Luísa Lucresia de Sales Ribeiro

Myrtaceae distribution in the different vegetation types of the Espinhaço Mountain Range: floristic composition and environmental influence.

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Distribuição de Myrtaceae em diferentes tipos vegetacionais da Cadeia do Espinhaço: composição florística e influência ambiental

Myrtaceae distribution in the different vegetation types of the Espinhaço Mountain Range: floristic composition and environmental influence

Dissertação apresentada ao Instituto de Biociências da Universidade de São Paulo para obtenção do título de Mestre em Ciências, área de concentração em Botânica.

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Prof. Dr. Paulo Takeo Sano

Orientador

À Jorge e Najla,

dedico.

"It (Successful research) depends to a large degree on

choosing an important problem and finding a way to solve it,

even if imperfectly at first."

– Edward O. Wilson (em *Letters to a Young Scientist*)

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Summary

Resumo

A Cadeia do Espinhaço (Espinhaço Mountain Range - EMR) é uma das regiões de maior diversidade florística da América do Sul, englobando um mosaico de fitofisionomias altamente diversas. Dentre os grupos de angiospermas que ocorrem nessas paisagens, Myrtaceae é destacada por sua diversidade e relevância ecológica. A família foi incluída em 13 inventários florísticos na EMR; contudo, esse número parece ser insuficiente para a compreensão de toda sua diversidade na área. Dessa forma, o objetivo desta dissertação foi revisar a composição, o esforço amostral e a distribuição de Myrtaceae em diferentes montanhas e vegetações da EMR e investigar os fatores ambientais que moldam esses padrões. Bancos de dados online, floras locais e descrições de espécies foram compilados, espécimes foram analisados em herbários e um banco de dados foi construído com 12.848 registros. Padrões florísticos foram investigados usando NMDS. Variáveis edáficas e climáticas associadas com a distribuição das espécies foram investigadas com GDM. Foram encontrados 17 gêneros e 281 espécies, das quais 42 spp. são endêmicas. Os gêneros mais diversos (*Eugenia* e *Myrcia*) também são os mais especiosos entre as Myrtaceae neotropicais, mas o endemismo foi desigual dentro dos clados. A maioria das espécies não é endêmica, estando distribuídas em domínios morfoclimáticos adjacentes – especialmente na Mata Atlântica, centro de diversidade de Myrteae e origem de grandes linhagens. A diversidade em diferentes subdivisões geomorfológicas foi correlacionada ao esforço amostral, ambos concentrados no Espinhaço Meridional, na Chapada Diamantina e no Quadrilátero Ferrífero. Florestas abrangeram o maior número de espécies e espécies exclusivas, embora o número de generalistas tenha crescido ao comparar o banco de dados com informações da literatura. Padrões de similaridade não recuperaram estruturas geomorfológicas ou subdivisões encontradas para outras famílias de angiospermas. Fatores edáficos relacionados à disponibilidade de nutrientes e capacidade de retenção de água do solo foram os preditores mais relevantes para a distribuição das espécies, alinhando-se com estudos que avaliam a distribuição de espécies em vegetações empobrecidas de nutrientes. Preditores climáticos e distância geográfica, embora citados anteriormente como expressivos para outras angiospermas em campos rupestres, não foram altamente significativos para Myrtaceae.

Palavras-chave: Banco de dados; Padrões florísticos; Myrteae; Biogeografia ecológica;

