The Gondwanan legacy in South American biogeography

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ABSTRACT

The tropical conservatism hypothesis (TCH) suggests that phylogenetic niche conservatism (the tendency for traits to be maintained during diversification) should be the main driver of latitudinal diversity gradients. For example, the tropical–temperate diversity gradient for woody angiosperms should reflect the tropical, older origin of most clades, the constrained evolution of cold tolerance, and the fact that few clades were able to persist in temperate zones after the beginning of the global cooling in the Eocene. Evidence for this explanation has been discussed primarily from a Northern Hemisphere perspective. Recently, two studies have presented diversity and clade–age relationships in South American forests that are inconsistent with the TCH, with older woody families being more frequent at higher latitudes and higher elevations in the Andes. We argue that a broader framework considering the ancient history of the Southern Hemisphere flora and the recent history of the Andean flora can help explain these discordant patterns. Here, we provide an initial discussion of this new perspective, emphasizing the historical development of a unique and rich palaeoflora of Gondwanan ancestry at mid- to high latitudes of South America and Antarctica. We suggest that the idea of Austral niche conservatism (ANC) of a warm-temperate Antarctic–South American biota should be explored further to improve our understanding of biogeographical patterns in the Southern Hemisphere.

Keywords
Austral niche conservatism, Andean flora, biodiversity, biogeographical patterns, extratropical evolution, latitudinal diversity gradients, palaeoflora, phylogenetic niche conservatism, Southern Hemisphere, tropical conservatism hypothesis.

INTRODUCTION

The central pursuit of historical biogeography is the identification of events that account for the evolutionary history of a biota on the basis of general biological principles that integrate evolution (phylogeny) and the space where diversification takes place (Anderson, 1996). Although hypotheses for ecological processes operating in the past are not testable by direct observation or experiment, inferences and predictions about present-day biota can be tested (Ball, 1976; Villagrán et al., 2014). In recent years, new methodologies based on the molecular analysis of phylogenies have been developed that allow researchers to test hypotheses about the origin and maintenance of modern biogeographical patterns (Wiens & Donoghue, 2004; Riddle et al., 2008).

Phylogenetic niche conservatism (PNC; Ricklefs & Latham, 1992; Wiens, 2004; Donoghue, 2008) has been suggested as a process that can explain modern biogeographical patterns and the main global diversity gradients, on the basis of phylogenetic structure (Hawkins et al., 2008; Wiens et al., 2010). A related hypothesis, the tropical conservatism hypothesis (TCH; Wiens & Donoghue, 2004), has been proposed to explain the high diversity in equatorial regions and its decline towards the poles. The TCH predicts that species richness will be high in regions characterized by warm temperatures and abundant rainfall because these conditions match the ancestral niches of many extant clades. According to this hypothesis, younger clades will be found in temperate regions because cold-temperate environments are geologically more recent (Wiens & Donoghue, 2004). The tropical–temperate
diversity gradient should thus reflect the tropical and older origin of most clades (Crane & Lidgard, 1989), the constrained responses of many lineages to cooling trends (Condamin et al., 2012), and the fact that only a limited number of clades survived in temperate zones after the global cooling initiated in the Eocene (Latham & Ricklefs, 1993; Donoghue, 2008; Graham, 2011). Hawkins et al. (2011) tested this hypothesis by analysing the ages and diversity of angiosperm families at a global scale, and found a positive ‘clade age–family richness’ relationship. More recently, however, both Segovia et al. (2013) and Qian (2014) have shown contrasting patterns in South American forests, suggesting that further studies are needed to assess how general the relationship is between clade age and diversity. These studies suggest that alternative hypotheses about the ancient history of the Southern Hemisphere flora and the recent history of the Andean flora should be explored. Here, we provide an initial discussion to highlight the fact that biogeographical hypotheses to explain floristic richness patterns in South America should consider the historical evidence for the development of a unique and rich, warm palaeoflora of Gondwanan ancestry at mid- to high latitudes of South America and Antarctica.

