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Thesis Abstract

Tree species distribution and phylogenetic diversity across southern South America

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Abstract. The present-day southern South American flora comprises a group of lineages with southern temperate affinities, which have been suggested to have evolved during and after the breakup of Gondwana, as well as a group of Neotropical elements which are largely found in northern South America. Here, I aim to assess the floristic coherence of the main vegetation types that inhabit this region and determine the principal drivers of variation in the evolutionary diversity of these forest communities. I compiled a database of 3662 species of shrubs and trees at 781 sampling sites spread over six countries in South America. To understand the vegetation types that occur in the region I conducted clustering and ordination analyses. I then compared the defined vegetation types using taxonomic distinction, indicator species and phylogenetic diversity analyses. My results indicated a high diversity of vegetation types in terms of woody floristic composition, with a large number of indicator species, many of which are endemic. Contradicting the idea that temperate floras are recently derived and evolutionarily poor subsets of tropical floras, I demonstrated that the forests of the far south of South America are characterized by exceptional evolutionary diversity.

Keywords. Temperate forest, tropical forest, tropical conservatism hypothesis, phylogenetic diversity, latitudinal gradients.

Introduction

The biogeographic history of southern South America (defined here as south of 15° 32'S latitude has led to a markedly distinct flora within the context of the Neotropics *sensu lato* (extending from the southern tip of South America through Central America to Mexico and including the Caribbean). In this region, the distribution of the present flora has been influenced principally by different events of expansion and retraction of biomes in response to paleoclimatic variation. These historical events have shaped the regional species pool, largely determining which lineages either adapt to new conditions, track their ancestral habitats or become extinct (Hoffmann and Sgro 2011). Elements of the ancient Gondwanan flora are thought to persist in these southern forests, generating diverse communities of mixed forests with or without the presence of Neotropical elements (1986).

Areas of transitional vegetation in southern South America have complicated attempts to classify this vegetation (Fittkau 1969). My first objective is therefore to define the main vegetation types that occur in this region (Rezende et al. 2016, Rezende 2017). I then analyse variation in species richness and taxonomic distinctiveness of vegetation types and determine which species are mainly driving the differences among these vegetation types (Rezende et al. 2016, Rezende 2017).

My second goal is to determine the principal drivers of variation in the evolutionary diversi-

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ty of forest tree communities. According to the tropical conservatism hypothesis (TCH; Wiens and Donoghue 2004), the latitudinal diversity gradient (the pattern whereby species richness declines from equatorial regions towards the poles) is largely governed by evolutionarily conserved ancestral preferences (Wiens and Graham 2005, Kozak and Wiens 2010, Romdal et al. 2013). This hypothesis assumes that most clades originated in tropical conditions that were widespread from the beginning of the Cretaceous to the end of the Eocene (Davies et al. 2004, Ruddiman 2006), and that most species in these clades have at least partly retained their ancestral physiological tolerances (Wiens and Donoghue 2004, Jansson et al. 2013). Thus, according to the TCH, species richness, evolutionary diversity and lineage age will be high in regions characterized by warm, non-freezing temperatures, since these conditions match the ancestral niches of many extant clades, while temperate regions will be occupied by fewer, younger and less diverse clades, because the transitions to cold, temperate environments have been relatively infrequent and recent (Wiens and Donoghue 2004).

Methods

The floristic data were retrieved from the NeoTropTree database (Oliveira-Filho 2015), which is a compilation of tree species checklists gathered from the literature with additional occurrence records obtained from verified herbarium specimens. Each site comprises a 5 km radius circle (see description, history and protocol at http: // www.icb.ufmg.br/treeatlan). NeoTropTree defines trees as freestanding plants with stems that can reach over 3 m in height. Thus, the NeoTropTree database includes, palms, tree ferns and bamboos, when they fit the inclusion criteria. My database consisted of 781 plant inventories of tree communities (I refer to all plant species sampled in these plots as trees) spread over six countries (Brazil, Bolivia, Argentina, Chile, Uruguay and Paraguay) with 249,374 occurrence records.

To define the main vegetation types, I performed a cluster analysis (with support assessed via 1000 replicates), non-metric multidimensional

scaling ordination (NMDS) and taxonomic distinction analyses. I generated the agglomerative dendrogram using the Jaccard coefficient of floristic similarity. I chose this coefficient because it produced the highest cophenetic correlation. To determine which species are responsible for the distinction between the main vegetation types, I performed an indicator species analysis using the method proposed by Tichý and Chytrý (2006).

