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Shedding light on the evolution of wood anatomical traits in some Myrtaceae species from subtropical Brazil

Danieli Graciela Schallemberger[1], Guilherme Bordignon Ceolin[1, 2]

Abstract. Shedding light on the evolution of wood anatomical traits in some Myrtaceae species from subtropical Brazil**.**
The historical and evolutionary parameters of wood anatomical traits for 31 Myrtaceae species from subtropical Brazil were investigated. This group is the richest in this climatic region. We selected the following traits: diameter, frequency and length of vessels, intervessel pit diameter and fiber length, because of the abundant material available in articles and public databases. We reconstructed a time-calibrated phylogeny and a climate envelope of each selected species and performed statistical tests to: elucidate which climate variables best explained the variation in the wood characters; disentangle the influence between ancestry and adaptation; find the best evolutionary model explaining the data variation; and infer the way in which evolution may have occurred. Our results showed that features related to precipitation had the greatest influence on most of the wood characters of the selected Myrtaceae species. We also demonstrated that most of the anatomical traits respond less to environmental demands than to common ancestry. In addition, evolutionary analyses showed that almost all wood variables are able to adapt rapidly, although they are confined to a narrow range of possible values. Hypotheses to explain these results are discussed and considered throughout the text.
Key words: Brownian motion, ecological anatomy, ecophysiology, niche analysis, phylogenetic signal.

Resumo. Esclarecendo a evolução das características anatômicas da madeira em algumas espécies de Myrtaceae do Brasil subtropical.
A história evolutiva das características anatômicas da madeira para 31 espécies de Myrtaceae do Brasil subtropical (grupo mais rico nesta região climática) foram investigadas. As seguintes características foram selecionadas: diâmetro, frequência e comprimento dos vasos, diâmetro das pontuações intervasculares e comprimento das fibras, devido ao abundante material disponível em artigos e bases de dados. A partir da construção de uma filogenia calibrada e uma análise de nicho climático de cada espécie foram realizados testes estatísticos para: elucidar quais variáveis climáticas melhor explicam a variação nos caracteres da madeira, particionar influência entre ancestralidade e adaptação, descobrir o melhor modelo evolutivo que explica a variação dos dados e inferir o modo mais provável de evolução dos traços anatômicos. Os resultados mostraram que variáveis de precipitação tiveram maior influência na maioria das características da madeira das espécies avaliadas. Também ficou demonstrado que a maioria dos traços anatômicos responde menos às demandas ambientais do que à ancestralidade comum. Além disso, as análises evolutivas mostraram que quase todas as variáveis da madeira são capazes de se adaptar rapidamente, embora confinadas a uma estreita faixa de valores possíveis. Hipóteses para explicar esses resultados são discutidas ao longo do texto.

Palavras-chave: análise de nicho, anatomia ecológica, ecofisiologia, movimento browniano, sinal filogenético.

Myrtaceae Juss. is certainly a remarkable plant family not only because its predominance as a tree element in most Brazilian forests (Giehl *et al.* 2015), but also because it is one of the most complex groups from the taxonomic point of view. Only considering Brazil, the Myrtaceae family comprises so far approximately 25 genera and 1,200 species (all belonging to the Myrteae DC. tribe), with new species being periodically described (Bünger *et al.* 2018). The outstanding taxonomic complexity of this group relies both on its specific richness and great morphological similarity among different genera and species (Martos *et al.* 2017). In fact, several species within this family are virtually indistinguishable when in a vegetative state, and this feature is captured in many Brazilian vernacular names as well (e.g., different species called simply “guamirim” or “camboim”). In addition, several other species are similar even in bloom, which has compelled

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[1] Universidade Federal de Santa Maria, Departamento de Engenharia Florestal, Linha 7 de Setembro, s/n, BR 386 Km 40, CEP 98400-000, Frederico Westphalen, Brasil, phone: 55-55-37440600, ORCID: https://orcid.org/0009-0009-2769-2418
[2] ceolingb@gmail.com. ORCID: https://orcid.org/0000-0003-1187-2528

researchers to use cryptic characters for the correct identification (e.g., morphology of the seed embryo [Sobral 2003]).

One of several hypotheses to explain this type of broad diversification pattern with little morphological disparity is the "Ecological Speciation Hypothesis" (ESH; Van Valen 1976). This hypothesis postulates that a species is a lineage that occupies an adaptive zone different from any other lineage in its distribution and that evolves separately from all other lineages outside this distribution. An adaptive zone is the combination of all the environmental variables under which a species or population can persist (ecological niche).

An intuitive perception in evolutionary ecology is that coexisting species must differ significantly and that most of the morphological variation between related species is an adaptive response to competition. The general prediction of this evolutionary model is that the difference in ecological traits must be large. However, some studies have shown that dominant ecological traits are rather conserved in many lineages (Ackerly 2003). This seems to be the case in Myrtaceae: several morphologically similar species live in the same places. Thus, a pertinent question to be answered for this peculiar family is: given that the morphology is so uniform, which characters could be adaptive?

The work of Santos & Marchiori (2011) showed that several Myrtaceae species can be recognized by quantitative variation in some attributes of the wood anatomy. Because wood is important in mediating the main water relationships of plants, it is directly involved in the adaptation of the species to different climate variables, principally those linked to hydraulic resources.

