Biogeographic anomalies in the species richness of Chilean forests: Incorporating evolution into a climatic – historic scenario

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Abstract Broad-scale richness gradients are closely associated with temperature and water availability. However, historical and evolutionary processes have also contributed to shape current diversity patterns. In this paper we focus on the potential influences of Pleistocene glaciation and phylogenetic niche conservatism (the tendency for traits to be maintained during diversification) on the tree diversity gradient in Chile, and we quantify its primary climatic correlates. Tree species richness is greatest at mid latitudes, particularly in the Andes and Coastal ranges, and decreases abruptly to the south and north. Regression tree analysis identified annual precipitation and annual temperature as the primary probable drivers of this gradient. Ice cover during the Last Glacial Maximum was also identified as an 'important' variable, but the contemporary and historical predictors are strongly collinear. Geographically weighted regression indicated that the relationships between richness and environmental variables vary regionally: the relationship between tree richness and precipitation is stronger in north-central Chile, whereas tree richness and temperature are most strongly associated in south-central Chile. By assigning each species the age of the family to which it belongs and averaging all species in each geographical unit, we also found that species from the oldest families are distributed mainly in mid to high latitudes and species from younger families are distributed mainly at lower latitudes. This pattern is closely associated with annual precipitation. Thus, the ecological component of tree richness follows contemporary climatic gradients of both energy and water, but the aridification of the Atacama Desert was an important driver over evolutionary time. The influence of recent Pleistocene glaciation remains unresolved but it cannot be discounted.

Key words: climate–richness relationship, diversity gradient, Pleistocene glaciation, tropical conservatism hypothesis.

INTRODUCTION

Broad-scale species richness gradients are closely associated with contemporary climate, primarily temperature and water availability (Wright *et al.* 1993; Hawkins & Porter 2003; Hawkins *et al.* 2003). This relationship, however, is not stationary: temperature tends to drive diversity gradients at high latitudes, whereas precipitation is more important at low latitudes (Hawkins *et al.* 2003). Some authors claim that the richness of species assemblages can be understood without recourse to historical or evolutionary processes (Francis & Currie 2003). However, this position has been criticized because ecological and evolutionary processes generating correlations between climate

and taxon richness can be strongly collinear (Qian & Ricklefs 2004; Hawkins *et al.* 2011). Besides, regional effects in comparisons of local diversity are consistent with the idea that regional evolutionary processes and historical events may also influence species richness, creating diversity 'anomalies' among ecologically comparable environments (Ricklefs *et al.* 1999).

One prominent historical hypothesis is related to distributional changes associated with Quaternary glaciations (Currie 1991; Montoya *et al.* 2007). The expectation is that species richness in areas that were covered by ice during the last glacial period (*c.* 21 kya) will be lower than in areas that were not covered by ice, due to recolonization lags by some taxa. Recent support for this hypothesis has been reported for northern North American mammals and birds (Hawkins & Porter 2003), southern South American mammals and butterflies (Samaniego & Marquet

2009), and Holarctic trees (Montoya *et al.* 2007), although historical effects are expected to be relatively small compared with those of current climate.

A hypothesis that appeals to an evolutionary mechanism, phylogenetic niche conservatism, is becoming increasingly invoked to explain global diversity gradients based on their phylogenetic structures (Hawkins *et al.* 2008; Wiens *et al.* 2010). For example, Hawkins *et al.* (2011) found that the spatial pattern of average ages of arboreal angiosperm families is fully consistent with the tropical conservatism hypothesis (TCH; Wiens & Donoghue 2004). That is, the age of the families is positively correlated with the diversity gradient equator poles. Assuming a tropical origin for angiosperms (Crane & Lidgard 1989), and that, at biogeographic scales, the evolution of cold tolerance represents the key innovation that permitted only a limited number of clades to persist in temperate zones after the global cooling initiated at the end of the Eocene (Latham & Ricklefs 1993; Ricklefs 2005; Donoghue 2008), older clades should be located in lower latitudes and younger clades in higher latitudes (Wiens & Donoghue 2004; Ricklefs 2006). Although this pattern has been described on a global scale, it appears to be clearer in the northern hemisphere than in the southern hemisphere. Apparently, the southern temperate forests presented similar or even older average ages than the tropical regions of the same continent (see Hawkins *et al.* 2011). Spatial structure in clade sorting and radiations due to historical patterns of climate change can at least partially underlie correlations between richness and current climate; however, a more detailed analysis of the characteristics of each region may show anomalous relationships between attributes that could explain the evolutionary history of their associated biota.