For the phylogenetic analysis, I generated an ultrametric phylogeny using Phylocom (v.4.2), starting with the following reference tree: R20120829.new (from http://phylodiversity.net/phylomatic/). For each tree community (each site), I calculated phylogenetic diversity *sensu stricto* (PD), which is the total sum of branch lengths in a phylogeny comprising species in the community and its equivalent, standardized for species richness (ses.PD). For this analysis I opted to study the pattern across multiple vegetation types, rather than just the gradient as a whole, as different vegetation types may have different histories and show different patterns of phylogenetic diversity. For this analysis, I excluded Pacific Insular Forest (only 1 sampling site) and combined Mediterranean Chile Forests with Temperate Pacific Forest, Dry Chaco with Wet Chaco and Pampa Deciduous Forest with Pampa Riverine Forest, since these vegetation types have a low number of sampling sites. I also divided Atlantic Semideciduous Forest into tropical and subtropical portions (see Rezende 2017 for details).

Results

The agglomerative dendrogram analysis showed a floristic differentiation among 16 Main Vegetation Types (Figs. 1, 2). There was a strong division into four major groups, which primarily differed in the phytogeographical domain to which they belong, thermal domain, leaf flush and the geographical location (east and west side of the Andes; Table 1). The Atlantic Rain Forest was the vegetation type with the highest number of indicator species. However, when I analyzed the proportion of the number of indicator species out of the number of species occurring in a given vegetation type, the Pacific Flora (Mediterranean and Temperate For-
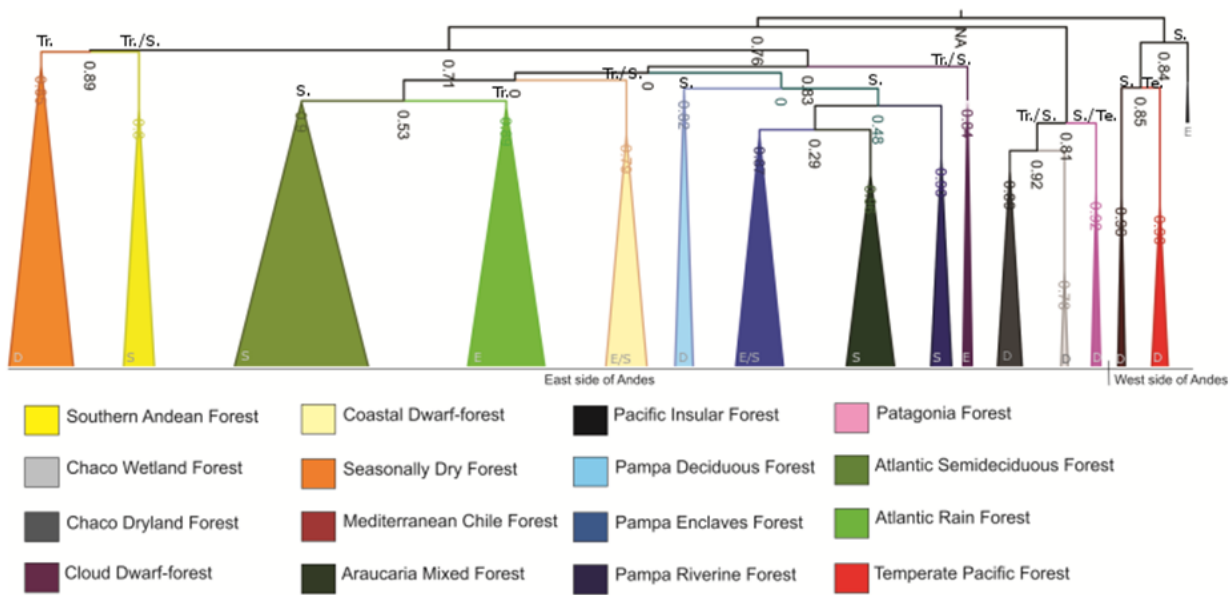
Figure 1. Dendrogram produced by clustering analysis based on a species occurrence matrix used to derive the floristic similarity among the 16 vegetation types that occur in southern South America. Tr = Tropical; S = Subtropical; Te = Temperate. D = Deciduous; S = Semideciduous; E = Evergreen.

est) had the highest proportion of indicator species (38 and 34 %), whereas the Atlantic Rain Forest had only 4 %. Also, the highest indicator values (IV) for species (IV > 0.95) were found for Mediterranean Chile and the Temperate Pacific. When analysing species richness (SR), Atlantic Rain Forest has the highest SR, with an average of 323 species per site, whereas the lowest SR was found in the Pacific Forest (29 species per community).

