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PHYLOGENETIC NICHE CONSERVATISM DOES NOT EXPLAIN ELEVATIONAL PATTERNS OF SPECIES RICHNESS, PHYLODIVERSITY AND FAMILY AGE OF TREE ASSEMBLAGES IN ANDEAN RAINFOREST

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With 3 figures, 3 tables and appendix
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Summary: Phylogenetic niche conservatism (PNC) is the tendency of species within a clade to retain ancestral traits and to persist in their primary ecological niches on geological time scales. It links evolutionary and ecological processes and has been hypothesized to explain patterns of species richness and the composition of species assemblages. Decreasing patterns of species richness along latitudinal gradients were often explained by the combination of ancient tropical climates, trait retention of tropical lineages and environmental filtering. PNC also predicts decreasing phylodiversity and family age with decreasing tropicality and has been invoked to explain these patterns along climatic gradients across latitudinal as well as elevational gradients. However, recent studies on tree assemblages along latitudinal and elevational gradients in South America found patterns contradicting the PNC framework. Our study aims to shed light on these contradictions using three different metrics of the phylogenetic composition that form a gradient from recent evolutionary history to deep phylogenetic relationships. We analyzed the relationships between elevation and taxonomic species richness, phylodiversity and family age of tree assemblages in Andean rainforests in Ecuador. In contrast to predictions of the PNC we found no associations of elevation with species richness of trees and increasing clade level phylodiversity and family age of the tree assemblages with elevation. Interestingly, we found that patterns of phylodiversity across the studied elevation gradient depended especially on the deep nodes in the phylogeny. We therefore suggest that the dispersal of evolutionarily old plant lineages with extra-tropical origins influences the recent composition of tree assemblages in the Andes. Further studies spanning broader ecological gradients and using better resolved phylogenies to estimate family and species ages are needed to obtain a deeper mechanistic understanding of the processes that drive the assembly of tree communities along elevational gradients.

Zusammenfassung: Das Konzept des „phylogenetischen Nischen-Konservatismus“ (englisch: „phylogenetic niche conservatism“; PNC) beschreibt die Tendenz von Arten und Kladen, ihre angestammten Arteigenschaften und ursprünglichen Nischen über geologische Zeitskalen hinweg zu erhalten. PNC verknüpft evolutionäre und ökologische Prozesse und wurde oft vorausgesetzt, um Muster im Artenreichtum und in der Zusammensetzung von Artgemeinschaften zu erklären. So wurde das generelle Muster abnehmenden Artenreichtums mit steigendem Breitengrad oft mithilfe der Kombination alter tropischer Klimate, der Beibehaltung von Arteigenschaften innerhalb tropischer Linien und der Filterfunktion von Umweltbedingungen erklärt. Außerdem prognostiziert der PNC eine Abnahme phylogenetischer Diversität und der Familienalter entlang klimatischer Gradienten von tropischen zu temperaten und arktischen Bedingungen. Diese Muster wurden bereits entlang von Breitengrad- und Höhengradienten gefunden und mit Hilfe des PNC erklärt. Vor kurzem fanden allerdings zwei Studien, die sich mit Baumgemeinschaften entlang von Breitengrad- und Höhengradienten in Südamerika befassten, Muster, die dem Rahmen des PNC widersprechen. Um diese Gegensätze näher zu beleuchten, verwenden wir in unserer Studie drei verschiedene Maße der phylogenetischen Zusammensetzung, die einen Gradienten von der jüngsten evolutiven Geschichte bis hin zu tiefen phylogenetischen Zusammenhängen abbilden. Im Speziellen haben wir den Effekt von Höhe auf den taxonomischen Artenreichtum, die phylogenetische Diversität und das Familienalter von Baumartengemeinschaften in Regenwäldern der ecuadorianischen Anden analysiert. Im Gegensatz zu den Annahmen des PNC konnten wir keinen Effekt von Höhe auf den Artenreichtum der untersuchten Baumgemeinschaft finden. Wir fanden außerdem zunehmende phylogenetische Diversität auf Kladenlevel sowie ein zunehmendes Familienalter der Baumartengemeinschaften mit steigender Höhe – Ergebnisse, welche ebenfalls im Kontrast zur PNC stehen. Interessanterweise hing das Muster der phylogenetischen Diversität entlang des untersuchten Höhengradienten insbesondere von den tiefen Knoten der Phylogenie ab. Daher nehmen wir an, dass die Ausbreitung evolutiv alter Pflanzenlinien außertropischen Ursprungs die heutige Zusammensetzung der Baumartengemeinschaften der Anden beeinflusst. Um die bestimmenden Prozesse hinter der Zusammensetzung von Baumartengemeinschaften entlang von Höhengradienten besser zu verstehen, sind weitere Studien entlang umfassenderer Gradienten und besser aufgelöste Phylogenien zur Schätzung der Familien- und Artenalter nötig.

Keywords: Ecuador, vegetation geography, tree species assembly, elevational gradient, orogeny

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1 Introduction

Although various exceptions at low taxonomic levels exist (Algar et al. 2009; Romdal et al. 2013), the decrease of species richness with increasing latitude is one of the most consistent patterns in ecology and biogeography (Gaston 2000, 2007; Hillebrand 2004; Lawton 1999). Numerous hypotheses have been proposed to explain this large scale pattern invoking ecological, historical, and evolutionary processes (e.g. Wiens et al. 2006; Willig et al. 2003). On the one hand, variables related to current climate and productivity were used to explain these gradients of species richness from an ecological point of view (for a recent meta-analysis see Field et al. 2009). For instance, optimum plant growth is found under humid conditions at tropical latitudes, whereas colder seasonal and, therefore, harsher climates decrease the probability that abiotic conditions match the tolerances of species. Therefore the match of niche requirements with the abiotic conditions, leads to the assortment of species along environmental gradients (environmental filtering), which influences not only species richness (Graham and Fine 2008; Pavoine and Bonsall 2011) but also the composition of regional species pools and local assemblages (Lebrija-Trejos et al. 2010; Pavoine and Bonsall 2011; Spasojevic and Suding 2012). On the other hand, the species pools on which these ecological processes operate are shaped by biogeographical and historical events that occurred during the geological history of the Earth (Raven and Axelrod 1974; Ricklefs 2004). For example, the breakup of the super-continent Gondwana (Morley 2003) influenced the location of landmasses, the global climate and the formation of mountains. This had consequences for speciation, extinction and dispersal, which in turn influenced the continental as well as regional species pools and thereby also local assemblages (Briggs 1995; Hoorn et al. 2010). Therefore, historical (e.g. speciation, extinction and migration) and ecological (e.g. environmental filtering) processes are not in conflict (Johnson and Stinchcombe 2007; Wiens and Donoghue 2004 but also see Algar et al. 2009), but should be considered jointly for a comprehensive understanding of recent patterns in species richness (Mittelbach and Schemske 2015).

The concept of phylogenetic niche conservatism (PNC) bridges the gap between historic and ecological processes (Ricklefs and Latham 1992; Wiens and Donoghue 2004). Niche conservatism in general describes the tendency of species and entire clades to retain their ancestral ecological traits (Wiens et al. 2010). If traits that influence the spatial distributions of species are phylogenetically conserved (which was found multiple times for plants; Chazdon et al. 2003; Prinzing et al. 2008), closely related species should have more similar traits than distantly related species and consequently the distribution of these species should be determined by similar environmental filters (Wiens and Graham 2005). Furthermore, PNC is closely linked with the time-for-speciation-effect (TSE) as the low probability of species to colonize habitats with different environmental conditions will lead to an accumulation of species in areas, in which a clade evolved (see review in Stephens and Wiens 2003). The combination of PNC and TSE was often used to explain the pattern of decreasing species richness along the latitudinal gradient from the tropics to the Arctic and Antarctic (Wiens et al. 2010). In this context, the PNC-TSE framework refers to the age of tropical (warm and wet) climates: Tropical climates are the oldest currently existing climates as the Earth's surface has been mainly tropical since the early Cretaceous (~ 146 mya; Raymo and Ruddiman 1992), whereas temperate and arctic environments have existed only since the global cooling during the Eocene (~ 50 mya; Graham 2011). According to the TSE, tropical lineages, therefore, had a considerable time span and area in which to speciate, leading to high species numbers within tropical lineages (Stephens and Wiens 2003; Wiens and Donoghue 2004). In turn, PNC implies that species in tropical lineages are adapted to tropical climates and the conservatism in traits constrains the evolution of adaptations to non-tropical conditions (e.g. cold-tolerance) and the colonization of extra-tropical regions (Wiens et al. 2006, 2010; Wiens and Donoghue 2004). Overall, PNC predicts that adaptation to tropical climate, niche conservatism and environmental filtering lead to a decrease of species richness, phylodiversity and age of clades with decreasing tropicality.

To date, patterns predicted by the PNC have been analyzed with emphasis on latitudinal gradients and many analyses detected results consistent with the PNC (Giehl and Jarenkow 2012; Hawkins et al. 2011, 2014; Hillebrand 2004; Jansson et al. 2013; Kerkhoff et al. 2014; Qian et al. 2013, 2014; Romdal et al. 2013; but see Boucher-Lalonde et al. 2015; Huang et al. 2014). As PNC should apply to different sorts of environmental gradients and elevational gradients are known for their possible contribution to answer important questions of macroecology (Körner 2000; for a review of elevational gradients see Rahbek 1995, 2005), PNC was also used to explain patterns of species richness along elevational gradients (Kozak and Wiens 2010). In Indonesia, for example, phylodiversity decreased with increasing elevation (Dossa et al. 2013) – a result consistent with PNC. However, patterns contradicting PNC were found in two studies which reported older instead of younger tree assemblages at high elevations and high latitudes. This was explained by the dispersal of ancient Gondwanan elements (Qian 2014; Segovia et al. 2013).

We selected a site in the Tropical Andes' hotspot of biodiversity (Myers et al. 2000), characterized by montane rain forests in Ecuador, for a further test of PNC along an elevational gradient. The tropical Andes are of great value for studying relationships between temperature and species assembly in plant assemblages (Antonelli et al. 2009; Pennington et al. 2010), especially in the context of PNC. First, the Andean mountain chain is geologically relatively young – its orogeny began in the Paleogene around 65 mya (which overlaps temporally with the emergence of temperate climate zones), but the Andes reached their highest and final elevations only between 2 mya and 15,000 years ago (Hoorn et al. 2010). Second, the Andean uplift had important effects on ecosystems through the creation of high elevation habitats and by acting as a barrier for the dispersal of tropical and corridor for dispersal of cold adapted species (Hoorn et al. 2010; Luebert and Weigend 2014). Consequently, the effect of (historical) biogeographic and of recent ecological processes should have left an imprint on the composition of the species assemblages along Andean slopes. We tested whether the predictions of PNC hold true for species richness, phylodiversity and family age along an elevational gradient in the Andes of Ecuador. In contrast to most of the published studies, we use three different metrics characterizing the phylogenetic composition of tree assemblages that cover a gradient from recent evolutionary history to deep phylogenetic relationships.

2 Methods

2.1 Study area

The study area is located in South Ecuador at 1000 – 3000 m a.s.l. on the eastern Cordillera of the Andes in the provinces of Loja and Zamora-Chinchipe. The topography in the study area is generally very steep (20–50°). Soil conditions are heterogeneous with a better nutrient supply at lower elevations and in valleys compared to more unfavorable nutrient conditions for plant growth at high elevations (Werner and Homeier 2015; Wilcke et al. 2008; Wolf et al. 2011). The climate of the study area is perhumid with peak rainfall occurring in June, July and August (Rollenbeck and Bendix 2011). Annual rainfall is high with ~ 2000 mm at 1000 m (Zamora), ~ 2200 mm at 2000 m (ECSF-Met. Station; ~ 2300 mm including occult precipitation) and ~ 4800 mm at 3000 m a.s.l. (Cerro Met. Station; ~ 6700 mm including occult precipitation; Bendix et al. 2008a; Bendix et al. 2008b). However, it should be stressed that the local amount of annual rainfall is strongly influenced by the strength of topographic sheltering against the easterlies (Bendix et al. 2006; Rollenbeck and Bendix 2011; Wagemann et al. 2015). The mean annual air temperature decreases with elevation from 20.0 at 1000 m to 15.5 at 2000 m to 9.5° C at 3000 m a.s.l., with a typical moist adiabatic lapse rate of around -0.6 K $(100\ m)^{-1}$ (Bendix et al. 2008b).

2.2 Study design

The study design comprised three different elevation levels (~ 1000 m a.s.l.; ~ 2000 m a.s.l. and ~ 3000 m a.s.l.) which harbor three different forest types (evergreen premontane rain forest at 1000 m, evergreen lower montane rain forest at 2000 m and evergreen upper montane rain forest at 3000 m a.s.l., see Homeier et al. 2008 for more details). Each elevation level contained 18 permanent plots, each 20 m x 20 m in size. The minimum distance between all plots was 0.02 km and the maximum distance was 24 km, with a mean of 14 km (maximum distance between plots within the same elevation level was 1.5 km, mean plot distance within the elevation levels ranged from 292 m to 704 m). For more detailed information on the location of the study sites see App. 1, for a map of the study area with study site locations see Jantz et al. (2014). All plots were located in homogenous mature forest without visible natural or human disturbance. In each plot all trees with a dbh $\geq$ 5 cm (at 1.3 m height) were recorded and determined to species level where possible (69 %), otherwise to morpho-species at genus level (31 %). Families were classified after APG III (The Angiosperm Phylogeny Group 2009). Tree ferns (Cyatheales) were excluded from the present analysis.

