Phylogenetic turnover during subtropical forest succession across environmental and phylogenetic scales

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Summary

- Although spatial and temporal patterns of phylogenetic community structure during succession are inherently interlinked and assembly processes vary with environmental and phylogenetic scale, successional studies of community assembly have yet to integrate spatial and temporal components of community structure, while accounting for scaling issues. To gain insight into the processes that generate biodiversity after disturbance, we combine analyses of spatial and temporal phylogenetic turnover across phylogenetic scales, accounting for covariation with environmental differences.
- We compared phylogenetic turnover, at the species- and individual-level, within and between five successional stages, representing woody plant communities in a subtropical forest chronosequence. We decomposed turnover at different phylogenetic depths and assessed its covariation with between-plot abiotic differences.
- Phylogenetic turnover between stages was low relative to species turnover and was not explained by abiotic differences. However, within the late successional stages, there was high presence/absence-based turnover (clustering) that occurred deep in the phylogeny and covaried with environmental differentiation.
- Our results support a deterministic model of community assembly where (i) phylogenetic composition is constrained through successional time, but (ii) towards late succession, species sorting into preferred habitats according to niche traits that are conserved deep in phylogeny, becomes increasingly important.

Key words: chronosequence, community assembly, depth of turnover, environmental filtering, null model, phylogenetic niche conservatism

Introduction

A better understanding of the processes that generate biodiversity during succession after disturbance is needed for more accurate predictions of ecosystem responses to future disturbance events (Garnier *et al.,* 2004; Dornelas, 2010). Community assembly during succession may be driven by deterministic (biotic and abiotic filtering) as well as stochastic processes (Keddy, 1992; Fukami *et al.,* 2005) that are often inferred using trait-based approaches (Bazzaz, 1979; Shipley *et al.,* 2006). However, the traits involved in assembly processes are *a priori* unknown and, particularly in species rich systems, it is difficult to choose and measure the most relevant traits. In communities with broad taxonomic sampling, such as hyper-diverse tropical plant communities, closely related species often share similar functional characteristics (Swenson, 2013), resulting from phylogenetic niche conservatism (Losos, 2008). In such systems, phylogenetic relatedness between species is often used as a proxy for overall trait similarity as it potentially integrates more trait information than a limited set of measurable traits (Pavoine & Bonsall, 2011; Mouquet *et al.,* 2012). Several studies have quantified spatial or temporal patterns of phylogenetic relatedness throughout succession, either by testing for non-random patterns of relatedness within successional stages (Letcher, 2010; Ding *et al.,* 2012) or by examining whether the observed temporal phylogenetic turnover between stages differed from the expected phylogenetic turnover, given the level of species turnover (Swenson *et al.,* 2012, Letten *et al.,* 2014). However, purely temporal approaches, that focus on phylogenetic turnover *between* stages, do not allow to evaluate whether non-random patterns of temporal phylogenetic turnover are simply a reflection of spatial turnover between sites belonging to the same successional stage (see Purschke *et al.,* 2013). In contrast, approaches that focus on spatial patterns of phylogenetic relatedness *within* successional stages only allow for inferences about assembly processes that act at a particular successional stage. Because spatial and temporal patterns of community composition are inherently interlinked (Preston, 1960; White *et al.,* 2010), studies based on partial analysis of either spatial or temporal patterns of community phylogenetic structure during succession will only give limited insight into the temporal dynamics of assembly processes.

Hardy and Senterre (2007) proposed a framework that allows to test the spatial phylogenetic structure of communities, based on the extent to which species within sites are

more, or less, related to each other than to species from different sites. If species that co-occur within a site are more related to each other than to species from different sites, phylogenetic turnover between sites is high, which is referred to as spatial phylogenetic clustering. Such high phylogenetic turnover is usually interpreted as a signature of abiotic filtering where distinct groups of closely related, and functionally similar, species are differentially selected in sites that differ in their environmental conditions (Baraloto *et al.,* 2012). Alternatively, phylogenetic clustering may reflect the exclusion of competitively inferior species, i.e. competitive hierarchies, if the traits conferring competitive dominance are phylogenetically conserved (Mayfield & Levine, 2010). In contrast, if species within sites are phylogenetically less related than species from different sites, phylogenetic turnover between sites is low, which is referred to as spatial phylogenetic overdispersion. This pattern is often interpreted as result of biotic filtering because of negative interactions due to limiting similarity competition between closely related species, but could also indicate abiotic filtering in case of convergent evolution of important niche traits (Cavender-Bares *et al.,* 2004). Because the Hardy & Senterre (2007) framework expresses community differentiation between sites, it can also be applied to pairs of communities at different successional stages (see Purschke *et al.,* 2013), allowing to compare spatial and temporal patterns of community differentiation within a consistent framework.

Despite the promise of combining spatial and temporal components of phylogenetic turnover to gain insight into assembly processes, there remain several difficulties with interpreting community phylogenetic structure. One main problem is that patterns of phylogenetic relatedness within communities and conclusions about assembly processes are highly scale-dependent (Swenson *et al.,* 2007; Graham *et al.*, 2016). For instance, patterns of phylogenetic overdispersion will only be detectable at small environmental, spatial and phylogenetic scales (i.e. between closely related species close to tips of the phylogeny, see Parmentier *et al.,* 2014). In contrast, phylogenetic clustering, resulting from abiotic filtering, has mainly been demonstrated over steep to moderate ecological gradients and at large phylogenetic scales, i.e. deep in the phylogeny (Cavender-Bares *et al.,* 2006). In addition, Hardy & Senterre (2007) pointed out that if such opposing assembly mechanisms, like overdispersion and clustering, act simultaneously at different phylogenetic scales, they may cancel out each other, resulting in an overall random phylogenetic structure. To address this

phylogenetic scaling issue, phylogenetic structure can be assessed at different depths in the phylogenetic tree (Hardy & Senterre, 2007; Cavender-Bares & Reich, 2012). The issue of environmental scaling may be accounted for by assessing the extent to which phylogenetic turnover is explained by environmental differences between sites (e.g. Hardy *et al.,* 2012).

Finally, inferences about assembly processes may be influenced by the level of biological organization considered in the analysis, i.e. whether phylogenetic structure is assessed on the level of species or individuals, respectively, giving more weight to rare or dominant species (Helmus *et al.,* 2007; Lozupone *et al.,* 2007). The joint use of abundance- and presence/absence-based indices allows to detect the relative importance of shifts in species abundances vs. changes in composition, and hence will be critical to understand the processes underlying community assembly (Vellend *et al.,* 2011).

In the context of succession, theory predicts that in early succession, disturbance acts as an environmental filter selecting for closely related species and that biotic filtering will become more important over time, selecting for more distantly related species in late succession (Cornell & Slatyer, 1977). While a number of studies found support for this hypothesis (e.g. Letcher, 2010; Whitfield *et al.,* 2012; Purschke *et al.,* 2013), a few recent studies detected an increase in phylogenetic relatedness during succession, and suggested that hierarchical competition and/or environmental filtering become more important during succession (e.g. Uriarte *et al.,* 2010; Kunstler *et al.,* 2012; Letten *et al.,* 2014; Buzzard *et al.,* 2015). However, existing studies of phylogenetic community structure (i) were usually based on metrics of phylogenetic structure that integrate across the whole phylogeny, and therefore did not allow for the possibility that assembly processes will only be detectable at particular phylogenetic scales, (ii) did not include information on environmental differentiation between sites, or (iii) focused either on spatial or temporal components of community change. To gain more accurate insights into the processes that underlie community assembly during succession after disturbance, there is therefore a need for integrative studies that account for phylogenetic community structure at different phylogenetic scales and that compare spatial and temporal turnover components in conjunction with environmental differentiation between sites. If, for example, abiotic filtering along an environmental gradient is the predominant process shaping communities at the beginning of succession and there is phylogenetic conservatism in species' traits conferring their environmental tolerances, spatial phylogenetic turnover between early

156 successional communities will (i) be higher than expected given the level of species turnover,
157 (ii) be explained by environmental differences between communities (Bartlett *et al.*, 2015;
158 Cadotte & Tucker, 2017) and iii) be detected only at large phylogenetic scales (Cavender-
159 Bares & Reich, 2012; Hardy *et al.,* 2012). If, in contrast, there is an increase in the relative
160 importance of biotic filtering, due to limiting similarity competition, during succession, we
161 predict that spatial phylogenetic turnover between late successional communities will be (i)
162 less than expected (spatial phylogenetic overdispersion), (ii) detected at small phylogenetic
163 scales, and (iii) unrelated to environmental differences between plots (Bartlett *et al.,* 2015).
164 Alternatively, if hierarchical competition is the predominant force shaping communities
165 during late succession, we predict that late successional communities will be comprised of
166 closely related species, but that phylogenetic turnover will not covary with environmental
167 differentiation (Bartlett *et al.,* 2015). If traits conferring competitive dominance are
168 phylogenetically conserved, and competitively superior species belong to a particular clade
169 (Roeder *et al.,* 2015), we additionally predict that hierarchical competition will cause
170 phylogenetic clustering at shallow phylogenetic scales. In contrast, if late successional
171 communities are primarily governed by the accumulation of closely related species that share
172 adaptations to the local abiotic conditions (Li *et al.,* 2015) and environmental filtering selects
173 for distinct sets of closely related species in plots that differ in their abiotic environment, we
174 predict that spatial phylogenetic turnover between communities belonging to the late
175 successional stages will be (i) higher than expected, (ii) explained by environmental
176 differences between sites, and (iii) detected at broad phylogenetic scales, resulting from
177 phylogenetic conservatism of abiotic niches. Finally, if deterministic community assembly
178 results in temporal shifts in phylogenetic community composition due to successional changes
179 in abiotic conditions (Swenson *et al.,* 2012), we predict that phylogenetic turnover between
180 stages will (i) be higher than expected by chance, (ii) be higher than spatial turnover between
181 plots from the same stage, and (iii) increase with environmental differences between stages.
182 Conversely, if relatively constant abiotic conditions cause a lack of phylogenetic shifts to over
183 time (Letten *et al.,* 2014), we predict that phylogenetic turnover between successional stages
184 will be (i) low relative to species turnover, (ii) lower than phylogenetic turnover between plots
185 from the same stage, and (iii) unrelated to environmental differences between stages.
186 To test these predictions, we use data on tree communities representing different

187 stages of a subtropical forest succession in south-eastern China. Successional subtropical
188 forests provide an ideal system for the study of temporal changes in the mechanisms
189 underlying community assembly as they represent community assembly in action and are
190 exceptionally species-rich (Uriarte *et al.,* 2010; Arroyo-Rodríguez *et al.,* 2017). While
191 subtropical forest areas were once widespread across South and East China, they are currently
192 under severe decline as a result of land use intensification (Wang *et al.,* 2007). Because of
193 frequent anthropogenic disturbance events, such as logging and burning, subtropical forests
194 often consist of a mosaic of different stages of secondary forest succession. Combining
195 analysis of spatial and temporal turnover (at the individual- and species-level), while
196 examining turnover (i) at different phylogenetic depths and (ii) with increasing environmental
197 differentiation, we will be able to address competing predictions about the temporal changes
198 in the relative importance of the processes that generate biodiversity after disturbance.
199
200 **Materials and methods**
201 ***Study area and sampling***
202 We studied woody plant communities in the comparative study plots that had been established
203 within the biodiversity-ecosystem functioning experiment BEF-China (Bruelheide *et al.,*
204 2011). The plots represent a chronosequence of subtropical forest succession in the
205 Gutianshan National Nature Reserve (GNNR), located in Zhejiang Province in south-eastern
206 China (29°8'18"-29°17'29" N, 118°2'14"–118°11'12" E). The GNNR comprises mixed broad-
207 leaved forests (Wu & others, 1980; Hu & Yu, 2008) within an elevational range of 250 m to
208 1258 m a.s.l.. A total of 1426 seed plant species of 648 genera and 149 families has been
209 recorded in GNNR (Lou & Li, 1988). The study area mainly consists of a mosaic of
210 secondary forest stands that represent different successional stages, with maximum tree age of
211 approximately 180 yrs (Bruelheide *et al.,* 2011).
212 Species abundance data was obtained from a vegetation inventory (May-October
213 2008) of all individuals of trees and shrubs (> 1 m height, 147 species in total) in each of the
214 27 30x30m plots (see Bruelheide *et al.,* 2011). The plots were distributed over the GNNR to
215 represent five successional stages (differing by 20 years), based on estimations of the age of
216 the largest tree individuals and on knowledge of the last logging event [see Bruelheide *et al.*
217 *(*2011) for more detailed information on type of disturbance that preceded succession]. The

number of plots per successional stage were 5 (<20 yr), 4 (20-39 yr), 5 (40-59 yr), 6 (60-79 yr) and 7 (≥80 yr). Because fewer individuals were recorded in the older plots relative to the younger plots (Fig. S1 in Supporting Information), we assessed whether the differences in the number of individuals between plots may potentially bias our results, which was not the case in our study (Table S1).

For each plot, a set of environmental variables (Table S2) related to topography [aspect (expressed as northness and eastness), slope, elevation], light (photosynthetically active radiation (PAR), red/far-red ratio) and soil characteristics (pH, moisture, C/N-ratio) were available from Bruelheide *et al.* (2011) and Kröber *et al.* (2012). Total phosphorus (P) content of the soil was measured with nitric acid digestion, a standard method recommended by the German forest soil survey (BMELV, 2009). The inorganic nitrogen concentration ($NO3^-$, $NH4^+$) of the mineral soil was determined by KCl extraction (1mol/L) followed by Flow Injection Analysis (FIAstar 500 Analyzer, FOSS, Hilerød, Denmark).