Across all sites, I found phylogenetic diversity sensu stricto (PD) to be strongly correlated with SR. These metrics showed a strong latitudinal pattern, where the highest value of PD was found for the communities in Atlantic Rain Forest (178), while the lowest values of PD where found for communities in the Pacific Forest (306). However, the standardized metric (ses.PD) showed an opposite result to that found for PD and SR. The highest value was found for the Pacific Forest communities (0.97), while the Atlantic Rain Forest had the lowest value (-6.35; Fig. 3).

Discussion

My results indicate that there are many vegetation types in southern South America that are distinct from tropical biomes and should therefore not be included in the Neotropical floristic prov-
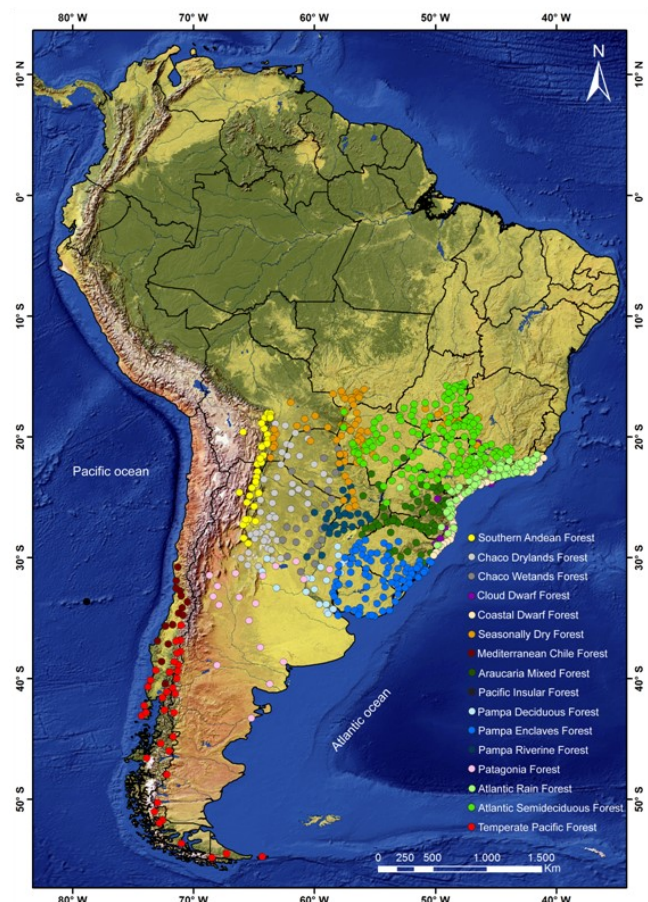

Figure 2. Map showing the location of the 16 vegetation types separated by floristic similarity analyses.

Table 1. Phytogeographic characteristics of the main vegetation types that occur in southern South America.

