and to compete for resources; (2) dominance inside the habitats occurs due to the presence of convergent traits under higher biotic and abiotic pressures, and divergent traits under lower pressures, due to improved fitness when there is less niche overlap. We used a PCA and the CSR strategies scheme to visualize the functional space occupied by the species. We calculated the functional diversity and the community's trait variance and mean considering only species occurrence for the first hypothesis (functional richness, variance and mean), and weighting by the relative coverage of the species in the community for the second hypothesis (functional dispersion, CWV and CWM). We used linear mixed models to measure the effect of the environmental variables on the effect size of the intended assembly process - calculated using specific null models to each hypothesis. Three axes of variation in species strategies were observed: the first related to drought resistance traits and the C strategy; the second related to resource economics and to the S and R strategies; and the third related to vertical growth. A reduction in the functional richness and in the variance of traits associated with the second axis occurred as a function of increasing altitude and coverage density. Negative effect sizes (which indicate filtering) were only observed at higher altitudes. There was also a reduction in the variance of traits associated with the first axis as a function of increasing altitude and decreasing soil availability. Negative effect sizes were only observed at higher altitude and higher soil availability. Convergence between dominant species throughout the functional space (FDis) and in traits associated with the first axis (CWV) increased as a function of altitude and soil availability. Idiosyncratic responses were observed for the mean

trait values (mean and CWM) as a function of the interaction between the predictors. Altitude acts reducing the functional space, however, this filter was only strong enough to exclude species from the community when soil availability and cover density were also high. This demonstrates the existence of traits that allow greater competitive ability, but also that these vary according to environmental conditions. The habitats at low altitude and with less soil availability showed the greater richness, functional dispersion, and high variance and CWV in drought resistance traits. This suggests that there is a strong partition in water use, favouring functionally distant species and allowing their coexistence.

Keywords: Brazilian *Páramos*. Assembly rules. Environmental filtering. Competition. Coexistence.

1. INTRODUCTION

Tropical mountains are important centres of biodiversity in the world, acting not just as hosts of a great number of species, but also as cradles of new species and tombs for many lineages (Silveira et al. 2016, Rangel et al. 2018, Rahbek et al. 2019). Such multiple roles of tropical mountains to biodiversity make them critical environments for conservation under human-induced climate change (Beniston 2003, Assis and de Mattos 2016, Rangel et al. 2018, Christmann and Menor 2021). In order to predict its impacts on high-altitude plant communities, many researchers have been using high-scale modelling approaches considering climate, soil, and topography dimensions of species niches (Bellard et al. 2012, Barbosa and Fernandes 2016, Fernandes et al. 2018). However, the fine-scale environmental heterogeneity of mountain landscapes creates certain limitations to broad-scale predictions (Bueno de Mesquita et al. 2018). Although several studies have already addressed the local responses of plant communities to environmental gradients (Negreiros et al. 2014, de Paula et al. 2015, Neri et al. 2016, Cordeiro and Neri 2019, Scherrer et al. 2019, Campos et al. 2021), most of them ignore the potential effect of biotic interactions on species distribution (Callaway et al. 2002, López-Angulo et al. 2020b). Also, constraints imposed by the environment on stable coexistence between species at habitat level still limit the reliability of the high-scale predictions (Chesson 2000, 2018, Pastore et al. 2021). Therefore, it is evident the need to comprehend the interplay between abiotic and biotic conditions and their influence on the selection of functional traits that allow plants to survive and coexist (Chesson 2000, Mayfield and Levine 2010, Kraft et al. 2015a). That can, thus, enhance our capacity to predict the outcomes of climate change on high-elevation ecosystems.

The trait-driven assembly process is pointed to as the main cause of the high species turnover among habitats in higher elevations, which creates its characteristic mosaic distribution of communities (Negreiros et al. 2014, de Paula et al. 2015, Neri et al. 2016). Differential selection for acquisitive and conservative strategies occurs due to variations in the resource levels caused by topography (Negreiros et al. 2014, de Paula et al. 2015, Kolb et al. 2018). However, some authors argue that coexistence and dominance in these patches may be caused by other traits not necessarily related to carbon use strategies (Rosado and de Mattos 2017, Cruz and Lasso 2021, Matos et al. 2021). In the outcrop areas, for example, where less soil is accumulated because of the high inclination, plants experience more intense droughts. Under these conditions, different drought resistance strategies emerge, like desiccation

tolerance and drought avoidance strategies (Porembski 2006, Matos et al. 2021, Porembski et al. 2021). Nevertheless, how the coexistence of these different strategies occurs in response to environmental gradients is still not clear (Alcantara et al. 2015, Males 2017).

At increased stress conditions environmental filtering is expected to act reducing the range of strategies able to colonize and survive in a habitat (Bernard-Verdier et al. 2012, Scherrer et al. 2019, de Bello et al. 2021). This hypothesis is supported by many studies, which found a decreasing functional and phylogenetic diversity along elevation and fertility gradients (Neri et al. 2016, Thakur and Chawla 2019, Gastauer et al. 2020). However, the presence of multiple suitable strategies to cope with stress conditions, like the different drought strategies present in water-limited environments, can enhance functional diversity instead of decreasing it (Marks et al. 2006, Matos et al. 2021, Porembski et al. 2021). Therefore, it's important to consider multiple traits in order to understand how the different filters act on the different dimensions of species niches (Marks et al. 2006, Kraft et al. 2015b, Pistón et al. 2019).

It is difficult to distinguish whether a species is not found in a site due to its inability to survive under the local environmental filters or because it has been excluded by a better competitor (Mayfield and Levine 2010, Kraft et al. 2015a, Cadotte and Tucker 2019). For example, increasing productivity can favour taller species because of light competition, excluding the smaller species not adapted to shading conditions. In this case, competition results in convergence for specific traits similarly to what is expected for abiotic filtering (Grime 2006, Mayfield and Levine 2010). In the Brazilian *Páramos*, for example, the presence of a bamboo species with resprouting ability after fire is associated with low functional diversity in tree islands, where it dominates after wildfires (Safford 2001, Christmann et al. 2021).

Nonetheless, if no set of traits allows better competitive ability, species are expected to diverge in niches to avoid competition for resources (MacArthur and Levins 1967, Chesson 2000, Bernard-Verdier et al. 2012, Scherrer et al. 2019). Pastore et al. (2021), using computational simulations, found that at evolutionary time and for a single trait and niche dimension, species presented greater divergence in broader environments. In this case, the costs of a species to lower its fitness by diverging from the optimal trait value compensate for the costs of overlapping its niche with other species. This might explain species coexistence at habitat level in mountain environments, where better fitness might result in a higher abundance of divergent strategies in habitats where species with distinct strategies are able to

survive. On the other hand, in habitats with strong environmental constraints, such as in high elevation habitats, better fitness might result in higher abundance of functionally similar species. The distribution of abundances between co-occurring strategies in mountain communities is, therefore, expected to respond to the elevation and topographic gradients, as well as to the presence of potential competitors at the habitat level (Scherrer et al. 2019). But which traits will present convergence or divergence is dependent on the importance of each specific trait for fitness under each specific condition (Zhu et al. 2017, Kearney et al. 2021).

In this study, we aim to understand how the interplay of elevation, topography-driven soil availability, and vegetation cover density can structure a tropical mountain community through the functional traits. We investigated the different dimensions of the functional strategies that composed the mountain's species pool. Then, a two-level null model approach was used to distinguish the rules that drive species occurrence due to its functional traits along the mountain gradients from those that drive species abundance inside the habitats (de Bello et al. 2012). We hypothesize that variation in the functional composition of communities occurs due to the filtering of suitable strategies into the habitats by the interplay of elevation, soil availability, and plant cover density. Increasing elevation and decreasing soil availability might favour conservative species and filter out more acquisitive species from the mountain pool, while increasing vegetation cover density might favour competitive exclusion of more conservative species. At the habitat level, we hypothesize that the dominance in stressful habitats occurs due to the presence of convergent traits, and in less stressful habitats, it occurs due to divergent traits, since species fitness is improved with less niche overlap with neighbour species.

2. MATERIAL AND METHODS

2.1. Study site

The present study was carried out in the Serra do Brigadeiro State Park, located at the northern border of the Serra da Mantiqueira mountain range in the state of Minas Gerais, between the meridians 42º 40' and 40º 20' West and the parallels 20º 33' and 21º 00' South (Engevix 1995). The Serra do Brigadeiro is formed by igneous and metamorphic rocks, mainly granite, gneiss, and migmatites (Benites et al. 2001), with the presence of quartz. The region's climate is tropical of altitude (Cwb), according to the classification of Köppen and

Geiger (1936), with an annual average temperature of 18º C, average annual precipitation of 1300 mm, and a marked seasonality (Engevix 1995). The park is located in the Atlantic Forest domain, with vegetation composed of secondary fragments of rainforest and high-altitude grasslands and shrublands, which are present above an elevation of 1600 m (Caiafa and Silva 2005).

The samples were all made on Brazilian *páramo* vegetation, also called *campos de altitude*, on the Pedra do Pato mountain. This mountain is one of the highest in the park, rising 1980 m above sea level. There is a wide variety of habitats in Pedra do Pato, like plateaus, rock outcrops, small valleys, and swamps. Each habitat has different species composition creating a mosaic of different physiognomies (Tinti et al. 2015). In order to cover the spectra of vegetation along the peak, the plots were established along an altitudinal gradient on the northern slope.

2.2. Data collection

In order to cover the spectra of vegetation along the peak, a total of 135 plots of 1 m^2 distributed within 45 quadrats of 3m^2 were established along a 200 m altitudinal gradient on the north side of the mountain. The elevation ranged from 1690 m until 1897 m a.s.l., at the summit. For each plot, a floristic survey of all the plants present was carried out and the cover percentage of each species was measured (BRAUN BLANQUET, 1979). Since the vegetation was highly heterogeneous, we divided it in three communities and calculated the importance value of each species using their relative cover and frequencies inside the community. This way, species that have low frequency and low cover along the whole gradient but are representative in a single habitat are not underrated. The ten vascular plant species with the highest importance value (VI) were selected for the collection of functional traits (Negreiros et al., 2014). Since some of the selected species were presented in more than one community, 27 different species had their functional traits collected as described below.

Five individuals of each species were selected for trait collection. Individuals' vegetative height (H) was measured in the field and two leaves of each individual were collected and transported in a cool box to a provisional laboratory in the Park's headquarters. Fresh leaves had their weight, thickness (LT), and area (LA) measured in the laboratory. Leaves were put in a drying oven and their dry weight was posteriorly collected. These measures were used to calculate leaf dry matter content and leaf water content (LDMC and

LWC); specific leaf area (SLA); leaf mass per area (LMA); and the leaf succulence index (LSI). We also used LA, dry and fresh weight to calculate the scores of CSR strategies using the StrateFy method (Pierce et al. 2017). All traits were measured following the methods proposed by Pérez-Harguindeguy et al. (2013). See Table S1 to check out the list of traits and the units of measure.

In order to determine the role of abiotic factors in structuring communities, we sampled the slope, soil depth, and the percentage of exposed rocks in each subplot. The slope was measured using a clinometer and soil depth was measured with a centimetre pointer, both at the middle of each subplot. Plot elevation was measured using a GPS. The vegetation cover density was calculated for each plot as a proxy of increased light and soil resource depletion by coexisting competitors. This metric was calculated by summing the cover of each species within a plot and dividing it by the effectively colonised area of the plot (plot area minus the area occupied by exposed rock).

2.3. Achieving assembly process

Two-level randomizations were used to access the community assembly process. The first randomization process was used to assess the strength of filtering on species occurrence across habitats. The null expectation for this process is that all species are able to colonise every plot in the mountain. We then shuffled species occurrences 10000 times for each plot, but always preserved plot species richness. For each turn of the algorithm, the plot mean and variance of each functional trait were calculated, as well as the functional richness (Mason et al. 2005). We calculated the probability of the observed value to be higher or lower than expected if all the species in the pool were able to colonise every site (Gotelli and Ulrich 2012, Mason et al. 2013, Botta-Dukát and Bálint 2016). We then used a probit transformation to calculate the effect size of filtering or limiting similarity on species assembly (Botta-Dukát 2018). Negative values of effect sizes for variance show that the local filters selected more convergent species from the pool, while positive values indicate the selection of more divergent. Additionally, the more negative or positive the effect sizes of mean trait values are, the higher the strength of the biotic and abiotic filters selecting for species with lower or higher trait values from the species pool, respectively.

