

JHONNY CAPICHONI MASSANTE

Phylogenetic structure of plant  
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gradients: a macroecological and  
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along environmental gradients:  
a macroecological and evolutionary approach



Department of Botany, Institute of Ecology and Earth Sciences,  
Faculty of Science and Technology, University of Tartu, Estonia

Dissertation was accepted for the commencement of the degree of *Doctor philosophiae* in Plant Ecology and Ecophysiology at the University of Tartu on 08 March 2021 by the Scientific Council of the Institute of Ecology and Earth Sciences University of Tartu.

Supervisor: Prof. Pille Gerhold, University of Tartu, Estonia

Opponent: Prof. Zdeňka Lososová, Masaryk University, Czech Republic

Commencement: MS Teams or Zoom, on 11 May 2021 at 10:15 a.m.

Publication of this thesis is granted by the Institute of Ecology and Earth Sciences, University of Tartu

ISSN 1024-6479

ISBN 978-9949-03-579-3 (print)

ISBN 978-9949-03-580-9 (pdf)

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University of Tartu Press  
[www.tyk.ee](http://www.tyk.ee)

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## LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which are referred to in the text by Roman numerals:

- I) **Massante, J.C.**, Götzenberger, L., Takkis, K., Hallikma, T., Kaasik, A., Laanisto, L., *et al.* (2019). Contrasting latitudinal patterns in phylogenetic diversity between woody and herbaceous communities. *Sci. Rep.*, 9, 6443.
- II) **Massante, J.C.** & Gerhold, P. (2020). Environment and evolutionary history depict phylogenetic alpha and beta diversity in the Atlantic coastal white-sand woodlands. *J. Veg. Sci.*, 31, 634–645.
- III) **Massante, J.C.**, Köbel, M., Pinho, P., Gerhold, P., Branquinho, C. & Nunes, A. (2020). Phylogenetic structure of understorey annual and perennial plant species reveals opposing responses to aridity in a Mediterranean biodiversity hotspot. *Sci. Total Environ.*, 144018.
- IV) **Massante, J.C.** & Gerhol, P. (2021). Evolutionary history of marginal habitats influences the diversity of tree communities in the Atlantic Forest. *Manuscript under review.*

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The author's contribution to the papers:

Was responsible for \*\*\*, contributed substantially \*\*, contributed \*

	I	II	III	IV
Study design	*	***	***	***
Data collection		***		***
Data analysis	***	***	***	***
Manuscript preparation	**	***	***	***

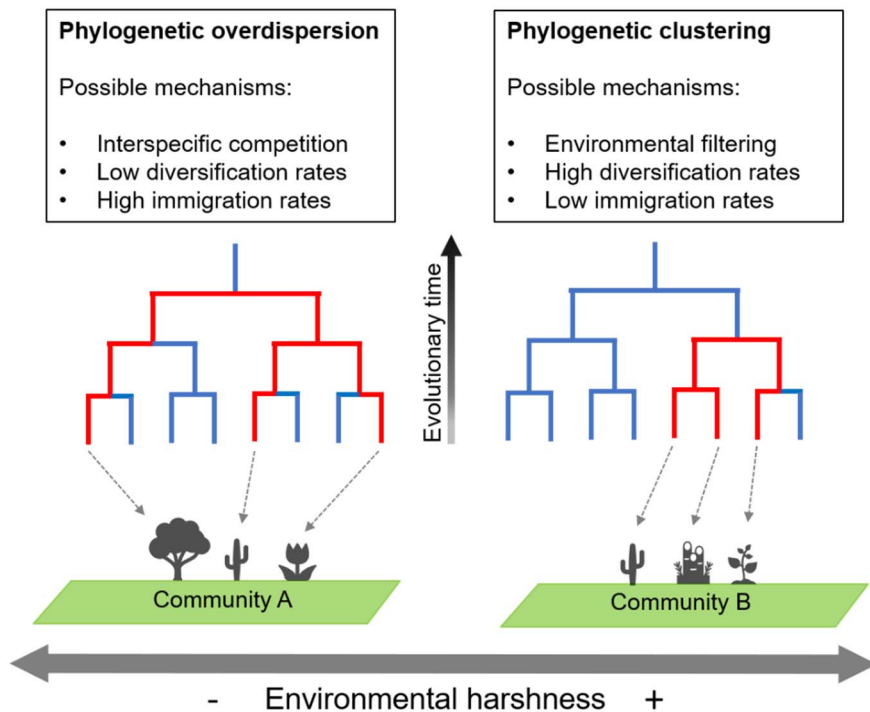
# 1. INTRODUCTION

## 1.1. Background

The distribution of biological diversity on Earth has fascinated naturalists for centuries, making the understanding of diversity patterns and their underlying mechanisms a long-standing goal in ecology and biogeography (Humboldt 1849; Whittaker 1956). Conversely, evolutionary biologists have deviated from that goal and focused on understanding evolutionary changes in organisms rather than how they could influence entire ecological communities. This decoupling between ecological and evolutionary studies prevailed until the second half of the 20<sup>th</sup> century, when ecologists and evolutionary biologists started investigating both mechanisms and diversity patterns (McGill *et al.* 2019). However, historically, studies addressing diversity patterns have focused on how the number of species is distributed along environmental gradients and across habitat types. For example, one of the earliest and most ubiquitous patterns on Earth is the latitudinal diversity gradient (LDG), in which the number of species decreases polewards (Hillebrand 2004; Mittelbach *et al.* 2007; Schemske & Mittelbach 2017; Kinlock *et al.* 2018). This striking pattern has been found in different taxa both from terrestrial and marine realms (Jablonski *et al.* 2013; Kerkhoff *et al.* 2014; Rolland *et al.* 2014; Piel 2018), although recent evidence has shown that it might not be universal (Fragnière *et al.* 2015; Gaucherel *et al.* 2018). Another conspicuous pattern is the decreasing species richness towards high elevations (Rahbek 1995; Antonelli *et al.* 2018). A clear clue of elevation gradients is the vegetation zonation in mountains, which varies at a far smaller spatial extent relative to LDG (Sanders & Rahbek 2012). It is evident that neither latitude nor elevation are real drivers of species richness. They are instead proxies for gradients in climatic variables, especially temperature (Willig *et al.* 2003). Moreover, species richness patterns along latitude and elevation depend on the way coexisting species are evolutionarily related to each other (phylogenetic relatedness), and how they are adapted to different climatic conditions. However, despite the recognition that ecological and evolutionary mechanisms are intertwined, and the balance between them underlies contemporary species diversity in ecological communities, integrating them to unravel diversity patterns is still challenging (Mouquet *et al.* 2012; Weber *et al.* 2017; McGill *et al.* 2019).

The implementation of the phylogenetic approach in community ecology over the last 20 years has offered a promising alternative to overcome the shortcomings of the classical approach of species richness to understand diversity patterns (Webb 2000; Webb *et al.* 2002; Cavender-Bares *et al.* 2009; Mouquet *et al.* 2012). Specifically, it is assumed that evolution plays a crucial role in the assembly of ecological communities, as coexisting species share evolutionary information that can be measured by the phylogenetic structure of a community (Webb *et al.* 2002). Two communities may have the same number of coexisting species but differ considerably in community phylogenetic structure due to the difference in the

way species have evolved and responded to different factors (Fig. 1). A community is phylogenetically clustered when coexisting species are evolutionarily closely related, whereas coexistence of distantly related species results in a phylogenetically overdispersed community (Cavender-Bares *et al.* 2009). The interpretation of these phylogenetic community structure patterns has been overly simplistic, focusing on ecological factors only, namely on the duality between environmental filtering and biotic interactions (Webb *et al.* 2002). Thus, assuming that species traits are conserved throughout evolutionary time, studies have suggested the environment and the interplay between competition and facilitation as drivers of non-random phylogenetic structure of coexisting species (Webb *et al.* 2002; Cavender-Bares *et al.* 2009; Vamosi *et al.* 2009; Valiente-Banuet & Verdú 2013). In communities where environmental filtering prevails,



**Fig. 1.** Schematic representation of phylogenetic community structure patterns. Both communities A and B display the same number of coexisting species. However, species in community A are phylogenetically distantly related (phylogenetic overdispersion), whereas species in community B are closely related (phylogenetic clustering). Some mechanisms that may be involved in the generation of these patterns are presented in the boxes. Red lines indicate the evolutionary path connecting extant coexisting species in communities, whereas blue lines indicate species that either were excluded or did not reach the community. Branch lengths were set to 1. The arrow between the two phylogenies indicates the evolutionary time before present. Copy of Fig. 1 in **III**.



phylogenetic clustering is expected because only a subset of evolutionary lineages may cope with the environmental stress. In contrast, in communities where competition between species is the most relevant factor, phylogenetic overdispersion is expected because closely related species often compete for the same resources, ultimately excluding weaker competitors (Webb *et al.* 2002).

However, traits may not always be conserved, nor competition necessarily leads to overdispersion (Mayfield & Levine 2010; Bennett *et al.* 2013; Gerhold *et al.* 2015). Additionally, in communities located under more extreme environmental conditions, facilitation may prevail over competition (Bertness & Callaway 1994) because some species may increase the realised niche of distantly related less tolerant species, therefore, increasing overdispersion (Butterfield *et al.* 2013; Pistón *et al.* 2016). The phylogenetic structure of communities may also depend on topo-edaphic variables such as soil fertility through habitat specialisation of lineages (Fine & Kembel 2011) and historical and macroevolutionary factors that have shaped the regional species pool (e.g., immigration and diversification, Ricklefs, 1987; Wiens, 2017; Zobel, 2016). Therefore, investigating diversity patterns through an integrative approach involving both ecological and evolutionary mechanisms offers the opportunity to understand how communities have been assembled and ultimately foster the improvement of predictions in ecology (Mouquet *et al.* 2012; Gerhold *et al.* 2018).

Climate is a powerful predictor of both species richness, phylogenetic diversity (i.e., the sum of evolutionary paths connecting species in a given community; Faith 1992) and phylogenetic structure of communities, globally (Kubota *et al.* 2018) and regionally (Kerckhoff *et al.* 2014; Qian & Sandel 2017). The phylogenetic diversity of mammals is unevenly distributed worldwide due to the variation in biogeographic history and diversification rate, with both processes reflecting global climatic gradients (Davies & Buckley 2011). Likewise, amphibian phylogenetic diversity can be traced back to past climate change, being unusually low on islands due to recent radiation of a few lineages and high in biogeographic contact areas (i.e. ecotones) due to high immigration or *in situ* diversification, combined with long-term persistence of old lineages (Fritz & Rahbek 2012). Angiosperm woody plant communities tend to be phylogenetically clustered in drier and historically unstable regions, probably due to tropical niche conservatism (Kubota *et al.* 2018). At a regional scale, phylogenetic diversity of woody angiosperms is low in temperate regions of the American continent (Kerckhoff *et al.* 2014) as an outcome of the tropical conservatism of lineages (Wiens & Donoghue 2004). Tropical niche conservatism has also been suggested as the mechanism underlying the phylogenetic structure of tree angiosperms in North America, where increasing phylogenetic clustering towards regions with extremely dry and cold climates has been shown (Qian & Sandel 2017). However, studies addressing the phylogenetic structure of plant communities were so far focused on a specific taxonomic group (e.g. woody angiosperms) and did not consider other taxonomic groups (e.g. gymnosperms). Gymnosperms occupy large areas both in the Southern Hemisphere (e.g. Podocarpaceae and Araucariaceae) and Northern Hemisphere (e.g. Pinaceae) and show a physiological advantage over angiosperms

in cold and dry regions (Bond 1989). Additionally, the presence of different growth forms (i.e. woody and herbaceous species) along the latitudinal gradient depends on their response to climatic variables that correlate with latitude (Engemann *et al.* 2016). Therefore, plant communities of different growth forms may show different responses to latitude. However, there is still insufficient knowledge about plant communities worldwide, with no global-scale study undertaken to examine variation in the phylogenetic structure across a wide taxonomic range of plant communities.

