



# Phylogenetic insights into Andean plant diversification

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Andean orogeny is considered as one of the most important events for the development of current plant diversity in South America. We compare available phylogenetic studies and divergence time estimates for plant lineages that may have diversified in response to Andean orogeny. The influence of the Andes on plant diversification is separated into four major groups: The Andes as source of new high-elevation habitats, as a vicariant barrier, as a North-South corridor, and as generator of new environmental conditions outside the Andes. Biogeographical relationships between the Andes and other regions are also considered. Divergence time estimates indicate that high-elevation lineages originated and diversified during or after the major phases of Andean uplift (Mid-Miocene to Pliocene), although there are some exceptions. As expected, Andean mid-elevation lineages tend to be older than high-elevation groups. Most clades with disjunct distribution on both sides of the Andes diverged during Andean uplift. Inner-Andean clades also tend to have divergence time during or after Andean uplift. This is interpreted as evidence of vicariance. Dispersal along the Andes has been shown to occur in either direction, mostly dated after the Andean uplift. Divergence time estimates of plant groups outside the Andes encompass a wider range of ages, indicating that the Andes may not be necessarily the cause of these diversifications. The Andes are biogeographically related to all neighboring areas, especially Central America, with floristic interchanges in both directions since Early Miocene times. Direct biogeographical relationships between the Andes and other disjunct regions have also been shown in phylogenetic studies, especially with the eastern Brazilian highlands and North America. The history of the Andean flora is complex and plant diversification has been driven by a variety of processes, including environmental change, adaptation, and biotic interactions.

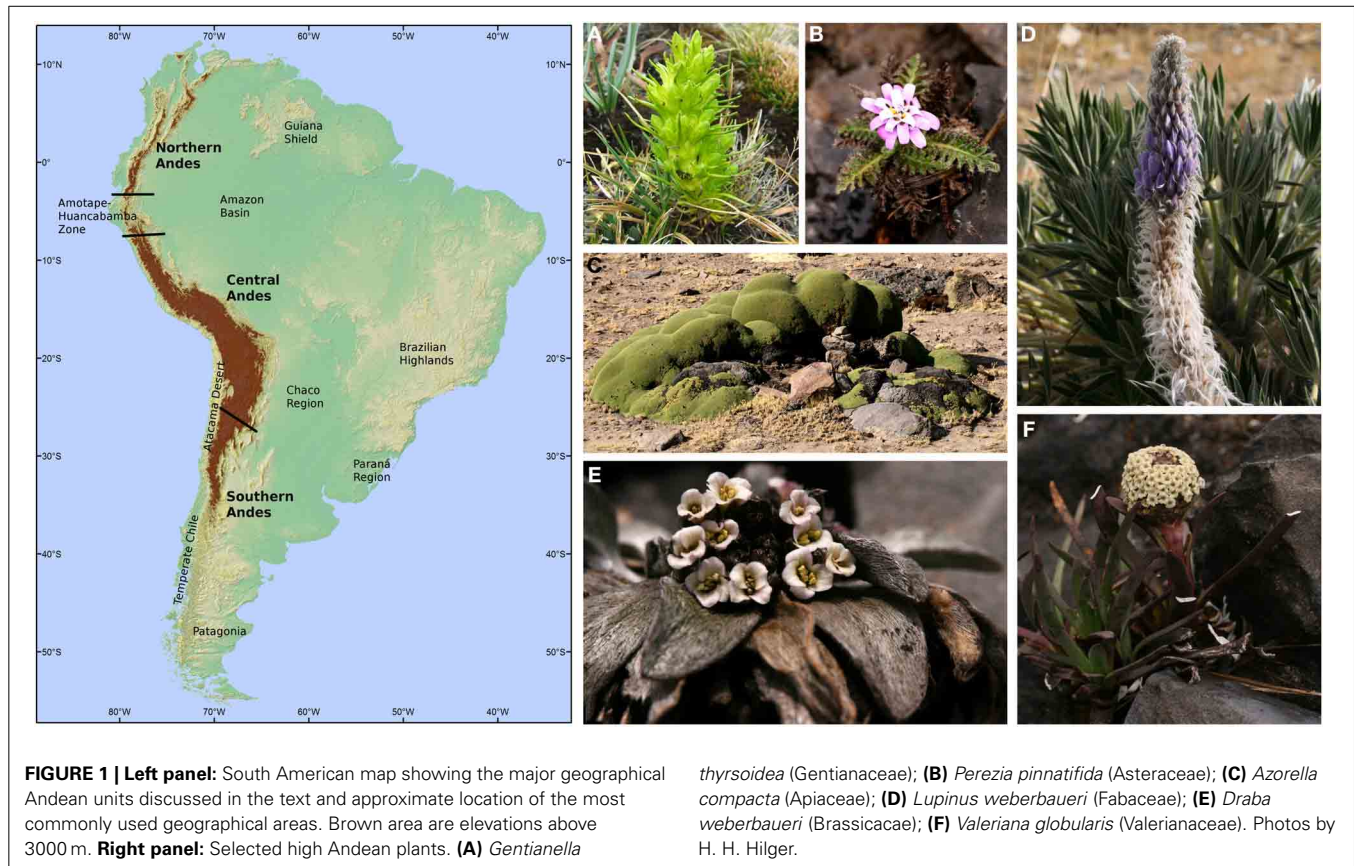
**Keywords:** Andes, divergence times, orogeny, phylogeny, plants, uplift

## 1. INTRODUCTION

The uplift of the Andes is considered as one of the most important events in the biogeographical history of the Neotropical biota (Hoorn et al., 2010) and the tropical Andes are one of the most diverse areas on earth in terms of vascular plant species (Barthlott et al., 2005). Gentry (1982) suggested that Andean uplift is responsible for nearly half of the Neotropical plant species diversity (Figure 1). Due to its geographical setting in the South American continent, the Andes have been proposed to act as a corridor, promoting North-South exchange of biotic elements, as a barrier, generating both East-West and internal vicariance, and as promoter of speciation, with new high elevation environments becoming available during their formation (Simpson, 1975, 1983; Luebert et al., 2009, 2011b; Antonelli and Sanmartín, 2011b; Hoorn et al., 2013). The rising Andes also influenced climatic and hydrological conditions at a continental level (Hartley, 2003; Blisniuk et al., 2005; Hoorn et al., 2010), affecting the evolutionary history of species groups outside the mountain chain (Antonelli et al., 2009). Currently, two major problems limit our understanding of the effects of the Andes and their orogeny on plant diversification: the scarcity of dated phylogenies (Antonelli

and Sanmartín, 2011b) and the controversy surrounding the detailed sequence and timing of the Andean orogeny (cf. Garzzone et al., 2008; Ehlers and Poulsen, 2009). The purpose of this review is to offer a synopsis of Andean plant diversifications as known today based on phylogenetic studies. It will become apparent that there are now a wider range of dated phylogenies than commonly assumed. Conclusions obtained from these phylogenies can also contribute to the debate about the timing of Andean uplift.

A precise definition of “Andes” is necessary to circumscribe the scope of this review. We follow the operational concept adopted by Nagy and Grabherr (2009), which includes the mountain regions from Venezuela to southern Chile and Argentina. This definition coincides with Körner et al. (2011), in which mountains are defined by the roughness of the landscape rather than a given elevation, which is useful for mountain chains such as the Andes with a long North-South extension and dramatic differences in elevation, especially toward the South. Absolute elevation of the thermal and vegetation belts on the mountains decreases with increasing latitude (Körner, 1998). In this circumscription, the Andes comprise the biogeographical provinces of Páramo, Puna, Yungas, Prepuna, and Subandean Patagonia



as defined in Morrone (2001). Within this region, three major geographical units can be identified: The Northern, the Central, and the Southern Andes (Figure 1, see Weigend, 2002). These units are also biogeographically meaningful. The Northern Andes comprise the mountains of Venezuela, Colombia, Ecuador, and the extreme North of Peru. At their southern edge a transition zone, the Amotape-Huancabamba zone, has been considered as a North-South biogeographical barrier, with high richness and endemism and many high-elevation groups reaching their northern and southern limits in this region (Weigend, 2002, 2004; Weigend et al., 2005). The Amotape-Huancabamba zone might represent a dispersal barrier for high-elevation lineages under current climatic conditions. Support for this idea has been found in the distribution of groups such as *Lithospermum* (Boraginaceae; Weigend et al., 2010), *Macrocarpea* (Gentianaceae; Struwe et al., 2009), *Nasa* (Loasaceae; Weigend, 2002), *Peperomia* (Piperaceae; Symmank et al., 2011). The Central Andes are situated between the Amotape-Huancabamba zone and the southern limit of the dry Puna around 25–29°S, where the precipitation regime changes from summer-rainfall to winter-rainfall (Lueberr and Plischoff, 2006), which is paralleled by floristic turnover (Villagrán et al., 1983; Martínez-Carretero, 1995; Arroyo et al., 1997, 1998). Here, aridity has been suggested as an environmental filter for Andean elements distributed to the North and to the South of this zone (Villagrán et al., 1983). Finally, the Southern Andes include the remaining Andean zones south of 29°S where elevation tends to decrease from North to South (Pankhurst and

Herve, 2007) an effect that—for plants—is compensated by latitude. Thus, “high-Andean flora” can be found from its northern limit in Colombia/Venezuela to the southern tip of South America (Troll, 1968). In spite of this subdivision, there are plant groups that are distributed along the entire Andes. This may suggest that the barriers identified do not act as filters for the dispersal of all plant groups, or that they developed after the respective groups occupied their present range. Dated phylogenies interpreted in the light of Andean geological history can contribute to clarifying this kind of questions.