Phylogenetic data and regional species pool

Based on the set of species present in the 27 plots and on the list of all woody species of the Gutianshan National Nature Reserve (Lou & Li, 1988), we constructed a regional species pool [the set of 438 woody species that occur in the whole GNNR (Table S3)] for which a phylogeny was inferred. For details on phylogenetic inference see Methods S1 and Tables S4 & S5. In short, we obtained sequence information (matK, rbcL and ITS region) for all species, or their closest relatives, from GenBank or de novo using standard barcoding protocols. A maximum likelihood tree was computed and dated using non-parametric rate smoothing and using published fossils as age constraints (Methods S2, S3). To avoid potential bias in the analysis of phylogenetic patterns due to their disproportionately long branch lengths (Letcher, 2010; Cadotte, 2014), non-angiosperm and one bamboo (*Pleioblastus amarus,* Poaceae) species, which generally occurred at low frequencies within the study area, were excluded from the regional species pool. We further excluded cultivated species, resulting in a total of 410 woody species of which 143 occurred in the 27 study plots (Table S3).

Phylogenetic structure

Using information on species composition and the phylogenetic tree pruned down to the 143

woody angiosperms found in the 27 plots, we estimated phylogenetic structure following the framework proposed by Hardy & Senterre (2007), which is based on the spatial decomposition of evolutionary relatedness between species into within- and between-community components. Within the Hardy & Senterre (2007) framework, spatial phylogenetic structure was quantified for presence/absence and abundance data, using the phylogenetic turnover (between-plot differentiation) statistics Π_{ST} and B_{ST}, respectively: $\Pi_{ST} = 1 - \Delta^{P}_{w}/\Delta^{P}_{a}$ and $B_{ST} = 1 - \Delta^{*P}_{w}/\Delta^{*P}_{a}$, where Δ^{P}_{w} and Δ^{*P}_{w} represent phylogenetic alpha diversity, and correspond to the mean within-community phylogenetic distance between distinct species and the mean phylogenetic distance between two individuals of distinct species, respectively, averaged over all communities belonging to the same successional stage. Δ^{P}_{a} and Δ^{*P}_{a} are the mean phylogenetic distance between distinct species and the mean phylogenetic distance between two individuals of distinct species, respectively, sampled from different communities belonging to a particular stage. Values of spatial phylogenetic turnover, Π_{ST} or B_{ST}, > 0 indicate spatial phylogenetic clustering – species, or individuals, within communities are phylogenetically more related than species, or individuals, from different communities. Spatial phylogenetic overdispersion is observed if Π_{ST} or $B_{ST} < 0$, indicating that species, or individuals, within communities are phylogenetically less related than species, or individuals, from different communities. When Π_{ST} and B_{ST} are calculated between pairs of plots belonging to the same successional stage, they address within-stage phylogenetic turnover. When Π_{ST} and B_{ST} are calculated between pairs of plots belonging to different successional stages, they address between-stage phylogenetic turnover. We tested, based on 100 simulation runs, whether levels of spatial phylogenetic turnover were affected by differences in the number of plots among stages (Methods S4). Mean Pearson correlations between Π_{ST} (or B_{ST}) for simulated communities and the number plots were close to zero, indicating that levels of phylogenetic turnover were not simply a reflection of the number of plots. To complement our main analyses of phylogenetic turnover, and in addition to measures of phylogenetic alpha diversity (Δ^{P}_{w} and Δ^{*P}_{w}), we also calculated Shannon evenness (Magurran, 2004) for each plot.

Null models

To test whether Π_{ST} or B_{ST} were significantly higher (or less) than zero, observed Π_{ST} or B_{ST} values were compared to those re-calculated for 999 random communities. Random

communities were generated using null model '1p' in Hardy (2008), shuffling species names across the phylogeny of all 410 woody angiosperms from the regional species pool. The latter corresponding to the set of species that are present in, or could potentially colonize, our study plots (see Ding *et al.,* 2012 and Letcher *et al.,* 2012). This null model maintains (i) the number of species within each community, (ii) species turnover between communities, (iii) the patterns of spatial autocorrelation in overall species abundances and occurrence frequencies, (iv) species' occurrence frequency across the study landscape and (v) species identity within each successional time step. This type of null model is appropriate for temporal data (Letcher *et al.,* 2012; Norden *et al.,* 2012) and has been demonstrated to provide exact tests (i.e. correct Type-I error rates) in situations where overall species frequencies (or abundances) are not phylogenetically structured (Hardy, 2008, see Methods S5). Significant positive (or negative) values of Π_{ST} (or B_{ST}) of within-stage phylogenetic turnover indicate that species, or individuals, co-occurring within successional stages are more (or less) related than expected by chance. Higher-than-expected Π_{ST}- or B_{ST}-values of between-stage phylogenetic turnover that are higher than within-stage phylogenetic turnover indicate phylogenetic shifts during the course of succession. Lower-than-expected values of between-stage turnover, that are lower than within-stage turnover, would indicate constant phylogenetic composition during succession.

Phylogenetic structure at different depths in the phylogeny

We assessed whether non-random phylogenetic structure, within each of the five successional stages, occurred at particular phylogenetic depths, following the approach in Hardy & Senterre (2007): phylogenetic turnover between plots was calculated based only on species pairs within clades younger than a given divergence time threshold. We chose eleven age thresholds, ranging between 30 Myr to 128 Myr, by steps of approximately 10 Myr. To test whether phylogenetic turnover significantly differed from zero at particular phylogenetic scales, we carried out partial randomizations, shuffling species names across the phylogeny, but restricting the randomization to species within clades younger than the respective age threshold. All calculations of phylogenetic community structure were carried out on phylogenetic, cophenetic distance matrices, using the packages 'vegan' (Oksanen *et al.,* 2017) and 'spacodiR' (Eastman *et al.,* 2011) in the R statistical package (R Development Core Team,

2017) and SPACoDi 0.10 (Hardy, 2010). To identify clades that signifcantly contributed to phylogenetic turnover between plots, we tested for each node in the phylogeny whether it had more decendent taxa than expected in a particular plot, using the 'nodesig' procedure in Phylocom v.4.2 (Webb *et al.,* 2009).

Relating phylogenetic structure to environmental variables

To quantify the extent to which spatial and temporal phylogenetic turnover was explained by differences in abiotic conditions, pairwise Π_{ST} (or B_{ST}) values were regressed on between-plot environmental distances. To control for covariation between phylogenetic turnover and spatial distance, we used the residuals from regressions of Π_{ST} (or B_{ST}) against the Euclidean distances calculated from the geographic x- and y-coordinates of the plots instead of the actual phylogenetic turnover values. Significance of the relationships was assessed by non-parametric randomization testing [5000 randomizations, R-package 'lmPerm' (Wheeler & Torchiano, 2016)]. Environmental distances were obtained from an inter-plot distance matrix based on the 11 topographic, light and edaphic descriptors. A principal components analysis (PCA) was carried out on the log-transformed and standardized (mean = 0, sd = 1) environmental data, to correct for the dominance of the distance matrix by highly correlated environmental variables. The resulting first six principal components (PCs) accounted for about 90% of the total variation (Table S6) and were used to construct the Euclidean inter-plot distance matrix from which the environmental distances were obtained. Because associations between phylogenetic turnover and environmental differentiation may be a reflection of differences in sample size among the successional stages, we additionally assessed relationships between environmental and phylogenetic turnover at each stage based resampling all possible combinations of four plots, the minimum number of plots across stages.

Phylogenetic signal in traits

To assess whether phylogenetic relatedness between species reflects their ecological similarity, we quantified phylogenetic signal in six traits [leaf area, specific leaf area (SLA), leaf nitrogen content, leaf phosphorus content, wood density, maximum height] that represent multiple axes of plant functional differentiation (Westoby *et al.,* 2002; Wright *et al.,* 2004;

Chave *et al.,* 2009; Moles *et al.,* 2009). Estimates of phylogenetic signal were based on the three metrics Blomberg' *K* (Blomberg *et al.,* 2003), Pagel's λ (Pagel, 1999) and Abouheif/Moran's *I* (Abouheif, 1999) (Table S7), and calculated in the R-packages 'phytools' (Revell, 2012) and 'adephylo' (Jombart *et al.,* 2010), for the subset of 121 species (of the 143 angiosperm species occurring in the 27 plots) for which data on all six traits were available from Kröber *et al.* (2012) and Böhnke *et al.* (2012, 2014).

Results

Temporal changes in alpha diversity

Phylogenetic alpha diversity (Δ^{P}_{w} and Δ^{*P}_{w}) showed no significant temporal trend in the course of succession (Fig. 1a,b). In contrast, there was a steep increase in species (Shannon) evenness over time (Fig. S2).

Comparisons between spatial and temporal phylogenetic turnover

Levels of overall phylogenetic turnover were significantly different from those predicted, given the levels of species turnover (Fig. 2). However, deviation from null expectations showed opposing patterns depending on whether phylogenetic turnover was estimated based on species presence/absence (Π_{ST}) or abundance (B_{ST}). Overall levels of presence/absence-based turnover were higher than expected, whereas overall abundance-based turnover was lower than expected. When overall phylogenetic turnover was dissected into turnover between pairs of plots belonging to the same successional stage (within-stage spatial turnover) and turnover between pairs of plots at different successional stages (between-stage temporal turnover) respectively, presence/absence-based within-stage turnover (Π_{ST}) was higher than expected, indicating that species within plots were more closely related to each other than to species from different plots. Levels of presence/absence-based between-stage turnover (Π_{ST}) did not differ from random expectations (Fig. 2a). In contrast, between-stage turnover was on average lower than predicted by chance, when based on abundance data (B_{ST}).

Phylogenetic turnover within and between single successional stages

Spatial phylogenetic turnover measures showed contrasting patterns of deviation from random expectations over the course of succession (Fig. 3). Presence/absence-based phylogenetic

turnover (Π_{ST}) did not significantly differ from zero within early and mid successional stages (stages 1, 2 and 3, Fig. 3a). However, Π_{ST}-values were higher than expected within the two latest successional stages (stages 4 and 5, Fig. 3a). In contrast, abundance-based spatial phylogenetic turnover (B_{ST}) was lower than predicted by chance within the first successional stage but did not significantly differ from null expectations within the mid- and late-successional stages (Fig. 3b). Presence/absence-based turnover (Π_{ST}) between pairs of consecutive successional stages was higher than expected between the mid and last successional stages (stage 3-4, stage 3-5 and stage 4-5, Fig. S3), but was never higher than levels of turnover within each of the stages 3, 4 and 5 (Fig. 3a). Presence/absence-based turnover (B_{ST}) was lower than predicted between the early and mid successional stage as well as between the first and the last stage (stage 1-2 and stage 1-5, Fig. S3), with values of B_{ST} that were lower than those estimated within stages (Fig. 3b).

Covariation between phylogenetic turnover and environmental differentiation

There were no significant relationships of presence/absence-based overall phylogenetic turnover and between-stage phylogenetic turnover (Π_{ST}), respectively, with environmental differences between plots (Fig. S4a,c). Instead, there was on average a significant positive association between within-stage phylogenetic turnover (Π_{ST}) and environmental distance (Fig. S4b), indicating an increase in phylogenetic turnover with increasing environmental differences (mainly related to soil moisture and light, see Table S6 & Fig. S7), between plots that belong to the same successional stage. When relationships between Π_{ST} and environmental distance were assessed within each of the five successional stages separately, significant increases in phylogenetic turnover with increasing environmental distance were only detected within the two last successional stages (stage 4 and 5, Fig. 4). The significant positive associations between phylogenetic turnover and environmental differences between plots within the two latest successional stages were maintained after accounting for differences in sample size between the stages using resampling down to the minimum number of plots (n=4) across stages (Stage 4: $R^2=0.24^*$; Stage 5: $R^2=0.19^*$). Abundance-based phylogenetic turnover (B_{ST}) was not associated with environmental distances, neither within nor between successional stages (results not shown).

Phylogenetic structure at different depths in the phylogeny

Presence/absence-based phylogenetic turnover (Π_{ST}) within the early and mid successional stages did not differ from random expectations throughout the phylogeny (Fig. 5). Non-random and higher-than expected phylogenetic turnover was only detected within the two latest successional stages (stage 4 and 5, Fig. 5) and occurred close to the root of the phylogeny (>100 Myr), indicating phylogenetic clustering at a deep phylogenetic scale. Abundance-based phylogenetic turnover (B_{ST}) did not differ from random expectations at any level in the in phylogeny within any successional stage (results not shown). Clades that were over-represented in, and contributed to the high turnover between, pairs of plots within the late successional stages diverged early in phylogeny (~100 Myr ago). Nodes that were significantly associated (i.e. had more taxa than expected by chance) with each of the plots are listed in (Table S8). For instance, the plot pair with the highest level of phylogenetic turnover within the late successional stage 4 (plot IDs CSPs 5 and 11), (i) had significantly more taxa than expected within the families Ericaceae (*Rhododendron*, *Vaccinium*, *Lyonia*, *Pieris*) and Theaceae (*Camellia*, *Schima*) (nodes 44 & 39) that diverged within the Ericales ~100 Myrs ago (Fig. S6) and (ii) was associated with dry and moist soil conditions, respectively (Fig. S7).

Phylogenetic signal in traits

All of the six traits considered showed significant phylogenetic signal, with values of Blomberg's *K*, Pagel's λ and Abouheif/Moran's *I* significantly greater than expected from a null model of no phylogenetic signal (Table S7). This suggests that, in our study, phylogenetic relatedness reflects overall trait similarity.