2.3 Phylogenies

We used the latest available and best resolved phylogenetic megatree (R20120829mod.new; Gastauer and Meira-Neto (in press); App. 2) to construct the phylogeny for our analysis of phylodiversity. We used the online-tool Phylomatic (http://www.phylodiversity.net/phylomatic; Webb et al. 2002) where we inserted the megatree and the list of observed tree taxa. Phylocom then assigned the 420 tree species on our plots to the megatree resulting in a phylogeny without branch lengths. To assign the branch length of the phylogenetic tree we used the 'bladj' module of Phylocom. We accessed the age file provided by Gastauer and Meira-Neto (in press; age_exp, App. 3) which is based on age estimates by Bell et al. (2010). The 'bladj' algorithm uses the provided age estimates for specific nodes in the phylogeny and distributes the remaining undated nodes evenly between the estimated nodes (Webb et al. 2008). This two-step approach is widely used in ecological studies using plant phylogenies (Kress et al. 2009; Slik et al. 2009; Swenson et al. 2007; Webb et al. 2008; but also see Swenson et al. 2006).

2.4 Diversity components

2.4.1 Taxonomic richness

As the number of species depends on sample size (Colwell et al. 2012) we applied a rarefaction method (Hurlbert 1971) using the function 'rarefy' in the package 'vegan' for R (Oksanen et al. 2014) to calculate the expected species richness in random subsamples of 17 individuals (smallest number of individuals sampled within a plot) per plot.

2.4.2 Phylogenetic diversity

We used two different measures for phylogenetic diversity, the mean nearest taxon distance (MNTD) which resembles the mean distance separating each individual in the assemblage (plot) from its closest relative and the mean pairwise distance (MPD) between individuals of all species in each assemblage. The MNTD is a useful measure to detect patterns close to the tips of the phylogenetic tree. In contrast, MPD uses pairwise phylogenetic distances between individuals and is useful to detect tree-wide patterns of phylogenetic clustering and evenness for locally co-occurring species (Kembel et al. 2010). We used a null model approach as proposed by Swenson et al. (2012) to test for phylogenetic clustering and overdispersion in the local tree assemblages. Following the approach we shuffled the tip labels of the phylogeny of our local tree 1000 times and calculated standardized effect sizes for both phylodiversity metrics (sesMNTD and sesMPD) as ses$X$ = (X_{observed} – mean(X_{random})) / sd(X_{random}), where X_{observed} was the observed value of either MNTD or MPD, mean (X_{random}) was the mean of the randomizations of the null-model and sd (X_{random}) was the standard deviation of the randomly calculated values of each metric. The calculations of both phylodiversity metrics were conducted using the packages 'ape', 'picante' and 'phytools' for R (Kembel et al. 2010; Paradis et al. 2004; Revell 2012). To test the effect of the gymnosperm species in our dataset we additionally calculated standardized effect sizes of both phylodiversity metrics for the dataset without gymnosperms (excluded species: *Podocarpus oleifolius* and *Prumnopitys montana*, both Podocarpaceae).

2.4.3 Age of families

We used Davies et al. (2004) family ages (App. 4) instead of ages by Bell et al. (2010) to calculate mean family ages on our plots because family ages by Davies et al. (2004) match fossil records closer than the ones by Bell et al. (2010; see method section in Hawkins et al. 2014). As phylogeny of Davies et al. (2004) comprised only angiosperm species we added the age for the gymnosperm family Podocarpaceae manually (132.7 my; Lu et al. 2014). We calculated the mean family age by allocating each species the age of its family and averaged the age across the species (unweighted mean family age) and across individuals (abundance weighted mean family age) at each plot. We calculated the mean family ages also after excluding gymnosperms.

Using mean values across species and correlating these with other variables extracted from the matrix of species occurrences (e.g. species richness) may lead to spurious correlations (Zelený and Schaffers 2012). This bias may also lead to spurious correlations with independent variables not extracted from the species by site matrix as long as these variables covary with species richness. To correct for this bias we calculated the standardized effect sizes of the mean family ages (ses family age) using the same approach as for the phylodiversity by randomizing the assigned family ages of the species 1000 times (see also Zelený and Schaffers 2012).

2.5 Statistical analyses

We tested for relationships between elevation and i) rarefied species richness, ii) sesMNTD, iii) sesMPD, and iv) mean family age of species within the tree assemblages in our study plots using linear models. To account for the effect of species richness on our measures of phylogenetic diversity, we included rarefied species richness as a covariate in models ii), iii) and iv). We compared the patterns of phylodiversity and phylogenetic family age for the complete assemblages and for the assemblage without gymnosperms. Additionally we tested for a correlation between observed and standardized MNTD and MPD values and mean family ages for the complete and the reduced dataset, respectively. All statistical analyses were done in the 'R' environment (R Core Team 2014).

3 Results

3.1 Species richness

Within our 54 study plots we recorded in total 3740 tree individuals (dbh ≥ 5 cm), belonging to 420 species, 178 genera and 72 families. Two species were gymnosperms (*Podocarpus oleifolius* and *Prumnopitys montana*). The most species rich families were Lauraceae (47 species), Rubiaceae (39 species), and Melastomataceae (37 species). The original numbers of individuals and species differed between the elevation levels: We found 994 tree individuals representing 177 species at 1000 m, 1172 individuals and 187 species at 2000 m, and 1574 individuals and 99 species at 3000 m a.s.l. The two gymnosperm species only occurred on the mid- and high elevation plots, the three youngest species only on the low- and mid elevation plots (Tab. 1). The rarefied species richness for a random sample of 17 tree individuals on each of the 400 m^2 plots ranged from 6.1 to 15 (12 ± 1.8; mean ± sd). There was no significant relationship between rarefied species richness and elevation (Fig. 1, Tab. 2).

3.2 Phylodiversity

For sesMNTD and sesMPD, effect sizes were mostly negative (63–82 % of values < 0; Tab. 2) indicating that the composition of assemblages was generally clustered. However, only few effect

Tab. 1: List of the ten oldest and five youngest tree families (those with phylogenetic ages > 100 myr and < 40 myr) recorded on our study plots. The table reports family, family age, total species richness, abundance (sum of individuals recorded on the three elevation levels), historical origin (reference: Raven and Axelrod (1974)). Note that the most abundant species per elevation level comprised 100 at 1000 m, 69 at 2000 m and 133 individuals at 3000 m a.s.l. and the most abundant family comprised in total 528 individuals (Melastomataceae)

Family	Age [myr]	Species richness	Abundance at 1000 m a.s.l.	 2000 m a.s.l.	 3000 m a.s.l.	Biogeographic origin
Chloranthaceae	143.8	7	5	40	40	Laurasia
Podocarpaceae (gymnosperms)	132.7	2	0	10	33	South Gondwana
Sabiaceae	127.2	5	4	2	3	West Gondwanaland, Australasia
Proteaceae	126.1	5	7	4	1	West Gondwanaland, Australasia
Hernandiaceae	116.7	1	0	2	0	West Gondwanaland, Australasia
Siparunaceae	109.5	2	0	7	5	unassigned
Winteraceae	106.8	1	0	0	17	West Gondwanaland
Picramniaceae	103.9	2	3	0	0	unassigned
Myricaceae	101.5	1	0	0	11	Laurasia
Palmae	101.0	4	3	4	2	unassigned
Lamiaceae	39.7	1	0	2	0	Laurasia
Primulaceae	36.7	6	0	30	79	West-Gondwanaland-Laurasia
Caryophyllales b	30.6	4	19	0	0	Laurasia
Urticaceae	25.2	5	22	18	0	Laurasia
Moraceae	25.2	21	200	35	0	Laurasia

Tab. 2: Table of statistical models for species richness and various metrics of the phylogenetic composition of tree assemblages in Southern Ecuador. We show results of linear models for relationships between rarefied species richness, standardized effect sizes of phylodiversity measure at the tip (sesMNTD) and at the clade level (sesMPD) and observed and standardized (ses) mean family ages. For all metrics (except rarefied species richness) we model two variants: one including gymnosperms and one excluding gymnosperms (column G). For each model we report intercept (Inter.), multiple R^2 (R^2), and degrees of freedom (df), as well as the slopes, t-value (slope divided by standard error) and error probability (P). For the standardized effect sizes we additionally specified the number of values < 0 and < - 2

			Elevation			Species richness						
	G	Inter.	Slope	t-value	P	Slope	t-value	P	R^2	df	< 0	< - 2
Rarefied species richness	Yes	13	-3.2×10^{-4}	-0.94	0.35				0.017	52		
sesMNTD	Yes	- 0.16	1.7×10^{-4}	1.0	0.30	-0.065	-1.0	0.32	0.045	51	39	2
sesMNTD	No	0.63	1.7×10^{-4}	1.0	0.31	-0.092	-1.4	0.16	0.05	51	41	3
sesMPD	Yes	-1.9	7.2×10^{-4}	4.5	**< 0.001**	0.035	0.54	0.59	0.28	51	35	0
sesMPD	No	-0.39	-1.7×10^{-4}	-0.85	0.40	-0.014	-0.18	0.86	0.01	51	46	9
Raw mean family age	Yes	38	4.9×10^{-3}	4.4	**< 0.001**	1.7	3.7	**< 0.001**	0.36	51		
Raw mean family age	No	39	4.1×10^{-3}	3.7	**< 0.001**	1.6	3.6	**< 0.001**	0.31	51		
ses mean family age	Yes	-2.9	6.6×10^{-4}	3.6	**< 0.001**	0.072	0.97	0.34	0.21	51	39	7
ses mean family age	No	-2.7	5.5×10^{-4}	3.0	**0.0047**	0.073	0.96	0.34	0.15	51	41	8

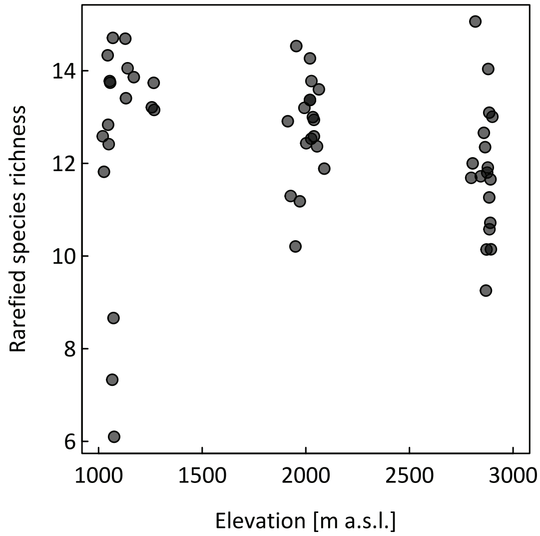

Fig. 1: Rarefied species richness (n = 17 trees) per study plot in relation to elevation

sizes were significantly clustered (standardized effect size < -2; Tab. 2). There was no significant relationship between elevation and phylodiversity with emphasis on the tip level (sesMNTD; Fig. 2 A, Tab. 2). The phylodiversity with emphasis on the clade level (sesMPD) increased with elevation with no additional effect of rarefied species richness (Fig. 2 C, Tab. 2). Excluding gymnosperms from the dataset we found neither an association of elevation with sesMNTD nor with sesMPD (Fig. 2 D, Tab. 2).

3.3 Age of species

The family age in the study plots ranged from 25.2 myr (species from the family Moraceae and Urticaceae) to 143.8 myr (species from the family Chloranthaceae). The two gymnosperm species *Prumnopitys montana* and *Podocarpus oleifolius* both from the family Podocarpaceae belonged to the second oldest family in our tree assemblage with an age of 132.7 myr.

We found a significant increase of the mean family age of species with elevation with an additional significant association with the rarefied species richness (Fig. 3 A, Tab. 2). The pattern was also significant for the standardized effect size of mean family age (App. 5 A, Tab. 2). Species richness was not related to the standardized effect size of mean family age suggesting that the significant contribution of species richness in the model of