In this paper we focus the analysis of plant diversity on the Pacific margin of southern South America (between 18°S and 55°S), encompassing a diversity of climate and vegetation formations. The presence of the Atacama Desert in the north of Chile generates a strongly non-linear latitudinal climatic gradient with respect to energy and water, very cold and wet to the south, relatively warm and wet in the mid latitudes, and hot and dry in the tropics (Di Castri and Hajek 1976; Luebert & Pliscoff 2006). Thus, trees are dense enough to form closed canopy forest only from mid latitudes to the south (30°S to 55°S). Due to the climatic structure of Chile (and of southern South America in general), its forests represent a biogeographic 'island', separated from other forest formations by more than 1000 km of arid and semiarid zones (Villagrán 1993, 1995; Armesto *et al.* 1996; Villagrán & Hinojosa 1997; Hinojosa *et al.* 2006). These forests were, however, continuous with other Neotropical forests before the development of the Arid Diagonal of South America (Garleff *et al.* 1991;

Villagrán & Hinojosa 1997; Abraham *et al.* 2000). The interruptions in the distribution of these forests date back to the Plio-Pleistocene transition, resulting from the strong rain shadow effect produced by the Andean uplift (Villagrán 1993, 1995; Villagrán & Hinojosa 1997). Due to their prolonged isolation, these forests are characterized by a high proportion (32%) of endemic genera (Arroyo *et al.* 1996; Villagrán & Hinojosa 1997; Hinojosa *et al.* 2006). Further, the emergence of arid and semiarid climates in this region has triggered a set of evolutionary processes to adapt to these new conditions (Arroyo *et al.* 1995).

Southern South American forests are composed of a mixture of paleofloras with variable origins and histories (Schmithüsen 1956; Villagrán & Hinojosa 1997). Fossil records indicate that during the Paleocene this region supported a widespread tropical flora (Hinojosa and Villagrán 1997). Then, a flora preadapted to cool temperate conditions, which was widely distributed in Gondwana (Poole *et al.* 2003), joined in this area during the mid-Eocene, associated with a northward displacement of vegetational belts (Hinojosa 2005a; Hinojosa *et al.* 2006). During the late Eocene and early Miocene, a mixed paleoflora, with similar proportions of Neotropical, Australasian and Australantarctic elements, established in response to colder and drier conditions arising from Antarctic glaciation and the drop of global temperature (Zachos *et al.* 2001; Hinojosa 2005b). At present, one-third of the woody genera in southern South America are related to ancient paleofloras that occupied southern South America in pre-Quaternary times (Villagrán & Hinojosa 1997; Wardle *et al.* 2001; Hinojosa *et al.* 2006).

In general, the vegetation of the southern hemisphere has a number of features that differentiate it from those of equivalent latitudes in the northern hemisphere, and their distinctiveness is usually attributed to a historical legacy associated with differing climatic (Markgraf *et al.* 1995) and phylogenetic histories (McGlone *et al.* 2010; Hinojosa *et al.* 2011). For example, southern South American forests show interesting biogeographic anomalies, including their richness gradient, with the concentration of woody species richness between 36°S and 40°S and an abrupt pauperization both south and north of this region (Villagrán *et al.* 1993, 1998; Markgraf *et al.* 1995; Villagrán 1995; Villagrán and Hinojosa 1997). This pattern has been explained by the influence of Quaternary climate dynamics over the distributional ranges of these forests, both by the impact of the drop in temperature and the presence of piedmont glaciers to the south (Villagrán *et al.* 1993; Markgraf *et al.* 1995; Villagrán & Hinojosa 1997), and by the fragmentation in response to pulses of aridity to the north (Villagrán 1995; Villagrán *et al.* 1998). Other anomalous patterns have also been described, such as a high

incidence of entire margin leaves (Hinojosa *et al.* 2011), and plant – animal mutualisms (Armesto & Rozzi 1989; Aizen & Ezcurra 2008). These anomalies have been explained as historical legacies associated with the persistence of lineages of Neotropical origins.

In this study we assess geographical patterns in tree species richness (total and distinguished by phytogeographic affinities) and family ages in order to understand how the current biogeographic patterns of this region represent the influence of current climate and historical or evolutionary legacies, both from Quaternary and pre-Quaternary periods. Specifically, we ask: (1) Do the environmental correlates of species richness vary spatially across the climatic structure of Chile? (2) Have Pleistocene glaciations affected the tree richness gradients? (3) Is the species richness gradient associated with the history of successions of paleofloras with different origins during the pre-Quaternary? (4) Is the diversity gradient correlated with the age of the families? Particularly, we expect that, as has been shown globally, rainfall should be the most influential variable on the gradient of species richness in lower latitudes, and that temperature should gain influence to the south. Secondly, we expect that if the forests experienced areal contractions in response to the climate changes of ice ages, then a historical variable as the extent of glaciers during the Last Glacial Maximum (LGM) should correlate positively with the loss of species richness in the affected area. Also, because deserts are relatively new, and these forests show a mixed floristic composition, we expect an anomalous pattern in this region with respect to the global distribution of family ages, that is, newer families in the deserts, and more ancient families in the central areas, which have the highest species richness.