Recently, an increasing number of studies focus on how species are affected by contemporary climate change and anthropogenic factors (e.g. desertification and habitat fragmentation). It has been proposed that changes in species immigration due to climate change will likely affect the phylogenetic diversity of plants, birds, and mammals in Southern Europe in the coming decades (Thuiller *et al.*, 2011). Likewise, rapid climate change may drive spatial phylogenetic homogenisation of woody species (Saladin *et al.* 2020). Among several threatened regions worldwide, coastal plant communities are perhaps the most critical. For example, the coastal vegetation of the South American Atlantic forest domain (hereafter AFD), also called restinga, has undergone massive fragmentation due to human occupation (Neves *et al.* 2017), and the number of extinct species and their evolutionary history is still unknown. Restingas originated in the Quaternary as a result of climatic instability and sea-level rise, and occur in Pleistocene and Holocene sandy sediments of marine origin along over 3,000 km of the Brazilian coast (Martin *et al.* 1993; Scarano 2002). Since climatic instability promoted forest contraction in the southern part of the AFD, whereas large forests remained historically stable in their central range (Carnaval & Moritz 2008), it might be expected that restingas have been influenced by the presence of both temperate and tropical lineages in southern Brazil (Duarte *et al.* 2014) in contrast to central regions of the AFD dominated by tropical lineages. As restingas comprise a geologically young ecosystem, there has been no time for local diversification (Scarano 2002); thus, the contemporary phylogenetic structure may reflect dispersal from neighbouring rainforests. Restingas have also experienced high soil salinity as the major environmental filter for plant species (Neves *et al.* 2017), and there are significant differences in phylogenetic community structure due to edaphic heterogeneity (Oliveira *et al.* 2014). However, no study has been undertaken to understand broad-scale patterns of phylogenetic structure in restingas and their relationship with contemporary and historical climatic variables.

An aspect of the current climatic threat is the risk of desertification due to increasing water scarcity (i.e., aridity) in some regions of the globe. Aridity is a critical factor for species diversity, especially in drylands that occupy ca. 41% of the land surface on Earth (Reynolds *et al.*, 2007). Recent evidence shows that different aspects of drylands are lost with increasing aridity, starting with plant productivity, followed by soil fertility and plant cover and richness (Berdugo *et al.* 2020). Comparably important for ecosystem functioning (Cadotte *et al.* 2009), but with controversies (Venail *et al.* 2015), the phylogenetic diversity and structure of plant communities in drylands have been far less understood than species

richness. Studies commonly address the influence of aridity on the phylogenetic structure of either perennial (e.g., Soliveres *et al.* 2012; Gong *et al.* 2019) or annual species (e.g., García-Camacho *et al.* 2017) separately and in different drylands. Annual and perennial species are found co-occurring along aridity gradients and are subjected to an interplay between facilitation and competition (Holzapfel *et al.* 2006). The difference in their life history strategies requires specific adaptations to environmental conditions that lead to an establishment-longevity tradeoff (Tilman 1994). For example, annuals are strongly affected by interannual climatic variability (Tielbörger & Kadmon 1997), which ultimately interfere in seed germination, establishment and dispersal (Facelli *et al.* 2005). As opposed to annuals, perennials must endure stressful conditions during the summer drought in drylands, and do so through a balance between conservative and acquisitive strategies (Liancourt *et al.* 2005). Given the intertwined co-occurrence of annuals and perennials, understanding how their phylogenetic structure responds to aridity is essential to predict diversity in drylands under scenarios of increasing aridity worldwide (Dai 2013).

Predicted scenarios of climate change may also influence species diversity along elevation gradients. It has been shown that the number of plant species in mountains has dramatically increased due to the increase in temperature over the last 145 years (Steinbauer *et al.* 2018). Such a modification has profound consequences on different taxa's phylogenetic structure, especially plants (Zhu *et al.* 2020), as it may inevitably drive mountaintop extinctions (Colwell *et al.* 2008). Studies on phylogenetic community structure along elevation gradients have shown that patterns might be contingent on the taxon investigated and differences in habitat types, especially in the tropics (e.g., Graham *et al.* 2009; Kluge & Kessler 2011; Dehling *et al.* 2014; Bose *et al.* 2019). Such a remarkable discrepancy of patterns in tropical areas may be linked to the fact that habitat types within a specific region display contrasting evolutionary histories based on lineages from different geological epochs (Bartish *et al.* 2016). However, understanding how phylogenetic community structure varies between habitat types along tropical elevation gradients is still challenging (Bose *et al.* 2019). Such information is crucial to understanding the evolution of these habitat types and how they are evolutionarily connected. Ultimately it will allow a more comprehensive understanding of how these systems respond to the effects of climate change.

## 1.2. Objectives of the thesis

The main objective of this thesis is to address potential ecological and evolutionary mechanisms underlying phylogenetic plant community structure along environmental gradients, with particular attention to possible differences between different growth forms (i.e., woody and herbaceous species worldwide; Massante *et al.* 2019, **I**) and life-history strategies (i.e., annual and perennial species in drylands; Massante *et al.* 2020, **III**). In **I**, data were extracted from original published papers and combined into a global dataset, whereas in **III**, data were previously

collected by co-authors in southwest Europe. The thesis also addresses the phylogenetic structure of angiosperm tree species in response to environmental variables and climatic stability (Massante & Gerhold 2020, **II**) as well as elevation and different habitat types (Massante & Gerhold manuscript, **IV**). In both **II** and **IV**, data were retrieved from Tree Flora of the Neotropical region database (NeoTropTree; Oliveira-Filho 2017). Two complementary metrics of phylogenetic community structure were used to reflect the variation at basal (mean pairwise phylogenetic distance, MPD) and terminal phylogenetic levels (mean nearest taxon distance, MNTD) coupled with null models to control for the effect of species richness gradients (Swenson 2014b). Specifically, the thesis addresses the following questions:

- Paper **I**: How does the phylogenetic community structure of different growth forms (i.e., woody and herbaceous plant species) relate to latitude?
- Paper **II**: What are the relative effects of the current climate, historical climatic stability, and edaphic factors on the phylogenetic structure of angiosperm tree communities in geologically young restinga habitats along the Atlantic coast of Brazil?
- Paper **III**: How does the phylogenetic structure of annual and perennial plant communities respond to aridity in Mediterranean semi-natural dryland?
- Paper **IV**: How does the phylogenetic structure of angiosperm tree communities respond to elevation in different habitat types in the tropical South American Atlantic forest domain?

## 2. MATERIAL AND METHODS

### 2.1. Data collection

A global dataset was compiled from papers indexed in the libraries JSTOR (from 1700 until 1945) and ISI of Web of Knowledge (1945–2016) to investigate latitudinal patterns in the phylogenetic structure of plant communities (paper **I**). Simultaneous occurrence of the keywords “community”, “vegetation”, “species list”, and “plant” were used. To be included in the analysis, papers must have had a full species list regardless of the sampling method (plots, transects, regional surveys). A community was recognised when there were coexisting species recorded in the sampling units. The dataset was further separated into woody communities (trees and shrubs) and herbaceous communities based on the information provided by the authors of the original studies. There were 223 woody communities added from Alwyn Gentry’s dataset (Phillips & Miller 2002), previously available from [http://salvias.net/pages/database\\_info.php](http://salvias.net/pages/database_info.php), now maintained by the Botanical Information and Ecology Network (BIEN – <https://bien.nceas.ucsb.edu/bien/>). Sampling unit size ranged from  $< 1 \text{ m}^2$  in herbaceous communities to  $> 1 \text{ km}^2$  in woody communities. Communities composed of both woody and herbaceous species and partial species lists (e.g. list of dominant species) were excluded from the analysis. Aquatic communities, communities located in anthropogenic habitats, and communities with fewer than three species were also excluded. Overall, there were 459 woody communities with 8,753 species and 589 herbaceous communities with 1,847 species. Woody communities included forests, scrublands and savannas, whereas herbaceous communities included the herbaceous layers of forests, grasslands, meadows, outcrops, salt marshes and dunes. Communities were located between the latitudes of  $54.79^\circ\text{S}$  and  $60.67^\circ\text{N}$  of the equator (Fig. 1 in **I**).

In paper **II** and **IV**, data were retrieved from the Tree Flora of the Neotropical Region database (NeoTropTree – NTT; Oliveira-Filho, 2017). In paper **II**, the phylogenetic diversity of coastal white-sand plant communities (called *Restingas* in Brazil) was analysed. In general, restingas are a mosaic of vegetation that originated in the Quaternary, occurring in Pleistocene and Holocene sandy sediments (Martin *et al.* 1993). Data of 136 restinga communities with 960 tree species, spanning  $20^\circ$  of latitude (Fig. 1 in **II**) were retrieved from the database. Communities were classified as northern, central, and southern restingas based on biogeographic and ecological information (Oliveira-Filho 2017). Southern restingas are considered older than restingas of central Brazil (Delaney 1962; Roncarati & Menezes 2005). Therefore southern restingas have experienced larger climatic instability due to stronger effects of the Quaternary sea-level rise (Delaney 1962). As paper **IV** investigated elevation gradients and differences in species richness and phylogenetic structure between the Atlantic rainforest and its marginal habitat types, data were retrieved for 108 communities within an area of  $\sim 44,000 \text{ km}^2$  (Fig. 1 in **IV**) that included 2,074 tree species. These communities

are located in a gradient spanning more than 2,000 meters above sea level and four different habitat types (including the rainforest, cloud forest, semideciduous forest and restinga). In both papers **II** and **IV**, the community is a circular area of 10k diameter in which species presence/absence was recorded.

In paper **III**, data were previously collected by members of the Environmental Changes (eChanges) workgroup from the University of Lisbon, with whom the study was developed. The data comprises 54 sites selected through a stratified random selection approach based on the United Nations aridity index (AI; Middleton and Thomas, 1997). These sites are located in Mediterranean drylands dominated by Holm-oak (*Quercus ilex*) woodlands in the southwestern Iberian Peninsula (Fig. S1 in **III**). The sampling of the understorey of Holm-oak woodlands was performed in April-June 2012 to optimise species identification. The point-intercept method was used to estimate plant cover. Six 20 m transects were systematically arranged over an area of ca. 1000 m<sup>2</sup> and 10 m apart from each other, with points spaced every 50 cm (246 points per site) (Nunes *et al.* 2015). At each point, a rod of 5 mm diameter was stuck to the ground with a 90° angle, and all plant species touching the rod only once at each point were recorded. Then, the species cover as the proportion of points intercepted along the six transects was estimated. There were 282 species from 41 families. The original dataset was separated into datasets composed of 191 annual species and 91 perennial species, respectively.

In all papers, species names were standardised according to The Plant List (<http://www.theplantlist.org/>) using the R package ‘Taxonstand’ (Cayuela *et al.* 2012) to match the nomenclature available in megaphylogenies. Synonyms of species were merged to their accepted names before further analysis.

## 2.2. Phylogeny and phylogenetic diversity

### 2.2.1. Phylogenetic trees

A megaphylogeny approach was used to produce the phylogenetic trees of interest in all papers. The use of megaphylogenies has been demonstrated to be a powerful tool in community phylogenetic analysis because the results obtained with them strongly correlate with the results obtained with precise purpose-built phylogenies (Li *et al.* 2019).

In paper **I**, the most updated megaphylogeny for seed plants available at that time was used, which comprised 79,881 taxa (Smith & Brown 2018), as a backbone to construct a phylogenetic tree containing all species in the dataset. The R function ‘S.PhyloMaker’ (Qian & Jin 2016) was used to bind species into the backbone within their parental taxa with dated branch lengths. Further, the complete phylogenetic tree was pruned down to two phylogenies that only included either woody or herbaceous species. In paper **II**, **III**, and **IV**, an updated version of the megaphylogeny proposed by Smith and Brown (2018) was used, including plant species from 479 monophyletic families (Jin & Qian 2019).

Species were bounded into the backbone using the same approach as in paper **I** but using the new R package ‘V.PhyloMaker’ (Jin & Qian 2019). Because gymnosperm and pteridophyte species were rare in all communities in papers **II** and **IV**, they were removed from the dataset to prevent bias in the phylogenetic analysis (Massante *et al.* 2019). Gymnosperms and pteridophytes were absent in paper **III**.

