CLIMATIC NICHE DETERMINES THE GEOGRAPHIC DISTRIBUTION OF MYRTACEAE SPECIES IN BRAZILIAN SUBTROPICAL ATLANTIC FOREST

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ABSTRACT – The understanding of factors determining species geographic distribution is a fundamental aim of ecology. We investigated the environmental niche for three Myrtaceae species in the Brazilian Subtropical Atlantic Forest (BSAF), part of a global conservation hotspot. Based on a literature review, we selected one representative Myrtaceae species in three important forest types in this region: Evergreen Rain Forest (coastal plains and associated mountains ranges); Araucaria Forest, and Seasonal Deciduous Forest (continental upland areas). Geographical coordinates of their distribution were obtained from the BIEN database. As explanatory variables, we considered altitude, climate, cloud cover, and soil classes. We summarized the environmental space occupied by each pair of species using Principal Components Analysis, determined niche overlaps, and applied statistical tests to verify niche equivalences and similarities. The selected species in Evergreen Rain Forest, Araucaria Forest, and Seasonal Deciduous Forest were *Myrcia splendens* (Sw.) DC., *Myrcia guianensis* (Aubl.) DC., and *Campomanesia xanthocarpa* O.Berg., respectively. *C. xanthocarpa* showed a more restricted geographic distribution than the two *Myrcia* species that occur from central America to southern Brazil. Species' geographic distribution were fundamentally determined by temperature and rainfall regimes. Only *C. xanthocarpa* and *M. guianensis*, from uplands forest formations, showed environmental niche equivalence. In conclusion, we found that both species of *Myrcia* showed high climatic niche amplitudes occurring throughout the climatic gradient, while *C. xanthocarpa* was more subtropical, distributed mostly in the south and southeast of Brazil.

Keywords: Biogeography; Niche analysis; Multivariate ordination.

NICHO CLIMÁTICO DETERMINA A DISTRIBUIÇÃO GEOGRÁFICA DE ESPÉCIES DE MYRTACEAE NA PORÇÃO SUL DA FLORESTA ATLÂNTICA SUBTROPICAL

RESUMO – O entendimento dos fatores que determinam as distribuições geográficas de espécies arbóreas é um objetivo de grande importância na ecologia florestal. Por isso, neste trabalho investigamos os nichos ambientais para três espécies de Myrtaceae, da Floresta Atlântica Subtropical (BSAF), que faz parte de um hotspot global para conservação da biodiversidade. Com base em revisão de literatura selecionamos três espécies de Myrtaceae, em três importantes formações florestais nesta região: Floresta Ombrófila Densa, FOD (planícies litorâneas e serras associadas), Floresta Ombrófila Mista, FOM, e Floresta Estacional Decidual, FED (áreas planálticas continentais). As coordenadas geográficas foram obtidas a partir do banco de dados BIEN. Como variáveis explicativas, consideramos altitude, clima, cobertura de nuvens e classes de solos. O espaço ambiental ocupado por cada par de espécies foi sintetizado por meio de uma Análise de Componentes Principais (PCA), a partir do qual verificamos a sobreposição de nichos e calculamos estatísticas de similaridade e equivalência de nichos. As espécies selecionadas para FOD, FOM e FED foram, respectivamente, ***Myrcia splendens*** *(Sw.) DC.,* ***Myrcia guianensis*** *(Aubl.) DC. e* ***Campomanesia xanthocarpa*** *O.Berg.* ***C. xanthocarpa*** *apresentou distribuição geográfica mais restrita do que as duas espécies de* ***Myrcia****, que ocorrem desde a América Central, até o Sul do Brasil. A distribuição das espécies foi determinada fundamentalmente por gradientes de temperatura e de precipitação. Apenas* ***C. xanthocarpa*** *e* ***M. guianensis****, representativas das formações florestais planálticas,*

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apresentaram equivalência de nicho. Como conclusão, observamos que ambas espécies de ***Myrcia*** *apresentam maior amplitude de nicho, com* ***C. xanthocarpa*** *apresentando caráter mais subtropical, com distribuição mais restritiva ao Sul e Sudeste do Brasil.*

Palavras-Chave: Biogeografia; Análise de Nicho; Ordenação multivariada.

1. INTRODUCTION

Identifying the determinants of the geographical distribution of species is one of the key objectives of ecology. It allows important inferences to be made about species' evolutionary history and their ecological niches (Loyola et al., 2008). Such information is essential as it can support the development of conservation strategies and sustainable management of natural resources (Schlottfeldt et al., 2015).

In natural conditions, species' geographic distributions represent an expression of their ecological niches. According to the classical concept proposed by G. Evelyn Hutchinson in the middle of the last century (Hutchinson, 1957), the fundamental niche of a species can be interpreted as being the n-dimensional hypervolume within which it can maintain a viable population over time. Studies worldwide have emphasized the importance of temperature and precipitation as fundamental to explaining the geographic distribution of species (Svenning and Skov, 2005). However, besides environmental factors that define the fundamental niche, the occurrence of a species is also limited by other ecological aspects, such as biotic interactions (e.g., competition, mutualism) and dispersal ability, which define the realized niche (Holt, 2009). Reproductive traits, such as those related to fruits and seeds, are considered being an important factor that affects the species geographic distributions (Lavergne et al., 2004), defining their biogeographic patterns. Thus, the species' geographic distributions in their natural habitats reflect complex interactions between several ecological factors, both biotic and abiotic, and both deterministic and stochastic.