Thus, our purpose with this work is to use some features of the wood anatomy to shed light on potential mechanisms responsible for the diversification and coexistence of countless Myrtaceae species in the Brazilian subtropical region. As all the morphological characteristics of living organisms are shaped by evolution, we aim to understand four particular aspects in the evolution of wood traits of the studied species: i) the occurrence of synchronicity, that is, the existence of a significant correlation between the climate characteristics and wood traits; ii) the relative weight of ancestry and adaptation in the differential evolution of the wood characters, that is, whether the variation in a trait was more correlated with phylogeny or with environmental influences; iii) if the variation in the wood characteristics would be better explained by models of neutral or restricted evolution, and iv) the mode of evolution, whether the diversification in the wood characteristics was either gradual (over time) or punctuated (occurred in jumps).

Material & Methods

Wood morphological data

We selected five quantitative wood attributes to illustrate the differences in the acquisition of resources between species, with their average values extracted from the paper published by Santos & Marchiori (2011). The characteristics were: frequency (vessels/mm^2), diameter and length of the vessels, diameter of the intervessel pits (DIVP) and length of the fibers. We show the selected species in Table 1.

Climate data

We extracted the georeferenced occurrence points of all species from digitized exsiccates available in the SpeciesLink online repository (http://splink.cria.org.br/; accessed in November 2024), totaling ~13,000 individuals. From these samples, we used the DIVA-GIS software (Hijmans *et al.* 2005a) to plot all specimens on a map, seeking both to check for inconsistencies in georeferenced locations (eg points in the ocean) and to restrict samples to those points occurring below the Tropic of Capricorn (latitude 23º S).

After this sifting, we retained 5,200 individuals, from which we extracted information on both altitude and 19 bio-climate variables (WorldClim database; Hijmans *et al.* 2005b). These variables aggregate diverse climate data of precipitation and temperature, which are biologically relevant for ecological niche analysis (Table 2). For statistical analysis, we firstly normalized all climate variables to have zero mean and unit standard deviation. This standardization was necessary to cope mathematically with the differences in the units of the climatedata (eg. ºC, m, mm). We used the PAST software (Hammer *et al.* 2001) to extract the average values of each bio-climate variable for each species, and then proceeded with both a Principal Component Analysis (PCA) and a Spearman correlation analysis to estimate which of these variables had the highest correlation with the species distribution. In addition, we also carried out exploratory univariate statistical analyses, of climate variables and of anatomical features, in order to have a general overview of the value distribution of these attributes within species. For this, we chose to use the coefficient of variation (CV), because it is a measure with both great powers to synthesize information, since it expresses dispersion around the mean, and useful statistical properties, especially as these are dimensionless.

Evolutionary analysis

We used the software Phylocom (Webb *et al.* 2008) to build a time-calibrated phylogeny of Myrtaceae. This tree served as a guide for tracing the evolutionary trajectories of the wood characters of the species studied. First, we used a phylogenetic autocorrelation analysis to break down how far the differences in wood attributes can be attributed to ancestry (phylogenetic signal) or to adaptation to different environments (equations below):

$$x=\rho Wx+\varepsilon \qquad [1]$$

$$R^2=1-Var(\varepsilon)/Var(x) \qquad [2]$$

In equation 1, x is a vector $n \times 1$ of standardized characteristic values for the various species, ρ is the phylogenetic autocorrelation coefficient, W is a phylogenetic connectivity matrix and ε is an estimate of residual error. The R^2 in equation 2 represents how much the variation of x can be explained only by phylogeny. Later, we attempted to answer whether the evolution of morphology is better explained by neutral or restricted models. Thus, we compared the goodness-of-fit for the wood variables to three different evolutionary models: Brownian motion (BM; random variation of traits over time), Ornstein-Uhlenbeck (O-U; random variation restricted by a central tendency or “attraction force”) and drift (DR; random variation with a component of directional deviation, that is, a tendency to lower or higher values). We considered as the best fitted model the one with the lowest AICc value (Akaike Information Criterion corrected for the sample size).

Thirdly, we verified the evolutionary mode of the wood anatomical characteristics. For this, we used Pagel’s κ statistics (Pagel 1999), which allows us to estimate whether the evolutionary changes were proportional to the length of the branches in the phylogenetic tree (gradual) or totally independent of them (punctuated). A value of κ equal to or very close to zero suggests independence from the evolution of the branch length characteristic, that is, a punctuated evolution mode. On the other hand, a value greater than zero suggests a gradual mode of evolutionary change. All analyses were performed with R statistical programs (R Development Core Team 2020).

Results

The first two axes of the PCA explained about 76% of the data variation, and, therefore, these were selected to synthesize the diversity in the climate characteristics. The first axis was highly correlated to altitude and the second one to precipitation (Figure 1). Due to the well-established high correlation between temperature and altitude, we decided to consider the first axis as an aggregate of these two variables.

Regarding the results of Speraman’s correlation tests, we found that vessel frequency correlates significantly with mean annual temperature amplitude (0.36; $P = 0.04$), mean temperature of the wettest quarter (-0.38922; $P = 0.02$), mean temperature of the coldest quarter (- 0.39545; $P = 0.02$), precipitation in the wettest month (-0.407; $P = 0.02$), precipitation in the driest month (0.42094; $P = 0.01$), precipitation seasonality (-0.44367; $P = 0.01$), precipitation of wettest quarter (-0.38959; $P = 0.02$), precipitation of driest quarter (0.39329; $P = 0.02$), precipitation of warmest quarter (-0.42185; $P = 0.01$), precipitation of coldest quarter (0.4092; $P = 0.02$).