### 2.2.2. Phylogenetic structure

The term phylogenetic diversity was used in papers **I** and **II** for simplicity. However, as the used indices reflect the community phylogenetic structure of coexisting species, in paper **III** and **IV**, this term was updated to the most commonly used term, “phylogenetic structure”, and kept in the present thesis. Two complementary indices were used to investigate the variation in the phylogenetic structure at both basal and terminal phylogenetic levels: mean pairwise phylogenetic distance (MPD) and mean nearest taxon distance (MNTD), respectively. MPD is considered a ‘basal phylogenetic metric’ because it estimates phylogenetic distances across the whole phylogenetic tree by averaging all species pairwise distances (Swenson 2014a). MNTD estimates phylogenetic distances at the phylogenetic tree tips, i.e. between each species and its closest relative, thus being considered a ‘terminal phylogenetic metric’ (Swenson 2014a). Gradients in species richness often influence phylogenetic indices (Miller *et al.* 2017). For example, MPD does not correlate with species richness, but its variance decreases with an increase in species richness, whereas MNTD decreases with species richness (Miller *et al.* 2017). Therefore, the standardised effect size of both indices (SESmprd and SESmntd) was calculated to account for the influence of species richness on community phylogenetic analysis. The observed indices values in the communities were compared to a null distribution of randomised communities (N = 1000 randomisations) with equal species richness (eq. 1). Because there was information on the relative abundance of species in paper **III**, the abundance was taken into account using the argument ‘abundance.weighted = TRUE’ implemented in the R package ‘picante’ (Kembel *et al.* 2010). The standardised values of MPD and MNTD are opposite in sign to the common used net related index (NRI) and nearest taxon distance index, respectively (Webb 2000).

$$\text{SESmprd} = \frac{\text{MPD}_{\text{observed}} - \text{MPD}_{\text{null}}}{\text{sd}(\text{MPD}_{\text{null}})} \quad (1),$$

where  $\text{MPD}_{\text{observed}}$  is the observed MPD in the community,  $\text{MPD}_{\text{null}}$  is the average of the expected MPD in the randomised communities (n = 1000 randomisations), and  $\text{sd}(\text{MPD}_{\text{null}})$  is the standard deviation of 1000  $\text{MPD}_{\text{null}}$  values.  $\text{SESmntd}$  was calculated based on equation (1) by replacing MPD with MNTD.

### 2.2.2. Taxonomic and phylogenetic beta diversity

Patterns of phylogenetic beta diversity were investigated in paper **II**, and taxonomic and phylogenetic spatial turnover in papers **III** and **IV**. In paper **II**, phylogenetic beta diversity was calculated at basal phylogenetic levels using mean phylogenetic dissimilarity between species in pairs of communities (Dpw, equivalent to the phylogenetic alpha diversity index MPD; Swenson, 2011). The mean nearest taxon distance separating species in two communities (Dnn, equivalent to the phylogenetic alpha diversity index MNTD; Swenson 2011) was used to capture phylogenetic beta diversity variation at terminal phylogenetic levels. Both indices were calculated in the R package ‘picante’ (Kembel *et al.* 2010). The focus in papers **III** and **IV** was on how species and lineages are replaced along environmental gradients as well as between different habitat types. The turnover component from the Sørensen pairwise dissimilarity, known as Simpson dissimilarity index, is not influenced by species richness gradients (i.e. nestedness – when communities with a low number of species are a subset of communities with a high number of species; Baselga 2010; Leprieur *et al.* 2012) was used as a measure of species turnover between communities. The R functions ‘beta.pair’ and ‘phylo.beta.pair’ in the R package ‘betapart’ (Baselga & Orme 2012) were used to calculate taxonomic and phylogenetic turnover, respectively. Further, in paper **IV**, the effects of nestedness on the overall taxonomic and phylogenetic beta diversity were accessed by calculating the relative importance of the nestedness-resultant component (BDratio and PBDratio, respectively) as follows:

$$\text{BDratio} = \frac{\text{BDnestedness}}{\text{BD}} \quad (2),$$

where BDnestedness is the nestedness-resultant component of the Sorensen pairwise dissimilarity index, and BD is the full Sorensen index (Baselga 2010). Values lower than 0.5 indicate that the variation in BD is basically influenced by spatial turnover. Values higher than 0.5 indicate that variation in BD results from differences in species richness between communities (Dobrovolski *et al.* 2012; Peixoto *et al.* 2017). PBDratio was calculated by replacing values in (2) with those produced with ‘phylo.beta.pair’. In that case, PBDnestedness represents the difference in Faith’s phylogenetic diversity(PD) between communities.

### 2.3. Environmental variables

The climatic variables used in most papers were originally retrieved from the database WorldClim at 1 km<sup>2</sup> resolution (Hijmans *et al.* 2005). In paper **II** and **IV**, environmental variables, including climatic and topo-edaphic measures, were already available from the NTT database (Oliveira-Filho 2017). In paper **II**, annual mean temperature and annual precipitation for the Last Glacial Maximum



(LGM, ~21,000 years before present; Hijmans *et al.* 2005) were also extracted and then used to calculate the absolute difference between current and past variables as a proxy for climatic stability to test its influence on the phylogenetic community structure of tree communities. The aridity index (AI) data used in paper **III** were retrieved from the global aridity database (<http://www.cgiar-csi.org/data/global-aridity-and-pet-database>; Trabucco and Zomer, 2009). The AI represents the ratio of annual precipitation to annual potential evapotranspiration, and its values increase with the decrease in aridity. The complement of the AI (1-AI, hereafter aridity) was used to ease interpretation. In that case, lower values indicate lower aridity (Delgado-Baquerizo *et al.* 2013). In paper **III**, the local slope and its standard deviation within a 250 m radius circular area around the site centroid were estimated as a measure of topographic roughness, based on digital elevation models with 10 m resolution using ArcGIS 10.1 (ESRI 2010). Edaphic variables were obtained by collecting soil samples at each site from the upper 10 cm (composite samples of 5 subsamples) and used to calculate soil nutrient content (soil organic matter, soil N, soil C, and C/N ratio).

The analysis of phylogenetic beta diversity in paper **II** and taxonomic and phylogenetic turnover in papers **III** and **IV** requires dissimilarity matrices between communities, in which the dissimilarity may be calculated using a variety of spatial and environmental variables. A matrix of geographic distance between communities was calculated using the function ‘spDists’ in the R package ‘sp’ (Pebesma & Bivand 2005; Bivand *et al.* 2013) and the Great Circle distance (WGS84 ellipsoid). Then a matrix of the environmental distance between communities was calculated in two steps. First, a principal component analysis (PCA) was applied on environmental variables relevant for the study system, available from each dataset (15 climatic variables in paper **II**, 20 in paper **III**, and 16 in paper **IV**) using the R function ‘prcomp’ (R Core Team 2017). All variables were scaled to have unit variance before calculation. The scores of the first three PCA axes were retrieved. A dissimilarity matrix was then calculated using the ‘dist’ R function (R Core Team 2017) coupled with the ‘Euclidian’ distance method.

## 2.4. Data analysis

In papers **I**, **II**, and **IV**, there was spatial autocorrelation in the data, and it was accounted for by fitting all models with an additional term describing the correlation structure using the ‘corExp’ function in the R package ‘nlme’ (Pinheiro *et al.* 2017). All continuous variables were centred and scaled to have zero mean and unit variance before parameter estimation to make them comparable within the models.

Due to the hierarchical nature of the data in paper **I**, patterns of SESmpd and SESmntd in both woody and herbaceous communities along the latitudinal gradient were analysed with linear mixed-effect models (LMM) using the function ‘lme’ in the R package ‘nlme’ (Pinheiro *et al.* 2017). Alternative models including combinations of latitude with biogeographic realms (Afrotropical, Australasian,

Indo-Malayan, Nearctic, Neotropical, Palearctic) as well as habitat types as fixed effects factors, and study identity as a random factor were built and compared using Akaike Information Criterion values (AIC; Burnham & Anderson 2004). Sampling unit size was included as a covariate in the fixed effects variables of all models to account for its influence on the response variables.

In paper **II**, the effect of latitude and climatic and edaphic factors on SESmpd and SESmtd was explored with generalised least square models (GLS) using the ‘gls’ function in the R package ‘nlme’ (Pinheiro *et al.* 2017). A model selection approach with the lowest Akaike Information Criterion values (AIC; Burnham and Johnson, 2004) was used as an indicator of the most parsimonious models. The final models were then refitted using restricted maximum likelihood (REML). Latitudinal patterns of the overall species richness and species richness in the ten most diverse families in restingas were also investigated using GLS.

In papers **III** and **IV**, *a priori* decision based on ecological relevance and collinearity (Pearson’s correlation  $< 0.7$ ) was used to select variables for statistical analysis, reaching out to six and five variables, respectively. Further, a model averaging approach based on Akaike Information Criterion (AIC; Burnham and Johnson, 2004) was applied to the variables using the R package ‘MuMIn’ (Barton 2019). Coefficients of each variable were estimated by averaging them across all models, then weighted according to the probability associated with each model. As there was no spatial autocorrelation in the data of paper **III**, they were analysed using ordinary least square models (OLS). In paper **IV**, data were analysed using GLS.

Because the use of partial Mantel tests on dissimilarity matrices has been criticised (Legendre & Legendre 2012), a residual approach was adopted to analyse phylogenetic beta diversity in paper **II** and taxonomic and phylogenetic spatial turnover in papers **III** and **IV**. First, linear models were fitted with dissimilarity matrices of diversity as a dependent variable and either the geographic or environmental dissimilarity matrices between communities, including both linear and quadratic terms, as an independent variable (e.g. phylogenetic beta diversity vs geographic distance). Each of these models’ residuals was extracted, representing the amount of phylogenetic beta diversity or taxonomic and phylogenetic spatial turnover not explained by geographic or environmental dissimilarity matrices. Mantel tests with 1000 randomisations were used to test the correlation between phylogenetic beta diversity and taxonomic and phylogenetic turnover with geographic and environmental dissimilarity matrices after accounting for each other’s effects (residuals from each linear model), using the ‘mantel’ function on the ‘ecodist’ R package (Goslee & Urban 2007). In paper **III**, the total variance in taxonomic and phylogenetic spatial turnover was partitioned into fractions explained by space (PCMN vectors; Borcard and Legendre, 2002), climate (matrix including aridity, winter temperature, and summer precipitation), and topo-edaphic variables (slope SD, soil nutrients, and soil C/N ratio) using the function ‘varpart’ in the ‘vegan’ R package (Oksanen *et al.* 2019). In paper **IV**, both taxonomic and phylogenetic spatial turnover across different habitat types were visualised using non-metric multidimensional scaling (NMDS). Differences

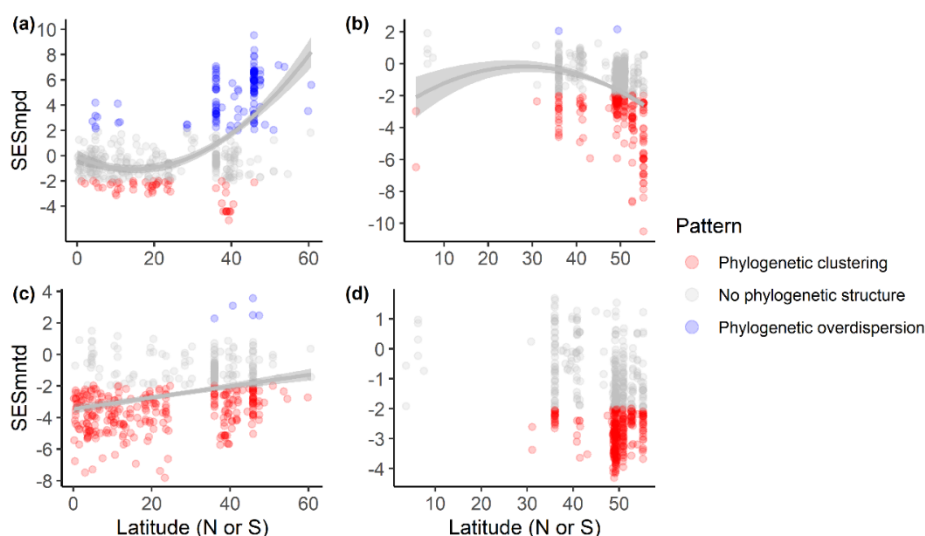
between habitat types were tested using analysis of similarity (ANOSIM) with 1000 permutations in the ‘vegan’ R package (Oksanen *et al.* 2019).