The second randomization was used to assess the strength of the relationship between species relative coverage and its traits. The null expectation is that abundance distribution

between coexisting species is not related to traits that confer better fitness than the neighbours. We defined a species pool for each plot based on the species observed in the plot plus the ones that could potentially colonise it, the so-called dark diversity. To account for these not observed species, we used the method ThresholdBeals from the package DarkDiv (Carmona 2020). As the result was a binary matrix, we made a separate matrix for each plot just with the species from the pool and assigned the observed abundances (species cover) for the species occurring in the plot and with zero abundance for those species appertaining to the dark diversity. We then shuffled the abundances between species 1000 times and calculated the weighted mean (CWM), the weighted variance (CWV), and functional dispersion (FDis) for each plot at each turn of the algorithm. The total abundance of species in the plot was preserved. We again calculated the effect size of the target process as the probit transformed the probability of the observed value to be higher or lower than expected. In this case, negative values of effect sizes for CWV show that more abundant species tend to converge in traits, while positive ones indicate that more abundant species tend to diverge. Negative effect sizes of CWM indicate that more abundant species have lower values than expected, while positive ones indicate the opposite pattern.

2.4. Statistical analyses

A principal component analysis (PCA) was conducted to investigate the functional space occupied by the species occurring in Pedra do Pato Mountain. The axis with the higher explanation of species variance in functional spaces was retained and plotted using the ggplot2 package (Wickham 2016). To synthesise the information on topography, we also conducted a PCA with soil depth, slope, and percentage of exposed rock. The axis with a higher explanation (PC1) was retained for the following analysis. We used linear mixed-effect models to test the effects of elevation, vegetation cover density, and PC1 of topographic variables on the effect sizes of each functional measure for both the across-habitat filtering hypothesis and the habitat-level coexistence hypothesis. Since plots in the same quadrat are expected to be more correlated with themselves than other plots, quadrat was used as a random effect variable. In order to isolate the independent effect of each predictor, we used multiple regressions and considered all the possible interactions among predictors. The models were produced with the lme4 package (Bates et al. 2015) and the significance of predictors was accessed using the lmerTest package (Kuznetsova et al. 2017). The coefficient

of determination (R^2) was obtained with the MuMIn package (Barton 2009). To plot the models, we used partial residual plots from the Visreg package (Breheny and Burchett 2017).

Elevation, soil depth, slope, rock exposure, and vegetation cover density were log transformed and scaled previous to the analysis for normalization. The variables LSI, LMA, LA, LT, and C-and R-strategy were log transformed; LWC, SLA and H were square-root transformed; and S-strategy was power transformed to achieve a more symmetric distribution of the data.

3. RESULTS

3.1.Functional strategies

The species whose traits were sampled in Pedra do Pato Mountain were mainly distributed along the C-S axis of the CSR triangle (Fig.1). The majority of species were classified as stress-tolerant and a few were classified as competitive. No ruderal species was found. The PCA revealed the presence of a more diverse set of strategies in the species pool (Fig. 2). The first three axes explained 89.1% of the species variation in the functional space (Fig. 2a). In general, traits related to water storage - such as leaf succulence index (LSI) and leaf water content (LWC) - as well as those related to greater leaf size - such as leaf area (LA) and leaf thickness (LT) - were positively correlated with PCA's first dimension (Dim1). On the other hand, leaf dry matter content (LDMC) was negatively related to this axis. The species *Acianthera teres*, *Dyckia cinerea*, and *Cryptangium comumatum* were the species with the greatest contribution to the variation in the first axis, the first two being positively correlated with it, while the last one being negatively correlated. Traits related to leaf economic spectrum and CSR strategies were more associated with the second dimension of the PCA (Dim2), with specific leaf area (SLA) and R-strategy (R) being the traits most positively correlated with this axis, while leaf mass per area (LMA) and stress tolerance (S) were negatively correlated. The species with the greatest contribution to this dimension were *Zygopetalum maculatum* and *Asteraceae* sp., both positively associated with this axis, while *Gaylussacia densa* was negatively correlated. Competitiveness (C) and leaf area (LA) had a considerable contribution to the first two axes; however, they had the greatest contribution in the third axis (Dim3) (Fig. 2b) where, together with plant height, which was the variable that

mostly contributed to this axis. *Acianthera teres* was the species that stood out the most, with a highly negative score.

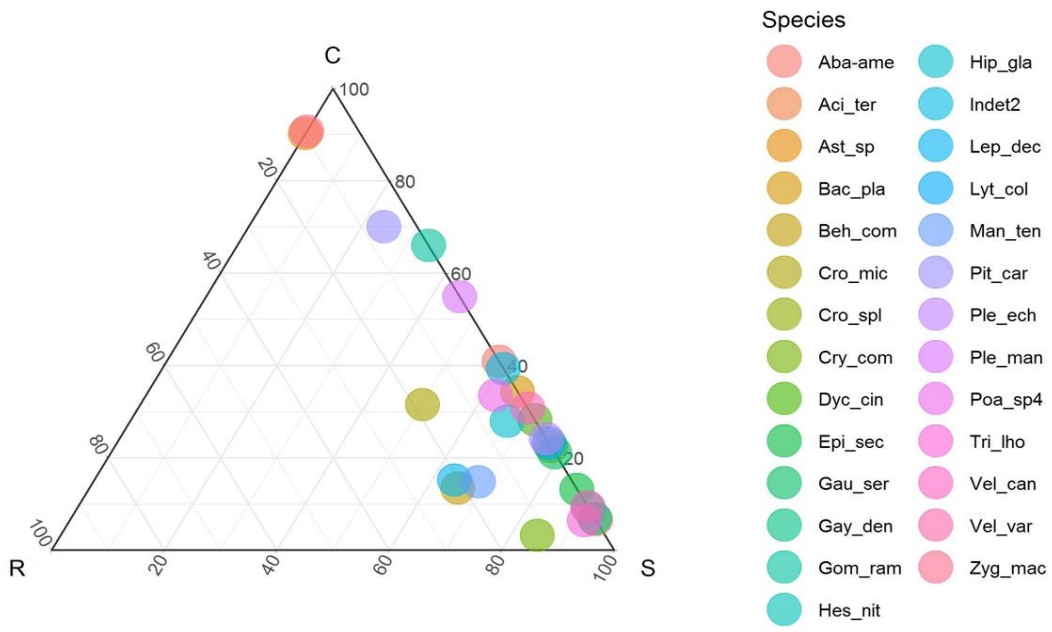

Figure 1: CSR strategies of species in Pedra do Pato Mountain, in Serra do Brigadeiro State Park, Minas Gerais - Brazil.

3.2. Topography-driven soil availability

The PCA of topographic variables revealed the presence of a soil gradient along the sampled area in Pedra do Pato. The three topographic variables were well represented by the first dimension (Dim1), which explained 62.97% of the total variation in the data. Because of the high explanatory power of this dimension, it was retained as a single variable, the principal component 1 (PC1). All variables had similar contributions to this axis, but rock exposure explained the higher proportion of it, with 37.25% of the explanation. Slope explained 32.65% of the variation in PC1, being positively correlated with this axis, together with rock exposure. Soil depth was negatively correlated to PC1, with a contribution of 30.10%. Soil availability was then higher at lower PC1 values and lower at higher PC1 values. Three different habitats with high species turnover were observed along the altitudinal gradient (Chapter 1): the top of the peak, associated with negative values of PC1; the upper slope, with higher altitudes and positive values of PC1; the bottom slope; with lower altitude and intermediary to positive PC1 values.

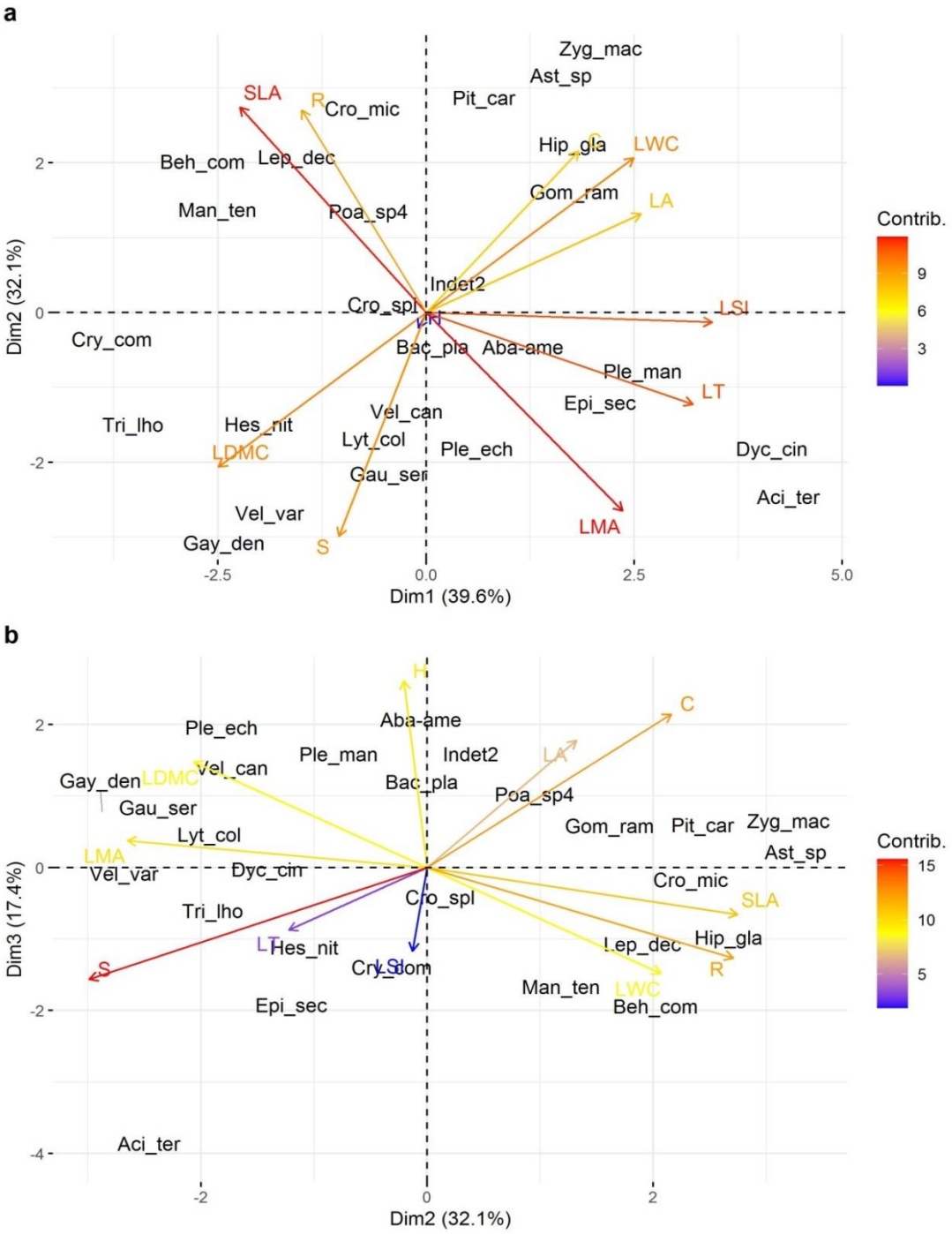

Figure 2. Multidimensional trait space of species in Pedra do Pato Mountain. (a) Biplot of the first and second components of species' strategies. (b) Biplot of the first and third component. Arrows represent the direction of trait vectors (see Table S1 to check the variables' names). Colours show the contribution of each trait.

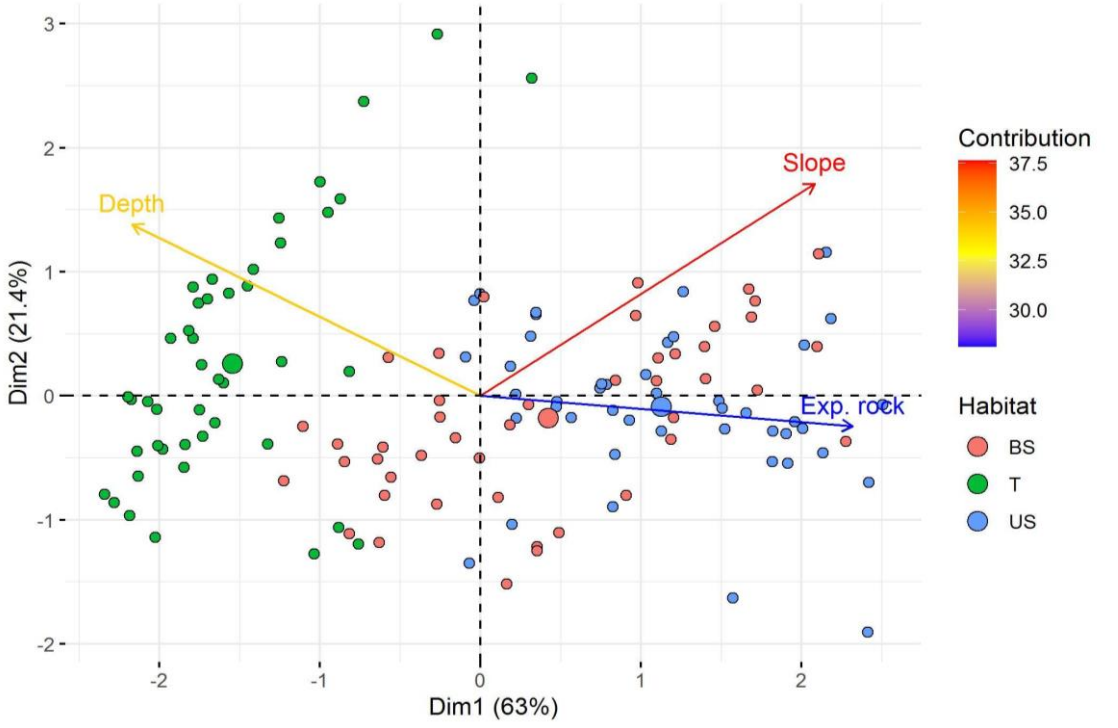

Figure 3: Topography-driven soil availability in Pedra do Pato. Points indicate the plots and the colours indicate the different habitats found: BS, bottom slope; T, top; US, upper slope. Arrows indicate the vectors of the environmental variables and the contribution of each to the variation explained by the first two dimensions (Contrib.).