In this sense, information on species' geographical distribution can be useful for investigating ecological niche patterns (Carretero and Sillero, 2016). Niche equivalency analysis, a statistical approach to testing whether species share the same multivariate environmental space (Broennimann et al., 2012), can indicate the potential for species coexistence, thus allowing insights into regional-scale biogeographic patterns.

In the Brazilian Subtropical Atlantic Forest (BSAF), part of a global hotspot for biodiversity conservation (Myers et al., 2000), altitudinal gradient and continentally have a great influence on plant species distribution (Oliveira-Filho et al., 2015). The BASF is characterized by three major forest physiognomies: the Evergreen Rain Forest (ERF), the Araucaria Forest (AF) and the Seasonal Deciduous Forest (SDF). While ERF occurs in the east, near the sea, occupying the coastal plains and slopes of its associated mountain ranges, AF and SDF occur to the west, in plateau areas, with the AF occupying higher altitudes than the SDF. Because they share the same river basins over a large extension of its natural areas and because there is no major geographical barrier separating them, in Southern Brazil AF and SFG have a greater floristic similarity to each other than with ERF (Higuchi et al., 2013; Oliveira-Filho et al., 2015).

In the BSAF, Myrtaceae is one of the most important botanical families, having the highest diversity of woody species at the family level (Oliveira-Filho and Fontes, 2000) and producing large quantities of fleshy fruits (Pessoa et al., 2017; Staggemeier et al., 2017) that are consumed by fauna (Bello et al., 2017). According to Bello et al. (2017), most Myrtaceae species have small black/red flesh-fruits (average diameter of 21.8 mm) and are dispersed by a wide range of animals, mainly primates and birds. Myrtaceae seeds have an average diameter of 6.21 mm (Bello et al., 2017), showing embryo morphological variation, related mostly to the hypocotyl (Lucas et al., 2007), that may affect seedlings emergence and growth rate (Hoyle et al., 2015). Also, because of its high ecological representativeness in BSAF, and well-documented species taxonomy and distribution, an increasing phylogenetic understanding and a historical timeframe that coincides with that of the BASF, the Myrtaceae is considered to be an excellent model group sensu Couvreur and Baker (2013) (Lucas and Bünger, 2015).

Considering the above, we investigated the geographic distribution and environmental niche of three Myrtaceae species representative of different BSAF sub-types (ERF, AF, and SDF). We hypothesized that only the representative species of AF and SDF (i.e., westward plateau formations) would show niche equivalence.

2. MATERIAL AND METHODS

The selection of species from the Myrtaceae was based on the Floristic and Forest Inventory of Santa Catarina (Vibrans et al., 2013a, 2013b, 2013c), currently the largest systematic vegetation sampling-based inventory for the BSAF. We selected the most abundant species of this family within the three main BSAF forest sub-types: *Myrcia guianensis* (Aubl.) DC. (Araucaria Forest), *Myrcia splendens* (Sw.) DC. (Evergreen Rain Forest) and *Campomanesia xanthocarpa* O.Berg (Seasonal Deciduous Forest). Given the greater abundance in each forest types, we expect that the selected species represent the climatic conditions observed in the ERF, AF, and SDF.

We obtained the distribution of selected species through the Botanical Information and Ecology Network – BIEN 3.4 (Fegraus, 2012; Enquist et al., 2016) (http://www.biendata.org/), assembled from registered specimens and plots. The BIEN database has been assembled from multiple sources (GBIF, SpeciesLink, SALVIAS) (Enquist and Boyle, 2012; SpeciesLink, 2012; GBIF.org, 2018) and undergone taxonomic validation by the Taxonomic Name Resolution Service (http://tnrs.iplantcollaborative.org/) (Maitner et al., 2018). Altitude, cloud cover, soil classes, and climate data at a spatial resolution of 2.5 minutes were selected as determinative variables for species occurrences (Table 1). Based on the work of Oliveira-Filho et al. (2015) and Higuchi et al. (2013), we assumed that the selected variables are influential on the distribution of species.

For each species, we verified dubious geographical occurrences and performed spatial filtering to select one occurrence in an area of 5 × 5 km, considering a spatial grid covering the species geographical distribution range, as bias caused by collections near specific sites, such as universities or research centers, might exist.