Abstract

The Espinhaço Mountain Range (EMR) is one of the most floristically diverse regions in South America, encompassing a mosaic of highly diverse phytophysiognomies. Among angiosperm groups that occur in these landscapes, Myrtaceae has been consistently highlighted for its diversity and ecological relevance. Although the family has been previously included in 13 comprehensive inventories in the EMR, this number is still insufficient to comprehend Myrtaceae richness and species distribution in the area. Therefore, the aim of the present dissertation was to review Myrtaceae composition, sampling effort and distribution in different mountains and vegetation types of the Espinhaço Mountain Range and investigate environmental drivers that shape these patterns. Online databases, local floras and species descriptions were compiled, specimens were analyzed in herbaria and a comprehensive database was constructed with 12,848 records. Floristic patterns were investigated using NMDS. Climatic and edaphic variables associated with species turnover in the study area were investigated with a GDM. There were found 17 genera and 281 species, from which 42 spp. are endemic to the EMR. The most diverse genera (*Eugenia* and *Myrcia*) were also the most speciose among neotropical Myrtaceae, but species endemism was proportionally uneven within clades. Contrary to previous assessments, Myrtaceae species were mostly not endemic, being distributed in the adjacent morphoclimatic domains – especially the Atlantic Forest, a center of Myrteae diversity and origin of major lineages. Diversity in different geological subdivisions were correlated to sampling effort, both concentrated in the Southern Espinhaço, Chapada Diamantina and Iron Quadrangle. Forests encompassed the highest number of overall and exclusive species, although the number of habitats generalists grew comprehensively when comparing the database with data from literature. Similarity patterns did not recover geomorphological groups or subdivisions previously found for other angiosperm families. Edaphic predictors related to nutrient availability and soils water holding capacity were the most relevant drivers of Myrtaceae species turnover in different vegetation types within the EMR, aligning with previous studies assessing species distribution in nutrient impoverished phytophysiognomies. Climatic predictors and geographical distance, though previously cited as expressive for other angiosperms in campos rupestres, were not highly significant for Myrtaceae.

Keywords: Botanical database; Floristic patterns; Myrteae; Ecological biogeography;

Introduction

Neotropical mountain formations have been highlighted for its enigmatic immense diversity since Humboldt expeditions in the XIX century, comprising large refugia for biodiversity in highly fragmented and vulnerable landscapes (Bitencourt *et al.* 2016; Martinelli 2007; Rahbek *et al.* 2019). Among mountain ecosystems worldwide, formations in east Brazil are underlined for its immense diversity despite small topographic complexity (Rahbek *et al.* 2019). The mountains in these regions were originally described as the Espinhaço Mountain Range (EMR) in 1822 by Wilhem von Eschwege (Derby 1906; Renger 2005). Since Eschwege, multiple studies have revaluated the EMR geology and circumscription: Derby (1906) reduced the EMR to the mountain ranges within the Minas series, therefore excluding areas known today as "Serra da Mantiqueira" and "Serra do Mar", and Bruni *et al.* (1974) proposed the denomination of the Espinhaço Supergroup, dividing the EMR in two stratigraphic groups and therefore excluding the Iron Quadrangle of its circumscription.

The current delimitation of Espinhaço Mountain Range follows, simultaneously, Bruni *et al.* (1974) and Derby (1906). Some biodiversity assessments focus on the Espinhaço *sensu lato* (*sensu* Derby 1906), extending over 1270 km from Juazeiro (BA) to Ouro Branco (MG) (Derby 1906; Harley 1995; Harley & Simmons 1986), and others focus on Espinhaço *sensu stricto* (*sensu* Bruni *et al.* 1974), extending over 1200 km from Juazeiro (BA) to Barão de Cocais (MG) – as this is the southern limit to the Espinhaço supergroup distribution (Renger 2005). Internally, multiple geomorphological subdivisions have been adopted. One of the most comprehensive of them segments the mountain range in three main structures: Southern Espinhaço, in central-south Minas Gerais; Northern Espinhaço, in north of Minas Gerais and southwest of Bahia; and Chapada Diamantina, in central Bahia (Danderfer & Dardenne 2002; Saadi 1995). Nonetheless, these structures are composed by smaller geological or political subdivisions: The Southern Espinhaço can be divided in Serra do Cabral and Diamantina Plateau; the Northern Espinhaço is usually divided according in North/South according to the distribution of Brazilian Semiarid; and the Chapada Diamantina is composed of a central structure and the "Piemonte da Diamantina", a portion in northeast deeply embedded within the Caatinga domain.