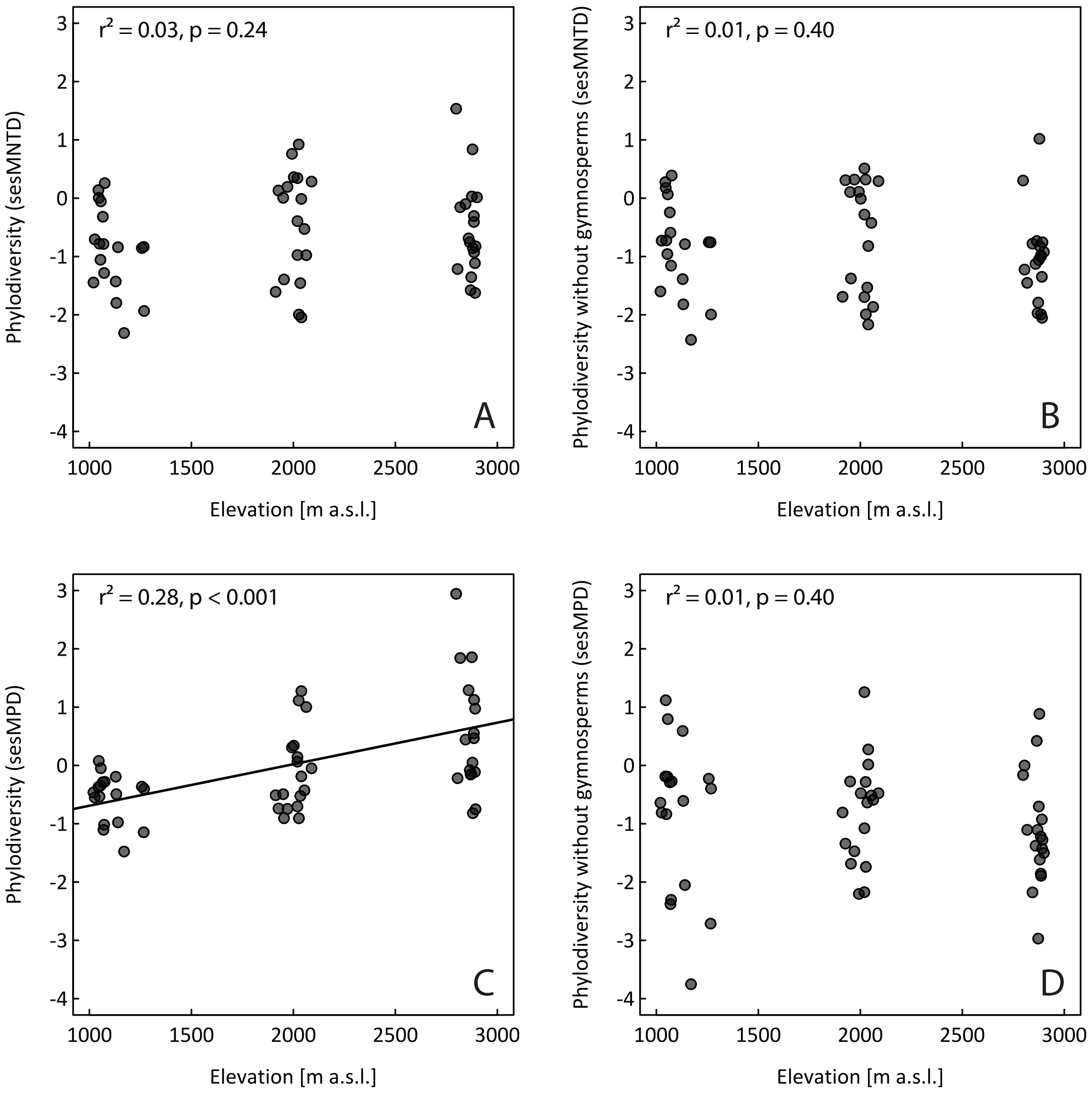

Fig. 2: Observed relationships between the different measures of phylodiversity of the tree assemblages (A, C) and of assemblages after removing gymnosperms (B, D) and elevation. For the tip level phylodiversity (sesMNTD; standardized effect size of the mean nearest taxon distance) we observed neither a significant relationship between sesMNTD for the complete tree assemblage (A) nor after excluding gymnosperms from the dataset (B). We observed a significant positive relationship between sesMPD for the complete tree assemblage (C) and no significant relationship after excluding gymnosperms from the dataset (D). Line indicates significant linear relationship ($p < 0.05$)

the raw mean family ages is due to a bias introduced by compositional similarity (see chapter 2).

The relationship between observed and standardized mean family age and elevation and the additional association with species richness was still significant when gymnosperms were excluded from the dataset (observed age: Fig. 3 B, Tab. 2; standardized age: App. 5 B, Tab. 2). The observed and standardized MNTD values were not significantly correlated with mean family age for the complete and reduced dataset excluding gymnosperms (all $r^2 < 0.034$, all $p > 0.18$, df = 52). The observed and standardized MPD values were positively correlated with mean family age for the complete dataset (MPD: $r^2 = 0.45$; sesMPD: $r^2 = 0.29$, both $p < 0.001$, df = 52); and also for the data set excluding gymnosperms (MPD: $r^2 = 0.46$; sesMPD : $r^2 = 0.31$, both $p < 0.001$, df = 52).

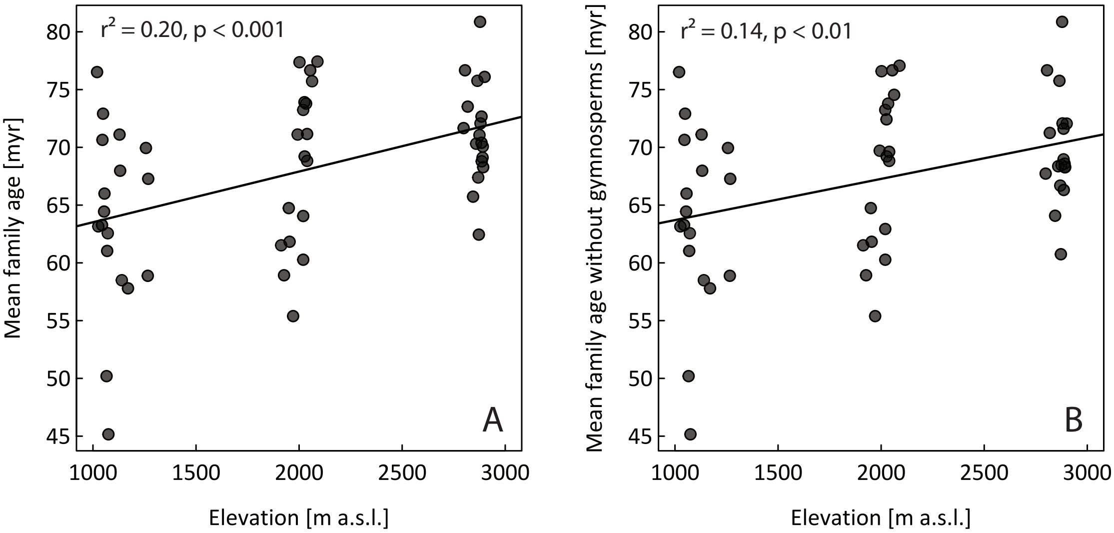

Fig. 3: Relationship between mean family age of species weighted by abundance and elevation. We observed a significant positive relationship between mean family ages and elevation for the complete tree assemblage (A) and after excluding gymnosperms from the calculation of the mean family age (B). Lines indicate significant linear relationships ($p < 0.05$)

4 Discussion

Overall the tree assemblages in our study plots were phylogenetically clustered suggesting that environmental filtering mainly drives community assembly. Furthermore, elevation was not related to species richness of trees across the sampled plots, whereas clade level phylodiversity and family age of tree assemblages increased with elevation. Therefore, our results do not support the phylogenetic niche conservatism hypothesis (PNC). Considering only angiosperms, we found no relationship between elevation and phylodiversity but a positive relationship between elevation and family age of tree species. This suggests that evolutionary patterns of Andean tree assemblages seem to be more distinct from predictions of the PNC when the phylogenetic structure deep within the phylogeny of plants is taken into account.

4.1 Taxonomic richness

Contrary to our expectation, species richness corrected for sample size did not decrease with increasing elevation. This finding contrasts the general hump-shaped or decreasing pattern of species richness along elevational gradients (LOMOLINO 2001; RAHBEK 1995). Three possible reasons might explain our findings: First, the high number of tree species at the mid and high elevation level on our plots and the high percentages of endemism for the Ecuadorian vascular plant flora above 1500 m a.s.l. (as many as 200 species are endemic in the Podocarpus National Park; JORGENSEN and LEÓN-YÁNEZ 1999; KESSLER 2002; VALENCIA et al. 2000) could indicate high speciation rates in lineages adapted to high elevations (HOMEIER et al. 2010). Second, our study design did not cover the entire elevation range of all tree species and our plots were not distributed continuously along the gradient (RAHBEK 1995). Third, factors other than elevation may have influenced the distribution of species richness. One likely driver is e.g. the high habitat heterogeneity along the studied gradient caused by a combination of complex topography and related climate and soil conditions (HOMEIER et al. 2010; PETERS et al. 2014; WERNER and HOMEIER 2015). At this time, we do not have the amount and type of data needed for a deeper understanding of species richness along the studied elevational gradient.

4.2 Phylodiversity

Assuming PNC we expected to find phylogenetically diverse assemblages at low elevations and a decrease in phylodiversity with increasing elevation, comparable to results from a tropical volcano in Indonesia (DOSSA et al. 2013). However, in contrast to these predictions we found no significant changes of the tip level phylodiversity and an increase in phylodiversity with elevation for the clade-level metric of phylodiversity. These results are in agreement with findings by Tallents et al. (2005) and Culmsee and Leuschner (2013), who analyzed the clade level phylodiversity of tree assemblages (including angiosperms and gymnosperms) in Tanzania and Malesia (see Tab. 3). Tallents et al. (2005) explain the high phylodiversity at high elevations by the presence of gymnosperms. Our findings support the results of this previous study, as we found gymnosperm species only within the mid and high elevation plots even though the gymnosperms were not among the most common species (see Tab. 1). The importance of gymnosperms is also emphasized by the fact that we detected a positive trend between phylodiversity and elevation at the clade level (sesMPD) but not at the tip level (sesMNTD). Gymnosperms originated during the Carboniferous around 319 mya (Beck 1966; Galtier and Rowe 1989) – long before the ancestral line of angiosperms originated in the Jurassic around 160 mya (De Bodt et al. 2005).

We detected no relationship between both phylodiversity measures and elevation when considering only angiosperms. In contrast to our results, previous studies showed that phylodiversity of angiosperms in the Rocky Mountains was hump-shaped with highest diversities at 3000 m a.s.l. whereas phylodiversity of angiosperms in China decreased with elevation (Bryant et al. 2008; Qian et al. 2014, see Tab. 3). Our finding (no relationship of angiosperm phylodiversity with elevation) and the finding from the Rocky Mountains (increasing angiosperm phylodiversity up to 3000 m a.s.l.) contradict the idea that the importance of environmental filtering increases with elevation (Hardy et al. 2012; Qian et al. 2014). Overall, our results of the phylodiversity analysis emphasize the role of gymnosperms in affecting phylodiversity along the elevational gradient, although gymnosperms had low abundances.

4.3 Family age

Mean family age and clade level phylodiversity of tree assemblages were significantly and positively correlated across plots irrespectively of whether we used presence-absence or abundance based metrics. This suggests that the phylodiversity and mean family age, which we used in our analysis, were not influenced by the distribution of abundances within plots. However, angiosperm assemblages containing species from old clades were not *per se* phylogenetically more diverse, which underlines that these two metrics – while using similar data sets – measure independent characteristics of the assemblages.

The observed values and the standardized effect sizes of the mean family age of our tree assemblages (including or excluding gymnosperms) increased with elevation. These findings contradict predictions according to PNC and latitudinal patterns species from younger clades were often found at higher latitudes (Hawkins et al. 2003, 2011; Jansson et al.

Tab. 3: Compilation of the results from different studies on tree assemblages analyzing the relationships between species richness and elevation (A, B), phylodiversity and elevation (A), family age and elevation and / or latitude (B). The datasets of the studies differed: Some studies included gymnosperms and some excluded gymnosperms (column G). Denoted are the observed patterns (increase (+), decrease (-) or hump-shaped (hump) of species richness, phylodiversity and age) in relation to increasing elevation or increasing latitude

	Study	Study area	G	Species richness ~ elevation	Phylodiversity ~ elevation		
A	(Bryant et al. 2008)	USA	No	hump	hump		
	(Tallents et al. 2005)	Tanzania	Yes	no pattern	+		
	(Culmsee and Leuschner 2013)	Malesia	Yes		+		
	(Dossa et al. 2013)	Indonesia	Yes		-		
	(Qian et al. 2014)	China	No	-	-		
B						**Age ~ elevation**	**Age ~ latitude**
	(Segovia et al. 2013)	Chile	No	-			+
	(Qian 2014)	South America	No	-		+	-

2013; Kerkhoff et al. 2014; Qian et al. 2013). In our study, gymnosperms were not the only driver of the increase in mean family age along the elevational gradient. While species from old families (up to the maximum family age of 143.8 my) occurred across the whole range of the elevational gradient with highest abundances at mid and high elevations (App. 6), species within the youngest families (25.2 myr to 36 myr) did not occur in the high elevation plots and were most abundant in the low elevation plots (App. 6). Therefore, our results are in line with two recent studies from South America that also found increases in mean family ages with increasing elevation and increasing latitude for assemblages of angiosperm trees, thus, contradicting the PNC (Qian 2014; Segovia et al. 2013; see Tab. 3). Qian (2014), Segovia and Armesto (2015) and Segovia et al. (2013) proposed that the occurrence of elements from old floras with extra-tropical origins in high elevation habitats causes higher average family ages of the tree assemblages. In addition, Segovia and Armesto (2015) pointed out that the flora at 40° S latitude in southern South America is dominated by Australasian and Austral-Antarctic elements (Kerkhoff et al. 2014). The Andean uplift during the Neogene created more temperate habitat at higher elevations and could have allowed the northward migration of Gondwanan taxa into tropical latitudes along the slopes of the mountains (Segovia and Armesto 2015). Our results support this idea as the historical origins of most of the oldest tree families (> 100 myr) were located on the Gondwanan landmass (Raven and Axelrod 1974; see Tab. 1) and macrofossils from *Podocarpus* have been reported from the Paleocene (~ 60 mya) of Patagonia (Morley 2011). We consequently suggest that the immigration of ancient lineages with Gondwanan origins into South America and their subsequent migration along the rising high elevation habitats has influenced the species composition of tree assemblages along the Andean slopes. Our study revealed that evolutionary patterns of Andean tree assemblages are more distinct when measures consider the phylogenetic structure deep within the phylogeny of plants. Generally, the observed elevational patterns of the three different measures (MNTD, MPD and mean family age) of the phylogenetic or evolutionary history got stronger the further these measures accessed deeper nodes of the phylogeny. The MNTD reflects patterns at the tip level, the MPD reflects patterns at the clade level, whereas family age is driven by the relatively deep family nodes in the phylogeny.