In turn, vessel length was correlated with the variables mean annual temperature (0.35; $P = 0.04$), minimum temperature of the coldest month (0.45; $P = 0.008$), mean temperature of the drier quarter (0.35; $P = 0.04$) and average temperature of the coldest quarter (0.35; $P = 0.04$).

Finally, fiber length has direct relationships with the largest number of variables, being significantly correlated with annual mean temperature (0.40; $P = 0.02$), temperature seasonality (-0.35; $P = 0.04$), minimum temperature of the coldest month (0.51; $P = 0.002$), mean temperature of the coldest quarter (0.56; $P < 0.001$), precipitation of the wettest month (0.50; $P < 0.001$), *P*recipitation of the driest month (-0.55; P < 0.01), precipitation seasonality (0.59; $P < 0.01$), precipitation of wetter quarter (0.49; $P < 0.01$), precipitation of driest quarter (-0, 56; P < 0.01), precipitation of warmest quarter (0.53; $P < 0.01$), precipitation of coldest quarter (-0.56; $P < 0.02$).

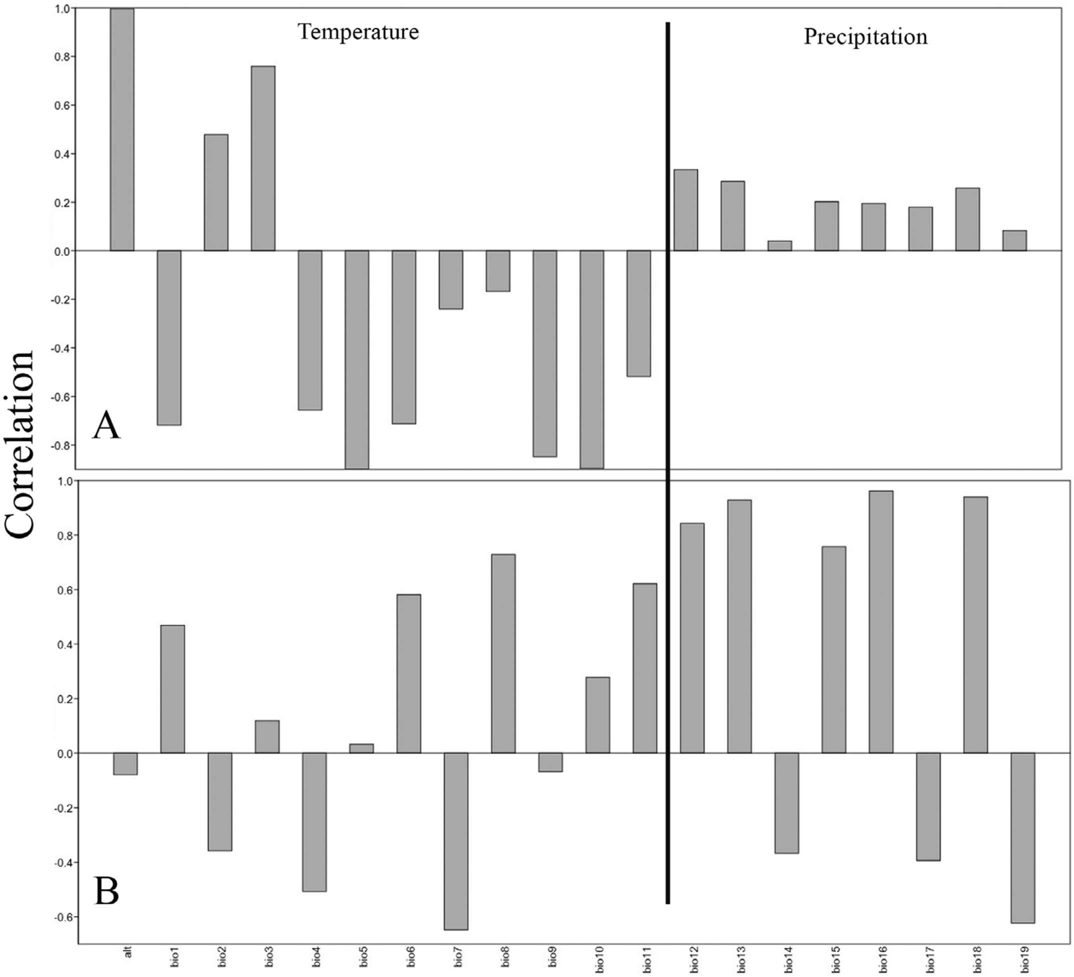

Figure 1. Principal component analysis (PCA) summary of correlation of bioclimatic variables used to explain the variation in the climate traits of Myrtaceae species. A) Axis 1. B) Axis 2. The black line divides the bioclimatic variables linked to temperature from those related to precipitation. Acronyms of bioclimatic variables: Alt = altitude; BIO1 = Annual Mean Temperature; BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp)); BIO3 = Isothermality (BIO2/BIO7) (×100); BIO4 = Temperature Seasonality (standard deviation ×100); BIO5 = Max Temperature of Warmest Month; BIO6 = Min Temperature of Coldest Month; BIO7 = Temperature Annual Range (BIO5-BIO6); BIO8 = Mean Temperature of Wettest Quarter; BIO9 = Mean Temperature of Driest Quarter; BIO10 = Mean Temperature of Warmest Quarter; BIO11 = Mean Temperature of Coldest Quarter; BIO12 = Annual Precipitation; BIO13 = Precipitation of Wettest Month; BIO14 = Precipitation of Driest Month; BIO15 = Precipitation Seasonality (Coefficient of Variation); BIO16 = Precipitation of Wettest Quarter; BIO17 = Precipitation of Driest Quarter; BIO18 = Precipitation of Warmest Quarter; BIO19 = Precipitation of Coldest Quarter.