To compare the ecological niches of selected species we applied an approach proposed by Broennimann et al. (2012), in which the multivariate environmental space is translated into a bi-dimensional space through Principal Component Analysis. The bi-dimensional space reveals the main environmental gradients, i.e., the most relevant explanatory variables for species distributions. For niche comparison, we determined the niche overlap between species using the D metric (Schoener, 1970), ranging from 0 (no overlapping) to 1 (completely overlapping). Also, we performed statistical tests for niche equivalence and similarity (Warren et al., 2008). We tested the hypothesis that species environmental niches are more equivalent (or similar) than would be expected by chance, considering 100 random permutations in the bi-dimensional environmental space defined by the ordinations produced (Broennimann et al., 2020).

All analyses were performed using the R statistical programming language (R Development Core Team, 2019), with the following packages: BIEN (Maitner et al., 2018), to obtain the geographical occurrence of the species, dismo (Hijmans et al., 2017), for spatial filtering, raster (Hijmans, 2015), for processing the environmental variables, ade4 (Thioulouse et al., 1997), for multivariate analysis, factoextra (Kassambara and Mundt, 2017), for ordination visualization, and ecospat (Broennimann et al., 2020), for niche comparations

3. RESULTS

The distributions of the three species revealed a restricted occurrence for *C. xanthocarpa* (Figure 1a), which occurs mainly in the southern and southeastern portion of the BSAF, with a lower frequency in central Brazil. The two species of *Myrcia* (Figure 1b, c) presented a broader distribution, with *M. splendens* and *M. guianensis* occurring in Mexico and Central América, respectively, to the south of Brazil, and both species being present in Amazonian, and the Atlantic and Cerrado domains.

The first two PCA axes that defined the bi-dimensional environmental space occupied by *C. xanthocarpa* (representative of the SDF) and *M. guianensis* (representative of the AF) explained 67.90% of the total inertia (Axis 1 = 44.90%; Axis 2 = 23.0%) (Figure 2a). Axis 1 synthesized a gradient related mainly to the Min Temperature of

Table 1 – Explanatory variables and data sources for the analysis of environmental niche comparison for selected species of the Myrtaceae from Brazilian Subtropical Atlantic Forest.
Tabela 1 *– Variáveis explicativas e fontes dos dados para a análise de comparação de nichos ambientais de espécies de Myrtaceae da Floresta Subtropical Atlântica do Brasil.*

Explicative variables	Data source
Altitude (ALT) (CGIARCSI, 2017)	Consortium for Spatial Information
Cloud cover (CLOUD)	EarthEnv (Wilson and Jetz, 2016)
Soil classes (SOIL)	SoilGrids (Hengl et al. 2017; Shangguan et al. 2016)
Mean Annual Temperature (BIO1)	WorldClim (Fick and Hijmans 2017)
Mean Diurnal Range (BIO2)	WorldClim (Fick and Hijmans 2017)
Isothermality (BIO3)	WorldClim (Fick and Hijmans 2017)
Temperature Seasonality (BIO4)	WorldClim (Fick and Hijmans 2017)
Max Temperature of Warmest Month (BIO5)	WorldClim (Fick and Hijmans 2017)
Min Temperature of Coldest Month (BIO6)	WorldClim (Fick and Hijmans 2017)
Temperature Annual Range (BIO7)	WorldClim (Fick and Hijmans 2017)
Mean Temperature of Wettest Quarter (BIO8)	WorldClim (Fick and Hijmans 2017)
Mean Temperature of Driest Quarter (BIO9)	WorldClim (Fick and Hijmans 2017)
Mean Temperature of Warmest Quarter (BIO10)	WorldClim (Fick and Hijmans 2017)
Mean Temperature of Coldest Quarter (BIO11)	WorldClim (Fick and Hijmans 2017)
Annual Precipitation (BIO12)	WorldClim (Fick and Hijmans 2017)
Precipitation of Wettest Month (BIO13)	WorldClim (Fick and Hijmans 2017)
Precipitation of Driest Month (BIO14)	WorldClim (Fick and Hijmans 2017)
Precipitation Seasonality (BIO15)	WorldClim (Fick and Hijmans 2017)
Precipitation of Wettest Quarter (BIO16)	WorldClim (Fick and Hijmans 2017)
Precipitation of Driest Quarter (BIO17)	WorldClim (Fick and Hijmans 2017)
Precipitation of Warmest Quarter (BIO18)	WorldClim (Fick and Hijmans 2017)
Precipitation of Coldest Quarter (BIO19)	WorldClim (Fick and Hijmans 2017)

Coldest Month (BIO6) and Mean Temperature of Driest Quarter (BIO9). From the left to the right of the ordination, we observe an increment in both the minimum temperature of coldest month and the mean temperature of the driest quarter.