Several articles based on geophysical and paleobotanical information argue for the “rapid rise model,” suggesting a recent and sudden uplift of the Andes, with more than half of the current elevation of the Central Andes uplifted between 10 and 6 Ma (Gregory-Wodzicki, 2000; Graham et al., 2001; Ghosh et al., 2006; Garzzone et al., 2008; Leier et al., 2013). The rapid rise model has generated considerable controversy and some authors have seriously challenged it. Ehlers and Poulsen (2009) suggest that paleoaltimetric estimates must be corrected with paleoclimatic data before the uplift history of the Andes can be reconstructed. According to Ehlers and Poulsen (2009), such correction would result in a more gradual uplift since, at least, Oligocene times and with most of the current elevation reached before 25 Ma. Other authors have suggested that the rapid rise model is at odds with geological evidence (e.g., Sempere et al., 2006; Hartley et al., 2007), but these authors place an emphasis on methodological issues and on the necessity of re-evaluating elevation estimates

rather than on explicitly proposing new dates for the Andean uplift.

In spite of the controversy, all of these views are an oversimplification if applied to the Andes as a whole. The evidence supporting one or the other view comes from the central Andean plateau, but there are studies indicating that the timing of the Andean uplift varies along its extension from North to South. While in the Northern Andes the timing of the uplift should be reflected in its different tectonic history (Gregory-Wodzicki, 2000), studies show that the northern Andean uplift appears to have been approximately simultaneous with the Central Andes, or even younger (Bayona et al., 2008; Bermúdez et al., 2010; Mora et al., 2010; Erikson et al., 2012). Some studies show that the uplift rate decreased toward the end of the Pliocene (Erikson et al., 2012) with a renewal of the uplift during Quaternary times (Regard et al., 2010; Rodríguez et al., 2013), and in general the Venezuelan Andes seem to be older than the rest of the Northern Andes (Mora et al., 2010). Within the Central Andes, Saylor and Horton (2014) showed that the timing of uplift pulses may differ between regions, with current elevations in the northern part of the central Andean plateau as old as 16 Ma, and thus ~6 Ma older than other parts of the central Andean plateau. Such non-uniform spatial patterns of uplift have also been suggested for the Northern Andes (Hoorn et al., 1995). For the Southern Andes, Blisniuk et al. (2005) indicates that most of the uplift would have occurred by 16.5 Ma, earlier than most of the Central Andes, and several studies are in line with the idea of an Early Miocene uplift of the Southern Andes (e.g., Jordan et al., 2001; Encinas et al., 2013; Fosdick et al., 2013), but Late Miocene phases of uplift have also been reported for the northern Patagonian Andes (Ramos et al., 2014).

The Andes exerted an enormous influence on climate and hydrology at continental scale. The most conspicuous effect is the disruption of large-scale atmospheric circulation (Garreaud et al., 2009). Asymmetries in rainfall between western and eastern South America are influenced by the elevation and orientation of the Andes, with two dry regions, the Atacama and Peruvian coastal deserts on the western side of the Andes and the extra-tropical plains in southern Argentina on the eastern side of the Andes (Garreaud, 2009), strongly affected by a rain-shadow effect caused by the Andes (Stern and Blisniuk, 2002; Houston and Hartley, 2003; Smith and Evans, 2007), with well-documented consequences for vegetation (Troll, 1968). In the Southern Andes, precipitation on the western slope is caused by frontal systems moving eastward from the Pacific. The effect of these frontal systems is orographically enhanced by the Andes (Garreaud, 2009), with precipitation maxima around 47°S (Luebert and Plissock, 2006) and an increase of precipitation with elevation and distance from the Pacific Ocean on the western Andes (Stern and Blisniuk, 2002). On the eastern side of the Southern Andes, precipitation strongly decreases due to a rain-shadow effect. Paleobotanical evidence (Barreda and Palazzesi, 2007) tend to confirm the relationship between Andean uplift and onset of arid conditions over Patagonia during the Miocene if the time estimates of Blisniuk et al. (2005) are accepted. In the Central and Northern Andes the asymmetry between East and West is reversed. Aridity is maximal a few kilometers off the Pacific coast on the western side

of the Andes, mostly due to the combined effects of the Pacific anticyclone, the Humboldt current and the rain-shadow effect of the Andes (Hartley, 2003; Houston and Hartley, 2003; Rutllant et al., 2003). The effect of the cold Humboldt current on aridity in western South America may have also been intensified or reinforced by Andean uplift (Sepulchre et al., 2009). No comparable paleobotanical evidence is available for the onset of aridity in the Peruvian and Atacama deserts, but phylogenetic studies in Atacama endemic taxa tend to indicate a rather recent (Miocene-Pliocene) origin of diversification of these lineages in response to aridity (e.g., Luebert and Wen, 2008; Dillon et al., 2009; Heibl and Renner, 2012), falling into the range of estimates for onset of present-day hyperaridity of the Atacama Desert (Alpers and Brimhall, 1988; Hartley, 2003; Hartley and Rice, 2005; Arancibia et al., 2006; Reich et al., 2009). These climatic changes exerted feedbacks on Andean uplift. While aridity on the western slope can be seen as a cause of uplift (Lamb and Davis, 2003), positive feedbacks between uplift and aridity are to be expected in the Central Andes. Conversely, in the Southern Andes uplift led to increases in precipitation in the western Andean side, so that negative feedback is to be expected (Blisniuk et al., 2005). Rainfall also tends to increase with elevation on the western side of the Central Andes, but rather due to the influence of the northeast summer monsoon over the Altiplano (Houston and Hartley, 2003). This summer monsoon is co-responsible for humid conditions on the eastern side of the continent at tropical and subtropical latitudes, the influence of which is prevented by the Andes on the western side (Garreaud et al., 2009).

Hydrological effects of the Andes are complex (Buytaert et al., 2009). One of the most important factors is related to the increase of precipitation with elevation, which makes the Andes one of the most important water sources on the continent and supports rivers, glaciers and ice fields (Houston, 2006; Garreaud, 2009), as well as sediment supply into the major water basins East and West of the Andes (e.g., Aalto et al., 2006; Hoorn et al., 2010). Drainage system formation requires topographic control. In particular, surface deformation and erosion required for drainage development has been documented to be coincident or posterior to the Andean uplift in the northern (Mora et al., 2010) and Central Andes (Hoke et al., 2007; Schildgen et al., 2009). The idea of a causal effect between Andean uplift and canyon formation has recently been challenged, arguing that surface uplift and canyon incision are temporally decoupled and putting forward the idea that climate change has been at least co-responsible for canyon formation in the Central Andes (Lease and Ehlers, 2013). This temporal decoupling between uplift and canyon formation is based on a divergent view of the timing Andean orogeny, as discussed above.

In this paper we discuss the available literature on dated and undated phylogenies of Andean lineages of vascular plants in the light of the various scenarios proposed for the timing of Andean uplift. We attempt to cover most of literature on vascular plant diversification related to the Andes, including some extra-Andean lineages whose diversification may have been influenced by the Andes. However, the number of lineages involved is potentially so high that it will exceed the capacity of the authors to finish this review before it becomes obsolete. Therefore, there is no intention



to exhaustively revise all the literature or to cover all Andean plant groups.

## 2. EFFECTS OF THE ANDES ON PLANT DIVERSIFICATION

According to Simpson (1975, 1983), Luebert et al. (2009), Antonelli and Sanmartín (2011b), and Hooen et al. (2013), effects of the Andes on plant diversification and evolution can be grouped into four major categories: (1) The Andes as source of new high-elevation habitats; (2) The Andes as a vicariant barrier, both on their eastern and western sides as well as internally; (3) The Andes as a North↔South corridor; (4) The Andes as generator of new environmental conditions outside the Andes. It has to be emphasized, that these factors acted in dramatically different ways for different ecosystems: The western and eastern slopes are today disjunct habitats, their disjunction came about by the final stages of Andean orogeny, when the central Andean chains and plateaus reached their current elevations. Exchange since then has only been possible via long-distance dispersal. Conversely, high-Andean habitats naturally formed later, in the last stages of orogeny, and—depending on topography—nowadays form more or less coherent or disjunct regions, which underwent dramatic changes in extent and connectivity during the glaciations. Although these factors may certainly act in combination upon some lineages, we will try to analyse the phylogenetic literature considering each of these causal mechanisms separately.

