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Phylogenetic patterns of rarity in a regional species pool of tropical trees

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Phylogenetic patterns of rarity in a regional species pool of tropical trees

Abstract

Species rarity is often defined in terms of: local abundance, geographic range size and habitat breadth. It is thought that each of these rarity axes has distinct effects on extinction risk. Thus, understanding phylogenetic patterns of these three axes is of considerable interest because they provide insights into the extent to which rarity is phylogenetically conserved and, in turn, how extinction risk is distributed across phylogenies. Here I examine the extent to which the three axes of rarity show phylogenetic signal (the tendency of related species to resemble each other more than species drawn at random from the same phylogenetic tree), and phylogenetic conservatism (stronger phylogenetic clustering than expected from a Brownian motion model of evolution) across a regional pool of woody plants in the Madidi region of the tropical Andes of Bolivia. I measured local abundance, geographic range size, and habitat breadth for 806 species in 101 families occurring in a set of 48 1-ha tree plots, and for 1,739 species in 141 families occurring in a set of 442 0.1-ha tree plots. I used three approaches to describe phylogenetic patterns of rarity: 1) hierarchical variance partitioning across taxonomic levels, 2) Blomberg's K statistic, and 3) disparity through time. I compared observed patterns described by these three approaches to patterns expected from a tip randomization null model that randomly assigns values of the axes of rarity to species. In addition, I compared observed patterns described by Blomberg's K statistic and disparity through time to patterns expected from a Brownian motion model of evolution. The hierarchical variance partitioning analysis showed that the three axes of rarity display phylogenetic signal: species belonging to the same genus tended to be more similar than expected from the tip randomization null model. At deeper phylogenetic levels the axes of rarity exhibited little or no phylogenetic signal and did not display phylogenetic conservatism. These findings suggest that, given the currently changing environment of the Tropical Andes, extinction risk could be phylogenetically clustered because certain genera may contain an unusually high number of threatened species.

INTRODUCTION

Many studies define rarity based on the local abundance of individuals and geographic range size (Harper 1981, Fidler 1987, Rabinowitz 1981, Hanski 1991, Fidler & Ahouse 1992, Gaston 1994a), while others add habitat breadth as a third axis of rarity (Rabinowitz 1981, Rabinowitz et al. 1986, Pitman et al. 1999, Romero-Saltos et al 2001). Each of these three axes of rarity is a species-level variable that describes a key aspect of abundance and distribution thought to have distinct effects on extinction risk: small local populations are vulnerable to demographic and environmental stochasticity (Lande 1993, Caughley & Gunn 1996); small geographic ranges are particularly likely to be affected by adverse conditions simultaneously across their entire extent (McKinney 1997, Gaston 2003, Harnik et al. 2012); species occupying a small number of habitats are most vulnerable to environmental change (McKinney 1997, Biesmeijer et al. 2006, Colles et al. 2009). Phylogenetic patterns of these axes of rarity are therefore of interest because they provide insights into change in extinction risk over evolutionary time. In particular, the extent to which the axes of rarity are phylogenetically conserved or labile determines in part how extinction risk is distributed across a given phylogeny and the amount of uniquely shared evolutionary history under threat, and it also bears on the possibility for species-level selection of distribution and abundance (Jablonski 1987, 2008, Waldron 2007, Borregaard et al. 2012).

Abundance, geographic range size, and habitat breadth might be more similar among closely related species than expected by chance because closely related species may have similar phenotypes related to dispersal ability, habitat requirements, and life history traits that, in turn, may determine the position of species along the axes of rarity (Gaston 2003, Vamosi & Vamosi 2012). More generally, to the extent that closely related species have similar temporal and spatial environmental templates, they might also share broad-scale geographic domains that determine species rarity (Mouillot & Gaston 2009, Machac et al. 2011). Alternatively, closely related species might differ more on the three axes of rarity than expected by chance because rarity might be largely determined by specialized inter-specific interactions (e.g., parasitism) that evolve faster than dispersal ability, habitat requirements, and life history traits (Ricklefs 2004, 2010, 2011). Empirical work is currently insufficient to determine the merit of these alternative hypotheses. The three axes of rarity have been found to be related to phylogenetic relationships in some studies (Jablonski 1987, Waldron 2007, Menken et al. 2009) and more phylogenetically labile in others (Gaston 2003, Ricklefs 2011).

Conclusions drawn from such studies may reflect differences in study systems, as well as in phylogenetic and spatial scales (Krasnov et al. 2011), but they are also colored by disagreements about the definition of phylogenetic conservatism and lability (Waldron 2007, Losos 2008, Wiens et al. 2010, Crisp & Cook 2012). Several studies have used "phylogenetic signal" as a measure of phylogenetic conservatism in traits (e.g., Blomberg 2003, Swenson & Enquist 2007), where phylogenetic signal is defined as the tendency of related species to resemble each other more than species drawn at random from the same phylogenetic tree (Blomberg et al 2003, Münkemüller et al 2012). One null model for testing this statistical hypothesis is "tip randomization", which is a "white noise" model of evolution (Kozak & Wiens, 2010) whereby non-random phylogenetic signal is accepted as phylogenetic trait conservatism (Fig. 1). Others have argued that phylogenetic trait conservatism should be defined as significant phylogenetic trait clustering relative to a Brownian motion model of evolution (Felsenstein 1985). Accordingly, phylogenetic trait lability would be defined as less phylogenetic trait clustering than expected from a Brownian motion model of evolution (Losos 2008, 2011)(Fig. 1).

The "tip randomization" null model assigns the trait values of species randomly across the phylogeny, so that any phylogenetic signal is eliminated. This model always produces less phylogenetic trait clustering than the null model based on the Brownian model of evolution (e.g., Baraloto et al. 2012, Fig. 1). The latter describes the evolution of a trait as a random walk along the branches of the phylogenetic tree, so that the expected covariance between species trait values is proportional to the history shared by the species (i.e., the length of shared branches along the phylogeny), and the expected sampling variance for the trait value of a given tip (species) is proportional to the branch length from the root to that tip (Felsenstein 1985, Revell et al. 2008). Thus, it is possible to relate the findings of these two approaches by adopting operational definitions that distinguish between phylogenetic signal and phylogenetic conservatism. Phylogenetic signal indicates that a relationship exists between the degree of phylogenetic relatedness and trait similarity, and it can be tested using a tip randomization null model. In contrast, phylogenetic conservatism indicates that species are more similar than would be expected by their phylogenetic relatedness (i.e. shared evolutionary history), and it can be tested using a Brownian null model. Using these definitions, phylogenetic signal is necessary but insufficient to demonstrate phylogenetic conservatism. That is, traits showing phylogenetic conservatism always show phylogenetic signal, but not vice versa (Losos 2008). However, the relative positions of the two null models along the axis of phylogenetic clustering may depend on the metric used to measure clustering (Fig. 1). Metrics commonly used to study phylogenetic patterns of trait evolution have various limitations and describe different aspects of the relationship between phylogenetic relatedness and trait similarity (Revell et al. 2008, Münkemüller et al. 2012), so that their relationship to various definitions of phylogenetic trait conservatism is complex (Crisp & Cook 2012).

The present study seeks to examine the extent to which the three axes of rarity (abundance, geographic range size, and habitat breadth) show phylogenetic signal or phylogenetic conservatism across a regional species pool of woody plants in the Madidi region of the tropical Andes of Bolivia.

METHODS

Study Area

The dataset used in this study is from quantitative inventories made within the Madidi region of Bolivia. This region is located in the northeastern slope of the Andes and covers approximately 111,000 km² in the northern part of the Department of La Paz (provinces Iturralde, Franz Tamayo, Bautista Saavedra, Muñecas, Larecaja, and Sud Yungas) and the western part of the Beni Department (province Ballivián) (Fuentes 2005) (Fig. 2). The region contains three protected areas: Madidi (18,854 km²), Apolobamba (4,765 km²) and Pilón Lajas (4,027 km²). The physiography of the region is complex: elevation ranges from 200 m elevation to more than 6,000 m (Fuentes 2005); average annual temperature varies from 26.1°C in the eastern lowlands to -2.5°C at the peak of Apolobamba (Navarro 2002); annual rainfall varies from 100 mm to 3,500 mm (Fuentes 2005). The vegetation of the region consists largely of mature tropical forest in different kinds of ecosystems, e.g., tropical rain forest, montane forest, cloud rain forest, and dry forest (Fuentes 2005).

Field sampling

Field work was conducted from 2001 to 2010, and two types of vegetation plots along an elevational gradient from 200 to 4500 m (Fig. 2) were established. There are 48 of

1.0 ha (100 x 100) in extent (hereafter "1 ha plots"). Within each plot all stems with a diameter at breast height (DBH, measured at 1.3 m above ground level) \geq 10 cm were recorded and uniquely marked with aluminum tags. There are, also 442 plots each having 0.1 (100 x 10 or 50 x 20 m) ha in extent (hereafter "0.1 ha plots"). Within those plots each individual stem with DBH \geq 2.5 cm was recorded, but not tagged. All plots were within closed-canopy mature forest with no sign of recent disturbance, and were at least 500 m from the nearest plot. Each stem was assigned to a morphospecies in the field, and all morphospecies were collected and vouchered at least once in each of the plots where they occurred. Voucher information was digitized in Tropicos[®] (http://www.tropicos.org/) and the vouchers are deposited at multiple herbaria (LPB, MO, MA, USZ, BOLV, HCB and CTES).

Taxonomy and dated phylogeny

The vouchers were identified by taxonomic specialists or by botanists with extensive experience in the Madidi region. In 2011 a comprehensive reconciliation process was undertaken to ensure that names were applied consistently across all plots. In the present analysis, the dataset includes only individuals that were identified to species, i.e., all trees that were identified only to genus or family, or were without a family, were excluded. In total, the dataset included 28,409 individuals representing a total of 806 named species in 101 families occurring in the 1 ha plots, and 112,494 individuals representing 1,739 named species in 141 families in 0.1 ha plots (families follow Stevens 2001 onwards)

A phylogeny resolved to the species level is currently not available for the species encountered in the study region. In its absence, I used a phylogeny that included all extant families in the Lignophyta (which includes angiosperms, gymnosperms, and ferns; Fig. S1) as terminal taxa, based on the topology of the Angiosperm Phylogeny Website (Stevens 2001 onwards) as well as phylogenetic information in Phylomatic version 3, R20120829 (Webb & Donoghue 2005). To create an ultrametric tree, I compiled information on node ages from the Angiosperm Phylogeny Website (Stevens 2001 onwards). Divergence ages were obtained for 74% of the nodes in the Lignophyta family-level phylogeny, either as a point estimate or range estimate (Table S1). Numerous nodes were dated more than once, so I conducted the analysis using three ultrametric trees to explore the effect of differences in divergence ages: a) a tree based on the minimum (youngest) divergence ages for each node, b) a tree based on the mean divergence age for each node, and c) a tree based on the maximum (oldest) divergence age for each node. For each of these three alternatives, I obtained pseudochronograms using the BLADJ function in Phylocom (version 4.2, Webb et al. 2011). BLADJ fixes nodes for which ages estimates are available, and evenly distributes other nodes between dated nodes (Webb et al. 2011).