Thus, when evaluating species occurrence density in the environmental space, it is observed that both differed fundamentally along Axis 1 (Figures 2b, c). *M. guianensis* showed the greatest expansion of its occurrence to the right of the ordination (Figure 2c), i.e., in more tropical sites (greater BIO6 and BIO9). *C. xanthocarpa* was more centered in the ordination space, then relatively more associated with less tropical sites (Figure 2b) (smaller BIO6 and BIO9). Since *M. guianensis* occupies a larger space in the environmental ordering, we inferred that it has a larger niche amplitude, mainly along Axis 1, related to tropicality (left side of the ordination). Despite these differences, the environmental niches, with an overlap of 25% ($D = 0.25$), were considered equivalent ($p < 0.05$) (Figure 2d). Although the niche of *C. xanthocarpa* was not similar to that of *M. guianensis* ($p > 0.05$) (Figure 2e), the niche of *M. guianensis* was similar to that of *C. xanthocarpa* ($p < 0, 05$) (Figure 2f). This means that *M. guianensis* shares all the environmental space in which *C. xanthocarpa* occurs, but that the opposite is not true.

When the comparison was conducted for *C. xanthocarpa* (SDF) and *M. splendens* (ERF), the first two axes of the ordering explained 66.80% of the total inertia (Axis 1 = 44.30%; Axis 2 = 22.50%) (Figure 3a). As in the previous comparison, axes 1 (BIO6 and BIO9) and 2 (BIO5 and BIO17) summarized the same environmental gradients. Although the pattern was like the previous comparison (*C. xanthorcarpa* × *M. guianensis*), with *M. splendens* showing greater occupation in areas of higher tropicality, on the right of the ordination (Figure 3b, c), the niche overlap was much lower, approximately 11% ($D = 0.11$), so that they were not equivalent ($p > 0.05$) (Figure 3d). Additionally, *M. splendens* showed a higher climatic niche amplitude than *C. xanthocarpa*. According to the similarity analysis, the niche of *M. splendens* did not differ significantly from that of *C. xanthocarpa* ($p < 0.05$) (Figure 3f), but the opposite is not true so that the niche of *C. xanthocarpa* differed from that of *M. splendens* ($p > 0.05$) (Figure 3e). This is the case because *M. splendens* occurs widely in places

Figure 1 – Geographical distribution of the three Myrtaceae species analyzed for similarity of environmental niches in South and Central America (a- *C. xanthocarpa*, b- *M. guianensis* and c- *M. splendens*).

Figura 1 *– Distribuição geográfica das três espécies de Myrtaceae analisadas quanto à similaridade de nichos ambientais (a-* ***C. xanthocarpa****, b-* ***M. guianensis*** *e c-* ***M. splendens****).*

with a tropical climate, differing from the conditions where *C. xanthorcarpa* occurs. On the other hand, the climatic conditions where *C. xanthocarpa* occurs do not differ from those where *M. splendens* occurs.

For the comparison between *M. guianensis* (AF) and *M. splendens* (ERF), the first two axes of the PCA explained 67.90% of the total inertia (Axis 1 = 43.90%, Axis 2 = 24.00%) (Figure 4a). As in both previous comparisons, Axis 1 synthesized the same environmental gradient related to tropicality (BIO6 and BIO9). Most of the variability on Axis 2 was accounted by BIO5 (Max Temperature of Warmest Month) and CLOUD (Cloud cover), showing that at the top of the ordination are the warmest areas with the lowest cloud cover throughout the year. Both species shared a large area of the bi-dimensional environmental space (Figure 4b, c). In fact, niche overlap was the greatest observed for all comparisons, with approximately 59% (D = 0.59) (Figure 4d), suggesting a significant climatic niche similarity of both *M. guianensis* with *M. splendens* ($p < 0.05$) and *M. splendens* with *M. guianensis* ($p < 0.05$) (Figure 4e, f). This indicates that, in general, where one species is observed, another species is also observed. However, despite the high overlap in the distribution and similarity of niches, they are not equivalent ($p > 0.05$) (Figure 4d). This apparent contradiction can be explained by the fact that both species occupy almost all the bi-dimensional space of the environmental PCA. Thus, in this situation, when both niches are randomized during the equivalency test, small distribution differences in the ordination space sufficed to indicate the non-equivalence of niches.

4. DISCUSSION

The results helped us to understand the biogeography of the evaluated species better, showing the importance of climate on their geographic distributions. While *M. splendens* and *M. guianensis*, representative of the ERF and AF respectively, presented a more tropical character, *C. xanthocarpa*, representative of the SDF, was more subtropical. It is noteworthy that the two species of *Myrcia*, with higher niche amplitude and broader geographical distribution, could occupy the same niche as *C. xanthocarpa*, but the opposite was not valid. *C. xanthocarpa*, with a narrower niche amplitude, was associated to southern and southeastern Brazil. Also,