### 2.1. THE ANDES AS SOURCE OF NEW HIGH-ELEVATION HABITATS

High plant diversity in the Andes is associated with high levels of endemism (Young et al., 2002). Simpson (1975) attempted to explain the high degree of diversity and endemism by colonization and diversification (extinction-speciation) processes that took place during the Pleistocene. This author postulated that Quaternary glaciations favored the expansion of Páramo environments, promoting floristic exchange across the region, followed by isolation during interglacial periods. This view is strongly influenced by the belief that the Andes reached their current elevation only just before the Pleistocene (Vuilleumier, 1971). After creation of high-Andean environments, vacant niches became available for colonization and speciation from lowland and mid-elevation elements, both from within and from outside the Neotropics (Simpson, 1983; Sklenář and Balslev, 2007). Results of phylogenetic studies tend to agree with this interpretation. This conclusion could automatically be extended to the Puna and Jalca habitats, which should have more or less parallel histories, but have been studied less extensively. Divergence time estimates for high- and mid-elevation Andean clades are summarized in **Figure 2**.

#### 2.1.1. Northern Andes

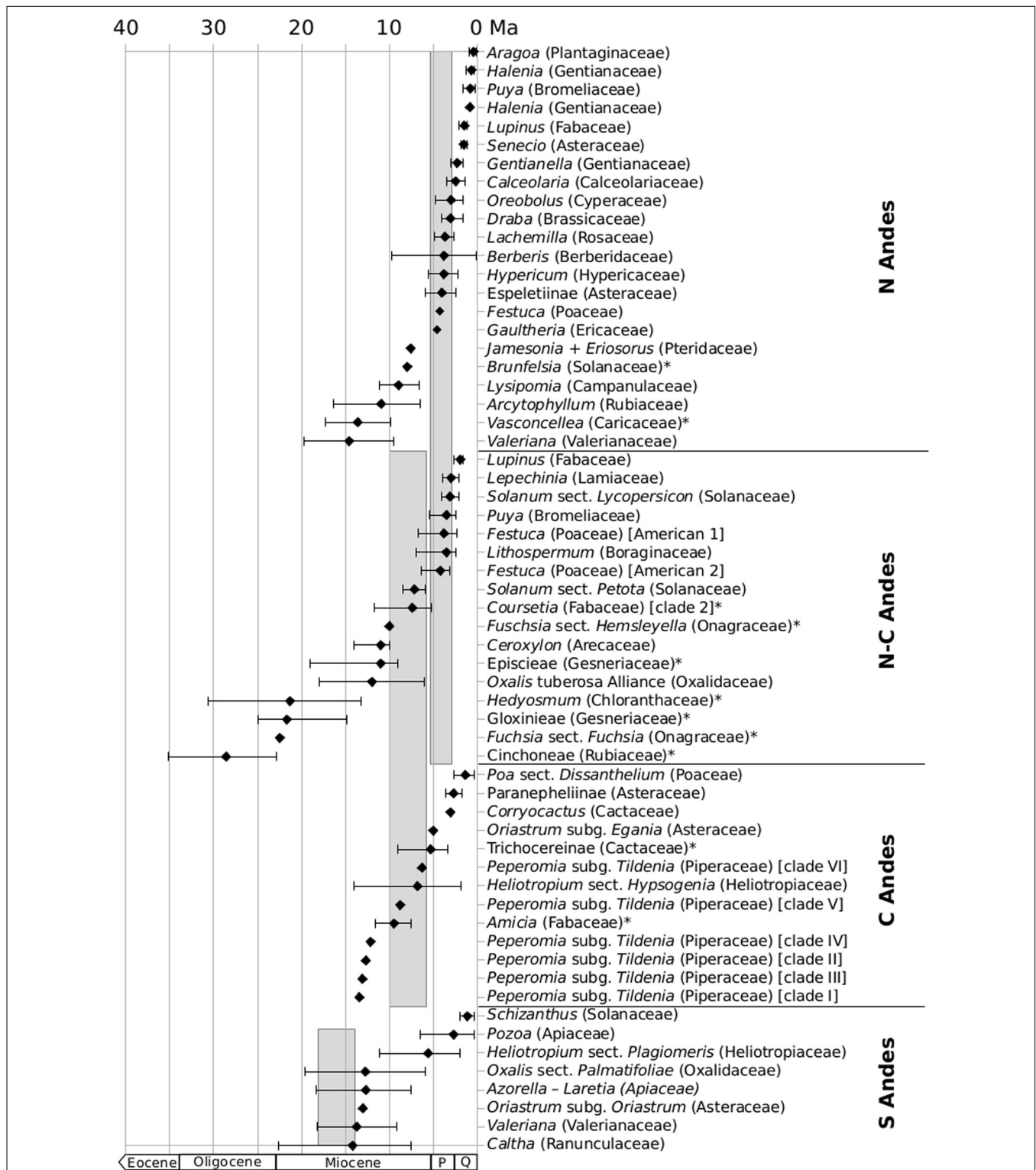
One of the best-known phylogenetic studies dealing with a species-rich high-Andean group was carried out on the genus *Lupinus* (Fabaceae; Hughes and Eastwood, 2006; Drummond et al., 2012). One of the centers of diversity of *Lupinus* (**Figure 1D**) are the northern and Central Andes with ~85 species, 81 of which represent a monophyletic group with most of its species growing above 3,000 m. The authors estimate a crown node age for this clade to ~2 Ma, suggesting a Pleistocene radiation. In addition,

this radiation is interpreted as the result of ecological opportunity, which is supported by the exceptional life-form diversity observed in high-Andean *Lupinus*, and it is claimed that an island-like diversification process can be invoked, driven by the isolation of the high-elevation areas in the Andes and reinforced by the geographical extension of the Andean region. Similar results and interpretations had been proposed for *Gentianella* (Gentianaceae; von Hagen and Kadereit, 2001, **Figure 1A**), or with a more recent age of diversification (<1 Ma) for Andean *Halenia* (Gentianaceae; von Hagen and Kadereit, 2003). High-Andean species in the genus *Lepechinia* (Lamiaceae) form a clade of ca. 30 species that may have started their divergence during the Early Pliocene (~3 Ma; Drew and Sytsma, 2013). The latter authors explain this diversification by climatic changes and the simultaneous rise of the Andes, leading to an increased availability of open habitats favored by *Lepechinia*.

Similar crown node ages have been reported for the Páramo clade of the genus *Hypericum* (Hypericaceae), with diversification rates that are greater than in any other clade in *Hypericum* (Nürk et al., 2013). High diversification rates in the Páramos have also been suggested for the Andean genus *Diplostegium* (Asteraceae; Vargas and Madriñán, 2012). In this line, Páramo flora has been recently studied extensively by Madriñán et al. (2013) who analyzed diversification rates for over 15 of the most diverse Páramo plant groups, including *Aragoa* (Plantaginaceae), *Arcytophyllum* (Rubiaceae), *Berberis* (Berberidaceae), *Calceolaria* (Calceolariaceae), *Draba* (Brassicaceae, **Figure 1E**), Espeletiinae (Asteraceae), *Festuca* (Poaceae), *Jamesonia* (Pteridaceae), *Lupinus* (Fabaceae), *Lysipomia* (Campanulaceae), *Oreobolus* (Cyperaceae), *Puya* (Bromeliaceae), and *Valeriana* (Valerianaceae, **Figure 1F**). They found the highest diversification rates among biodiversity hotspots across the world in these groups. Since most of the speciation events detected in these lineages occurred during the Pleistocene, the authors suggest that these exceptional diversification rates may have been a consequence of range expansion and contraction of populations due to Quaternary climatic oscillations.

However, for the Páramo clade of Valerianaceae Bell and Donoghue (2005) and Madriñán et al. (2013) estimated older ages, ranging from ~20 to ~5 Ma. Andean uplift has been suggested as a possible explanation for all these diversifications and similar scenarios are plausible for mid-elevation taxa.

Most of the diversity of the genus *Vasconcellea* (Caricaceae) is in the Northern Andes, with 18 out of its 20 species (Antunes Carvalho and Renner, 2012). Crown node age of *Vasconcellea* was dated to the Middle Miocene (ca. 14 Ma), originating *in situ* from a Central American ancestor, with a later secondary colonization of Central America (Antunes Carvalho and Renner, 2012). Andean orogeny has been invoked to explain the diversification of *Vasconcellea*. Two early diverging (Late Miocene, ~8 Ma) species of *Brunfelsia* (Solanaceae) inhabit the Andean foothills and montane forests of the Northern Andes (Filipowicz and Renner, 2012). For the tribe Cinchoneae (Rubiaceae), Antonelli et al. (2009) suggested that diversification at mid-elevation habitats in the northern and Central Andes during the Middle and Late Miocene was favored by ecological adaptation to higher altitudes. New World Gesneriaceae have a center of



**FIGURE 2 | Divergence times for high- and mid-elevation Andean groups that may have diversified in response to the Andean uplift.** Mid-elevation groups are signalled by asterisk. Groups are sorted by their geographical distribution in the Northern, Central, and Southern Andes and putative age ranges for the rapid phases of

uplift of these Andean regions are marked as gray bars. Error bars represent 95%HPD intervals for all estimates using BEAST. Reported Standard Deviations were transformed to 95% Confidence Intervals. Q, Quaternary; P, Pliocene. For source of data and details see Supplementary Material.

diversity in the Northern Andes and Perret et al. (2013) document at least two Andean radiations (in Gloxinieae and Episcieae). Gloxinieae originated in the Andes during the Early Miocene, but did not start their diversification until the Middle or Late Miocene. Andean diversification of Episcieae started during the Middle Miocene (ca. 10 Ma), coincident with a period of presumably rapid Andean uplift. According to Perret et al. (2013), the latter radiation accounts for more Andean species than any other clade of Gesneriaceae. Diversification of the genus *Hedyosmum* (Chloranthaceae) in the Northern Andes has been dated to ca. 10 Ma (Antonelli and Sanmartín, 2011a), similar to the age reported for the Andean palm genus *Ceroxylon* (Arecaceae; Trénel et al., 2007).