METHODS

Data

Species richness

The geographic richness pattern was derived from the 102 tree species (>2 m tall) recognized by FLORA ARBOREA (Rodriguez *et al.* 1983). A GIS database was constructed using the collection points registered in the Herbarium of University of Concepción (CONC) and the records of the Laboratory of Paleoecology of the University of Chile. The geographic distribution of each species was represented by the minimum area polygon that best fitted the distribution of collection points. Species richness was then calculated using a grid with a 50 by 50-km grain for analysis. Only cells that had at least 75% of their area within Chile were used for analysis. A finer grain of 10×10 km was used for mapping.

Genus phytogeographic affiliation

Each genus was grouped according to its biogeographic affiliation. Thus, species richness was calculated for each of the groups as classified by Hinojosa (2005b): Endemic, Tropical (the sum of Neotropical and Pantropical genera) and Austral (the sum of Austral-Antarctic and Australasian genera). These affiliations are defined by Hinojosa *et al.* (2006) as following: (1) Austral-Antarctic – temperate elements (AA): genera with disjunct distributions at mid and high latitudes of the southern hemisphere, including New Zealand, Tasmania, south-east and southern Australia, and southern South America (e.g. *Eucryphia*, *Laurelia*); (2) Australasian Tropical elements (AU): genera distributed in southern hemisphere areas, occasionally extending their range into tropical regions of the Americas; (3) Neotropical elements (N): genera with disjunct distributions in southern South American forests and montane forests of the eastern Andes (NW Argentina, Bolivia and Peru) and/or the Atlantic coast of southern Brazil, sometimes extending to Central America (e.g. *Azara*, *Myrceugenia*); (4) Pantropical elements (P): genera occurring in the circumtropical belt, incorporating South America, Indo-Malaysia, Africa and Madagascar (e.g. *Prosopis*, *Cryptocarya*). Some of these genera are absent from tropical Australasia; (5) Endemic elements (E): genera presently restricted to Chilean subtropical and temperate forests, south of 30°S. Widespread elements were not included in the classification.

Families average ages

Family ages were obtained from a dated version of the megatree of Davies *et al.* (2004) (available at http://www.phylodiversity.net/phylomatic/davies_dated.new; accessed March 2012). Each species was assigned the age of its family, and ages were averaged across all species in each grid cell.

Environmental data

Six climatic variables expected to potentially influence tree diversity were extracted from the 30 arc second database in WorldClim (Hijmans *et al.* 2005): annual mean temperature, minimum temperature of coldest month, annual precipitation, precipitation seasonality (coefficient of variation in monthly precipitation), precipitation of warmest quarter and cell range in temperature (the highest annual temperature pixel – the lowest annual temperature pixel in each cell). To explore possible glacial influences on the richness gradient, cells under ice at the LGM (21 kya) were registered based on the model put forward by Holling and Schilling (1981). A total of 33% cells would have been covered by ice.

Analytical protocols

We combined two analytical approaches to evaluate climatic and historical influences on tree richness patterns. First, spatial heterogeneity in the relationships between tree richness and climate variables (non-stationarity) was

quantified with geographically weighted regressions (GWR, Fotheringham *et al.* 2002). For all models a Gaussian function was assumed for the decay of the weight with distance, with a fixed bandwidth obtained using the AIC-based optimization algorithm (Burnham & Anderson 2002) included in SAM 4.0 (Rangel *et al.* 2010). Because of the extreme non-stationarity of the relationships among predictors and response variables identified by the GWR (see below), neither OLS regression nor spatially explicit autoregression would be informative and so were not used.

Regression trees (Breiman *et al.* 1984) were generated for species richness and average family age patterns to evaluate the detailed structure of the data. Regression trees are well suited for data that contain both continuous and categorical predictors and complex response surfaces. They also work well for spatially structured data and can explicitly partition trans-scalar relationships between environmental variables and ecological response variables. Because all possible alternative variable splits are evaluated at each branch of the tree, the relative contributions of collinear predictors can be quantified using variable importance values. The tree was pruned using v-fold cross validation, and we reported variance improvement (the sum of variances explained across the entire tree by each variable), variable importance (the degree

of masking of collinear predictors) and cross-validated relative error (a metric of model fit). The trees were generated using CART v. 6.6 (Salford Systems, San Diego, CA).