INCONGRUENT CLADE AGE AND FLORISTIC RICHNESS IN SOUTH AMERICA

Segovia et al. (2013) analysed the species richness pattern of woody angiosperms along the Pacific margin of southern South America (18°–55° S) and revealed interesting biogeographical anomalies with respect to tropical–temperate gradients in the Northern Hemisphere. In particular, the woody species richness gradient in Chile had a marked bell-shaped pattern, with a concentration of diversity at mid-latitudes, between 36° S and 40° S, and abrupt declines in richness to both the north and south of the mid-latitude region (Villagrá, 1993, 1998; Markgraf et al., 1995; Villagrá, 1995; Villagrá & Hinojosa, 1997). Segovia et al. (2013) also showed that the pattern of distribution of average clade ages (of woody families) in southern South America is contradictory to the pattern expected according to the TCH, which predicts a concentration of older clades at low latitudes (see also Fig. 4b in Hawkins et al., 2011). In southern South America, in turn, woody species from older families were found to be concentrated mainly at higher latitudes, while woody species from younger families were found to be distributed mainly towards lower (mediterranean and arid climate) latitudes. Therefore, the clade-age pattern did not follow the bell-shaped curve of woody species richness in south-west South America and was inconsistent with the TCH, where family ages should correlate positively with species richness.

On the other hand, Qian (2014) analysed forest composition in 127 plots set along latitudinal and elevational gradients in the Neotropics, testing for a positive relationship between clade ages and minimum temperatures. Qian (2014) found positive relationships among taxonomic richness, mean clade age (measured as mean family age of each forest plot) and minimum temperature (measured as mean temperature of the coldest month) in plots along the latitudinal gradient (0–30° S), but the opposite pattern for forest plots sampled along the elevational gradient, with mean clade age negatively correlated with habitat minimum temperature and, consequently, with taxonomic richness. Even when differences in water availability among sites were considered as possibly accounting for these results, the contrasting relationships persisted.

We propose that the incongruent pattern in the distribution of average clade age in South American forests can be explained at least in part by the history of a large portion of the extratropical woody flora, which in modern times has occupied temperate latitudes in western South America as well as high elevations in the Andes. During the period when South America and Antarctica were connected as part of Gondwanaland, this large continental mass became a globally important centre of floral diversification, with woody taxa often originating there before spreading to other southern areas (Mildenhall, 1980; Hill, 1994). Similar evidence of major clade diversification before the complete breakup of Gondwanaland has been provided by phylogenetic studies of birds and amphibians (Feller & Hedges, 1998; Edwards & Boles, 2002; Ericson et al., 2002, 2014). Elements of the ancient and rich Gondwanan flora and fauna persisted in subtropical regions of South America, giving rise to diverse communities of mixed forests with or without the presence of Neotropical elements in subtropical and temperate latitudes (Romero, 1986). The presence of ancient lineages with an extratropical history, representing the Gondwanaland heritage, could explain the deviation from the patterns expected based on the TCH, questioning the assumptions of a common tropical origin of clades and the constrained evolution of cold tolerance among temperate woody taxa and the application of this model to South America.

A SOUTHERN PERSPECTIVE

Gondwanaland legacy

Early naturalists of the 19th century observed that temperate floras in the Southern Hemisphere were markedly different from those in tropical regions and bore little resemblance to their counterparts in northern continents. Schuw (1823) proposed that South America could be divided into an Antarctic and a Tropical realm, and that New Zealand and the Cape Floristic Region should also be awarded the status of realms (Moreira-Muñoz, 2007). One key naturalist, during the period of a Northern Hemisphere-biased biogeography, who contributed to a significant advance in the floristic knowledge of the southern continents, was Joseph Dalton Hooker (1817–1911). This botanist and traveller, a contemporary of Charles Darwin, studied the floristic composition of the landmasses in
southern regions during expeditions to the Antarctic continent in HMS Erebus and Terror under the command of Sir James Ross. In a letter addressed to Darwin in November 1851, Hooker wrote, trying to offer an explanation for the floristic affinities among the southern continents that he had described: ‘recent discoveries rather tend to ally the New Zealand Flora with the Australian – though there is enough affinity with extratropical South America to be very remarkable and far more than can be accounted for by any known laws of migration. I am becoming slowly more convinced of the Southern Flora being a fragmentary one – all that remains of a great Southern Continent’ (Huxley, 1918, p. 445). Moreover, Hooker proposed that the distribution and abundance of vegetation in Austral regions depended not only on the high mean temperatures but also on the amount of moisture in the air and the equable levels of heat and cold, free from extremes (Skottsberg, 1960).