5 Conclusion

Patterns of species richness, phylodiversity, and mean family age for tree assemblages along the studied elevational gradient in the tropical Andes contradict the phylogenetic niche conservatism (PNC). We could show that two gymnosperm species that occur on high elevation habitats of the Andes strongly influence the pattern of increasing phylodiversity with elevation. Importantly, we found that average family ages of tree species increased along the elevational gradient and this increase was not merely driven by the occurrence of gymnosperms at high elevations. To this end, we suggest that the dispersal of evolutionarily ancient lineages into the tropical Andes was one important process affecting the current composition of tree assemblages along elevational gradients in the Andes. Our results highlight that PNC does not necessarily drive patterns of tree assembly along elevational gradients in Ecuador, but that the biogeographical history of the Andes may play a more important role for today's composition of tree assemblages. To obtain more definitive conclusions, we recommend further studies using broader elevational gradients and more highly resolved phylogenies to estimate family and species ages.

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Appendix

Appendix 1: Locations of the study plots

Study site	Elevational range	Geographic position	Area
Bombuscaro	1020 to 1268 m a.s.l.	S 04°07‘, W 78°58’	Podocarpus National Park
San Francisco	1913 to 2089 m a.s.l.	S 3°58‘, W 79°4‘	Reserva San Francisco
Cajanuma	2789 to 2900 m a.s.l.	S 04°07‘, W 79°11‘	Podocarpus National Park

Appendix 2: Newick version of the megatree (R20120829mod.new, Markus Gastauer, personal communication), which was used for the construction of the tree phylogeny.