### 2.1.2. Central Andes

In the genus *Puya*, an Andean radiation gave rise to ~200 species during the Late Miocene-Early Pliocene (Givnish et al., 2011) and this may have been favored by the evolution of CAM photosynthetic pathway in some species (Givnish et al., 2014) plus allopatric speciation driven by Pleistocene glacial cycles (Jabaily and Sytsma, 2013). Evolution of CAM photosynthetic pathway was also put forward as an explanation for the diversification of the genus *Deuterocohnia* (also Bromeliaceae) at various elevations in the Andes during the Late Miocene (Givnish et al., 2014). Andean uplift associated with the development of root tubers was proposed for the origin of the high-Andean *Heliotropium* sect. *Hypsogenia* (two species, Heliotropiaceae) in the Central Andes (Luebert et al., 2011a), whose diversification has been dated to ca. 5 Ma (Luebert et al., 2011b). In *Lithospermum* (Boraginaceae), a genus with a center of diversity in the Central Andes (Weigend et al., 2010), Weigend et al. (2009) estimated a crown node age for the South American to ca. 3.5 Ma. In the high-Andean *Corryocactus* (Cactaceae), Hernández-Hernández et al. (2014) estimated a Pliocene age for its diversification (~3 Ma). Shifts in diversification rates were inferred for the subtribe Trichocereinae (Cactaceae), centered on the Central Andes, whose diversification started after 7 Ma, coincident with the Andean uplift in that region (Arakaki et al., 2011; Hernández-Hernández et al., 2014). However, according to the phylogeny presented by Schlumpberger and Renner (2012), many subsequent dispersal events between the Andes and eastern South America can be inferred in both directions. Taxonomic complexity and the lack of detailed dated phylogenies and biogeographical analyses in this group of Cactaceae make it difficult to provide an explanation for its diversification. Nonetheless, based on the distribution of its Andean taxa both in the inter-Andean valleys and at high-elevation habitats (Anderson, 2005), it is likely that a combination of inner Andean vicariance and upward colonizations played a role in the divergence of this group with well over 100 extant species. The study of Schlumpberger and Renner (2012) suggests that pollination syndromes are evolutionarily labile in this group. Therefore, repeated evolution of pollination syndromes may have contributed to reproductive isolation in recent speciation events. In *Peperomia* subg. *Tildenia* (Piperaceae), there are several central-Andean clades, all of which started their diversification after ca. 13 Ma, coincident with the onset of central Andean uplift (Symmank et al., 2011). *Poa* sect. *Dissanthelium*

(Poaceae), with a center of diversity in the Central Andes, forms a monophyletic group of 20 species (Refugio-Rodríguez et al., 2012) that diversified in the last ca. 1 Ma (Hoffmann et al., 2013). In another central Andean example, Soejima et al. (2008) estimated that the stem node of Paranepheleinae, a high Andean plant group, to be around 13 Ma old. However, the main diversification of the group did not occur until around 2 Ma. Hybridization may have played a role in the diversification of this group. Two genera of Paranepheleinae, *Paranepheleus* (seven species) and *Pseudoonosseris* (three species), are distributed at higher (2500–4000 m) and lower elevations, respectively. They seem to be sister groups, which indicates that the group originated at lower elevations during the Miocene and one of the lineages, *Paranepheleus*, later diversified at higher elevations. One of the odd endemic Central Andean groups is *Laccopetalum* + *Krapfia*, sister to subcosmopolitan *Ranunculus* (Ranunculaceae). Species of this clade are currently restricted to very high elevations (>3500 m), but their divergence from *Ranunculus* is placed into the early Miocene (ca. 21 Ma), with a divergence of *Laccopetalum* and *Krapfia* placed at ca. 6 Ma (Emadzade and Hörandl, 2011).

Polyploidization has often been associated with speciation in high-Andean environments. Polyploidy was suggested to be involved in the diversification of the *Oxalis tuberosa* Alliance (Oxalidaceae; Emshwiller and Doyle, 1998, 2002), with a center of diversity in the Central and Northern Andes (Emshwiller, 2002). The main diversification of this group was dated to be of Late Miocene age (Heibl and Renner, 2012). In monophyletic and widespread American *Solanum* sect. *Petota* (Solanaceae), a high concentration of polyploid species relative to total number of species was reported for the Northern Andes, while diploid species predominate in the Central Andes (Hijmans et al., 2007). This possibly originally South American group (Simon et al., 2011), started its diversification about 7 Ma (Särkinen et al., 2013). Polyploidization was also suggested as a driver of diversification for the central and northern Andean genus *Polylepis* (Rosaceae; Schmidt-Lebuhn et al., 2010), but divergence times estimates are not provided. The genus *Tarasa* (incl. *Nototriche*; Malvaceae), which includes several high-elevation species of the Central Andes, also comprises some polyploids (Tate et al., 2005). While diploid species predominate in low-elevation habitats, most polyploids are high-Andean. In *Tarasa*, allopolyploidization and shifts to autogamous breeding systems (both of which occurred several times) may have enabled species to colonize high Andean environments (Tate and Simpson, 2003). The process is suggested to be relatively recent (Quaternary; Tate and Simpson, 2004), but molecular dating is not available.

### 2.1.3. Southern Andes

In the Southern Andes, the genus *Schizanthus* (Solanaceae) possesses two high Andean species that have been resolved as sister to each other and are estimated to have diverged ca. 1 Ma (Särkinen et al., 2013), probably associated with a shift to hummingbird pollination (Pérez et al., 2006). The divergence time estimates for *Valeriana* (Valerianaceae) by Bell et al. (2012) are considerably higher (~13 Ma). These authors suggest that *Valeriana* originated in the Southern Andes before final uplift, and that the group diversified into the higher elevations from

either sides of the Andes once the Southern Andes reached their current elevation (see above). For the southern Andean *Palmatifoliae* clade of *Oxalis*, Heibl and Renner (2012) suggested an origin in alpine habitats and a start of diversification during the Middle Miocene (~19 Ma). The same authors estimate a more recent origin (Late Miocene to Pliocene) of alpine species of the *Alpinae* clade, which entered the alpine habitats several times with no subsequent radiations in high-elevation environments. The southern Andean representatives of the genus *Caltha* (Ranunculaceae) form two independent lineages, both with Late Miocene crown node ages (Cheng and Xie, 2014). Similar ages (~5 Ma) were proposed for southern Andean *Heliotropium* sect. *Plagiomeris* (Heliotropiaceae; Luebert et al., 2011b). This is the only Neotropical section of the genus *Heliotropium* with ephemeral annual life form, which is associated with the relative aridity of their habitats (Luebert et al., 2011a). Palazzesi et al. (2012) found a divergence of the major southern/central Andean lineages of Geraniales in the Oligocene and Early Miocene, with actual species divergence only in the Pleistocene and argue for an early south-temperate diversification of the order with much later speciation in an Andean context. The subantarctic, Andean species of *Nothofagus* s.str. (Nothofagaceae; see Heenan and Smissen, 2013) diverged around 20 Ma (scenario 1 of Sauquet et al., 2012). Unfortunately, the phylogeny of *Nothofagus* in this part of the tree is not yet well-resolved (Sauquet et al., 2012; Heenan and Smissen, 2013). Also in the Southern Andes, the diversification of the genus *Oriastrum* (Asteraceae; nomenclature following Davies, 2010) in high-elevation environments contrasts between southern and central Andean clades (Hershkovitz et al., 2006): while the southern Andean centered subgenus *Oriastrum* may have diversified about 13 Ma, crown node age of the central Andean subgenus *Egania* was estimated to ca. 5 Ma, possibly correlated to the differences in the timing of the Andean uplift between the central and the Southern Andes as discussed above.

## 2.2. THE ANDES AS A VICARIANT BARRIER

### 2.2.1. East-West Andean vicariance

Disjunct patterns in plants groups inhabiting both sides of the Andes have long been noticed in the literature. One of the earliest authors mentioning this pattern was Kuntze (1895) and it has since been interpreted by Neotropical biogeographers as a sign of the effects of the Andean uplift and the subsequent development of aridity in South America (e.g., Schmithüsen, 1956; Smith, 1962; Landrum, 1981; Moreira-Muñoz, 2011).