All statistical analyses performed in papers **I–V** were carried out in R version 3.4.3 (R Core Team 2017), and figures were produced using the R package ‘ggplot2’ (Wickham 2016).

### 3. RESULTS

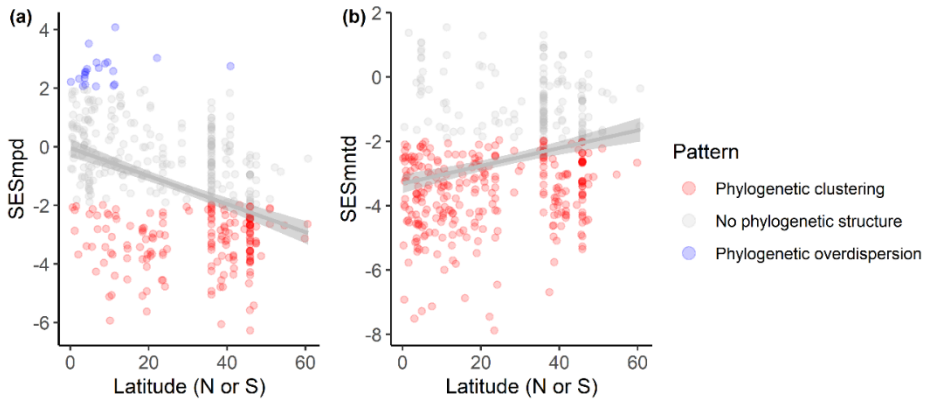
#### 3.1. Woody and herbaceous communities display contrasting latitudinal patterns of phylogenetic structure

There were contrasting latitudinal patterns in woody and herbaceous plant communities. In woody communities, SESmpd, which estimates variation at basal levels of phylogeny, showed a concave-up relationship with latitude, whereas SESmntd (variation at terminal levels of phylogeny) increased linearly (Fig. 2a, c). In herbaceous communities, SESmpd showed a concave-down relationship with latitude, whereas SESmntd did not show a clear relationship (Fig. 2b, d).



**Figure 2.** Effect of latitude on the phylogenetic structure of plant communities. The standardised effect size of mean pairwise distance (SESmpd) in woody (a) and herbaceous (b) communities. The standardised effect size of mean nearest taxon distance (SESmntd) in woody (c) and herbaceous (d) communities. Lines represent the top-ranked models' predicted values (Full parameter estimates are available in Table 2 in I). Shaded areas represent 95% confidence intervals. Modified from figure 2 in I.

While habitat type (closed, semi-open, open) influenced patterns of SESmpd in woody communities, it was the most crucial variable for both SESmpd and SESmntd in herbaceous communities, in which both indices were comparably lower in open habitats than in closed ones (Table 2 in I; Fig. S2b and d in I). Despite an overall phylogenetic clustering in SESmpd, herbaceous communities showed lower values of SESmpd in the Neotropical and Palearctic biogeographic realms than in the Afrotropical realm (Table 2 in I; Table S2 and Fig. S2a in I). Once gymnosperm species were removed from woody communities, an opposite pattern of SESmpd related to latitude appeared: SESmpd decreased towards higher latitudes (Fig. 3a), whereas SESmntd was not affected by the removal of gymnosperms (Fig. 3b).

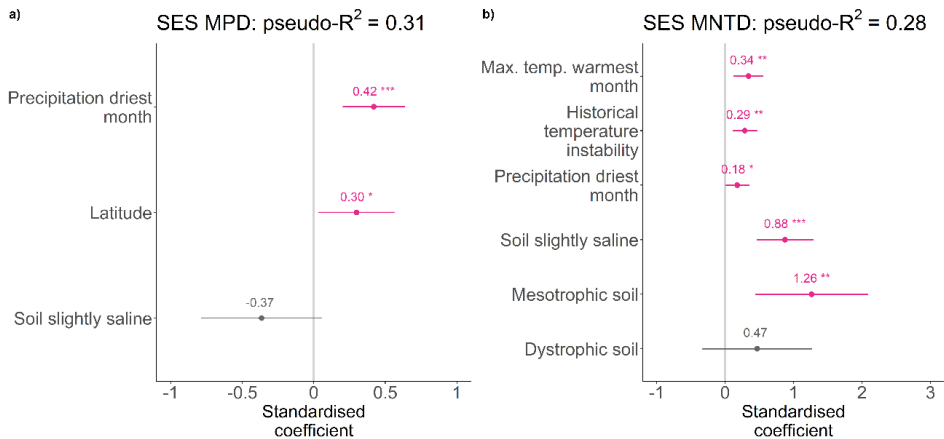


**Figure 3.** Effect of latitude on the phylogenetic structure of woody communities without gymnosperm species. **(a)** The standardised effect size of mean pairwise distance (SESmpd). **(b)** The standardised effect size of mean nearest taxon distance (SESmntd). Lines represent the top-ranked models' predicted values (Full parameter estimates are available in Table S3 in **I**). Shaded areas represent 95% confidence intervals. Modified from figure S3 in **I**.

### 3.2. Taxonomic and phylogenetic patterns of Atlantic white-sand coastal vegetation (restingas) in response to differences in climate and soil

The overall angiosperm tree species richness and species richness in the most dominant families showed a unimodal relationship with latitude in restingas (Fig. 2 and 3 in **II**). Both indices of phylogenetic structure showed an overall positive relationship with latitude towards southernmost restingas (Fig. S2 in **II**). SESmpd was lower in northern restingas (Fig. S5c in **II**) than in central and southern restingas. SESmntd was lower in northern and central restingas than in southern restingas (Fig. S5d in **II**).

After accounting for other environmental variables, the phylogenetic structure of restinga communities was no longer correlated with latitude, at least in SESmntd. While SESmpd correlated with precipitation of the driest month and latitude (Fig. 4a), SESmntd positively correlated with the maximum temperature of the warmest month and precipitation of the driest month, as well as historical temperature instability (Fig. 4b). SESmntd also tended to be higher in communities with more fertile and less saline soils (Fig.4b). There was no correlation between phylogenetic beta diversity at basal phylogenetic levels (Dpw) and spatial or environmental distances between communities (Fig. 5a and b in **II**). At terminal phylogenetic levels (Dnn), phylogenetic beta diversity correlated with spatial and environmental distances between communities (Fig. 5c and d in **II**).

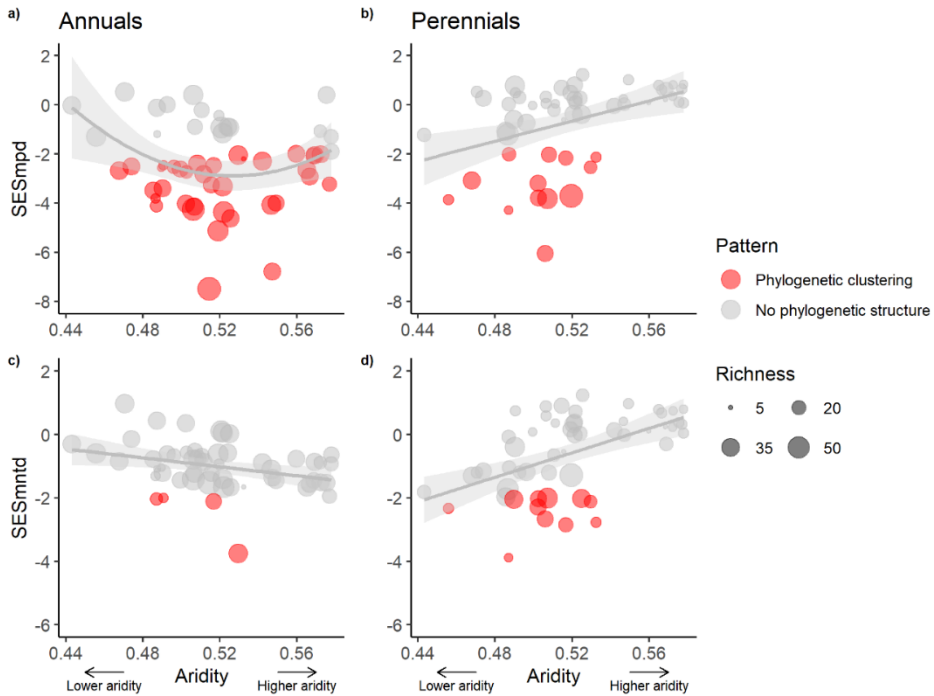


**Figure 4.** Standardised regression coefficients of model predictors and associated 95% confidence intervals (CI) for the phylogenetic structure of angiosperm tree communities in the Atlantic white-sand coastal woodlands (restingas). **(a)** The standardised effect size of the mean pairwise distance (SESmpd) and **(b)** the standardised effect size of the mean nearest taxon distance (SESmntd). CIs that do not cross the zero line are coloured in green and indicate a statistically significant effect (\*\*\*,  $p < 0.0005$ , \*\*,  $p < 0.005$ ; \*,  $p < 0.05$ ) on changes in the phylogenetic structure. Pseudo-R<sup>2</sup> values were calculated as the square of the correlation between fitted and observed values in the models. Full parameter estimates are available in Table S5.1 and S5.2 in II. Copy of Fig. 4 in II.

### 3.3. Phylogenetic structure of annual and perennial species along an aridity gradient in a Mediterranean dryland

Annual species richness did not show a clear pattern along the aridity gradient, whereas perennials showed a unimodal relationship (Fig. 2a and b in III). In both cases, there was a high dispersion of values at intermediate aridity levels. After accounting for other climatic and topo-edaphic variables, annual richness decreased with topographic heterogeneity, whereas that of perennials decreased with aridity and increased with winter temperature (Fig. 4a and b in III).

The phylogenetic structure of annuals and perennials showed opposite relationships with aridity. In annuals, SESmpd showed a quadratic relationship (quadratic slope =  $3.81 \pm 1.63$ ,  $p = 0.024$ ; Fig. 5a), and SESmntd decreased linearly with aridity (linear slope =  $-7.06 \pm 2.92$ ,  $p = 0.019$ ; Fig. 5c). Both indices showed phylogenetic clustering at intermediate to high aridity level. In perennials, both SESmpd and SESmntd showed a positive linear relationship with aridity, being more clustered in communities with lower aridity (SESmpd, linear slope =  $20.53 \pm 6.17$ ,  $p = 0.001$ ; SESmntd, linear slope =  $19.30 \pm 4.32$ ,  $p < 0.001$ ; Fig. 5b and d).



**Figure 5.** Phylogenetic structure of plant communities along the aridity gradient in Mediterranean drylands. SESmpd = the standardised effect size of the mean pairwise phylogenetic distance, and SESmtd = the standardised effect size of the mean nearest taxon distance. Lines and shaded areas represent the fitted values from linear regression with a quadratic (**a**) and a linear term (**b, c, d**), and their 95% confidence intervals, respectively. The size of the circle is proportional to the number of species in the community.

After combining aridity with other climatic and topo-edaphic variables, aridity was still a strong predictor of the phylogenetic structure of both annual and perennial communities. Both SESmpd and SESmtd of annuals negatively correlated with aridity and soil nutrient content, indicating clustering in drier communities and communities with higher soil nutrient content (Fig. 4c, e in **III**). In contrast, SESmpd and SESmtd of perennials were more clustered at both phylogenetic levels (SESmpd and SESmtd) in communities located at low to medium aridity and high soil C/N ratio (Fig. 4b, f in **III**).

There was a high taxonomic and phylogenetic turnover between plant communities in both annual and perennial species. After accounting for spatial effects, taxonomic and phylogenetic turnover of both annuals and perennials correlated with the environmental distance between communities (Table 1). Once controlled for the environmental effects, there was no correlation with the spatial distance between communities in either case (Table 1).