| Main Vegetation Type	Domain	Thermic realm	Climatic regime	Leaf flush
Atlantic Coastal Dwarf-forests	Atlantic Forest	Tropical and Subtropical	Maritime/ Seasonally dry	Evergreen and Semideciduous
Pampa Riverine forests	Pampa	Subtropical	Seasonally cold	Semideciduous
Atlantic Rain Forests	Atlantic Forest	Tropical and Subtropical	Rain/ Cloud	Evergreen
Pacific Temperate Forests	Temperate Pacific	Temperate/ Sub-antarctic	Rain/ Seasonally cold	Evergreen/ Semideciduous
Atlantic Cloud Dwarf-forests	Atlantic Forest	Tropical and Subtropical	Cloud	Evergreen
Pacific Insular Rain Forests	Pacific Islands	Subtropical	Rain	Evergreen
Andean Forests	Southern Andean	Tropical and Subtropical	Seasonally Cloudy	Semideciduous
Atlantic Mixed Forests	Atlantic Forest	Subtropical	Seasonally cold	Semideciduous
Atlantic Semideciduous Forests	Atlantic Forest/ Cerrado	Tropical and Subtropical	Seasonally dry and Seasonally cold	Semideciduous
Pampa Enclaves Forests	Pampa	Subtropical	Seasonally cold/ Maritime	Semideciduous/ Evergreen
Seasonally Dry Forest	Cerrado/ Gran Chaco	Tropical	Seasonally dry	Deciduous
Pampa Deciduous Forests	Pampa	Subtropical	Seasonally cold	Deciduous
Chaco Wetlands Forests	Gran Chaco	Tropical and Subtropical	Seasonally dry and Seasonally cold	Deciduous
Chaco Drylands Forests	Gran Chaco	Tropical and Subtropical	Semi-arid	Deciduous
Mediterranean Forest	Mediterranean Chile	Subtropical	Semi-arid/ Seasonally cold	Deciduous
Patagonia Forest	Patagonia	Subtropical/ Temperate	Seasonally cold/ Semi-arid /Arid	Deciduous
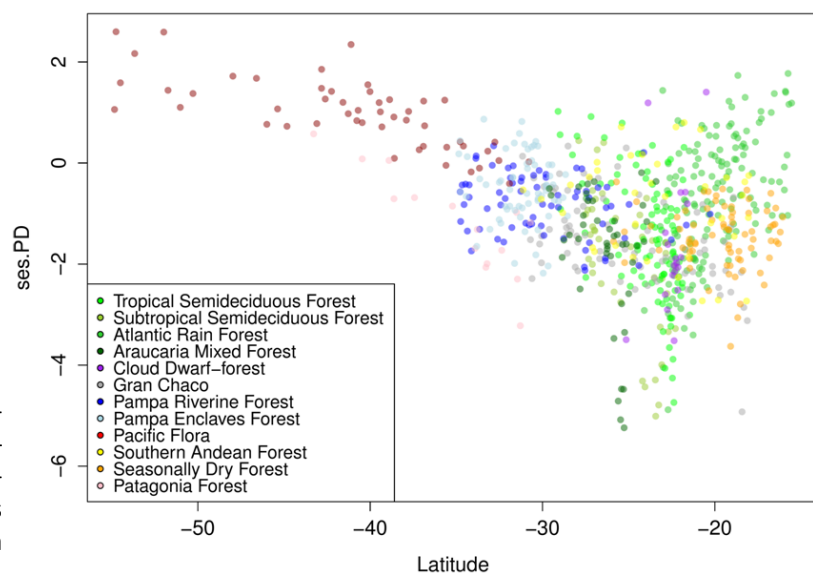
Figure 3. Latitudinal variation in phylogenetic diversity *sensu stricto* standardised for variation in species richness (ses.PD). Each point represents the estimated value of ses.PD for a single tree community.

ince (Rezende et al. unpubl. data). The large number of vegetation types is due to the floristic complexity found in the region (Rezende et al. 2016, Rezende 2017). The highest number of indicator species was recorded for the Atlantic Rain Forests, which was expected because this vegetation type also has the largest number of species. However, the largest proportional values (indicator species in relation to total richness) and the largest IV values (IV > 0.95) were recorded for the Mediterranean and Temperate Pacific forests (Rezende et al. 2016, Rezende 2017). These vegetation types located west of the Andes have a wide spectrum of biogeographic elements, including genera with many endemic species that appear to have radiated within them (Arroyo et al. 2008).

As with species richness (SR), phylogenetic diversity (PD) declines with distance from the equator, which is expected given how tightly correlated SR and PD are (Rezende et al. unpubl. data, Rezende 2017). However, once I controlled for this correlation and evaluated phylogenetic diversity with a standardized metric (ses.PD), I found that lineage diversity increases further south. Thus tree communities in the far south of South America show greater lineage diversity than expected given their species richness (Rezende et al. unpubl. data, Rezende 2017). This unexpected result may be because the temperate flora has high richness at the family level with low generic and species diversity, as well as a high proportion of monotypic genera, with several of these genera even representing monogeneric families (e.g., Aextoxicaceae, Gomortegaceae, Desfontainiaceae and Eucryphiaceae; Vilagran and Hinojosa 1997).

Overall, my findings show that the flora of South America's extratropical regions is not a narrow, cold-adapted subset of that of tropical regions. Rather, as suggested by Segovia and Armesto (2015) the extratropical floras also include diverse lineages that likely have a temperate southern hemisphere origin. My findings demonstrate that these southern forests are evolutionarily distinct with a distinct evolutionary history from the tropics and allow us to refute the Tropical Conservatism Hypothesis (TCH). Moreover, my results do not support the idea that temperate floras are recently derived from tropical floras. Indeed, the distinctive ecology and biogeographical history of each biome could be a key to understanding the distribution of tree species in southern South America.

Acknowledgements

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