RESULTS

Geographic patterns

Tree species richness is greatest at mid latitudes, particularly in mid altitudes of the Andes and coastal ranges, and decreases abruptly to the south and north (Fig. 1a). The distribution of species richness calculated for the biogeographic affinity groups is similar to the general pattern, that is, most species near the centre of the country and few to the north and to the south (Fig. 2). Furthermore, this pattern indicates that the Tropical flora is the only element present in the Atacama Desert, with a tendency to be distributed mainly in north-central Chile, while Austral flora shows a tendency to be distributed mainly in south-central
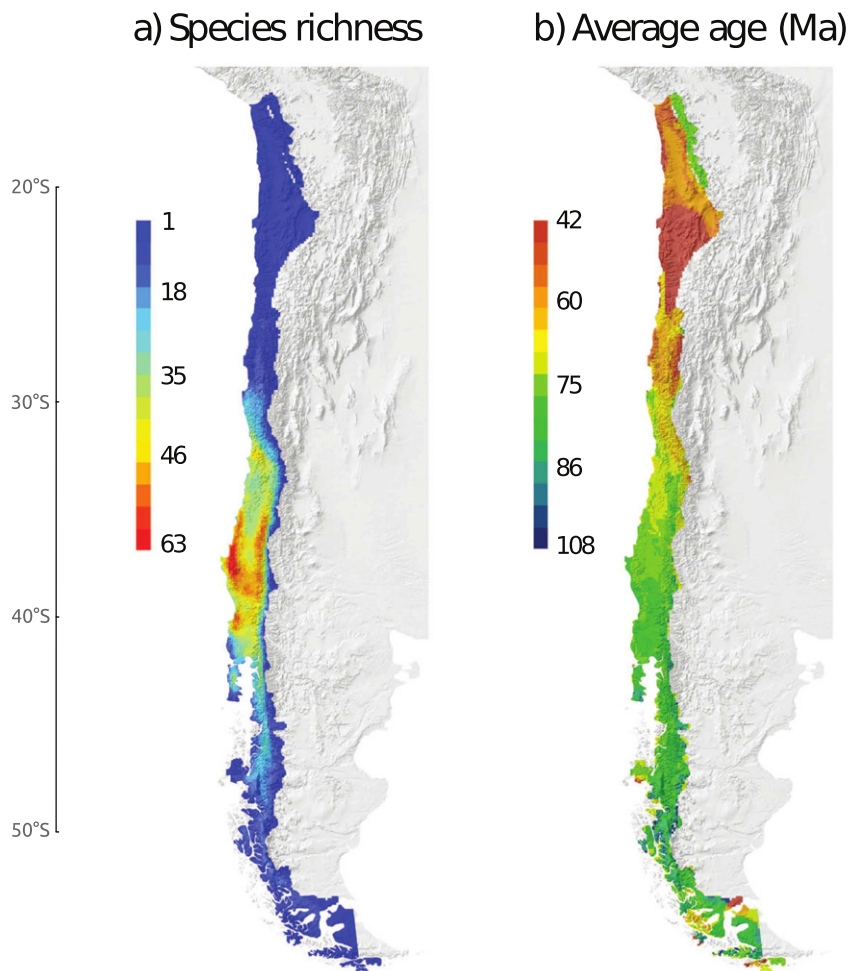

Fig. 1. (a) Pattern of tree species richness in a 10×10-km grid. (b) Spatial distribution of mean family age.
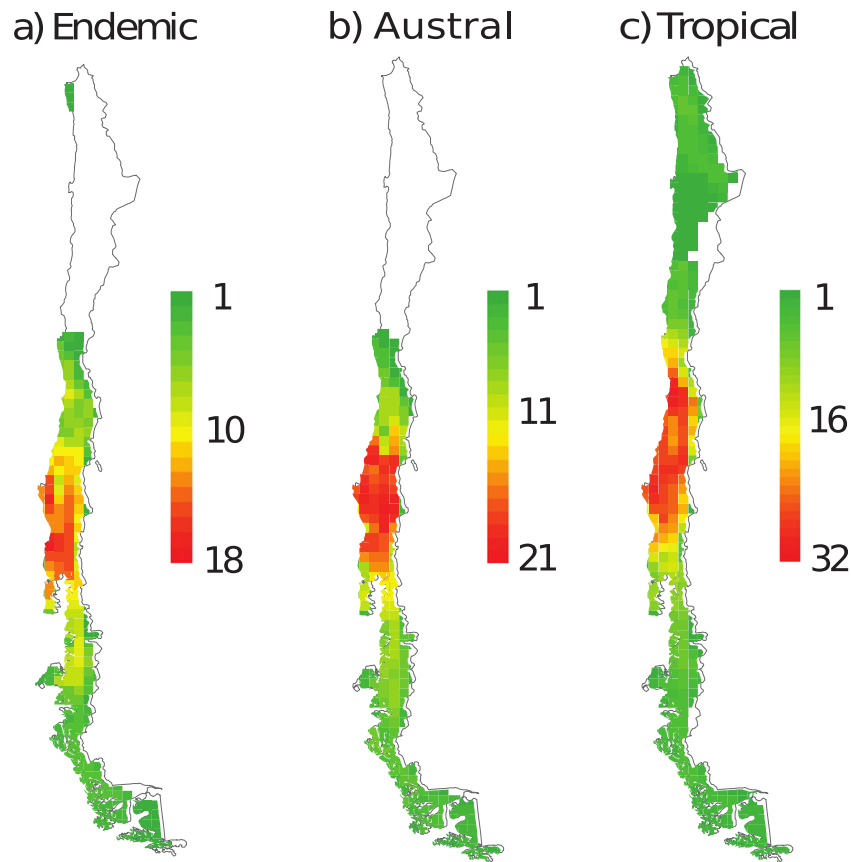
Fig. 2. Pattern of tree species richness grouped by generic biogeographic affiliations in a 50×50-km grid: (a) Endemic; (b) Austral (Austral-Antarctic and Australasian); (c) Tropical (Neotropical and Pantropical).