**Table 1.** Mantel test results comparing taxonomic and phylogenetic turnover of annual and perennial components of plant communities with spatial and environmental distances between communities. The relationship between taxonomic and phylogenetic turnover and spatial distance was calculated after accounting for the effect of the environmental distance (i.e. residuals of turnover ~ Env). The relationship between taxonomic and phylogenetic turnover and environmental distance was calculated after accounting for the spatial distance effect (i.e. residuals of turnover ~ spatial).

Life-history strategy	Response	Predictor	Mantel R [95% CI]	p-value
Annuals	Taxonomic turnover	Spatial Env	0.006 [−0.0 – 0.02]	0.801
		<b>Env Spatial</b>	<b>0.36 [0.33 – 0.41]</b>	<b>0.001</b>
	Phylogenetic turnover	Spatial Env	0.007 [−0.01 – 0.03]	0.780
		<b>Env Spatial</b>	<b>0.25 [0.21 – 0.29]</b>	<b>0.001</b>
Perennials	Taxonomic turnover	Spatial Env	−0.008 [−0.02 – 0.01]	0.765
		<b>Env Spatial</b>	<b>0.22 [0.18 – 0.27]</b>	<b>0.001</b>
	Phylogenetic turnover	Spatial Env	−0.017 [−0.03 – 0.00]	0.531
		<b>Env Spatial</b>	<b>0.17 [0.12 – 0.21]</b>	<b>0.001</b>

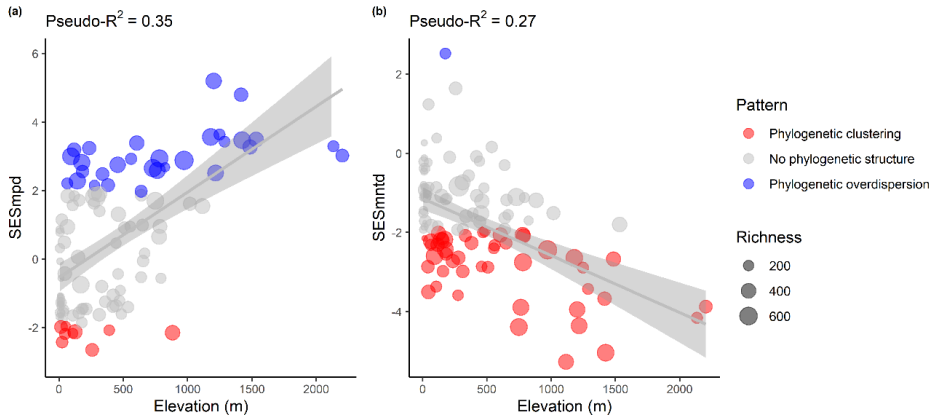
### 3.4. Phylogenetic structure of tree communities in the southeast Atlantic forest

Angiosperm tree species richness displayed a tremendous variation across communities in the southeast Atlantic forest domain, ranging from 85 species in restinga to 755 species in rainforest (mean = 285.5, sd = 137.5). Species richness peaked at middle elevations (Fig. 3a in **IV**) and was higher in rainforest and cloud forest than in semideciduous forest and restinga (Fig. 4a and Table S1 in **IV**). Once controlled for elevation and other environmental variables, species richness responded negatively to salinity and water deficit severity and increased with annual precipitation (Fig. 6a in **IV**). Phylogenetic endemism (PE) increased with elevation (Fig. 3b in **IV**) and was higher in cloud and semideciduous forests (Fig. 4b and Table S1 in **IV**). PE did not vary with annual precipitation but was negatively correlated with precipitation seasonality and positively correlated with all other variables (Fig. 6b in **IV**).

The phylogenetic structure of communities at different phylogenetic levels revealed opposing directions along the elevation gradient. SESmpd increased with elevation: communities consisted of species from rather distantly related lineages at high elevations (linear slope =  $8.77 \pm \text{SE } 1.42$ ,  $p < 0.001$ ; Fig. 6a), whereas SESmntd decreased with elevation, with communities consisting of more close relatives at high elevations (linear slope =  $-6.63 \pm 1.13$ ,  $p < 0.001$ , Fig. 6b). After accounting for other environmental variables, elevation was still a relevant



predictor of SESmpd, together with salinity and water deficit: communities located in areas with high salinity and water deficit consisted of close relatives (Fig. 6c in IV). SESmntd responded negatively to precipitation seasonality and increased with water deficit, i.e. communities consisted of close relatives at the tips of phylogeny in areas of high precipitation seasonality and distant relative in areas with high water deficit (Fig. 6d in IV).

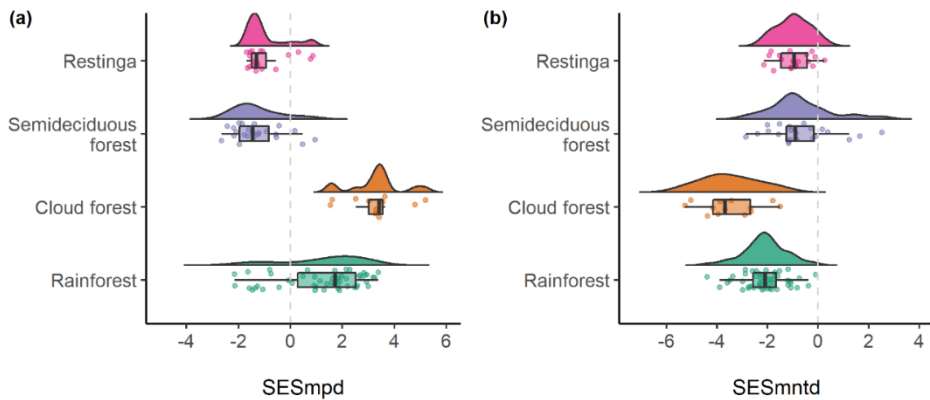


**Figure 6.** Phylogenetic structure of angiosperm tree communities along elevation gradients in the southeast Atlantic forest domain. **(a)** the standardised effect size of the mean pairwise phylogenetic distance (SESmpd); **(b)** the standardised effect size of the mean nearest taxon distance (SESmntd). Lines were drawn from generalised least squares (GLS), accounting for spatial autocorrelation between communities. Shaded areas represent 95% confidence intervals. Pseudo-R<sup>2</sup> values were calculated as the square of the correlation between fitted and observed values in the models.

Community phylogenetic structure differed significantly across habitat types. While SESmpd was higher in cloud forest and rainforest than in semideciduous forest and restinga (Fig. 7a; Table S1 in IV), SESmntd was lower in cloud forest and rainforest compared to semideciduous forest and restinga (Fig. 7b; Table S1 in IV). Both indices showed no difference in phylogenetic structure between semideciduous forest and restinga.

The taxonomic and phylogenetic beta diversity analyses showed that the restinga tree communities are likely a subset of rainforest and semideciduous forest communities due to the nestedness effect (i.e. loss of species richness and phylogenetic diversity, respectively; Fig. 7a and b in IV). The spatial turnover of species and lineages was the main determinant of the overall habitat types dissimilarity, indicating a high degree of species replacement between them (Fig. 7a and b in IV). There was a significant difference in the taxonomic (ANOSIM  $R = 0.87$ ,  $p = 0.001$ ) and phylogenetic turnover between habitat types (ANOSIM  $R = 0.65$ ,  $p = 0.001$ , Fig. 7c and d in IV). Overall, there was an overlap of 128 species (6% of the total) between all habitat types (Fig. 7e in IV). Rainforest and cloud forest showed the highest number of species that did not occur elsewhere

(14% and 13%, respectively), followed by semideciduous forest (4%) and restinga (1.7%). Rainforest shared comparably more species with semideciduous forest and cloud forest (17% and 13.7%, respectively) than with restinga (2.3%, Fig.7e in IV).



**Figure 7.** Phylogenetic structure of angiosperm tree communities across habitat types in the southeast Atlantic forest domain. **(a)** the standardised effect size of the mean pairwise phylogenetic distance (SESmpd); **(b)** the standardised effect size of the mean nearest taxon distance (SESmtd). Curves show the probability distribution of the variables, dots represent the real data points, and boxplots show their median and the interquartile ranges.

## 4. DISCUSSION

Over the past decades, many studies have shown the potential to address the evolutionary history of coexisting species to understand contemporary patterns in ecological communities. However, most of the approaches focused on ecological mechanisms only, either biotic interactions or environmental filtering as drivers of species diversity patterns (Webb *et al.* 2002; Cavender-Bares *et al.* 2009). Some studies have recently defended that both evolutionary and ecological mechanisms are intertwined and contribute to explaining diversity patterns (Kerkhoff *et al.* 2014; Gerhold *et al.* 2015, 2018; Carlucci *et al.* 2017; Weber *et al.* 2017; Kubota *et al.* 2018). By adopting a broader hypothesis formulation in which both evolutionary and ecological mechanisms are considered factors that influence species richness and phylogenetic structure of plant communities, the results in this thesis reinforce this integrated view.

This thesis shows that on a global scale, woody and herbaceous communities display contrasting patterns of phylogenetic structure along the latitudinal gradient and that species of both growth forms tend to be more closely related in open habitat types, probably due to recent colonisation (paper I). In geologically young restingas, where local diversification is unlikely to have occurred, the current phylogenetic structure of angiosperm tree communities probably results from the coexistence of Gondwanan restricted lineages with species from widespread families in historically unstable areas of southern Brazil. Phylogenetic clustering in restingas in historically more stable areas likely results from local diversification in the neighbouring rainforest with subsequent dispersal to restingas (paper II). In semi-natural drylands, where water availability is the most limiting factor, annual plant species are phylogenetically clustered in communities with intermediate to high aridity levels, whereas clustering in perennials is found at low to intermediate aridity levels. This contrasting response to aridity probably results from historical environmental filtering and endemism of recent diversified annual species and local dominance of a few perennial species in more mesic areas (paper III). Finally, the variation in the phylogenetic structure of angiosperm tree species along elevation and across habitat types in the Atlantic forest domain largely depends on whether the basal or terminal phylogenetic level is considered. For example, higher SESmpd and phylogenetic endemism and lower SESmtd at high elevations show that cloud forest is phylogenetically more distinct from rainforest, semideciduous forest and restinga due to local diversification in a few lineages. In contrast, higher SESmtd in semideciduous forest and restinga demonstrates that these habitat types are likely colonised by lineages that underwent past diversification and are adapted to harsh environmental conditions such as water limitation and high salinity, respectively (paper IV).

#### **4.1. Latitudinal patterns of phylogenetic structure in woody and herbaceous plant communities suggest an effect of local diversification and habitat age**

Woody plant communities were phylogenetically more clustered at low latitudes and tended to become overdispersed at high latitudes. The decreasing relatedness between species towards high latitudes contrasts with previous studies showing phylogenetic clustering in colder and drier regions. The latter pattern has been proposed to result from tropical lineages retaining their ancestral niches and failing to disperse into temperate regions (Qian *et al.* 2013; Kerkhoff *et al.* 2014; Kubota *et al.* 2018). The present study suggests, however, that tropical niche conservatism might not be the most important mechanism for assembling plant communities when a broad taxonomic scale is considered (e.g. including gymnosperm species). In the present study, gymnosperms were considered in the woody communities because they occupy and dominate many communities worldwide (e.g. the Podocarpaceae and Araucariaceae in the Southern Hemisphere, and the Pinaceae in the Northern Hemisphere) and have physiological advantages over angiosperms in cold and dry regions (Bond 1989). Therefore, phylogenetically distant gymnosperms at high latitudes contribute significantly to the phylogenetically overdispersed pattern in woody communities. Since most woody species originated in warm tropical regions (Axelrod 1966; Richards 1996; Ricklefs 2005), the pattern of increasing overdispersion towards high latitudes probably results from high diversification of angiosperms at low latitudes due to larger area and greater time for diversification (Fine & Ree 2006), and from temperate niche conservatism of gymnosperms at high latitudes due to their physiological advantage over angiosperms in cold and nutrient-poor environments (Bond 1989; Berendse & Scheffer 2009). Considering only angiosperms in the analysis, SESmpd decreases towards high latitudes, supporting the findings in previous studies (Qian *et al.* 2013; Kerkhoff *et al.* 2014; Kubota *et al.* 2018). SESmtd is not affected by the exclusion of gymnosperms because the division between angiosperms and gymnosperms deep in the phylogeny does not affect the relationships at the tips of the phylogeny.