Discussion

The present study combines analysis of within- and between-stage phylogenetic turnover during succession across phylogenetic scales, while accounting for between-plot environmental differentiation, and demonstrates that, despite a lack of temporal phylogenetic turnover between stages, there was a shift from abundance-based phylogenetic overdispersion in early succession towards presence/absence-based phylogenetic clustering in late succession. Low between-stage turnover that was not explained by environmental differences

435 between stages suggests that (i) relatively constant environmental conditions and (ii) shifts in
436 species abundances (towards higher evenness) that were counterbalanced by increasing
437 relatedness towards late succession, resulted in an absence of net change in phylogenetic
438 composition over time. Within the late successional stages, phylogenetic turnover was higher
439 than expected, increased with environmental differentiation between sites and occurred at
440 broad phylogenetic scales, indicating (i) deep phylogenetic conservatism of species' abiotic
441 niches, and (ii) that environmental filtering along an abiotic gradient becomes more important
442 towards late succession.
443
444 ***Comparisons between spatial and temporal phylogenetic turnover: high turnover within***
445 ***and low turnover between successional stages***
446 Within-stage and between-stage phylogenetic turnover showed, on average, opposing levels
447 of deviation from random, depending whether they were based on presence/absence or
448 abundance data. While turnover between plots belonging to the same successional stage was
449 higher than expected, relative to the levels of species turnover, when based on
450 presence/absence data, phylogenetic turnover between plots at different successional stages
451 was lower than expected when based on abundance data (Fig. 2). Preceding studies
452 (Lozupone *et al.,* 2007; Fine & Kembel, 2011) have demonstrated that using both
453 presence/absence- and abundance-based metrics may reveal different patterns of phylogenetic
454 structure for rare and abundant species, and thus may help to distinguish species composition
455 from dominance effects. The previous study by Norden *et al.* (2012) revealed that temporal
456 changes in phylogenetic community structure during tropical rainforest succession were
457 influenced by shifts in species' abundance rather than species occurrence, whereas Letten *et*
458 *al.* (2014) found low temporal phylogenetic turnover during heathland succession, because
459 closely related, dominant species replaced each other over time. The previous study of
460 Bruelheide *et al.* (2011), in the same system that was used in our study, demonstrated a lack of
461 species turnover with only few species restricted to a particular successional stage,
462 reminescent of the concept of initial floristic composition, but that there were substantial
463 shifts in species' abundance towards a more even distribution of abundance in late
464 successional communities. Therefore, in our study, the low levels of abundance-based
465 phylogenetic turnover, relative to the turnover of species between successional stages, reflect

the fact that the temporal increase in evenness is counterbalanced by the increase in relatedness between the most dominant species towards late succession (Figs. 1c & S2): the most dominant species within the early successional stages *(Loropetalum chinense*, *Quercus serrata*, *Rhododendron simsii*) are distantly related, whereas late successional communities were comprised of closely related species, i.e. belonging to the genera *Castanopsis*, *Rhododendron*, *Camellia* and *Eurya*, respectively – resulting in an absence of a net change in phylogenetic diversity and composition over time. Further, low levels of temporal functional turnover during tropical forest succession, were detected in an earlier study by Swenson *et al.* (2012), presumably due to relatively constant local environmental conditions through time. In our study, environmental differences between communities at different successional stages were similar to those between communities at the same stage (Fig. S4b,c), indicating that the lack of phylogenetic shifts likely reflects the constant abiotic conditions throughout succession.

In spite of the lack of temporal phylogenetic turnover between stages, we found a higher than expected presence/absence-based phylogenetic turnover (Π_{ST}) between plots that belong to the same successional stage, suggesting that there are filtering processes that have selected for different groups of closely related species. Our finding that the within-stage phylogenetic turnover (Π_{ST}) significantly increased with environmental distance (Fig. S4b) indicates that phylogenetic differentation between communities belonging to the same successional stage was due to an underlying environmental gradient (mainly related to soil moisture and light; see Table S6), and that the higher-than-expected levels of spatial phylogenetic turnover reflect differential abiotic filtering selecting for closely related species within communties that belong to the same successional stage (see following section). The strong association between within-stage phylogenetic turnover and environmental differences may also be a reflection of the fact that, in contrast to previous studies of community turnover in subtropical forest systems that have focussed on indirect abiotic descriptors such as elevation or habitat types (Legendre *et al.,* 2009), we used a large set of environmental (edaphic, light & topographic) descriptors. And it has been demonstrated recently that the quality of environmental data may influence conclusions about assembly processes (Chang *et al.,* 2013).

Temporal changes in within-stage turnover

We found that there was a shift from (abundance-based) spatial phylogenetic overdispersion within the first successional stage towards (presence/absence-based) spatial phylogenetic clustering within the two late successional stages (Fig. 3). This contrasts with a number of previous studies of successional tropical and subtropical forests (Letcher, 2010; Ding *et al.,* 2012; Norden *et al.,* 2012; Whitfeld *et al.,* 2012) that found high levels of phylogenetic relatedness in young, disturbed forest communities, compared to older communities. Those studies concluded that disturbance in early succession acts as an abiotic filter and selects for closely related species but that competitive exclusion of closely related species becomes increasingly important towards late succession. Our finding that the most dominant species within plots were less related to each other than to species from different plots within the first successional stage may be explained in a number of different ways: First, phylogenetic overdispersion may reflect abiotic filtering if the traits conferring environmental tolerance are not phylogenetically conserved and distantly related species are filtered by the same environment (Cavender-Bares *et al.,* 2004). However, we detected significant phylogenetic signal in a set of six traits reflecting multiple axes of plant functional differentiation, and Eichenberg *et al.* (2015) found even stronger phylogenetic signal in the same study system when intraspecific trait variation was taken into account. This indicates that phylogenetic relatedness reflects ecological similarity between species and that abiotic filtering of convergent niche traits is unlikely to explain phylogenetic overdispersion in our study. Second, phylogenetic overdispersion may result from competitive exclusion of closely related species that share similar traits – a process that is expected to result in overdispersion at small phylogenetic scales. However, in our study, we did not detect phylogenetic overdispersion at shallow phylogenetic depth (Fig. 5). Third, it has recently been demonstrated that early-successional communities may be comprised of distantly related species in cases where (i) early-successional pioneers are distributed all over the phylogeny (Letcher *et al.,* 2015) and/or (ii) remnant species, which have persisted from former management, have a wide range of phylogenetically conserved traits that allow them to tolerate early successional environmental conditions (Bhaskar *et al.,* 2014). Because in our study, (i) most species were present throughout succession, and (ii) remnant species were represented by only a few individuals (e.g. *Nyssa sinensis*, *Castanea henryi*, *Cyclobalanopsis glauca, Castanopsis fargesii*; see Fig.

528 1c & Bruelheide *et al.,* 2011) and hence did not substantially contribute to abundance-based
529 phylogenetic structure, the abundance-based phylogenetic overdispersion in early succession
530 is unlikely to reflect the presence of pioneer or remnant species. Finally, phylogenetic
531 overdispersion may reflect successful dispersal of species that have different dispersal
532 stategies (Du *et al.,* 2012), provided that dispersal traits are phylogenetically conserved
533 (Baeten *et al.,* 2015). In our study, the most abundant species within the first successional
534 stage (e.g. *Loropetalum chinense, Quercus serrata, Rhododendron simsii*) were both, distantly
535 related (Fig. 1c) and dispersed by different dispersal modes (animal-dispersed acorns,
536 ballistic- and wind-dispersed seeds for *Quercus*, *Loropetalum* and *Rhododendron*,
537 respectively), suggesting that the abundance-based phylogenetic overdispersion in early
538 succession likely reflects the coexistence of a wide range of different dispersal strategies
539 (Levin & Muller-Landau, 2000; Purschke *et al.,* 2014).
540 Within the two late successional stages, presence/absence-based phylogenetic turnover
541 was higher than expected relative to the levels of species turnover, indicating deterministic
542 filtering that selects for distinct sets of closely related species in the different plots. There are
543 a few studies that found increasing functional similarity in (sub-)tropical forest communities
544 over time (Uriarte *et al.,* 2010; Buzzard *et al.*, 2015), concluding that the relative importance
545 of abiotic filtering increases with forest age. Further, the previous studies by Hardy *et al.*
546 (2012) and Fine & Kembel (2011), focussing on phylogenetic turnover between tree
547 communities along environmental gradients, pointed out that, if environmental niches are
548 evolutionarily conserved, abiotic filtering is predicted to result a in strong covariation between
549 phylogenetic turnover and environment differentiation between plots (Cadotte & Tucker,
550 2017). Therefore, our finding that phylogenetic turnover within late successsional stages was
551 higher than expected and explained by environmental differentation [mainly related to to soil
552 and light conditions (Table S6), and independent of spatial distance] between plots (Fig. 4), is
553 consistent with phylogenetic niche conservatism and indicates that the relative importance of
554 environmental filtering along an environmental gradient increased during the course of
555 succession. The high phylogenetic turnover within the late successional stages, together with
556 the lack of temporal between-stage phylogenetic turnover, further suggests that phylogenetic
557 clustering in late succession reflects the local colonization of species that (i) are closely
558 related to residents (Li *et al.,* 2015) and (ii) were already present in the early-successional

559 species pool, indicating that species sorting into their preferred habitat takes time to develop.
560 Spatial phylogenetic clustering in late succession was only detected close to the root of the
561 phylogenetic tree (Fig. 5). Previous studies of community turnover across phylogenetic scales
562 (Parmentier & Hardy, 2009; Cavender-Bares & Reich, 2012) found that phylogenetic turnover
563 increased both with phylogenetic depth as well as with environmental differentiation between
564 sites, and concluded that ancient diversification events, together with niche conservatism, still
565 show an imprint on the assembly of current plant communities. The fact that, in our study,
566 spatial phylogenetic clustering (Π_{ST}) within late successional communities was only detected
567 at large phylogenetic scales (i.e. between taxa that diverged >100 Myrs years ago), together
568 with the finding that phylogenetic turnover was explained by abiotic differences (related to
569 soil and light conditions) between plots is consistent with deep phylogenetic signal in species'
570 soil moisture and light niche. Clades that contributed to the high phylogenetic turnover within
571 the late successional stage diverged early in phylogeny and were associated with one or the
572 other end of the environmental gradient (Table S8, Fig. S7), indicating environmental niche
573 differentiation between species that diverged early in phylogeny.
574 Alternatively, phylogenetic clustering in late succession can also result from
575 hierarchical competition if early successional pioneers are replaced by competitively superior
576 closely related species in late succession (Kunstler *et al.,* 2012; Letten *et al.,* 2014). However,
577 most early-successional species in our study were still present in late succession. Further,
578 hierarchical competition is predicted to result in phylogenetic clustering that is unrelated to
579 environmental differentiation between plots (Bartlett *et al.,* 2015), which was not the case in
580 our study. This suggests that competition hierarchies are unlikely to explain the phylogenetic
581 clustering in our study. Our finding that non-random phylogenetic structure within the two
582 latest successional stages was only detected based on presence/absence-data (Fig. 3a), is
583 likely to reflect the high number of rare species found in late compared to early succession
584 (Fig. 1c, see also Bruelheide *et al.,* 2011), and in such situations presence/absence metrics
585 (such as Π_{ST}), giving high weight to rare species, will provide greater testing power to detect
586 significant community phylogenetic structure than metrics based on abundance (Helmus *et*
587 *al.,* 2007; Vellend *et al.,* 2011).
588 In conclusion, the integrated analysis of the spatial and temporal components of
589 phylogenetic relatedness during succession, across phylogenetic and environmental scales,

allowed to test competing hypothesis about the temporal dynamics of community processes after disturbance. Our results do not support a model that predicts a progression towards decreasing phylogenetic relatedness over time. Instead, our findings support a deterministic model of community assembly where the phylogenetic composition is constrained though time but different assembly processes act at different ends of the successional gradient: colonization of species that differ in their dispersal strategies likely plays an important role in early succession, whereas, despite the lack of phylogenetic shifts between stages, environmental filtering of niche traits that are conserved deep in phylogeny becomes increasingly important towards late succession. Such insights into the temporal dynamics of post-disturbance community assembly processes were not apparent from previous analyses that focused either on single (spatial or temporal) phylogenetic turnover components or single phylogenetic scales.

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Author contributions

H.B. established the BEF-China experimental platform. O.P. developed the main idea for this manuscript with contributions from W.D., S.G.M. & H.B.. O.P. analysed the data and interpreted the results with input from all co-authors. S.G.M. generated the phylogenetic tree with contributions from W.D.. O.P. wrote the first draft of the manuscript with all other authors substantially contributing to revisions.

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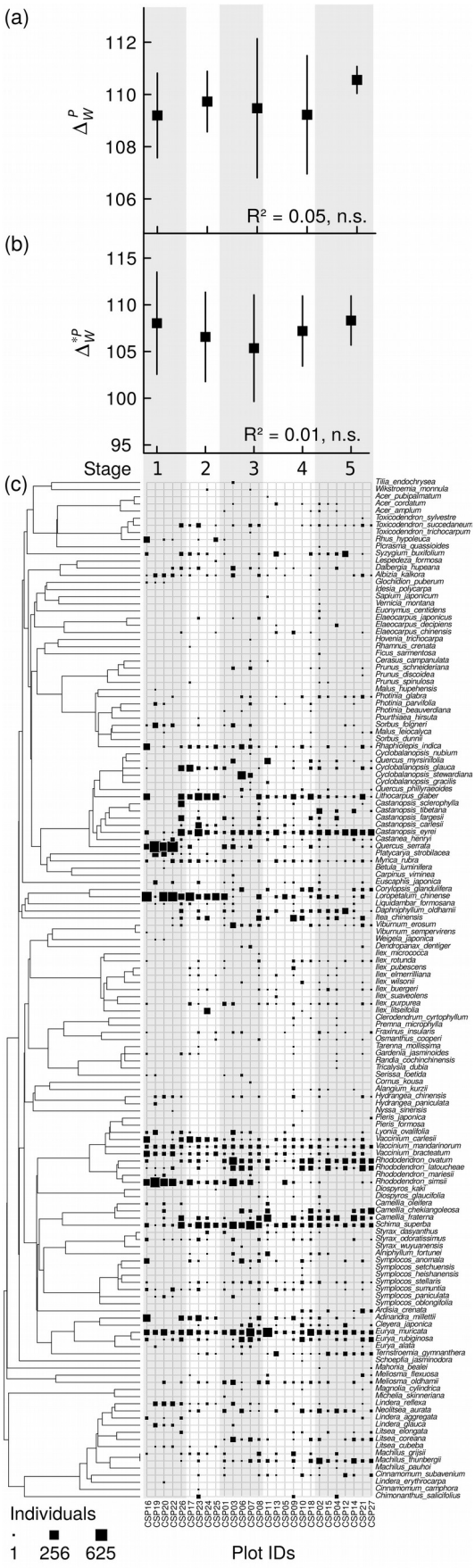