The mountain range encompasses a wide latitudinal variation, crossing three highly diverse and very ecologically distinct Brazilian Morphoclimatic domains: the Caatinga, the Cerrado and the Atlantic Forest. Variations in elevation and soil

properties, in addition to these heterogeneous climatic influences, render a fragmented landscape with a mosaic of different phytophysiognomies that have been described in detail by a few comprehensive floras (*e.g.* Harley & Simmons 1986; Harley 1995; Pirani *et al.* 2003; Zappi *et al.* 2003). As the northern portion of the EMR is surrounded by the Caatinga Domain, lower elevations in this area are usually occupied by vegetation types intrinsically linked to leaf loss and desiccation, such as caatinga *sensu lato* (Andrade-Lima 1981). Intermediate elevations or lower elevations within the southmost portion of the EMR are usually covered by the wide continuum of cerrado *sensu lato* (campos limpos, campos sujos, campos cerrado, cerrado *sensu stricto* and cerradão), usually associated with marked seasonality and deep, aluminum-rich soils (Coutinho 1978). Mountaintops in the EMR are covered by shallow, rocky, and impoverished soils, with an overall predominance of highly diverse rocky outcrops like campos rupestres and cangas ferruginosas (ferruginous ironstones). Finally, throughout the mountain range, in areas with favorable edaphic conditions, there is the occasional occurrence of a wide array of forest vegetations that vary according to water availability: deciduous, semi-deciduous, nebular, riparian forests and "capões de mata" (disjunct evergreen and broadleaved tropical forests located on mountain slopes or swamps, according to Coelho 2014).

Although there are multiple studies assessing geological subdivisions in the EMR (*e.g.* Abreu, 1995; Chemale Jr. *et al.*, 2011; Dossin *et al.*, 1990; Martins-Neto, 1998), few investigations have emphasized biodiversity distribution in the region and proposed biogeographical subdivisions that accords to biota current distribution and the evolutionary history. Among them, few papers have investigated these patterns for specific taxonomical groups solely occurring in campos rupestres, like subdivisions proposed for *Minaria* – Apocynaceae (Ribeiro *et al.* 2014), Asclepiadoideae – Apocynaceae (Bitencourt *et al.* 2016), Asteraceae (Campos *et al.* 2019) and Microlicieae – Melastomataceae (Pacifico *et al.* 2021), and one comprehensive paper recognized biogeographical regions for campos rupestres using the distribution of endemic species (Colli-Silva *et al.* 2019). Nonetheless, these subdivisions are still incongruent, potentially indicating that distinct biological models present different distribution patterns. Since the EMR comprehends one of the most floristically diverse areas in South America, more investigations are needed to fully comprehend its diversity distribution (Giulietti *et al.* 1996; Harley 1995; Harley & Simmons 1986; Neves *et al.* 2018; Silveira *et al.* 2016).

Among one of the most species-rich families in the mountain range and surrounding biomes (Bridgewater *et al.* 2004; Oliveira-Filho & Fontes 2000), Myrtaceae

is an angiosperm family with pantropical distribution. Worldwide it is represented by ca. 130 genera and over 6000 species with diversity centers in southeast Asia, Australia and tropical America (Lucas *et al.* 2019; Wilson *et al.* 2001). The family is divided, according to molecular data, in subfamilies Psiloxyloideae – with two tribes, and Myrtoideae – with fifteen tribes (Wilson *et al.* 2005). In South America, Myrtaceae is almost exclusively represented by species of the Myrteae tribe, the richest of the Myrtoideae subfamily with ca. 49 genera and over 2500 species, including large genera *Eugenia* and *Myrcia*. Myrteae is morphologically characterized by its simple opposite leaves with oil glands, flowers with numerous stamens, inferior ovaries and indehiscent fleshy fruits (Lucas *et al.* 2007; Wilson *et al.* 2005). Myrteae morphological characters provide the group with a unique ecological relevance, maintaining strong interactions with pollinators and animal dispersers due to high quantity of pollen produced and year-round production of fleshy fruits – being of central relevance for the upkeep of frugivores in tropical environments (Gressler *et al.* 2006; Staggemeier *et al.* 2017).

Despite its great ecological and taxonomical relevance, studies including Myrtaceae are still insipient, mostly due to difficulty in taxon recognition. This can be mostly attributed to the homogeneous morphology and consequent taxonomical complexity of the group, that historically has been based on cryptic morphological characters such as embryo shape and the number of ovules and locules in the ovary (Landrum & Kawasaki 1997; McVaugh 1968). Consequently, floristic inventories including Myrtaceae frequently included extensive lists with imprecise identifications, reinforcing the existing knowledge gap (Soares-Silva 2000). Nevertheless, in the last 20 years there has been a significant breakthrough in Myrtaceae taxonomy, with multiple phylogenies and taxonomical revisions elucidating the relationships within subfamilies, tribes, genera, and sections within massive genera. This combined effort of taxonomists around the globe allowed future papers to reassess Myrtaceae distribution within complex landscapes based on more accurate and reliable taxonomical identifications. Therefore, though there is still major taxonomical progress to be made within Myrtaceae, we have reached a prime point where we can reevaluate what we already know about its species.