Chile (Fig. 2). In contrast, the gradient of average family age is monotonic, with older average ages in the south and younger ages in the north (Fig. 1b).

Species richness and current environmental variables

Relation between species richness is non-stationary with climate (Fig. 3a,b). The correlation between tree richness and temperature (measured by the local regression coefficient) is most strongly positive in south-central Chile (Fig. 3a). This is associated with the drop in tree species richness from the centre of diversity to the south. In the rest of Chile the relationship between temperature and richness is weakly negative. The relationship between tree richness and precipitation is strongest in north-central Chile (Fig. 3b). As with temperature, this precipitation gradient represents a drop in diversity from the central richness peak, but towards north rather than south. The steep rainfall gradient from the central region to the Atacama Desert accounts for this. In the rest of Chile the relationship between precipitation and

richness is close to zero or weakly negative in the extreme north and south.

Richness and glacial influence

The environmental regression tree for species richness had 26 terminal branches and identified annual precipitation as having the most explanatory power, with ice cover at the LGM ranking second (Fig. 4). The model had a relatively low error rate of <8%. Although the final tree was dominated by precipitation, the variable importance values indicated that the 'effect' of annual temperature on tree richness was the strongest across all alternative splits in the tree, whereas LGM ice cover had a moderate importance. Thus, the contemporary and historical predictors are substantially collinear, making it difficult to evaluate unambiguously relationships between species richness and past *versus* present environmental drivers or the dominant contemporary variable. On the other hand, cell range in temperature – our measure of the strength of climatic gradients up the sides of the mountains – was essentially absent from our best model and had by
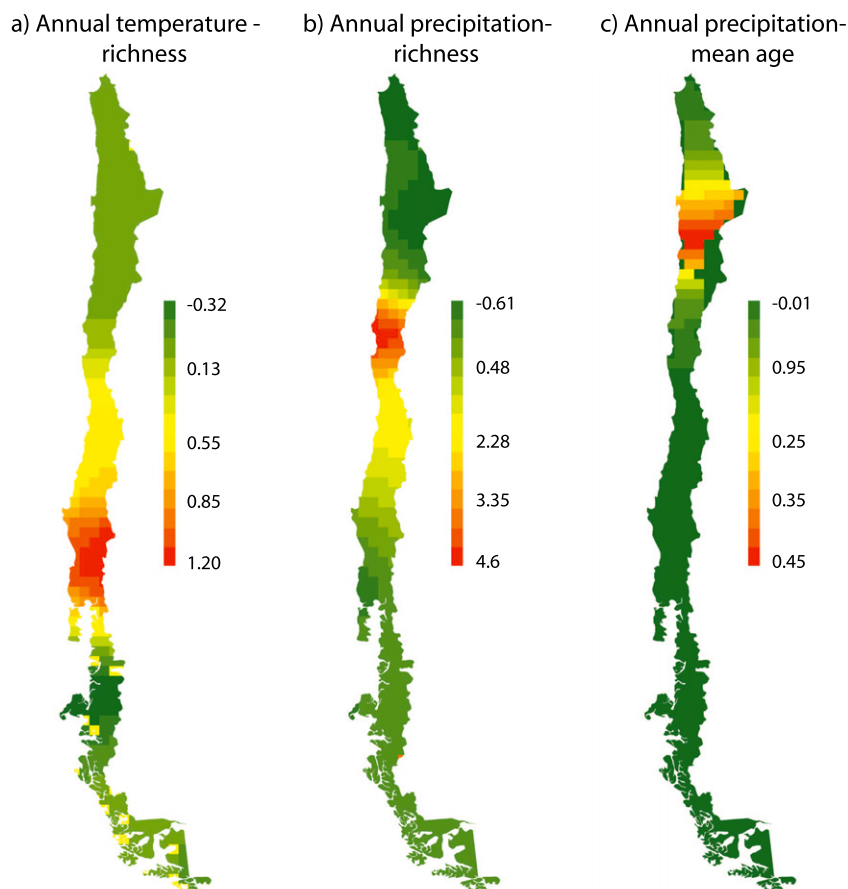
Fig. 3. Standardized regression coefficients from geographically weighted regressions (GWR) of: (a) tree richness and annual temperature; (b) tree richness and annual precipitation; (c) average family age and annual precipitation.

far the lowest variable importance, indicating that the richness gradient across the entire country is dominated by macroscale climatic gradients rather than mesoscale gradients associated with the Andean and Coastal ranges.