878 **Fig. 1** Phylogenetic alpha diversity within the five successional stages (mean ± 1 SE; Stage 1
879 (<20 yr): n=5, Stage 2 (20-39 yr): n=4, Stage 3 (40-59 yr): n=5, Stage 4 (60-79 yr): n=6,
880 Stage 5 (≥80 yr): n=7), based on (a) presence/absence (Δ^{P}_{w}) and (b) abundance data (Δ^{*P}_{w}).
881 Δ^{P}_{w} and Δ^{*P}_{w} are equivalent to the mean phylogenetic distance between distinct species (Δ^{P}_{w}),
882 and the mean phylogenetic distance between individuals of distinct species (Δ^{*P}_{w}) within
883 communities, respectively. R^2 values are given. None of the two alpha diversity measures
884 showed a significant successional trend. (c) Distribution of abundances within the 27
885 comparative study plots [assigned to one of the five successional stages (Stage 1-5)] mapped
886 onto the phylogeny of the 143 species. The size of the black squares corresponds to the
887 number of individuals.
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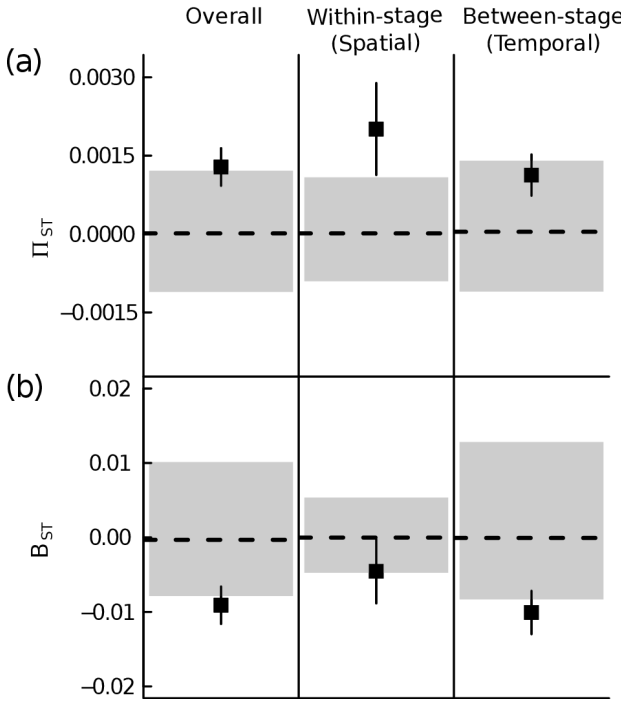

Fig. 2 Phylogenetic turnover for all pairs of plots (combining spatial and temporal turnover, n=351, left panel) dissected into spatial, i.e. within-successional stage, (n=62, middle panel) and temporal, i.e. between-stage, (n=289, right panel) turnover (black squares, mean ± 1 SE). Phylogenetic turnover was calculated for (a) presence/absence (Π_{ST}) and (b) abundance data (B_{ST}) and is based on the partitioning of the mean phylogenetic distance between distinct species, or between individuals of distinct species, into within- and between-community components. Π_{ST} or $B_{ST} > 0$ indicate that the species, or individuals, co-occurring within communities are phylogenetically more related to each other than to species from other communities (high turnover). B_{ST} or $\Pi_{ST} < 0$ indicate that the species, or individuals, co-occurring within communities are phylogenetically less related to each other than to species from other communities (low turnover). The black dashed line and grey-shaded area represent the mean and the 95% CI, respectively, from the 999 random communities. B_{ST} and Π_{ST} values outside the interval indicate non-random phylogenetic turnover.

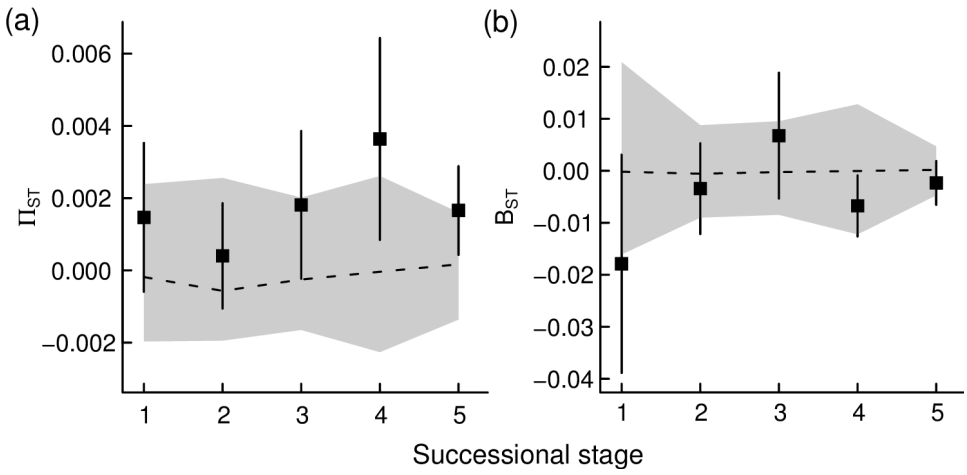

Fig. 3 Spatial phylogenetic turnover between all pairs of communities within each of the five successional stages (black squares, mean ± 1 SE; Stage 1: n=10, Stage 2: n=6, Stage 3: n=10, Stage 4: n=15, Stage 5: n=21), based on (a) presence/absence (Π_{ST}) and (b) abundance data (B_{ST}). B_{ST} or Π_{ST} values above (or below) the grey-shaded area (i.e. the 95% CI for the B_{ST} or Π_{ST} values from the 999 random communities) indicate spatial phylogenetic clustering (or overdispersion).

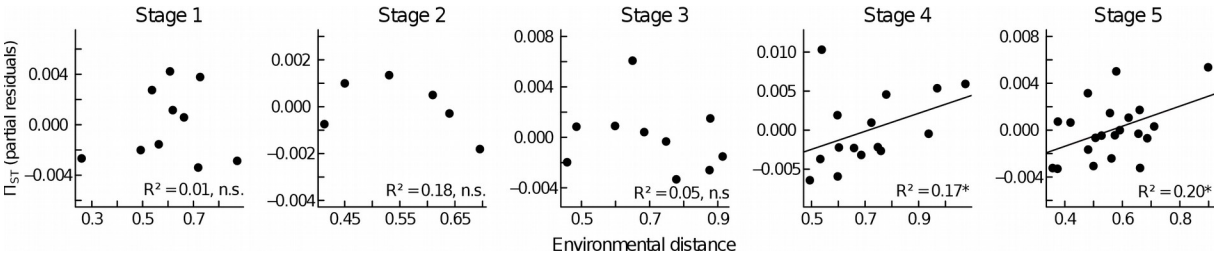

Fig. 4 Relationship between presence/absence-based phylogenetic turnover (Π_{ST}) and environmental differences (with respect to topography, light and soil characteristics) between communities, within each of the five successional stages. Π_{ST} values are given as partial residuals after accounting for spatial distance as a covariable. R^2 values are given. Significant relationships (based on randomization testing) are indicated by solid lines and are only detected in the two late successional stages. *$P \leq 0.05$, n.s. not significant.

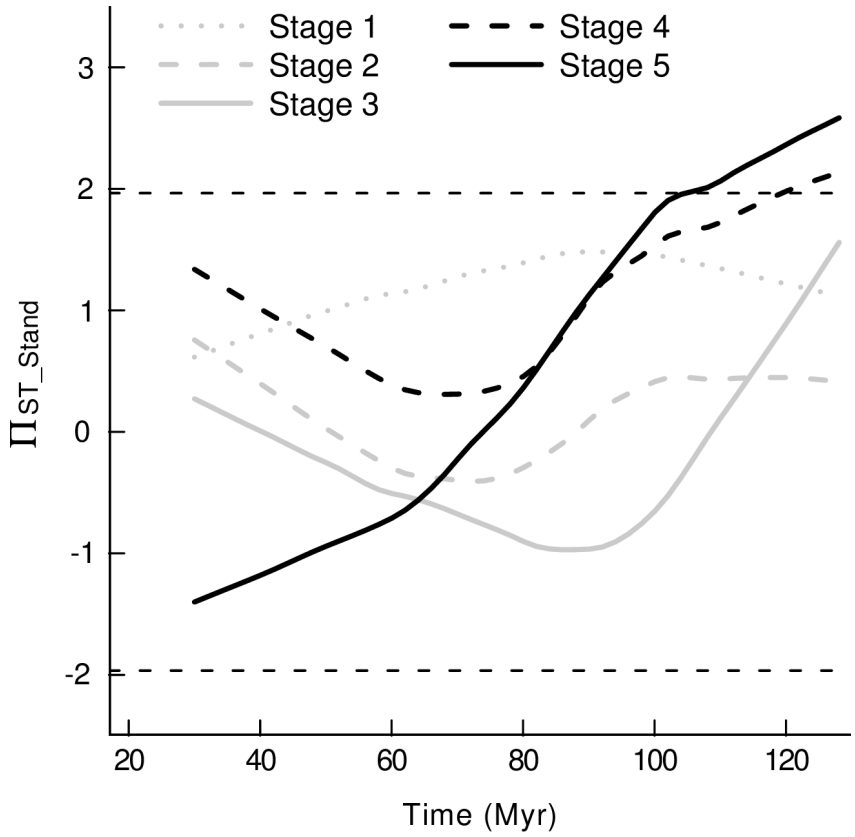

Fig. 5 Phylogenetic turnover, based on presence/absence data (Π_{ST}), at different phylogenetic depths, within the five successional stages. The lines represent, for each successional stage, fitted curves from local polynomial regression (loess, smoothing span = 0.66, polynomial degree = 1), of node age against the standardized effect size of phylogenetic turnover (Π_{ST_Stand}). Π_{ST_Stand} values were calculated as the ratio between observed to expected values of Π_{ST}: $\Pi_{ST\_Stand}=(\Pi_{ST\_obs} - \Pi_{ST\_exp})/sd(\Pi_{ST\_exp})$, where Π_{ST_obs} is the observed Π_{ST} value at a particular node, and Π_{ST_exp} and $sd(\Pi_{ST\_exp})$ are the mean and standard deviation of the expected Π_{ST} values from 999 partial phylogenetic tree randomizations among clades younger than that particular node. The two horizontal dashed lines indicate the 0.05 significance levels. Non-random and higher-than-expected turnover (spatial phylogenetic clustering) was only detected within the two late successional stages and at broad phylogenetic scales (from approximately 128 to 100 Myr).

996 ***Supporting Information***

997 **Fig. S1** Rarefaction curves of the 27 woody plant communities (CSPs), giving the estimated
998 number of species for any number of individuals. The five successional stages are indicated
999 by different line colors. The vertical line depicts the minimal number of individuals (n=175)
1000 sampled in a plot. The intersection between the rarefaction curves and the vertical line
1001 corresponds to the estimated number of species if only 175 individuals per plot were sampled.
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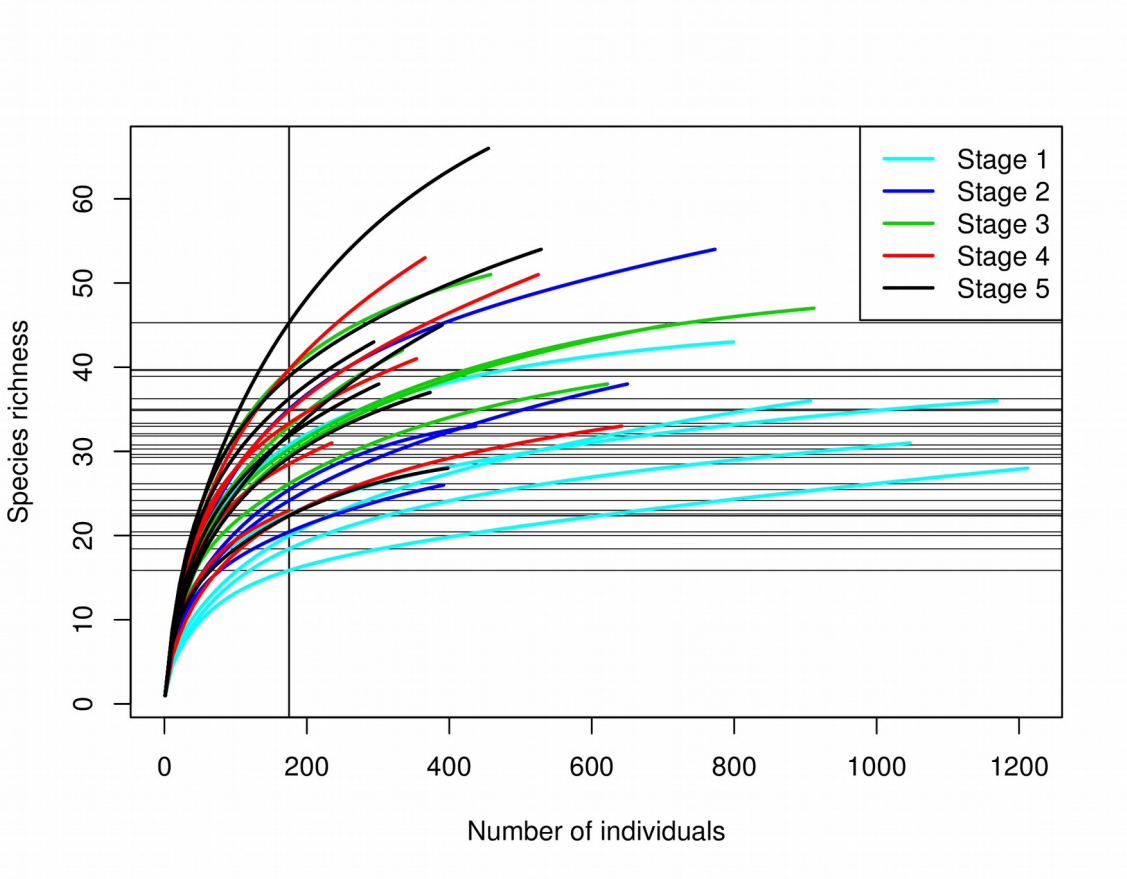

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Fig. S2 Shannon evenness within each of the five successional stages (black squares, mean ± 1 SE). R^2-value is given. The solid line indicates the significant relationship between evenness and successional stage. ** $P \leq 0.01$.