Measuring rarity

For each species I estimated: local abundance, geographic range, and habitat breadth. These axes of rarity were estimated using data from both types of plots (1 ha and 0.1 ha plots) separately because the species pools included in each type of plot differ substantially.

Local abundance was calculated as the mean number of individuals in all plots where the species was found (mean abundance). For example if a species was found in 10 of 442 (0.1 ha) plots with 30 individuals in total, then local abundance would be 30/10 = 3 individuals/0.1ha.

Geographic range size was calculated as the extent of occurrence (EOO), a measure of the geographic area occupied by a species (Gaston 1994a, Gaston & Fuller 2009) that is thought to provide information about the degree to which risks from threatening factors are spread spatially across the species' geographical distribution (IUCN 2014). I estimated extent of

occurrence as the area encompassed by a convex polygon enclosing all occurrence points (following IUCN 2014). For each species, all georeferenced records of occurrence in the Neotropics were downloaded from Tropicos[®] (<u>http://tropicos.org/</u>). Before calculating EOO, I excluded records showing conflict between the geographic coordinates of the specimen and the description of the collecting locality in terms of administrative units at the level of country.

Habitat breadth was quantified as the number of habitats where a species was known to occur. Habitats were defined as vegetation types in the "Mapa de vegetación de Bolivia" (Navarro 2002) (Fig. S2). These vegetation types were delineated according to bioclimatic, geological, geomorphological, and edaphic features, as well as aspects of the vegetation that emphasize the presence of endemic and dominant species (Navarro 2002).

Because abundance, geographic range size, and habitat breadth showed distributions with markedly positive-skew, they were log-transformed for analysis.

Measuring phylogenetic patterns of rarity

I used three approaches to describe phylogenetic patterns (hierarchical variance partitioning across taxonomic levels, Blomberg's K statistic, and disparity trough time) in the axes of rarity (local abundance, geographical range size, and habitat breadth) across the regional species pool in Madidi. The first approach was based on hierarchical taxonomic levels, and did not require a dated phylogenetic tree. In contrast, the other two approaches did require a dated phylogenetic tree. As explained above, the phylogenetic tree available for these analyses was only resolved to the family level, while the rarity variables were at the species level. Thus, for the analyses based on phylogenetic trees, I randomly chose one species per family and, based on that sample, I gauged phylogenetic patterns of rarity. This random selection procedure was repeated 1,000 times to provide a distribution of parameter estimates obtained from different samples of species, which therefore did not depend on the particular species sampled. The estimates based on dated phylogenetic trees quantify phylogenetic patterns in rarity among species that belong to different plant families, and not patterns among species that belong to the same plant family. In contrast, the first approach based on hierarchical taxonomic levels does quantify patterns of rarity among species within and across plant families.

Using the first approach, I estimated variation in each axis of rarity among species within genera, genera within families, families within orders, orders within superorders and superorders within subclasses. The taxonomic hierarchy was based on the Tropicos® database (http://tropicos.org/) and Stevens (2001 onwards, http://www.mobot.org/MOBOT/research/APweb/). This analysis was based on a linear mixed effects model, with nested random effects representing hierarchical taxonomic levels and for which within-group errors are allowed to be correlated and/or have unequal variances. I compared the observed variation within hierarchical taxonomic levels to expected values according to a "tip randomization" or "white noise" null model (Kozak & Wiens2010) that randomly assigns species across the taxonomic hierarchy and, therefore, eliminates any phylogenetic signal that may exist. I calculated the 95% confidence intervals for expected variation within each hierarchical taxonomic level as the range between the 2.5 and 97.5 percentiles of 1,000 iterations of the null model and examined whether observed values fell within these confidence intervals.

The second approach used Blomberg's K statistic, which is the ratio of the mean squared error of the tip data, measured from the phylogenetic mean (i.e., the estimated trait value at the root node), divided by the mean squared error of the data calculated using the variance-covariance matrix derived from the tree (Blomberg et al. 2003). When the tree

accurately describes the variance-covariance pattern observed in the data, the value of K will be relatively large; otherwise the value of K will be relatively small. Observed K values are often scaled by the expected K value under a Brownian model of evolution, so that K < 1 implies that relatives resemble each other less than expected under Brownian motion evolution, and K > 1 implies that relatives are more similar than expected under a Brownian motion model (Blomberg et al. 2003). I compared phylogenetic patterns of rarity, as described by Blomberg's K statistic, against 1,000 iterations of each of two null models. Here, I used an analysis of variance followed by a Dunnet-Tukey test designed to examine differences among groups with no assumption of equal population variances (Dunnett 1980).

The third approach for describing phylogenetic patterns in the three axes of rarity is a disparity through time analysis (Harmon et al. 2003). For any given clade, disparity is the average Euclidian distance in trait space between pairs of species. The disparity of each clade defined by a node in the phylogeny is standardized by dividing the value by the disparity across the whole phylogeny. These standardized disparity values are known as relative disparity (Harmon et al. 2003). For every node in the phylogeny, I calculated the mean relative disparity as the average relative disparity across all clades in the whole tree originated at that node or earlier. Mean relative disparity values below one imply that clades contain relatively little of the variation present across the phylogeny as a whole and, consequently most variation is found between clades (rather than within clades). Conversely, values >1 imply that most of the total variation across the phylogeny is contained within clades. I compared observed values of disparity through time to expected values derived from 1,000 iterations of each of two null models: tip randomization and the Brownian motion model of evolution. I estimated 95% confidence intervals for mean relative disparity at each node of the phylogeny, defined as the range of values between the 2.5 and 97.5 percentiles.

All analyses were performed in R version 3.0.2 (R Development Core Team, 2013), using packages, "Ime" (Pinheiro & Bates 2000), "ape" (Paradis 2004), "picante" (Kembel et al. 2013), "geiger" (Harmon et al. 2008), and "DTK" (Matthew 2009).

RESULTS

Partitioning of variation in rarity across taxonomic levels to a limited extent supported, the hypothesis that the three axes of rarity exhibit phylogenetic signal. For both data sets (0.1 ha and 1.0 ha plots) most variance in each of the three axes of rarity was concentrated among species within genera, ranging between 65 and 80% (Fig. 3). Variation in rarity associated with all other taxonomic levels was <20%. Nonetheless, observed variation among species within genera was significantly less than expected from the tip randomization null model for the three axes of rarity; except for habitat breadth in the 1.0 ha plot data set (Fig. 3d). Accordingly, observed variations in rarity associated with higher taxonomic levels, most notably genus and family were higher than expected. Thus, overall, species belonging to the same genus were more similar to each other in each of the three axes of rarity than expected by chance.

The other two approaches to measuring phylogenetic patterns of rarity focused on species belonging to different plant families (and are therefore blind to patterns among species within the same plant families), revealed little or no phylogenetic signal. Observed values of Blomberg's K in both data sets (0.1 ha and 1.0 ha plots) were usually closer to the values generated by the tip randomization null model than to the Brownian model of evolution (Fig. 4, Fig. S3-S5). Some values of Blomberg's K were indistinguishable from those generated by the tip randomization null model (Fig. 4a, 4d, 4e and 4f) although they were often somewhat higher (Fig. 4b, 4c), suggesting weak phylogenetic signal. This weak

phylogenetic signal was particularly evident in habitat breadth for the 0.1 ha plots (Fig. 4c) and abundance for the 1.0 ha plots (Fig. 4b). The observed values of Blomberg's K for local abundance, geographic range size and habitat breadth were lower than the respective values under a Brownian model of evolution (Fig. 4).

Observed mean relative disparities for all three axes of rarity exceeded the corresponding values generated by the Brownian model of evolution, at least towards the terminal nodes of the phylogeny (Fig. 5). These terminal nodes therefore contained more of the variation in the three axes of rarity than would be expected from a Brownian model of evolution; this is consistent with the results from the Blomberg's K values. However, relative disparities across the basal nodes of the phylogeny were often similar to those generated by the Brownian model of evolution, except in the case of local abundance for 1.0 ha plots (Fig. 5b).

In sharp contrast to the Brownian model of evolution, the tip randomization null model produced values of mean relative disparities that frequently mimicked observed values across most nodes of the phylogeny (Fig. 5, Fig. S6-S11). The most obvious exception was local abundance for 1.0 ha plots with higher than expected mean relative disparities in early nodes of the phylogeny (Fig. 5b). These results suggest that a tip randomization null model is a reasonable description of disparity through time, and that the three axes of rarity display little if any phylogenetic signal. Indeed, in contrast to the results based on analysis of Blomberg's K values, it seems that analysis of disparity through time does not reveal evidence of even weak phylogenetic signal.

Both analyses showed that the three axes of rarity do not exhibit phylogenetic conservatism in the sense of showing stronger phylogenetic trait clustering than expected from a Brownian motion model of evolution (Fig. S3-S11).

DISCUSSION

Several authors claim that local abundance, habitat breadth, and geographic range describe important aspects of the distribution and abundance of species linked to extinction risk (Biesmeijer et al. 2006, Caughley & Gunn 1996, Colles et al. 2009, Gaston 2003, Lande 1993, McKinney 1997). Hence, there is considerable interest in understanding phylogenetic patterns of these axes of rarity because they provide insights into phylogenetic patterns of extinction risk and the related issue of clade selection (Jablonski 1987, Waldron 2007). Here, I used data on rarity for a regional species pool of tropical woody plants to test for phylogenetic signal, defined as the tendency of related species to resemble each other more than species drawn at random from the same phylogenetic tree (Blomberg et al 2003, Münkemüller et al 2012), and phylogenetic conservatism, defined as stronger phylogenetic trait clustering than expected from a Brownian motion model of evolution (Losos 2008, 2011). My analyses showed that local abundance, habitat breadth and geographic range size of woody plants in the Madidi Region display phylogenetic signal, but only among species belonging to the same genus. However, at deeper phylogenetic levels these axes of rarity exhibit little or no phylogenetic signal and do not display phylogenetic conservatism. At these deeper levels, phylogenetic patterns of rarity were reasonably well described by a null model that randomly assigns species values across the phylogeny (the tip randomization null model). I will, in the following, expand on possible caveats of the analysis and explore implications of the findings, in particular implications of our perception of the phylogenetic patterns of rarity, our understanding of the processes that generate those patterns, and the future of Andean floras.

A potential criticism of the analysis could be the exclusion of morphospecies (species without a specific epithet), which most likely are local endemics of limited distribution, and the exclusion of unidentified individuals. In total, 666 morphospecies (12,223 individuals) and 5,775 unidentified individuals for the 0.1 ha plots, in addition to 212 morphospecies (3,025 individuals) and 246 unidentified individuals for the 1.0 plots, were removed. Including morphospecies and unidentified individuals might have given the analysis more accuracy. However, comparing the number of morphospecies removed to the species used in the analysis (1,757 and 813 species for 0.1 ha and 1.0 ha, respectively) and the individuals removed to the individuals used in the analysis (112,494 and 28,404 individuals for 0.1 ha and 1.0 ha respectively), suggests that the results would remain the same because for both data sets the individuals removed were approximately only 20 % of the total. Nonetheless, exclusion of the unidentified individuals might have influenced the abundance and habitat breadth of some species.