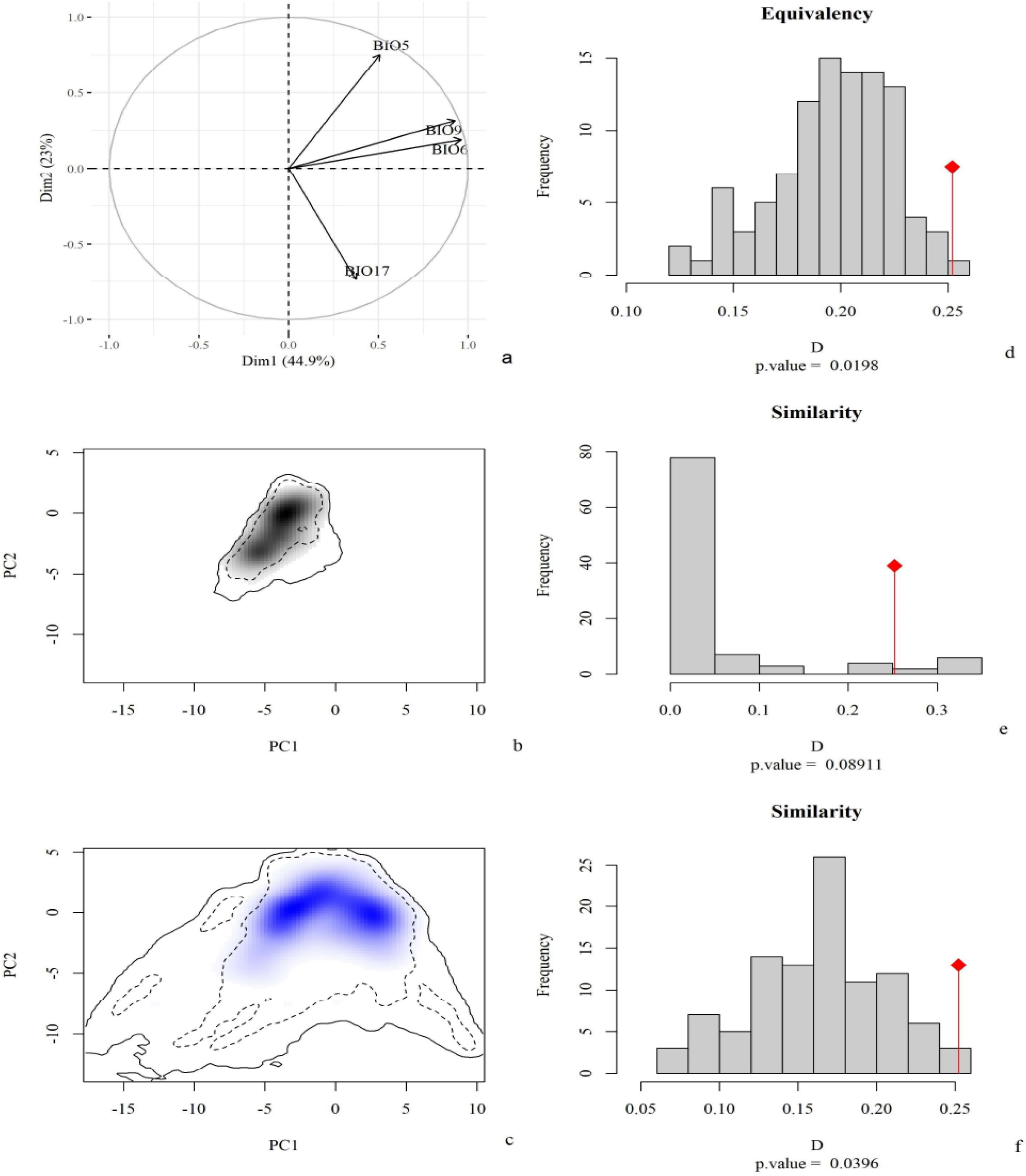

Figure 2 – PCA of *C. xanthocarpa* and *M. guianensis* sites based on environmental data. a) Explanatory variables with the greatest contribution to the PCA; b) ordination of *C. xanthocarpa* and c) *M. guianensis* sites; d) significance test for niche equivalence between *C. xanthocarpa* and *M. guianensis*; e) test of significance for niche similarity of *C. xanthocarpa* in relation to *M. guianensis* and f) of *M. guianensis* in relation to *C. xanthocarpa*. BIO5 (Max Temperature of Warmest Month), BIO6 (Min Temperature of Coldest Month), BIO9 (Mean Temperature of Driest Quarter) and BIO17 (Precipitation of Driest Quarter).

Figura 2 *– PCA para as áreas de ocorrência de* ***C. xanthocarpa*** *and* ***M. guianensis*** *em função dos dados ambientais. a) Variáveis explicativas de maior contribuição para a PCA; b) ordenação das áreas de ocorrência de* ***C. xanthocarpa*** *e c) de* ***M. guianensis****; d) teste de significância para equivalência de nicho entre* ***C. xanthocarpa*** *e* ***M. guianensis****; e) teste de significância para similaridade de nicho de* ***C. xanthocarpa*** *em relação a* ***M. guianensis*** *e f) de* ***M. guianensis*** *em relação a* ***C. xanthocarpa****. BIO5 (temperatura máxima no mês mais quente), BIO6 (temperatura mínima no mês mais frio), BIO9 (temperatura média no trimestre mais seco) e BIO17 (precipitação no trimestre mais seco).*