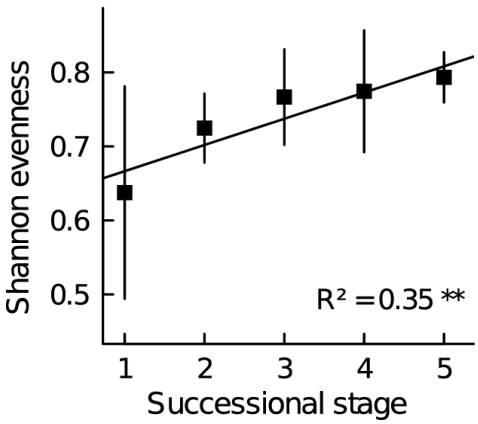

Fig. S3 Phylogenetic turnover between successional stages (black squares, mean ± 1 SE), calculated for (a) presence/absence (Π_{ST}) and (b) abundance data (B_{ST}). The black dashed line and grey-shaded area represent the mean and the 95% CI, respectively, from the 999 random communities. B_{ST} and Π_{ST} values above the interval indicate higher than expected temporal phylogenetic turnover. B_{ST} and Π_{ST} values below the interval indicate lower than expected temporal phylogenetic turnover.

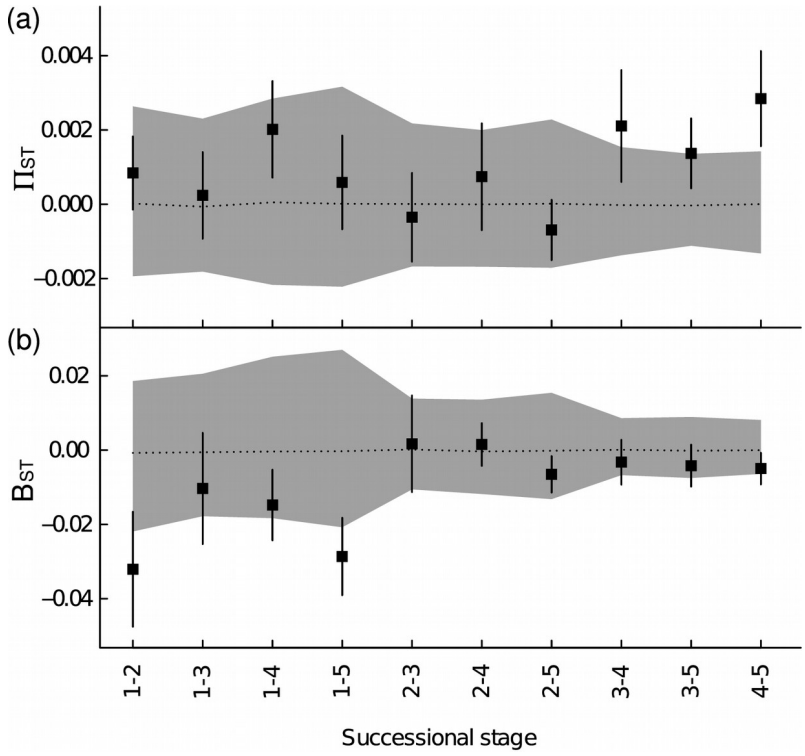

Fig. S4 Relationships between presence/absence-based phylogenetic turnover and environmental differences (with respect to topography, light and soil characteristics) between communities for (a) all pairs of plots (combining spatial and temporal turnover, n=351), (b) pairs of plots of the same successional stage (spatial turnover, n=62) and (c) pairs of plots belonging to different successional stages (temporal turnover, n=289). Π_{ST} values are given as partial residuals after accounting for spatial distance as a covariable. R^2 values are given. The significant relationship (based on randomization testing) between spatial phylogenetic turnover and environmental distance is indicated by the solid red line. * $P \leq 0.01$, . $P \leq 0.1$, n.s. not significant.

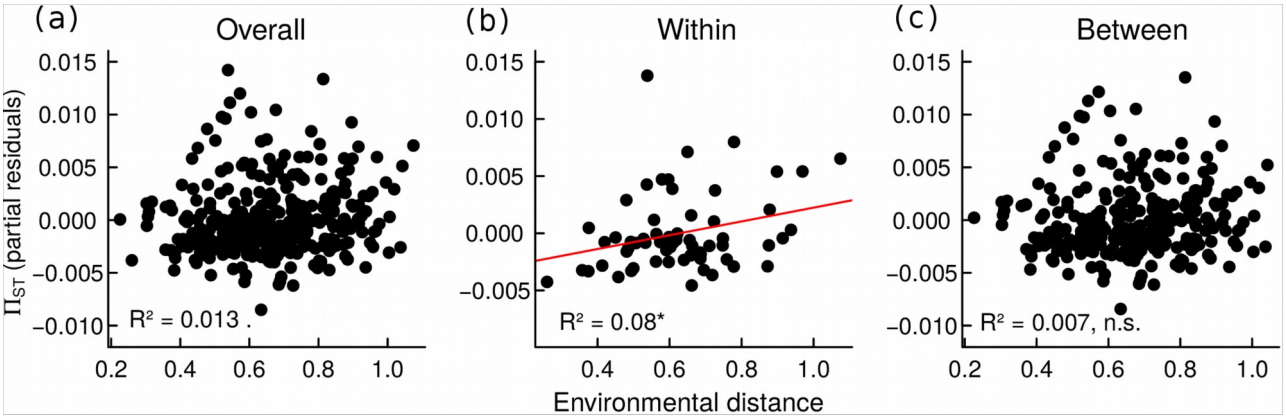

Fig. S5 Phylogenetic turnover, based on presence/absence data (Π_{ST}), at different phylogenetic depths, within the five successional stages. Standardized Π_{ST} values (Π_{ST_Stand}) are given, calculated as the ratio between observed to expected values of Π_{ST}: $\Pi_{ST\_Stand}=(\Pi_{ST\_obs} - \Pi_{ST\_exp})/sd(\Pi_{ST\_exp})$, where Π_{ST_obs} is the observed Π_{ST} value at a particular node, and Π_{ST_exp} and $sd(\Pi_{ST\_exp})$ are the mean and standard deviation of the expected Π_{ST} values from 999 partial phylogenetic tree randomizations among clades younger than that particular node. The dashed lines indicate the 0.05 significance levels. Non-random and higher-than-expected turnover (spatial phylogenetic clustering) was only detected within the two late successional stages and at broad phylogenetic scales (from approximately 128 to 100 Myr).

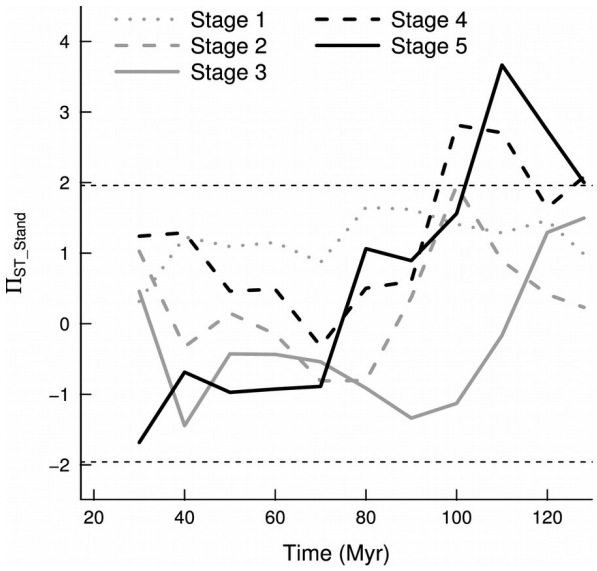

Fig. S6 Illustration of results from the nodesig analysis. Highlighted are clades (shaded areas) that had significantly more taxa than expected in plot pairs with the highest levels of phylogenetic turnover at the two latest successional stages (blue: plot pair CSP 5 & 11 at stage 4; red: CSPs 4 & 12 at stage 5, see also Fig. 1c). For instance, node N39 and N44, respectively, i) were significantly associated with the plots CSPs 5 and 11 (the plot pair that that had the highest phylogenetic turnover in stage 4, see also Table S8), and ii) correspond to the families Theaceae (*Camellia, Schima*) and Ericaceae (*Rhododendron, Vaccinium, Lyonia, Pieris*), that diverged early in phylogeny ~100 Myrs ago within the Ericales at node N22 (red vertical line). See Table S8 for a complete list of nodes that were significantly associated with each of the plots.

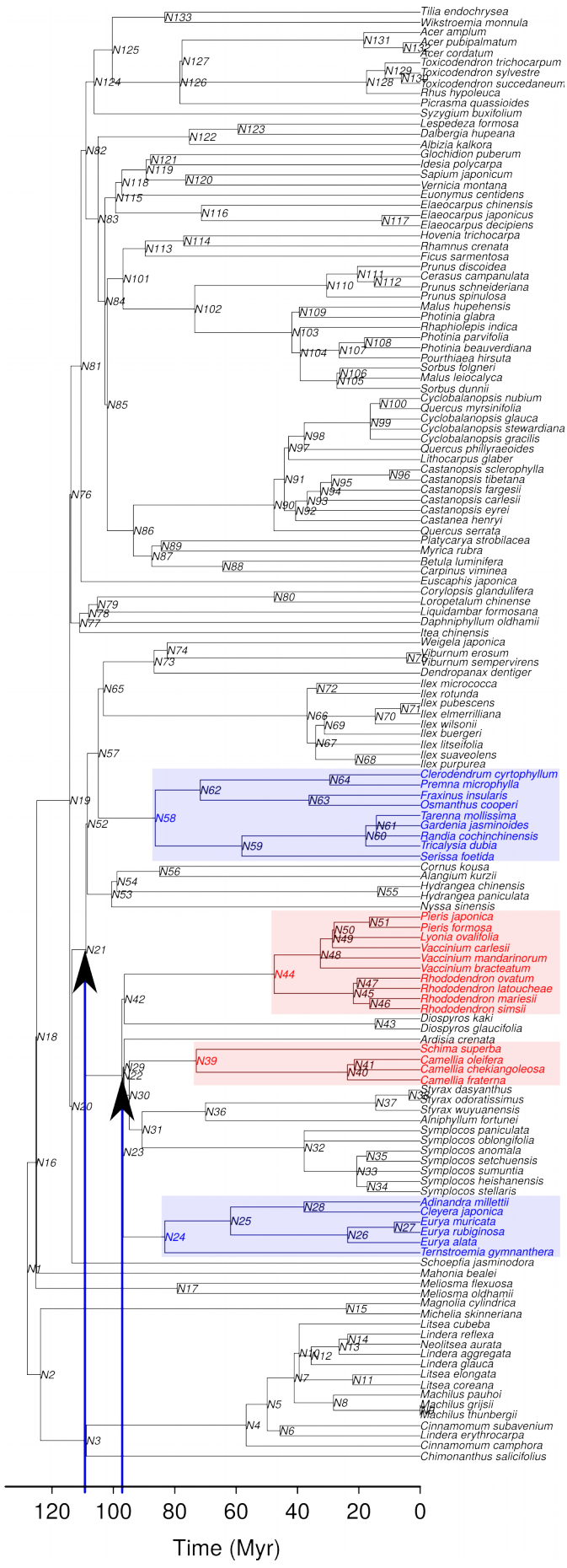

Fig. S7 PCA biplot illustrating the association between the 11 environmental variables and the 27 plots (CSPs). See Table S6 for variable loadings and Table S2 for Pearson correlations.

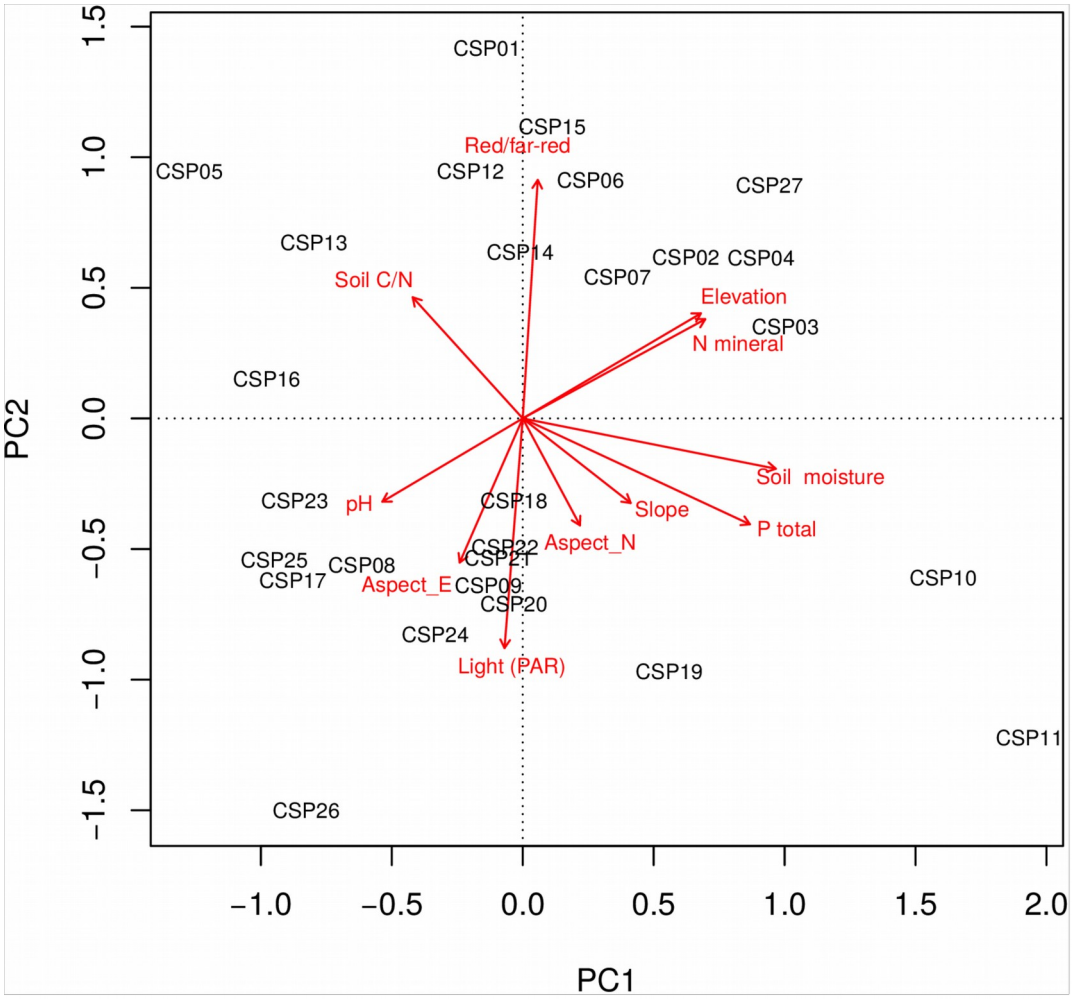

Table S1 Correlations between non-rarefied and rarefied phylogenetic metrics. Estimates of phylogenetic diversity and turnover were recalculated (100 times) for rarefied communities containing 175 individuals each (the minimum number of individuals recorded in a plot). Rarefied and non-rarefied estimates for all of the metrics were strongly ($P < 0.05$) correlated.