In the Espinhaço Mountain Range, the family is highlighted for its diversity in different phytophysiognomies, especially in areas of rocky outcrops and forests (Giulietti *et al.* 1987; Zappi *et al.* 2003). Myrtaceae have been included in 13 comprehensive floristic inventories in the area, with a total of 14 genera and 152 species (Lucresia *et al.* 2021). Still, these occurrences are limited to floristic surveys in restricted areas and there are major knowledge gaps concerning the overall distribution

of these species in different vegetation types and areas that lack formal assessments. Though these investigations provided valuable insight onto species richness, it is relevant not only to assess the overall number of species, but also to understand the patterns and causes of current distribution to understand how diversity was shaped across time and space (Soininen 2010). Though biodiversity studies have historically focused on alpha-diversity, patterns of species distribution have been recognized as useful to understand and develop hypothesis about the underlying processes that drive diversity patterns, which is extremely valuable in a scenario of climate change and biodiversity crisis (Gaston 2000; Soininen *et al.* 2007).

Species distribution are a combination of multiple factors, such as biogeographical history, ecological interactions, and suitability to abiotic variables, which directly impact colonization, survival and dispersal of organisms and species (Cox & Moore 2005). Nonetheless, the proportion of variation driven by these factors varies. For flowering plants, previous investigations stressed the relevance of temperature and precipitation – as they affect vital processes related to plant growth and reproduction (Hedhly *et al.* 2009; Lawson & Rands 2019; Saiter *et al.* 2016; Toledo *et al.* 2011), but others pointed to a high overall relevance of edaphic factors – as these variables pose a bigger challenge to plant establishment and growth in environments with low nutrient or water availability (Bueno *et al.* 2018; Ulrich *et al.* 2014). Nevertheless, since beta diversity is related to organisms' physiology and evolutionary biogeographical processes, multiple studies are required to understand how different communities respond to similar constraints (Soininen *et al.* 2007).

Few studies have investigated environmental drivers of species beta diversity turnover in the Espinhaço Mountain Range. A few investigations have explored the relation between edaphic variations and community composition in campos rupestres, all of them in local scales (*e.g.* Carmo & Jacobi, 2016; Conceição & Pirani, 2005). Other studies have investigated large-scale patterns, all of which focused in campos rupestres, either with one taxonomic group or overall species composition (Campos *et al.* 2019; Neves *et al.* 2018; Pacifico *et al.* 2021). Since no previous study has investigated environmental influence in different vegetation types of the Espinhaço Mountain Range using the same biological model, and given Myrtaceae representativeness in different landscapes, the family is a prime model to compare environmental drivers of species turnover with other previously investigated biological models and across different vegetation types.

Therefore, the present work aims to (1) List Myrtaceae species for the Espinhaço Mountain Range and their distributions regarding vegetation preferences and geographical ranges; (2) Investigate if distinct geomorphological structures reflect distinct floristic patterns for Myrtaceae; (3) Identify areas with little collection effort that should be prioritized in future assessments; and (4) Identify which environmental predictors, if any, are relevant drivers of Myrtaceae species turnover in the study area. This dissertation comprises two manuscripts formatted according to their target journals. The first chapter is a comprehensive analysis of Myrtaceae distribution in the Espinhaço Mountain Range, including species occurrence within different geomorphological structures and vegetation types, similarity patterns across the study area and the recognition of the most relevant knowledge gaps for this angiosperm group. The second chapter assesses Myrtaceae biogeographical ecology in the EMR, investigating which climatic or pedological predictors are drivers of Myrtaceae turnover in different vegetation types of the study area – and comparing these results with other angiosperm groups.