There are some recent phylogenetic studies documenting the age of disjunct clades inhabiting both the eastern and the western versant of the Andes but not the intervening area. Marquinez et al. (2009) report a mid-Miocene age (~13–16 Ma) for the crown node of a disjunct South American clade of *Drimys* (Winteraceae). The authors suggest that speciation in the genus *Drimys* in South America coincides with Central Andean uplift. In *Fuchsia* sect. *Quelusia* (Onagraceae) Berry et al. (2004) report a similar age for the disjunction between *F. magellanica*, practically restricted the south-western Andes, and the other members of the section, distributed in southern Brazil (Berry, 1989), which would thus indicate the onset of aridity in SE South America around that time. Chacón et al. (2012) also report

mid-Miocene ages for the separation of the Brazilian clade of *Alstroemeria* (Alstroemeriaceae) from the western clades. Three species of *Brunfelsia* inhabit the Pacific coast of South America and they diverged from their disjunct sister species in Venezuela about 7 Ma, coincident with the peak of the Colombian Andean uplift according to Filipowicz and Renner (2012). In the genus *Phytelephas* (Arecaceae), distributed on the eastern and western slopes of the Central and Northern Andes, crown node ages were estimated to be of Middle to Late Miocene age (Trénel et al., 2007). Finally, for the genus *Monttea* (Plantaginaceae), disjunctly distributed on the arid zones of both sides of the Andes, the split between eastern and western species was estimated to be of Late Miocene age (~5–10 Ma; Baranzelli et al., 2014), coinciding with the Andean uplift according to the rapid model. **Figure 3A** illustrates divergence time estimates for all vicariant groups mentioned above.

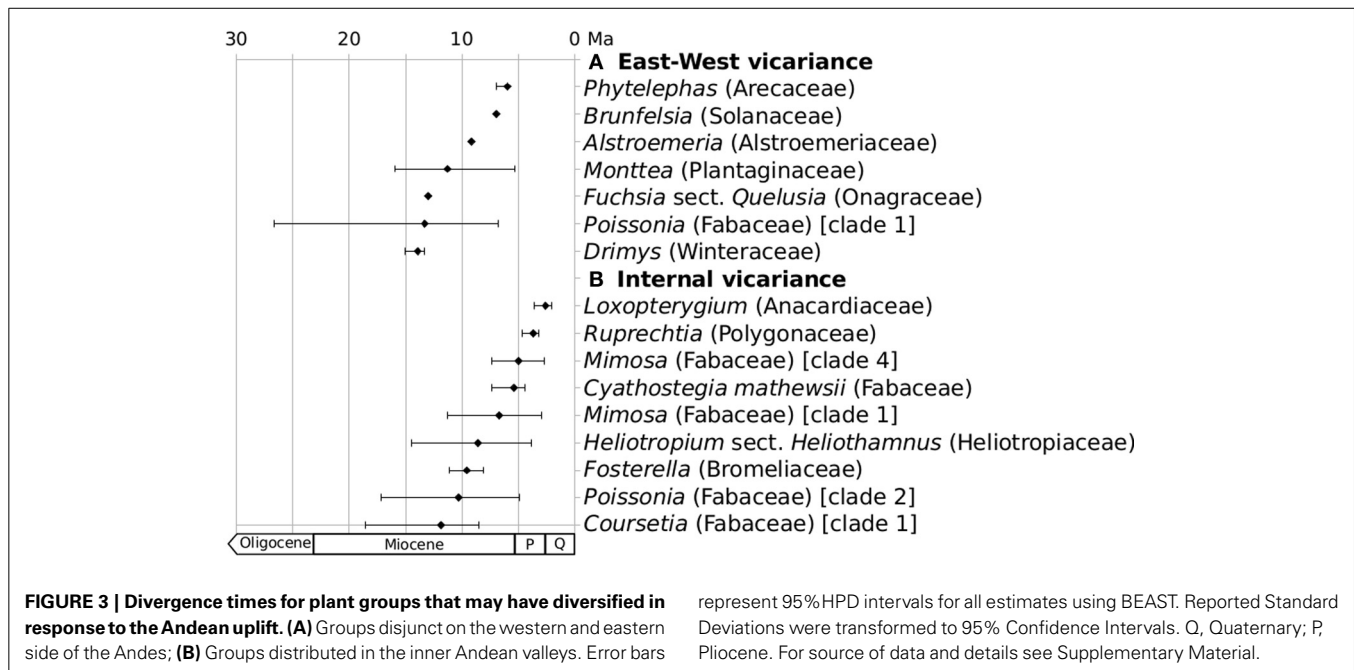
Monophyly of several other disjunct plant groups has been documented in recent phylogenetic studies, but dates have not been proposed. For example, the genus *Myrceugenia* (Myrtaceae) has long been considered a typical example of a South American disjunction mediated by Andes uplift (Landrum, 1981). Murillo-A. et al. (2012) suggest that the disjunction of *Myrceugenia* may have taken place during the Early Miocene. Another example are the sister genera *Balsamocarpon* and *Zuccagnia* (Fabaceae). The former is distributed in the southern portion of the Atacama Desert, on the western side of the Andes, while the latter has a distribution in the Chaco region on the eastern side of the Andes (Ulibarri, 2005). These genera form a monophyletic group together with *Hoffmannseggia* and *Stenodrepanum* (Nores et al., 2012). These authors suggest that the Andes acted as a barrier in the divergence of *Balsamocarpon* and *Zuccagnia*, followed by diversification and long-distance dispersal events in *Hoffmannseggia*. *Bulnesia* subg. *Bulnesia* (Zygophyllaceae) is a monophyletic group (Comas et al., 1998) with a similar distribution pattern to *Balsamocarpon/Zuccagnia* on both sides of the Andes. Similarly, *Suaeda foliosa* (Amaranthaceae) is distributed in the Atacama and Peruvian deserts on the western side of the Andes and has been shown to be sister to *S. divaricata* from the Chaco region (Schütze et al., 2003). Davis and Anderson (2010) showed the monophyly of the genera *Dinemandra* and *Dinemagonum* (Malpighiaceae), both from north central Chile on the western slope of the Andes, and the genus *Ptilochaeta* from the Chaco and Paraná regions on the eastern side. Mexican *Lasiocarpus* is nested in *Ptilochaeta* and Anderson (2013) argues that *Lasiocarpus* represents a secondary colonization of this group from South America to Mexico.

### 2.2.2. Inner Andean vicariance

The inner-Andean valleys also represent habitats that were isolated by Andean orogeny and should thus promote vicariant speciation. This idea has been suggested in several papers (e.g., Struwe et al., 2009).

One example is *Heliotropium* sect. *Heliothamnus*, with a center of diversity in the inner-Andean valleys of Ecuador and Peru and for which a Miocene age of its crown node was proposed (Luebert et al., 2011b). Pennington et al. (2010) studied different populations of the species *Cyathostegia mathewsii* (Fabaceae), distributed





disjunctly in inner-Andean valleys from southern Ecuador to southern Peru. The authors found a strong phylogenetic signal in the distribution of the populations and identified four geographically well-defined clades. They estimated the crown-node age of *C. mathewsii* to be Late Miocene/Early Pliocene ( $5.4 \pm 1$  Ma), which they associate with the vicariant effect of valley formations just before the origin of *C. mathewsii*. The crown node of the genus *Poissonia* (Fabaceae) was dated to the Early Miocene ( $\sim 20$  Ma; Pennington et al., 2004; Särkinen et al., 2011). This genus is composed of two well-supported clades of seasonally dry tropical forests (SDTF) species, one inhabiting both sides of the Andes (Chaco and Peruvian Desert) and the other distributed along the Central Andes (Pennington et al., 2004; Särkinen et al., 2011). Both clades started their diversification around 10 Ma (Särkinen et al., 2011). The northern Andean species of *Ruprechtia* (Polygonaceae), also from SDTF, diversified during the Early Pliocene (clade C; Pennington et al., 2004). An even more recent diversification was suggested for the northern and central Andean SDTF species of *Loxopterygium* (Anacardiaceae), which was dated to Late Pliocene age (clade B; Pennington et al., 2004). Other examples are provided by Särkinen et al. (2011) for several Fabaceae lineages from Andean SDTF. These authors found that the crown node ages of the lineages from the SDTF range from ca. 19 to 4 Ma, suggesting that isolation of SDTF fragments in the Andes dates back to the Early Miocene and has persisted since, which they regard as in agreement with the “rapid rise” model described above. In the Andean genus *Fosterella* (Bromeliaceae), allopatric speciation associated with the Andean uplift was invoked to explain the diversification of this genus, whose origin was dated to Middle Miocene age (Wagner et al., 2013). Outside the Andes (SDTF and Yungas), *Fosterella* has some species distributed in azonal rock outcrops of the Brazilian highlands, lowlands of central Amazonia and Central America; the latter three areas were reached in different and recent colonization

events after the Andean diversification of the group (Wagner et al., 2013). **Figure 3B** summarizes divergence time estimates for all these inner-Andean clades.