In both a letter sent to Joseph Hooker in December 1858 (Darwin, 1903, p. 116) and later in the Origin of species (Darwin, 1859, p. 466), Charles Darwin acknowledged the idea of a large flora that could have occupied Antarctica before it was covered by ice. Further, Engler (1879, 1882) recognized a close relationship between floras from southern Chile and New Zealand’s South Island, the sub-Antarctic islands, most of Australia and Africa’s Cape Region. Engler (1899) was surprisingly perceptive at the time in realizing that, scattered over the islands and landmasses of the southernmost part of the world, lay the remains of a single flora, the ‘Ancient Ocean’ flora, that he eventually called the Austral Antarktischen Florenelement (Engler, 1899; cited in Moreira-Munoz, 2007). The validity of this hypothesis was confirmed only in 1892, when the first fossil woods from the Antarctic Peninsula were recovered (Skottsberg, 1960). In 1902, the first leaf impressions belonging to two different horizons were recovered, one Jurassic (Halle & Seward, 1913) and the other presumably Oligocene. These fossil leaves were shown to belong to genera present nowadays in South America and New Zealand, such as Nothofagus (Dusen, 1908).

Aware of these findings, Skottsberg (1960) recognized two main centres of floristic distribution in South America, one strictly sub-Antarctic and the other Austral, applied to a southern element that migrated into a warm-temperate flora of subtropical character and then, removed from its source, southern element that migrated into a warm-temperate flora strictly sub-Antarctic and the other Austral, applied to a main centres of floristic distribution in South America, one

Andean legacies

Some floristic affinities of forests on the middle and upper slopes of the tropical Andes suggest a relationship with floras of higher latitudes in temperate regions of southern South America and other landmasses in the Southern Hemisphere (Hill, 1929). The geological evidence discussed below indicates that the final uplift of the central and southern Andes to their current elevations (above 3000 m) did not occur until the late Miocene or Pliocene. Empirical data show that this region had achieved no more than half of its current height by the late Miocene (Gregory-Wodzicki, 2000; Giambiagi, 2003). Assuming that a correlation exists between the age of a place and the age of its biota, the geological chronology of Andean uplift and the time of radiation of Andean taxa implies a correspondingly recent origin of the central and southern high Andean flora (Hughes & Eastwood, 2006; Antonelli et al., 2009). In situ evolutionary radiation, the upwards migration of lowland elements (Arroyo et al., 1983) along with recent long-distance dispersal of high-elevation plants established elsewhere (Soltis et al., 2001), would probably have been the main sources for the high Andean flora.

During the process of Andean uplift and the expansion of arid land west and east of the Cordillera (the arid diagonal of South America; Rambo, 1952, 1953), subtropical mixed forests would have become largely extinct in lowland areas as a result of intensifying drought. Remnants of these mixed forests (climate relicts; sensu Woolbright et al., 2014) would have remained at specific locations along the Pacific coast of South America (Villagrán & Hinojosa, 2005), on the Brazilian plateau and on the slopes of the tropical Andean Range (Hinojosa & Villagrán, 1997). Southwards migration does not appear to have been important for lowland tropical plants. In contrast, certain elements moved northwards into the tropical Andes of South America, particularly during the late Pliocene (1.5–3.2 Ma) (Hooghiemstra, 1984; Pennington & Dick, 2004). Examples of this northwards migration route are members of the Cunoniaceae, of which Weinmannia is an important genus in Andean montane forests, along with a number of species of Podocarpus, Drimys and others.
(Hooghiemstra, 1984). The diversification and migration patterns of these and other southern lineages with a tropical Andean distribution deserve further study.