References

Abreu, P.A.A. (1995) O Supergrupo Espinhaço da Serra do Espinhaço Meridional (Minas Gerais): o Rifte, a Bacia e o Orógeno. *Geonomos* 3: 1–18. https://doi.org/10.18285/geonomos.v3i1.211

Andrade-Lima, D. de (1981) The Caatingas dominium. *Revista Brasileira de Botanica* 4: 149–153.

Bitencourt, C., Rapini, A., Santos Damascena, L. & De Marco Junior, P. (2016) The worrying future of the endemic flora of a tropical mountain range under climate change. *Flora: Morphology, Distribution, Functional Ecology of Plants* 218: 1–10. https://doi.org/10.1016/j.flora.2015.11.001

Bridgewater, S., Ratter, J.A. & Ribeiro, J.F. (2004) Biogeographic patterns, beta-diversity and dominance in the Cerrado biome of Brazil. *Biodiversity and Conservation* 13: 2295–2318. https://doi.org/10.2307/1931725

Bruni, M.A.L., Almeida, J.T. de & Bruni, D.C. (1974) Folha Rio São Francisco (SC. 23). *Carta Geológica do Brasil ao Milionésimo*. Departamento Nacional da Produção Mineral (DNPM), Brasília.

Bueno, M.L., Dexter, K.G., Pennington, R.T., Pontara, V., Neves, D.M., Ratter, J.A. &

Oliveira-Filho, A.T. (2018) The environmental triangle of the Cerrado Domain: Ecological factors driving shifts in tree species composition between forests and savannas. *Journal of Ecology* 106: 2109–2120. https://doi.org/10.1111/1365-2745.12969

Campos, L., Freire Moro, M., Funk, V.A. & Roque, N. (2019) Biogeographical review of Asteraceae in the Espinhaço Mountain Range, Brazil. *The Botanical Review* 85: 293–336. https://doi.org/10.1007/s12229-019-09216-9

Carmo, F.F. & Jacobi, C.M. (2016) Diversity and plant trait-soil relationships among rock outcrops in the Brazilian Atlantic rainforest. *Plant and Soil* 403: 7–20. https://doi.org/10.1007/s11104-015-2735-7

Chemale Jr., F., Dussin, I.A., Martins, M. & Santos, M.N. (2011) Nova abordagem tectono-estratigráfica do Supergrupo Espinhaço em sua porção meridional (MG). *Geonomos* 19: 173–41. https://doi.org/10.18285/geonomos.v19i2.52

Colli-Silva, M., Vasconcelos, T.N.C. & Pirani, J.R. (2019) Outstanding plant endemism levels strongly support the recognition of campo rupestre provinces in mountaintops of eastern South America. *Journal of Biogeography* 46: 1723–1733. https://doi.org/10.1111/jbi.13585

Conceição, A.A. & Pirani, J.R. (2005) Delimitação de habitats em campos rupestres na Chapada Diamantina, Bahia: substratos, composição florística e aspectos estruturais. *Boletim de Botânica da Universidade de São Paulo* 23: 85–111.

Coutinho, L.M. (1978) O conceito de cerrado. *Revista Brasileira de Biologia* 1: 17–23.

Cox, C.B. & Moore, P.D. (2005) *Biogeography: An Ecological and Evolutionary Approach*. 7th ed. C. B. Cox & P. D. Moore (eds.). Blackwell Publishing. 208 pp.

Danderfer, A. & Dardenne, M.A. (2002) Tectonoestratigrafia da Bacia Espinhaço na porção Centro-Norte do cráton do São Francisco: registro de uma evolução poliistórica descontínua. *Revista Brasileira de Geociências* 32: 449–460. https://doi.org/10.25249/0375-7536.2002324449460

Derby, O.A. (1906) The Serra do Espinhaço, Brazil. *The Journal of Geology* 14: 374–401.

Dossin, I.A., Dossin, T.M. & Chaves, M.L.S.C. (1990) Compartimentação estratigráfica do Supergrupo Espinhaço em Minas Gerais - Os Grupos Diamantina e Conselheiro Mata. *Revista Brasileira de Geociências* 20: 178–186. https://doi.org/10.25249/0375-7536.1990178186

Gaston, K.J. (2000) Global patterns in biodiversity. *Nature* 405: 220–227. https://doi.org/10.1038/35012228

Giulietti, A.M., Menezes, N.L., Pirani, J.R., Meguro, M. & Wanderley, M.G.L. (1987) Flora da Serra do Cipó, Minas Gerais: caracterização e lista das espécies. *Boletim de Botânica da Universidade de São Paulo* 9: 1–151.