3.3. Across habitats filtering

The effect sizes of trait variance and FRic for across-habitat environmental filtering showed a strong response to the predictors (Table 1). The predictive power of the models was higher than 20%, with models for FRic, var-LSI, var-LWC and var-LDMC reaching the highest variance explained ($r^2 > 0.6$). Elevation showed a highly significant effect on FRic and the variance of LT, LSI, LA, LMA, SLA, LDMC, and R-strategy, causing a reduction in functional space along the altitudinal gradient. The decrease of soil availability – measured by PC1 – also had a strong contribution to the reduction in functional space, having a positive relationship with the variance in LT, LSI, LA, LDMC, and the C- and S-strategies. Density had a negative, but weaker, restricting effect on trait space, reducing FRic and the variance in SLA and LMA. Effect sizes predicted by the models were in general positive, reaching negative values just under high elevation and low PC1 values or high elevation and high densities (Fig. 4). Plant height was the only trait that didn't show any response of variance

inside the community to the predictors. However, all effect sizes predicted by the model were negative, showing a convergence pattern for height inside all communities (Fig. S1f).

The models for effect sizes of community trait means had a weaker predictive power ($r^2 < 0.6$), showing many significant interaction effects (Table 2). The elevation caused an increase in the mean-H and mean-C, and a decrease in mean-LT. The only trait that was influenced by the PC1 as a main effect predictor was LT, which presented an increase with increasing PC1. Density had only negative effects, causing a reduction in the means of LT, LSI, and LA. The interaction between elevation and PC1 had a negative effect on mean-LT, -LWC and -LSI, while its effect was positive on LDMC, and SLA. The three-way interaction between elevation, density, and PC1 had negative effects on LA and C-strategy. No significant effect was found for elevation-density and density-PC1 interactions on any trait. Mean-LT showed more positive effect sizes under low PC1, showing increasing effect sizes moving upwards in the mountain (Fig. 5a). However, with high density, effect sizes were negative at higher elevations while they stayed positive at lower elevations (Fig. 5b). SLA moved from negative to positive effect sizes at higher elevations in response to PC1, but decreased at lower elevations, moving from zero to negative (Fig. 5c). Predicted effect sizes of mean-H went from highly negative at lower elevations to closer to zero at higher elevations, achieving positive values with increasing density (Fig. 5d). Mean-LSI also decreased with density, showing a very similar response to mean-LT under lower densities (Fig. S2a-b). Mean-LWC tended from negative to positive effect sizes in response to increasing PC1 at a lower elevation, but remained close to zero at a higher elevation (Fig. S2c). Mean-LDMC had a very similar, but mirrored, response, showing positive values at lower elevation and PC1 values (Fig. S2d). Furthermore, LA and C-strategy, under lower densities, presented highly positive effect sizes when PC1 and elevation were high, as well as when elevation and PC1 were low (Fig. S2e, h). Increasing density caused the same pattern observed for mean-LSI on mean-LA at the same conditions (Fig. S2f). The response of mean-C under high densities was also similar but showed mostly negative values along the whole altitudinal and topographic gradient (Fig. S2i).

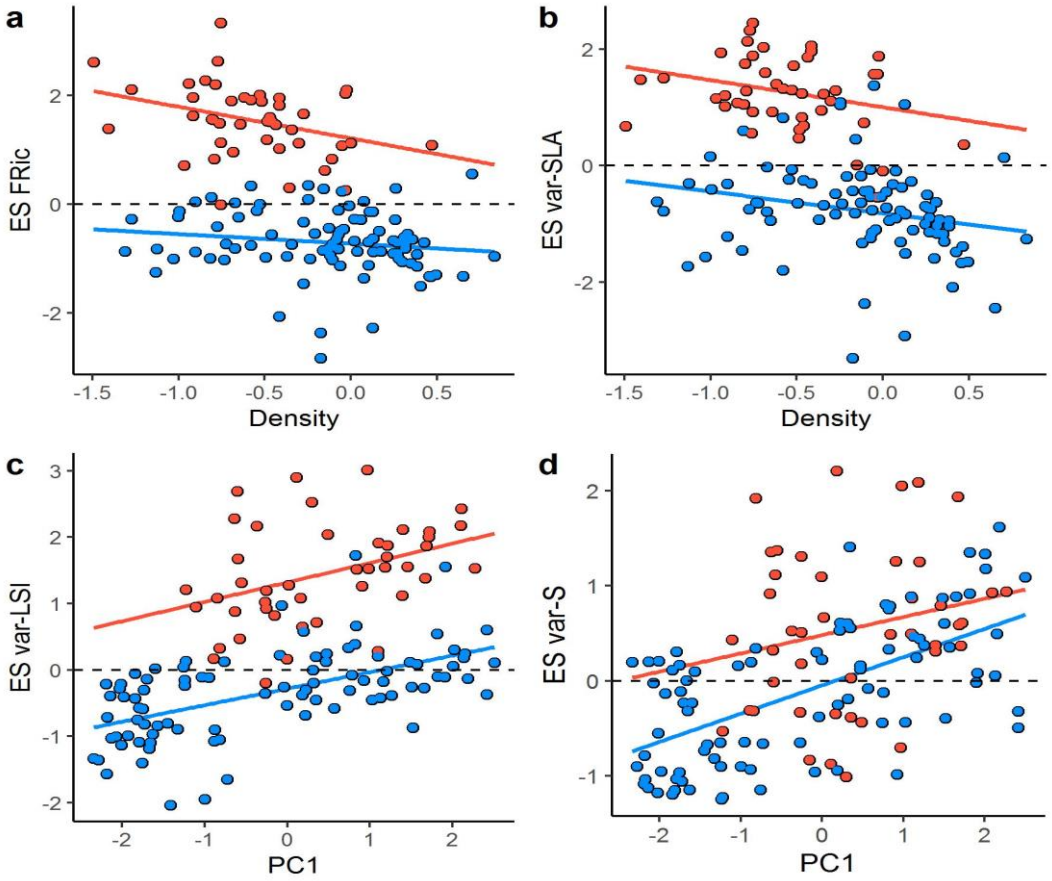

Figure 4. Partial residual plots showing the effects of environmental filters across habitats on the effect sizes (ES) of functional richness (a), variance in specific leaf area (b), leaf succulence index (c), and S-strategy (d). Conditional effects of elevation are shown in blue for high elevation and in red for low elevation. PC1 and density were set to their median values for plots *a* and *b*, and *c* and *d,* respectively. The dashed line marks the effect sizes = 0, which represents an absolutely random assembly. See Table 1 to check for the significance of predictors.

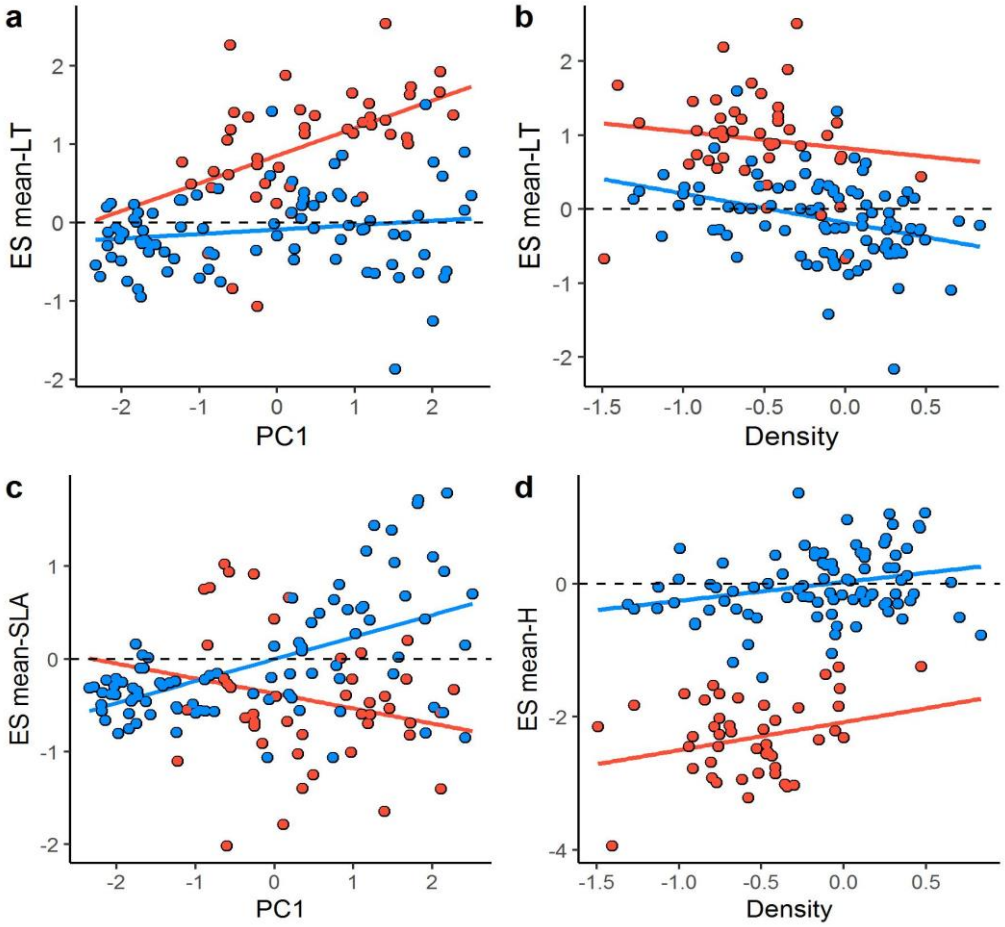

Figure 5. Effects of environmental filters across habitats on effect sizes (ES) of mean leaf thickness (a-b), specific leaf area (c), and plant height (d). Conditional effects of elevation are shown in blue for high elevation and in red for low elevation. Density and PC1 were set to their median values for plots *a* and *c*, and *b* and *d,* respectively. The dashed line marks the effect sizes = 0, which represents an absolutely random assembly. See Table 1 to check for the significance of predictors.

3.4. Species abundance at habitat level

The models for species abundance at habitat level had lower predictive power than those obtained for environmental filtering, with the exception of FDis, which presented a coefficient of determination of 0.60 (Table 2). The power of explanation was smaller than 40% for all models of the weighted variance and smaller than 28% for models of CMW. Elevation had an important role in structuring the diversity of strategies that co-occur inside the plots, causing a strong decrease in FDis ($p < 0.001$), and a weaker decrease in CWV-LDMC, -LSI, and -LA ($p < 0.05$). Otherwise, elevation also caused an increase in the

weighted means of C and SLA, concurrently with a decrease in S. PC1 had a strong influence on FDis, CWV-LDMC,-LSI, CWV-H, -LT, -LA, and -R ($p < 0.01$), leading to an increase in the first ones and a decrease in the last one. Furthermore, PC1 also caused an increase in the weighted means of plant height. No significant effect of density and the interactions among predictors was found for the weighted variance of any trait. However, density had a negative main effect, as well as a negative interaction effect with PC1 on weighted means of LA. Additionally, negative density-elevation and positive elevation-PC1 interaction effects occurred for weighted means of LA and C. The elevation-PC1 interaction also had a negative effect on the weighted means of S.