### 2.3. THE ANDES AS A CORRIDOR

Floristic and paleoecological studies suggest that the Andes acted as a dispersal corridor, overcoming dispersal barriers such as the most arid zone of the Atacama Desert or the low-lying Amotape-Huancabamba zone (e.g., van der Hammen and Cleef, 1983; Moreno et al., 1994; Weigend, 2002; Linares-Palomino et al., 2003; Pinto and Luebert, 2009; Schwarzer et al., 2010). Andean North-South exchanges may have been favored by Quaternary climatic oscillations (van der Hammen, 1974; Moreno et al., 1994; Dillon et al., 1995). This may not only explain the distribution of several widely distributed plant groups of the Andes. Phylogenetic studies in the recent decades have contributed to clarify this question.

Doan (2003) proposed a general south-to-north diversification patterns for plants and animals based on the earlier uplift of the Southern Andes. This theory has found support for a range of plant groups. The genera *Azorella* (p.p., **Figure 1C**), *Laretia* and *Mulinum* (p.p.) (Apiaceae) form a well-supported clade distributed from Costa Rica to Patagonia along the Andes. Its geographical origin was inferred for the southern part of its distribution range, from which it migrated northwards since about 12 Ma (Nicolas and Plunkett, 2012, 2014). These authors suggest that this group colonized the Central and Northern Andes after the Mid-Miocene climatic optimum (5–17 Ma), when the global climate became cooler (Zachos et al., 2001) and the Andes reached their current elevation (see above). In the genus *Oreobolus* (Cyperaceae), there is a South American clade with a wide Andean distribution; this clade may also have originated in the Southern Andes and migrated northwards during the Early Pliocene ( $\sim 4$  Ma; Chacón et al., 2006). In the genus *Perezia* (Asteraceae, **Figure 1B**), Simpson et al. (2009) suggest that



the genus colonized high-elevation habitats from low-elevation ancestors in the Southern Andes and subsequently migrated northwards along the Andes to eventually diversify in the Central Andes. An essentially parallel hypothesis is provided by Meudt and Simpson (2006) based on data on *Ourisia* (Plantaginaceae), which clearly originated in the Southern Andes and subsequently dispersed to the Central and Northern Andes, where further speciation took place. In *Chuquiraga* (Asteraceae), distributed from Patagonia to Venezuela along the Andes (Ezcurra, 2002; Gruenstaeudl et al., 2009), a southern origin was inferred (Gruenstaeudl et al., 2009). Unfortunately, no time framework is provided for *Perezia* or *Chuquiraga*. Extensive northward migrations from south-temperate regions are also documented by a combination of fossils and a dated phylogeny for several lineages in Geraniales (Palazzesi et al., 2012).

Antonelli et al. (2009) suggested a considerable importance of the Western Andean Portal (WAP) in Andean biogeography. The WAP was an East-West corridor located around the present Ecuadorian/Peruvian border (i.e., the Amotape-Huancabamba zone) that enabled Pacific marine incursions into the Amazonian basin until the Middle Miocene, when the marine incursions ceased due to Andean uplift (Hoorn, 1993). Biogeographical reconstructions in the genera *Cinchona* and *Ladenbergia* (Rubiaceae) suggest multiple migrations from the northern to the Central Andes around 12–10 Ma, attributed to the closing of the WAP (Antonelli et al., 2009). High Andean-species of the genus *Puya* (Bromeliaceae) are concentrated in the Northern Andes, a diversity reached after this area was colonized by high-elevation, central-Andean ancestors that crossed the WAP (Jabaily and Sytsma, 2013) around 6–4 Ma (Givnish et al., 2011, 2014). A similar pattern was proposed for *Solanum* sect. *Petota*, which diversified in the Northern Andes from central Andean ancestors (Simon et al., 2011) during the Late Miocene (Särkinen et al., 2013). The opposite route was inferred for the genus *Hedyosmum* (Chloranthaceae), which colonized the central Andes from northern Andean ancestors several times after Andean uplift (Antonelli and Sanmartín, 2011a). For the genus *Festuca* (Poaceae), Inda et al. (2008) suggested that Patagonian species originated from North America through a North to South migratory route along the Andes during the Late Miocene - Early Pliocene (10–3.8 Ma). A similar dispersal pattern was reported in *Cleome* (Cleomaceae), with a well-supported clade (incl. *Podandrogynne*) originating in the Northern Andes during the Late Miocene and a subsequent dispersal into and radiation in the Central Andes (Feodorova et al., 2010).

In a study of *Macrocarpaea* (Gentianaceae), a genus of montane forest species, an Andean origin around the Amotape-Huancabamba zone, with radiations in both north- and southwards directions was postulated (Struwe et al., 2009). These radiations correspond to two well-supported subclades distributed to the South and to the North of the Amotape cross, within which allopatric speciation between adjacent zones of the same mountain range were hypothesized (Struwe et al., 2009). Migrations from the Southern Andes through the Amotape-Huancabamba zone into the Northern Andes suggest that the Amotape-Huancabamba zone was not a dispersal barrier for lineages of mid-elevations. Although these authors did not provide divergence time estimates, they suggest that these diversification

events occurred after the major phases of Andean uplift since Miocene times.

In the genus *Nolana* (Solanaceae), with a center of diversity in the Atacama and Peruvian Deserts, several events of dispersal between both these deserts were suggested to have taken place along the Andes (Dillon et al., 2009). These events may have taken place during the Late Pliocene and Pleistocene, as shown by different molecular dating analyses (Dillon et al., 2009; Särkinen et al., 2013). Andean exchanges may have been followed by diversification in the coastal range. A very similar pattern of distribution and dispersal can be observed in *Malesherbia* sect. *Malesherbia* (Malesherbiaceae), where Gengler-Nowak (2002) argued for Pleistocene or even Holocene floristic exchanges. Phylogenetic and biogeographical analyses of the allied genera *Polyachyrus*, *Moscharia* and *Oxyphyllum* (Asteraceae; Katinas and Crisci, 2000; Katinas et al., 2008; Luebert et al., 2009) would also suggest this pattern, with Pleistocene southwards colonizations from the Central Andes to central Chile, but no dating analysis is available for these groups.

#### 2.4. THE ANDES AS PROMOTERS OF DIVERSIFICATION OUTSIDE THE ANDES

Several studies have highlighted the possible effects of Andean uplift on the diversification of lineages outside the Andean range. The idea that Andean uplift is important in the diversification of Neotropical lowland plant taxa has been mentioned in the literature at least since Gentry (1982) and Kubitzki (1989).

Rapid diversification in the genus *Inga* (Fabaceae) is a classical example. This genus is particularly diverse on the eastern Andean foothills and in the Amazonian basin. Rapid diversification of *Inga* in this area was suggested to have been promoted by the later phases of Andean orogeny (Richardson et al., 2001). In the mostly extra-Andean tribe Bignoniaceae (Bignoniaceae), Lohmann et al. (2013) suggested that the Andean orogeny played an important role in the diversification of some lineages in the Amazon basin and eastern South America. In the tribe Cinchoneae (Rubiaceae), the Andean orogeny was suggested to have played a role in diversification in lowland Amazonia (Antonelli et al., 2009). These authors argue that the connection between the Andean uplift and the demise of Lake Pebas during the Late Miocene is consistent with colonizations by eastern Andean ancestors into lowland Amazonia from the Late Miocene onwards. Miocene diversification of the rain forest genus *Renealmia* (Zingiberaceae) also gives support to the idea that its diversification was influenced by the rise of the Andes (Särkinen et al., 2007), similar to what was proposed to several genera of the Annonaceae with Miocene diversifications (Pirie et al., 2006).

Diversification of the tribe Protieae (Burseraceae) in the western Amazon was suggested to be associated with the creation of new edaphic habitats during the uplift of the Andes (Fine et al., 2005). However, divergence times for this group (~40 Ma; Becerra et al., 2012) seem to predate Andean uplift. In the family Chrysobalanaceae, the lowland Amazon genera *Hirtella* and *Couepia* diversified during the Middle Miocene (~12 Ma; Bardon et al., 2013), but their diversification was probably not causally linked to Andean uplift. In fact Amazonian lowland taxa in general are a mixture of old and young lineages, with ages ranging from 40 to 5.6 Ma in the analysis of Hoorn et al. (2010)

and the data currently available do not paint a clear picture as to the overall importance of Andean uplift for Amazonian diversifications.

Luebert and Wen (2008) and Luebert et al. (2011b) proposed the Middle Miocene as the minimum age for the origin of *Heliotropium* sect. *Cochranea* (Heliotropiaceae). The diversification of this group in the Atacama Desert during the Pliocene, isolated on the western slope of the Andes, was probably facilitated by Andean uplift and the subsequent development of aridity (Sepulchre et al., 2009). This scenario was also suggested for the origin of monotypic *Gypothamnium* (Asteraceae) in the Atacama Desert (Luebert et al., 2009) and for *Plectocephalus* in South America (Asteraceae; Susanna et al., 2011). On the south-eastern side of the Andes, the onset of diversification of *Heliotropium* sect. *Heliotrophytum* around 8.5 Ma has also been related to increasing aridity as a consequence of Andean orogeny (Luebert et al., 2011b).