In short, Spearman's correlation analyses showed that frequency and length of vessels and also the length of fibers had significant (all values $P < 0.05$) although moderate (~35%) correlations with a greater number of precipitation-related parameters (such as seasonality and precipitation in the driest month) rather than with variables related to temperature.

Still, the exploratory statistical analyses showed that values of the coefficient of dispersion of most climate attributes were frequently low (~10%; Figure 2), indicating that the ecological niche of Myrtaceae species is quite restricted. On the other hand, wood traits have showed a wide range of coefficient values (~15 – 70 %; Figure 3), suggesting more plasticity.

Further, the results of phylogenetic auto-correlation analysis showed that the influence of ancestry is soundly in several anatomical parameters analyzed, ranging from 35% (length of fibers) to 65% (diameter of the vessels; Figure 4). This finding suggests that there is a predisposition to relatively low adaptability in most of the wood traits, which is corroborated by the fact that the Ornstein-Uhlenbeck evolutionary model provided the best fit for almost all morphological characteristics.

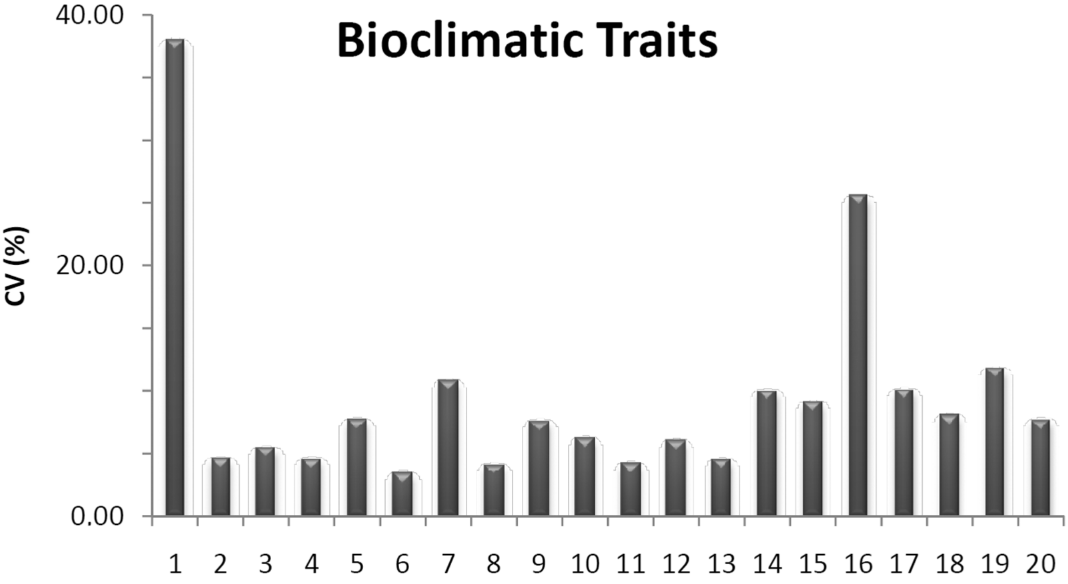

Figure 2. Coefficient of variation of bioclimatic traits. 1 = altitude. 2 = annual mean temperature; 3 = mean diurnal range; 4 = isothermality; 5 = temperature seasonality; 6 = max temperature of warmest month; 7 = min temperature of coldest month; 8 = temperature annual range; 9 = mean temperature of wettest quarter; 10 = mean temperature of driest quarter; 11 = mean temperature of warmest quarter; 12 = mean temperature of coldest quarter; 13 = annual precipitation; 14 = precipitation of wettest month; 15 = precipitation of driest month; 16 = precipitation seasonality; 17 = precipitation of wettest quarter; 18 = precipitation of driest quarter; 19 = precipitation of warmest quarter; 20 = precipitation of coldest quarter.

With the exception of the diameter of the intervessel pits (DIVP), which was better modeled by Brownian motion (Table 3).

Finally, the results showed a gradual mode of evolution for most of the wood anatomical traits (Table 3), except for vessel frequency, which showed a punctuated mode.

Discussion

The question of why some groups are so “large” while others are not having puzzled researchers for decades (Frodin 2004). In most cases, the answer to this question depends on differences in the diversification rate, that is, when there is a positive balance between the rates of speciation and extinction, the former being greater than the latter (Ricklefs 2007). Increases in speciation rate (or decreases in extinction rate) may occur as a response to several causes, for example, the emergence of a key trait (Drummond *et al.* 2012) or changes in the fundamental niche (Joly *et al.* 2013). For the Myrtaceae studied here, however, nothing found so far seems to explain why this particular family is so diverse in most of the forests in subtropical Brazil, since we neither found large discrepancies in the variation of the wood traits (absence of key traits) nor a wide range of climate variables (fundamental niche conserved).

The outstanding fact our results show is that most of the variation observed in the wood traits is phylogeny-dependent, meaning that the traits exhibit noticeable hereditary restrictions in their evolution. In other words, the wood of the Myrtaceae has a strong phylogenetic signal, that is, a significant tendency for evolutionarily related species to be more similar to each other than to distant species (Borges *et al.* 2019). In parallel, it was also found that the evolutionary model that best fits the observed patterns is the O–U model.