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((((ophioglossaceae)ophioglossales,(psilotaceae)psilotales)ophioglossaceae_to_psilotaceae,((equisetaceae)equisetales,(marattiaceae)
marattiales,((osmundaceae)osmundales,((hymenophyllaceae)hymenophyllales,(gleicheniaceae,(dipteridaceae,matoniaceae))gleicheniales,((lygodiaceae,(anemia
ceae,schizaeaceae))schizaeales,((marsileaceae,salviniaceae)salviniales,((thyrsopteridaceae,((loxomataceae,(culcitaceae,plagiogyriaceae)),(cibotiaceae,cyatheaceae,
dicksoniaceae,metaxyaceae)))cyatheales,(lindsaeaceae,saccolomataceae,(dennstaedtiaceae,pteridaceae,((aspleniaceae,woodsiaceae,thelypteridaceae,(blechnacea
e,onocleaceae))aspleniaceae_to_onocleaceae),(dryopteridaceae,(lomariopsidaceae,(tectariaceae,(oleandraceae,(davalliaceae,polypodiaceae)))))drypteridaceae_
to_polypodiaceae)dennstaedtiaceae_to_polypodiaceae)polypodiales)cyatheales_to_polypodiales)marsileaceae_to_polypodiales)lygopodiaceae_to_
polypodiales)hymenophyllaceae_to_polypodiales)osmundales_to_polypodiales)equisetales_to_polypodiales)monilophyte,(((cycadaceae,zamiaceae)cycadales,
(ginkgoaceae,((pinaceae,((araucariaceae,(podocarpaceae,phyllocladaceae))araucariaceae_to_podocarpaceae,((cupressaceae,taxaceae)taxaceae_to_
cupressaceae,sciadopityaceae)))pinales,(gnetum,ephedra,welwitschia)gnetales)gnetales_to_pinales)ginkgoaceae_to_gnetales)gymnosperms,((amborellaceae)
amborellales,((hydatellaceae,(cabombaceae,nymphaeaceae))nymphaeales,((austrobaileyaceae,(trimeniaceae,schisandraceae))austrobaileyales,(((chloranthaceae)
chloranthales,(((myristicaceae,(magnoliaceae,((degeneriaceae,himantandraceae),(annonaceae,eupomatiaceae))))magnoliales,(calycanthaceae,((siparunaceae,(go
mortegaceae,atherospermataceae)),(monimiaceae,(hernandiaceae,lauraceae))))laurales),((canellaceae,winteraceae)canellales,((hydnoraceae,lactoridaceae,aristol
ochiaceae),(piperaceae,saururaceae))piperales))magnoliids),(((((((((((commelinaceae,hanguanaceae),(philydraceae,(haemodoraceae,pontederiaceae)))commelin
ales,(musaceae,heliconiaceae,(strelitziaceae,lowiaceae)strelitziaceae_to_lowiaceae,((marantaceae,cannaceae),(zingiberaceae,costaceae)))ingiberales),((typhaceae
,bromeliaceae),(rapateaceae,(((xyridaceae,eriocaulaceae),(mayacaceae,(thurniaceae,(cyperaceae,juncaceae)cyperaceae_to_juncaceae))),((anarthriaceae,(centrole
pidaceae,restionaceae)),(flagellariaceae,((joinvilleaceae,ecdeiocoleaceae),((anomochloa,streptochaeta),(pharus,((guaduella,puelia),((((streptogyna,(ehrharta,(ory
za,leersia))),((pseudosasa,chusquea),(buergersiochloa,((lithachne,olyra),(eremitis,pariana))))),(brachyelytrum,((lygeum,nardus),((melica,glycer),(((diarrhena,(bra
chypodium,(avena,(bromus,triticum)))),((phaenosperma,anisopogon),(ampelodesmos,(piptatherum,(stipa,nassella))))))))))bep,(micraira,(((chasmanthium,(thy
sanolaena,zeugites)),(gynerium,(danthoniopsis,((miscanthus,zea),(panicum,pennisetum))))),(eriachne,(((aristida,stipagrostis),(merxmuelleraa,(danthonia,(karo
ochloa,austrodanthonia)))),(((molinia,phragmites),(amphiopogon,arundo)),((merxmuellerab,centropodia),((pappophorum,(eragrostis,uniola)),(distichlis,(zoys
ia,(spartina,sporobolus))))))))))pacc))))poaceae)poaceae_to_flagellariaceae)))))poales,(arecaceae)arecales,dasypogonaceae)commelinids,(orchidaceae,((boryace
ae,(blandfordiaceae,(lanariaceae,(asteliaceae,hypoxidaceae)))),((ixioliriaceae,tecophilaeaceae),(doryanthaceae,(iridaceae,(xeronemataceae,(xanthorrhoeaceae,(a
maryllidaceae,asparagaceae))))))))asparagales),((corsiaceae,campynemataceae),((melanthiaceae,(petermanniaceae,(colchicaceae,alstroemeriaceae))),((rhipogon
aceae,philesiaceae),(smilacaceae,liliaceae))))liliales),((velloziaceae,triuridaceae,(stemonaceae,(pandanaceae,cyclanthaceae)))pandanales,(nartheciaceae,(burmann
iaceae,dioscoreaceae))dioscoreales)),(petrosaviaceae)petrosaviales)petrosaviidae,(araceae,(tofieldiaceae,(((hydrocharitaceae,butomaceae),alismataceae),(scheuc
hzeriaceae,(aponogetonaceae,(juncaginaceae,((posidoniaceae,(ruppiaceae,cymodoceaceae)),(zosteraceae,potamogetonaceae))))))))alismatales)
narthecidae,(acoraceae)acorales)monocots,((ceratophyllaceae)ceratophyllales,((eupteleaceae,(((lardizabalaceae,circaeasteraceae)lardizabalaceae_to_circaeastera
ceae,(menispermaceae,(berberidaceae,ranunculaceae)ranunculaceae_to_berberidaceae)),papaveraceae))ranunculales,(sabiaceae,(nelumbonaceae,(platanaceae,(
((((((((macadamia_grandis,macadamia_claudiensis),macadamia_whelanii),((orites_megacarpus,panopsis),brabejum)),((macadamia_integrifolia,macadamia_
tetraphylla),(macadamia_ternifolia,macadamia_jansenii))),((malagasia,catalepidia),((heliciopsis,athertonia),virotia))),(cardwellia,((euplassa,(sleumerodendron,(t
urrillia,kermadecia))),gevuina,(bleasdalea,hicksbeachia)))),(((floydia,lambertia),(roupala,orites_diversifolius)),((((((banksia_ilicifolia,banksia_
oligantha),banksia_cuneata)isostylis,banksia_elegans,banksia_attenuata),(banksia_candolleana,((banksia_menziesii,banksia_burdetii,banksia_
victoriae,(banksia_hookeriana,banksia_prionotes)),(banksia_sceptrum,banksia_ashbyi),(banksia_lindleyana)lindleyanae)),(dryandra_sessilis,dryandra_
serratuloides,dryandra_foliosissima,dryandra_calophylla,dryandra_speciosa)dryandra,((banksia_baxteri,banksia_speciosa),banksia_coccinea)),((((banksia_
lemanniana,banksia_caleyi,banksia_aculeata),banksia_elderiana,banksia_baueri,banksia_lullfitzii,(banksia_repens,banksia_chamaephyton,banksia_
blechnifolia,banksia_goodii),banksia_hiemalis,banksia_petiolaris,banksia_brevidentata),(banksia_benthamiana,banksia_audax),banksia_laevigata,(banksia_
ornata,banksia_serrata,banksia_aemula)),(banksia_pilostylis,banksia_media,banksia_epica,banksia_praemorsa)cyrtostylis))cryptostomata,(((banksia_
dentata,((banksia_oblongifolia,banksia_robur),banksia_plagiocarpa,banksia_integrifolia_aquilonia),(banksia_integrifolia_integrifolia,banksia_integrifolia_
monticola,banksia_integrifolia_compar,(banksia_marginata,banksia_saxicola),banksia_paludosa),banksia_canei)salicinae,((banksia_spinulosa_
spinulosa,(banksia_spinulosa_collina,banksia_spinulosa_neoanglica),banksia_spinulosa_cunninghamii),banksia_ericifolia_ericifolia)),(((banksia_
occidentalis,banksia_littoralis),banksia_brownii,banksia_verticillata),(banksia_nutans_nutans,banksia_nutans_cernuella)),(banksia_quercifolia,banksia_
oreophila)quercinae,(((((banksia_telmatiaea,banksia_scabrella,banksia_leptophylla_melletica,banksia_leptophylla_leptophylla,banksia_lanata),banksia_
grossa),(banksia_micrantha,(banksia_sphaerocarpa_sphaerocarpa,banksia_sphaerocarpa_caesia)),(banksia_dolichostyla,banksia_violacea,(banksia_
laricina,banksia_incana))),banksia_tricuspis),((banksia_pulchella,banksia_meisneri_cendens),(banksia_dryandroides)dryandroideae),(banksia_
grandis,banksia_solandri)grandes))phanerostomata)banksia)),carnarvonia),grevillea)proteaceae)platanaceae_to_proteaceae)proteales,((buxaceae,haptanthace
ae)buxales,(trochodendraceae)trochodendrales,((gunneraceae,myrothamnaceae)gunnerales,((((((((((anisophylleaceae,((coriariaceae,corynocarpaceae),(cucurbit
aceae,(tetramelaceae,(begoniaceae,datiscaceae)))))cucurbitales,(nothofagaceae,(fagaceae,((myricaceae,juglandaceae)juglandaceae_to_myricaceae,(casuarinacea
e,(ticodendraceae,(((((ostrya_rehderiana,ostrya_virginiana)ostrya,(((carpinus_putoensis,carpinus_hupeana),(carpinus_polyneura,carpinus_
turczaninowii)),carpinus_cordata)carpinus,ostryopsis_davidiana),(corylus_heterophylla,corylus_chinensis)corylus)coryloideae,((betula_
alleghaniensis,(betula_glandulosa,betula_pendula))betula,(((alnus_glutinosa,alnus_incana),alnus_crispa),alnus_maritima)alnus)betuloideae))betulaceae)))))
fagales)fagales_to_urbitales,((((((adenostoma,(chamaebatiaria,(sorbaria,spiraeanthus)))sorbarieae,(((((((((amelanchier,peraphyllum),malacomeles),(crataegus,m
espilus)),aria,aronia,(chaenomeles,osteomeles),((chamaemeles,malus),cotoneaster),(chamaemespilus,torminalis),cormus,(cydonia,(photinia,pseudocydonia))-
,dichotomanthes,docyniopsis,((((eriobotrya,rhaphiolepis),heteromeles),pyrus),stranvaesia),eriolobus,pyracantha,sorbus)pyrinae),vauquelinia),(kageneckia,lindl
eya))pyreae,gillenia)pyrodae,(((aruncus,luetkea),holodiscus),((kelseya,petrophyton),spiraea))spiraeeae),(((coleogyne,kerria,neviusia),rhodotypos)kerrieae,(exoc
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horda,(oemleria,prinsepia))osmaronieae)kerriodae),((maddenia,pygeum,prunus)amygdaleae,(neillia,physocarpus)neillieae)),lyonothamnus)spiraeoideae,((cercocarpus,(chamaebatia,cowania,purshia)),dryas)dryadoideae)rosaceae,((barbeyaceae,(dirachmaceae,((((sageretia,scutia,(rhamnus,frangula),(rhamnella,krugiodendron,rhamnidium,(karwinskia,condalia),reynosia,berchemia)rhamneae),maesopsis),ventilago)rhamnoids,((bathiorhamnus,ampeloziziphus,doerpfeldia)ampeloziziphoids,((hovenia,(paliurus,ziziphus))paliureaeanothus,(spyridium,(trymalium,(pomaderris,siegfriedia)),cryptandra)pomaderreae,(phylica,(nesiota,noltea))phyliceae,schistocarpaea,((discaria,(adolphia,trevoa)),colletia)colletieae,colubrina,alphitonia,emmenosperma,lasiodiscus,((gouania,helinus),(reissekia,(crumenaria,pleuranthodes))gouanieae))ziziphoids))mnaceae,elaeagnaceae)),(ulmaceae,(cannabaceae,((((((((((antiaris_toxicaria)antiaris,(mesogyne_insignis)mesogyne),((((((castilla_elastica,castilla_ulei)castilla,(helicostylis_pedunculata,helicostylis_tomentosa)helicostylis),((perebea_angustifolia,perebea_humilis),perebea_longepedunculata),perebea_rubra,perebea_xanthochyma),(maquira_costaricana)maquira),((pseudolmedia_laevigata,(pseudolmedia_laevis,pseudolmedia_macrophylla)),pseudolmedia_spuria)pseudolmedia),(((naucleopsis_caloneura,naucleopsis_ternstroemiifolia),naucleopsis_guianensis),((naucleopsis_krukovii,naucleopsis_ulei),naucleopsis_naga))naucleopsis)),(poulsenia_armata)poulsenia),((antiaropsis_decipiens)antiaropsis,(sparratosyce_dioca)sparratosyce)),(((((ficus_asperula,(ficus_copiosa,ficus_wassa)),(ficus_racemosa,ficus_variegata)),ficus_virens),(ficus_edelfeltii,ficus_habrophylla)),ficus_insipida)ficus),(((((bleekrodea_madagascariensis)bleekrodea,streblus_elongatus),((((brosimum_alicastrum,brosimum_utile),((brosimum_guianense,brosimum_rubescens),(helianthostylis_sprucei)helianthostylis,(trymatococcus_amazonicus,trymatococcus_oligandrus)trymatococcus)),brosimum_lactescens),((dorstenia_bahiensis,dorstenia_choconiana)dorstenia,(utsetela_neglecta)utsetela))),((brousonettia_papyrifera)brousonettia,trophis_scandens)),(fatoua_pilosa)fatoua)),((maclura_amboinensis,maclura_tricuspidata),maclura_pomifera)maclura),(((((artocarpus_altilis,artocarpus_heterophyllus),artocarpus_vrieseanus)artocarpus,((parartocarpus_venenosus)parartocarpus,(prainea_limpato,prainea_papuana)prainea)),(batocarpus_amazonicus,(batocarpus_costaricensis,(clarisia_biflora,clarisia_ilicifolia)clarisia))),(((bagassa_guianensis)bagassa,(((milicia_excelsa)milicia,((streblus_glaber,streblus_pendulinus),streblus_smithii)),((morus_alba,morus_nigra)morus,(trophis_involucrata,trophis_racemosa)trophis))),(((sorocea_affinis,sorocea_pubivena),sorocea_briquetii),sorocea_bonplandii)sorocea)))moraceae,urticaceae)cannabaceae_to_moraceae))))rosales),(quillajaceae,(((bauhinia,cercis)cercideae,(((((berlinia,brachystegia,oddoniodendron),brownea,cynometra,amherstia),((hymenaea,guibourtia,peltogyne),tessmannia)),(barnebydendron,goniorrhachis),schotia,(colophospermum,prioria))detarieae,(((((dialium,martiodendron),petalostylis),apuleia),poeppigia)dialiinae,((((arcoa,ceratonia,gymnocladus,gleditsia)umtiza_clade,diptychandra,(((chamaecrista,cassia,senna)cassiinae,(((hoffmannseggia,zuccagnia),(caesalpinia,libidibia,cenostigma,pomaria,poincianella,guilandia,stuhlmannia,haematoxylum,erythrostemon))caesalpinia_group,pterogyne)pterogyne_group),(tachigali,((conzattia,parkinsonia,peltophorum)core_peltophorum_group,((mora,dimorphandra,erythrophleum)dimorphandra_group,(dinizia,pentaclethra,mimozyganthus,((amblygonocarpus,adenanthera,tetrapleura,xylia,pseudoprosopis,calpocalyx)adenanthera_group,(piptadeniastrum,(entada,(plathymenia,((neptunia,prosopis,prosopidastrum)prosopis_group,(desmanthus,leucaena)leucaenae_group,(dichrostachys,gagnebina)dichrostachys_group,(parkia,(microlobius,parapiptadenia,stryphnodendron,anadenanthera,pseudopiptadenia,adenopodia,piptadenia,mimosa)piptadenia_group,(acacia,((faidherbia,zapoteca),lnterolobium,albizia,((chloroleucon,leucochloron,blanchetiodendron)chloroleucon_alliance,(abarema,pararchidendron)abarema_alliance,(samanea,pseudosamanea)samanea_alliance,(havardia,ebenopsis,pithecellobium)pithecellobium_alliance,(calliandra,cojoba,zygia,macrosamanea,cedrelinga,archidendron,inga)inga_alliance))ingeae)))))))))mimosoids))))),((((swartzia,bobgunnia,bocoa,candolleodendron),(trischidium,cyathostegia,ateleia)),((((amburana,mildbraediodendron,cordyla,aldina),(dussia,myrocarpus,myroxylon,myrospermum,monopteryx)),((dipteryx,pterodon),taralea)),(xanthocercis,angylocalyx,castanospermum,alexa),(((styphnolobium,pickeringia),cladrastis),(((calia,uribea),(zollernia,holocalyx,lecointea)),((sweetia,luetzelburgia,vatairea,vataireopsis),(harleyodendron,exostyles)),((hymenolobium,andira),(((apoplanesia,((parryella,amorpha),(errazurizia,eysenhardtia))),((psorodendron,psorothamnus),(marina,dalea)))amorpheae,((adesmia,amicia,zornia,poiretia,nissolia,chaetocalyx)adesmia_group,(((riedeliella,discolobium),((cranocarpus,brya),platymiscium,(platypodium,inocarpus,maraniona,tipuana,ramorinoa,centrolobium,paramachaerium,etaballia,pterocarpus),(cascaronia,geoffroea),(fissicalyx,fiebrigiella,chapmannia,stylosanthes,arachis),grazielodendron))pterocarpus_group,((dalbergia,machaerium,aeschynomene_a),(aeschynomene_b,cyclocarpa,soemmeringia,smithia,kotschya,humularia,bryapsis,geissaspis),(pictetia,diphysa,zygocarpum,ormocarpum,ormocarpopsis,peltiera),weberbauerella)dalbergia_group))dalbergieae)),(((((cyclolobium,poecilanthe),tabaroa,(harpalyce,((brongniartia,plagiocarpus),((templetonia,hovea),(cristonia,(thinicola,lamprolobium)))))),((euchresta,((ammopiptanthus,(anagyris,piptanthus)),(thermopsis,baptisia)),((ammondendron,ammothamnus,maackia,sophora_ss,salweenia),camoensia)),((cyclopia,((xiphotheca,amphithalea),(stirtonanthus,(podalyria,(liparia,(virgilia,calpurnia)))))),((spartidium,(lebeckia,wiborgia,rafnia,aspalathus),((lotononis,bolusia,crotalaria),(pearsonia,rothia,robynsiophyton)))crotalarieae,((melolobium,dichilus,polhillia),(argyrolobium_a,((lupinus,anarthrophyllum,sellocharis),(argyrolobium_b,(adenocarpus,((cytisophyllym,argyrocytisus,petteria,laburnum,podocytisus,hesperolaburnum,cytisus,lembotropis,calicotome),(echinospartum,erinacea,retama,gonocytisus,genista,spartium,stauracanthus,ulex)))))))genisteae)))),(ormosia,haplormosia,pericopsis,acosmium,bowdichia,diplotropis,clathotropis,petaladenium,sakoanala,neoharmsia,bolusanthus,platycelyphium,dicraeopetalum,cadia)ormosieae)genistoids,(((baphia,baphiastrum,bowringia,leucomphalos,airyantha,dalhousiea),baphiopsis)baphieae,((hypocalyptus,((goodia,((bossiaea,platylobium),(muelleranthus,(ptychosema,aenictophyton)))),gompholobium,sphaerolobium,((daviesia,erichsenia),viminaria),(isotropis,(jacksonia,leptosema,latrobea,euchilopsis,phyllota,otion,aotus,urodon,stonesiella,almaleea,eutaxia,dillwynia,pultenaea,irbelia,chorizema,oxylobium,podolobium,callistachys,gastrolobium))))mirbelieae,((((((callerya,endosamara,sarcodum,afgekia,antheroporum),wisteria),glycyrrhiza),((((erophaca,((oxytropis,(astragalus,(biserrula,(ophiocarpus,barnebyella)))),(((colutea,((oreophysa,smirnowia,eremosparton),sphaerophysa)),(lessertia,sutherlandia)),(swainsona,(clianthus,(montigena,carmichaelia),streblorrhiza))))),(chesneya,spongiocarpella,(gueldenstaedtia,tibetia))),(((caragana,halimodendron),calophaca),(alhagi,(eversmannia,(hedysarum,corethrodendron,sulla,taverniera),(onobrychis,sartoria,ebenus)))))),(parochetus,(galega,(cicer,(((trifolium,((lathyrus,(pisum,vavilovia)),((lens,viciaa),viciab))),((melilotus,trigonella),medicago)),ononis))))))irlc,(((hebestigma,lennea),((gliricidia,poitea),(((olneya,(poissonia,sphinctospermum)),(coursetia,(peteria,genistidium))),robinia)))robinieae,(sesbania,(((lotus,dorycnium,tetragonolobus),(hammatolobium,cytisopsis,tripodion)),(((coronilla,securigera),scorpiurus),hippocrepis),(anthyllis,hymenocarpos),(((acmispon,syrmatium),ottleya),(dorycnopsis,(kebirita,(ornithopus,hosackia)))),antopetitia,pseudolotus,podolotus)loteae))),((phylloxylon,((((rhynchopis,microcharis),indigastrum),cyamopsis),(vaughania,indigofera)))indigofereae,((austrosteenisia,leptoderris,dalbergiella,aganope,ostryocarpus,xeroderris,fordia_ss,platysepalum,sylvichadsia,schefflerodendron,craibia,disynstemon,platycyamus,kunstleria,burkilliodendron,craspedolobium),(abrus,(((dioclea,luzonia,macropsychanthulimbosema,cleobulia,camptosema,cratylia,galactia,collaea,lackeya,rhodopis,neorudolphia),((cruddasia,ophrestia),pseudoeriosema))galactinae,(((fordia_pp,millettia_pp),philenoptera),((hesperothamnus,piscidia),((dahlstedtia,deguelia,lonchocarpus,behaimia,bergeronia,margaritolobium,muellera),(derris,paraderris),(millettia_ss,pongamiopsis),(pyranthus,chadsia,mundulea,tephrosia,apurimacia,paratephrosia,requienia,ptycholobium))))millettioids)),(((((((((otholobium,psoralea),((orbexilum,hoita),(rupertia,psoralidium,(pediomelum,(bituminaria,cullen)))))psoraleeae,calopogonium,cologania,pachyrhizus,herpyza,neorautanenia,neonotonia,teyleria,dumasia,pueraria,nogra,eminia,sinodolichos,pseudeminia,pseudovigna,amphicarpaea,teramnus,glycine,phylacium,neocollettia)glycininae,(wajira,shenostylis,nesphostylis,alistilus,austrodolichos,dolichos,macrotyloma,spathionema,vatovaea,physostigma,((dipogon,lablab),(vigna,oxyrhynchus,phaseolus,ramirezella,((strophostyles,dolichopsis),macroptilium,mysanthus,oryxis))))haseolinae),(erythrina,psophocarpus,dysolobium,otoptera,descorea)erythrininae,strongylodon),(adenodolichos,paracalyx,bolusafra,carrissoa,chrysoscias,rhynchosia,eriosema,dunbaria,cajanus,flemingia)cajaninae),(spatholobus,butea,meizotropis)),((apios,cochlianthus,shuteria,mastersia,diphyllarium),((mucuna,(((campylotropis,kummerowia),lespedeza),((dendrolobium,phyllodium,ougeinia,aphyllodium,ohwia,hanslia,arthroclianthus,nephrodesmus,tadehagi,akschindlium,droogmansia),(monarthrocarpus,trifidacanthus,desmodium,codariocalyx,hylodesmum,hegnera,pseudarthria,pycnospora,mecopus,uraria,christia,alysicarpus,desmodiastrum,meliniella,leptodesmia,eliotis)))desmodieae),(kennedia,hardenbergia,vandasina)nedinae))),(barbieria,clitoria,centrosema,periandra,clitoriopsis)clitorinae)phaseoloids))))))))))papilionoideae))))fabaceae,(surianaceae,polygalaceae)))fabales)nitrogenfixing,((lepidobotryaceae,celastraceae)celastrales,((huaceae,((connaraceae,oxalidaceae),(((((((((weinmannia,(cunonia,pancheria)),vesselowskya),((callicoma,codia),pullea)),(((ackama,spiraeopsis),opocunonia),caldcluvia),((geissois,pseudoweinmannia),lamanonia),acrophyllum,gillbeea,aistopetalum,eucryphia),bauera),(((anodopetalum,platylophusratopetalum),schizomeria)),davidsonia),(acsmithia,spiraeanthemum))cunoniaceae,((