The relationship between the phylogenetic structure of herbaceous communities and latitude is less evident than in woody communities. The lack of relationship probably arises because, despite the unimodal relationship between SESmpd and latitude, both SESmpd and SESmtd are most influenced by differences in habitat types, with more closely related species coexisting in open habitats. Therefore, phylogenetic clustering of herbaceous communities at high latitudes may reflect recent geological origin of temperate and boreal habitat types relative to the tropics (Fine & Ree 2006), together with the presence of evolutionarily young lineages that diversified following the rise of angiosperm-dominated herbaceous flora in open habitats during global cooling in the Late Cretaceous and Eocene-Oligocene transition, such as C<sub>4</sub> Poaceae, Brassicaceae and Ranunculaceae (Couvreur *et al.* 2010; Linnert *et al.* 2014; Spriggs *et al.* 2014; Wang *et al.* 2016).

Phylogenetic clustering has also been attributed to recent radiation of lineages in relatively young fynbos and grasslands vegetation in South Africa (Proches *et al.* 2006). Alternatively, phylogenetic clustering in local herbaceous communities may result from historical environmental filtering acting in evolutionarily young species pools, such as grasslands of Tertiary origin, in which only a few lineages had enough time to establish (Lososová *et al.* 2015). This result finds support in the coexistence of more closely related species in the Nearctic and Neotropical biogeographic realms than in the Afrotropical realm, probably because herbaceous communities in the first two realms are located at high latitudes, where only species adapted to cold conditions are expected to coexist. However, the weaker relationship between phylogenetic structure and biogeographic realm probably resulted from the fact that the Afrotropical realm was underrepresented in the dataset. Furthermore, results in herbaceous communities must be interpreted with caution because of spatial limitation in the distribution of the original studies and a comparably higher number of communities in Central Europe than in other regions.

#### **4.2. Phylogenetic structure of angiosperm tree communities in the Atlantic coastal white-sand vegetation (restingas) is contingent on climate and evolutionary history of the neighbouring rainforest**

The unimodal relationship between species richness and latitude reflects the distribution of the most dominant families with higher species richness in the central region of restingas. The central region of restingas is characterised by a stable historical climate (Carnaval & Moritz 2008) and high endemism rates (Werneck *et al.* 2011), which may have contributed to the high total number of species in restingas. Species richness in restingas is generally lower than in the Atlantic rainforest because only a few lineages have traits to cope with environmental harshness (Scarano 2002). Recent studies have argued that dioecy, fleshy fruit formation and asexual reproduction are the traits related to the successful colonisation of species in restingas (Matallana *et al.* 2005; Scarano 2009). However, the processes by which restingas have been colonised remain little understood.

Contrary to species richness, the phylogenetic structure (both SESmpd and SESmntd) positively correlates with latitude, with species becoming more distantly related in the southernmost and wetter restingas. The coexistence of distantly related species in southern restingas may be related to the availability of forest remnants in periods of unfavourable climatic conditions during Quaternary (Behling *et al.* 2007). These remnants were crucial for maintaining old Gondwanan lineages (Segovia & Armesto 2015). Therefore, the results in paper II suggest that species in southern restingas belong to old and restricted Gondwanan lineages and species from lineages widespread in the Atlantic forest domain.

Even after including environmental variables such as temperature, precipitation, soil salinity and soil fertility, SESmpd is still correlated with latitude. SESmpd also correlates with precipitation, indicating the presence of distantly related lineages in wetter restingas. SESmntd, on the other hand, positively correlates with more variables after accounting for latitude. SESmntd increases with temperature, precipitation, and displays high values in more fertile and less saline soils. These variables are related to the main limiting environmental factors proposed for species distribution in restingas (Scarano 2002). Thus, lower values of SESmntd indicate the coexistence of closely related species in more stressful communities due to adaptations of a few lineages to extreme conditions, supporting previous studies (Kubota *et al.* 2018). Additionally, phylogenetic clustering towards more stable regions may reflect regional diversification in the neighbouring rainforest with subsequent dispersal to restingas nearby (Fernandes & Queiroz 2015). Higher values of SESmntd in historically unstable regions indicate a lack of recent radiation among close relatives and may have resulted from close relatives evolving early in the evolutionary time and persisting in stable refugia (Behling *et al.* 2007; Leonhardt & Lorscheitter 2010).

Phylogenetic beta diversity at terminal levels of the phylogeny is more pronounced than at basal levels across restingas, supporting previous studies in other Atlantic forest habitat types (Duarte *et al.* 2014). This pattern may result from the availability of several local species pools nested within a large lineage pool along the latitudinal gradient in the Atlantic forest, in which tropical species adapted to local conditions fail in colonising colder and wetter subtropical restingas. This hypothesis finds support in the correlation between phylogenetic beta diversity and both geographic and environmental dissimilarities between communities, indicating that dispersal limitation and niche conservatism seem to be the factors underlying high phylogenetic beta diversity at terminal levels in the geologically young restingas (Daru *et al.* 2017). In the dispersal limitation scenario, species that evolved in the rainforest and colonised nearby restingas probably had insufficient time to disperse to other regions, especially during climatic oscillation events (Carnaval & Moritz 2008). In the niche conservatism scenario, species may have found suitable empty niches in restingas similar to those in the rainforest, and through slow evolution of niches, species remained in their area of origin, regardless of their dispersal capacity (Daru *et al.* 2017). As expected, the lack of correlation between phylogenetic beta diversity at basal levels and either geographic or environmental distances between communities reflects widespread plant families in the Atlantic forest domain that probably colonised restingas during the Quaternary, homogenising the phylogenetic structure deep in the phylogeny. Low phylogenetic beta diversity at basal levels has also been found in the Atlantic rainforest due to sympatric speciation (Gastauer *et al.* 2015) and in white-sand forests of the Amazonian basin due to recent diversification (Guevara *et al.* 2016), supporting the hypothesis of older lineages tending to be uniformly distributed in lowland habitat types.

### 4.3. Phylogenetic structure of annual and perennial species responds contrastingly to aridity in a Mediterranean dryland

Species richness of annuals does not correlate with aridity, whereas that of perennials shows a unimodal relationship. Annual species have a short life-span and high potential for seed dispersal and dormancy, and their germination and establishment are strongly dependent on interannual water availability (Guterman 2002). Therefore, neutral processes such as dispersal and stochastic colonisation (Hubbell 2001) as well as seed germination strategies to increase seedling survival (Guterman 2002; Volis & Bohrer 2013) are likely the factors related to the lack of pattern in annuals. Unlike annuals, perennial species have a longer life-span and must endure summer droughts over the years and do so through conservative or acquisitive strategies (Liancourt *et al.* 2005). Thus, environmental filtering at the drier extreme of the gradient selects species that can cope with harsh conditions such as water limitation. In contrast, at the other extreme of the gradient, a few dominant species such as those from the genera *Cistus* and *Cynodon* are probably strong competitors and exclude other species from communities, thus contributing to the unimodal pattern in perennials (Michalet *et al.* 2006). Despite the lack of relationship between annuals and aridity, the greater number of both annual and perennial species at intermediate levels of aridity may indicate the presence of an ecotone where both species of the aridest and those of the least arid communities still find conditions to live.

The phylogenetic structure of annuals and perennials responded contrastingly to aridity. Both SESmpd and SESmntd decreased with aridity in annuals, with phylogenetic clustering occurring at intermediate to high aridity. Two different processes may explain this pattern. Firstly, phylogenetic clustering in SESmpd indicates that environmental filtering affects entire lineages in the regional species pool, selecting species from dry-adapted lineages and excluding those lacking mechanisms to cope with water scarcity. Secondly, assuming that lineages were already filtered out (low SESmpd), clustering in SESmntd is likely dependent on annuals' capacity to disperse to neighbouring communities coupled with endemism of recently diversified species within dry-adapted lineages (Verdú & Pausas 2013). Additionally, in Mediterranean ecosystems, species may descend from lineages adapted to specific soil conditions, therefore outcompeting other less specialised species (Fine & Kembel 2011).

In contrast to that found in annuals, SESmpd and SESmntd in perennials decrease towards regions with lower aridity, and communities tend to be phylogenetically clustered at intermediate to low aridity. Aridity has increased over geological time in the Mediterranean basin and contributed to local diversification (Valente *et al.* 2010; Verdú & Pausas 2013). Therefore, lineages have already been filtered out regionally, reflecting the phylogenetic clustering found at intermediate to low aridity. The coexisting closely related species in these regions likely display traits that may reduce competitive exclusion in the absence

of niche differentiation (e.g. among the above mentioned *Cistus* species) (Mayfield & Levine 2010) or high trait dissimilarity (Prinzing et al., 2008), allowing better partitioning of resources. Even after accounting for other environmental variables such as temperature, precipitation and soil nutrient availability, aridity is still a strong predictor of phylogenetic structure. Additionally, SESmpd and SESmntd negatively correlate with soil C/N ratio, indicating that locally dominant species (e.g. those from the genus *Cistus*) may have more efficient use of scarce nitrogen than other species in areas with low aridity and high soil C/N ratio (Zhang *et al.* 2020).

Spatial phylogenetic turnover (i.e. the replacement of lineages across communities) did not correlate with geographic distance between communities in either annuals or perennials, indicating that species in the Mediterranean basin may not be dispersal limited or that there has been enough time for species sorting to occur despite dispersal limitation. In contrast, phylogenetic turnover correlated with the environmental distance between communities, which shows that even within a filtered group of lineages, species may still have specific adaptations to different environmental conditions and are mostly related to variables at a finer scale such as soil specificity (Fine & Kembel 2011).

#### **4.4. Evolutionary history of marginal habitats influences the diversity of tree communities in the Atlantic Forest**

Angiosperm tree species richness in the southeast Atlantic forest domain shows a unimodal pattern along the elevation gradient, peaking at middle elevations, reinforcing previous studies (Rahbek 1995; McCain & Grytnes 2010). Species richness is higher in rainforest and cloud forest than in semideciduous forest and restinga. Therefore, the unimodal relationship between species richness and elevation may reflect environmental filtering at both extremes of the gradient. Salinity may filter species in restingas, and water scarcity in semideciduous forests at low elevations, whereas temperature could filter species in cloud forests at high elevations.

Unlike species richness, phylogenetic endemism increases with elevation, highlighting mountainous regions as areas of high endemism rates (Hoorn *et al.* 2013; Rahbek *et al.* 2019). Interestingly, rainforests show lower phylogenetic endemism despite their high number of species, suggesting that rainforests' richness may partly depend on the species generated in cloud forests. As expected, restingas do not show either lower or higher phylogenetic endemism levels, mainly because restingas did not have sufficient time for plant diversification (Scarano 2002).

SESmpd and SESmntd show contrasting relationships with elevation and across habitat types. SESmpd increases with elevation and is higher in rainforest and cloud forest than in restinga and semideciduous forest. The increasing phylogenetic distance at basal levels along the elevation gradient is probably related to



the Atlantic forest domain's evolutionary history. The Atlantic forest domain is the oldest forest in South America (Rizzini 1997), and it holds a mix of species and higher-level taxa that evolved while South America was separating from Africa during the last 165 million years (Sanmartín *et al.* 2004). Throughout the geological time, lineages had sufficient time to disperse from lowlands towards other habitat types such as cloud forests. Therefore, communities at higher elevations may be composed of pre-adapted distantly related lineages dispersed from other mountainous regions and lowland lineages in the same region. Similar findings have been shown in other tropical regions such as Malesian mountain forests (Culmsee & Leuschner 2013) and the Indian Western Ghats (Bose *et al.* 2019), reinforcing the idea that species in tropical elevation gradients are sorted from lineages with different biogeographical and evolutionary histories (Duarte *et al.* 2014; González-Caro *et al.* 2020). The decreasing of SESmntd with elevation indicates diversification within lineages adapted to the mountainous climate and topographic heterogeneity. Therefore, mountains in the Atlantic forest domain could be considered a 'Cradle' (Stebbins 1974) of angiosperm tree species, indicated by the high level of phylogenetic endemism and phylogenetic clustering in SESmntd. On the other side of the gradient, SESmntd tends to increase towards semideciduous forest and restinga, indicating a lack of recent diversification. Diversification may have happened before species arrive in these habitat types, and only lineages able to cope with high temperatures, dry seasons and saline soils were able to colonise them, indicating environmental filtering and possibly phenotypic plasticity in anatomical and physiological traits beneficial in the specific environment (Herzog *et al.* 1999; Rôças *et al.* 2001; Scarano *et al.* 2001; Scarano 2009). The tendency of no phylogenetic structure or clustering in restinga may also be related to the geologically young age of the habitat type, as discussed in more detail in section 4.2. Furthermore, SESmpd decreasing with salinity and water deficit severity indicates that not all lineages can tolerate such constraints.