	Correlation	
Metric	**Mean**	**SD**
Δ^{P}_{w}	0.821	0.036
Δ^{*P}_{w}	0.970	0.006
Π_{ST}	0.632	0.049
B_{ST}	0.967	0.004

Table S2 Pearson correlations between successional stage and the 11 abiotic environmental descriptors and successional stage. Significant correlations ($P < 0.05$) are highlighted in bold.

	Elevation	Aspect_E	Aspect_N	Slope	Light (PAR)	Red/far-red	Soil moisture	pH	Soil C/N	N mineral	P total
Stage	0.29	-0.26	-0.26	0.11	**-0.41**	**0.59**	0.29	-0.36	0.1	**0.59**	0.07
Elevation		-0.29	0.03	-0.11	-0.28	0.21	**0.51**	**-0.43**	-0.06	**0.47**	0.29
Aspect_E			0.24	0.23	**0.39**	-0.31	-0.21	0.11	0.1	-0.18	0.03
Aspect_N				**0.4**	0.21	-0.21	0.15	-0.26	0.13	-0.18	0.28
Slope					0.04	-0.06	0.33	-0.15	0.05	0.14	**0.48**
Light (PAR)						**-0.82**	0.14	0.09	-0.27	-0.25	0.12
Red/far-red							-0.13	-0.27	**0.38**	0.3	-0.18
Soil moisture								-0.34	**-0.43**	**0.5**	**0.83**
pH									-0.24	**-0.4**	-0.15
Soil C/N										-0.13	**-0.58**
N mineral											0.31

1204 **Table S4** Sequence information for the woody plant species in the Gutianshan National
1205 Nature Reserve.
1206

		GeneBank accession number		
Species	**Species substitute or synonym**	***mat*K**	***rbc*L**	**5.8s+ITS**
Abelia_chinensis		AY310461	HQ680737	FJ745388
Abutilon_theophrasti		HM850990	HM849734	DQ006017
Acanthopanax_trifoliatus		U58603	U50239	
Acer_amplum	*Acer campestre*	JN894032	DQ978399	DQ238431
Acer_buergerianum			DQ978396	U89908
Acer_cordatum	added manually to ML tree			
Acer_davidii		JF952989	DQ978406	JF975773
Acer_elegantulum		HQ427339	HQ427191	
Acer_mono			DQ978416	AY605447
Acer_olivaceum		HQ427338		
Acer_pubipalmatum	added manually to ML tree			
Acer_tataricum			DQ978436	AY605363
Acer_wilsonii		HQ427337	HQ427189	HM352665
Actinidia_callosa		AF322620	AJ549061	AF323829
Actinidia_chinensis		U61324	L01882	
Actinidia_hemsleyana		AF322608	AJ549036	AF323802
Actinidia_lanceolata			AJ549072	
Actinidia_melanandra		AF322600		AF443211
Adina_rubella			AJ346965	AJ346856
Adinandra_millettii		AF380069	HQ427223	AY626848
Aesculus_chinensis		EU687709		JF421459
Ailanthus_altissima		EF489111	HM849750	JF755934
Akebia_quinata		AF542587	L12627	GQ339575
Akebia_trifoliata		GQ434168	AF335305	AY029788
Alangium_kurzii		FJ644650	DQ340449	FJ610018
Alangium_platanifolium		FJ644640	JF308649	FJ610006
Albizia_julibrissin		AY386855	GU135262	FJ572041
Albizia_kalkora		HQ427295	HQ427141	JF708202
Alniphyllum_fortunei		HQ427279	AF396149	AF396437
Amelanchier_asiatica				JQ392362
Antidesma_japonicum	*Antidesma venosum*	HQ415372	JF265291	
Aphananthe_aspera		AF345320	AF500339	
Aralia_chinensis		HQ427393	HQ427250	U63181
Aralia_dasyphylla				DQ007355
Aralia_echinocaulis				AF273525
Ardisia_brevicaulis				FJ482141
Ardisia_crenata		HQ427412	L12599	JN645186
Ardisia_crispa				FJ482139
Ardisia_hanceana				JN645190
Ardisia_japonica		JF416274	GQ436756	JN645201
Berberis_soulieana	*Berberis fortunei*		FJ449857	FJ980428
Berchemia_huana	*Berchemia zeyheri*	JF270656	JF265303	
Betula_luminifera		FJ011821		AY761116

Bischofia_polycarpa	*Bischofia javanica*	GU135116	AY663571	
Broussonetia_papyrifera		AF345326	JF317478	HM623778
Buddleja_lindleyana	*Buddleja davidii*	HQ384530	AJ001757	
Buxus_sinica	*Buxus sempervirens*	AF543728	HM849831	EF123195
Caesalpinia_decapetala		HM049555		JF708207
Callicarpa_bodinieri		HQ427330	HQ427182	
Callicarpa_giraldii		HQ427332	HQ427184	FJ593347
Callicarpa_japonica		FM163257		FM163230
Callicarpa_rubella		HQ427329	HQ427181	FM163232
Camellia_brevistyla				HM061465
Camellia_chekiangoleosa		HQ427374	HQ427229	EU579685
Camellia_cuspidata		HQ427370	HQ427225	EU579693
Camellia_fraterna			HQ427224	EU579705
Camellia_oleifera			GQ436647	HM061454
Camellia_sinensis		AJ429305	AF380037	HM061514
Camptotheca_acuminata		JF953409	L11211	JF976064
Campylotropis_macrocarpa		AY386870	EU717277	GU572164
Caragana_sinica		HM049541	FJ537233	FJ537284
Carpinus_londoniana		AY211990		AF432040
Carpinus_viminea		AY212000	HQ427161	AF432058
Castanea_henryi		EF057123		
Castanea_mollissima		EF057124		
Castanea_seguinii		AY263920	AY263937	
Castanopsis_carlesii		AY040496	HQ427175	AY040372
Castanopsis_eyrei		EF057125	HQ427167	EF057109
Castanopsis_fargesii		EF057133	HQ427173	AY040383
Castanopsis_sclerophylla		EF057137		EF057106
Castanopsis_tibetana		AY263921	AY147096	
Celastrus_aculeatus				JQ424095
Celastrus_angulatus		EU328938		JQ424098
Celastrus_gemmatus				JQ424102
Celastrus_oblanceifolius				JQ424119
Celastrus_rosthornianus		EU328940		JQ424130
Celastrus_stylosus				JQ424136
Celtis_biondii		KF569895	KF569888	
Celtis_tetrandra			JF317479	
Cephalotaxus_fortunei		AF228109	AY450863	
Cephalotaxus_sinensis		AF228110	EF660728	
Cerasus_campanulata	syn. *Prunus campanulata*		AF411501	AF318658
Chimonanthus_salicifolius		HQ427325	HQ427177	AY786102
Choerospondias_axillaris		HQ427341	HQ427193	GQ434625
Cinnamomum_camphora		AJ247154	L12641	AY878325
Cinnamomum_chekiangense		HQ427409	HQ427267	
Cinnamomum_subavenium		HQ427408	HQ427266	GU598529
Cladrastis_wilsonii	*Cladrastis sikokiana*		U74232	JQ676968
Clerodendrum_bungei				U77744
Clerodendrum_cyrtophyllum		HQ427333	HQ427185	JF755940
Clerodendrum_trichotomum		AF477760	HQ427186	U77771
Clethra_barbinervis		AB697681	AF421089	AY190573
Cleyera_japonica		HQ427371	EU980811	AF456257

Coptosapelta_diffusa			EU145453	DQ358882
Cornus_controversa		U96893	AF190433	AY530918
Cornus_kousa		DQ341345	L14395	DQ340555
Corylopsis_glandulifera	syn. *Corylopsis hypoglauca*	HQ427314	HQ427165	EF456719
Corylopsis_sinensis		AF013038	AB237032	EF456711
Crataegus cuneata	*Crataegus monogyna*	JN893932	JN890652	
Cryptomeria_fortunei		AB030117		
Cunninghamia_lanceolata		AB030125	AY140260	
Cyclobalanopsis_glauca	syn. *Quercus glauca*	AB060062	AB060571	AY040458
Cyclobalanopsis_gracilis	syn. *Quercus ciliaris*	HQ427318	HQ427169	
Cyclobalanopsis_nubium	syn. *Quercus sessilifolia*	AB060068	AB060577	
Cyclobalanopsis_stewardiana		KF569896	KF569889	
Cyclocarya_paliurus		AY147098	AY147094	AF303817
Dalbergia_hupeana		HQ427296	U74236	GU217673
Daphne_genkwa	*Daphne laureola*	JN894952	HM849946	GQ167533
Daphniphyllum_macropodum			AM183400	
Daphniphyllum_oldhamii		HQ427311	HQ427162	JN040993
Dendropanax_dentiger		HQ427394	HQ427251	GU054694
Deutzia_glauca	*Deutzia setchuenensis*	JF308687	JF308658	
Diospyros_glaucifolia		HQ427382	EU980694	FJ624405
Diospyros kaki		GQ434247	EU980698	FJ624403
Diospyros_morrisiana		HQ427383	HQ427240	
Diospyros_oleifera		AB174997		AB175016
Diospyros_rhombifolia		AB174999	EU980741	AB175018
Distylium_myricoides		GU576683	AM183408	GU576648
Edgeworthia_chrysantha			AJ297920	AJ744932
Ehretia_thyrsiflora			EU599831	
Elaeagnus_glabra				JQ062502
Elaeagnus_multiflora				JQ062478
Elaeagnus_pungens		GU135102	GU135269	JQ062488
Elaeagnus_umbellata		AY257529	HM849968	JQ062486
Elaeocarpus_chinensis			HQ427153	
Elaeocarpus_decipiens		HQ415261	HQ415077	
Elaeocarpus_japonicus		HQ415264	HQ415080	
Eleutherococcus_gracilistylus			GQ436710	FJ980422
Emmenopterys_henryi		FJ905360	Y18715	FJ984985
Euchresta_japonica			AB127040	
Euodia_faugeaii	*Euodia hupehensis*	EF489105	FN552679	
Euonymus_alatus		EU328950		EU328755
Euonymus_carnosus		HQ427389	HQ427246	
Euonymus_centidens		HQ427390	HQ427247	
Euonymus_fortunei		HQ393828	HM755927	HQ393699
Euonymus_myrianthus		HQ427388	HQ427245	HQ393721
Euonymus_oblongifolius	syn. *Euonymus nitidus*	HQ393835	HQ427248	JQ424144
Euonymus_oxyphyllus		HQ393836		HQ393704
Eurya_alata				AF456259
Eurya_hebeclados				AY626865
Eurya_loquaiana		HQ427372	HQ427227	AY626870
Eurya_muricata		HQ427373	HQ427228	AY626872
Eurya_nitida				AY096026

Eurya_rubiginosa		HQ427368	HQ427222	AY626877
Euscaphis_japonica		DQ663628	DQ307099	
Fagus_engleriana		AY042391	JF941501	AY232907
Fagus_longipetiolata		AY042402	JF941508	AY232955
Fagus_lucida		EF057139	JF941510	AY232963
Ficus_erecta		HQ427366	HQ427220	HQ890729
Ficus_heteromorpha			JF941536	
Ficus_pandurata		HQ415327	HQ415153	
Ficus_pumila		HM851109	AF500352	AY063580
Ficus_sarmentosa				AB485901
Firmiana_platanifolia			AY328192	AF460185
Fontanesia_fortunei	syn. *Fontanesia phillyreoides*			AF534815
Forsythia_viridissima		FJ263957		AF534810
Fraxinus_chinensis		HM171509	DQ673301	HQ705225
Fraxinus_insularis		HQ427335	HQ427187	
Gardenia_jasminoides		HQ427344	GQ436564	GQ434646
Gardneria_multiflora				JF937929
Gleditsia_sinensis		AM086835		AF510019
Glochidion_puberum		HQ427285	AY663586	AY936659
Gymnocladus_chinensis				AF510033
Hamamelis_mollis		AF128827	L01922	GU576659
Helwingia_japonica		AJ430195	L11226	AF200593
Hibiscus_syriacus		AF345329	AY328174	AF460188
Holboellia_coriacea	*Holboellia grandiflora*	FJ626513	AF398181	AY029779
Hovenia_dulcis				DQ146607
Hovenia_trichocarpa		JF317429	JF317489	DQ146608
Hydrangea_angustipetala		GU217336		
Hydrangea_anomala		GU369710	AF323202	JF976651
Hydrangea_chinensis		KF569897	KF569890	AB377211
Hydrangea_paniculata		HQ427310	AB236036	
Hydrangea_strigosa	syn. *Hydrangea aspera*	AJ429277	JF941958	JF976653
Idesia_polycarpa		FJ670040	AF206781	AJ006441
Ilex_buergeri			FJ394593	FJ394663
Ilex_cornuta		GQ997309	FJ394601	EU647650
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Ilex_ficoidea		HQ427288	HQ427133	FJ394682
Ilex_latifolia		HQ427289	X98731	DQ200798
Ilex_litseifolia		KF569898		
Ilex_macrocarpa			AJ4927271	AJ492689
Ilex_micrococca		HQ427290	X98721	JF976691
Ilex_pubescens		HQ427291	AJ492722	AJ492686
Ilex_purpurea		HQ427292	AJ492710	FJ394708
Ilex_rotunda		HQ415255	X98720	FJ394710
Ilex_suaveolens		HQ427293	HQ427139	
Ilex_triflora			AJ4927131	AJ492675
Ilex_tsoi			FJ394645	FJ394718
Ilex_wilsonii		HQ427294	FJ394649	FJ394722
Illicium_lanceolatum		HQ427283	HQ427126	JQ180205
Indigofera_decora				AF534797
Itea_chinensis		HQ415356	HQ415186	