Null models are central to our perception of phylogenetic patterns of rarity. In particular, metrics that compare rarity across all species in a phylogeny (i.e., Blomberg's K) are gauged against values expected under a null model (Krasnov et al. 2011, Machac et al 2011). Likewise, metrics that compare rarity between sister species (e.g., intra-class correlation for sister species pairs) are also evaluated in the light of null models (Waldron 2007, Hunt et al. 2005). However, we are unaware of the use of null models in assessments of phylogenetic patterns of rarity based on nested analysis of variance across taxonomic levels. The nested analysis of variances showed that the three axes of rarity were most variable among species within genera (Fig. 3), a result similar to previous studies (Gaston 2003, Ricklefs 2010). Nonetheless, variation among species within genera was generally less than expected by the tip randomization null model, indicating some phylogenetic signal. According to the operational definitions adopted in this study, this phylogenetic signal in the axes of rarity is a necessary but insufficient condition to demonstrate phylogenetic conservatism (Losos 2008). To demonstrate phylogenetic conservatism the observed values of variation in rarity among species should be compared against what is expected from the Brownian model of evolution. This comparison is not possible at the moment due to incomplete phylogenetic knowledge, but it is a subject for future studies.

Although few studies describe phylogenetic patterns of local abundance, habitat breadth, or geographic range, the available information does suggest that the axes of rarity show marked phylogenetic signal, and perhaps even phylogenetic conservatism, across very ancient clades. For example, metazoans may tend to have smaller geographic ranges than protists (Fenchel 1993), and plants and insects may tend to have smaller geographic ranges than vertebrates (Gaston 1994b, Brown et al. 1996, Gaston et al. 1998). In contrast, at shallower phylogenetic levels phylogenetic signal in axes of rarity may often be weak or absent, as in the cases of birds in the order Anseriformes (Webb et al. 2001) and birds occurring in eastern North America deciduous and mixed forests (Ricklefs 2011). Nonetheless, fairly strong phylogenetic signal in rarity has been reported at these shallower phylogenetic levels, including habitat breadth across British Lepidoptera (Menken et al. 2009), and abundance and habitat breadth among Palaearctic and Nearctic parasitic fleas on small mammals (Krasnov et al. 2011). Finally, at the most terminal nodes of phylogenies, rarity might show phylogenetic signal between sister species (Jablonski 1987, Waldron 2007). In this context, the findings presented here describe phylogenetic patterns of rarity at intermediate phylogenetic scales, rather than very deep or very shallow levels. Although the most basal nodes of the phylogeny used in this analysis reach back more than 400 million years, the regional species pool of Madidi includes few species of non-Angiosperms and, thus, most of the rarity data are concentrated in lineages that diverged from each other no more than approximately 200 million years ago. The regional species pool analyzed here might include few sister species if plant speciation in the Andes is commonly broadly allopatric (e.g., Bell & Donoghue 2005, Moore & Donoghue 2007), potentially exceeding the extent of the Madidi study region.

Phylogenetic signal (or conservatism) in axes of rarity is often thought to follow from phylogenetic signal (or conservatism) in other biological variables such as body size, dispersal ability, habitat requirements and use, as well as life history traits (Gaston 2003, Menken et al. 2009, Krasnov et al. 2011). Among woody plants of the Madidi region, phylogenetic signal in the three axes of rarity was present among species within genera, but was weak or absent at deeper phylogenetic levels. This phylogenetic signal in rarity might be related to phylogenetic patterns in the habitats occupied by different clades in the Madidi region. Species turnover across the elevation gradient in Madidi reflects replacement of clades that diverged from each other more than 60–30 million years ago, often corresponding to the taxonomic level of family (Jiménez et al. in prep.). Elsewhere in the Andes, plant families also exhibit high turnover with respect to elevation (Gentry 1995, Loza et al. 2010), and diversification of clades at or below the family level seems to occur often within relatively narrow elevation bands in the Andes (e.g., Von Hagen & Kadereit 2001, Bell & Donoghue 2005, Moore & Donoghue 2007). Thus, Andean plants, including woody plants in Madidi, seem to show substantial phylogenetic signal (perhaps even conservatism) in the environments they occupy, below the taxonomic level of family. Species composition is also determined by pH levels, phosphorus, calcium, and magnesium available in the soil (Loza 2008). To the extent that the environment occupied by a species reflects habitat requirements, and given that habitat requirements are thought to determine habitat breadth, local abundance, and geographic range size (Gaston 2003), phylogenetic signal in the three axes of rarity might result from phylogenetic signal in habitat requirements.

Beyond habitat requirements, rarity in tropical trees is sometimes thought to be largely determined by vulnerability to negative density-dependent effects of conspecifics (Comita et al. 2010) driven by host-specific natural enemies that compose the soil biota (Mangan et al. 2010). If these inter-specific interactions are indeed a major driver of rarity among woody plants in the Madidi region, then it would seem that species within genera would show phylogenetic signal in vulnerability to negative-density dependence imposed by pathogens, despite the fact that these interactions could potentially evolve rapidly and thus erase any phylogenetic signal (Ricklefs 2004, 2010, 2011). However, there is some evidence that vulnerability to pathogens attacking plant leaves show phylogenetic signal across tropical tree species (Gilbert & Webb 2007). Future studies designed to critically examine the above hypothesis on the phylogenetic patterns of rarity would be enhanced by the addition of evidence for specialization in both pathogenic and mutualistic soil fungi.

Rarity has been associated with differential persistence of species during times of background levels of extinction as well as during mass extinction events (Jablonski 1986, 2008, Colles et al. 2008, Harnik et al. 2012). The phylogenetic signal in the three axes of rarity described here among species within genera (Fig. 3) has potentially important implications for our understanding of the biotic impacts of ongoing climate change on Andean floras, and for biodiversity conservation plans. My study region has experienced no recent spatially coherent temporal trends in precipitation (Vuille et al. 2003), but temperature has increased by 0.2–0.3 °C per decade during the last 30 years, and these rates of increase are positively related to elevation (Vuille & Bradley 2000, Ruiz et al. 2012). In the future, this trend may result in the disappearance of modern climates at high altitudes in the study region and,

more generally, in the tropical Andes (Williams et al. 2007). Species responses to this type of temporal climate trend are often classified into three broad modes (Jackson & Overpeck 2000, Parmesan 2006, Aitken et al. 2008): 1) the geographic distribution of a species does not change because the species tolerates the climatic change through either phenotypic plasticity or evolutionary change; 2) the geographic distribution of a species changes as the species tracks the geographic shift of its climatic environment; 3) extinction.

Many ecologists believe that species with small population sizes, narrow habitat breadths, and restricted geographic distributions are more likely to respond in the third way, i.e., becoming extinct, than species with larger populations and broader habitat breadths and geographic ranges (Bush et al. 2004, Aitken et al. 2008, Lenoir et al. 2010, Angert et al. 2011). If that were the case, then my results showing phylogentic signal in rarity would suggest that extinction risk from climate change is phylogenetically clustered across the species pool of Madidi trees. Extinction risk would be unusually high for species in particular genera, so that the amount of evolutionary history under threat is higher than would be expected by chance (Jones et al. 2005). Ongoing work in Madidi, aimed to examining responses of tree species to ongoing climate change using re-census of the 1.0 ha plots used here, will determine if rarity helps to predict which species are more at risk of extinction from climate change, and may provide a basis for distributing limited resources for the conservation of biodiversity in a fashion that maximizes the number of species protected.

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Figure 1: Tip randomization null model and Brownian motion null model showing the direction of phylogenetic clustering and the places where is expected to have phylogenetic signal and conservatism



Figure 2: Geographic distributions of plots. A. Map of South America with Bolivia in gray B. Map of Bolivia with plots located in the Madidi region. C. Location of 0.1-ha (white circles) and 1-ha (dark triangles) plots across the elevation gradient in Madidi.



Figure 3: Percentage of variation explained at different taxonomic levels. The blue circles are the observed values and the boxplots are the distribution for the tip randomization null model. The (-) and (+) symbols represent whether observed values fall in the area of 2.5 and 97.5 percentile. a) Local Abundance 0.1 ha plot, b) Local abundance 1.0 ha plot, c) Habitat breadth 0.1 ha plot, d) Habitat breadth 1.0 ha plot, e) Geographic range size 0.1 ha plot and f) Geographic range size 1.0 ha plot. Variance components are estimated using a linear mixed effect model. The level of significance is given by (*) p< 0.05, (**) p< 0.005 and (***) p< 0.001



Figure 4: Boxplots of Blomberg's K values for the two null models (Tip randomization and Brownian motion) and for the observed values (Observed). In the middle of the boxplot is the median of the distribution and the projecting bars show the minimum and maximum values. The horizontal line at the bottom show whether the observed distribution of Blomberg's K differ from the two null models according to an analysis of variance (p< 0.05). a) Local Abundance 0.1 ha plot, b) Local Abundance 1.0 ha plot, c) Habitat breadth 0.1 ha plot, d) Habitat breadth 1.0 ha plot, e) Geographic range size 0.1 ha plot and f) Geographic range size 1.0 ha plot.



Figure 5: Relative disparity plots for the observed values and the two null models (tip randomization and Brownian model of evolution). The plots show the distribution of the 95% of the confidence interval of the data. The "y" axes are the evolutionary time in million years. The left side is the root of the phylogeny. a) Local Abundance 0.1 ha plot, b) Local Abundance 1.0 ha plot, c) Habitat breadth 0.1 ha plot, d) Habitat breadth 1.0 ha plot, e) Geographic range size 0.1 ha plot and f) Geographic range size 1.0 ha plot.

APPENDIX :SUPPORTING FIGURES

Figure S1: Phylogenetic tree of the Lignophyta clade used in the analysis is based on the topology of the Angiosperm Phylogeny Website (Stevens (2001 onwards). An * indicate families found in the 0.1 ha plots and ** indicate families found in 1.0 ha plots. The node numbers correspond to those given in appendix 2.




































Figure S2: A. Map of South America with Bolivia in gray. B Map of Bolivia with the protected areas Madidi, Apolobamba, and PilonLajas in white. C Map of the plots distribution in the Madidi Region of Bolivia on the vegetation map by Navarro (2002), the numbers indicate the type of vegetation: "1" *Bosques yungueños montanos pluviales,* "2" *Bosque yungueño montano inferior pluvial de los Yungas de Apolobamba,* "3" *Bosque yungueño montano superior pluvial de los Yungas de Apolobamba,* "4" *Bosque yungueño montano superior pluvial de los Yungas de Apolobamba,* "4" *Bosque yungueño montano superior pluviestacional de los Yungas de Muñecas,* "5" *Bosque yungueño inferior pluviestacional de los Yungas de Muñecas,* "6" *Bosque yungueño altoandino de Polylepis,* "7" *Bosque yungueño montano superior húmedo de los Yungas de Coroico,* "8" *Bosque siempre verde subandino del suroeste de la Amazonia,* "9" *Bosques siempreverdes estacionales yungueños basimontanos,* "10" *Bosque húmedo estacional basimontano de los Yungas,* "11" *Bosque húmedo estacional basimontano de los Yungas de Apolobamba,* "12" *Bosque semideciduo basimontano superior de los Yungas de La Paz,* "13" *Bosque semideciduo basimontano superior de los Yungas de Munecas,* "14" *Bosque yungueño.*





Figure S3: Boxplots of Blomberg's K values for abundance (log-transformed data) for the two null models (Tip and Brownian) and for the observed values (Observed). The horizontal line at the bottom shows whether the observed distribution of Blombergs' K differ from the two null models according to an analysis of variance (p< 0.05). The first row shows values for 1.0 ha plots and the second row for the 0.1 ha plots. From left to right, the first column is based on a tree of young ages, the second a tree of central ages and the third a tree of the old ages. The middle of the boxplot is the median of the distributions and the projecting bars show the minimum and maximum values.