This model, by carrying a restriction parameter in its mathematical formulation, allows the modeling of processes in which natural selection stabilizes around an ideal value (Blomberg *et al.* 2020). This stabilizing selection can cause morphological stasis in the long run, because it favors certain phenotypic characters over others, avoiding divergences in form and function. This can occur, for example, when the morphological similarity is driven by adaptations to a given selective regime (Pfenninger *et al.* 2003).

Figure 3. Coefficient of variation of wood anatomical traits of the Myrtaceae species analyzed. 1 = vessel frequency; 2 = vessel diameter; 3 = vessel length; 4 = DIPV; 5 = fiber length.

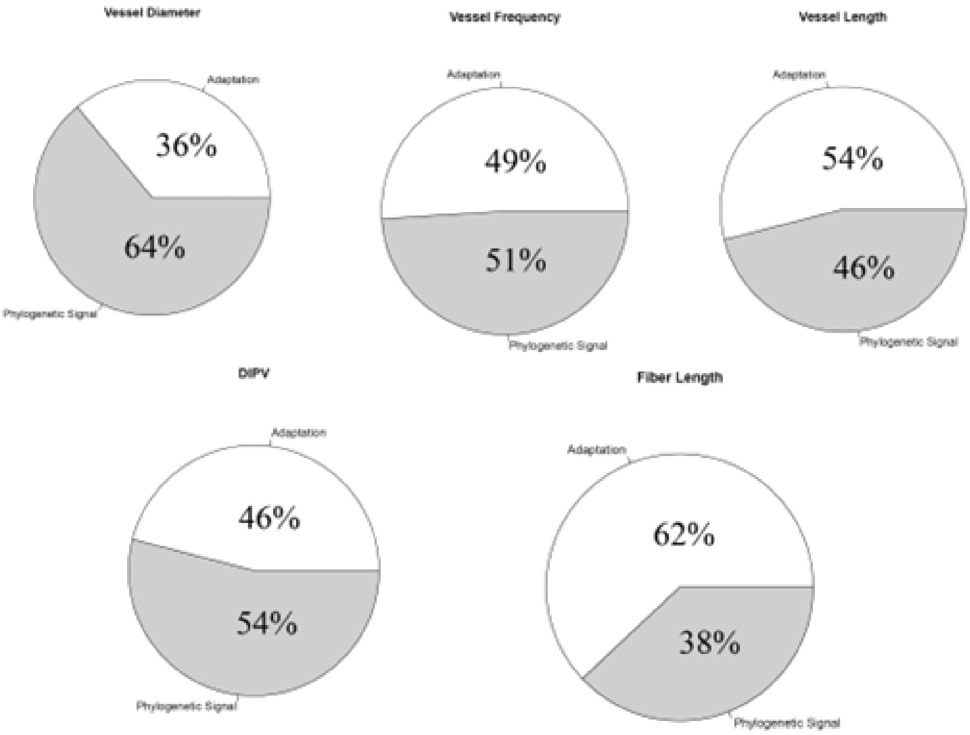

Figure 4. Comparative analysis of influence of adaptation and phylogenetic signal on the variability of wood traits in Myrtaceae analyzed.

Table 1. Myrtaceae species and their respective wood traits. VF = vessel frequency (vessels/mm^2); VD = vessel diameter (μm); VL = vessel length (μm); DIVP = diameter of the intervessel pits (μm); FL = fiber length (μm).

	VF	VD	VL	DPIV	FL
Acca sellowiana	266	33	444	5.1	744
Blepharocalyx salicifolius	90	38	471	5.4	926
Calyptranthes concinna	11	58	510	6.3	999
Calyptranthe tricona	17	70	487	5.8	1064
Campomanesia guazumifolia	93	49	551	4.3	1168
Campomanesia xanthocarpa	18	78	423	4.5	1246
Eugenia burkartiana	46	25	565	4.7	1077
Eugenia hiemalis	26	61	448	4.8	1086
Eugenia involucrata	21	58	582	5.4	1226
Eugenia mansoi	143	30	592	4.4	990
Eugenia rostrifolia	134	42	514	4.2	995
Eugenia verticillata	20	51	690	5.5	1495
Eugenia uniflora	86	37	486	4.7	888
Eugenia uruguayensis	50	48	621	4.7	1236
Myrcia palustris	44	58	681	5.4	1246
Eugenia myrcianthes	52	52	526	5.4	1154
Myrceugenia euosma	254	29	541	9.6	936
Myrceugenia glaucescens	116	40	596	9.5	1083
Myrceugenia miersiana	201	35	460	12.1	1163
Myrceugenia myrtoides	140	43	594	6.8	959
Myrcia oblongata	34	58	461	7.5	893
Myrcia selloi	25	46	606	5.7	1364
Myrcianthes cisplatensis	178	25	441	5.2	899
Myrcianthes gigantea	125	28	496	5.4	924
Myrcianthes pungens	136	37	505	4.9	1023
Myrciaria cuspidata	131	29	439	3.8	937
Myrciaria tenella	178	30	469	4.5	1013
Myrhinium atropurpureum	54	42	503	5.7	977
Plinia rivularis	89	48	535	5.2	1316
Plinia peruviana	140	25	476	4.1	969.00
Psidium cattleianum	49	43	809	4.5	1570
Siphoneugena reitzii	131	36	407	3.9	1023

In such cases, morphology is correlated with habitat use (Smith *et al.* 2011). For the studied Myrtaceae, the exploratory analyses enabled us to demonstrate that there is low volatility in the environmental conditions tolerated by the species. Thus, in restrictive conditions such as these, it is expected that the variation in the characteristics of the wood will occur in a limited range of values, due to the selective forces that act against those variants that deviate too much from the evolutionary solution considered "optimal".