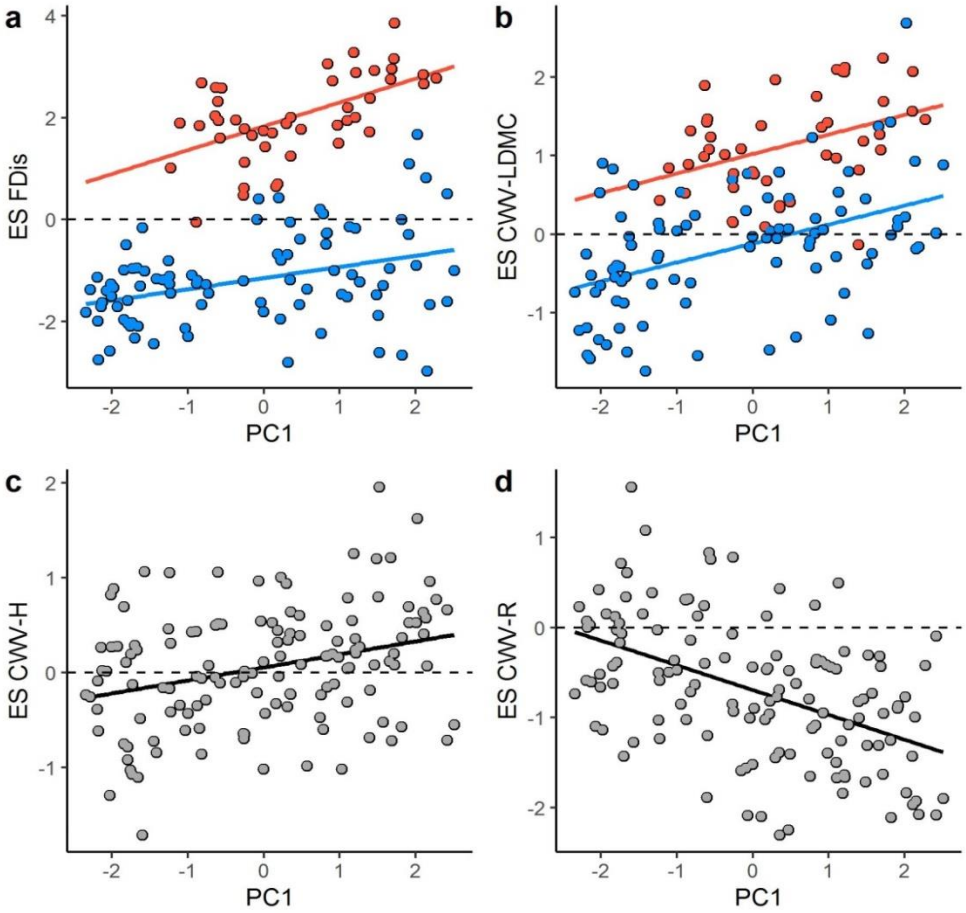

Figure 6. Partial residual plots showing habitat level effects of environmental variables on effect sizes of functional dispersion (a) and community weighted variances of leaf dry matter content (b), plant height (c), and R-strategy (d). Blue shows the conditional effects for high elevation, and red for low elevation. Non-significant results for altitude are shown in gray. Cover density was set to its median value for all plots. The dashed line marks the effect sizes = 0, which represents an absolutely random assembly. See Table 2 to check for the significance of predictors.

The predicted effect sizes of FDis were negative at higher elevations and highly positive at lower elevations (Fig. 6a). Effect sizes of CWV-LDMC were positive along most of the gradient but became negative at higher elevations and low PC1 values (Fig. 6b). A shift from negative to positive effect sizes was predicted by CWV-H (Fig. 6c), with increasing PC1 values but varying very close to the zero line. CWV-R tended to zero with lower PC1 values and became more negative the higher the PC1 values. ES of CWV-LA were positive at lower elevations, tending to zero as higher the elevation was (Fig. S3e). CWV-LSI and CWV-LWC presented similar patterns to CWV-LDMC, while CWV-LT responded similarly to CWV-H (Fig. S3). Predictions of the effect sizes for weighted means of H tended to be zero with low PC1 and decreased with high PC1 and low density (Fig. 7a). S-strategy showed positive effect sizes at lower elevations, where it increased with PC1 (Fig. 7b). However, at higher elevations, it went from positive to negative ES with increasing PC1. CWM of R was negative along the altitudinal gradient, tending to zero at higher elevations (Fig. 7c). Effect sizes of CWM-LA and C-strategy were negative at lower elevations, decreasing with PC1, but increasing with PC1 at higher elevations (Fig. S4) Low density favoured higher LA and C values at higher elevations, accentuating their increase with PC1, showing positive effect sizes at extreme values of this variable.

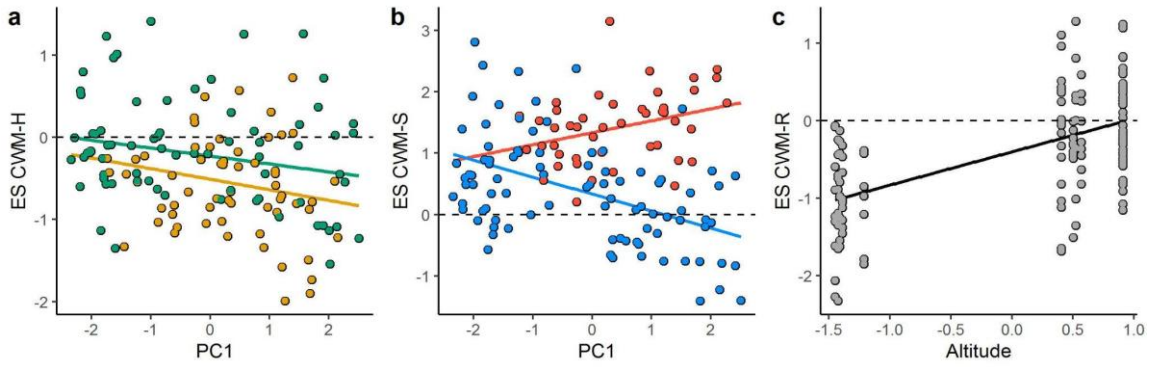

Figure 7. Conditional plots showing habitat level effects of environmental variables on effect sizes of community weighted means of plant height (a), S-strategy (b), and R-strategy (c). Conditional effect of density is shown in green for high density and yellow for low density in a. Conditional effects of elevation are shown in blue for high elevation and in red for low elevation when its effect was significant, and grey for median elevation, in plots where its effect was not significant. The dashed line marks the effect sizes = 0, which represents an absolutely random assembly. See Table 2 to check for the significance of predictors.

Table 1: Models' estimates and coefficients of determination for the across-habitats environmental filtering hypothesis. Significant estimates are in bold and the significance levels were represented with asterisks (*p ≤ 0,05, **p ≤ 0,01, ***p ≤ 0,001). Marginal R^2 (R^2_{mar}) is the coefficient of determination of the fixed factors, while conditional R^2 (R^2_{cond}) is the coefficient of determination of the entire model, considering the fixed and random effects.

Distribution measure	Effect size	Intercept	Elevation	Density	PC1	Alt*Den	Alt*PC1	Den*PC1	Alt*Den* PC1	R^2_{mar}	R^2_{cond}
Variance	FRic	0.02	**-0.84*** **	**-0.35***	0.13	0.18	0.05	0.18	-0.08	0.56	0.80
	LT	0.05	**-0.48****	-0.25	**0.24****	0.06	-0.01	0.1	0.01	0.49	0.62
	LSI	**0.31***	**-0.69*** **	-0.18	**0.28*** **	0.01	-0.01	0.04	0.05	0.63	0.71
	LWC	**0.85*** **	**-0.82*** **	-0.22	**0.25****	-0.12	0.18	-0.06	0.14	0.63	0.76
	LDMC	**0.85*** **	**-0.82*** **	-0.22	**0.25****	-0.12	0.18	-0.06	0.14	0.63	0.76
	LA	**0.29***	**-0.49*** **	-0.03	0.11	0.12	0.07	0.11	-0.07	0.47	0.67
	SLA	-0.21	**-0.8****	**-0.41***	0.16	0.12	-0.11	0.18	-0.18	0.45	0.74
	LMA	-0.12	**-0.78****	**-0.42***	0.16	0.05	-0.12	0.15	-0.22	0.43	0.71
	H	**-0.62*** **	-0.15	0.11	0.02	-0.02	-0.03	0.04	-0.01	0.09	0.44
	C	-0.05	-0.23	-0.06	**0.22****	0.02	0.03	0.05	-0.07	0.28	0.57
	S	0.1	-0.26	-0.26	**0.26****	-0.11	0	0.01	-0.21	0.29	0.42
	R	**-1.01*** **	**-0.32****	0.06	-0.03	0.06	0.05	0.05	0.03	0.27	0.55
Mean	LT	0.2	**-0.42****	**-0.33***	**0.2***	-0.06	**-0.16***	0.1	-0.15	0.36	0.63
	LSI	0.01	-0,30	**-0.3***	0.12	-0.06	**-0.23****	0.08	-0.19	0.30	0.57
	LWC	-0.2	0.12	-0.24	0.13	-0.12	**-0.17***	0.05	-0.23	0.05	0.54

	LDMC	0.2	-0.12	0.24	-0.1	0.12	**0.17***	-0.05	0.23	0.05	0.54
	LA	0.15	-0.11	**-0.38****	0.13	-0.22	-0.01	-0.05	**-0.3***	0.10	0.69
	SLA	-0.13	0.15	0.05	0.06	-0.04	**0.18***	-0.08	0.04	0.10	0.49
	LMA	0.13	-0.25	-0.08	-0	0.04	-0.17	0.1	-0.05	0.13	0.47
	H	**-0.79*****	**0.91*****	**0.33***	-0.1	-0.05	-0.03	0.07	-0.09	0.59	0.86
	C	-0.18	**0.31***	-0.28	0.05	-0.22	0.03	-0.12	**-0.25***	0.25	0.46
	S	**0.52****	-0.18	0.25	-0.1	0.14	-0.05	0.13	0.22	0.09	0.54
	R	**-0.42***	-0.34	-0.02	0.06	-0.02	0.14	-0.04	0.02	0.20	0.75

Table 2: Models' estimates and coefficients of determination for habitat-level effects of environmental factors on species abundance. Significant estimates are in bold and the significance levels were represented with asterisks (*p ≤ 0,05, **p ≤ 0,01, ***p ≤ 0,001). Marginal R^2 (R^2_{mar}) is the coefficient of determination of the fixed factors, while conditional R^2 (R^2_{cond}) is the coefficient of determination of the entire model, considering the fixed and random effects.

Distribution measure	**Effect size**	**Intercept**	**Elevation**	**Density**	**PC1**	**Alt*Den**	**Alt*PC1**	**Den*PC1**	**Alt*Den* PC1**	**R^2_{mar}**	**R^2_{cond}**
Weighted variance (CWV)	FDis	-0.05	**-1.25*****	-0.31	**0.34****	0.14	-0.09	0.1	0.07	0.60	0.83
	LT	-0.02	-0.08	-0.07	**0.21****	-0.03	-0.14	0.08	-0.06	0.12	0.40
	LSI	0.17	**-0.29***	-0.07	**0.27****	-0.06	-0.12	0.06	-0.04	0.31	0.44
	LWC	0.26	**-0.5***	-0.28	**0.26****	-0.03	0.03	0.07	0.14	0.40	0.68
	LDMC	0.26	**-0.5***	-0.28	**0.26****	-0.04	0.03	0.07	0.14	0.40	0.68
	LA	**0.37****	**-0.35***	0.16	-0.09	0.17	0.02	0.04	0.13	0.22	0.44

	SLA	-0.08	-0.09	-0.15	0.03	-0.3	-0.04	-0.02	-0.01	0.02	0.41
	LMA	0.03	-0.14	-0.17	0.05	-0.36	-0.08	0.02	-0.09	0.03	0.41
	H	0.09	-0.08	-0.02	**0.21****	0.03	-0.14	0.12	-0.2	0.10	0.38
	C	-0.22	-0.07	0.02	0.11	0.29	-0.06	0.06	0.03	0.13	0.42
	S	**-0.32***	-0.13	-0.07	0.13	0.2	-0.01	0.03	-0.01	0.13	0.35
	R	**-0.66*****	0.02	0.15	**-0.26****	0.07	0.04	0.02	0.26	0.14	0.36
Weighted mean (CWM)	LT	-0.08	-0.22	-0.04	0.1	-0.09	-0.08	-0.04	-0.08	0.10	0.50
	LSI	-0.16	0.01	-0.05	0.08	-0.1	-0.1	-0.01	-0.04	0.03	0.54
	LWC	**-0.36***	0.29	-0.05	0.06	-0.1	-0.03	-0.09	0.03	0.11	0.61
	LDMC	**0.36***	-0.28	0.05	-0.06	0.1	0.03	0.09	-0.03	0.11	0.61
	LA	**-0.45***	0.06	-0.08	0.09	**-0.19***	0.14	**-0.13***	-0.08	0.08	0.56
	SLA	-0.12	**0.32***	-0.07	-0.02	0.06	0.06	-0.08	0.1	0.11	0.42
	LMA	0.12	-0.3	0.06	0.03	-0.08	-0.05	0.07	-0.1	0.10	0.42
	H	-0.19	-0.34	**0.18***	**-0.17***	-0.06	0.12	0.04	-0.04	0.12	0.52
	C	**-0.48*****	**0.37****	-0.09	0.07	**-0.16***	**0.2***	-0.09	-0.05	0.26	0.38
	S	**0.72*****	**-0.44*****	0.13	-0.1	0.12	**-0.2****	0.09	0.03	0.28	0.38
	R	**-0.39****	**0.42*****	-0.07	0	0	0.06	-0.05	0.1	0.23	0.38