Figure S4: Boxplots of Blomberg's K values for habitat breadth (log-transformed data) for the two null models (Tip and Brownian) and for the observed values (Observed). The horizontal line at the bottom shows whether the observed distribution of Blombergs' K differ from the two null models according to an analysis of variance (p< 0.05). The first row shows values for 1.0 ha plots and the second row for the 0.1 ha plots. From left to right, the first column is based on a tree of young ages, the second a tree of central ages and the third a tree of the old ages. The middle of the boxplot is the median of the distributions and the projecting bars show the minimum and maximum values.



Figure S5: Boxplots of Blomberg's K values for geographic range size (log-transformed data) for the two null models (Tip and Brownian) and for the observed values (Observed). The horizontal line at the bottom shows whether the observed distribution of Blombergs' K differ from the two null models according to an analysis of variance (p< 0.05). The first row shows values for 1.0 ha plots and the second row for the 0.1 ha plots. From left to right, the first column is based on a tree of young ages, the second a tree of central ages and the third a tree of the old ages. The middle of the boxplot is the median of the distributions and the projecting bars show the minimum and maximum values.



Figure S6: Relative disparity plots for abundance in 0.1 ha plots (log-transformed data) compared with the two null models (tip randomization and Brownian model of evolution). Relative disparity plot begin in the left side that is the root of the phylogeny and continue until all the extant taxa. The "y" axis is the evolutionary time in million years. The first row shows the distribution of the 95% of the confidence interval of the data and the second row shows the mean of average sublclade disparity for each node in the phylogeny. From left to right, the first column is based on a tree of young ages, the second a tree of central ages and the third a tree of the old ages.



Figure S7: Relative disparity plots for habitat breadth in 0.1 ha plots (log-transformed data) compared with the two null models (tip randomization and Brownian model of evolution). Relative disparity plot begin in the left side that is the root of the phylogeny and continue until all the extant taxa. The "y" axis is the evolutionary time in million years. The first row shows the distribution of the 95% of the confidence interval of the data and the second row shows the mean of average sublclade disparity for each node in the phylogeny. From left to right, the first column is based on a tree of young ages, the second a tree of central ages and the third a tree of the old ages.



Figure S8: Relative disparity plots for geographic range size in 0.1 ha plots (log-transformed data) compared with the two null models (tip randomization and Brownian model of evolution). Relative disparity plot begin in the left side that is the root of the phylogeny and continue until all the extant taxa. The "y" axis is the evolutionary time in million years. The first row shows the distribution of the 95% of the confidence interval of the data and the second row shows the mean of average sublclade disparity for each node in the phylogeny. From left to right, the first column is based on a tree of young ages, the second a tree of central ages and the third a tree of the old ages.



Figure S9: Relative disparity plots for abundance in 1.0 ha plots (log-transformed data) compared with the two null models (tip randomization and Brownian model of evolution). Relative disparity plot begin in the left side that is the root of the phylogeny and continue until all the extant taxa. The "y" axis is the evolutionary time in million years. The first row shows the distribution of the 95% of the confidence interval of the data and the second row shows the mean of average sublclade disparity for each node in the phylogeny. From left to right, the first column is based on a tree of young ages, the second a tree of central ages and the third a tree of the old ages.



Figure S10: Relative disparity plots for habitat breadth in 1.0 ha plots (log-transformed data) compared with the two null models (tip randomization and Brownian model of evolution). Relative disparity plot begin in the left side that is the root of the phylogeny and continue until all the extant taxa. The "y" axis is the evolutionary time in million years. The first row shows the distribution of the 95% of the confidence interval of the data and the second row shows the mean of average sublclade disparity for each node in the phylogeny. From left to right, the first column is based on a tree of young ages, the second a tree of central ages and the third a tree of the old ages.



Figure S11: Relative disparity plots for geographic range size in 1.0 ha plots (log-transformed data) compared with the two null models (tip randomization and Brownian model of evolution). Relative disparity plot begin in the left side that is the root of the phylogeny and continue until all the extant taxa. The "y" axis is the evolutionary time in million years. The first row shows the distribution of the 95% of the confidence interval of the data and the second row shows the mean of average sublclade disparity for each node in the phylogeny. From left to right, the first column is based on a tree of young ages, the second a tree of central ages and the third a tree of the old ages.

APPENDIX: SUPPORTING TABLE

Table S1: Estimated ages for World Family Phylogenetic Tree (old, central and young ages) that come from different resources (references S1). (Angiosperm Phylogeny Website (Stevens (2001 onwards))

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
1	400	400	400	Theißen et al. 2001
1	452	434	410	Clarke et al. 2011
1	401	390.5	380	Leebens-Mack et al. 2005
1	422	408	404	Magallón et al. 2013
2	348	316.5	285	Becker et al. 2000
2	368	351	330	Clarke et al. 2011
2	351	332.05	324.3	Magallón et al. 2013
2	356	327	296	Smith et al. 2010
2	366	330	301	Smith et al. 2010
2	300	300	300	Theißen et al. 2001
2	457	385	313	Zimmer et al. 2007
4	231	197	169	Clarke et al. 2011
4	229	229	229	Magallón and Castillo 2009
4	127	127	127	Magallón and Castillo 2009
4	183.4	183.4	183.4	Magallón et al. 2013
4	162	155	145	Moore et al. 2010
4	211	179	158	Zhang et al. 2012
4	180	156	132	Soltis et al. 2008
4	179	162	153	Wikström et al. 2001
5	187	173	160	Bell et al. 2010
5	150	144	138	Bell et al. 2010
5	208	177	152	Clarke et al. 2011
5	235.5	235.5	235.5	Magallón and Castillo 2009
5	129.7	129.7	129.7	Magallón and Castillo 2009
5	170.4	170.4	170.4	Magallón et al. 2013
5	151	144	138	Moore et al. 2010
5	185	161	146	Zhang et al. 2012
5	174	150.5	127	Soltis et al. 2008
5	172	156	147	Wikström et al. 2001
8	138.4	138.4	138.4	Xue et al. 2012
8	168	156	146	Bell et al. 2010
8	142	136	130	Bell et al. 2010
8	201.4	201.4	201.4	Magallón and Castillo 2009
8	128	128	128	Magallón and Castillo 2009
8	132.5	132.5	132.5	Magallón et al. 2013

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
8	140	132	125	Moore et al. 2010
8	160	141.5	123	Soltis et al. 2008
8	162	147.5	140	Wikström et al. 2001
9	122	121	120	Anderson et al. 2005
9	145	131	129	Bell et al. 2010
9	125	125	125	Magallón and Castillo 2009
9	129.4	124.2	120.2	Magallón et al. 2013
9	131.1	124.8	118.5	Moore et al. 2007
9	147	137	128	Smith et al. 2010
9	172	153	138	Smith et al. 2010
9	152	131	110	Soltis et al. 2008
9	153	139	131	Wikström et al. 2001
9	127	126	123	Zhang et al. 2012
10	143	129.5	126	Bell et al. 2010
10	121.5	121.5	121.5	Magallón et al. 2013
10	126.4	121.4	110.2	Xue et al. 2012
11	122.7	122.7	122.7	Magallón and Castillo 2009
11	124.1	122.6	121.1	Vekemans et al. 2012
12	119	119	119	Anderson et al. 2005
12	121.5	121.5	121.5	Magallón and Castillo 2009
12	123	122.4	121.4	Vekemans et al. 2012
12	142	130.5	124	Wikström et al. 2004
12	115.3	115.3	115.3	Xue et al. 2012
13	116	115.5	115	Anderson et al. 2005
13	139	124	119	Bell et al. 2010
13	127	117	117	Bell et al. 2010
13	114.4	114.4	114.4	Magallón and Castillo 2009
13	115.1	115.1	115.1	Magallón and Castillo 2009
13	118.3	111.8	111.7	Magallón et al. 2013
13	113	110	105	Moore et al. 2010
13	180	180	180	Schneider et al. 2004
13	132	119	89	Soltis et al. 2008
13	131	121	116	Wikström et al. 2003
13	116	112	107	Zhang et al. 2012
14	112	108	103	Moore et al. 2010
15	107	103	98	Moore et al. 2010
16	112.5	112.5	112.5	Magallón and Castillo 2009
16	113.1	113.1	113.1	Magallón and Castillo 2009
16	112.5	112.5	112.5	Magallón and Castillo 2009
16	113.1	113.1	113.1	Magallón and Castillo 2009

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
16	104	101	96	Moore et al. 2010
16	104	101	96	Moore et al. 2010
17	116	115	114	Anderson et al. 2005
17	115	115	115	Anderson et al. 2005
17	110.7	110.7	110.7	Magallón and Castillo 2009
17	111.3	111.3	111.3	Magallón and Castillo 2009
17	110.7	110.7	110.7	Magallón and Castillo 2009
17	111.3	111.3	111.3	Magallón and Castillo 2009
17	104	100	95	Moore et al. 2010
17	104	100	95	Moore et al. 2010
17	111	107.5	104	Wikström et al. 2001
17	107.5	107.5	107.5	Wikström et al. 2001
17	93.5	93.5	93.5	Xue et al. 2012
18	109	109	109	Anderson et al. 2005
18	122	111	106	Bell et al. 2010
18	128	128	128	Janssens et al. 2009
18	128	128	128	Bremer et al. 2004
18	106.35	106.35	106.35	Magallón and Castillo 2009
18	89	84	80	Moore et al. 2010
18	103	93	81	Zhang et al. 2012
18	135	135	135	Schneider et al. 2004
18	130	115	86	Soltis et al. 2008
18	122	112	107	Wikström et al. 2003
19	116	104.5	99	Bell et al. 2010
19	116	104.5	99	Bell et al. 2010
19	133.5	123	112.5	Janssens et al. 2009
19	133.5	118.5	103.5	Janssens et al. 2009
19	127	127	127	Bremer et al. 2004
19	127	127	127	Bremer et al. 2004
19	132	128	124	Lemaire et al. 2011
19	132	128	124	Lemaire et al. 2011
19	105.3	105.3	105.3	Magallón and Castillo 2009
19	105.3	105.3	105.3	Magallón and Castillo 2009
19	105.3	105.3	105.3	Magallón et al. 2013
19	105.3	105.3	105.3	Magallón et al. 2013
19	85	81	76	Moore et al. 2010
19	85	81	76	Moore et al. 2010
19	114	110	106	Wikström et al. 2001
19	11	11	11	Wikström et al. 2001
20	109	97	93	Bell et al. 2010