In fact, the significant correlations found between some characteristics of the wood and several climate variables, although not high, suggest that the challenges imposed by the environment are strong enough to maintain the variation of the morphological traits within a certain range. Natural selection still needs to "choose", from a set of possible ways, those character combinations that adapt to a given environment.

Table 2**.** Myrtaceae species and their respective average bioclimatic variables. Alt = altitude; BIO1 = Annual Mean Temperature; BIO2 = Mean Diurnal Range; BIO3 = Isothermality; BIO4 = Temperature Seasonality; BIO5 = Max Temperature of Warmest Month; BIO6 = Min Temperature of Coldest Month; BIO7 = Temperature Annual Range; BIO8 = Mean Temperature of Wettest Quarter; BIO9 = Mean Temperature of Driest Quarter; BIO10 = Mean Temperature of Warmest Quarter; BIO11 = Mean Temperature of Coldest Quarter; BIO12 = Annual Precipitation; BIO13 = Precipitation of Wettest Month; BIO14 = Precipitation of Driest Month; BIO15 = Precipitation Seasonality; BIO16 = Precipitation of Wettest Quarter; BIO17 = Precipitation of Driest Quarter; BIO18 = Precipitation of Warmest Quarter; BIO19 = Precipitation of Coldest Quarter.

	Alt	**BIO1**	**BIO2**	**BIO3**	**BIO4**	**BIO5**	**BIO6**	**BIO7**	**BIO8**	**BIO9**	**BIO 10**	**BIO 11**	**BIO 12**	**BIO 13**	**BIO 14**	**BIO 15**	**BIO 16**	**BIO 17**	**BIO 18**	**BIO 19**
Acca sellowiana	750.56	16.96	10.67	54.73	314.77	26.79	7.29	19.49	18.00	15.28	20.64	13.11	1636.75	177.80	101.83	18.26	486.21	343.31	465.17	362.90
Blepharocalyx salicifolius	561.97	18.09	10.40	54.02	315.87	27.70	8.45	19.25	19.79	15.81	21.82	14.21	1562.37	184.49	87.37	24.11	506.33	296.59	483.28	321.11
Calyptranthes concinna	721.62	18.02	11.43	58.01	300.99	27.59	7.93	19.66	19.89	15.70	21.49	14.25	1601.19	181.99	90.68	22.33	494.23	317.19	476.67	340.78
Calyptranthes tricona	491.12	18.58	10.82	54.57	320.43	28.51	8.73	19.78	20.90	15.46	22.31	14.64	1606.52	181.60	95.76	20.26	488.80	320.08	470.64	341.20
Campomanesia guazumifolia	609.22	18.67	11.55	57.67	306.76	28.34	8.33	20.02	20.46	16.48	22.19	14.81	1594.65	190.45	87.05	26.62	514.90	301.35	490.08	324.25
Campomanesia xanthocarpa	607.70	18.30	10.85	55.95	304.55	27.76	8.45	19.31	20.52	15.97	21.84	14.51	1592.99	190.91	86.90	25.98	518.56	300.81	500.98	323.52
Eugenia burkartiana	540.97	18.89	10.86	55.99	306.62	28.26	8.96	19.30	21.79	15.77	22.44	15.03	1616.55	202.45	83.98	28.42	545.99	290.27	536.84	310.70
Eugenia hiemalis	393.97	19.24	10.76	55.13	315.13	28.76	9.31	19.45	20.67	17.37	22.87	15.29	1495.48	175.46	81.85	24.78	479.27	281.47	461.38	313.64
Eugenia involucrata	551.66	18.53	10.55	55.26	303.43	27.87	8.87	18.99	21.00	15.85	22.06	14.76	1605.27	196.31	85.06	27.80	534.63	291.24	520.02	311.67
Eugenia mansoi	140.64	19.24	11.06	50.58	392.82	30.71	8.85	21.86	20.55	17.89	23.99	14.58	1621.43	170.71	105.21	14.50	476.64	344.14	433.21	350.93
Eugenia rostrifolia	259.24	18.76	9.62	50.77	329.18	28.59	9.70	18.89	19.14	17.55	22.60	14.79	1596.98	164.65	105.13	13.89	456.61	347.84	429.34	374.63
Eugenia verticillata	147.56	21.00	9.09	52.14	289.32	29.51	12.08	17.44	23.70	18.16	24.48	17.47	1803.08	243.71	76.56	39.15	690.92	257.77	675.28	264.21
Eugenia uniflora	490.42	18.62	10.51	54.73	311.40	28.13	8.95	19.18	20.22	16.57	22.26	14.78	1597.52	189.58	87.80	24.47	517.59	303.05	489.84	331.01
Eugenia uruguayensis	404.53	18.12	10.00	51.50	335.40	28.06	8.66	19.40	17.37	17.98	22.07	14.04	1503.24	160.66	93.87	17.04	445.38	314.59	416.30	360.04
Myrcia palustris	438.53	18.44	9.87	52.61	313.99	27.78	9.10	18.68	19.69	16.69	22.18	14.61	1581.68	184.61	88.66	23.38	512.50	299.08	497.15	322.83
Eugenia myrcianthes	315.24	19.08	10.34	53.25	327.27	28.76	9.40	19.37	18.82	19.22	22.92	15.06	1489.88	172.26	85.18	22.54	466.12	291.24	441.54	339.28
Myrceugenia euosma	755.35	17.16	11.05	55.62	316.46	27.10	7.24	19.86	18.73	15.53	20.85	13.27	1614.28	181.05	97.25	19.88	489.41	332.73	470.13	355.98
Myrceugenia glaucescens	648.79	17.56	10.41	54.30	312.98	27.32	8.12	19.21	18.56	16.01	21.22	13.74	1641.45	186.54	96.78	22.09	510.51	327.00	483.66	346.58
Myrceugenia miersiana	663.08	17.92	10.25	55.05	296.41	26.97	8.46	18.52	20.53	15.21	21.41	14.25	1565.47	193.22	82.03	28.00	527.28	281.75	518.47	296.28
Myrceugenia myrtoides	139.30	18.91	9.91	49.35	362.30	29.52	9.44	20.08	18.83	18.05	23.15	14.57	1496.07	147.03	102.47	11.33	419.26	333.41	391.41	361.24
Myrcia oblongata	844.44	16.98	10.96	56.47	302.06	26.51	7.10	19.41	17.55	15.12	20.54	13.25	1617.56	184.56	93.65	22.51	507.40	319.17	482.36	339.10