4. DISCUSSION

The species pool of Pedra do Pato consisted mainly of pure stress-tolerant species, which was expected because of the harsh conditions found in high elevation areas, such as the poor soil, high radiation, strong wind, and colder temperatures (Negreiros et al. 2014, de Paula et al. 2015, Matos et al. 2021). Additionally, the competitive dimension had a great contribution to the strategy spectrum found, as observed for other *campos de altitude* and *Páramos* sites (Christmann et al. 2021, Cruz and Lasso 2021, Matos et al. 2021). The presence of so many competitive and competitive/stress-tolerant species might be related to the high precipitation during the rainy season and the presence of fog all over the year (Safford 1999, Assis and de Mattos 2016), and it is an indicator of more productivity in comparison with the high elevation formations of central Brazil, like the *campos rupestres*, composed primarily of more stress-tolerant species (Negreiros et al. 2014). The PCA analysis integrating more ecophysiological traits revealed the importance of other dimensions of strategy variation among the species in the mountain's pool. The higher variation explained by the water-storage axis emphasizes the importance of different drought-resistance strategies, which are expected to have a critical role in species survival under drought events (Griffiths and Males 2017, Matos et al. 2021, Porembski et al. 2021). The independence of this dimension from carbon-use strategies highlights that drought-resistance strategies do not necessarily relate to plant economy, as discussed by Males (2017), and is shown in other studies in tropical mountains, although not discussed by the authors (Cruz and Lasso 2021, Matos et al. 2021). Interpreting the first and the second axis together, we can disentangle species into 4 different strategies: more acquisitive species with smaller leaves and low leaf water storage investment (top left corner of Fig. 2a) - which might be related to resprouting ability after the dry season, like *Mandevilla tenuifolia* (J.C.Mikan) Woodson (Caiafa and Silva 2005); more acquisitive species with bigger leaves and higher leaf succulence - composed mainly by orchids and bromeliads, species known to have adaptations for absorbing atmospheric moisture (Silva et al. 2006, Matos et al. 2022); highly conservative species, with small leaves and higher leaf dry matter content - traits characteristics from drought-tolerant species; and highly conservative species with bigger and highly succulent leaves - typical traits of drought avoidance strategies (Griffiths and Males 2017).

Despite the small altitude gradient, elevation was the main driver of strategy selection in the mountain. High altitude plots presented more restricted assemblies when the whole functional space was considered as well as when traits were considered apart. These results

corroborate previous observations using functional and phylogenetic approaches in the same mountain range (Neri et al. 2016, Gastauer et al. 2020). However, the effects of elevation on mean trait values were quite different from what was expected and were highly dependent on interactions with other predictors. Elevation alone selected for taller plants with thinner leaves and intermediately conservative species, also with intermediary values of leaf water storage. Although these results apparently contradict the literature (Scherrer et al. 2019, Thakur and Chawla 2019), they can be explained by the differences in scale. Long altitudinal gradients reflect mostly variations in temperature, irradiation, and air pressure (Rahbek et al. 2019), which were not captured by the small gradient considered here. Alternatively, increasing elevation in this mountain might reflect changes in exposure, like increased cloud interception and wind incidence, which cause variation in microclimatic conditions (Sparacino et al. 2020). Evidence of this hypothesis can be found in surveys made on other peaks in the same mountain range, but with lower maximum elevations (Caiafa and Silva 2007, Neri et al. 2016, Campos et al. 2021). Despite the differences in elevation, the gradient between the lower parts until the top of each peak had similar patterns of species composition. Although climatic variables were not collected, the presence of more xeromorphic species at lower elevations suggests the presence of a moisture gradient, with higher plots probably subjected to higher atmospheric moisture incomes.

The soil availability gradient did not significantly affect the overall trait space of communities but had a strong effect on the variance of traits related to drought strategies and on the variance of C and S dimensions from the CSR triangle. Plots with bigger soil deposition had species with more restricted trait values than those with little soil available, which agrees with the hypothesis of increased competitive exclusion with productivity (Grime 2006, Mudrák et al. 2016). However, which mean trait values are favoured under higher soil availability depended on the elevation and resource depletion. For instance, in plots at higher elevations, more conservative species are favoured probably due to the strong winds (Sparacino et al. 2020). Nonetheless, the higher cloud moisture interception associated with a greater amount of soil may increase productivity, favouring species with less investment on drought resistance, which exclude species with different strategies (Alcantara et al. 2015). Alternatively, in plots with higher soil availability but lower elevation - which are expected to experience drier conditions - more drought-tolerant species are favoured. These results highlight the fact that no single strategy could allow higher competitive ability under all environmental conditions (Mouillot et al. 2007, Enquist et al. 2015).

Higher densities also caused a reduction in the functional space of communities, but this reduction was caused mainly by its effects on traits related to resource economy (SLA and LMA). As pointed out for the effect of soil availability, the mean strategy selected by increased densities depended on other factors. For mean-SLA and -LMA, for example, no effect of cover density was found, which emphasizes that the outcome of competitive interactions is highly dependent on the local conditions. The species excluded by higher cover densities were determined by the interaction of elevation and soil availability. The effects of cover density on mean-LT, -LSI, and -LA might be related to reductions in the fitness of these species under more intense resource depletion and high shading. The energetic cost of producing large and succulent leaves might be too high for succulent species to handle under high resource depletion rates (Milla and Reich 2007, Díaz et al. 2016). Meanwhile, as less light achieves the mesophyll of succulent plants, shade caused by the neighbours is a problem for them, due to decreased photosynthetic rates (Griffiths and Males 2017, Males 2017). Shading can also explain the increased vegetative height, since a taller body enhances the ability to compete for light (Alcantara et al. 2015, Thakur and Chawla 2019). However, no reduction of variance in LT, LSI, and H was observed, suggesting that light competition is not strong enough to filter out more succulent and smaller species.

Our results showed that, at habitat level, limiting similarity is an important process that drives community assembly in campos de altitude. At lower elevations and low soil availability, better fitness is achieved by species with the most divergent strategies, resulting in higher functional dispersion. This response was caused mainly by high divergence in drought-resistant strategies among the most abundant species. Although it seems to contradict the theoretical predictions that divergence increases in broader environments - since water is apparently a more limiting resource under these conditions - it's important to notice that more drought-resistant species can obtain resources from different sources and at different times (Dawson et al. 2012, Matos et al. 2022). Atmospheric moisture can be an important water source for orchids and bromeliads like *Dyckia cinerea* Mez during the dry season (Benzing et al. 1976), when water becomes more limited, as *Vellozia variegata* Goethart & Henrard and *Trilepis lhotzkiana* Nees ex. Arn. are desiccation-tolerant species (Porembski et al. 2021), able to cope with dehydration. For these species, therefore, dry environments are broad enough to support different strategies with high abundance (Pastore et al. 2021, Matos et al. 2022). However, as both elevation and soil availability increase, which creates more restricted assemblies, coexistent species are not different enough for diverging in resource use to compensate for fitness differences between them (Pastore et al. 2021) - which is supported by

the negative effect sizes for FDis and CWV at these conditions. The result is communities dominated by a single strategy that allows better fitness, while species with other trait values remain with low abundance. The permanence of this subordinate species in the community might be, nonetheless, determined by environmental fluctuations (Chesson 2000, 2008), as the marked precipitation seasonality of the *campos de altitude* (Safford 1999). Climate change is expected to modify this typical regime, causing an increase in regional scale droughts, which can disturb the stable coexistence between dominant and subordinate species in these ecosystems (Assis and de Mattos 2016, Scarano et al. 2016, Matos et al. 2021).

Leaf economy strategies did not show any response in weighted variance to the predictors, which suggests that these traits are evenly distributed along the environmental gradients sampled. Nevertheless, CWM of C and S strategies had a strong effect from the interaction between elevation and soil availability, with better fitness always associated with high stress-tolerant strategy - with the exception of the high elevation outcrops, where dominance was achieved by species with the mean local trait optimum. The lack of response in CWV but in CWM occurred due to the high number of S-strategists where it is dominant, which results in a flatter distribution of abundances among the species. R strategy was the only trait that responded in an opposite way to soil availability, with strong convergence at more soil-limited plots. Under this condition, the mean plot R-value is dominant at higher elevations, while lower values provide greater fitness differences at lower elevations, which highlights the disadvantage of this strategy under harsh conditions. The great R^2 of models for CSR strategies highlight that greater fitness is not provided by a single trait, but by a combination of different traits, since CSR strategies incorporate different trade-offs in a single variable (Kraft et al. 2015b, Pistón et al. 2019).

Smaller plants had better fitness than the taller ones at lower elevations and lower soil availability. Even where the environment was supposed to offer better conditions and for them to dominate, there were no indications of better fitness associated with taller plants. The nutrient limitation and the altitude conditions - like wind and lower air pressure - make the cost of investing resources in vertical growth too high to exist any strong compensation for capturing light before the neighbours (Wright et al. 2004, Onoda et al. 2017). However, although no evidence of better competitive ability was found for taller plants among coexisting species, the effect sizes of variance in height for the whole peak were highly negative along the gradient. This indicates that plants with height too far from the optimal value (i.e., herbs and rosettes at lower elevations or forbs and shrubs at higher elevations), are

competitively excluded along the whole environmental gradient, resulting in a highly homogeneous community with regard to vegetative height.

Models for variance and weighted variance presented a higher explanation power than those for mean and weighted means. The whole form of a species depends on many traits that can vary independently as far as biophysical and phylogenetic constraints allow that (Grime 1977, Wright et al. 2004, Díaz et al. 2016). Each response in the community mean traits to the environment reflects just part of the whole architecture of co-occurring plants' relationship with abiotic and biotic conditions. This results in small explanation power of species response (Van Cleemput et al. 2021), unless a single dimension of functional space is responsible to confer high adaptability and provide higher fitness, as observed for LT, LSI, H, C-strategy and R-strategy in the first case and CSR strategies in the latter. However, the exclusion of species with a non-suitable trait value, for example, can restrict the range of variation of that specific trait but also other traits' ranges if they are correlated or even by chance (Agrawal et al. 2010). So the multidimensional information carried by the variance of a single trait increases its ability to explain patterns of functional response to the environment. Therefore, we highlight the importance of considering multiple trait measures to detect the multidimensionality of species niches and to investigate the correlations between them to detect their adaptive and fitness characters (Kraft et al. 2015b, Pistón et al. 2019, Sosiak and Barden 2021). The greatest power of explanation of the predictors on FDis, FRic, and the CWM of CSR strategies also shows the advantage of considering multidimensional measures or whole plant architecture to better understand community patterns.

Our results show that biotic interactions have a critical role in trait-driven species distribution and coexistence in a mountain ecosystem. The increased resource depletion by competitors and the presence of species with a strategy that allows them to monopolize resources might filter out species not able to cope with biotic-induced stress, which results in convergent strategies. Furthermore, our results suggest a strong dependence of mountain species on different water sources especially the ones inhabiting rock outcrops. Decreasing fog events will narrow the environment to the point that diverging species will no longer be able to co-occur (Matos et al. 2021, 2022, Pastore et al. 2021). With less moisture entering the environment opportunistic acquisitive plant species may also be extinct, causing a strong biodiversity loss (Dawson et al. 2012, Rosado and de Mattos 2017).

5. CONCLUSION

Understanding the main drivers of species distribution and coexistence is a key step to enhancing our ability to predict the effects of human-induced global changes on mountain ecosystems. Our study shows the main strategies that co-occur along a mountain gradient in the *campos de altitude* vegetation in Brazil and how the environment shapes their distribution and coexistence. Although the species composition for the whole mountain was highly restricted concerning the CSR strategies, they presented a great diversity in alternative strategies that were not just related to carbon use trade-offs. The drought resistance strategies had the highest variation between species and were strongly connected with the environmental gradients observed. High niche partitioning in water sources could explain species coexistence in this environment, especially in the outcrops. Therefore, change in fog and precipitation regimes can probably disrupt species coexistence and cause diversity loss in these ecosystems. Our results also highlight the importance of the interaction between abiotic and biotic variables on community assembly. This reflects not just in species occurrence, but also in their abundance, indicating that no trait value could offer better competitive ability in every site. Knowing the key traits related to dominance can help the predict the outcome of the shifts in species distribution due to climate change.