Average family age and current environmental variables

The regression tree for average age was substantially simpler than the regression tree for species, with 10 terminal branches (Fig. 5), indicating that the data contained less structure than the richness regression tree across a wide range of scales. Model fit was also weaker than in the richness tree (relative error *c.* 23%). Annual precipitation dominated the optimal tree and was clearly identified as the strongest predictor of average age of families among all alternative splits. As with the GWR of richness, average age has a highly localized positive relationship with climate, with a strong local relationship with precipitation only in the Atacama Desert (Fig. 3c). This is consistent with the spatial pattern of age (Fig. 1b).

DISCUSSION

Tree species richness is concentrated in the interface of the Mediterranean subtropical and temperate wet regions (36°S and 40°S), particularly in mid altitudes of the Andes and Coastal ranges, and decreases abruptly to the south and north. This pattern has been previously described and has been considered a legacy of Quaternary glacial oscillations and the development of the Arid Diagonal of South America (Villagrán *et al.* 1993, 1998; Markgraf *et al.* 1995; Villagrán 1995; Villagrán & Hinojosa 1997). A similar pattern, previously reported for mammals and butterflies, has been found to be strongly correlated with environmental variables (Samaniego & Marquet 2009; Hawkins 2010).

Annual temperature was the most important explanatory variable over the tree richness gradient of Chile based on the regression tree, but other variables, including annual precipitation, were also important, and the relationship between each variable and the gradient changed with latitude (Fig. 3a,b). In northern Chile, where the Tropical elements of the flora tend to dominate (Fig. 2c; Schmithüsen 1956), changes in
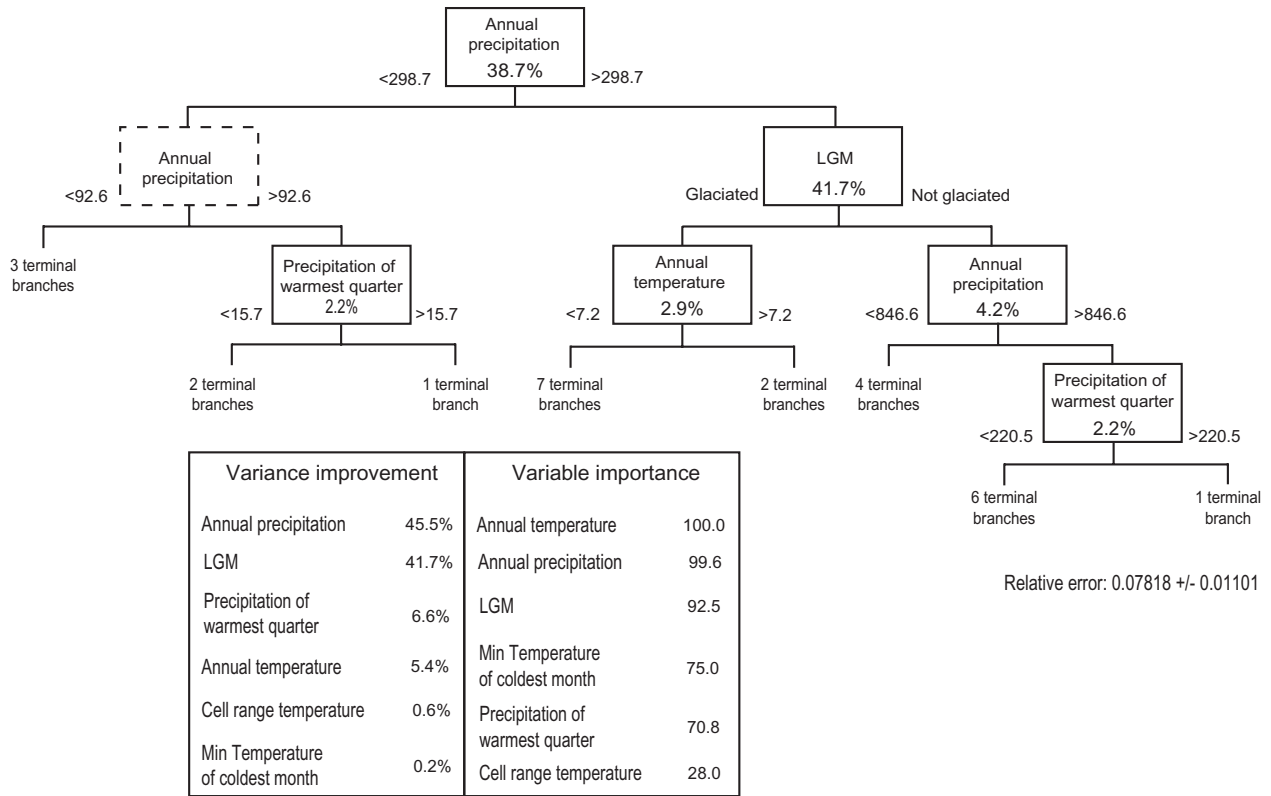
Fig. 4. Regression tree for tree species richness. The percentage of variation explained by each split is provided at each node, but only splits accounting for >2% of the variance in richness are shown. Also provided are the variance improvements of each predictor summed over the entire tree, and the variable importance values based on competing splits. Relative error reflects the proportion of cases (cells) misassigned to a terminal branch. LGM, Last Glacial Maximum.