Giulietti, A.M., Wanderley, M.G.L., Longhi-Wagner, H.M., Pirani, J.R. & Parra, L.R. (1996) Estudos em "sempre-vivas": taxonomia com ênfase nas espécies de Minas Gerais, Brasil. *Acta Botanica Brasilica* 10: 329–377. https://doi.org/10.1590/s0102-33061996000200007

Gressler, E., Pizo, M.A. & Morellato, L.P.C. (2006) Polinização e dispersão de sementes em Myrtaceae do Brasil. *Revista Brasileira de Botanica* 29: 509–530. https://doi.org/10.1590/S0100-84042006000400002

Harley, R.M. (1995) Introduction. *In*: B. L. Stannard (ed.) *Flora of the Pico das Almas.* Kew, Royal Botanic Gardens, pp. 1–37.

Harley, R.M. & Simmons, N.A. (1986) *Florula of Mucugê, Chapada Diamantina, Bahia, Brazil: A descriptive check-list of a campo rupestre area.* 1st ed. Royal Botanical Gardens. 228 pp.

Hedhly, A., Hormaza, J.I. & Herrero, M. (2009) Global warming and sexual plant reproduction. *Trends in Plant Science* 14: 30–36. https://doi.org/10.1016/j.tplants.2008.11.001

Landrum, L.R. & Kawasaki, M.L. (1997) The genera of Myrtaceae in Brazil: An illustrated synoptic treatment and identification keys. *Brittonia* 49: 508–536. https://doi.org/10.2307/2807742

Lawson, D.A. & Rands, S.A. (2019) The effects of rainfall on plant–pollinator interactions. *Arthropod-Plant Interactions* 13: 561–569. https://doi.org/10.1007/s11829-019-09686-z

Lucas, E.J., Harris, S.A., Mazine, F.F., Belsham, S.R., Nic Lughadha, E.M., Telford, A., Gasson, P.E. & Chase, M.W. (2007) Suprageneric phylogenetics of Myrteae, the generically richest tribe in Myrtaceae (Myrtales). *Taxon* 56: 1105–1128. https://doi.org/10.2307/25065906

Lucas, E.J., Holst, B., Sobral, M., Mazine, F.F., Nic Lughadha, E.M., Barnes Proença, C.E., Ribeiro da Costa, I. & Vasconcelos, T.N.C. (2019) A new subtribal classification of Tribe Myrteae (Myrtaceae). *Systematic Botany* 44: 560–569.

https://doi.org/10.1600/036364419x15620113920608

Lucresia, L., Stadnik, A., Campos, L. & Roque, N. (2021) Myrtaceae floristic survey and vegetation distribution in a central portion of Chapada Diamantina, Brazil. *Phytotaxa* 498: 71–86. https://doi.org/10.11646/phytotaxa.498.2.1

Martinelli, G. (2007) Mountain biodiversity in Brazil. *Revista Brasileira de Botanica* 30: 587–597. https://doi.org/10.1590/S0100-84042007000400005

Martins-Neto, M.A. (1998) O Supergrupo Espinhaço em Minas Gerais: registro de uma bacia rifte-sag do Paleo/Mesoproterozóico. *Revista Brasileira de Geociências* 28: 151–168. https://doi.org/10.25249/0375-7536.1998151168

McVaugh, R. (1968) The genera of American Myrtaceae: an interim. *Taxon* 17: 354–418. https://doi.org/10.2307/1217393

Neves, D.M., Dexter, K.G., Pennington, R.T., Bueno, M.L., Miranda, P.L.S. & Oliveira-Filho, A.T. (2018) Lack of floristic identity in campos rupestres — A hyperdiverse mosaic of rocky montane savannas in South America. *Flora: Morphology, Distribution, Functional Ecology of Plants* 238: 24–31. https://doi.org/10.1016/j.flora.2017.03.011

Oliveira-Filho, A.T. & Fontes, M.A.L. (2000) Patterns of floristic differentiation among atlantic forests in southeastern Brazil and the influence of climate. *Biotropica* 32: 793–810. https://doi.org/10.1111/j.1744-7429.2000.tb00619.x