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
20	123	123	123	Bremer et al. 2004
20	125	114	101	Lemaire et al. 2011
20	118	98	87	Lemaire et al. 2011
20	96	83	68	Zhang et al. 2012
20	124	106	85	Soltis et al. 2008
20	117	107	102	Wikström et al. 2001
21	119	119	119	Bremer et al. 2004
21	121.3	112	102.7	Janssens et al. 2009
21	96.85	96.85	96.85	Magallón and Castillo 2009
21	80	76	71	Moore et al. 2010
21	112	103.5	100	Wikström et al. 2001
22	96	86.5	83	Bell et al. 2010
22	102	90.5	86	Bell et al. 2010
22	108	108	108	Bremer et al. 2004
22	97	76	56	Lemaire et al. 2011
22	81	81	81	Magallón and Castillo 2009
22	57.6	57.6	57.6	Xue et al. 2012
24	93	80.5	72	Bell et al. 2010
24	77	77	77	Magallón and Castillo 2009
25	97	97	97	Bremer et al. 2004
26	78	69.5	69	Bell et al. 2010
26	106.9	95	83.1	Janssens et al. 2009
26	62.8	62.8	62.8	Magallón and Castillo 2009
27	87	87	87	Bremer et al. 2004
28	72	64	61	Bell et al. 2010
28	78	78	78	Bremer et al. 2004
28	60	50.5	45	Wikström et al. 2001
29	76	76	76	Bremer et al. 2004
30	75	75	75	Bremer et al. 2004
32	70	60.5	54	Bell et al. 2010
35	70	70	70	Bremer et al. 2004
39	58	42	38	Bell et al. 2010
39	64	64	64	Bremer et al. 2004
40	108.6	67.4	46.7	Nylinder et al. 2012
43	85	73.5	71	Bell et al. 2010
43	100	100	100	Bremer et al. 2004
43	93	71	50	Lemaire et al. 2011
43	73	73	73	Magallón and Castillo 2009
43	82	77	76	Wikström et al. 2001
44	74	61.5	59	Bell et al. 2010

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
44	69.7	62.1	54.4	Paape et al. 2008
44	71	66	65	Wikström et al. 2001
45	79	63	61	Bell et al. 2010
45	92	92	92	Bremer et al. 2004
45	71	65.5	65	Wikström et al. 2001
47	104.7	90.4	76.5	Bremer and Eriksson 2009
47	108	93	78	Bremer et al. 2004
47	89.2	79	68.8	Janssens et al. 2009
47	86	73	60	Lemaire et al. 2011
47	75	52	35	Lemaire et al. 2011
47	75	70	68	Wikström et al. 2001
47	68	62.5	61	Wikström et al. 2001
48	69	58	57	Bell et al. 2010
49	61	55.5	54	Wikström et al. 2001
50	57	49	45	Wikström et al. 2001
51	96	73.5	70	Bell et al. 2010
51	91	63	31	Lemaire et al. 2011
51	89	82	80	Wikström et al. 2001
52	115	104	95	Beaulieu et al. 2013
52	115	104	95	Beaulieu et al. 2013
52	109	97	100	Bell et al. 2010
52	109	97	100	Bell et al. 2010
52	121	121	121	Bremer et al. 2004
52	121	121	121	Bremer et al. 2004
52	122.8	113	103.2	Janssens et al. 2009
52	122.8	113.8	104.8	Janssens et al. 2009
52	99.5	99.5	99.5	Magallón and Castillo 2009
52	99.5	99.5	99.5	Magallón and Castillo 2009
52	81	75	71	Moore et al. 2010
52	81	75	71	Moore et al. 2010
52	112	103	99	Wikström et al. 2001
52	112	103	99	Wikström et al. 2001
53	109	99	89	Beaulieu et al. 2013
53	94	81.5	77	Bell et al. 2010
53	114	114	114	Bremer et al. 2004
53	95	95	95	Magallón and Castillo 2009
53	64.2	64.2	64.2	Xue et al. 2012
53	89	74	52	Zhang et al. 2012
54	106	96	85	Beaulieu et al. 2013

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
54	96	80.5	74	Bell et al. 2010
54	96	80.5	74	Bell et al. 2010
55	93	93	93	Beaulieu et al. 2013
55	93	93	93	Beaulieu et al. 2013
55	93.75	93.75	93.75	Magallón and Castillo 2009
55	93.75	93.75	93.75	Magallón and Castillo 2009
56	101	91	79	Beaulieu et al. 2013
56	101	91	79	Beaulieu et al. 2013
56	113	113	113	Bremer et al. 2004
56	113	113	113	Bremer et al. 2004
56	105	84	58	Lemaire et al. 2011
56	105	84	58	Lemaire et al. 2011
56	92	92	92	Magallón and Castillo 2009
56	92	92	92	Magallón and Castillo 2009
57	111	111	111	Bremer et al. 2004
57	111	111	111	Bremer et al. 2004
58	94	80	87	Beaulieu et al. 2013
58	74	60	57	Bell et al. 2010
58	111	106.5	102	Bell and Donoghue 2005
58	101	101	101	Bremer et al. 2004
58	90	62	32	Lemaire et al. 2011
58	82	68	45	Zhang et al. 2012
58	87	80	78	Wikström et al. 2001
60	95	84	71	Beaulieu et al. 2013
60	63	51	49	Bell et al. 2010
60	101.1	87	72.9	Janssens et al. 2009
60	84	84	84	Bremer et al. 2004
60	74.9	74.9	74.9	Magallón and Castillo 2009
60	74	66	63	Wikström et al. 2001
62	55	44	41	Bell et al. 2010
62	52	47	46	Wikström et al. 2001
63	48	36.5	35	Bell et al. 2010
63	49	43	41	Wikström et al. 2001
64	42	31	29	Bell et al. 2010
64	42	35.5	33	Wikström et al. 2001
65	110	110	110	Bremer et al. 2004
67	86	78.5	76	Wikström et al. 2001
69	79	68.5	67	Bell et al. 2010
69	88	80	76	Wikström et al. 2001
70	71	57.5	56	Bell et al. 2010

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
70	73	67.5	66	Wikström et al. 2001
71	68	62.5	62	Wikström et al. 2001
73	71	59.5	58	Bell et al. 2010
73	73	67	65	Wikström et al. 2001
74	50	40	40	Bell et al. 2010
74	80	64.5	49	Kim et al. 2005
74	43	42	44	Wikström et al. 2001
75	51	51	51	Bremer et al. 2004
75	49	45.5	42	Kim et al. 2005
76	101	93	87	Bell et al. 2010
76	113	113	113	Bremer et al. 2004
77	65	65	65	Beaulieu et al. 2013
77	72	53.5	51	Bell et al. 2010
77	73.9	62	50.1	Janssens et al. 2009
77	69	69	69	Manen et al. 2010
77	80	80	80	Martin 1977
78	66	66	66	Bremer et al. 2004
79	90	66.5	66	Bell et al. 2010
79	90	74	65	Wikström et al. 2001
80	103	101	99	Anderson et al. 2005
80	102	97	92	Bell et al. 2010
80	126.2	117	107.8	Janssens et al. 2009
80	114	114	114	Bremer et al. 2004
80	125	118	110	Lemaire et al. 2011
80	98.85	98.85	98.85	Magallón and Castillo 2009
80	126	113	85	Soltis et al. 2008
80	109	106	103	Sytsma etal.2006
80	97	88.5	85	Wikström et al. 2001
81	95	83.5	82	Bell et al. 2010
82	107	107	107	Bremer et al. 2004
83	103	103	103	Bremer et al. 2004
83	106	106	106	Bremer et al. 2004
84	68	55.5	51	Bell et al. 2010
84	89	89	89	Magallón et al. 1999
84	72	63	59	Wikström et al. 2001
86	89	89	89	Bremer et al. 2004
88	78	58.5	51	Bell et al. 2010
88	60	50	45	Wikström et al. 2001
89	100	100	100	Bremer et al. 2004
89	68	62	61	Wikström et al. 2001

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
92	90	90	90	Warren and Hawkins 2006
93	102	102	102	Bremer et al. 2004
94	77	62.5	61	Bell et al. 2010
95	66	50	49	Bell et al. 2010
95	58.9	58.9	58.9	Janssens et al. 2009
95	65	65	65	Bremer et al. 2004
95	56	56	56	Bremer et al. 2004
95	52	46	44	Wikström et al. 2001
96	64	64	64	Bremer et al. 2004
97	101	99	97	Anderson et al. 2005
97	112	112	112	Bremer et al. 2004
97	117.1	104	90.9	Janssens et al. 2009
97	123	106	92	Lemaire et al. 2011
97	101.55	101.55	101.55	Magallón and Castillo 2009
97	106	97.5	94	Wikström et al. 2001
99	90	90	90	Warren and Hawkins 2006
100	64	50	49	Bell et al. 2010
100	96	86.5	82	Wikström et al. 2001
101	102	100.5	99	Anderson et al. 2005
101	115	103	99	Bell et al. 2010
101	94.35	94.35	94.35	Magallón and Castillo 2009
101	90	86.5	83	Wikström et al. 2001
102	90	86.5	83	Wikström et al. 2001
103	102	90.5	88	Bell et al. 2010
103	72	69.5	67	Wikström et al. 2001
104	95	81.5	79	Bell et al. 2010
104	61	56.5	52	Wikström et al. 2001
106	47	43	39	Wikström et al. 2001
107	72	58	55	Bell et al. 2010
107	38	33.5	29	Wikström et al. 2001
108	94	67.2	46	Masson and Kadereit 2013
111	55	54	53	Arakaki et al. 2011
111	74	60.5	58	Bell et al. 2010
111	40	35	30	Wikström et al. 2001
114	47	37	27	Bell et al. 2010
115	28	24.5	21	Wikström et al. 2001
116	61.9	56.1	50.3	Christin et al. 2011
116	35	29.5	24	Wikström et al. 2001
117	33.7	18.8	6.7	Ocampo and Columbus 2010
120	26.6	14.3	5.1	Ocampo and Columbus 2010