diversity were associated primarily with the rainfall gradient (see Fig. 3b), whereas south of the richness centre, where the Austral elements (taxa with Australasian and Antarctic distributions, Hinojosa 2005b; Hinojosa *et al*. 2006) of the flora tend to dominate (Fig. 2b; Schmithüsen 1956), changes in diversity were associated primarily with annual temperature (Fig. 3a). The latitudinal differences in diversity – environment relationships could reflect the biogeographic history of the region and the evolutionary responses of the species, but a latitudinal shift from temperature-driven diversity gradients at high latitudes to rainfall-driven diversity gradients at low latitudes has been hypothesized to be a global phenomenon (Hawkins *et al*. 2003).

Ice cover in the Last Glacial Maximum was the unique historical variable incorporated in our analysis, but covariation with current temperature gradients (the coldest areas during the Pleistocene remain the coldest areas today) makes it difficult to evaluate it unambiguously. This variable did enter the regression tree for richness where annual precipitation is high (at high latitudes), but current annual temperature still explained more variation over all competing splits (Fig. 3). Patterns of southwards richness pauperiza-

tion in southern South America (Villagrán & Hinojosa 1997) as well as in other southern hemisphere forests (Markgraf *et al*. 1995) have been attributed to the repeated process of range contraction and expansion in response to the glacial – interglacial cycles of the Pleistocene. In the case of Chile, pollen records from the Lake District and Chiloé (40°S–43°S) (Villagrán 1988, 1990; Heusser & Heusser 2006) and phylogeographic studies (Segovia *et al*. 2012) show that the thermophilous taxa of the temperate rainforest contracted their ranges during cold phases, restricting themselves to areas of low to medium altitude of the Coastal range north of 40°S, whereas cold-tolerant species were able to survive near the ice line and even further south (Villagrán *et al*. 1998; Mathiasen & Premoli 2010). Therefore, distributional changes associated with the LGM may not be sufficient to explain the contemporary gradient. Perhaps this hypothesis should be extended to repeated distributional changes associated with multiple Quaternary glacial cycles, but evaluating this would require an assessment of the extinction rates in the region during this period.

We found that the pattern of distribution of average ages in southern South America (defined at the family level) opposes the pattern described at the global scale
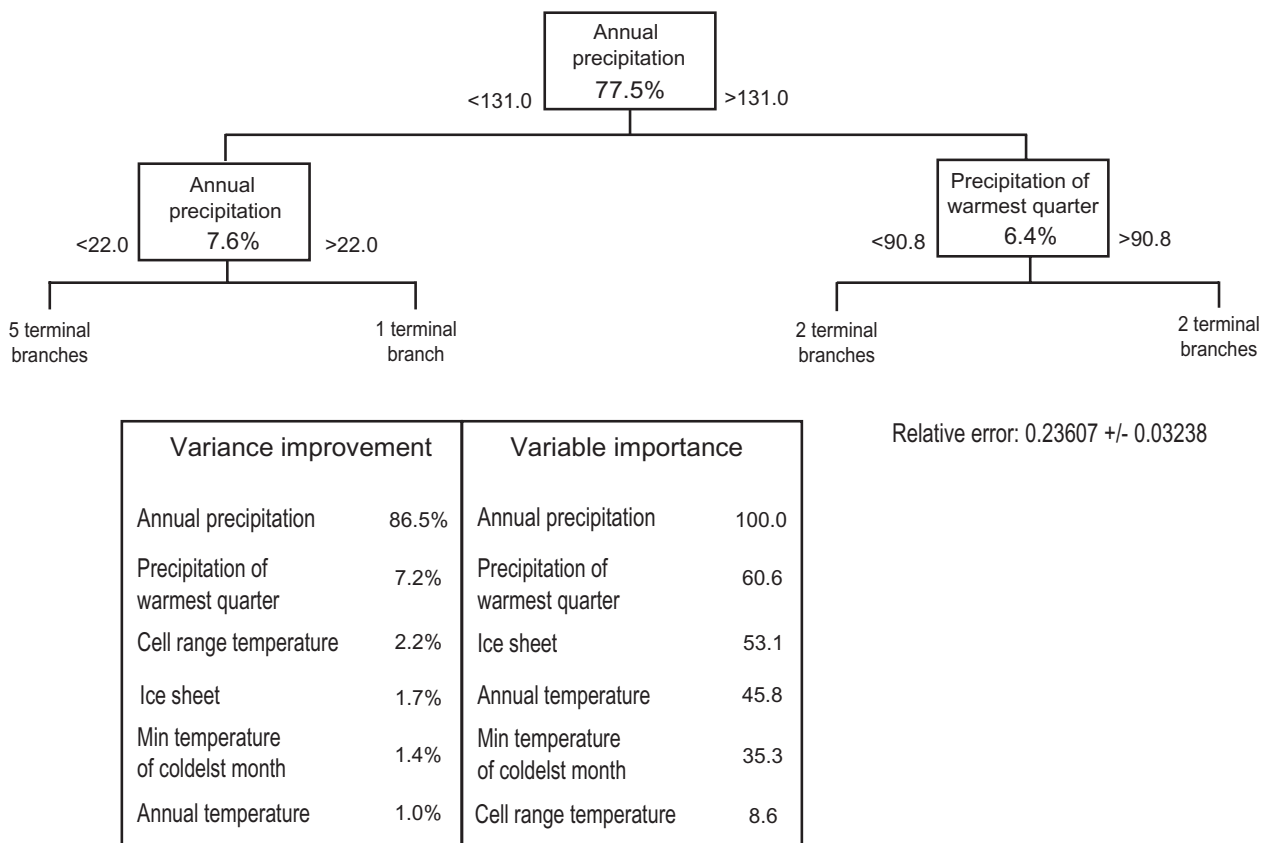
Fig. 5. Regression tree for angiosperm average age, calculated by assigning each species the age of its family. Presentation as in Figure 4.