The high degree of tree species and lineages replacement across habitat types, indicated by spatial taxonomic and phylogenetic turnover, is the main factor of overall taxonomic and phylogenetic beta diversity in the southeast Atlantic forest. An exception was found between rainforest and restinga and between semideciduous forest and restinga, in which taxonomic and phylogenetic beta diversity are mainly driven by the nestedness effect (i.e. loss of species richness and phylogenetic diversity, respectively). In that case, restinga communities are likely a subset of more species-rich habitat types such as rainforest and semideciduous forest. High phylogenetic beta diversity has been found in other regions of the Atlantic forest domain. It has been argued to result from the presence of lineages with different biogeographical origin (Duarte *et al.* 2014), such as those native to Gondwana (Segovia & Armesto 2015). These results contradict the idea that habitat types such as cloud forest and semideciduous forest are a subset of species from the rainforest (Scarano 2002). According to the results presented in paper **IV**, restinga is the only habitat type that can be considered a subset of the rainforest, probably because species are still dispersing into this coastal vegetation.

## 5. CONCLUSIONS

The results presented in this thesis showed that on a global scale, plant communities' phylogenetic structure along the latitudinal gradient might depend on the plant growth form and phylogenetic scale considered (i.e. basal and terminal diversifications in the phylogeny). Patterns of phylogenetic structure in woody communities changed from overdispersed to clustered in high latitudes once gymnosperm species were excluded from analysis, highlighting that only a few angiosperm lineages can cope with environmental harshness. Phylogenetic clustering in herbaceous communities at high latitudes may be related to the young geological age of open habitat types. However, further studies must consider broader global sampling. In geologically young ecosystems (restingas), where angiosperm tree species had no time for diversification, plant communities' phylogenetic structure strongly depends on the available lineage pool that comprises different habitat-specific species pools across the Atlantic forest domain. Moreover, environmental harshness and the presence of Quaternary refugia also influence whether coexisting species are more closely or distantly related to each other. The age of restingas also prevents more derived species from dispersing from their local distribution, increasing phylogenetic beta diversity at terminal levels of the phylogeny. In the historically dry Mediterranean basin, annual and perennial plant species' phylogenetic structure responds contrastingly to aridity and can be important in land use management and restoration strategies. Furthermore, species with both life-history strategies seem not to be dispersal limited across the region but instead are adapted to specific local climatic and edaphic conditions. In the Atlantic forest domain, tree communities tend to show basal phylogenetic overdispersion and terminal clustering towards higher elevations, highlighting the influence of the Atlantic forest domain's evolutionary history on the contemporary communities. More specifically, the coexistence of distantly related lineages towards high elevations reflects the assembly of lineages with different biogeographic histories that once reached mountainous regions and underwent local diversification, reflected in terminal clustering. Results also show that not all habitat types should be considered marginal to the rainforest, for example, cloud forest and semideciduous forest. Restinga, instead, contains species that occur in both rainforest and semideciduous forest.

Overall, the results in this thesis add insights into the use of phylogenetic information to investigate the origin and maintenance of diversity patterns. These results have relevant implications for future studies aiming to predict how species diversity patterns will be affected under climate change scenarios (Colwell et al. 2008; Thuiller et al. 2011) and should be explored in more detail in the context of conservation and restoration strategies of ecological communities.

## 6. SUMMARY

The accelerated climate change and habitat destruction have affected biological diversity in ways never seen before. Preventing a species from its extinction goes beyond counting numbers. It also means conserving the evolutionary history it shares with its relatives. Evolution plays an important role in the way species are assembled into communities of different habitat types and along environmental gradients. For example, two grasslands may have the same number of herbaceous species but differ enormously in their constituent species' evolutionary history. Species that evolved in distantly related lineages may live together in one grassland because closely related species often compete for the same resources, thus causing the exclusion of the weaker species. It generates a pattern of phylogenetic structure, which in the first grassland is called phylogenetic overdispersion. In the second grassland, closely related species may share characters that give them a competitive advantage over others and allow them to outcompete distantly related species. Thus, the grassland where closely related species live together is considered phylogenetically clustered. Because patterns of biological diversity (e.g. phylogenetic overdispersion or clustering) result from complex processes that happen both on the contemporary time scale (e.g. species interactions and requirements to specific environmental conditions) and the evolutionary time scale (e.g. generation of new species), understanding how these processes act to shape community's diversity adds valuable insights into the way species will respond to future changes. This thesis investigates how plant communities' phylogenetic structure responds to changes in the environment such as elevation, climate, nutrients in the soil, and changes driven by humans such as desertification. Specifically, this thesis asks the following questions:

- 1) How does the phylogenetic community structure of different growth forms (i.e., woody and herbaceous plant species) relate to latitude, biogeographic realms and habitat types worldwide?
- 2) What are the relative effects of the current climate, historical climatic stability, and edaphic factors on the phylogenetic structure of angiosperm tree communities in geologically young restinga habitats along the Atlantic coast?
- 3) How does the phylogenetic structure of annual and perennial plant communities respond to aridity in Mediterranean semi-natural dryland?
- 4) How does the phylogenetic structure of angiosperm tree communities respond to elevation in different habitat types in the tropical Atlantic forest domain?

The analysis of woody and herbaceous plant communities worldwide (1) showed that their phylogenetic structure responds contrastingly to latitude, considered a surrogate for temperature. Woody communities become phylogenetically overdispersed towards high latitudes, probably because most woody species originated in warm and stable tropical regions. However, due to a lack of adaptations to cope with freezing, they did not reach cold regions at high latitudes. Only a few woody species, including both flowering plants and the evolutionarily distant related

gymnosperms, have physiological adaptations to cope with freezing, thus contributing to the phylogenetic overdispersion. Once gymnosperms are removed from the analysis, communities become clustered because those flowering species that are adapted to cold climate come from closely related lineages. Herbaceous communities do not show a clear pattern along the latitudinal gradient. Instead, they are more sensitive to the habitat type, being more phylogenetically clustered in open habitats (e.g. grassland) than in closed habitat types (e.g. forest). That difference may be related to some lineages' recent origin, including herbaceous species such as grasses.

In the analysis of how species with different life-cycle strategies respond to desertification (i.e. increasing aridity) (3), communities of species that complete their life-cycle within one year (annual species) become phylogenetically clustered in drier areas. This result reflects historical environmental filtering acting on the dry-adapted lineages available in the region and the limited dispersal of young species adapted to specific soil conditions. Communities of species with a longer lifespan, that is, those that must endure stressful conditions during the summer drought (perennial species), become phylogenetically clustered at intermediate to low levels of aridity, indicating the presence of closely related species with specific characters that allow them to outcompete weaker distantly related competitors.

Analyses in (2) and (4) were carried out in the Atlantic Forest biodiversity hotspot and focused exclusively on tree species communities in coastal vegetation and along elevation, respectively. Using a metric that explores deep past evolutionary events, (2) coastal communities become phylogenetically overdispersed towards southernmost areas, suggesting the coexistence of distantly related and cold-adapted species with species that come from widespread lineages in the Atlantic Forest. Once the phylogenetic structure is calculated using a metric that explores recent evolutionary events, communities become clustered in areas of great climatic stability with a high number of spatially restricted species, indicating a potential limitation in the dispersal of the coexisting species and *in situ* diversification. Communities are also clustered in drier areas with high soil salinity and low soil fertility, indicating environmental filtering. The phylogenetic structure of tree communities responds contrastingly to elevation gradients (4). Considering deep past evolutionary events, communities become overdispersed towards high elevations, indicating a process of long-term colonisation of distantly related lowland lineages that share common characters to cope with cold temperatures. These lineages probably generated new species in the mountains because communities are clustered in high elevations when considering recent evolutionary events. Additionally, in communities associated with water limitation and high salinity, there is phylogenetic clustering when using the deep past metric and nearly no phylogenetic structure when using the metric that accounts for recent events. This result indicates that only a few lineages were able to establish in harsh conditions, and most lineages did not generate new species in these communities.

This thesis shows how the phylogenetic structure of plant communities responds to variation in different environmental variables. These results add insights into the use of phylogenetic information to investigate the origin and maintenance of diversity patterns. Additionally, these results are significant in the context of current climate change and habitat destruction because these events threaten the number of species that live in different biological communities, their function and the evolutionary history that they share.

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## 8. SUMMARY IN ESTONIAN

### Taimekoosluste fülogeneetiline struktuur piki keskkonnagradiente makroökoloogilisest ja evolutsioonilisest vaatepunktist

Kliimamuutus ja elupaikade kadu ohustavad bioloogilist mitmekesisust, mille tõttu kahaneb liigirikkus ning kaob ka evolutsiooniline pärand, mis on geenides liigitunnustes. Tänapäevased taimkattetüüpide kooslused keskkonnagradiendil on kujunenud evolutsiooniliste protsesside tulemil. Näiteks võib kahel niidul olla sarnane taimede liigirikkus, kuid erinev liikide evolutsiooniline pärand. Kauges suguluses olevad liigid võivad koosluses koos elada sellepärast, et lähisugulased konkureerivad tihti sarnaste ressursside pärast, mistõttu nõrgem konkurent välja tõrjutakse – areneb fülogeneetiliselt üledisperseerunud kooslus. Lähisugulased võivad koosluses koos olla, kui neil esinevad tunnused, mis annavad konkurentsile eelise kauges suguluses olevate liikide ees. Lähisugulaste kooseksisteerimisel tekib fülogeneetiliselt klasterdunud kooslus. Kuna bioloogilise mitmekesisuse mustrid (sh fülogeneetiline üledispersioon ja klasterdumine) arenevad nii tänapäevaste (nt biotilised interaktsioonid ja liikide nõudlused keskkonnaparameetrite suhtes) kui ka evolutsiooniliste protsesside (nt liigitekke) tulemil, on bioloogilise mitmekesisuse säilitamiseks oluline teada, milline on nende protsesside suhteline roll. Dissertatsioon uuribki, kuidas mõjutavad taimekoosluste fülogeneetilist struktuuri keskkonnategurid nagu näiteks kõrgus merepinnast, kliima, mulla toitainete sisaldus ja inimtekkeline kõrbestumine. Täpsemalt otsitakse vastuseid küsimustele:

- 1) Kuidas on koosluse eri kasvuvormide (st puittaimed ja rohttaimed) fülogeneetiline struktuur seotud laiuskraadi, biogeograafilise piirkonna ja taimkattetüübiga globaalsel skaalal?
- 2) Kuidas mõjutavad piki Atlandi ookeani kallast leviva *restinga* taimkattetüübi puittaimede fülogeneetilist struktuuri tänane kliima, ajalooline kliimaatiline stabiilsus ja kasvukoha mulla omadused?
- 3) Kuidas mõjutab kõrbestumine ühe- ja mitmeaastaste rohttaimede fülogeneetilist struktuuri poollooduslikes kuivades Vahemere kooslustes?
- 4) Kuidas mõjutab kõrgus merepinnast puittaimede fülogeneetilist struktuuri erinevates taimkattetüüpides bioloogilise mitmekesisuse tulipunktis Atlantilise vihmametsa kompleksis?