A phylogeny of *Weinmannia* (Bradford, 2002) is still insufficiently resolved to determine whether the Neotropical species of this genus can be considered immigrants into tropical latitudes, but the extensive Palaeogene fossil record of Cunoniaceae from southern Australia, including *Weinmannia*, plus Late Cretaceous fossil wood from Antarctica attributed to Cunoniaceae, implies that this family originated in the south and probably migrated north along this route (Pennington & Dick, 2004). Similarly, recent phylogenetic studies have suggested that the Andean uplift and associated topographical gradients acted both as a dispersal route for boreotropical lineages (Bell & Donoghue, 2005; Winkworth & Donoghue, 2005) and stimulated rapid diversification, via allopatric speciation and ecological displacement in highland (Bell & Donoghue, 2005; Hughes & Eastwood, 2006) and montane habitats (Pirie et al., 2006).

**ANTARCTIC AND SOUTH AMERICAN PALAEOFLORAS**

**Palaeozoic and Mesozoic**

Antarctica was covered by forests from the Permian onwards (Taylor et al., 1992). Indeed, many elements found today in the southern continents can be traced back to the Gondwanan era, when the large continent would have been dominated by a continuous cool-temperate flora, which is now scattered into a relict distribution by tectonic movements and the breakup of Gondwana (McLoughlin, 2001). In the Early Jurassic, when the southern territories were still united into a single landmass, the southern cone of South America, west Antarctica and New Zealand/Australia would have constituted the south-west border of the supercontinent (Shields, 1998; McLoughlin, 2001; McCarthy, 2003, 2007). These primate connections could explain the strong current biotic affinities among the continents of the Southern Hemisphere.

In the Early Cretaceous, the Antarctic forest ecosystem was dominated by a conifer–tree fern forest community (Falcon-Lang et al., 2001). During the Late Cretaceous, flowering plants must have radiated throughout Gondwanaland, gradually changing the lowland vegetation to forests dominated by angiosperms (Crane & Lidgard, 1989; Lupia et al., 1999; Cantiroll & Poole, 2005). The shifting forest composition would have made ancestral vegetation more similar at the family level to the angiosperm-dominated canopy of today’s Valdivian rain forest in Chile, where evergreen and broad-leaved tree species predominate in a cool-temperate environment with strong oceanic influence: Nothofagaceae, Myrtaceae, Eucryphiaceae/ Cunoniaceae, Lauraceae, Monimiaceae and the gymnosperms Araucariaceae, Cupressaceae and Podocarpaceae (Villagrán, 1991; Armesto et al., 1996; Poole et al., 2003 and references therein). To this impressive Antarctic palaeoflora it would be possible to add Late Cretaceous fossil flowers related to extant Winteraceae, now widespread in temperate Chilean and Neotropical forests (Eklund, 2003). The Antarctic palaeofloras strongly suggest that the ancestors of today’s tropical and temperate South American flora were much more widespread in the Late Cretaceous (Poole et al., 2003, 2005).

**Cenozoic**

The proxy data for Antarctica during the Palaeocene epoch (65–56 Ma) generally show cool temperate conditions supporting vegetation dominated by *Podocarpites* spp. (Podocarpaceae), highly diverse *Nothofagus*-dominated forests developing in the mid-Eocene (49–37 Ma), followed by the final demise of angiosperm-dominated woodlands as a result of Cenozoic cooling and the inception of the Antarctic cryosphere around the Eocene–Oligocene boundary (Francis, 1996; Poole et al., 2005; Truswell & Macphail, 2009).

During the Palaeocene–Eocene transition, the fossil record from South America shows that woody species shared between tropical and extratropical (northern Argentina) sites were practically non-existent (Jaramillo & Cárdenas, 2013). The number of fossil species recorded in Eocene Neotropical sites is 572, but only 93 in extratropical sites of Argentina, with only two species present in both Neotropical and Argentinian palaeosites. The few shared species include *Podocarpites*, common in Argentina but very rare in the Neotropics, and *Polypodiacoisporites* sp. (a fern), rare in both regions (Jaramillo & Cárdenas, 2013). This floristic differentiation reflects the absence of a tropical biome expansion into extratropical latitudes even during the warmest period of the Cenozoic, in the early to middle Eocene (Zachos et al., 2001). Moreover, the historical distinction of these two adjacent, but non-overlapping, floras could indicate that the flora of the extratropical regions is not a narrower cold-adapted subset of that of tropical regions, but a much richer element that diversified much earlier.