Table 2 cont. (...)

	Alt	**BIO1**	**BIO2**	**BIO3**	**BIO4**	**BIO5**	**BIO6**	**BIO7**	**BIO8**	**BIO9**	**BIO 10**	**BIO 11**	**BIO 12**	**BIO 13**	**BIO 14**	**BIO 15**	**BIO 16**	**BIO 17**	**BIO 18**	**BIO 19**
Myrcia selloi	450.38	18.44	9.81	51.84	322.37	28.05	9.20	18.85	19.80	16.66	22.28	14.52	1594.84	187.33	90.90	23.78	517.81	303.46	490.57	325.63
Myrcianthes cisplatensis	113.41	18.73	10.24	47.83	397.09	30.02	8.71	21.31	17.99	17.81	23.62	14.02	1415.61	145.48	87.09	15.40	406.09	293.46	354.02	336.02
Myrcianthes gigantea	685.25	17.25	10.68	54.38	321.11	27.08	7.46	19.62	18.15	15.75	21.03	13.33	1624.85	175.24	100.45	17.69	480.22	343.55	462.73	365.12
Myrcianthes pungens	491.91	18.36	10.77	53.92	331.96	28.59	8.60	20.00	18.84	16.95	22.20	14.30	1581.65	170.31	99.47	17.23	468.35	333.22	432.20	356.52
Myrciaria cuspidata	484.53	18.53	10.55	54.24	319.76	28.28	8.84	19.44	19.72	16.78	22.23	14.59	1518.24	172.08	89.48	21.63	473.07	301.91	439.92	336.33
Myrciaria tenella	593.33	17.97	10.73	54.67	318.13	27.72	8.12	19.60	19.53	16.04	21.66	14.04	1559.47	180.28	90.18	22.98	493.74	307.16	472.07	326.41
Myrhinium atropurpureum	578.59	17.35	10.21	52.59	327.15	27.27	7.88	19.39	17.15	16.51	21.22	13.38	1584.52	166.71	101.48	15.64	458.42	340.42	432.05	372.15
Plinia rivularis	506.70	19.87	11.63	59.13	291.16	29.18	9.56	19.62	22.60	16.73	23.17	16.14	1515.94	190.24	70.15	31.07	516.61	252.16	496.05	285.00
Plinia peruviana	577.24	18.57	11.24	57.08	305.74	28.13	8.50	19.63	19.82	17.42	22.08	14.73	1568.33	177.57	91.05	21.03	481.05	314.33	458.81	342.05
Psidium cattleianum	405.77	19.14	9.81	53.54	299.28	28.07	9.87	18.20	21.63	16.48	22.71	15.46	1643.02	206.93	82.12	29.78	572.82	280.02	556.98	298.00
Siphoneugena reitzii	698.32	17.71	10.35	55.01	299.20	26.99	8.27	18.72	20.31	15.54	21.23	14.04	1733.17	207.95	96.25	25.50	567.41	329.67	550.48	346.64

Table 3.Estimated values for the evolution mode (Pagel’sκ) of the morphological characters and AICc of the different evolutionary models tested. Bold numbers indicate the lowest AICc value (best model). VF = vessel frequency; VD = vessel diameter; VL = vessel length; DIVP = diameter of the intervessel pits; FL = fiber length.

			Traits		
Evol. Model	VF	VD	VL	DIVP	FL
Pagel’sκ	0	0.48	0.8	1.0	0.21
Brownian Motion	388.85	261.33	371.04	**176.22**	438.26
Ornstein-Uhlenbeck	**357.34**	**255.81**	**369.84**	178.54	**417.45**
Drift	391.23	263.78	373.24	178.43	440.68