## 2.5. BIOGEOGRAPHICAL RELATIONSHIPS OF THE ANDEAN FLORA

Many of the aforementioned phylogenetic studies included lineages that also occur outside of the Andes and therefore provide insights into the biogeographical relationships between the Andes and other regions.

One of the most obvious patterns is the connection between Central America, and especially the central American Cordillera, and the Andes. Floristic interchange in both directions is documented in Gesneriaceae (Perret et al., 2013). In Gloxinieae a colonization event Andes to Central America occurred during the early Miocene and at least one more after the Late Miocene. Episcieae dispersed from Central America to the Andes several times from the Late Miocene onwards. The closing of the Panama Isthmus may have facilitated northward dispersals of South American lowland lineages into Central America, as inferred for *Joosia* and *Isertia* (Rubiaceae) (Antonelli et al., 2009). The same route and time frame was suggested for *Pitcairnia* and *Tillandsia* (Bromeliaceae; Givnish et al., 2014), which reached Central America from Andean ancestors independently around 5 Ma (Givnish et al., 2011). In *Peperomia* subg. *Tildenia*, Central American taxa originated from central Andean ancestors around 15 Ma (Symmank et al., 2011). These authors suggest a northern Andean track and subsequent extinction of the group in the Northern Andes, since the current northern limit of *Peperomia* subg. *Tildenia* in the Andes is around the Amotape-Huancabamba zone. The separation of Central American and Andean lineages in *Ruprechtia* (Polygonaceae) occurred ca. 6 Ma, but their respective diversifications did not start until 4–3 Ma (Pennington et al., 2004). All these time estimates indicate a dispersal across the Panama Isthmus before it closed ca. 3.5 Ma. This has also been suggested for *Inga* (Richardson et al., 2001). On the other hand, *Coursetia* (Fabaceae) colonized the Andes from Central America before its diversification started ca. 7 Ma (Pennington et al., 2004). *Costus* (Costaceae) dispersed from Central America into the Andean region between ca. 1–6 Ma (Kay et al., 2005). In *Halenia*, the colonization of the South American Andes from Central America occurred more recently (~1 Ma), according to the estimates of von Hagen and Kadereit (2003). Similar timing and direction were estimated for *Lupinus*

by Drummond (2008). Overall, these estimates would be in agreement with the ideas of Simpson (1983), who argued that colonizations of the Andean flora by Nearctic elements occurred gradually since the Middle Miocene, and the closing of the Panama gap had little effect on it. In the case of alpine *Lupinus* and *Halenia*, dispersal must have been from mountain range to mountain range, and the presence or absence of the Isthmus can not conceivably have had an effect—the taxa can not have migrated via the lowland Darién, whether covered by water or not. A generally limited importance of the Panama Isthmus is supported by various dated molecular phylogenies showing dispersal across the region older than the closing of the Panama Isthmus (Cody et al., 2010). However, as pointed out by Antunes Carvalho and Renner (2012), the colonization of South America by Caricaceae during the Early Miocene may have also been favored by a first closing of the Panama Isthmus ca. 24 Ma (Farris et al., 2011), an earlier date than generally accepted.

Relationships between the northern and the Central Andes and the Brazilian highlands have been suggested for *Tibouchina* (Melastomataceae; Michelangeli et al., 2013), a connection also retrieved in phylogenetic studies on *Elapghoglossum* (Dryopteridaceae; Vasco et al., 2009), *Sinningia* (Gesneriaceae; Perret et al., 2006), *Macrocarpaea* (Gesneriaceae; Struwe et al., 2009), and Bromelioideae (Bromeliaceae; Givnish et al., 2014). The latter is the only dated dispersal scenario available (~8 Ma; Givnish et al., 2011). Ecotopical similarity rather than geographical proximity may have played a role in the origin an floristic connections of those regions (Simpson, 1983). A similar rationale must necessarily explain the relationships between the Andes and the Guiana Shield, demonstrated for taxa such as *Chaetolepis* (Melastomataceae; Michelangeli et al., 2013), since they were never connected.

In a recent review, Luebert (2011) showed direct relationships between the Atacama Desert and the Central and Southern Andes in many genera with phylogenetic studies. Among the groups with relationships between the Central Andes and the Atacama Desert are *Bomarea* (Alstroemeriaceae), *Cleome* (Cleomaceae), *Croton* (Euphorbiaceae), *Eremocharis* (Apiaceae), *Gypothamnium* (Asteraceae), *Krameria* (Krameriaceae), *Malesherbia* sect. *Malesherbia* (Malesherbiaceae), *Nasa* (Loasaceae), *Oxalis* (Oxalidaceae), *Oziroë* (Asparagaceae), *Prosopis* ser. *Cavernicarpae* (Fabaceae), *Solanum* sect. *Lycopersicon* (Solanaceae), and *Tarasa* (Malvaceae), *Vasconcellea* (Caricaceae). Among the groups with relationships between the Atacama Desert and the Southern Andes are *Asteriscium* (Apiaceae), *Chaetanthera* (Asteraceae), *Conanthera* (Tecophilaeaceae) *Montiopsis* subg. *Montiopsis* (Montiaceae), *Oxyphyllum* (Asteraceae), *Schizanthus* (Solanaceae), *Schizopetalon* (Brassicaceae), *Tropaeolum* sect. *Chilensia* (Tropaeolaceae) (see references in Luebert, 2011). However, only few of them have been dated at the crown node of that relationship: *Bomarea* (~5 Ma; Chacón et al., 2012), *Asteriscium* and *Eremocharis* (both ~11 Ma; Nicolas and Plunkett, 2014), *Oxalis* (~20 Ma; Heibl and Renner, 2012), *Prosopis* (~1 Ma; Catalano et al., 2008), *Solanum* sect. *Lycopersicon* (~2 Ma; Särkinen et al., 2013), *Vasconcellea* (~10 Ma; Antunes Carvalho and Renner, 2012), *Alstroemeria* (~18 Ma; Chacón et al., 2012), *Chaetanthera* (~10 Ma; Hershkovitz et al.,

2006), *Schizanthus* (~24 Ma; Särkinen et al., 2013). Floristic interchange between the Andes and the Atacama Desert has therefore been taking place continuously since Miocene times.

Surprisingly, fewer studies have shown the connection between the Andes and the immediately adjacent areas of eastern South America (incl. Amazon basin). Examples can be found in *Brunfelsia*, which made its way from eastern South America into the Andes around ca. 10 Ma (Filipowicz and Renner, 2012), and the tribe Cinchoneae, whose Amazonian representatives originated from Andean ancestors during the late Miocene (Antonelli et al., 2009). Conversely, an eastern South American origin for Andean taxa in *Chuquiraga* for Andean taxa was inferred by Gruenstaedl et al. (2009). Simpson et al. (2009) suggest that the geographical origin of the Andean lineages in *Perezia* is in the lowlands of Patagonia. Finally, in *Oxalis* subg. *Trifidus*, distributed in the Altiplano and temperate Chile, Heibl and Renner (2012) estimated a Middle Miocene split between its two component species.

Direct relationships between the Andean region and North America can be inferred for *Urtica* (Farag et al., 2013; Henning et al., 2014). American *Urtica gracilis* can be shown to be sister to an Australasian clade, *U. gracilis* then splits up into temperate North American subsp. *gracilis* as sister to the remaining subspecies, and western North American subsp. *holosericea* in turn sister to three subspecies distributed in Mexico/Guatemala, Peru and Chile/Argentina, respectively, with at likely two dispersal events from North America into South America along the American Cordillera. Conversely, the other group in American *Urtica* is sister to a Macaronesian clade, but also seems to have had at least two dispersal events between South and Central America, with a minor diversification in Mexico and a major diversification in the Andes. Timing has not been investigated for *Urtica*. On the other hand, colonization from North America to the northern Andes by *Festuca* took place ca. 4 Ma (Inda et al., 2008). The same biogeographical connection but more recent origin was suggested for *Gentianella* (von Hagen and Kadereit, 2001). Weigend et al. (2010) show that *Lithospermum* arrived from Southern North America initially to the Central Andes, and then migrated northwards and diversified in the Amotape-Huancabamba zone. According to Bell and Donoghue (2005), “Valerianaceae arrived in South America, most likely via long-distance dispersal. . .when the northwestern Andes were not at their current elevations.” Dispersal from the north-temperate zone and especially the North American Cordillera into the Andes and subsequent diversification seems to be a fairly common pattern, although few detailed phylogenies are available. A clear Andes-North America direction was shown for the bulb-bearing *Oxalis* (Gardner et al., 2012). The dispersal of that group into North America may have occurred after its Middle Miocene origin (Heibl and Renner, 2012) by long distance dispersal.

More geographically distant relationships between the Andean *Prumnopitys* (Podocarpaceae) and its close relatives in Oceania (Knopf et al., 2012) date back to the Paleocene (Biffin et al., 2011), while in *Nothofagus* s. str. this separation seems to be more recent (~42 Ma, Middle Eocene; Sauquet et al., 2012). In Cunoniaceae, Bradford (2002) showed phylogenetic relationships between Andean *Weinmannia*, and *W. tinctoria* from the Mascarenes.