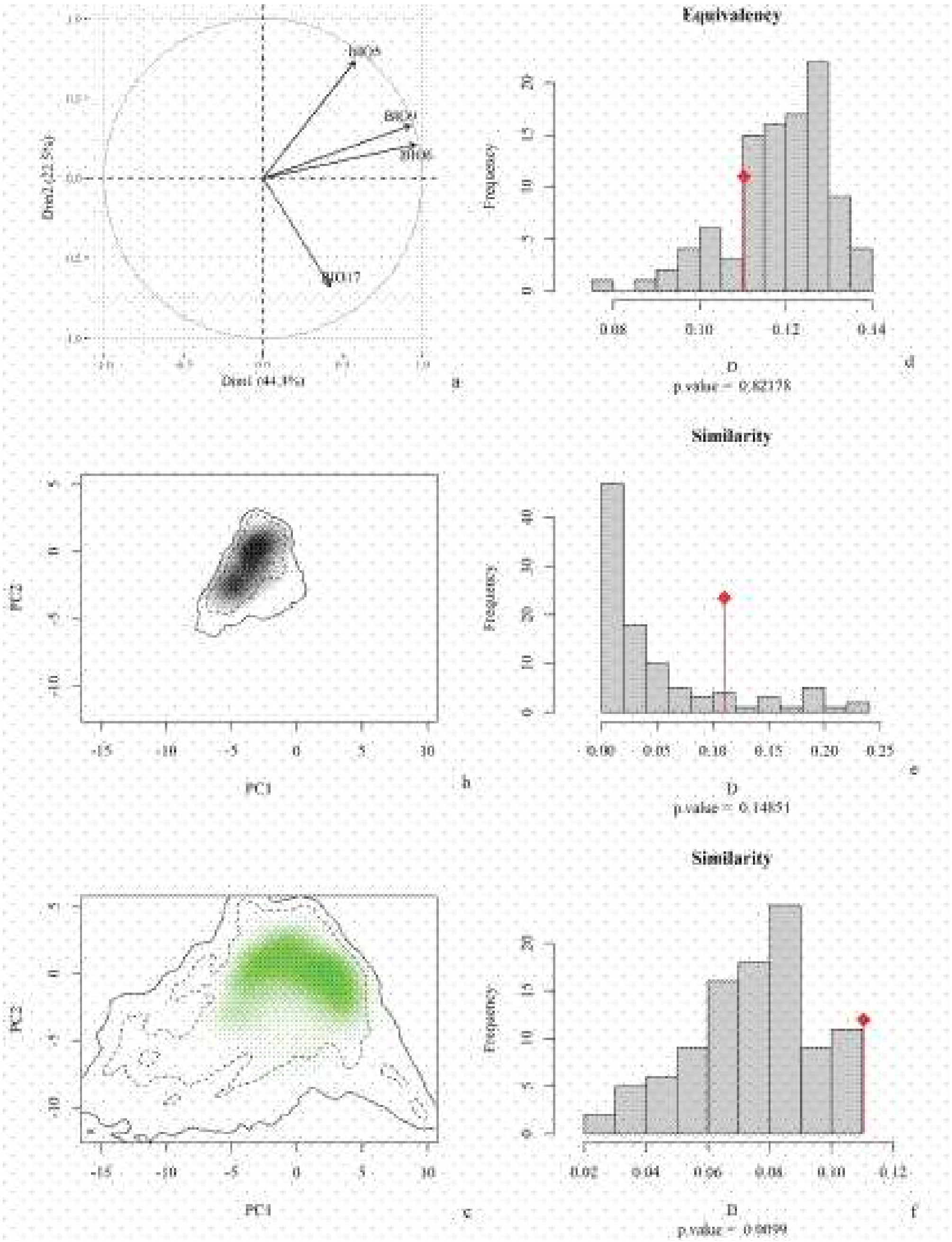

Figure 3 – PCA of *C. xanthocarpa* and *M. splendens* sites based on environmental data. a) Explanatory variables with the greatest contribution to the PCA; b) ordination of *C. xanthocarpa* and c) *M. splendens* sites; d) significance test for niche equivalence between *C. xanthocarpa* and *M. splendens*; e) test of significance for niche similarity of *C. xanthocarpa* in relation to *M. splendens* and f) of *M. splendens* in relation to *C. xanthocarpa*. BIO5 (Max Temperature of Warmest Month), BIO6 (Min Temperature of Coldest Month), BIO9 (Mean Temperature of Driest Quarter) and BIO17 (Precipitation of Driest Quarter).