Temperate floras of the Eocene of South America integrate some Neotropical elements, or tropical taxa that migrated south during Eocene global warming (Romero, 1986, 1993; Hinojosa & Villagrán, 2005; Wilf et al., 2005). Romero (1978, 1986, 1993) called this temperate Palaeogene biome the Mixed Palaeoflora, which would have characterized the Palaeocene south of 44° S. By the middle Eocene, this flora would have expanded north to occupy the entire region south of 24° S (Romero, 1986). The widespread Mixed Palaeoflora of South America must be considered a unique ecosystem with no modern analogue. It developed over a vast temperate region, under a climate warmer than today, and presumably with higher annual precipitation distributed rather uniformly during the whole year (Hinojosa & Villagrán, 2005). In the fossil evidence this palaeoflora was represented by a rich mixture of angiosperm and gymnosperm lineages, the latter mainly Araucariaceae and Podocarpaceae (Romero, 1978, 1986, 1993; Hinojosa & Villagrán, 2005). This widespread and diverse warm-temperate flora
combined Neotropical elements, temperate elements from Gondwana (sub-Antarctic in origin) and Chaco forest elements that evolved in situ (Jaramillo & Cárdenas, 2013).

The high abundance and diversity of gymnosperm trees (e.g. Araucariaceae and Podocarpaceae) in the forests of the extratropical region, the numerous families that are rare in the tropics but much more abundant in southern temperate latitudes (e.g. Proteaceae, Myrtaceae, Casuarinaceae, Cunoniaceae, Atherospermataceae and Akaniaceae) and the conspicuous absence of major Neotropical clades (e.g. Zingiberales, Meliaceae, Anacardiaceae, Sapotaceae, Moraceae, Annonaceae andViolaceae, except for one Euphorbiaceae) suggest that equatorial tropical rain forests did not expand south during global warming events, as the rich mixed flora that occupied the mid-latitudes acted as a barrier to the dispersal of the tropical flora. The tropical forests did not expand into southern regions even during the early Eocene climatic optimum (Jaramillo & Cárdenas, 2013). In turn, it was the unique and rich mixed flora, which according to Romero (1978, 1986, 1993) developed at the mid-latitudes of South America, that expanded to occupy all the areas immediately south of the tropical rain forest biome during the warm periods of the Palaeogene (Jaramillo & Cárdenas, 2013).

**FINAL REMARKS**

Recent evidence from community phylogenetic analyses, floristic affinities, fossil records and molecular phylogenetic reconstructions is being used in a renewed effort to understand South American biogeography. This new evidence reinforces the proposal of an early differentiated mixed palaeoflora of extratropical origin, similar to that of present-day forests in temperate regions of the Southern Hemisphere. The relationship between average clade age along latitude and elevation gradients found by both Segovia et al. (2013) and Qian (2014) indicates that the distribution of richness of South American woody angiosperms does not conform to the standard TCH. This could be a sign of the relative antiquity of the lineages comprising the present extratropical floras in South America. This perspective therefore raises questions about the relationships between the historical rates of speciation and extinction in generating the present-day floras, taking into account the fact that they are often remnants of ancient and fragmented palaeofloras that were once widely distributed. Moreover, the perspective presented here accounts for the current distribution pattern of woody species richness in forests of the western margin of southern South America (Segovia et al., 2013).