brunelliaceae,cephalotaceae),elaeocarpaceae))))oxalidales,((achariaceae,(goupiaceae,(violaceae,passifloraceae),(lacistemataceae,salicaceae))),centroplacaceae,caryocaraceae,(rafflesiaceae,euphorbiaceae),humiriaceae,irvingiaceae,ixonanthaceae,linaceae,(putranjivaceae,lophopyxidaceae),pandaceae,(phyllanthaceae,picrodendraceae),(ctenolophonaceae,(erythroxylaceae,rhizophoraceae)),((bonnetiaceae,clusiaceae),(calophyllaceae,(hypericaceae,stemaceae))),(malpighiaceae,elatinaceae),ochnaceae,(balanopaceae,((trigoniaceae,dichapetalaceae),(chrysobalanaceae,euphroniaceae))))malpighiales))celastrales_to_malpighiales),(zygophyllaceae,krameriaceae)zygophyllales)fabids,(((((((neuradaceae,(thymelaeaceae,(sphaerosepalaceae,bixaceae,(cistaceae,(sarcolaenaceae,dipterocarpaceae))sarcolaenaceae_to_dipterocarpaceae,(cytinaceae,muntingiaceae),malvaceae)))malvales,((akaniaceae,tropaeolaceae),((caricaceae,moringaceae)moringaceae_to_caricaceae,(setchellanthaceae,(limnanthaceae,((koeberliniaceae,(bataceae,salvadoraceae)),(emblingiaceae,(pentadiplandraceae,(gyrostemonaceae,resedaceae),tovariaceae,(capparaceae,(cleomaceae,brassicaceae)brassicaceae_to_cleomaceae))))))))brassicales)malvales_to_brassicales,(gerrardinaceae,(dipentodontaceae,tapisciaceae))huerteales)huerteales_to_brassicales,(biebersteiniaceae,(nitrariaceae,((kirkiaceae,(anacardiaceae,burseraceae)bursa_to_anaca),(sapindaceae,(simaroubaceae,((((((aglaia,aphanamixis,lansium,dysoxylum,guarea,heckeldora,ruagea,synoum),(((calodecaryia,turraea),nymania),munronia,cipadessa,malleastrum,trichilia)),walsura),(ekebergia,quivisianthe)),(azadirachta,melia)melieae)melioideae,(((((capuronianthus,lovoa),(carapa,khaya,swietenia)),(cedrela,toona)),neobeguea),(chukrasia,schmardaea))swietenioideae)meliaceae,rutaceae)meliaceae_to_rutaceae))))sapindales),(picramniaceae)s),((staphyleaceae,(guamatelaceae,(stachyuraceae,crossosomataceae)crossosomataceae_to_stachyuraceae)),(aphloiaceae,(geissolomataceae,strasburgeriaceae)))crossosomatales),((combretaceae,((onagraceae,lythraceae),((((((((((((((((neomitranthes_cordifolia,siphoneugena),plinia_pauciflora),myrciaria)pliniagroup,algrizea_macrochlamys),((calyptranthes,(marlierea_eugeniopsoides,myrcia1),myrcia2,myrcia3),((marlierea,myrcia_multiflora,myrcia),myrcia_racemosa),myrcia4,myrcia_bicarinata)myrciagroup),((blepharocalyx_cruckshanksii,luma),myrceugenia)myrceugeniagroup),(((((neomyrtus_pedunculata,lophomyrtus_obcordata),lophomyrtus_bullata),ugni_mollinae),myrteola_nummularia)myrteolagroup,(((((campomanesia,psidium),acca_sellowiana,myrrhinium_atropurpureum),pimenta),(amomyrtus,legrandia_concinna))pimentagroup,(eugenia,myrcianthes)eugeniagroup))),blepharocalyx_salicifolius),((rhodamnia,(decaspermum_humile,(octamyrtus_pleiopetala,rhodomyrtus_psidioides))),(gossia,austromyrtus_dulcis))australasiangroup),myrtus_communis)myrteae,((syzigium,backousieae),(metrosidereae,tristanieae)),(tristaniopsis,sphaerantia)kanieae)myrteaestem,((((((chamelaucium,homoranthus)chamelaucieae,micromyrtus),(homalocalyx,calytrix)),leptospermeae),(eucalypteae,syncarpieae)eucalypteaestem),lindsayomyrtus)),((((beaufortia,calothamnus),melaleuca),callistemon),osbornia)),(xanthostemom,(kjellbergiodendron,lophostemon))),(heteropyxis,psiloxylum)psiloxydeae)myrtaceae,vochysiaceae),(melastomataceae,(crypteroniaceae,(alzateaceae,penaeaceae))))))myrtales,(geraniaceae,(melianthaceae,vivianiaceae))geraniales))malvids),(vitaceae)vitales)rosids,(peridiscaceae,((paeoniaceae,(altingiaceae,(hamamelidaceae,(cercidiphyllaceae,daphniphyllaceae)))),((crassulaceae,(aphanopetalaceae,(tetracarpaeaceae,(penthoraceae,haloragaceae)penthoraceae_to_haloragaceae))),(iteaceae,(grossulariaceae,saxifragaceae)))))saxifragales)subrosid,dilleniaceae,((aextoxicaceae,berberidopsidaceae)berberidopsidales,((balanophoraceae,olacaceae,(((misodendraceae,schoepfiaceae),loranthaceae),(opiliaceae,santalaceae)))santalales,((((drose,(nepenthaceae,(drosophyllaceae,(ancistrocladaceae,dioncophyllaceae)dioncophyllaceae_to_ancistrocladaceae))),((tamaricaceae,frankeniaceae),(polygonaceae,plumbaginaceae)plumbaginaceae_to_polygonaceae)),(rhabdodendraceae,(simmondsiaceae,((asteropeiaceae,physenaceae),((amaranthaceae,achatocarpaceae,caryophyllaceae)amaranthaceae_to_caryophyllaceae,(stegnospermataceae,(limeaceae,((lophiocarpaceae,(barbeuiaceae,((((((trianthema_portulacastrum,(trianthema_turgidifolia,(trianthema_cussackiana,(trianthema_compacta,trianthema_glossistigma,trianthema_oxycalyptra,(trianthema_patellitecta,(trianthema_rhynchocalyptra,(trianthema_megasperma,trianthema_pilosa))))))),zaleya),(trianthema_triquetra,(trianthema_parvifolia,(trianthema_sheilae,trianthema_triquetra_africa)))),((cypsela,(sesuvium_maritimum,sesuvium_portulacastrum,sesuvium_sessile,sesuvium_verrucosum)sesuvium),(sesuvium_sesuviodes,sesuvium_hydaspicum))),mesembryanthemum)aceae,(nyctaginaceae,gisekiaceae,sarcobataceae,phytolaccae)))),(molluginaceae,((((anacampserotaceae,cactaceae),portulacaceae)cactaceae_to_portulaceae,talinaceae),halophytaceae,didiereaceae,montiaceae,basellaceae))))))))))caryophyllales,((hydrostaeae,((loasaceae,hydrangeaceae),cornaceae,(curtisiaceae,grubbiaceae)))cornales,(((balsaminaceae,(marcgraviaceae,tetrameristaceae)),(((polemonioideae,cobaeoideae,acanthogilioideae)polemoniaceae,fouquieriaceae),lecythidaceae,((sladeniaceae,pentaphylacaceae),(sapotaceae,(ebenaceae,primulaceae)),(mitrastemonaceae,theaceae,(symplocaceae,(styracaceae,diapensiaceae)styracaceae_to_diapensiaceae),(((actinidiaceae,roridulaceae),sarraceniaceae),(clethraceae,(cyrillaceae,(enkianthoideae,(monotropoideae,(arbutoideae,((cassiopoideae,ericoideae)cassiopoideae_to_ericoideae,(harrimanelloideae,(styphelioideae,vaccinioideae)styphelioideae_to_vaccinioideae)harrimanelloideae_to_vaccinioideae)cassiopoideae_to_vaccinioideae)arbutoideae_to_vaccinioideae)monotropoideae_to_vaccinioideae)ericaceae)))))))ericales,((icacinaceae,metteniusaceae,oncothecaceae,(garryaceae,eucommiaceae)garryales,(((((pauridiantha,amphidasya),(ophiorrhiza,((hindsia,(coussarea,faram)),(schradera,((psychotria,palicourea),morinda)),(pentanisia,(serissa,paederia),hedyotis,(theligonum,rubia),mycetia,nertera))))rubioideae,luculia,(((bathysa_veraguensis,bathysa,condaminea,dioicodendron,elaeagia,emmenopterys,hippotis,macbrideina,parachimarrhis,pentagonia,picardaea,pinckneya,pogonopus,rustia,simira,sommera,wittmackanthus,((chimarrhis_hookeri,chimarrhis_glabriflora),chimarrhis_turbinata,chimarrhis_microcarpa,capirona,dolicodelphys,warszewiczia),(calycophyllum,alseis)),((mussaenda,pseudomussaenda),(retiniphyllum,(((vangueria,(keetia,psydrax)),(greenea,((aleisanthiopsis,aleisanthia),ixora))),((wendlandia,(augusta_rivalis,augusta_longifolia)augusta),((randia,(genipa,gardenia)),duroia,((tarenna,pavetta),(tricalysia,coffea),bertiera),(didymosalpinx,paragenipa)))))),((maguireothamnus,(((sipanea_biflora,sipanea_stahelii),sipanea_pratensis)sipan,(sipaneopsis,neobertiera))),((posoqueria,molopanthera),gleasonia)))ixoroideae,((ladenbergia,cinchona),(((hoffmannia,hamelia),cosmibuena),chione),(isertia_hypoleuca,isertia_coccinea)isertia,((uncaria,sarcocephalus),cephalanthus),((coutaportia_ghiesbreghtiana,coutaportia_guatemalensis,hintonia,exostema_lineatum,exostema_purpureum,erithalis,(coutarea_andrei,coutarea_hexandra)coutarea,((cubanola,((portlandia,(isidorea_pedicellaris,isidorea_pungens)isidorea),(catesbaea_parviflora,(catesbaea_spinosa,phyllacanthus)))),((bikkia,badusa,siemensia,(schimidtottia,(phialanthus,ceratopyxis))),(scolosanthus,(chiococca,asemnantha))))),strumpfia),((((rogiera_amoena,rogiera_cordata)rogiera,(neoblakea,machaonea,allenanthus),((guettarda_speciosa,guettarda_ferruginea,timonius,antirhea,(guettarda_crispiflora,chomelia),(guettarda_boliviana,guettarda_odorata)guettarda),(javorkaea,gonzalagunea_veraguensis,arachnothryx_laniflora,arachnothryx_fosbergii,arachnothryx_leucophylla,(gonzalagunia_dicocca,gonzalagunia_rosea,gonzalagunia_kallunkii)gonzalagunia))),(blepharidium,(suberanthus_stellatus,suberanthus_neriifolius)suberanthus,(acrosynanthus,(roigella,rachicallis,(phyllomelia,mazaea_phialanthoides,mazaea_shaferi),(rondeletia_sp1,(rondeletia_alaternoides,rondeletia_odorata),(rondeletia_intermixta,rondeletia_portoricensis,rondeletia_pilosa,rondeletia_inermis))rondeletia))))))cinchonoideae))rubiaceae,(gentianaceae,(logani,(gelsemiaceae,((alstonia_scholaris)alstonieae,(((kopsia_fruticosa,rauvolfia_mannii)vinceae,(molongum_laxum,tabernaemontana_divaricata)tabernaemontaneae),((((chilocarpus_suaveolens)alyxieae),picralima_nitida),((thevetia_peruviana,(allamanda_cathartica,plumeria_rubra)),(acokanthera_oblongifolia,(nerium_oleander,(strophanthus_divaricatus,((beaumontia_grandiflora,apocynum_androsaemifolium),((((raphionacme_welwitschii,schlechterella_abyssinica),((hemidesmus_indicus,cryptostegia_grandiflora),(periploca_graeca,camptocarpus_mauritianus)))periplocoideae,(((((secamone_bosseri,secamone_cristata),(secamone_buxifolia,(secamone_sparsiflora,secamone_uncinata)),secamone_falcata,secamone_elliottii,secamone_parvifolia,secamone_geayii,(secamone_minutifolia,secamone_ecoronata))secamone,(pervillaea_venenata,pervillaea_phillipsonii),(secamonopsis_microphylla,secamonopsis_madagascariensis)secamonopsis,secamone_volubilis)secamonoideae,(fockea_capensis,((riocreuxia_burchellii,dregea_sinensis),(pergularia_daemia,(pentarrhinum_insipidum,((vincetoxicum_nigrum,tylophora_indica),(araujia_sericifera,(gonolobus_xanthotricus,matelea_quirosii)gonolobeae))))))asclepiadoideae)))))))))))apocynaceae))))gentianales,((plocospermataceae,((oleaceae,carlemanniaceae),(tetrachondraceae,((calceolariaceae,gesneriaceae),(plantaginaceae,(scrophulariaceae,(stilbaceae,(((((((((((salvia_africana_caerulea,salvia_aurita),salvia_brachyantha,salvia_nilotica,salvia_taraxicifolia,salvia_verticillata),((salvia_henryi,salvia_summa),salvia_roemeriana),salvia_aethiopis,(salvia_argentea,salvia_indica),(salvia_bucharica,salvia_canariensis),(salvia_cadmica,salvia_candidissima),(salvia_penstemonoides,salvia_texana),salvia_amplexicaulis,salvia_candelabrum,salvia_disermis,salvia_verbenaca,salvia_lavandulifolia,salvia_lyrata,salvia_officinalis,salvia_palestina,salvia_pratensis,salvia_ringens,salvia_sclarea,salvia_sylvestris,salvia_staminea,salvia_viridis,salvia_viscosa,((monarda_didyma,monarda_fistulosa),monarda_menthaefolia)monarda,origanum_laevigatum,origanum_vulgare,(thymus_alsinoides,thymus_vulgaris)thymus,majorana_hortensis,mentha_longifolia,mentha_rotundifolia),rosmarinus_officinalis),(perovskia_abrotanoides,perovskia_atriplicifolia) perovskia),(((salvia_fruticosa,salvia_glutinosa),salvia_nubicola),((salvia_digitaloides,salvia_barrelieri),salvia_hians))),(((((((((salvia_polystachya,salvia_tiliifoilia),salvia_farinacea),(salvia_coccinea,salvia_hirsuta),salvia_cedrocensis),salvia_involucrata),(salvia_amarissima,salvia_lycioides,salvia_microphylla)),salvia_chamaedryoides,salvia_divinorum,salvia_greggii,salvia_guaranitica,salvia_misella,salvia_section_biflorae),(((salvia_elegans,salvia_uliginosa),salvia_corrugata),salvia_subincisa),salvia_ballotiflora),salvia_cf.sagittata)calosphace,(((salvia_brandegei,salvia_dorrii,salvia_pachyphylla,salvia_spathacea),(salvia_chionopeplica,salvia_clevelandii,salvia_eremostachya)),salvia_columbariae),(salvia_californica,salvia_greatai),dorystaechas_hastata),((((((dracocephalum_grandiflorum,dracocephalum_moldavica),dracocephalum_ruyschiana)dracocephalum,(satureja_hortensis,satureja_montana)satureja),((agastache_foeniculum,agastache_mexicana,agastache_rugosa)agastache,glechoma_hederacea)),((nepeta_cataria,nepeta_tuberosa),nepeta_faassenii)nepeta),horminum_pyrenaicum),((((prunella_grandiflora,prunella_hyssopifolia),prunella_vulgaris)prunella,lepechinia_chamaedryoides),(lepechinia_calycina,lepechinia_fragrans)),(melissa_officinalis,ocimum_basilicum)),(((((lavandula_angustifolia,lavandula_stoechas),lavandula_latifolia),lavandula_lanata)lavandula,plectranthus_barbatus),collinsonia_canadensis)),(((((marrubium_incanum,marrubium_peregrinum),marrubium_vulgare)marrubium,(lamium_amplexicaule,lamium_garganicum),lamium_album),lamium_galeobdolon,lamium_maculatum,lamium_purpureum,stachys_lavandulaefolia),(caryopteris_bicolor,trichostema_dichotomum),vitex_agnuscastus,westringia_rosmariniformis))lamiaceae,(phrymaceae,orobanchaceae,paulowniaceae)),((thomandersiaceae,verbenaceae),(acanthaceae,bignoniaceae,byblidaceae,linderniaceae,lentibulariaceae,martyniaceae,pedaliaceae,schlegeliaceae))))))))))lamiales,((montiniaceae,(hydroleaceae,sphenocleaceae)),(convolvulaceae,((((((((((((((((brevantherum,geminata),leptostemonum),unclear1),unclear2),cyphomandra),unclear3),(((dulcamaroid,morelloid),((normania,archeosolanum),africannonspiny)),potatoe,regmandra)),thelopodium)solanum,jaltomata)solaneae,(((capsicum,lycianthes2),lycianthes1)capsiceae,(((((((physalis2,margaranthus_solanaceus),chamaesaracha),quincula_lobata),oryctes_nevadensis,physalis1,leucophysalis,(((witheringia1,brachistus_stramonifolius),witheringia_solanacea),witheringia_mexicana))physalinae,(((acnistus_arborescens,iochroma_australe,eriolarynx_lorentzii,vassobia_dichotoma),saracha_punctata,iochroma_fuchsioides,iochroma_umbellatum,dunalia_solanacea)iochrominae,larnax)),((withamia,mellissia_begonifolia),(aureliana_fasciculata,athenaea_sp),((tubocapsicum_anomalum,nothocestrum),discopodium_penninervum))withaninae),(cuatresia_riparia,(cuatresia_exiguiflora,witheringia_cuneata)))physaleae,(salpichroa_origanifolia,nectouxia_formosa))),(datura,brugmansia,iochroma_cardenasianum)datureae),mandragora),((((markea,merinthopodium_neuranthum,juanulloa_mexicana),dyssochroma_viridiflora)juanulloeae,solandra),schultesianthus)),nicandra_physalodes),exodeconus_miersii),((atropa,(anisodus,((atropanthe_sinensis,(physochlaina,scopolia_carniolica,(scopolia_japonica,przewalskia_tangutica))),hyoscyamus)))hyoscyameae,(((grabowskia,lycium_cestroides,phrodus_microphyllus,lycium_sandwicense),lycium_barbarum,lycium_pallidum)lycieae,nolana,sclerophylax),jaborosa,latua_pubiflora))solanoideae,(((((((((cyphanthera_albicans,duboisia_myoporoides),duboisia_leichhardtii,duboisia_hopwoodii),cyphanthera_anthocercidea),crenidium_spinescens),cyphanthera_microphylla),anthotroche),(cyphanthera_odgersii,grammosolen)),anthocercis),symonanthus,nicotiana)nicotianoideae),(schwenckia,melananthus_guatemalensis)schwenckieae,((((((plowmania_nyctaginoides,hunzikeria_texana),bouchetia_erecta),nierembergia),leptoglossis_darcyana),brunfelsia),(petunia_axillaris,(calibrachoa_parviflora,fabiana_imbricata)))petunieae,((benthamiella_skottsbergii,(combera_paradoxa,pantacantha_ameghinoi))benthamielleae,(salpiglossis_sinuata,(((streptosolen_jamesonii,browallia_eludens),browallia_speciosa)browallieae,(protoschwenckia_mandonii,(vestia_foetida,(sessea_corymbiflora,cestrum))cestreae)))cestroideae)),duckeodendron_cestroides,(((goetzea,espadaea_amoena,henoonia_myrtifolia),coeloneurum_ferrugineum),(tsoala_tubiflora,metternichia_principis))goetzeoideae),schizanthus)solanaceae)solanaceae_to_convolvulaceae)solanales),boraginaceae))lamiids,(((stemonuraceae,cardiopteridaceae),(phyllonomaceae,(helwingiaceae,aquifoliaceae)helwingiaceae_to_aquifoliaceae))aquifoliales,((escalloniaceae)escalloniales,(((rousseaceae,campanulaceae),pentaphragmataceae),(((argophyllaceae,phellinaceae),alseuosmiaceae)argophyllaceae_to_alseuosmiaceae,stylidiaceae,(menyanthaceae,(goodeniaceae,(calyceraceae,(((barnadesia,huarpea),(dasyphyllum,((chuquiraga,doniophyton),(schlechtendalia,(dasyphyllum_diacanthoides,(fulcaldea,arnaldoa)))))),(stifftia,(onoseris,(aphylloclados,plazia)),(((pachylaena,((duidaea,(chaetanthera,mutisia)),(chaptalia,(leibnitzia,(piloselloides,gerbera))))),((leucheria,jungia),((acourtia,(proustia,trixis)),(adenocaulon,(perezia,(triptilion,nassauvia)))))),((gochnatia,cnicothamnus),(hecastocleis,(((dicoma,pasaccardoa),(oldenburgia,(brachylaena,tarchonanthus),(cardopatiinae,((atractylodes,(carlina,atractylis)),((echinops,acantholepis),((xeranthemum,chardinia),((berardia,(onopordum,(synurus,alfredia))),(((ptilostemon,galactites),(cynara,((picnomon,notobasis),(cirsium,silybum,(tyrimnus,carduus))))),(((outreya,jurinea),(cousinia,arctium)),(serratula,((acroptilon,callicephalus),(zoegea,centaurea)))))))))))),((ainsliaea,(myripnois,pertya)),(gymnarrhena,((((warionia,gundelia),((scolymus,(tragopogon,scorzonera)),(((uropappus,microseris),(arnoseris,cichorium)),(((picris,leontodon),(hyoseris,sonchus)),((urospermum,chondrilla),(youngia,(rhagadioulus,lapsana))))))),(((haplocarpha,(cymbonotus,(arctotis,arctotheca))),(eremothamnus,((didelta,berkheya),(hirpicium,(gazania,gorteria))))),(((oligactis,(liabum,sinclairia)),(paranephelius,((munnozia,chrysactinium),(erato,philoglossa)))),(distephanus,(((linzia,vernonia),((vernonia2,baccharoides),(gymnanthemum,hesperomannia))),((cabobanthus,(centrapalus,((centauropsis,vernonia3),((orbivestus,(vernonastrum,vernonia4)),(gutenbergia,(ethulia,(hilliardiella,muschleria))))))),(stokesia,(hololepis,(stramentopappus,(lepidonia,bolanosa))),((chresta,(critoniopsis,(elephantopus,(lessingianthus,(chrysolaena,lepidaploa))))),((albertinia,sipolisia),vernonanthura))))))))),(corymbium,((blennosperma,((gynoxys,gynoxys2),roldana,(tussilago,petasites),(ligularia,parasenecio),(othonna,euryops),(senicio_scaposa,senicio_medley woodii),((pericallis,(cineraria,dendrosenecio)),((senicio_flaccidus,(senicio_costaricensis,(senicio_sphaerocephalus,senicio_serra))),(senicio_inornatus,senicio_subsessilis,senicio_ochrocarpus,(senicio_umbrusus,(senicio_vulgaris,(senicio_squalida,senicio_glauca)))),((packera,(senicio_incanus,(senicio_paludosus,senicio_jacobea))),((gynura,kleinia),(delairea,senicio_rowleyanus))))))),(((((dimorphotheca,(osteospermum,calendula)),((athrixia,(arrowsmithia,(rosenia,oedera))),(phaenocoma,(vellereophyton,((stoebe,edmondia),((gamochaetopsis,(plecostachys,antennaria,(tenrhynea,gamochaeta))),(jalcophila,(pterygopappus,(((anaxeton,(langebergia,petalacte)),(anaphalis,(pseudognaphalium,helicrhysum))),((telfordia,(ozothamnus,cassinia)),((apalochlamys,ammobium),((myriocephalus,(leucophyta,craspedia)),(podolepis,(millotia,hyalosperma))))))))))))))),((amellus,(commidendron,((chiliotrichum,olearia),(pteronia,(orithrophium,(conyza,((remya,(olearia2,calotis)),((grangea,olearia3),(vittadinia,brachyscome)),(lagenifera,(erigeron,(diplostephium,(podocoma,(solidago,(grindelia,(erigeron2,conyza2))))))))))))))),(osmitopsis,(athanasia,(hippia,(schistostephium,(soliva,(lidbeckia,((ursinia,eriocephalus),(((hymenolepis,((cotula,cotula2),lasiospermum)),(leucanthemella,(seriphidium,(kaschgaria,artemisia)),(crossostephium,arctanthemum,(ajania,tripleurospermum)))),((oncosiphon,(cymbopappus,pentzia)),(microcephala,((anthemis,tanacetum,matricaria,anacyclus,achillea,(gonospermum,lugoa)),((leucanthemum,(rhodanthemum,glossopappus)),(lonas,((chamaemelum,santolina),(aaronsohnia,(chrysanthemum,ismela)))))))))))))))))),(((zoutpansbergia,callilepis),((inula,blumea),(pegolettia,(cratystylis,(epaltes,(streptoglossa,pluchea)))))),((athroisma,blepharispermum),((marshallia,pelucha,plateilema,(psathyrotes,trichoptilium),((helenium,(balduina,gaillardia)),(psilostrophe,((amblyolepis,tetraneuris),(baileya,hymenoxys))))),((cosmos,(bidens,coreopsis)),((neurolaena,(((coulterella,varilla),(jaumea,(flaveria,(haploesthes,sartwellia))),((oxypappus,pseudoclappia),((pectis,porophyllum),(nicolletia,((tagetes,(adenophyllum,thymophylla)),(clappia,(arnicastrum,jamesianthus))))))),((chaenactis,dimeresia,orochaenactis),(loxothysanus,(((bartlettia,chamaechaenactis),(hymenopappus,thymopsis)),(((peucephyllum,psathyrotopsis),(espejoa,(chaetymenia,hypericophyllum))),(schkuhria,((achyropappus,bahia),((florestina,palafoxia),(platyschkuhria,(amauriopsis,hymenothrix)))))))))),(polymnia,((wyethia,(chromolepis,(ambrosia,(helianthus,(rudbeckia,trichocoryne))))),((galinsoga,melampodium,smallanthus),(((eutetras,(amauria,(pericome,perityle))),(hofmeisteria,(ageratina,((carminatia,(brickellia,kuhnia)),((fleischmannia,(ageratum,conoclinium)),(steviopsis,((eupatoriadelphus,eupatorium,liatris),((chromolaena,praxelis),(stomatanthes,(trichogonia,(acritopappus,campuloclinium))))))))))),((monolopia,(lasthenia,(amblyopappus,baeriopsis))),(constancea,syntrichopappus,(eriophyllum,pseudobahia)),(venegasia,(eatonella,hulsea),(arnica,(achyrachaena,adenothamnus,blepharipappus,calycadenia,holocarpha,lagophylla,raillardella,(blepharizonia,hemizonia),(holozonia,layia),((hemizonella,kyhosia),(anisocarpus,(carlquistia,madia),(argyroxiphium,dubauta,wilkesia))))))))))))))))))))))))))))))asteraceae)))))asterales,((((adoxaceae,caprifoliaceae)dipsacales,(paracryphiaceae)paracryphiales),(pennantiaceae,(torricelliaceae,(griseliniaceae,(pittosporaceae,(araliaceae,(myodocarpaceae,apiaceae))))))apiales),(bruniaceae,columelliaceae)bruniales)))campanulids)lamiids_to_campanulids)ericales_to_asterales)asterids)))subasterids)pentapetalids)core_eudicots)trochodendrales_to_asterales)sabiales_to_asterales)eudicots)ceratophyllales_and_eudicots)poales_to_asterales)magnoliales_to_asterales)austrobaileyales_to_asterales)nymphaeales_to_asterales)angiosperms)seedplants)euphyllophyte;