Figura 3 *– PCA para as áreas de ocorrência de* ***C. xanthocarpa*** *e* ***M. splendens*** *em função dos dados ambientais. a) Variáveis explicativas de maior contribuição para a PCA; b) ordenação das áreas de ocorrência de* ***C. xanthocarpa*** *e c) de* ***M. splendens****; d) teste de significância para equivalência de nicho entre* ***C. xanthocarpa*** *e* ***M. splendens****; e) teste de significância para similaridade de nicho de* ***C. xanthocarpa*** *em relação a* ***M. splendens*** *e f) de* ***M. splendens*** *em relação a* ***C. xanthocarpa****. BIO5 (temperatura máxima no mês mais quente), BIO6 (temperatura mínima no mês mais frio), BIO9 (temperatura média no trimestre mais seco) e BIO17 (precipitação no trimestre mais seco).*

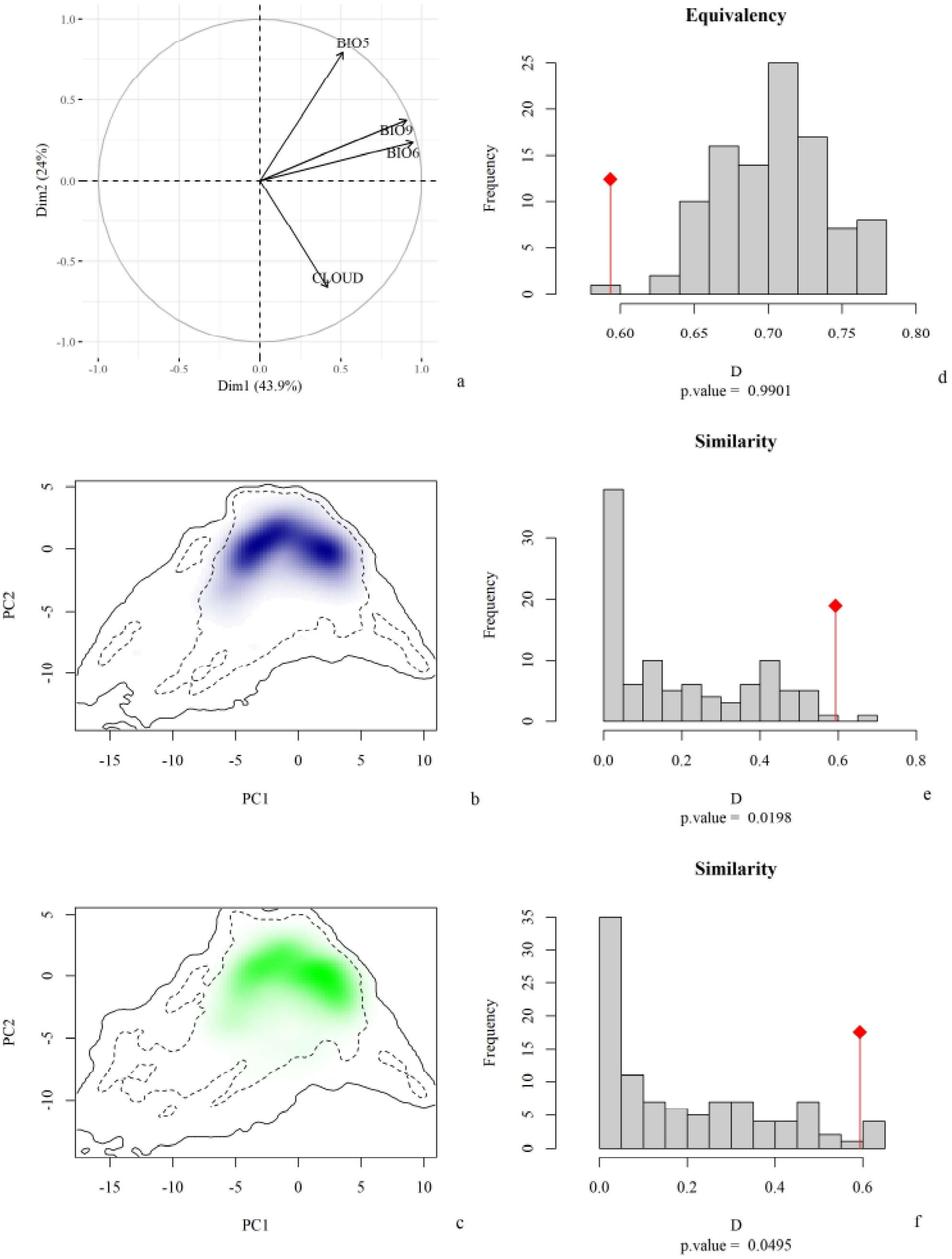

Figure 4 – PCA of *M. guianensis* and *M. splendens* sites based on environmental data. a) Explanatory variables with the greatest contribution to the PCA; b) ordination of *M. guianensis* and c) *M. splendens* sites; d) significance test for niche equivalence between *M. guianensis* and *M. splendens*; e) test of significance for niche similarity of *M. guianensis* in relation to *M. splendens* and f) of *M. splendens* in relation to *M. guianensis*. BIO5 (Max Temperature of Warmest Month), BIO6 (Min Temperature of Coldest Month), BIO9 (Mean Temperature of Driest Quarter) and CLOUD (Cloud cover).