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
121	35	35	35	Arakaki et al. 2011
121	33	22	21	Bell et al. 2010
121	26.5	13.9	4.9	Ocampo and Columbus 2010
121	18	14.5	11	Wikström et al. 2001
122	28.5	14.9	3.9	Ocampo and Columbus 2010
124	100	88.5	86	Bell et al. 2010
124	75	71	67	Wikström et al. 2001
125	90	75	72	Bell et al. 2010
126	65	60	55	Wikström et al. 2001
128	61	40.5	37	Bell et al. 2010
128	47	38	29	Wikström et al. 2001
130	72	58	58	Bell et al. 2010
130	125	107.85	110.9	Schuster et al. 2013
130	52	44.5	37	Wikström et al. 2001
131	43	36.5	30	Wikström et al. 2001
132	100	100	100	Forest et al. 2009
133	108	104.5	101	Anderson et al. 2005
134	99	96	91	Moore et al. 2010
136	115	95.5	91	Bell et al. 2010
136	90.6	90.6	90.6	Magallón and Castillo 2009
136	102	91	85	Wikström et al. 2001
137	106	85	82	Bell et al. 2010
137	85	74.5	69	Wikström et al. 2001
138	81	81	81	Vidal-Russell and Nickrent 2008
139	75	75	75	Vidal-Russell and Nickrent 2005, 2007
140	108	108	108	Anderson et al. 2005
140	135	123	117	Bell et al. 2010
140	114.5	114.5	114.5	Magallón and Castillo 2009
140	110.5	110.5	110.5	Magallón et al. 2013
140	111	108	103	Moore et al. 2010
140	125	116	111	Wikström et al. 2004
140	112	107	101	Zhang et al. 2012
141	123	123	123	Arakaki et al. 2011
141	132	125	118	Bell et al. 2010
141	105	101	97	Bell et al. 2010
141	112.6	112.6	112.6	Magallón and Castillo 2009
141	113.2	113.2	113.2	Magallón and Castillo 2009
141	108.7	108.7	108.7	Magallón et al. 2013
141	115	111	109	Wang et al. 2009

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
141	96	92	88	Wang et al. 2009
141	119	119	119	Wang et al. 2009
141	113	113	113	Wang et al. 2009
141	121	112.5	108	Wikström et al. 2001
141	97.6	97.6	97.6	Xue et al. 2012
143	77	77	77	Arakaki et al. 2011
143	114	106.5	103	Bell et al. 2010
143	114	108	102	Wang et al. 2009
143	97	91	85	Wang et al. 2009
143	104	98	95	Wikström et al. 2001
145	107	99	91	Bell et al. 2010
145	107	104	100	Moore et al. 2010
145	96	91.5	89	Wikström et al. 2001
145	32.2	32.2	32.2	Xue et al. 2012
146	110	105	100	Wang et al. 2009
146	94	89	84	Wang et al. 2009
147	110	103	96	Bell et al. 2010
147	107	103	99	Wang et al. 2009
147	92	88	84	Wang et al. 2009
147	109	109	109	Wang et al. 2009
147	102.4	102.4	102.4	Magallón and Castillo 2009
147	84	84	84	Wikström et al. 2001
148	85	79	78	Wang et al. 2009
149	78	63	61	Bell et al. 2010
149	86.7	86.7	86.7	Magallón and Castillo 2009
149	68	65.5	65	Wikström et al. 2001
150	64	46.5	43	Bell et al. 2010
150	55	50	48	Wikström et al. 2001
151	74	58.5	56	Bell et al. 2010
151	69	63	61	Schaefer et al. 2009
152	60	53.5	50	Wikström et al. 2001
153	15.8	15.8	15.8	Plana et al. 2004
153	73	73	73	Schaefer et al. 2009
154	95	85	75	Cook and Crisp 2005
155	68	54	55	Bell et al. 2010
155	93	88.5	88	Wang et al. 2009
155	93.5	93.5	93.5	Magallón and Castillo 2009
155	65	61	57	Wikström et al. 2001
156	50	39	37	Bell et al. 2010
156	47	46.5	46	Wikström et al. 2001

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
157	43	27	29	Bell et al. 2010
157	38	37	36	Wikström et al. 2001
159	36	27	27	Bell et al. 2010
159	36	35.5	35	Wikström et al. 2001
160	302	256.5	211	Forest et al. 2005
160	143	143	143	Grimm and Renner 2013
160	88	88	88	Grimm and Renner 2013
161	104	88.5	82	Bell et al. 2010
161	96	90.5	88	Wang et al. 2009
161	94	94	94	Magallón and Castillo 2009
161	79	76	73	Wikström et al. 2001
162	86	75.5	73	Bell et al. 2010
162	70	66	65	Wikström et al. 2001
163	81	70.5	69	Bell et al. 2010
163	67	63	62	Wikström et al. 2001
164	77	64	62	Bell et al. 2010
165	76	65.5	64	Bell et al. 2010
165	61	56	55	Wikström et al. 2001
166	65	55	54	Bell et al. 2010
166	52	45.5	42	Wikström et al. 2001
167	89	89	89	Zerega et al. 2005
168	90	87	84	Hengcheng Wang et al. 2009
168	75	72	69	Hengcheng Wang et al. 2009
168	83	77	74	Wikström et al. 2001
169	82	76.5	74	Wikström et al. 2004
170	71	67	66	Wikström et al. 2004
171	111	104	101	Bell et al. 2010
171	108	104	100	Wang et al. 2009
171	95	91	87	Wang et al. 2009
171	108	108	108	Wang et al. 2009
171	102	102	102	Magallón and Castillo 2009
171	90	81	70	Zhang et al. 2012
171	97	91.5	89	Wikström et al. 2001
172	109	96.5	91	Wang et al. 2009
172	112	112	112	Wang et al. 2009
172	94	89.5	88	Wikström et al. 2001
173	97	92.5	89	Bell et al. 2010
173	114	107.5	101	Davis et al. 2005
173	93	91	90	Wang et al. 2009
173	89.3	89.3	89.3	Magallón and Castillo 2009

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
173	84	79	77	Wikström et al. 2001
176	79	61.5	60	Bell et al. 2010
176	58	51.5	49	Wikström et al. 2001
177	113.8	113.8	113.8	Davis et al. 2005
179	104	94	92	Davis et al. 2005
179	95	89	87	Davis et al. 2005
181	73	52	45	Bell et al. 2011
181	57	49.5	45	Wikström et al. 2001
182	42	38	36	Bell et al. 2010
182	82	76	69	Davis et al. 2005
182	74	72	66	Davis et al. 2005
182	28	26	24	Wikström et al. 2001
185	85	85	85	Davis et al. 2005
187	113	99	85	Davis et al. 2005
188	83	70.5	70	Bell et al. 2010
188	106.2	99.6	95.5	Davis et al. 2005
188	94.9	90.2	88.5	Davis et al. 2005
188	62	58	57	Wikström et al. 2001
189	72	59	59	Bell et al. 2010
189	53	45.5	41	Wikström et al. 2001
190	66	50	48	Bell et al. 2010
190	43	40	37	Wikström et al. 2001
190	32	29	26	Wikström et al. 2001
194	89	81.5	79	Bell et al. 2011
194	72	67	65	Wikström et al. 2001
195	86	78.5	76	Bell et al. 2011
195	69	64.5	63	Wikström et al. 2001
196	105.7	105.7	105.7	Davis et al. 2005
197	66	61.5	60	Wikström et al. 2001
198	81	72.5	72	Bell et al. 2010
198	60	55	53	Wikström et al. 2001
199	74	70	69	Wikström et al. 2001
201	109.5	96.3	83.1	Bendiksby et al. 2010
203	114	108	105.8	Davis et al. 2005
203	101.9	97.1	95.6	Davis et al. 2005
203	111	105.5	100	Xue et al. 2012
204	111	105.5	100	Davis et al. 2005
205	105	91.5	89	Bell et al. 2010
206	78	61	59	Bell et al. 2010
206	74	65.5	62	Wang et al. 2009

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
206	90.5	90.5	90.5	Magallón and Castillo 2009
206	80	74.5	72	Wikström et al. 2001
208	64	49	46	Bell et al. 2010
208	70	65	64	Wikström et al. 2001
211	87	81	75	Wang et al. 2009
211	62	56	50	Wang et al. 2009
212	88	66.5	65	Bell et al. 2010
212	88	79	70	Wang et al. 2009
212	64	55	46	Wang et al. 2009
212	74	67	64	Wikström et al. 2001
213	104	102	97	Moore et al. 2010
213	113	95	76	Wang et al. 2009
213	83.5	83.5	83.5	Xue et al. 2012
214	86	86	86	Anderson et al. 2005
214	119	109	106	Bell et al. 2010
214	112	105	98	Wang et al. 2009
214	88	81	74	Wang et al. 2009
214	106.7	106.7	106.7	Magallón and Castillo 2009
214	91	85	77	Zhang et al. 2012
214	108	100.5	97	Wikström et al. 2001
216	102	96	90	Wang et al. 2009
216	80	76	72	Wang et al. 2009
216	98.25	98.25	98.25	Magallón and Castillo 2009
216	88	71	63	Zhang et al. 2012
217	104	89.5	86	Bell et al. 2010
218	59	59	59	Arakaki et al. 2011
218	94	89	85	Wang et al. 2009
218	80	74	68	Wang et al. 2009
218	96	96	96	Wang et al. 2009
218	92	92	92	Magallón and Castillo 2009
218	82	73	60	Zhang et al. 2012
219	94	81.5	82	Bell et al. 2010
219	76	73	70	Wang et al. 2009
219	63	69	57	Wang et al. 2009
219	65.9	65.9	65.9	Magallón and Castillo 2009
219	79	75	71	Wikström et al. 2001
220	56	37	34	Bell et al. 2010
220	61	57.5	54	Wikström et al. 2001
221	90	72.5	65	Bell et al. 2010
221	90.5	72	47.9	Couvreur et al. 2010

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
221	68	54	38	Zhang et al. 2012
221	72	70	68	Wikström et al. 2001
222	85	73	71	Bell et al. 2010
222	60	57	54	Wikström et al. 2001
223	54	53	52	Wikström et al. 2001
225	71	59.5	59	Bell et al. 2010
225	43	40	37	Wikström et al. 2001
228	68	56.5	54	Halletal.2010
228	42	37.5	33	Wikström et al. 2001
230	83.2	71.3	59.7	Beilstein et al. 2010
230	55	42.5	41	Bell et al. 2010
230	39.6	39.6	39.6	Magallón et al. 2013
230	41	41	41	Schranz and Mitchell-Olds 2006
230	31	27.5	24	Wikström et al. 2001
231	50	50	50	Al-Shehbaz et al .2006
231	76.5	64.5	54.4	Beilstein et al. 2010
231	43	32	31	Bell et al. 2010
231	41	41	41	Schranz and Mitchell-Olds 2006
231	23	20.5	18	Wikström et al. 2001
232	86	65.5	64	Bell et al. 2010
232	61	59.5	58	Wikström et al. 2001
233	80	78	76	Wang et al. 2009
233	76	74	72	Wang et al. 2009
233	75	69	67	Wikström et al. 2001
234	81	73	72	Bell et al. 2010
235	33.9	33.9	33.9	Magallón and Castillo 2009
237	56	42	42	Bell et al. 2010
237	41	39	37	Wikström et al. 2001
237	25	23	21	Wikström et al. 2001
238	88	88	88	Ducousso et al. 2004
238	30	28	26	Wikström et al. 2001
238	16	14	12	Wikström et al. 2001
241	66	63	60	Wang et al. 2009
241	73	71	69	Wang et al. 2009
241	117.4	117.4	117.4	Muellner et al. 2007
241	104.9	104.9	104.9	Muellner et al. 2007
241	90.5	90.5	90.5	Muellner et al. 2007
243	75	71	70	Bell et al. 2010
243	66	59.5	57	Wikström et al. 2001
244	93.6	93.6	93.6	Muellner et al. 2007