6. REFERENCES

Agrawal, A. A., J. K. Conner, and S. Rasmann. 2010. Tradeoffs and Negative Correlations in Evolutionary Ecology. Page *in* W. E. and J. L. Michael Bell, Douglas Futuyma, editor. Evolution since Darwin: the first 150 years. SinauerAssociates, Inc., Sunderland.

Alcantara, S., R. de Mello-Silva, G. S. Teodoro, K. Drequeceler, D. D. Ackerly, and R. S. Oliveira. 2015. Carbon assimilation and habitat segregation in resurrection plants: A comparison between desiccation- and non-desiccation-tolerant species of Neotropical Velloziaceae (Pandanales). Functional Ecology 29:1499–1512.

Assis, M. V., and E. A. de Mattos. 2016. Vulnerabilidade da vegetação de campos de altitude às mudanças climáticas. Oecologia Australis 20:24–36.

Barbosa, N. P. U., and G. W. Fernandes. 2016. Rupestrian Grassland: Past, Present and Future Distribution. Pages 531–544 Ecology and Conservation of Mountaintop Grasslands in Brazil.

Barton, K. 2009. Mu-MIn: Multi-model inference. R Package Version 0.12.2/r18.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1–48.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters 15:365–377.

de Bello, F., C. P. Carmona, A. T. C. Dias, L. Götzenberger, M. Moretti, and M. P. Berg. 2021. Community Metrics. Handbook of Trait-Based Ecology From Theory to R Tools. Cambridge University Press, Cambridge.

de Bello, F., J. N. Price, T. Munkemuller, J. Liira, M. Zobel, W. Thuiller, P. Gerhold, L. Götzenberger, S. Lavergne, J. Lepš, K. Zobel, and M. Partel. 2012. Functional species pool framework to test for biotic effects on community assembly. Ecology 93:2263–2273.

Beniston, M. 2003. Climatic change in mountain regions: a review of possible impacts. Climatic Change 59:5–31.

Benites, V. M., C. E. G. R. Schaefer, E. S. Mendonça, and L. Martin Neto. 2001. Caracterização da matéria orgânica e micromorfologia de solos sob Campos de Altitude no Parque Estadual da Serra do Brigadeiro (MG). Revista Brasileira de Ciência do Solo 25:661–674.

Benzing, D. H., K. Henderson, B. Kessel, and J. Sulak. 1976. The Absorptive Capacities of Bromeliad Trichomes. American Journal of Botany 63:1009–1014.

Bernard-Verdier, M., M. L. Navas, M. Vellend, C. Violle, A. Fayolle, and E. Garnier. 2012. Community assembly along a soil depth gradient: Contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. Journal of Ecology 100:1422–1433.

Botta-Dukát, Z. 2018. Cautionary note on calculating standardized effect size (SES) in randomization test. Community Ecology 19:77–83.

Botta-Dukát, Z., and C. Bálint. 2016. Testing the ability of functional diversity indices to detect trait convergence and divergence using individual-based simulation. Methods in Ecology and Evolution 7:114–126.

Breheny, P., and W. Burchett. 2017. Visualization of Regression Models Using visreg. The R Journal 9:56–71.

Bueno de Mesquita, C. P., L. S. Tillmann, C. D. Bernard, K. C. Rosemond, N. P. Molotch, and K. N. Suding. 2018. Topographic heterogeneity explains patterns of vegetation response to climate change (1972 – 2008) across a mountain landscape , Niwot. Arctic, Antarctic, and Alpine Research 50.

Cadotte, M. W., and C. M. Tucker. 2019. Should Environmental Filtering be Abandoned ? Trends in Ecology & Evolution.

Caiafa, A. N., and A. F. da Silva. 2007. Structural analysis of the vegetation on a highland granitic rock outcrop in Southeast Brazil 1 3:657–664.

Caiafa, A. N., and A. F. da Silva. 2005. Composição florística e espectro biológico de um campo de altitude no Parque Estadual da Serra do Brigadeiro, Minas Gerais – Brasil. Rodriguésia 56:163–173.

Callaway, R. M., R. W. Brooker, P. Choler, Z. Kikvidze, C. J. Lortie, R. Michalet, L. Paolini, F. I. Pugnaire, B. Newingham, E. T. Aschehoug, C. Armas, D. Kikodze, and B. J. Cook. 2002. Positive interactions among alpine plants increase with stress. Nature 417:844–848.

Campos, P. V., P. M. Villa, C. Ernesto, G. Reynaud, J. A. Nunes, S. Porembski, and A. V. Neri. 2021. Community composition , beta diversity and structure of high altitude grasslands along an altitudinal gradient in southeastern Beta diversity , community composition and structure of high altitude grasslands along an altitudinal gradient in southeastern B.

Carmona, M. C. P. 2020. Package ‘ DarkDiv .’

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology, Evolution, and Systematics 31:343–366.

Chesson, P. 2008. Quantifying and Testing Species Coexistence Mechanisms. Pages 119–164 *in* F. Valladares, A. Camacho, A. Elosegui, C. Gracia, M. Estrada, J. C. Senar, and J. . Gili, editors. Unity in Diversity: Reflections on Ecology after the Legacy of Ramon Margalef. Fundacion BBVA, Bilbao.

Chesson, P. 2018. Updates on mechanisms of maintenance of species diversity. Journal of Ecology 10:1773–1794.

Christmann, T., and I. O. Menor. 2021. A synthesis and future research directions for tropical mountain ecosystem restoration. Scientific Reports 11:1–17.

Christmann, T., B. H. P. Rosado, G. Delhaye, I. S. Matos, J. S. Drummond, H. L. Roland, Y. C. Moraes, and I. O. Menor. 2021. Functional assembly of tropical montane tree islands in the Atlantic Forest is shaped by stress tolerance , bamboo presence , and facilitation. Ecology and Evolution 11:10164–10177.

Van Cleemput, E., K. Helsen, H. Feilhauer, O. Honnay, and B. Somers. 2021. Spectrally defined plant functional types adequately capture multidimensional trait variation in herbaceous communities. Ecological Indicators 120:106970.

Cordeiro, A. de A. C., and A. V. Neri. 2019. Spatial patterns along an elevation gradient in

high altitude grasslands, Brazil. Nordic Journal of Botany 37:1–10.

Cruz, M., and E. Lasso. 2021. Insights into the functional ecology of páramo plants in Colombia. Biotropica 00:1–17.

Dawson, T. E., E. Nicola, I. Querejeta, C. Moreno-gutie, and C. Moreno-gutie. 2012. Isotopes reveal contrasting water use strategies among coexisting plant species in a Mediterranean ecosystem.

Díaz, S., J. Kattge, J. H. C. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, M. Kleyer, C. Wirth, I. Colin Prentice, E. Garnier, G. Bönisch, M. Westoby, H. Poorter, P. B. Reich, A. T. Moles, J. Dickie, A. N. Gillison, A. E. Zanne, J. Chave, S. Joseph Wright, S. N. Sheremet Ev, H. Jactel, C. Baraloto, B. Cerabolini, S. Pierce, B. Shipley, D. Kirkup, F. Casanoves, J. S. Joswig, A. Günther, V. Falczuk, N. Rüger, M. D. Mahecha, and L. D. Gorné. 2016. The global spectrum of plant form and function. Nature 529:167–171.

Engevix. 1995. Caracterização do meio físico da área autorizada para criação do Parque Estadual da Serra do Brigadeiro: relatório técnico final dos estudos-8296-RE-H4-003/94.

Enquist, B. J., J. Norberg, S. P. Bonser, C. Violle, C. T. Webb, A. Henderson, L. L. Sloat, and V. M. Savage. 2015. Scaling from Traits to Ecosystems : Developing a General Trait Driver Theory via Integrating Trait-Based and Metabolic Scaling Theories. Advances in Ecological Research 52:249–318.

Fernandes, G. W., N. P. U. Barbosa, B. Alberton, A. Barbieri, R. Dirzo, F. Goulart, T. J. Guerra, L. P. C. Morellato, and R. R. C. Solar. 2018. The deadly route to collapse and the uncertain fate of Brazilian rupestrian grasslands. Biodiversity and Conservation 27:2587–2603.

Gastauer, M., J. Thiele, S. Porembski, and A. V. Neri. 2020. How do altitude and soil properties influence the taxonomic and phylogenetic structure and diversity of Brazilian páramo vegetation? J. Mt. Sci:17.

Gotelli, N. J., and W. Ulrich. 2012. Statistical challenges in null model analysis. Oikos 121:171–180.

Griffiths, H., and J. Males. 2017. Succulent plants. Current Biology 27:890–896.

Grime, J. 2001. Plant strategies, vegetation processes, and ecosystem properties. 2nd edition. Wiley, Chichester.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111:1169–1194.

Grime, J. P. 2006. Trait convergence and trait divergence in herbaceous plant communities :

Mechanisms and consequences. Journal of Vegetation Science 17:255–260.

Kearney, M. R., M. Jusup, M. A. McGeoch, S. A. L. M. Kooijman, and S. L. Chown. 2021. Where do functional traits come from? The role of theory and models. Functional Ecology 35:1385–1396.

Kolb, R. M., L. F. A. De Paula, R. Marta, S. Porembski, F. A. O. Silveira, and D. Rodrigo. 2018. Rocks and leaves : Can anatomical leaf traits reflect environmental heterogeneity in inselberg vegetation ? Rocks and leaves : Can anatomical leaf traits re fl ect environmental heterogeneity in inselberg vegetation ?

Köppen, W., and R. Geiger, editors. 1936. Das geographische System der Klimate (1936). Gebrüder Borntl'aeger, Berlin.

Kraft, N. J. B., P. B. Adler, O. Godoy, E. C. James, S. Fuller, and J. M. Levine. 2015a. Community assembly, coexistence and the environmental filtering metaphor: 592–599.

Kraft, N. J. B., O. Godoy, and J. M. Levine. 2015b. Plant functional traits and the multidimensional nature of species coexistence. Proceedings of the National Academy of Sciences of the United States of America 112:797–802.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. lmerTest Package: Tests in Linear Mixed Effects Models. Journal of Statistical Software 82:1–26.

López-Angulo, J., D. S. Pescador, A. M. Sánchez, A. L. Luzuriaga, L. A. Cavieres, and A. Escudero. 2020. Impacts of climate, soil and biotic interactions on the interplay of the different facets of alpine plant diversity. Science of the Total Environment 698:133960.

MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist 101:377–385.

Males, J. 2017. Secrets of succulence. Journal of Experimental Botany 68:2121–2134.

Marks, C. O., M. J. Lechowicz, C. O. Marks, and M. J. Lechowicz. 2006. Alternative Designs and the Evolution of Functional Diversity. The American Naturalist 167:55–66.

Mason, N. W. H., F. de Bello, D. Mouillot, and S. Pavoine. 2013. SPECIAL FEATURE : FUNCTIONAL DIVERSITY A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients 24:794–806.

Mason, N. W. H., D. Mouillot, W. G. Lee, and J. B. Wilson. 2005. Functional richness , functional evenness and functional divergence : the primary components of functional diversity. Oikos 111:112–118.

Matos, I. S., O. Binks, C. B. Eller, B. B. Zorger, P. Meir, T. E. Dawson, and B. H. P. Rosado. 2022. Revisiting plant hydrological niches: the importance of atmospheric resources for ground-rooted plants. Journal of Ecology n/a.

Matos, I. S., C. B. Eller, I. Oliveras, D. Mantuano, and B. H. P. Rosado. 2021. Three eco-physiological strategies of response to drought maintain the form and function of a tropical montane grassland. Journal of Ecology 109:327–341.

Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecology Letters 13:1085–1093.

Milla, R., and P. B. Reich. 2007. The scaling of leaf area and mass: The cost of light interception increases with leaf size. Proceedings of the Royal Society B: Biological Sciences 274:2109–2114.

Mouillot, D., N. W. H. Mason, and J. B. Wilson. 2007. Is the abundance of species determined by their functional traits? A new method with a test using plant communities. Oecologia 152:729–737.

Mudrák, O., Š. Janeček, L. Götzenberger, N. W. H. Mason, J. Horník, I. de Castro, J. Doležal, J. Klimešová, and F. de Bello. 2016. Fine-scale coexistence patterns along a productivity gradient in wet meadows: shifts from trait convergence to divergence. Ecography 39:338–348.

Negreiros, D., S. Le Stradic, G. W. Fernandes, and H. C. Rennó. 2014. CSR analysis of plant functional types in highly diverse tropical grasslands of harsh environments. Plant Ecology 215:379–388.