Pacifico, R., Almeda, F. & Fidanza, K. (2021) Modeling of Microlicieae (Melastomataceae) species composition provides insights into the evolution of campo rupestre vegetation on eastern Brazilian mountaintops. *Flora: Morphology, Distribution, Functional Ecology of Plants* 281. https://doi.org/10.1016/j.flora.2021.151850

Pirani, J.R., Mello-Silva, R. & Giulietti, A.M. (2003) Flora de Grão-Mogol, Minas Gerais, Brasil. *Boletim de Botânica da Universidade de São Paulo* 21: 1–24. https://doi.org/10.11606/issn.2316-9052.v21i1p1-24

Rahbek, C., Borregaard, M.K., Colwell, R.K., Dalsgaard, B., Holt, B.G., Morueta-Holme, N., Nogues-Bravo, D., Whittaker, R.J. & Fjeldså, J. (2019) Humboldt's enigma: What causes global patterns of mountain biodiversity? *Science* 365: 1108–1113. https://doi.org/10.1126/science.aax0149

Renger, F.E. (2005) O "Quadro Geognóstico Do Brasil" De Wilhelm Ludwig Von Eschwege: breves comentários à sua visão da geologia no Brasil. *Geonomos* 13:

91–95. https://doi.org/10.18285/geonomos.v13i1e2.139

Ribeiro, P.L., Rapini, A., Damascena, L.S. & Van den Berg, C. (2014) Plant diversification in the espinhaço range: Insights from the biogeography of *Minaria* (Apocynaceae). *Taxon* 63: 1253–1264. https://doi.org/10.12705/636.16

Saadi, A. (1995) A Geomorfologia da Serra do Espinhaço em Minas Gerais e de suas margens. *Geonomos* 3: 41–63. https://doi.org/10.18285/geonomos.v3i1.215

Saiter, F.Z., Brown, J.L., Thomas, W.W., Oliveira-Filho, A.T. & Carnaval, A.C. (2016) Environmental correlates of floristicregions and plant turnover in the Atlantic Forest hotspot.pdf. *Journal of Biogeography* 43: 2322–2331. https://doi.org/10.1111/jbi.12774

Silveira, F.A.O., Negreiros, D., Barbosa, N.P.U., Buisson, E., Carmo, F.F., Carstensen, D.W., Conceição, A.A., Cornelissen, T.G., Echternacht, L., Fernandes, G.W., Garcia, Q.S., Guerra, T.J., Jacobi, C.M., Lemos-Filho, J.P., Le Stradic, S., Morellato, L.P.C., Neves, F.S., Oliveira, R.S., Schaefer, C.E., Viana, P.L. & Lambers, H. (2016) Ecology and evolution of plant diversity in the endangered campo rupestre: a neglected conservation priority. *Plant and Soil* 403: 129–152. https://doi.org/10.1007/s11104-015-2637-8

Soininen, J. (2010) Species turnover along abiotic and biotic gradients: Patterns in space equal patterns in time? *BioScience* 60: 433–439. https://doi.org/10.1525/bio.2010.60.6.7

Soininen, J., Lennon, J.J. & Hillebrand, H. (2007) A multivariate analysis of beta diversity across organisms and environments. *Ecology* 88: 2830–2838. https://doi.org/10.1890/06-1730.1

Staggemeier, V.G., Cazetta, E. & Morellato, L.P.C. (2017) Hyperdominance in fruit production in the Brazilian Atlantic Rainforest: the functional role of plants in sustaining frugivores. *Biotropica* 49: 71–82. https://doi.org/10.1111/btp.12358

Toledo, M., Poorter, L., Peña-Claros, M., Alarcón, A., Balcázar, J., Leaño, C., Licona, J.C., Llanque, O., Vroomans, V., Zuidema, P. & Bongers, F. (2011) Climate is a stronger driver of tree and forest growth rates than soil and disturbance. *Journal of Ecology* 99: 254–264. https://doi.org/10.1111/j.1365-2745.2010.01741.x