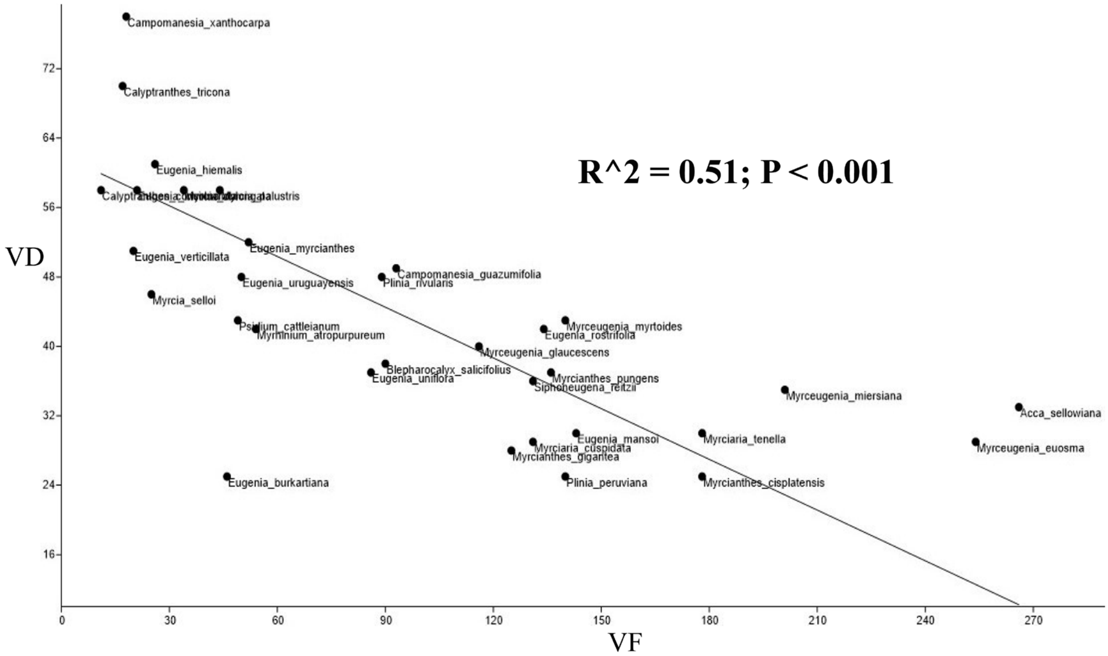

Figure 5. Linear regression showing inverse relationship between vessel frequency (VF) and vessel diameter (VD) in the Myrtaceae species analyzed.

However, because there are relatively few viable solutions to certain "problems", Myrtaceae species present a restricted range of combinations of the same characters, regardless of whether these are vegetative, reproductive or anatomical. Especially considering the latter attributes, environmental restrictions are even more influential, since they exert intense pressure on the establishment and survival of individuals, as far as they are directly linked to the acquisition and transport of water.

Ideally, in terms of competition for resources, individuals with a larger diameter of the xylematic vessels would have an evolutionary advantage, since this would increase the water capacity in the plant. However, this condition also increases the chance of embolisms. Although the Myrtaceae family has its origin and center of diversity in forests with high rainfall levels and low seasonality (e.g., Atlantic rainforest, annual precipitation >1,500 mm; Amorim *et al.* 2019), some species have evolved adaptations in order to tolerate environments subject to water stress, either occasional (e.g., Pampa Biome) or frequent (e.g., Cerrado Biome). To cope with this type of climate challenge, one of the evolutionarily stable strategies most used is making both the dimensions and the number of vessels malleable, since the presence of abundant vessels with short vascular elements provides greater safety for hydraulic conductivity in xeric environments (Lindorf 1994). This strategy can be observed in the analyzed Myrtaceae species, since the traits "length" and "frequency" of the vessels showed less phylogenetic signal, the latter also showing a saltatory evolution mode ($\kappa = 0$), that is, subject to sudden changes. In fact, regression tests we carried out contrasting vessel diameter against frequency showed that there is a significant negative relationship ($R^2 = 0.51$; $P < 0.0001$; Figure 5) between these two traits, a previously described trade-off pattern for the family (Marques *et al* 2007).

Moreover, when we observe that "vessel diameter" has a high phylogenetic signal (64%), it is clear that the evolutionarily stable strategy used by natural selection in the studied Myrtaceae species is one that increases the number of xylematic vessels, because even though embolisms occur in some vessels, the sap flow is ensured by others found in large numbers.

Finally, we found the trait "fiber length" to be highly plastic and adaptable, as it is one of the attributes with the lowest percentages of influence of ancestry and the highest correlations with climate variables. Although they do not have a direct role in the rise of the water column along the stem, the fibers have an auxiliary support function, influencing the wood density and its hygroscopic movement (Santini *et al.* 2016). Thus, the evolutionary lability of these elements can be of great value for some species to be able to establish themselves in environments different from that of their direct ancestors.

This is, so far, the first evolutionary study of Myrtaceae wood in which the authors tried not only to identify some patterns in the characteristics of the wood but also to hypothesize about their influence on diversification. It is important to note that the sample size and geographic area are small compared to the Myrtaceae family's species richness as a whole. Even so, we found interesting results that explain some peculiar aspects of this outstanding family. In short, we demonstrated that the wood anatomical traits of the selected Myrtaceae have relative homogeneity due mainly to evolutionary restrictions, which makes the species preferentially occur in areas with abundant and constant rainfall. Thus, the hypothesis of ecological speciation does not hold up, since the environment where species preferentially grow is relatively homogeneous, restricting the evolution of morphology around some optimal values.

It is imperative to emphasize the need for additional studies, involving a larger coverage area (*eg* Cerrado) and using other environmental variables (*eg* soil type), in order to clarify the putative evolutionary processes that cause the great diversity of Myrtaceae. Nonetheless, our results are potentially useful as a guide for several activities, for instance, fruit production, landscaping projects or even management and recovery of degraded areas. Additionally, since our findings suggest the existence of relative evolutionary inertia in the traits of Myrtaceae wood, this might restrict the type of environments in which certain Myrtaceae species can grow.

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