With this evidence in mind, questions about the relationships between biodiversity patterns and the historical role of cradles and museums of the tropical and temperate zones (Stebbins, 1974), particularly in the case of South America, can be reformulated. Such ideas have prevailed in the biogeographical literature when examining tropical–temperate patterns of biodiversity from a Northern Hemisphere perspective, assuming that Southern Hemisphere biotas would conform to these patterns. However, considering the history of the southern biotas, it becomes more important to detect the relationships between geographical patterns of speciation and extinction rates in entire biomes, incorporating biogeographical history rather than current geographical locations at lower or higher latitudes (e.g. Crisp et al., 2009). In the light of new data, we can hypothesize that the biota of Austral continents, which was much more diverse in the Mesozoic under a warm-temperate and equitable climate than today (cradle, sensu Stebbins, 1974), should have experienced high extinction rates as a result of the breakup of Gondwanaland and the freezing of the Antarctic continent. The Austral biota would have further changed its clade representation while migrating towards lower latitudes (both in South America and Australasia). Tropical forests, in the meantime, would have maintained higher speciation rates compared with extinction under geologically and climatically more stable conditions, but their flora did not colonize southern high latitudes, at least not in South America. This could explain the woody diversity patterns found in the southern regions of South America, where Australasian and Austral–Antarctic elements are predominant, giving this flora an older average age than that of lower latitude regions, where the proportion of Neotropical elements tends to increase (Segovia et al., 2013), and producing a remarkable peak of phylogenetic diversity of woody species at around 40° S in southern South America (see Fig. 1A in Kerkhoff et al., 2014). Concomitantly, the Andean uplift in the Neogene generated new environmental conditions that allowed the progress of the southern woody flora towards tropical latitudes, making headway particularly on the wetter eastern flank of the Andes. Thus, the higher average clade age in the cold mountains of the continent (Qian, 2014) could be understood as the product of Austral or extratropical palaeoflora museums, or climate relicts, associated with ancient northwards migrations and relatively low rates of speciation and extinction. The average age of clades represented in montane forests of the Andes compared with lowland rain forest in the tropics suggests that the communities that make up this montane forest biome in South America are legacies of a southern biogeographical history. This is a very interesting argument because the rich biota of tropical mountains was presumably further enriched by the contribution of extratropical flora (and biota) to tropical biodiversity.

With respect to the historical shaping of biogeographical patterns, the incongruent relationship between average clade age and tree species richness in temperate forests of western South America could also be explained because present-day mixed forests (Hinojosa et al., 2006) contain a rich stock of extratropical lineages. These elements might represent an extratropical deviation from the assumed tropical niche of early angiosperms; that is, the Gondwanan flora that differentiated early outside the tropics would have experienced periods of high diversification that would have led to niche differentiation in multiple habitat contexts and under a
variety of selective pressures. Accordingly, for the analysis of diversity patterns in the Southern Hemisphere at least, it is necessary to consider the unexplored idea of Austral niche conservatism (ANC). This means that the diversity patterns could be explained better by a process of niche conservatism of an anciently fragmented biome, similar to Crisp et al.’s (2009) hypothesis of biome niche conservatism. Thus, to pursue evolutionary explanations for PNC, it is necessary to consider the biogeographical history of multiple biomes that have shaped the current biogeographical patterns. This involves distinguishing their ancestral floristic composition and understanding the evolutionary and tectonic processes that would have influenced their origin and spatial configuration. For example, the regional distribution pattern of tree species richness in western South American forests and its unexpected relationship with family age (Segovia et al., 2013) seems incongruent with the principle of tropical conservatism, but the abundance of Southern Hemisphere elements with a long extratropical history suggests that the pattern could be the product of the combined effects of tropical and Austral conservatism.

Finally, we emphasize that, to understand the current distribution patterns of diversity and clade diversification in the Southern Hemisphere, it will be necessary to examine further the influence of a diverse, warm-temperate Austral biota that became differentiated early during the fragmentation of Gondwana, and whose biogeographical history occurred completely outside the tropics. If we accept the principle of phylogenetic conservatism, we can predict that the configuration of an extratropical niche for this rich southern biota would have had a strong impact on the present distribution and community composition of South American biomes, especially through their interaction and mixing with the diverse tropical biota. We posit that incorporating this southern perspective into the analysis of modern biogeographical patterns could help explain apparently incongruent findings such as those described by Qian (2014) and Segovia et al. (2013).

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REFERENCES


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