Jasminum_sinense	*Jasminum nudiflorum*	AF531779		AF361301
Juglans_cathayensis		AF118028		
Juniperus_chinensis		HM024014	HM024292	
Juniperus_formosana		HM024028	HM024306	
Kerria_japonica		AB073686	AF132893	
Koelreuteria_bipinnata			DQ978447	
Lasianthus_japonicus		HQ427345	HQ427196	
Lespedeza_buergeri				JN402408
Lespedeza_cyrtobotrya				JN402422
Lespedeza_dunnii				JN402431
Lespedeza_floribunda		HM049538	GQ436353	JN402438
Lespedeza_formosa	syn. *Lespedeza thunbergii*		HQ427143	JN402486
Ligustrum_lucidum		EU669873	GQ436542	JF976848
Ligustrum_sinense		JF830514	JF830433	JF830366
Lindera_aggregata		AB442057	HM019473	AB470487
Lindera_erythrocarpa		AB259065		HQ697215
Lindera_glauca		AB442056	HM019478	AB500615
Lindera_megaphylla		AF244404		AY265406
Lindera_reflexa		AF244401	HQ427264	AY265407
Liquidambar_acalycina		AF015649	DQ352380	GU576668
Liquidambar_formosana		AF133221	AJ131772	AF015436
Liriodendron_chinense		AF123481	AY841593	
Lithocarpus_cleistocarpus		EF057117		EF057114
Lithocarpus_glaber		HQ427322	AB060568	AY040435
Lithocarpus_hancei				AY040451
Litsea_coreana		HQ427405	HQ427263	AF272286
Litsea_cubeba		AF244398	AY337734	AB260863
Litsea_elongata		HQ427403	HQ427261	DQ120606
Lonicera_hypoglauca		HM228434	HM228478	FJ372916
Lonicera_japonica		GQ997392	HM850134	JQ780992
Lonicera_macranthoides		HM228448	HM228492	FJ372918
Lonicera_modesta				EU240716
Loropetalum_chinense		HQ427312	AF061999	GU576672
Lyonia_ovalifolia		U61305	AF124580	
Maackia_chinensis				EF457721
Machilus_grijsii		KF569899	KF569893	JF976985
Machilus_leptophylla		HM019350	HM019490	EF538697
Machilus_pauhoi		HQ427418	HM019496	EF538695
Machilus_thunbergii		KF569890	KF569894	FJ755429
Maesa_japonica				JF708192
Magnolia_cylindrica		HQ427420	AY008914	
Magnolia_denudata		AF123465	AY008913	EU593545
Magnolia_officinalis		AF548641	AY008933	EU593549
Mahonia_bealei		DQ478617	L12657	FJ424229
Mallotus_japonicus		AB268027	AY794934	
Mallotus_repandus		EF582678	GU441787	DQ866617
Malus_hupehensis		AF309179	JQ391346	JQ392455
Malus_leiocalyca		HQ427351	HQ427202	
Manglietia_fordiana		AY952412	L12658	
Melastoma_dodecandrum			GQ436727	GQ265883

Melia_azedarach		EF489117	AY128234	AY695595
Meliosma_flexuosa		HQ427361	HQ427214	
Meliosma_oldhamii		HQ427360	HQ427213	
Meliosma_rigida		HQ415309	HQ415132	
Michelia_maudiae		HQ415276	HQ415093	EU593553
Michelia_skinneriana		HQ427417	HQ427275	
Microtropis_fokienensis		HQ393848		HQ393683
Millettia_dielsiana	syn. *Callerya cinerea*		GQ436360	FJ980295
Millettia_reticulata	syn. *Callerya reticulata*	AF142733		AF467031
Morus_alba		AB038183	L01933	JN407493
Morus_australis		GU145559	GU145573	AY345152
Morus_cathayana		GU145565	GU145579	AM042001
Mussaenda_shikokiana				AJ846854
Myrica_rubra	syn. *Morella rubra*	HQ427396	HQ427253	AJ626784
Myrsine_stolonifera	*Myrsine_retusa*	HM850887	HM850193	
Neolitsea_aurata		HM019358	HM019498	JF977135
Nyssa_sinensis		JF308675	JF308651	EU734444
Orixa_japonica		EF489106		HM851496
Ormosia_henryi		HM049514		
Osbeckia_chinensis			AF215525	
Osmanthus_cooperi		EU669875	HQ427188	EF362772
Osmanthus_fragrans		FM208253		EU314904
Osmanthus_matsumuranus		EU409435		EF362770
Persea_grijsii		AJ247180		
Pertusadina_hainanensis		HQ427346	AJ347002	AJ346892
Philadelphus_brachybotrys	*Philadelphus pekinensis*	GU217268		
Phoebe_bournei		HM019369	HM019509	EF538706
Phoebe_sheareri		HQ427400	HM019513	FM957848
Photinia_beauverdiana		HQ427353	HQ427204	JQ392492
Photinia_glabra		HQ427354	HQ427205	FJ796905
Photinia_parvifolia		HQ427355	HQ427206	GQ368497
Photinia_serrulata	syn. *Photinia serratifolia*	AF288111	GQ436594	GQ368486
Photinia_villosa				FJ810016
Phyllanthus_glaucus			AY765271	HM106990
Phyllanthus_urinaria			AY765268	AY936735
Picrasma_quassioides		HQ427327	EU043008	GQ434548
Pieris_formosa		U61303	AF124581	EU547690
Pieris_japonica		AB206598	AB206589	EU547692
Pieris_taiwanensis		AB206599	AB206593	
Pinus_massoniana		DQ353716	DQ353732	
Pinus_taiwanensis		AB161016	DQ156493	
Pistacia_chinensis			FN599457	EF193079
Pittosporum_illicioides		HQ427307	HQ427157	
Platycarya_strobilacea		HQ427308	AY263933	AF303808
Pleioblastus_amarus	*Arundinaria tecta*	EF125165	AJ746179	HQ292267
Podocarpus_macrophyllus		AF228111	AF249616	
Podocarpus_nagi	syn. *Nageia nagi*	AB644449	AB644468	
Polygala_arillata			AM234210	
Populus_adenopoda	*Populus tremula*	AJ506086	AJ418827	
Pourthiaea_hirsuta				GQ368494

Premna_microphylla		HQ427331	U28883	
Prunus_discoidea			HQ427208	
Prunus_mume		JF955822	AF411491	JF978116
Prunus_persica		AF288117	AF411493	JF978127
Prunus_phaeosticta		HQ415272	HQ415089	EU669095
Prunus_salicina			AF411494	AF318725
Prunus_schneideriana		HQ427356	HQ427209	EU370928
Prunus_serrulata		GU363780	AF411487	AF318721
Prunus_spinulosa		HQ427357	AF411503	AF411513
Prunus_undulata				EU669108
Pseudolarix_kaempferi		AB019866	X58782	
Pterocarya_insignis	syn. *Pterocarya macroptera*			AF303814
Pterocarya_stenoptera		AF118042		AF179587
Pyrus_calleryana			JQ391379	JQ392478
Quercus_acutissima		AB060069	AB060578	AF098428
Quercus_fabri				HE591366
Quercus_myrsinifolia		AB060063	AB060572	AF098414
Quercus_phillyraeoides		HQ427324	AB060573	AY040462
Quercus_serrata		AB060067	AB060576	
Quercus_variabilis		AB060065	AB060574	AY040463
Randia_cochinchinensis	syn. *Aidia cochinchinensis*	HQ427347	HQ427198	
Rhamnella_franguloides			AJ3900271	AY626454
Rhamnus_crenata		HQ427385	HQ427242	AY626443
Rhamnus_utilis		JF317432	JF317492	
Rhaphiolepis_indica		HQ427352	HQ427203	JQ392494
Rhododendron_fortunei		AF454850	HQ706905	AF393407
Rhododendron_latoucheae		HQ427298	HQ427145	
Rhododendron_mariesii		AF454860	HQ427147	AF297202
Rhododendron_ovatum		U61330	HQ427144	JF978354
Rhododendron_simiarum			HQ706935	HQ707070
Rhododendron_simsii		HQ427299	GQ997829	JF978401
Rhus_chinensis			FN599458	EF682845
Rhus_hypoleuca		HQ427342		
Rosa_bracteata		HM490026		
Rosa_cymosa		AB039317		HM593924
Rosa_henryi		AB039310		AB038454
Rosa_laevigata		AB011997	GU363797	JN407516
Rosa_multiflora		AB039304	GQ436573	HM593923
Rosa_rubus		FJ472525		FJ416660
Rubus_amphidasys				AY083367
Rubus_buergeri				FJ472903
Rubus_chingii		HQ427358	HQ427211	
Rubus_corchorifolius				JF708203
Rubus_coreanus				FJ472906
Rubus_hirsutus		GU363753	GU363792	FJ472891
Rubus_hunanensis				FJ472902
Rubus_irenaeus				EF034131
Rubus_lambertianus				FJ472904
Rubus_parvifolius		AB073699	GU363802	JN407526
Rubus_pungens				FJ472893

Rubus_reflexus		JN407197	JN407362	JN407520
Rubus_swinhoei				EF034143
Rubus_tephrodes				EF034144
Rubus_trianthus				AY083366
Sabia_campanulata			AM183414	
Sabia_japonica		AM396512		
Sabia_swinhoei		GU266603	FJ626616	
Sageretia_thea			AJ2257851	AY626453
Salix_babylonica		AJ849593	FJ788588	
Sambucus_williamsii				JN040994
Sapindus_mukorossi			FN599461	
Sapium_discolor	syn. *Triadica cochinchinensis*	HQ415366	HQ415199	JF733770
Sapium_japonicum	syn. *Neoshirakia japonica*		AY794856	
Sapium_sebiferum	syn. *Triadica sebifera*	GU135113	AY794859	GU441830
Sassafras_tzumu		AF244391	HM019516	GU082375
Schima_superba		AJ429306	Z80208	HM100443
Schoepfia_jasminodora		HQ415321	HQ415146	
Securinega_suffruticosa	*Securinega capuronii*		AY663621	
Serissa_foetida	syn. *Serissa serissoides*		Z68822	FJ980385
Skimmia_reevesiana		FN668822	FN599464	
Sloanea_sinensis			HQ427152	
Sorbus_alnifolia	syn. *Aria alnifolia*	DQ860451		FJ810006
Sorbus_dunnii	syn. *Aria dunnii*			GQ368505
Sorbus_folgneri		HQ427359	HQ427212	
Sorbus_hemsleyi				FJ810010
Spiraea_blumei		JQ041791		JQ041773
Spiraea_cantoniensis		AF288127		DQ897609
Spiraea_chinensis		JQ041792		JQ041774
Spiraea_japonica				DQ897617
Spiraea_prunifolia		JQ041787		DQ897623
Spiraea_vanhouttei			L11206	U16205
Stachyurus_chinensis		AM396501	JF944501	DQ307102
Stauntonia_hexaphylla		FJ626517	L37922	AY029784
Stephanandra_chinensis		AF288128		AF487153
Stewartia_sinensis		AF380106	AF380061	AY070322
Styrax_calvescens				AF327468
Styrax_dasyanthus		HQ427280	HQ427123	AF327469
Styrax_faberi				AF327484
Styrax_japonicus				AF327465
Styrax_odoratissimus		HQ427282	HQ427125	AF327460
Styrax_suberifolius		HQ427281	HQ427124	AF327493
Styrax wuyuanensis	added manually to ML tree			
Symplocos_anomala		AY679808	HQ427233	AY336291
Symplocos_chinensis		AY336341		AF396229
Symplocos_heishanensis				AY630642
Symplocos_lancifolia		HQ415339	HQ415167	AB114887
Symplocos_laurina		AY336368		AY336318
Symplocos_oblongifolia	added manually to ML tree			
Symplocos_paniculata		AF440433	Z83139	AY336263
Symplocos_phyllocalyx		AY336357		AY336293

Symplocos_setchuensis		AY336359	HQ427235	AY336294
Symplocos_stellaris		HQ427379	HQ427236	AY336329
Symplocos_sumuntia		HQ427377		AY336322
Syzygium_buxifolium		HQ415314	HQ427244	EF026624
Tarenna_mollissima		HQ415401		
Taxodium_distichum		JQ512482	AF119185	
Taxus_chinensis			AY450856	
Ternstroemia_gymnanthera		AF380109	AF421106	HM061522
Tilia_endochrysea		HQ427306	HQ427156	
Toona_ciliata				FJ462489
Toona_sinensis		JN680343	JN654542	FJ462490
Torreya_grandis		AF228108	DQ478794	
Toxicodendron_succedaneum		HQ427343	AY510144	FJ945957
Toxicodendron_sylvestre		HQ415319	AY510145	FJ945938
Toxicodendron_trichocarpum			AY510143	FJ945927
Trachycarpus_fortunei		HQ720315	AY012460	
Trema_cannabina	*Trema micrantha*	GQ982115	AF062004	AY635571
Tricalysia_dubia	*Diplospora dubia*	HQ427350	HQ427201	
Tutcheria_microcarpa		HQ427376	HQ427231	AF456277
Ulmus_parvifolia		AF345321	D86316	
Vaccinium_bracteatum		AB623177	KF569892	
Vaccinium_carlesii			KF569891	
Vaccinium_japonicum	syn. *Vaccinium erythrocarpum*	AF419710		AF419781
Vaccinium_mandarinorum	added manually to ML tree			
Vernicia_fordii		GU135095	GU135180	
Vernicia_montana		AB268057	AY794899	
Viburnum_dilatatum		HQ591575	HQ591719	JF979005
Viburnum_erosum		HQ427362	HQ427216	JF979007
Viburnum_fordiae		JF956802	JF944784	
Viburnum_plicatum		HQ591613	HQ591754	AY265143
Viburnum_propinquum		HQ591614	HQ591755	EF462987
Viburnum_sempervirens		HQ427363	HQ427217	HQ591976
Viburnum_setigerum		EF490251	GQ248708	HQ591977
Viburnum_sympodiale		HQ591630	HQ591770	EF462988
Vitex_negundo		AB284176	JQ322525	FM200123
Weigela_japonica		HQ427364	HQ427218	AF078716
Wikstroemia_indica		HQ415322	HQ415147	
Wikstroemia_monnula			HQ427215	
Xylosma_japonica	syn. *Xylosma congesta*	AB233834	AB233938	DQ521290
Zanthoxylum_ailanthoides			FN599470	HM851475
Zanthoxylum_armatum			GQ436751	HM851465
Zanthoxylum_austrosinense				HM851488
Zanthoxylum_simulans		EF489100		HM851466
Zelkova_schneideriana		AF345328		AJ622867
Zelkova_serrata			AF206835	AJ622877

Table S5 Age constraints for nodes used to create the ultrametric tree.