Since the position of *W. trichosperma*, from southern South American temperate forests, was resolved as sister to the tropical Andes—Mascarene clade, this author argued that exchanges between tropical America and the Indian Ocean occurred more recently than between temperate and tropical America. Although Bradford (2002) indicated that these results await confirmation, no study has challenged them so far. The diversification of *Weinmannia* occurred during Oligocene–Miocene transition (Heibl and Renner, 2012).

### 3. DISCUSSION

The exact timing and process of Andean uplift has been repeatedly invoked to explain Neotropical diversifications in plants, shaping the diversity of both Andean and extra-Andean groups (see reviews in Hoorn et al., 2010; Graham, 2011a; Särkinen et al., 2011; Madriñán et al., 2013). When the available evidence is analyzed, we only find partial support for that explanation. There is a trend in high-Andean lineages to be of more recent origin in the northern than in the Central Andes and in the central than in the Southern Andes (Figure 2), which agrees with the assumption that the Andean uplift progressed from South to North (see above). Plant groups inhabiting mid-elevation environments (such as *Brunfelsia*, *Fuchsia*, Fabaceae, Geraniaceae, *Hedyosmum*, *Oxalis tuberosa* Alliance, Rubiaceae, *Vasconcellea*, see Figure 2) also tend to be older than high-Andean groups, which also agrees with progression of uplift. These trends are fairly stable and independent of the conflicting views on the exact timing of Andean uplift. However, these trends do not fit all studied plant groups. Some high-Andean lineages (*Valeriana*, several groups in Geraniales) are older than the presumed timing of the Andean uplift, while most are younger, especially in the Northern Andes (Figure 2).

For the latter, ecological opportunities to colonize high-Andean environments may have differed between lineages, so that the speed of the diversification of life histories or other adaptive traits necessary to survive in extreme environments are lineage-specific. This may be the reason for a delayed evolutionary response in some lineages, explaining the evident lag times in diversification with respect to the formation of high-elevation habitats. However, such an explanation lacks power, since this can be argued for any young group whose diversification started after the uplift of the Andes regardless of cause-effect links. Moreover, Late Miocene increases in Andean uplift rate coincides with a global cooling trend (Zachos et al., 2001, 2008), which can also be seen as a possible trigger of plant diversifications. Regarding the role of the Andes as vicariant barrier, the available data tend to be more consistent with the timing of the Andean orogeny. The separation of western South American *Drimys* (~14 Ma) and *Fuchsia* (~13 Ma) are consistent with the uplift times proposed for the Southern Andes (Figure 3). Groups distributed West and East of the Central and Northern Andes are younger (~11–7 Ma) with the exception of *Poissonia* (~13 Ma). A narrower range of ages (~12–3 Ma) is shown for putatively vicariant lineages distributed in the inner-Andean valleys (Figure 3). All groups for which the Andes have likely acted as a corridor for latitudinal dispersal diversified after the Andes reached their present elevation (~3–5 Ma, see Figure 3). An alternative

explanation for younger lineages is proposed by Rull (2011a,b), partially in response to the general assumption that Andean uplift has driven Neotropical biotic diversification. This author argues that Pleistocene climatic fluctuations are at least co-responsible of present Neotropical diversity, since most speciation events occurred during this period, which fits the data available so far. This explanation, however, has the same inherent problems of power mentioned above. Moreover, current lineage diversity is always overestimated in phylogenetic studies compared to historical diversity, because newer lineages have had less time to go extinct than ancient lineages (Harvey et al., 1994). In this line, Hoorn et al. (2011) argued that crown node ages of clades “lead to more robust age estimation of deeper nodes even when many species are missing.” However, disentangling the relative effects of different events that overlap in time may prove impossible using dated phylogenies (Pennington and Dick, 2010).

Older-than-uplift lineages also require an explanation. One possibility would be accepting an older origin of the high-Andes as suggested by Ehlers and Poulsen (2009). This would imply that most of the studied groups diversified with considerable lag times with respect to Andean uplift. On the other hand, these lineages could have initially diversified at lower elevations before the Andean uplift, with later colonization of the high elevation environments as they were forming. Since the global climates during the Middle Miocene were considerably warmer (the Mid-Miocene Climatic optimum has been dated around 14–16 Ma, see Zachos et al., 2008), initially diverging species should have had more tolerance to higher temperatures than they have now. In *Valeriana* that is more likely because many species related to the Páramo clade are found out of high-elevation habitats (Bell and Donoghue, 2005). Palazzesi et al. (2012) argue for a northward displacement of an originally south-temperate floristic element with climatic cooling, eastern Patagonian aridization and Andean uplift and this could explain various “too old” lineages nowadays restricted to Andean habitats in groups such as Ranunculaceae, Geraniales, Apiaceae. This argument is also in line with the relatively common phenomenon of south-to-north diversifications in the high Andes and along the Andean slopes, as shown for, e.g., *Malesherbia* (Gengler-Nowak, 2002). Overall, the detailed spatial patterns of Andean diversifications are still very incompletely understood, not least because most phylogenies use a rough “geographical subdivision” pattern for interpreting historical biogeography instead of analysing explicit distribution data.

The range of ages obtained for Andean lineages (~20–1 Ma) are similar to those reported for several lineages on the Qinghai-Tibetan Plateau (QTP; Wen et al., 2014). This may be due to the fact that the Andes and the QTP are of similar age (Favre et al., 2014). However, the relatively high frequency of Miocene or younger Angiosperm diversifications revealed by molecular phylogenies in relation to older ones suggests that a further possibility must also be taken into account: These diversifications may respond to the age constraints given by the origin of Angiosperms in time. This origin has been dated to the Early Jurassic the oldest (Magallón, 2010; Magallón et al., 2013). This time constraint imposes a boundary for diversification of modern lineages within the Angiosperms.

A range of published papers highlight the strong biogeographical connections between the Andean region and neighboring areas of Central America, eastern and western South America, as well as with more distant regions, such as North America, Oceania and Mascarenes. Biogeographical connections between the Andes and different areas of the Neotropics shown in molecular phylogenies confirm the long recognized mixed character of the Andean flora (Katinas et al., 1999). All connections with neighboring areas seem to have originated in Miocene times, or later. In particular, the closing of the Panama Isthmus might have been an important event for many lineages, which experienced floristic exchanges with Central America since Miocene times. The importance of the closing of the Panama Isthmus has long been claimed in Neotropical biogeography (e.g., Graham, 2011b). However, the closing of the Panama Isthmus must have occurred before the Pliocene in order to explain plant interchanges between Central and South America (Cody et al., 2010). Older ages for the closing of the Panama Isthmus have indeed been recently proposed by Farris et al. (2011), which has begun to be acknowledged by biogeographers (e.g., Antunes Carvalho and Renner, 2012; Hughes et al., 2013). However, few explicit analyses have included altitudinal species/lineage distributions in the discussion and a role of the closing of the Panama Isthmus in the exchange between montane and alpine biota is very implausible.

In summary, the data available in the literature confirm a temporal time-frame for most Neotropical diversifications which roughly agrees with Andean uplift, but also point to a complex history of the Andean flora (Antonelli and Sanmartín, 2011b; Rull, 2011a). As long as there are controversial models of uplift history, rigorous hypothesis testing must wait and each taxonomic group tends to have independent histories. There can be little doubt that diversification was driven by a range of processes, some directly linked to Andean uplift, such as climate changes and new ecological niches, others rather based in biotic responses such as polyploidization, morphological and physiological adaptations, and shifts in plant-pollinators interactions. Evaluation of the relative importance of these drivers is still a pending task in Neotropical biogeography.

## FUNDING

German Academic Exchange Service (DAAD), SYNTHESYS, Nees Institute for Biodiversity of Plants, University of Bonn.

## ACKNOWLEDGMENT

We are grateful to Hartmut Hilger (Berlin) for granting permission to publish his pictures, to Patricio Plissock (Santiago) for the map of **Figure 1** and to the reviewers for comments.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <http://www.frontiersin.org/journal/10.3389/fevo.2014.00027/abstract>

Divergence times of Andean diversifications according to the major processes discussed in the text. Data on number of species, distribution, and habitat were obtained from the cited works, from Mabberley (2008), or from taxonomic treatments of the groups. Presence in the high-Andes were obtained from the cited



works, and from Sklenář et al. (2005), Jørgensen and Ulloa Ulloa (1994), Freiberg (1985), Arroyo et al. (1992), Muñoz-Schick et al. (2000), and Brako and Zarucchi (1993). For references see main text.

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**Conflict of Interest Statement:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 31 March 2014; paper pending published: 05 May 2014; accepted: 31 May 2014; published online: 19 June 2014.

Citation: Luebert F and Weigend M (2014) Phylogenetic insights into Andean plant diversification. *Front. Ecol. Evol.* 2:27. doi: 10.3389/fevo.2014.00027

This article was submitted to *Evolutionary and Population Genetics*, a section of the journal *Frontiers in Ecology and Evolution*.

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