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
244	83.6	83.6	83.6	Muellner et al. 2007
244	74.1	74.1	74.1	Muellner et al. 2007
245	73	64	56	Bell et al. 2010
245	51	50	49	Bell et al. 2010
245	56	49	47	Wikström et al. 2001
246	70	64	57	Bell et al. 2010
246	54	51	49	Bell et al. 2010
246	70.7	70.7	70.7	Magallón and Castillo 2009
246	61	56	55	Wikström et al. 2001
247	51	46	45	Wikström et al. 2001
248	110	85.5	84	Bell et al. 2010
248	94	88	82	Wang et al. 2009
248	57	51	45	Wang et al. 2009
248	99	93	91	Wikström et al. 2001
249	101	77	75	Bell et al. 2010
249	86	81	76	Wikström et al. 2001
252	47	43.5	40	Anderson et al. 2005
252	48	31	34	Bell et al. 2010
252	76.3	76.3	76.3	Magallón and Castillo 2009
252	68	59	56	Wikström et al. 2001
254	40	26	24	Bell et al. 2010
254	49	211	42	Wikström et al. 2001
254	78.61	68.25	57.89	Zhu et al. 2006
255	86	86	86	Anderson et al. 2005
255	121	112	107	Bell et al. 2010
255	122	113	108	Bell et al. 2010
255	114	107	100	Wang et al. 2009
255	90	83	76	Wang et al. 2009
255	108	108	108	Magallón and Castillo 2009
255	99	91	77	Zhang et al. 2012
255	103	100	97	Wikström et al. 2001
255	78.9	78.9	78.9	Xue et al. 2012
256	99	94	89	Bell et al. 2010
256	89	81.5	78	Wang et al. 2009
256	90	90	90	Sytsma and Berger 2011.
256	98	92.5	85.7	Thornhill et al. 2012
256	83	77	75	Wikström et al. 2001
257	100	100	100	Sytsma et al. 2004
258	90	74.5	73	Bell et al. 2010
258	84	76.5	74	Wikström et al. 2001

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
259	84	84	84	Morley and Dick 2003
259	80	80	80	Renner et al. 2001
260	141	123.5	106	Conti et al. 2002
260	68	68	68	Morley and Dick 2003
260	78.6	68	57.4	Moyle 2004
260	21	21	21	Renner et al. 2001
260	152.6	94.25	58.9	Rutschmann et al. 2004
261	135.6	80.8	53	Rutschmann et al. 2004
262	100	96.5	93	Sytsma et al. 2004
263	80	64.5	63	Bell et al. 2010
263	94	94	94	Sytsma et al. 2004
263	71	62	57	Wikström et al. 2001
264	86	83	80	Anderson et al. 2005
264	106	90	87	Bell et al. 2010
264	109	103	97	Wang et al. 2009
264	74	68	62	Wang et al. 2009
264	50	50	50	Palazzesi et al. 2012
264	98	91	88	Wikström et al. 2001
265	94	72.5	70	Bell et al. 2010
265	42.8	31.4	20.2	Palazzesi et al. 2012
265	74	63	59	Wikström et al. 2001
267	32	19	8	Bell et al. 2010
267	17.7	11.2	5.9	Palazzesi et al. 2012
267	45	38	31	Wikström et al. 2001
268	90	87	84	Hermsen et al. 2006
268	103	93	83	Jian et al. 2006
268	103	98	94	Moore et al. 2010
269	102	102	102	Anderson et al. 2005
269	111	101.5	95	Bell et al. 2010
269	106.7	106.7	106.7	Magallón and Castillo 2009
269	116	101.5	92	Wikström et al. 2001, 2004
273	102	102	102	Forest et al. 2009
274	88	78.5	77	Bell et al. 2010
274	96	84.5	78	Wikström et al. 2001, 2004
275	88	78.5	77	Bell et al. 2010
275	82	73	69	Wikström et al. 2001
277	72	59	58	Bell et al. 2010
277	62	55.5	53	Wikström et al. 2001
278	63	49	48	Bell et al. 2010
278	51	45	43	Wikström et al. 2001

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
279	86	77	73	Wikström et al. 2001
280	81	81	81	Forest et al. 2009
282	90	72.5	55	Anderson et al. 2005
282	132	98	95	Bell et al. 2010
282	77	77	77	Magallón et al. 2013
282	123	113	108	Wikström et al. 2001
283	99	99	99	Anderson et al. 2005
283	103	100	98	Bell et al. 2010
283	111.5	111.5	111.5	Magallón and Castillo 2009
283	118.4	118.4	118.4	Magallón et al. 2013
283	130	119.5	113	Wikström et al. 2001
284	122.8	122.8	122.8	Magallón and Castillo 2009
284	123.6	123.6	123.6	Magallón and Castillo 2009
285	117	117	117	Anderson et al. 2005
285	131	116	110	Bell et al. 2010
285	105	105	105	Magallón et al. 2013
285	143	131	125	Wikström et al. 2001
285	122.8	109.3	75.2	Xue et al. 2012
286	119	114.5	110	Anderson et al. 2005
286	126.7	118.5	110.3	Barker et al. 2007
286	102	99.5	88	Bell et al. 2010
286	124	112.5	108	Wikström et al. 2001
287	121	117.5	114	Anderson et al. 2005
287	113.2	113.2	113.2	Magallón and Castillo 2009
287	146	133	126	Wikström et al. 2001
288	404	393	389.9	Magallón et al. 2013
288	100	100	100	Zhang et al. 2012
289	106	88.5	85	Bell et al. 2010
289	126	115.5	111	Wikström et al. 2001
290	116	111.5	107	Anderson et al. 2005
290	102	84	81	Bell et al. 2010
290	121	110.5	106	Wikström et al. 2001
291	116	110.5	105	Anderson et al. 2005
291	99	81	77	Bell et al. 2010
291	125	120.3	115.6	Jacques et al. 2011
291	65.9	65.9	65.9	Magallón et al. 2013
291	119	108	103	Wikström et al. 2001
292	104	97	90	Anderson et al. 2005
292	87	70.5	67	Bell et al. 2010
292	106	92	84	Wikström et al. 2001

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
293	157	133	130	Bell et al. 2010
293	134	134	134	Bremer 2000
293	176	160	154	Goremykin et al. 1997
293	135	133	131	Leebens-Mack et al.2005
293	177	177	177	Magallón and Castillo 2009
293	127	127	127	Magallón and Castillo 2009
293	154.4	138.9	134.1	Magallón et al. 2013
293	133.8	128.9	124	Moore et al. 2007
293	129	122	117	Moore et al. 2010
293	228.6	178.45	128.3	Nauheimer et al. 2012
293	220	200	180	Savard et al. 1994
293	167	156	139	Smith et al. 2010
293	191	164	141	Smith et al. 2010
293	125	125	125	Xue et al. 2012
293	142	124	108	Zhang et al. 2012
295	138	115.5	102	Bell et al. 2010
295	103	103	103	Bremer 2000
295	128	128	128	Janssen and Bremer 2004
295	147	147	147	Magallón and Castillo 2009
295	126	126	126	Magallón and Castillo 2009
295	122.6	122.6	122.6	Magallón et al. 2013
295	133	123	97	Merckx et al. 2008
295	124	117.5	111	Wikström et al. 2001
296	134	111.5	103	Bell et al. 2010
296	112	109.5	107	Wikström et al. 2001
297	115	90.5	83	Bell et al. 2010
297	107	107	107	Janssen and Bremer 2004
297	91	86	81	Wikström et al. 2001
298	47	47	47	Janssen and Bremer 2004
298	127	103.6	74	Chen et al. 2012
299	88	88	88	Janssen and Bremer 2004
300	98	98	98	Janssen and Bremer 2004
304	73	73	73	Janssen and Bremer 2004
305	27	27	27	Coyer et al. 2013
307	47	47	47	Janssen and Bremer 2004
307	100	100	100	Kato et al. 2003
309	127	110.5	105	Bell et al. 2010
309	83.1	83.1	83.1	Xue et al. 2012
311	117	117	117	Janssen and Bremer 2004
311	131	118	78	Merckx et al. 2008

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
312	123	97.5	86	Bell et al. 2010
312	125.5	125.5	125.5	Magallón and Castillo 2009
312	114.4	114.4	114.4	Magallón and Castillo 2009
312	112	96.5	87	Wikström et al. 2001
316	64.7	64.7	64.7	Chacón et al. 2012
316	91	91	91	Janssen and Bremer 2004
317	50.7	50.7	50.7	Chacón et al. 2012
318	104	77.5	63	Bell et al. 2010
318	64.7	64.7	64.7	Chacón et al. 2012
318	73	65.5	63	Wikström et al. 2001
320	114	98.5	92	Bell et al. 2010
320	119	119	119	Janssen and Bremer 2004
320	125	125	125	Magallón and Castillo 2009
320	112.6	112.6	112.6	Magallón and Castillo 2009
320	127	119	101	Merckx et al. 2008
320	101	96.5	92	Wikström et al. 2001
322	98	83	78	Bell et al. 2010
322	84	84	84	Eguiarte 1995
323	107	107	107	Janssen and Bremer 2004
324	92	77	72	Bell et al. 2010
325	84	70.5	67	Bell et al. 2010
325	100	100	100	Janssen and Bremer 2004
326	72	60.5	58	Bell et al. 2010
326	93	93	93	Janssen and Bremer 2004
326	61	57.5	54	Wikström et al. 2001
327	69	57	54	Bell et al. 2010
327	91	91	91	Janssen and Bremer 2004
327	58	54.5	51	Wikström et al. 2001
330	98	77	74	Bell et al. 2010
332	37	37	37	Bremer et al. 2000
332	67.3	67.3	67.3	Gustafsson et al. 2010
332	104	104	104	Janssen and Bremer 2004
332	85	85	85	Ramirez et al 2007
333	113	99.5	96	Bell et al. 2010
333	116	116	116	Bremer 2000
333	120	120	120	Janssen and Bremer 2004
333	128	128	128	Magallón and Castillo 2009
333	115	115	115	Magallón and Castillo 2009
333	83.4	83.4	83.4	Magallón et al. 2013
333	93	91.5	90	Mennes etal. 2013

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
333	122	116	94	Merckx et al. 2008
333	104	95	91	Wikström et al. 2001
333	104	95	91	Wikström et al. 2001
333	64.5	64.5	64.5	Xue et al. 2012
334	108	108	108	Bremer 2000
334	98.6	98.6	98.6	Givnish et al. 2000
334	89	89	89	Janssen and Bremer 2004
334	123	117	111	Magallón and Castillo 2009
334	105	94.5	84	Mennes etal. 2013
334	120	109	89	Merckx et al. 2008
334	91	85	83	Wikström et al. 2001
335	101	88	86	Bell et al. 2010
335	84	84	84	Bremer 2000
335	114	114	114	Janssen and Bremer 2004
335	158	158	158	Kress and Specht 2005
335	109.7	109.7	109.7	Magallón and Castillo 2009
335	99.9	99.9	99.9	Magallón and Castillo 2009
335	85	84	83	Mennes etal. 2013
335	114	92	83	Merckx et al. 2008
335	85	77	73	Wikström et al. 2001
336	91	73	70	Bell et al. 2010
336	110	110	110	Janssen and Bremer 2004
336	104	75	50	Merckx et al. 2008
336	75	68.5	66	Wikström et al. 2001
337	104	104	104	Janssen and Bremer 2004
339	79	79	79	Bremer et al. 2000
339	98	98	98	Janssen and Bremer 2004
340	89	86.5	84	Bell et al. 2010
340	62	62	62	Bremer 2000
340	88	88	88	Janssen and Bremer 2004
340	97	97	97	Kress and Specht 2005
340	110	108	106	Kress and Specht 2006
340	87	87	87	Magallón and Castillo 2009
340	79.5	79.5	79.5	Magallón and Castillo 2009
340	96	67	52	Merckx et al. 2008
340	66	60	57	Wikström et al. 2001
340	42	38	34	Wikström et al. 2001
341	84	84	84	Janssen and Bremer 2004
341	88	88	88	Kress and Specht 2005
341	106	105.5	105	Kress and Specht 2006