(Hawkins *et al.* 2011). That is, trees from older families are distributed mainly in high latitudes, while trees from younger families are distributed mainly towards lower latitudes (see Fig. 1b). This average age pattern did not follow the bell-shaped pattern of species richness, inconsistent with the TCH hypothesis, where the distribution of older families is expected to correlate with the richest areas. This could be explained by the extratropical origins of part of the flora (20% of Austral elements, Villagrán & Hinojosa 1997). When South America and Antarctica were connected during late Cretaceous, the area became a centre of floral diversification, with taxa often originating there before spreading to other southern areas (Mildenhall 1980; Hill 1994; Markgraf *et al.* 1995, 1996), a fact that would account for previous adaptations to cold in these lineages. These extratropical floras persisted in South America with diversification and extinction rates lower than in the rest of the southern hemisphere, because this region showed more moderated climatic changes after the separation of Antarctica (Markgraf *et al.* 1995).

An alternative explanation for the pattern of average ages of families can be associated with the relatively recent development of extreme aridity in the

tropics and the establishment of the Arid Diagonal of South America during the Neogene (between 15 and 10 Myr) (Hinojosa and Villagrán 1997). Hawkins *et al.* (2011) found that angiosperm families in the wet tropics were older, as expected by tropical niche conservatism hypothesis, but that deserts were occupied globally by species of younger families. Aridification and the establishment of the South American Arid Diagonal would have promoted evolutionary processes *in situ* associated with adaptation to aridity (Axelrod 1979; Arroyo *et al.* 1995). Meanwhile, the emergence of a Mediterranean climate in response to a trend to drier climates from Oligocene onwards progressively produced an essentially modern-looking flora with numerous arid and semiarid sclerophyllous species evolving from the tropical – subtropical pool of taxa (Arroyo *et al.* 1995; Markgraf *et al.* 1995, 1996), which could be also contributing to the gradient of average family ages. There could be bias in using an arbitrary classification criterion, as the family rank, as well as in assigning ages to the origins of these families. However, this bias should be relatively low, since the definition of the clades and their relative ages are derived from a single phylogenetic megatree.

In sum, the contemporary species richness gradient for Chilean trees shares a number of commonalities with those of other regions, with strong associations of diversity and contemporary climatic gradients. The shift in the relative influences of temperature and rainfall on richness moving from high to low latitudes found in other parts of the world would also occur in the southern hemisphere. Besides, Pleistocene glaciations may have left a lingering influence on the contemporary tree richness gradient, as has been suggested for northern hemisphere forests. On the other hand, some aspects of Chilean tree richness may be unique to the region, including the tendency for species from older clades to dominate extratropical forests, and a flora comprising a complex mix of cool Austral, Tropical and Endemic elements with different origins. It is necessary to conduct quantitative comparisons to assess whether the age pattern found in Chile is repeated in the rest of the southern temperate forests, which would represent a Gondwanic legacy. But it is clear that to understand current distribution patterns we need to take into account the origins and evolution of the lineages that form these forests.

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