Clade	Node defined by MRCA to	Calibration type	Age [ma]	Reference
Seed plants	*Taxodium distichum* - *Abutilon theophrasti*	max	385	(Gerrienne et al. 2004)
Gymnosperms	*Pseudolarix kaempferi* - *Taxodium distichum*	min	318	(Renner 2009)
Cupressaceae	*Cunninghamia lanceolata* - *Taxodium distichum*	min	90	(LePage 2003)
Pinaceae	*Pseudolarix kaempferi* - *Pinus massoniana*	min	90	(Gandolfo et al. 2001) (Hughes and McDougall 1987,
Angiosperms	*Pleioblastus amarus* - *Abutilon theophrasti*	max	130	Hughes et al. 1991)
Laurales	*Chimonanthus salicifolius* - *Litsea cubeba*	min	108.8	(Crane et al. 1994)
Eudicots	*Holboellia coriacea* - *Abutilon theophrasti*	fixed	125	(Hughes and McDougall 1990)
Ranunculales	*Holboellia coriacea* - *Mahonia bealei*	min	91	(Knobloch and Mai 1986)
Berberidaceae	*Berberis soulieana* - *Mahonia bealei*	min	33.9	(Manchester 1999) (Magallon-Puebla et al. 1996,
Hamamelidaceae	*Liquidambar acalycina* - *Corylopsis sinensis*	min	83.5	Magallón et al. 2001)
Fabales	*Polygala arillata* - *Albizia kalkora*	min	60	(Lavin et al. 2005)
Malpighiales	*Vernicia fordii* - *Phyllanthus urinaria*	min	89.3	(Crepet and Nixon 1998)
Salicaceae	*Idesia polycarpa* - *Populus adenopoda*	min	48	(Boucher et al. 2003) (Pacltová 1966, Batten 1981,
Fagales	*Quercus serrata* - *Juglans cathayensis*	min	93.5	Kedves 1989)
Juglandaceae	*Cyclocarya paliurus* - *Juglans cathayensis*	min	55.8	(Crane et al. 1990)
Rosaceae	*Rosa cymosa* - *Prunus pseudocerasus*	min	37.2	(Manchester 1999)
Ulmaceae	*Ulmus parvifolia* - *Zelkova schneideriana*	min	33.9	(Manchester 1999)
Rutaceae-Meliaceae	*Melia azedarach* - *Skimmia japonica*	min	50	(Corbett and Manchester 2004)
Myrtales	*Melastoma dodecandrum* - *Syzygium buxifolium*	min	60	(Pigg et al. 1993)
Ericales	*Actinidia melanandra* - *Ardisia crenata* *Actinidia melanandra* - *Rhododendron*	min	89.6	(Nixon and Crepet 1993)
Actinidiaceae (stem node)	*latoucheae*	min	77.05	(Schenk and Hufford 2010)
Cornaceae	*Alangium kurzii* - *Cornus kousa*	min	55.8	(Manchester 1999)
Nyssaceae	*Camptotheca acuminata* - *Nyssa sinensis*	min	33.9	(Manchester 1999)
Hydrangeaceae	*Deutzia glauca* - *Hydrangea strigosa*	min	37.2	(Manchester 1999)
Cornales	*Camptotheca acuminata* - *Cornus kousa*	min	89	(Schenk and Hufford 2010)
Oleaceae	*Osmanthus matsumuranus* - *Fraxinus chinensis*	min	33.9	(Manchester 1999) (Manchester and Donoghue
Dipsacales	*Viburnum sympodiale* - *Lonicera modesta*	min	33.9	1995)
Apiales	*Pittosporum illicioides* - *Dendropanax dentiger*	min	37.2	(Manchester 1999)

Table S6 Loadings and percentage of total variation explained of the first six principal components (PCs) of a PCA on the eleven environmental variables. The first two PCs correspond to variation in soil moisture and light, respectively. See Fig. S7 for PCA biplot.

	PC1	PC2	PC3	PC4	PC5	PC6
Elevation	0.8	0.47	-0.09	0.5	-0.08	0.47
Aspect_Eastness	-0.28	-0.65	0.51	-0.06	0.67	0.54
Aspect_Northness	0.26	-0.48	0.83	0.17	-0.54	0.22
Slope	0.49	-0.38	0.7	-0.65	0.04	-0.29
Light (PAR)	-0.08	-1.03	-0.09	0.5	0.2	-0.29
Red/far-red	0.07	1.07	0.23	-0.36	0	0.11
Soil moisture	1.14	-0.23	-0.15	0.03	-0.05	-0.1
pH	-0.63	-0.38	-0.58	-0.58	-0.12	0.29
Soil C/N	-0.49	0.55	0.83	0.2	0.08	-0.13
N mineral	0.82	0.45	-0.09	-0.03	0.64	-0.13
P total	1.02	-0.48	-0.07	-0.34	-0.12	0.16
Cumulative variance explained (in %)	27.7	52.3	67.6	76.9	84.2	89.5

Table S7 Phylogenetic signal (Blomberg's *K*, Pagel's λ and Abouheif/Moran's *I*) in each of the six traits.Values of Blomberg's *K* and Pagel's λ equal to one correspond to a Brownian motion model of trait evolution, while values of *K* or λ close to zero indicate no phylogenetic signal. Unlike *K* and λ, Abouheif/Moran's *I* is a measure of phylogenetic autocorrelation and is not based on an evolutionary model. *P*-values for the *K*- and *I*- statistics were obtained by randomly shuffling (999 times) the tips on the phyogeny. *P*-values for Pagel's λ were obtained based on likelihood-ratio tests.

	Leaf area	SLA	Leaf N	Leaf P	Wood density	Height
Blomberg's *K*	0.902	0.385	0.726	0.576	0.534	0.46
P	< 0.001	0.023	< 0.001	< 0.001	< 0.001	0.005
Pagel's λ	0.991	0.45	0.902	0.596	0.612	0.479
P	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Abouheif/Moran's *I*	0.266	0.22	0.32	0.246	0.248	0.125
P	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.028

Table S8 Nodes with significantly more taxa than expected within a particular plot (CSP). Columns correspond to successional stage (Stage 1-5), Plot ID (see also Fig. 1c), node name (see Fig. S6), and ranks in the null distribution across 999 randomization runs, shuffling the tips in the phylogeny. Only nodes that are within the upper 2.5-percentile of the null distribution are listed. Highlighted (for illustration purposes) are the most significant nodes, associated with the plot pairs that had the highest levels of phylogenetic turnover at the two late successional stages (red: stage 4, CSPs 5 & 11; blue: stage 5, CSPs 4 & 12) (see also Fig. 1c and Fig. S6).

Successional Stage	Plot ID (CSP)	Node name	Rank
1	16	N22	990
1	16	N42	975
1	16	N44	989
1	19	N42	980
1	19	N44	992
1	20	N39	994
1	20	N40	985
1	22	N44	989
1	26	N86	983
1	26	N92	986
2	23	N92	974
2	24	N22	995
2	24	N23	982
3	1	N8	976
3	3	N44	985
3	3	N78	991
3	6	N20	981
3	6	N21	985
3	6	N22	999
3	6	N23	987
3	6	N24	992
3	6	N26	983
3	6	N44	974

1267	3	7	N22	999
1268	3	7	N24	990
1269	3	7	N25	999
1270	3	7	N42	989
1271	3	7	N44	998
1272	3	7	N45	983
1273	3	8	N22	974
1274	3	8	N92	974
1275	3	8	N93	993
1276	3	8	N94	984
1277	4	11	N22	995
1278	4	11	N23	982
1279	4	11	N29	988
1280	4	11	N30	993
1281	4	11	N39	999
1282	4	11	N40	988
1283	4	13	N24	975
1284	4	5	N22	988
1285	4	5	N42	995
1286	4	5	N44	999
1287	4	5	N48	991
1288	4	10	N20	983
1289	4	10	N22	999
1290	4	10	N23	999
1291	4	10	N24	990
1292	4	10	N25	979
1293	4	10	N29	994
1294	4	10	N30	988
1295	4	10	N33	997
1296	4	18	N22	996
1297	4	18	N23	997
1298	4	18	N24	977
1299	5	4	N58	980
1300	5	12	N24	978

5	14	N77	999
5	14	N78	997
5	14	N79	986

Methods S1 We gathered sequence information, i.e. *mat*K, *rbc*L and the ITS region including the 5.8s gene for all woody species from Gutianshan National Nature Reserve (Lou & Li, 1998) or closely related species available in GenBank (http://www.ncbi.nlm.nih.gov/genbank/, accessed between May and June 2012). For some species of the CSPs, *mat*K and *rbc*L were sequenced using standard barcoding protocols (Fazekas *et al.*, 2012) (Accession numbers: KF569888-KF569899, Table S4). All sequences were aligned separately for the different markers using MAFFT v6 (Katoh *et al.*, 2002). Sequences for *mat*K and *rbc*L were aligned with the 'Auto' option in the online version of the program (http://mafft.cbrc.jp/alignment/server/). The ITS region was aligned with the 'Q-INS-I' option considering secondary structure of RNA using the MAFFT application at Bioportal (https://www.bioportal.uio.no/, Kumar *et al.*, 2009)). Aligned sequences were concatenated for each species resulting in a total alignment of 3521 nucleotide positions. A phylogenetic tree was inferred using a Maximum Likelihood (ML) method implemented in PhyML (Guindon & Gascuel, 2003). For ML inference, the best fitting model (GTR+I+G) selected by Modeltest (Posada and Crandall 1998) was applied with the following options: tree topology search operation: best of NNI and SPR search, number of substitution rate categories =6, all other parameters were estimated (Gamma Distribution Parameter Alpha, Proportion of Invariable Sites, Transition/Transversion Ratio).

Species occurring in the CSPs but without sequence information available (Table S4) were added manually to the obtained ML tree by the following procedure. *Acer cordatum* was added within *Acer* as a polytomy to the most recent common ancestor (MRCA) of a monophyletic clade formed by other members of *Acer* sect. *Palmata* (i.e. *A. elegantulum*, *A. wilsonii*, *A. olivaceum*). Its branch length was defined as the average distance from the MRCA of that clade to the tips. *Styrax wuyuanensis*, *Symplocos oblongifolia* and *Vaccinium mandarinorum* were added similarily as polytomy emerging from the MRCA for all other

members of the respective genus included, with branch lengths equalling the average branch length from that MRCA to the tips of congeners.

Using the ML topology and branch lengths an ultrametric tree was created by non-parametric rate smoothing (nprs) as implemented in r8s (Sanderson, 1997). Absolute node ages were obtained using 27 published fossils or dates as age constrains. A fixed age of 125 million years was applied to the crown node of the Eudicots (Table S5).

Methods S4 Because non-random phylogenetic structure at the plot scale may simply reflect non-random pattern in overall species frequencies (or abundances) across the phylogeny (Mouquet *et al.*, 2012), we tested for phylogenetic signal in species occurrences as well as abundances at the scale of the whole data set using the APD (abundance phylogenetic deviation) index proposed by Hardy (2008). There was no phylogenetic signal in overall species' occurrence frequencies or abundances in our study (APD = 0.014, $P = 0.056$ and APD = 0.053, $P = 0.996$), so there was no need to implement a null model that restricts permutations to species with similar occurrence frequencies (or abundances).

Methods 5 We tested, based on 100 simulation runs, whether differences in the number of plots (communities) among stages affect the estimates or phylogenetic turnover (Π_{ST} and B_{ST}) using the following procedure: in each simulation run we (i) generated 10 communities with 10 species each, and 20 species in total, (ii) calculated Π_{ST} (or B_{ST}) based on different numbers of plots (3-10 plots) and assessed the Pearson-correlation between Π_{ST} (or B_{ST}) and the number of plots, and (iii) tested (using a one sample t-test) whether the mean correlation obtained from the 100 simulations significantly differed from zero. Calculations of Π_{ST} (or B_{ST}) were based on a random Yule (pure-birth) tree for 20 tips [R-package 'phytools' (Revell, 2012)]. We found that the mean correlation between Π_{ST} (and B_{ST}) and the number plots was close to zero, indicating that there is no intrinsic correlation between the phylogenetic turnover estimates used in our study and the number of plots.

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