Figura 4 *– PCA para as áreas de ocorrência de **M. guianensis** e **M. splendens** em função dos dados ambientais. a) Variáveis explicativas de maior contribuição para a PCA; b) ordenação das áreas de ocorrência de **M. guianensis** e c) de **M. splendens**; d) teste de significância para equivalência de nicho entre **M. guianensis** e **M. splendens**; e) teste de significância para similaridade de nicho de **M. guianensis** em relação a **M. splendens** e f) de **M. splendens** em relação a **M. guianensis**. BIO5 (temperatura máxima no mês mais quente), BIO6 (temperatura mínima no mês mais frio), BIO9 (temperatura média no trimestre mais seco) e CLOUD (cobertura de nuvem).*

it was observed that the most abundant species in the plateau forest formations, AF and SDF, showed significant niche equivalence among themselves. This did not occur when niches were compared to the most abundant species of ERF.

A historical and evolutionary view of the species under discussion allows a better understanding of our results. All neotropical Myrtaceae originated at the beginning of the Paleocene (60 million years ago), in eastern Gondwana, in the region that today is New Caledonia and New Zealand, dispersing westward into present-day Antarctica and South America, which had a warmer and wetter climate than today (Vasconcelos et al., 2017). On the South American continent, the family diversified into eight main phylogenetic clades, in which *Campomanesia* is part of the "*Pimenta*" group, with Curitiba, *Acca*, *Legrandia* and *Pimenta*; *Myrcia* is part of the "*Myrcia*" group, together with *Mitranthes*, *Marlieria*, and *Calyptranthes* (Vasconcelos et al., 2017). Santos et al. (2017) suggested that the genus *Myrcia*, which is endemic to the neotropical region, originated in the mountains of the southern and southeastern Atlantic Forest during the late Eocene and late Miocene, followed by rapid diversification and northward expansion. Through a continuous process of diversification and several dispersal events, both from the south to the north and the north to the south (Vasconcelos et al., 2017), various *Myrcia* species spread throughout the neotropical region. According to Santos et al. (2017), while *M. splendens* originated in the Amazon, *M. guianensis* speciated in the rupestrian areas of Central Brazil, which explains the tropical associations of both species. Studies focusing on the "*Pimenta*" clade are few, but there is evidence that the origin of this clade is associated with the south and west of South America, and possibly the Andes Mountains (Lucas et al., 2007), which may explain the subtropical character of *C. xanthocarpa* and its restricted distribution in the south and southeast of Brazil.

In addition, reproductive functional traits are among the most important factors determining species dispersion capacity. According to Lucas et al. (2007), *Myrcia* and *Campomanesia* differ in their seed embryo traits. While *Myrcia* has an embryo with well-developed cotyledons in relation to the hypocotyl, *Campomanesia's* cotyledons are much smaller in relation to the hypocotyl (Lucas et al., 2007). According to Hoyle et al. (2015), larger cotyledons, with larger nutritional reserves, can provide for newly germinated seedlings both a greater establishment capacity and a greater initial growth rate. Additionally, considering the fruit size and type of dispersal vector, based on the study by Clark et al. (2005), we can infer that *C. xanthocarpa*, with relatively larger fruits, dispersed predominantly by primates, have a more space-limited dispersal than *Myrcia* species, with smaller fruits, dispersed mostly by small birds (Bello et al., 2017). Thus, it is reasonable to assume that the respective reproductive functional traits of the evaluated species, related to ecological strategies for seed germination and dispersal ability, could have been relevant in defining their biogeographic pattern.

Given this evolutionary history and the functional reproductive attributes of the studied species, our environmental analysis supports the idea that the ecological and evolutionary processes linked to isolation (Anacker and Strauss, 2014), dispersal (Ai et al., 2012) and adaptation to environmental conditions (Pearman et al., 2008) are driving forces behind the definition of niche similarity among species and, hence, biogeographic patterns. Both *Myrcia* species showed a wide climatic niche range, occurring in both tropical and subtropical regions. Furthermore, most of the multivariate space defined by their climatic niche was not filled by *Campomanesia xanthocarpa*, which, with a more subtropical nature, showed an occurrence more limited to South and Southeast Brazil.

Despite niche similarities and overlaps, the only species with significant equivalence were those that are representatives of the plateau forest formations, *M. guianensis*, and *C. xanthocarpa*. On the other hand, *M. splendens*, relatively more common in the coastal formation (ERF), showed no niche equivalence with *M. guianensis* and *C. xanthocarpa*. It is worth noting that in southern Brazil, the SDF and AF share relatively more similar climatic conditions, which differ from those of the ERF (Higuchi et al., 2013). In fact, Higuchi et al. (2013) and Oliveira-Filho et al. (2015) have noted floristic divergence between the ERF and plateau forests formations (SDF and AF) in southern Brazil, reflecting marked climatic differences, influenced by altitudinal gradient and continentality.

5. CONCLUSION

In conclusion, we confirmed our hypothesis that only the two species of the plateau forest formation presented niche equivalence. Furthermore, both species of *Myrcia* showed high climatic niche amplitudes occurring throughout the climatic gradient, while *C. xanthocarpa* was more subtropical, distributed mostly in the south and southeast of Brazil.

6. AUTHOR CONTRIBUTIONS

P.H., A.C.S. and J.T.A conceived the ideas, designed the methodology, analyzed the data, and contributed to the writing.

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