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
341	51	47	43	Wikström et al. 2001
341	32	28	24	Wikström et al. 2001
342	79	79	79	Janssen and Bremer 2004
342	88	88	88	Kress and Specht 2005
342	105	102	99	Kress and Specht 2006
343	54	45	43	Bell et al. 2010
343	68	68	68	Janssen and Bremer 2004
343	80	80	80	Kress and Specht 2005
343	101	96	91	Kress and Specht 2006
343	96	93.5	91	Kress and Specht 2006
344	78	78	78	Janssen and Bremer 2004
344	49	49	49	Kress and Specht 2005
344	96	88	80	Kress and Specht 2006
344	52	46.5	45	Wikström et al. 2001
344	30	26	22	Wikström et al. 2001
345	103	88	85	Bell et al. 2010
345	83	83	83	Janssen and Bremer 2004
345	109	107.5	106	Leebens-Mack et al. 2005
345	109	109	109	Magallón and Castillo 2009
345	99	99	99	Magallón and Castillo 2009
345	109	109	109	Magallón and Castillo 2009
345	99.2	99.2	99.2	Magallón and Castillo 2009
345	116	106	88	Merckx et al. 2008
345	72	70.5	69	Wikström et al. 2001
346	62	62	62	Givnish et al. 2000
346	87	87	87	Givnish et al. 2004
347	96	82	79	Bell et al. 2010
348	76	60.5	58	Bell et al. 2010
348	108	108	108	Janssen and Bremer 2004
348	52	47	45	Wikström et al. 2001
349	96	96	96	Janssen and Bremer 2004
349	97	97	97	Janssen and Bremer 2004
350	58	58	58	Bremer et al. 2000
350	40	40	40	Bremer et al. 2000
350	97	97	97	Janssen and Bremer 2004
351	76	59	58	Bell et al. 2010
352	90	90	90	Janssen and Bremer 2004
353	89	89	89	Janssen and Bremer 2004
355	100	100	100	Janssen and Bremer 2004
356	98	98	98	Janssen and Bremer 2004

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
357	74	58.5	55	Bell et al. 2010
357	100	100	100	Besnard et al. 2009
357	88	88	88	Janssen and Bremer 2004
357	39	33.5	28	Wikström et al. 2001, 2004
358	105	105	105	Janssen and Bremer 2004
360	124	124	124	Janssen and Bremer 2004
360	134.4	134.4	134.4	Magallón and Castillo 2009
360	119.6	119.6	119.6	Magallón and Castillo 2009
360	123	109.5	96	Mennes etal. 2013
360	130	121	119	Merckx et al. 2008
361	117	91	72	Bell et al. 2010
361	50	50	50	Bremer 2000
361	114	114	114	Janssen and Bremer 2004
361	130	117	116	Merckx et al. 2008
361	96	87	84	Wikström et al. 2001
362	84	67	66	Bell et al. 2010
362	101.7	101.7	101.7	Magallón and Castillo 2009
363	71	51	47	Bell et al. 2010
363	98	98	98	Janssen and Bremer 2004
363	74	67	66	Wikström et al. 2001
364	123	123	123	Janssen and Bremer 2004
364	126	116	113	Merckx et al. 2008
364	120	116	111	Merckx et al. 2010
365	111	89.5	83	Bell et al. 2010
365	116	116	116	Janssen and Bremer 2004
365	127	127	127	Magallón and Castillo 2009
365	118	109	98	Merckx et al. 2010
365	115	115	115	Wikström et al. 2001
366	92	79	68	Merckx et al. 2010
367	116	116	116	Janssen and Bremer 2004
368	176	149	128	Clarke et al. 2011
368	149.1	149.1	149.1	Magallón et al. 2013
368	141	136	129	Moore et al. 2010
368	168	131	126	Soltis et al. 2008
368	143.2	143.2	143.2	Xue et al. 2012
370	198.2	198.2	198.2	Magallón and Castillo 2009
370	127.7	127.7	127.7	Magallón and Castillo 2009
370	137.2	137.2	137.2	Magallón et al. 2013
370	104.5	104.5	104.5	Xue et al. 2012
371	96	73	69	Bell et al. 2010

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
371	171.5	171.5	171.5	Magallón and Castillo 2009
371	116.6	116.6	116.6	Magallón and Castillo 2009
371	119	110.5	108	Wikström et al. 2001
372	120	110	100	Doyle et al. 2004
372	71.1	71.1	71.1	Magallón et al. 2013
372	106	102	98	Su and Saunders 2009
372	108	99	97	Wikström et al. 2001
374	69	52	50	Bell et al. 2010
374	110.4	106.3	102	Couvreur et al. 2011
374	84.7	73.65	62.6	Erkens et al. 2009
374	101.5	98	94.9	Su and Saunders 2009
374	110.4	101.7	99.4	Surveswaran et al. 2010
374	97	86.5	82	Wikström et al. 2001
375	59	40.5	38	Bell et al. 2010
375	80	68	63	Wikström et al. 2001
376	133	120	112	Bell et al. 2010
376	171.4	171.4	171.4	Magallón and Castillo 2009
376	119.3	119.3	119.3	Magallón and Castillo 2009
376	117.5	117.5	117.5	Magallón et al. 2013
376	130.2	130.2	130.2	Renner 2005
376	121	111	108	Wikström et al. 2001
377	91	91	91	Crepet et al. 2004
377	127	127	127	Renner 2005
377	103	92.5	89	Wikström et al. 2001
379	44	28	25	Bell et al. 2010
379	116	114	112	Renner 2005
379	56	50.5	50	Wikström et al. 2001
379	44	39	34	Wikström et al. 2001
380	67	49.5	45	Bell et al. 2010
380	134	122	110	Merckx et al. 2010
380	124	124	124	Renner 2005
381	96	96	96	Forest et al. 2009
382	119.8	119.8	119.8	Arakaki et al. 2011
382	143	143	143	Magallon et al. 2005
382	122	122	122	Moore et al. 2007
382	170	170	170	Sanderson et al. 2004
382	149	149	149	Wikstrom et al. 2007
383	138	112.5	104	Bell et al. 2010
383	175	175	175	Magallón and Castillo 2009
383	119	119	119	Magallón and Castillo 2009
Node	Estimated Old	Estimated Central	Estimated Young	Source
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	Age (Myr)	Age (Myr)	Age (Myr)	
383	110	110	110	Magallón et al. 2013
383	139	127.5	122	Wikström et al. 2001
384	96	70.5	67	Bell et al. 2010
384	64.1	64.1	64.1	Magallón et al. 2013
384	106	95	90	Wikström et al. 2011
385	111	80.5	77	Bell et al. 2010
385	128	128	128	Magallón and Castillo 2009
385	125	125	125	Magallón and Castillo 2009
385	122.8	122.8	122.8	Magallón et al. 2013
385	111	102	99	Wikström et al. 2001
386	145	122	99	Bell et al. 2010
386	130	114	110	Bell et al. 2010
386	203	203	203	Magallón and Castillo 2009
386	125	125	125	Magallón and Castillo 2009
386	103.4	103.4	103.4	Magallón et al. 2013
386	168	126.5	85	Schneider et al. 2004
386	155	140.5	133	Wikström et al. 2001
389	56	40.5	38	Bell et al. 2010
389	90	90	90	Crepet et al. 2004
389	75	56.4	38	Löhne et al. 2008
389	112	112	112	Magallón and Castillo 2009
389	122.7	122.7	122.7	Magallón et al. 2013
389	152	127.5	111	Wikström et al. 2001
389	52.5	44.6	36.7	Yoo et al. 2005
390	337	316	306	Clarke et al. 2011
390	311.6	311.6	311.6	Magallón et al. 2013
390	316	304.5	301	Smith et al. 2010
391	293.2	293.2	293.2	Hedges and Kumar 2013
391	307	307	307	Magallón et al. 2005
391	307	307	307	Magallón et al. 2005
391	277.5	277.5	277.5	Soltis et al. 2002
391	277.5	277.5	277.5	Soltis et al. 2002
391	348	348	348	Wikström et al. 2001
391	322	322	322	Wikström et al. 2001
392	222.9	222.9	222.9	Soltis et al. 2002
392	348	348	348	Wikström et al. 2001
393	286	252	212	Clarke et al. 2011
393	259	219	174	Davies et al. 2011
393	350	312.5	275	Leslie et al. 2012
393	278.1	278.1	278.1	Magallón et al. 2013

Node	Estimated Old	Estimated Central	Estimated Young	Source
	Age (Myr)	Age (Myr)	Age (Myr)	
394	276.6	260.5	256.9	Magallón et al. 2013
395	318	263	223	Biffin et al. 2010
395	255	206	177	Biffin et al. 2010
395	205	205	205	Biffin et al. 2011
395	230	203	176	Leslie et al. 2012
395	278	278	278	Magallón et al. 2005
395	243	243	243	Magallón et al. 2013
396	250	250	250	Leslie et al. 2012
397	217	207	197	Leslie et al. 2012
397	175.4	175.4	175.4	Magallón et al. 2013
397	293	243.5	242	Mao et al.2012
397	237	214.5	192	Yang et al.2012
398	192.3	166.6	90.6	Ickert-Bond et al. 2009
398	140	130	120	Magallón et al. 2013
398	202	155	104	Smith et al. 2010
399	127	111.3	87.2	Ickert-Bond et al. 2009
399	81.9	81.9	81.9	Magallón et al. 2013
400	200	200	200	Crisp and Cook 2011
400	250	250	250	Hermsen et al. 2006
400	181	171.5	167	Magallón et al. 2013
400	92	92	92	Wink 2006
401	404	393	389.9	Magallón et al. 2013
411	74.1	74.1	74.1	Schneider et al. 2004
415	93.6	93.6	93.6	Pryier et al. 2004
421	173	173	173	Pryier et al. 2004
421	161.6	161.6	161.6	Schneider et al. 2004
421	91.1	91.1	91.1	Soltis et al. 2004
423	135	135	135	Pryier et al. 2004
424	263	263	263	Pryier et al. 2004
424	278	278	278	Schuettpelz et al. 2006
425	227	227	227	Pryier et al. 2004
425	239.4	239.4	239.4	Schuettpelz et al. 2006
426	275.6	275.6	275.6	Magallón et al. 2013

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