Neri, A. V., G. R. A. Borges, J. A. A. Meira-Neto, L. F. S. Magnago, I. M. Trotter, C. E. G. R. Schaefer, and S. Porembski. 2016. Soil and altitude drive diversity and functioning of Brazilian Páramos (campo de altitude) . Journal of Plant Ecology 10:rtw088.

Onoda, Y., I. J. Wright, J. R. Evans, K. Hikosaka, K. Kitajima, Ü. Niinemets, H. Poorter, T. Tosens, and M. Westoby. 2017. Physiological and structural tradeoffs underlying the leaf economics spectrum. New Phytologist 214:1447–1463.

Pastore, A. I., G. Barabás, M. D. Bimler, M. M. Mayfield, and T. E. Miller. 2021. The evolution of niche overlap and competitive differences. Nature Ecology and Evolution 5:330–337.

de Paula, L. F. A., D. Negreiros, L. O. Azevedo, R. L. Fernandes, J. R. Stehmann, and F. A. O. Silveira. 2015. Functional ecology as a missing link for conservation of a resource-limited flora in the Atlantic forest. Biodiversity and Conservation 24:2239–2253.

Pérez-Harguindeguy, N., S. Diaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. S. S. Bret-Harte, W. K. K. Cornwell, J. M. M. Craine, D. E. E. Gurvich, C. Urcelay, E. J. J. Veneklaas, P. B. B. Reich, L. Poorter, I. J. J. Wright, Etc., P. Ray, Etc., S. Díaz, S. Lavorel, H. Poorter, P. Jaureguiberry, M. S. S. Bret-Harte, W. K. K. Cornwell, J. M. M.

Craine, D. E. E. Gurvich, C. Urcelay, E. J. J. Veneklaas, P. B. B. Reich, L. Poorter, I. J. J. Wright, P. Ray, L. Enrico, J. G. Pausas, A. C. De Vos, N. Buchmann, G. Funes, F. Quétier, J. G. Hodgson, K. Thompson, H. D. Morgan, H. ter Steege, M. G. A. Van Der Heijden, L. Sack, B. Blonder, P. Poschlod, M. V Vaieretti, G. Conti, A. C. Staver, S. Aquino, and J. H. C. Cornelissen. 2013. New Handbook for standardized measurment of plant functional traits worldwide. Australian Journal of Botany 61:167–234.

Pierce, S., D. Negreiros, B. E. L. Cerabolini, J. Kattge, S. Díaz, M. Kleyer, B. Shipley, S. J. Wright, N. A. Soudzilovskaia, V. G. Onipchenko, P. M. van Bodegom, C. Frenette-Dussault, E. Weiher, B. X. Pinho, J. H. C. Cornelissen, J. P. Grime, K. Thompson, R. Hunt, P. J. Wilson, G. Buffa, O. C. Nyakunga, P. B. Reich, M. Caccianiga, F. Mangili, R. M. Ceriani, A. Luzzaro, G. Brusa, A. Siefert, N. P. U. Barbosa, F. S. Chapin, W. K. Cornwell, J. Fang, G. W. Fernandes, E. Garnier, S. Le Stradic, J. Peñuelas, F. P. L. Melo, A. Slaviero, M. Tabarelli, and D. Tampucci. 2017. A global method for calculating plant CSR ecological strategies applied across biomes world-wide. Functional Ecology 31:444–457.

Pistón, N., F. de Bello, L. Götzenberger, B. H. P. Rosado, E. A. De Mattos, R. S. Gómez, and C. P. Carmona. 2019. Multidimensional ecological analyses demonstrate how interactions between functional traits shape fitness and life history strategies. Journal of Ecology 107:2317–2328.

Porembski, S. 2006. Vegatative Architecture of Desiccation-tolerant Arborescent Monocotyledons. Aliso: A Journal of Systematic and Evolutionary Botany 22:129–134.

Porembski, S., J. Rexroth, K. Weising, L. Bondi, R. Mello-silva, D. C. Centeno, M. N. Datar, A. Watve, A. Thiombano, M. N. Rabarimanarivo, and L. F. A. de Paula. 2021. An overview on desiccation-tolerant mat-forming monocotyledons on tropical inselbergs. Flora 285.

Rahbek, C., M. K. Borregaard, A. Antonelli, R. K. Colwell, B. G. Holt, D. Nogues-bravo, C. M. Ø. Rasmussen, K. Richardson, M. T. Rosing, R. J. Whittaker, and J. Fjeldså. 2019a. Building mountain biodiversity: Geological and evolutionary processes 1119:1114–1119.

Rangel, T. F., N. R. Edwards, P. B. Holden, J. A. F. Diniz-Filho, W. D. Gosling, M. T. P. Coelho, F. A. S. Cassemiro, C. Rahbek, and R. K. Colwell. 2018. Modeling the ecology and evolution of biodiversity: Biogeographical cradles, museums, and graves. Science 361.

Rosado, B. H. P., and E. A. de Mattos. 2017. On the relative importance of CSR ecological strategies and integrative traits to explain species dominance at local scales. Functional

Ecology 31:1969–1974.

Safford, H. D. 1999. Brazilian Páramos II . Macro- and mesoclimate of the *campos de altitude* and affinities with high mountain climates of the tropical Andes and Costa Rica. Journal of Biogeography:713–737.

Safford, H. D. 2001. Brazilian Paramos . III . Patterns and Rates of Postfire Regeneration in the Campos de Altitude. Biotropica 33:282–302.

Scherrer, D., L. Pellissier, A. Guisan, H. K. Mod, P. Vittoz, J. Pottier, A. Litsios, L. Götzenberger, and M. Zobel. 2019. Disentangling the processes driving plant assemblages in mountain grasslands across spatial scales and environmental gradients. Journal of Ecology 107:265–278.

Silva, I. V. da, R. M. S. A. Meira, A. A. Azevedo, and R. M. de A. Euclydes. 2006. Estratégias anatômicas foliares de treze espécies de Orchidaceae ocorrentes em um campo de altitude no Parque Estadual da Serra do Brigadeiro (PESB) - MG, Brasil. Acta Botanica Brasilica 20:741–750.

Silveira, F. A. O., D. Negreiros, N. P. U. Barbosa, E. Buisson, F. F. Carmo, D. W. Carstensen, A. A. Conceição, T. G. Cornelissen, L. Echternacht, G. W. Fernandes, Q. S. Garcia, T. J. Guerra, C. M. Jacobi, J. P. Lemos-Filho, S. Le Stradic, L. P. C. Morellato, F. S. Neves, R. S. Oliveira, C. E. Schaefer, P. L. Viana, and H. Lambers. 2016. Ecology and evolution of plant diversity in the endangered campo rupestre: a neglected conservation priority. Plant and Soil 403:129–152.

Sosiak, C. E., and P. Barden. 2021. Multidimensional trait morphology predicts ecology across ant lineages. Functional Ecology 35:139–152.

Sparacino, J., D. Renison, A. M. Devegili, and R. Suarez. 2020. Wind protection rather than soil water availability contributes to the restriction of high-mountain forest to ravines. New Forests 51:101–117.

Thakur, D., and A. Chawla. 2019. Functional diversity along elevational gradients in the high altitude vegetation of the western Himalaya. Biodiversity and Conservation 28:1977–1996.

Tinti, B. V., C. E. R. G. Schaefer, J. A. Nunes, A. C. Rodrigues, I. F. Fialho, and A. V. Neri. 2015. Plant diversity on granite/gneiss rock outcrop at Pedra do Pato, Serra do Brigadeiro State Park, Brazil. Check List 11.

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-

Bares, T. Chapin, J. H. C. Cornellssen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M. L. Navas, Ü. Niinemets, J. Oleksyn, H. Osada, H. Poorter, P. Pool, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Zhu, L., B. Fu, H. Zhu, C. Wang, L. Jiao, and J. Zhou. 2017. Trait choice profoundly affected the ecological conclusions drawn from functional diversity measures. Scientific Reports 7:1–13.

APPENDIX B: SUPPLEMENTARY MATERIALS

Table S1: Functional traits measured in Pedra do Pato Mountain, Minas Gerais, Brazil.

Functional trait	Abbreviation	Unit
Leaf thickness	LT	mm
Leaf succulence index	LSI	$g_{water}\ dm^{-2}$
Leaf water content	LWC	% (g_{water}/ $g_{fresh\ weight}$)
Leaf dry matter content	LDMC	% ($g_{dry\ weight}$/ $g_{fresh\ weight}$)
Leaf area	LA	mm^2
Specific leaf area	SLA	$mm^2\ mg^{-1}$
Leaf mass per area	LMA	$g\ mm^2$
Vegetative height	H	cm
Competitive strategy	C	%
Stress-tolerant strategy	S	%
Ruderal strategy	R	%

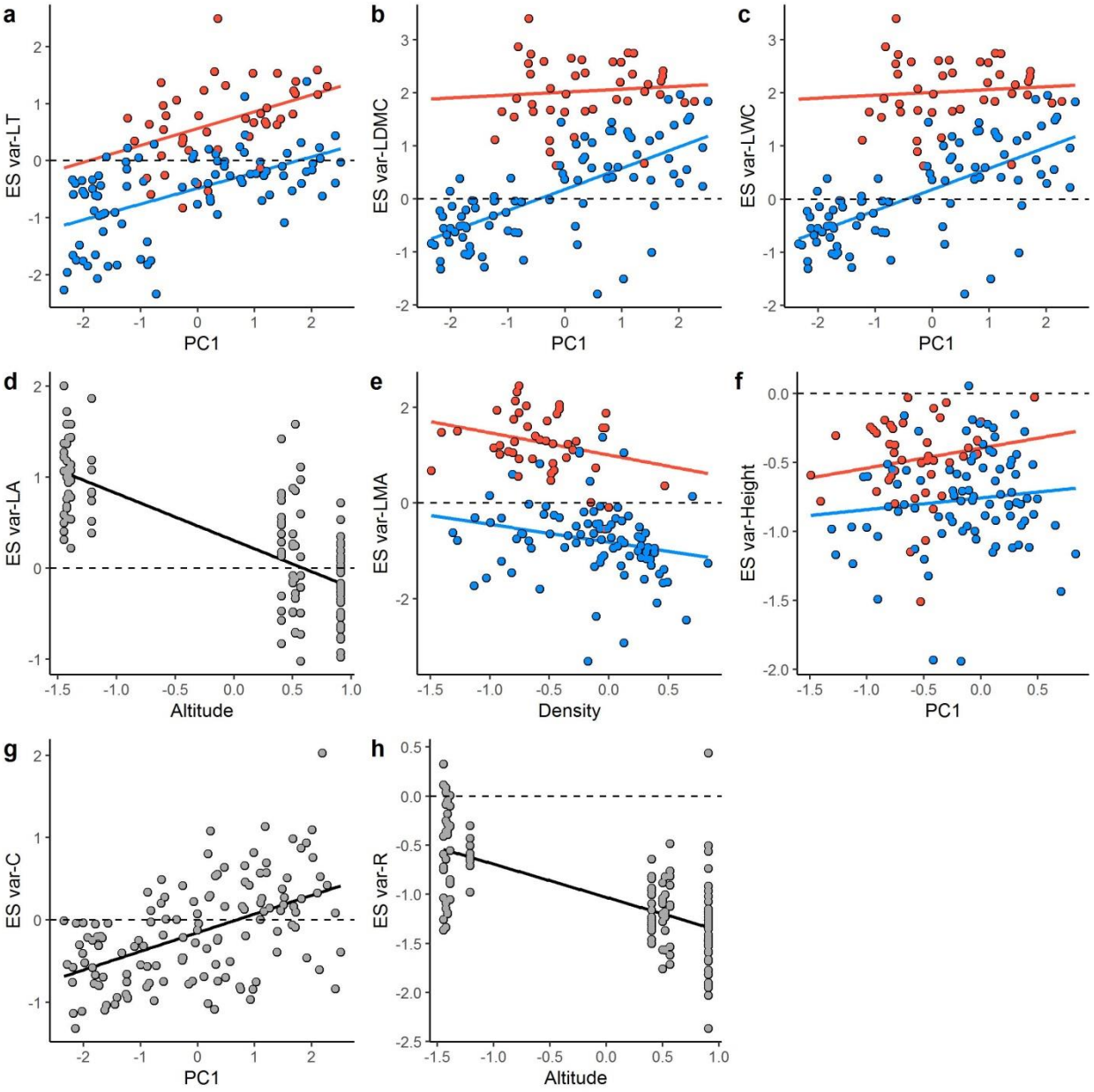

Figure S1. Partial residual plots showing the effects of environmental filters across habitats on the effect sizes (ES) of the community variance in functional traits. Significant conditional effects of elevation are shown in blue for high elevation and in red for low elevation. Non-significant variables are set to their median value. The dashed line marks the effect sizes = 0, which represents an absolutely random assembly. See Table 1 to check for the significance of predictors.