Ulrich, W., Soliveres, S., Maestre, F.T., Gotelli, N.J., Quero, J.L., Delgado-Baquerizo, M., Bowker, M.A., Eldridge, D.J., Ochoa, V., Gozalo, B., Valencia, E., Berdugo, M., Escolar, C., García-Gómez, M., Escudero, A., Prina, A., Alfonso, G.,

Arredondo, T., Bran, D., Cabrera, O., Cea, A.P., Chaieb, M., Contreras, J., Derak, M., Espinosa, C.I., Florentino, A., Gaitán, J., Muro, V.G., Ghiloufi, W., Gómez-González, S., Gutiérrez, J.R., Hernández, R.M., Huber-Sannwald, E., Jankju, M., Mau, R.L., Hughes, F.M., Miriti, M., Monerris, J., Muchane, M., Naseri, K., Pucheta, E., Ramírez-Collantes, D.A., Raveh, E., Romão, R.L., Torres-Díaz, C., Val, J., Veiga, J.P., Wang, D., Yuan, X. & Zaady, E. (2014) Climate and soil attributes determine plant species turnover in global drylands. *Journal of Biogeography* 41: 2307–2319. https://doi.org/10.1111/jbi.12377

Wilson, P.G., O'Brien, M.M., Gadek, P.A. & Quinn, C.J. (2001) Myrtaceae revisited: A reassessment of infrafamilial groups. *American Journal of Botany* 88: 2013–2025. https://doi.org/10.2307/3558428

Wilson, P.G., O'Brien, M.M., Heslewood, M.M. & Quinn, C.J. (2005) Relationships within Myrtaceae *sensu lato* based on a matK phylogeny. *Plant Systematics and Evolution* 251: 3–19. https://doi.org/10.1007/s00606-004-0162-y

Zappi, D.C., Lucas, E., Stannard, B.L., Nic Lughadha, E., Pirani, J.R., Queiroz, L.P., Atkins, S., Hind, D.J.N., Giulietti, A.M., Harley, R.M. & Carvalho, A.M. (2003) Lista das plantas vasculares de Catolés, Chapada Diamantina, Bahia, Brasil. *Boletim de Botânica da Universidade de São Paulo* 21: 345–398.

General Conclusions

The present work contributed with the knowledge of Myrtaceae species distribution in the Espinhaço Mountain Range (EMR) by refining and exploring historical data. Combining multiple sources of information and analyzing the full extension of the mountain range allowed a better comprehension of large-scale endemism and distribution patterns: While previous investigations described Myrtaceae as an endemic group in the EMR, according to the dataset most species are also distributed in the adjacent morphoclimatic domains, especially the Atlantic Rainforest. These results not only contributed to the biodiversity knowledge in the EMR, but also sparked new questions for future investigations regarding the uneven distribution of endemism within Myrtaceae clades.

Previously surveyed areas presented the highest number of records and species, reinforcing that local floristic surveys are essential towards building a database that can be used to assess overall species diversity and distribution. Nonetheless, the accumulation curves and number of new species occurrences reported in this investigation (57 spp.; 20.5%) reinforces how the sampling effort is still insufficient to fully assess the mountain range diversity. In that regard, the present work also highlights areas with knowledge gaps for Myrtaceae and therefore suggests locations that should be included in future assessments. In addition, the compilation of species and specimens vegetation of occurrence – and the rarefaction curves from each vegetation type – suggests sampling effort is strongly targeted in open habitats while forest diversity is still overlooked.

The present work also contributed with an assessment of species turnover in the EMR using a new model organism. Previous investigations on environmental drivers of species distribution in the EMR have mainly focused in campos rupestres and specific organisms that possess wildly different biological and ecological characteristics. In this regard, Myrtaceae was the first model in which distribution patterns were mostly driven by edaphic predictors rather than variables related to temperature and precipitation. These results possibly indicate that patterns in beta diversity are more intrinsically linked to the biological group rather than the investigated environment. The present work is also the first evidence of a higher geographical isolation among forests, contradicting the well-documented pattern of endemic distribution among campos rupestre. It is interesting to note, however, that this investigation is one of the few focusing on an animal-dispersed plant model, which could indicate that zoochoric species present a different and yet underexplored pattern

of distribution in mountaintops – reinforcing the need to investigate distinct biological models in the EMR and explore the combination of different methods to fully comprehend species distribution patterns.