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 Gondwana 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-
ty of forest tree communities. According to the tropical conservatism hypothesis \cite{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 \cite{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 \cite{Davies et al. 2004, Ruddiman 2006}, and that most species in these clades have at least partly retained their ancestral physiological tolerances \cite{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 \cite{Wiens and Donoghue 2004}.

**Methods**

The floristic data were retrieved from the NeoTropTree database \cite{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 \cite{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 \cite{2006}.

For the phylogenetic analysis, I generated an ultrametric phylogeny using Phylcom \cite{v.4.2}, starting with the following reference tree: R20120829.new \cite{http://phylodiversity.net/phylomatic/}. For each tree community (each site), I calculated phylogenetic diversity \textit{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 \cite{Rezende 2017 for details}.

**Results**

The agglomerative dendrogram analysis showed a floristic differentiation among 16 Main Vegetation Types \cite{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-
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 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.

**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.

<table>
<thead>
<tr>
<th>Main Vegetation Type</th>
<th>Domain</th>
<th>Thermic realm</th>
<th>Climatic regime</th>
<th>Leaf flush</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atlantic Coastal Dwarf-forests</td>
<td>Atlantic Forest</td>
<td>Tropical and</td>
<td>Maritime/</td>
<td>Evergreen and</td>
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<td></td>
<td></td>
<td>Subtropical</td>
<td>Seasonally dry</td>
<td>Semideciduous</td>
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<tr>
<td>Pampa Riverine forests</td>
<td>Pampa</td>
<td>Subtropical</td>
<td>Seasonally cold</td>
<td>Semideciduous</td>
</tr>
<tr>
<td>Atlantic Rain Forests</td>
<td>Atlantic Forest</td>
<td>Tropical and</td>
<td>Rain/ Cloud</td>
<td>Evergreen</td>
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<tr>
<td></td>
<td></td>
<td>Subtropical</td>
<td></td>
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</tr>
<tr>
<td>Pacific Temperate Forests</td>
<td>Temperate Pacific</td>
<td>Temperate/ Sub-</td>
<td>Rain/</td>
<td>Evergreen/</td>
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<td>antarctic</td>
<td>Seasonally cold</td>
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<tr>
<td>Atlantic Cloud Dwarf-forests</td>
<td>Atlantic Forest</td>
<td>Tropical and</td>
<td>Cloud</td>
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<td>Subtropical</td>
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<tr>
<td>Atlantic Mixed Forests</td>
<td>Atlantic Forest</td>
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<td>Semideciduous</td>
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<td>Atlantic Forest/</td>
<td>Tropical and</td>
<td>Seasonally dry and</td>
<td>Semideciduous</td>
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<td></td>
<td>Cerrado</td>
<td>Subtropical</td>
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<td>Pampa Enclaves Forests</td>
<td>Pampa</td>
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<td>Maritime</td>
<td>Evergreen</td>
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<td>Seasonally Dry Forest</td>
<td>Cerrado/ Gran Chaco</td>
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<td>Seasonally dry</td>
<td>Deciduous</td>
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<td>Pampa Deciduous Forests</td>
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<td>Seasonally cold</td>
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<tr>
<td>Chaco Wetlands Forests</td>
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<td>Tropical and</td>
<td>Seasonally dry and</td>
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<td>Subtropical</td>
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<tr>
<td>Chaco Drylands Forests</td>
<td>Gran Chaco</td>
<td>Tropical and</td>
<td>Semi-arid</td>
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<td>Subtropical</td>
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<td>Subtropical</td>
<td>Semi-arid/</td>
<td>Deciduous</td>
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<td></td>
<td>Chile</td>
<td></td>
<td>Seasonally cold</td>
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<tr>
<td>Patagonia Forest</td>
<td>Patagonia</td>
<td>Subtropical/</td>
<td>Seasonally cold/</td>
<td>Deciduous</td>
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<td></td>
<td></td>
<td>Temperate</td>
<td>Semi-arid/Arid</td>
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</tbody>
</table>

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.

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