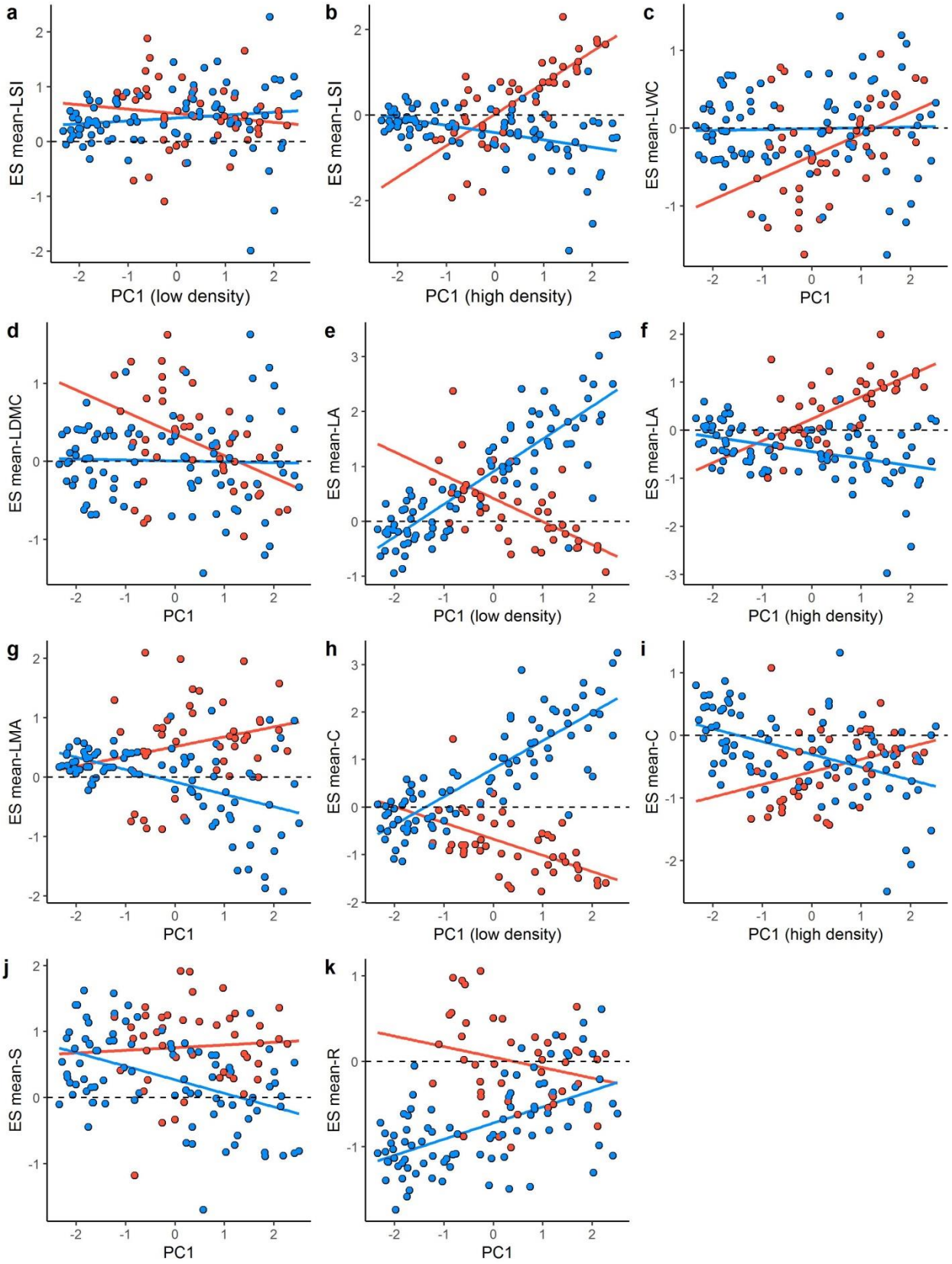

Figure S2. Partial residual plots showing the effects of environmental filters across habitats on the effect sizes (ES) of community mean functional traits. Significant conditional effects of elevation are shown in blue for high elevation and in red for low elevation. Significant

conditional effects of density are assigned with “low density” and “high density”. Non-significant variables are set to their median value. The dashed line marks the effect sizes = 0, which represents an absolutely random assembly. See Table 1 to check for the significance of predictors.

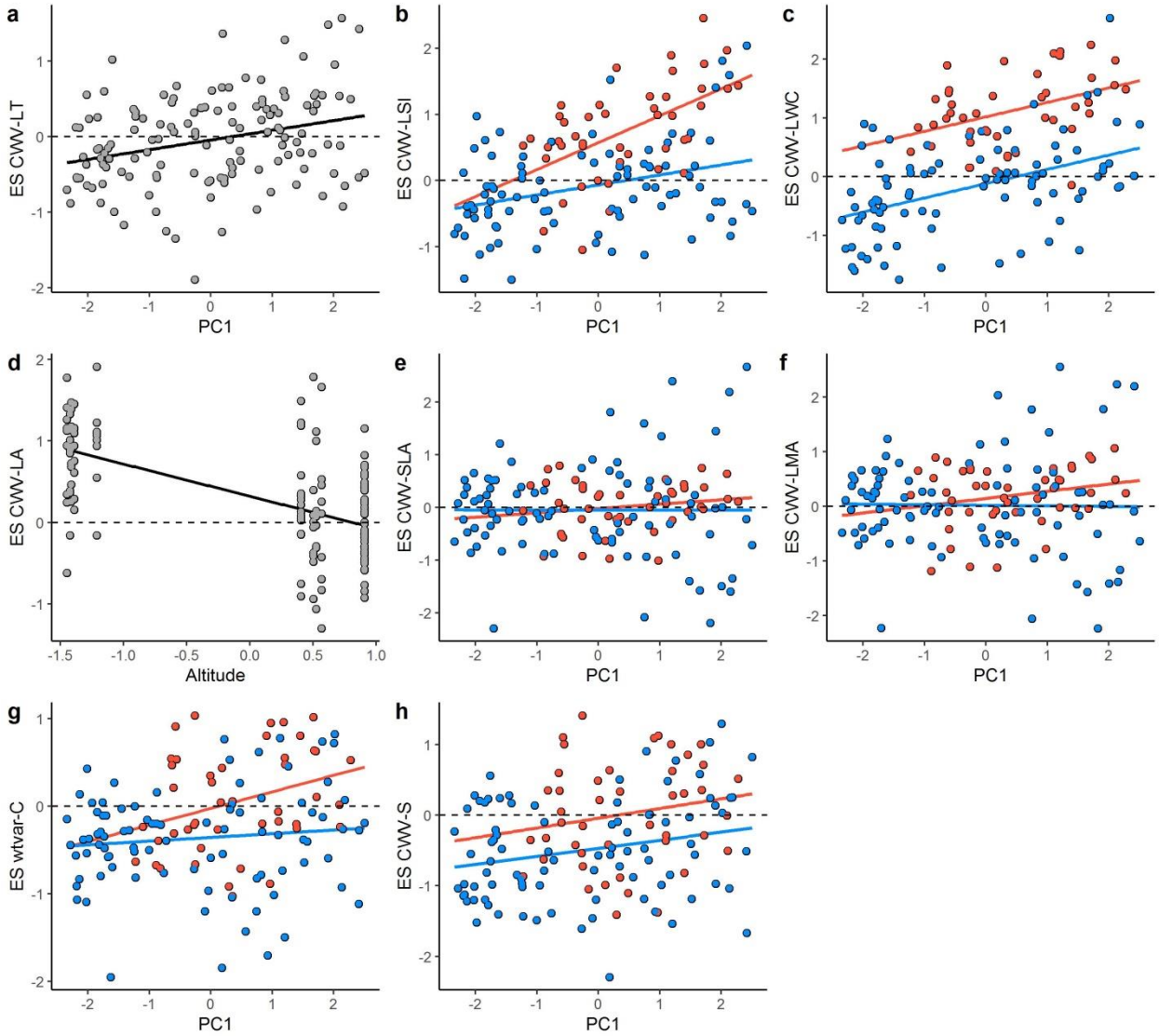

Figure S3. Partial residual plots showing the effects of environmental variables on the effect sizes (ES) of the community weighted variance in functional traits. Conditional effects of elevation are shown in blue for high elevation and in red for low elevation. Non-significant variables are set to their median value. The dashed line marks the effect sizes = 0, which represents an absolutely random assembly. See Table 1 to check for the significance of predictors.

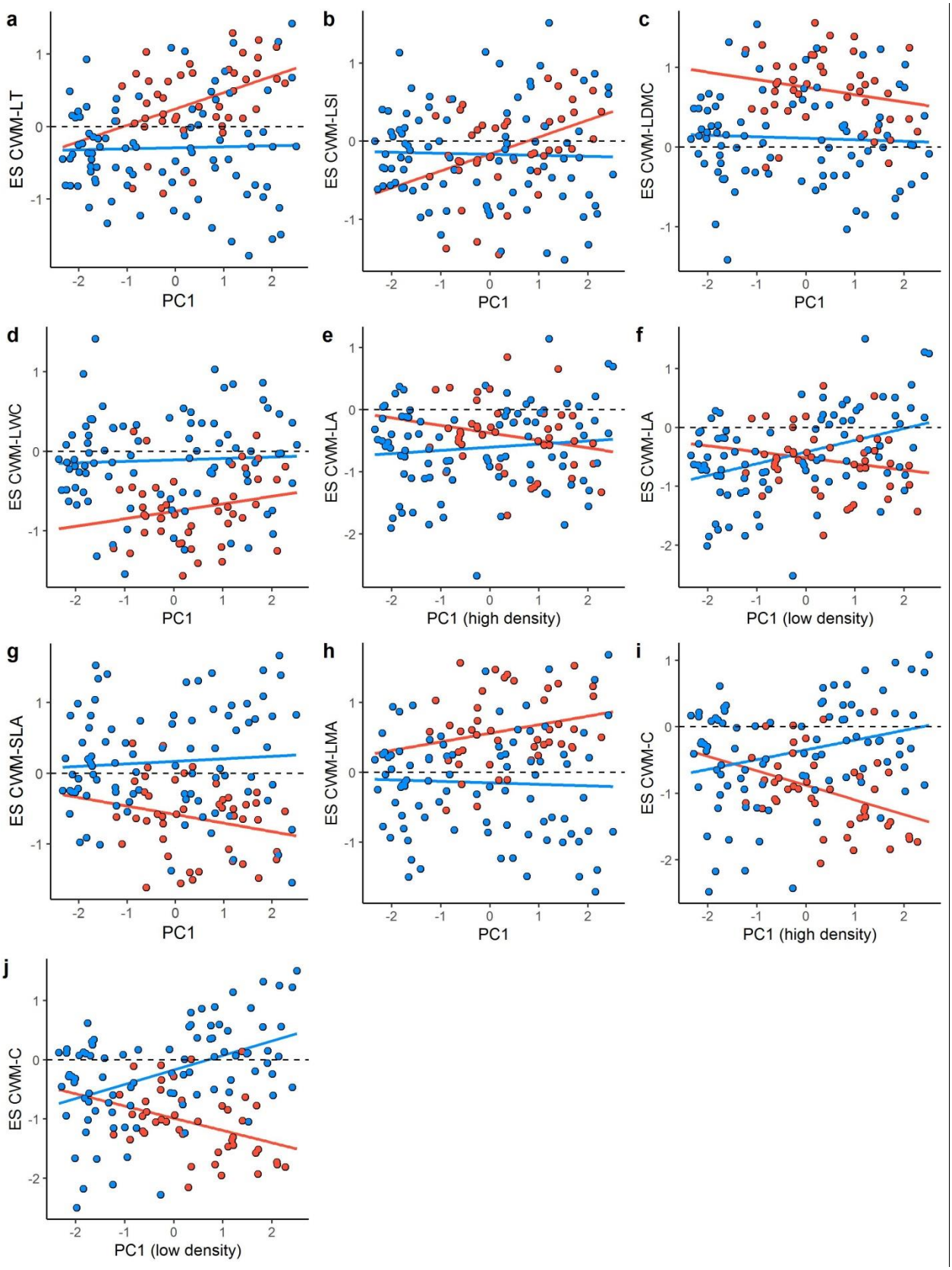

Figure S4: Partial residual plots showing the effects of environmental variables on the effect sizes (ES) of community weighted mean of functional traits. Conditional effects of elevation are shown in blue for high elevation and in red for low elevation. Significant conditional

effects of density are assigned with “low density” and “high density”. Variables not shown in the plot are set to their median value. The dashed line marks the effect sizes = 0, which represents an absolutely random assembly. See Table 1 to check for the significance of predictors.