Puit- ja rohttaimeliikide uurimine globaalsel skaalal (1) näitas, et laiuskraad mõjutab koosluste fülogeneetilist struktuuri erinevalt. Puittaimeliikide lähisugulus on suurem väiksematel laiuskraadidel tõenäoliselt sellepärast, et enamasti puittaimi arenes soojas ja stabiilses troopikas. Külbumise vastaste kohastumuste puudumise tõttu ei levinud paljud liigid jahedamasse parasvöötmesse. Ainult mõnedel puittaimeliikidel, sh nii õis- kui ka kaugemas suguluses olevatel paljasseemnetaimedel, on külbumise vastased füsioloogilised kohastumused. Selliste liikide kooseksisteerimisel tekib koosluses fülogeneetiline üledispersioon. Paljasseemnetaimede mitte arvestamise tulemusel klasterdub koosluse fülogeneetiline

struktuur, mille tingib külmumise vastaste kohastumustega õistaimeliikide omavaheline lähisugulus. Rohttaimeliikide fülogeneetiline struktuur koosluses piki laiuskraadi ei ole nii selge kui puittaimedel. Rohttaimeliikide fülogeneetilist struktuuri mõjutab pigem taimkattetüüp: rohttaimed on omavahel lähemas suguluses avatud (nt niidud) kui suletud võradega (nt mets) kasvukohtades. See tulemus võib olla seotud mõnede rohttaimeklaadide (nt kõrrelised) evolutsioonilise noorusega.

Erineva elustrateegiaga rohttaimeliikide uurimine kõrbestavas piirkonnas (3) näitas, et üheaastased rohttaimed on lähemas suguluses kuivemates tingimustes. See on tõenäoliselt tingitud pikaajalisest liikide selekteerimisest regionaalsest liigifondist kuivadesse kooslustesse. Pikema elueaga, st mitmeaastased liigid, mis peavad taluma kuivastressi suvise põua ajal, on fülogeneetiliselt lähemas suguluses niiskemates oludes. See on tõenäoliselt võimalik sellepärast, et neil on sarnased tunnused, mis annavad neile eelise kaugemalt sugulastest konkurentide ees.

Uurides evolutsioonilisi liikide lahknemisi Atlantilise vihmametsa kompleksi puittaimekooslustes rannikul (2) ja kõrgusvööndites (4) selgus, et (2) kaugmineviku lahknemiste valguses on rannikukoosluste liigid omavahel kaugemas suguluses lõunapoolsematel aladel. See on ilmselt tingitud kauges suguluses olevate ja jahedale kliimale kohastunud ning laialt levinud Atlantilise vihmametsa liikide kooseksisteerimisest. Lähimineviku liikide lahknemine näitab, et liigid on lähemas suguluses kliimaatilisel stabiilsemates piirkondades; neis piirkondades esineb ka palju ainuomaseid liike. See viitab võimalikule levimistõkkele ja kohapealsele liigitekkele. Liigid on lähemas suguluses ka kuivadel ning kõrge soolsuse ja väheviljaka mullaga aladel, mis viitab sugulasliikide spetsiaalsete kohastumuste selekteerimisele nendes kooslustes. Puittaimede fülogeneetiline struktuur erines kõrgusgradiendil (4). Kauges minevikus toimunud liikidevahelised lahknemised näitavad, et merepinnast kõrgemate taimekattetüüpide kooslustes on liigid omavahel pigem kauges suguluses. See näitab tõenäoliselt pikaajalist kauges suguluses olevate ning jaheda temperatuuriga kohastunud liikide levimist kõrgusgradiendil ülespoole. Neist liikidest arenes tõenäoliselt mägedes uusi liike, sest lähimineviku liikidevahelist lahknemist uurides selgus, et kõrgemal asuvate koosluste liigid on omavahel lähisugulased. Kuivas ja kõrge soolsusega mullal levivates kooslustes on liigid lähisugulased, kui vaadata kaugmineviku lahknemisi, kuid fülogeneetiline struktuur on juhuslik lähiminevikus toimunud lahknemiste valguses. Tulemus näitab, et vaid vähesed liigid suutsid minevikus karmide keskkonnatingimustega kooslusi asustada ning neist liikidest ei arenenud kohapeal uusi liike.

Dissertatsioon näitab, kuidas keskkonnategurid mõjutavad taimekoosluste fülogeneetilist struktuuri. Tulemused toetavad fülogeneetiliste andmete laialdasemat kasutamist, et uurida eluslooduse mitmekesisuse muustrite päritolu ja säilimise mehhanisme. Tulemused on olulised ka tänaste kliimamuutuste ja elupaikade kao kontekstis, sest liikide väljasuremine tähendab ka evolutsioonilise ajaloo kadumist looduslikes kooslustes.



## ACKNOWLEDGEMENTS

I am deeply grateful to my wife for embarking with me on the journey to Estonia and for being supportive and kind in all moments, including the darkest ones. I sincerely thank my supervisor Pille Gerhold for accepting me as a PhD student and for her guidance and support throughout this important period of my life. I thank Lauri and Lars for scientific and sometimes emotional advice and Alice, Francesco and Triin for collaboration opportunities. A deep and special thank goes to the University of Tartu and its staff. One of the best things about doing a PhD at UT is to feel welcome and interact with lovely, efficient and detail-oriented people.

My special thank goes to Helen Kaptein, who kindly accommodated me in her house when I arrive in Tartu and Nemailla Bonturi, a Brazilian who found me talking to my wife on the street and introduced us to the unexpected lusophone community in Tartu. Life in Tartu would have been very hard without friends and colleagues from all over the world that made some moments easier. I thank everyone, especially Sofia, Lisandra, Guilherme, Jerome, Diego, Jessica, Paola, Marina, Raul, Lena, Inga, Aurele, Guille, John, Marge, and Mickael, for words of advice or for simply being there listening to my complainings and, of course, for a few fun and relaxing moments. I could not forget to thank all colleagues and friends I met at the University of South Bohemia in the Czech Republic, especially my roommate Guillaume for the fun statistical related moments in our apartment, and Anibal, Lindsay, and Nina.

Finally, a profound and special thank goes to my family and friends back in Brazil, who always supported and encouraged me, even though they do not understand exactly what I do. I am especially grateful to my parents, sisters, father-in-law, and mother-in-law for always being supportive; my friends Alan, Andreia, Wanderson and Bianca for the fun moments. I thank you for understanding why I was not present in important moments. I love you all!

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The research included in this thesis was funded by the Estonian Research Council [PUT 1006], European Regional Development Fund (Contract No. 36.9-6.1/1476) and University of Tartu.

## **PUBLICATIONS**

# CURRICULUM VITAE

Jhonny Capichoni Massante

ORCID: <https://orcid.org/0000-0003-2764-4976>

University of Tartu – Institute of Ecology and Earth Sciences  
Vanemuise 46, Tartu, Estonia, 51014

Email: [jhonny.massante@ut.ee](mailto:jhonny.massante@ut.ee)

Tel: +351 912522287

Last updated December 2020

## Education

- 2016–present, **Ph.D.** Institute of Ecology and Earth Sciences, University of Tartu, Estonia.
- 2014–2016, **M.S.** Marine Biology and Coastal Environments, Fluminense Federal University, Brazil.
- 2007–2013, **B.S.** Biology, State University of Rio de Janeiro, Brazil.

## Professional appointments

- 2018–2018, Fieldwork specialist, Department of Botany, University of Tartu
- 2016–2018, Teaching assistant, University of Tartu

## Supervising

Annika Kumar (B.S.), “Variation in ecological and evolutionary drivers of phylogenetic beta diversity in plant communities” (at University of Tartu).

## Publications

- Jhonny C. Massante** and Gerhold, P. Evolutionary history of marginal habitats influences the diversity of tree communities in the Atlantic Forest. *Manuscript under review*.
- Mendes, G. et al. (including **Jhonny C. Massante**, 38/48). (2020). How much leaf area do insects eat? A dataset of insect herbivory sampled globally with a standardized protocol. *Accepted at Ecology*.
- Jhonny C. Massante**, Kobel, M., Pinho, P., Gerhold, P., Branquinho, C., Nunes, A. (2020). Phylogenetic structure of understorey annual and perennial plant species reveals opposing responses to aridity in a Mediterranean biodiversity hotspot. *Science of The Total Environment*, vol. 761, article 144018.
- Blaus, A., Reitalu, T., Gerhold, P., Hiiesalu, H., **Jhonny C. Massante**, Veski, S. (2020). Modern pollen-plant diversity relationships inform palaeoecological reconstructions of functional and phylogenetic diversity in Calcareous fens. *Frontiers in Ecology and Evolution*, vol. 8, article 207.
- Jhonny C. Massante** and Gerhold, P. (2020). Environment and evolutionary history depict phylogenetic alpha and beta diversity in the Atlantic coastal white-sand woodlands. *Journal of Vegetation Science*, 31 (4).

- Brown, J.J., Mennicken, S., **Jhonny C. Massante**, Dijoux, S., Telea, A., Benedek, A.M., Götzenberger, L., Májeková, M., Lepš, J., Šmilauer, P., Hrček, J., de Bello, F. (2019). A novel method to predict dark diversity using unconstrained ordination analysis. *Journal of Vegetation Science*, 30 (4).
- Jhonny C. Massante**, Götzenberger, L., Takkis, K., Hallikma, T., Kaasik, A., Laanisto, L. Hutchings, M.J., Gerhold, P. (2019). Contrasting latitudinal patterns in phylogenetic diversity between woody and herbaceous communities. *Scientific Reports*, vol: 9, article 6443.
- Jhonny C. Massante**. Mining disaster: restore habitats now. (2015). *Nature*, 528 (7580).

### Awards and Grants

- 2020 Erasmus+ traineeship to work on phylogenetic structure of semi-natural and restored plant communities in Mediterranean drylands – Erasmus+ Programme of the European Union (2,880 EUR).
- 2019 Dora Plus activity 1.2 (PhD student mobility) to visit the University of Lisbon for a collaboration of 10 months – European Regional Development Fund and Archimedes Foundation (8,852 EUR).
- 2019 IAVS Travel grant, International Association for the Vegetation Science (550 EUR).
- 2019 Kristjan Jaak Scholarship for short study visits to attend the 15<sup>th</sup> European Ecological Federation Congress in Lisbon, Portugal – European Regional Development Fund and Archimedes Foundation (1,114 EUR).
- 2018 Doctoral Expedition to Reunion Island, University of Tartu (selected with the project: “Phylogenetic structure of plant communities along an elevational gradient in the tropical Reunion Island”).
- 2018 Dora Plus activity 1.1 grant (short study visits) to attend the Meta-Analysis course delivered by dr. Wolfgang Viechtbauer at Maastricht University, The Netherlands – European Regional Development Fund and Archimedes Foundation (1,284 EUR).
- 2018 Dora Plus activity 1.1 grant (short study visits) to attend the Climate Change Biogeography meeting promoted by the International Biogeography Society in Évora, Portugal – European Regional Development Fund and Archimedes Foundation (1.355 EUR).
- 2017 Erasmus+ grant student mobility to attend the Quantitative Ecology Module at the University of South Bohemia, Czech Republic – Erasmus+ Programme of the European Union (1,983 EUR).
- 2017 IAVS Travel grant, International Association for the Vegetation Science (550 EUR).
- 2015 Field course: Ecology and Conservation the Brazilian Seasonally Dry Tropical Forest (Caatinga). Selected with the project: “Positive interactions among plants can increase regeneration niches in the Caatinga”. (21 days of intensive training on sampling design, data analysis, scientific writing, and scientific presentation).

### **Selected presentations**

**Jhonny C. Massante**, Neves, D., Gerhold, P. (July 2019). Environment and evolutionary history control phylogenetic turnover in Atlantic white-sand plant communities. *European Ecological Federation Congress – Ecology across borders: Embedding ecology in sustainable development goals*, Lisbon, Portugal. (Oral presentation).

**Jhonny C. Massante**, Götzenberger, L., Takkis, K., Hallikma, T., Laanisto L., Hutchings, M.J., Gerhold, P. (March 2018). Contrasting latitudinal patterns in phylogenetic diversity between woody and herbaceous communities. *Climate Change Biogeography – International Biogeographical Society meeting*, Évora, Portugal. (Poster).

### **Professional Service**

Manuscript reviewer, 2019 –

*Journal of Ecology*, *Journal of Biogeography*, *Journal of Vegetation Science*  
(certified review record available at

<https://publons.com/researcher/3411727/jhonny-massante/peer-review/>),  
*Ecological Indicators*, *Agronomy Research*, *Biodiversidade Brasileira*.

## DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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