Appendix 3: Node ages that were used for the age calibration of the phylogeny for the phylodiversity analysis. All age estimates were extracted from the age file 'age_exp' (Markus Gastauer, personal communication) which uses age estimates from Bell et al. (2010).

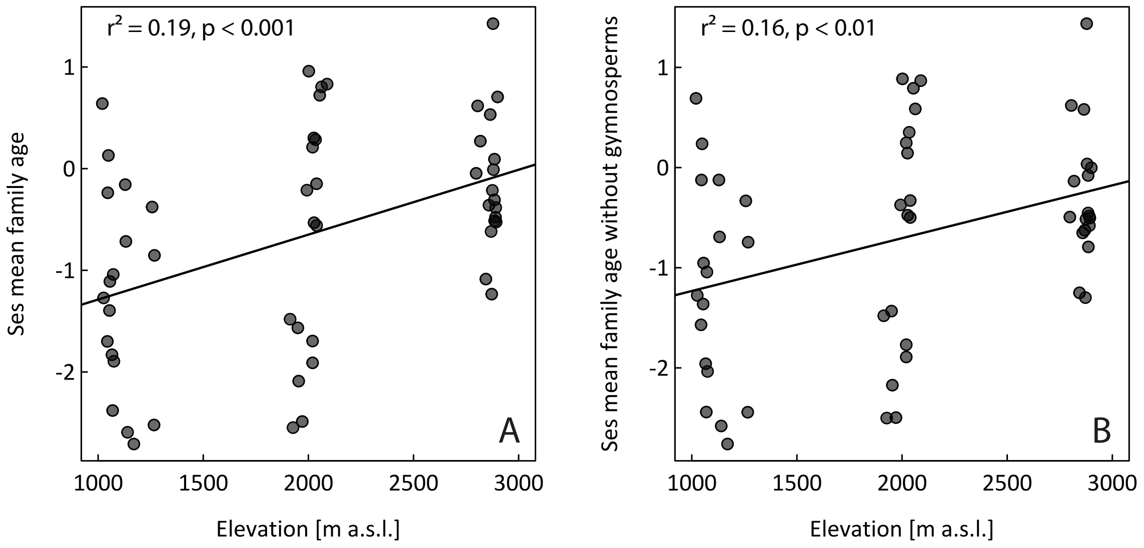
Node	Age [myr]
Acanthaceae	38
Achariaceae	79
Adoxaceae	31
Akaniaceae	6
Alismatales	107
Altingiaceae	7
Amaranthaceae	37
Amaranthaceae to Caryophyllaceae	55
Amaryllidaceae	30
Angiosperms	147
Annonaceae	23
Apiaceae	29
Apiales	49
Apocynaceae	21
Aquifoliales	88
Araceae	79
Araliaceae	18
Araucariaceae to Podocarpaceae	257
Arecaceae	31
Argophyllaceae to Alseuosmiaceae	49
Aristolochiaceae	91
Asparagaceae	42
Asparagales	92
Aspleniaceae to Onocleaceae	95
Asteraceae	40
Asterales	77
Asterids	104
Austrobaileyales	89
Austrobaileyales to Asterales	144
Berberidaceae	33
Betulaceae	18
Bignoniaceae	25
Boraginaceae	54
Brassicaceae	31
Brassicaceae to Cleomaceae	41
Brassicales	83
Bromeliaceae	20
Bursa to Anaca	50
Buxaceae	98
Cactaceae to Portulaceae	21
Calycanthaceae	98
Campanulaceae	53
Campanulids	93
Canellaceae	10
Canellales	77
Cannabaceae	36
Cannabaceae to Moraceae	54
Caprifoliaceae	36
Caryophyllales	99
Celastraceae	53
Celastrales	71
Celastrales to Malpighiales	101
Ceratophyllales and Eudicots	129
Chloranthaceae	121
Chrysobalanaceae	16
Circaeasteraceae	45
Combretaceae	21
Commelinales	70
Commelinids	96
Convallariaceae	19
Convolvulaceae	24
Core eudicots	117
Cornaceae	67
Cornales	87
Costaceae	19
Crassulaceae	47
Crossosomataceae to Stachyuraceae	24
Crossosomatales	84
Cucurbitaceae	21
Cucurbitales	61
Cunoniaceae	27
Cyatheales	183
Cyatheales to Polypodiales	211
Cycadales	283
Cyclanthaceae	30
Cyperaceae	32
Cyperaceae to Juncaceae	55
Dasypogonaceae	38
Dennstaedtiaceae to Polypodiaceae	151
Dilleniaceae	55
Dioncophyllaceae to Ancistrocladaceae	37

Dioscoreales	83
Dipsacaceae	10
Dipsacales	57
Drypteridaceae to Polypodiaceae	94
Elaeagnaceae	20
Elaeocarpaceae	38
Equisetales to Polypodiales	360
Ericaceae	14
Ericales	92
Ericales to Asterales	104
Escalloniaceae	65
Eudicots	128.9
Euphyllophyte	466
Fabaceae	61
Fabales	79
Fabids	103
Fagaceae	28
Fagales	52
Fagales to Cucurbitales	96
Garryales	70
Gentianales	65
Geraniaceae	48
Geraniales	87
Gesneriaceae	52
Ginkgoaceae to Gnetales	346
Gleicheniales	263
Gnetales	159
Gnetales to Pinales	298
Gymnosperms	354
Haloragaceae	23
Hamamelidaceae	25
Helwingiaceae to Aquifoliaceae	42
Hyacinthaceae	30
Hydrangeaceae	44
Hymenophyllaceae to Polypodiales	286
Iridaceae	31
Juglandaceae	4
Juglandaceae to Myricaceae	29
Lamiaceae	38
Lamiales	69
Lamiids	96
Lamiids to Campanulids	99
Lardizabalaceae	35
Lardizabalaceae to Circaeasteraceae	81
Lauraceae	12
Laurales	112
Lecythidaceae	46
Lentibulariaceae	37
Liliaceae	52
Liliales	86
Limnanthaceae	12
Linaceae	71
Loasaceae	31
Lygopodiaceae to Polypodiales	266
Lythraceae	46
Magnoliaceae	33
Magnoliales	69
Magnoliales to Asterales	130.1
Magnoliids	125
Malpighiaceae	61
Malpighiales	89
Malvaceae	66
Malvales	78
Malvids	107
Marantaceae	17
Marsileaceae to Polypodiales	220
Melanthiaceae	59
Meliaceae	39
Meliaceae to Rutaceae	53
Melianthaceae	34
Menispermaceae	33
Menyanthaceae	44
Monilophyte	364
Monimiaceae	35
Monocots	129.9
Moraceae	33
Moringaceae to Caricaceae	64
Musaceae	34
Myristicaceae	12
Myrtales	89
Narthecidae	118
Nitrogenfixing	99
Nyctaginaceae	22
Nymphaeales	38
Ochnaceae	49
Oleaceae	41

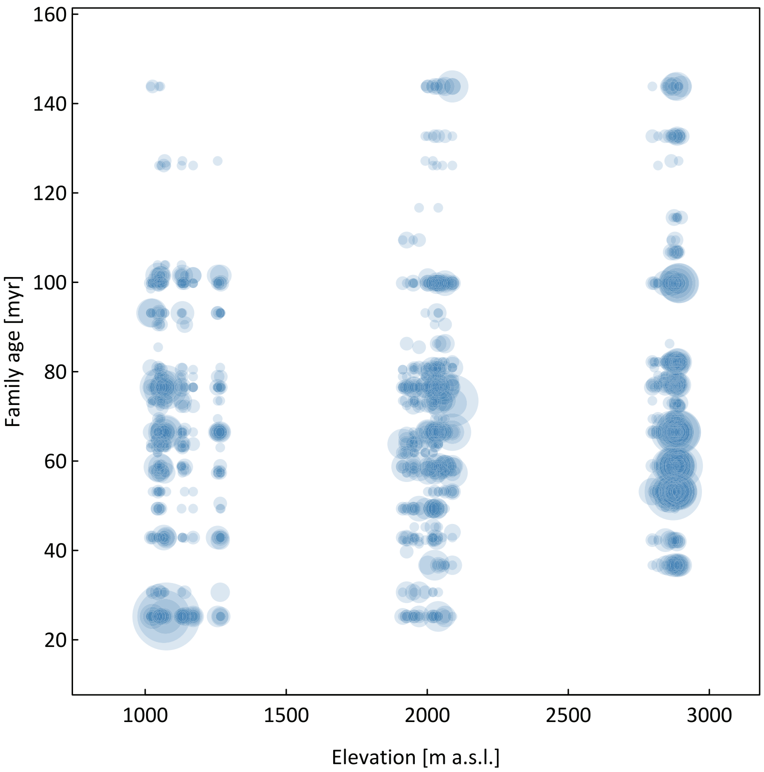
Onagraceae	23
Ophioglossaceae to Psilotaceae	306
Orchidaceae	42
Osmundales to Polypodiales	323
Oxalidaceae	34
Oxalidales	89
Pandanales	72
Papaveraceae	82
Parnassiaceae	29
Passifloraceae	68
Pentapetalids	116.9
Penthoraceae to Haloragaceae	48
Petrosaviidae	109
Philydraceae	29
Pinales	288
Piperaceae	32
Piperales	104
Pittosporaceae	11
Plantaginaceae	42
Platanaceae to Proteaceae	98
Plumbaginaceae	43
Plumbaginaceae to Polygonaceae	58
Poaceae	28
Poaceae to Flagellariaceae	58
Poales	85
Poales to Asterales	130
Polemoniaceae	32
Polygalaceae	44
Polygonaceae	41
Polypodiales	176
Primulaceae	57
Proteaceae	35
Proteales	110
Ranunculaceae	55
Ranunculaceae to Berberidaceae	67
Ranunculales	100
Rhamnaceae	59
Rhizophoraceae	60
Rosaceae	40
Rosales	82
Rosids	108
Rubiaceae	57
Rutaceae	40
Sabiaceae	87
Sabiales to Asterales	126
Salicaceae	61
Salviniales	173
Santalaceae	43
Santalales	91
Sapindaceae	41
Sapindales	71
Sarcolaenaceae to Dipterocarpaceae	35
Saururaceae	47
Saxifragaceae	38
Saxifragales	95
Schizaeales	212
Scrophulariaceae	51
Seedplants	355
Solanaceae	37
Solanaceae to Convolvulaceae	59
Solanales	71
Strelitziaceae	23
Strelitziaceae to Lowiaceae	40
Stylidiaceae	65
Styracaceae	36
Styracaceae to Diapensiaceae	51
Subasterids	116.8
Subrosid	116.8
Taxaceae to Cupressaceae	227
Tecophilaeaceae	45
Ternstroemiaceae	51
Thymelaeaceae	36
Tofieldiaceae	61
Trochodendraceae	19
Urticaceae	34
Verbenaceae	29
Vitaceae	65
Winteraceae	18
Zingiberaceae	18
Zingiberales	84

Appendix 4: Family ages that were used for the analysis of family ages of the tree assemblages. All family age estimates were extracted directly from the phylogeny provided by Davies et al. (2004) which is available online (http://biology.mcgill.ca/faculty/davies/Data/Dated tree Ultrametric.phy, accessed 11/2015).

Family	**Age [myr]**
Actinidiaceae	64.655587
Adoxaceae	86.272046
Alzateaceae	58.2997
Anacardiaceae	42.881471
Annonaceae	78.890161
Apocynaceae	67.046339
Aquifoliaceae	77.025746
Araliaceae	69.439409
Asteraceae	42.307411
Bignoniaceae	45.247531
Boraginaceae	85.473059
Brassicaceae	50.503186
Brunelliaceae	49.651267
Burseraceae	42.881471
Cannabaceae	41.479856
Caryophyllales b	30.642085
Celastraceae	41.983088
Chloranthaceae	143.833806
Chrysobalanaceae	63.027391
Clethraceae	78.134138
Clusiaceae	58.922056
Combretaceae	74.034094
Cunoniaceae	53.150235
Elaeocarpaceae	53.150235
Ericaceae	76.805507
Euphorbiaceae	57.379803
Fabaceae	63.803841
Hernandiaceae	116.66751
Hypericaceae	44.060641
Icacinaceae	98.569468
Lacistemataceae	58.039526
Lamiaceae	39.728399
Lauraceae	99.807051
Lecythidaceae	90.558439
Malpighiaceae	73.492593
Malvaceae	65.834252
Melastomataceae	66.475919
Meliaceae	49.350353
Monimiaceae	99.807051
Moraceae	25.229981
Myricaceae	51.00971
Myristicaceae	101.535374
Myrtaceae	80.913749
Olacaceae	114.500865
Santalaceae	114.500865
Loranthaceae	114.500865
Palmae	100.975677
Pentaphylacaceae	79.141798
Phyllanthaceae	73.492593
Picramniaceae	103.862183
Piperaceae	80.450584
Podocarpaceae	NA
Polygalaceae	72.281677
Polygonaceae	59.246611
Primulaceae	36.689299
Proteaceae	126.136464
Rhizophoraceae	76.370622
Rosaceae	72.977131
Rubiaceae	76.504911
Rutaceae	53.366445
Sabiaceae	127.156694
Salicaceae	58.039526
Sapindaceae	58.745333
Sapotaceae	93.138822
Siparunaceae	109.456993
Solanaceae	61.877995
Staphyleaceae	42.744786
Styracaceae	60.783984
Symplocaceae	82.167251
Theaceae	82.167251
Thymelaeaceae	72.421904
Urticaceae	25.229981
Violaceae	58.675148
Winteraceae	106.76463



Appendix 5: Standardized effect sizes (ses) of the mean family ages of the tree assemblages (A) and of assemblages after removing gymnosperms (B) in relation to elevation. We observed significant positive relationships for the complete tree assemblage (A) and after excluding gymnosperms from the dataset (B). Lines indicate significant linear relationship ($p < 0.05$).



Appendix 6: Family age of observed tree species in relation to elevation. Each circle represents one species at its observed elevation. The radius of the circles is proportional to the number of individuals.