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Anthropogenic disturbance shapes phylogenetic and functional tree community structure in a subtropical forest

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ABSTRACT

Forests across the world are increasingly affected by human activities, with unmanaged forests often in early- and mid-successional phases after anthropogenic disturbances. In consequence, it is important to obtain a better understanding of these successional dynamics and their implications for the functioning of forest ecosystems. Here, we investigate this issue for a highly diverse subtropical forest in China, as it is particularly relevant here. China naturally harbors large forested areas and much forest biodiversity, but its forests are also subject to strong anthropogenic pressures, with only 2% of its forest remaining undisturbed. We assess how anthropogenic disturbance shapes two important aspects of forest biodiversity, namely phylogenetic and functional community structure. Comparing plots that have not been disturbed within the last 100 years, plots clear-cut ~50 years ago, and plots clear-cut ~50 years ago and then selectively cut ~20 years ago, we find that the abundant gymnosperm species which are important pioneer species in southern China strongly affect phylogenetic structure, causing over-dispersion among large stems in disturbed stands. A tendency for decreasingly clumped phylogenetic structure over succession when considering only angiosperms may reflect an initial filtering by disturbance whose legacy decreases during succession. Multi-trait functional structure, which was not significantly affected by gymnosperms, has similar patterns to the phylogenetic structure without gymnosperms. Phylogenetic and functional structure differs among stem size classes, but with partially divergent trends. Functional structure is more strongly linked to a disturbance indicator, the proportion of light-demanding species, than phylogenetic structure. Our results illustrate that past tree harvesting has left strong legacies in the phylogenetic and functional structure of tree stands in a highly diverse southern Chinese forest and thus may also shape their functioning.

1. Introduction

Forests across the world are increasingly impacted by human activities, with unmanaged forests often in early- and mid-successional phases after anthropogenic disturbances and only 36% of the World's forest area can be considered primary forest (Li et al., 2010; Lindquist et al., 2012; Liu, 2006). In consequence, it is important to obtain a better understanding of these successional dynamics and the implications for the functioning of forest ecosystems.

There is increasing evidence that species diversity may affect ecosystem functioning in plant communities (Cardinale et al., 2006). However, ecosystem functioning and community stability may be more strongly depend on phylogenetic and functional structure than on species richness. Notably, Cadotte et al. (2009) found that phylogenetic diversity is better than species richness at explaining community productivity. Flynn et al. (2011) concluded that functional diversity and phylogenetic diversity had similar strength in predicting the relationship between biodiversity and ecosystem functioning. Cadotte et al. (2012) showed that phylogenetically over-dispersed communities (where species are less related than expected by chance) are more stable than clustered ones.

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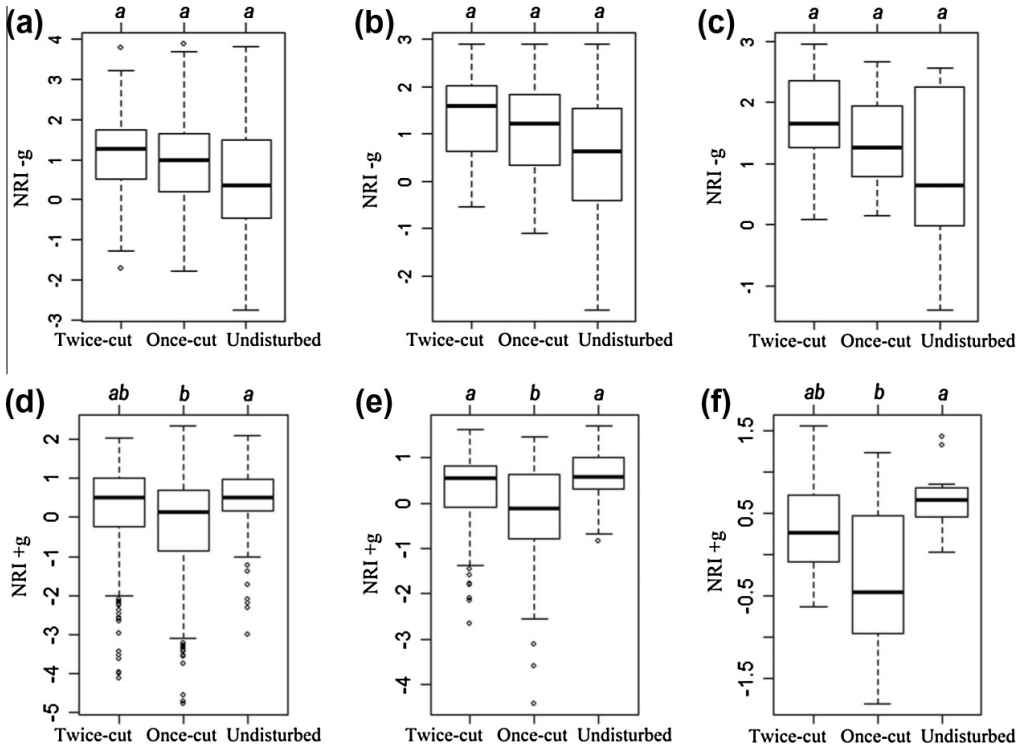

Fig. 1. Phylogenetic community structure (Net Relatedness Index, NRI) when including or excluding gymnosperms species (+g, including gymnosperms species; −g, excluding gymnosperms species) in relation to disturbance regime at three spatial scales: (a) and (d) 10 × 10 m scale, (b) and (e) 20 × 20 m scale and (c) and (f) 50 × 50 m scale. Different letters indicate significant differences in mean NRI between forest types ($P < 0.05$).

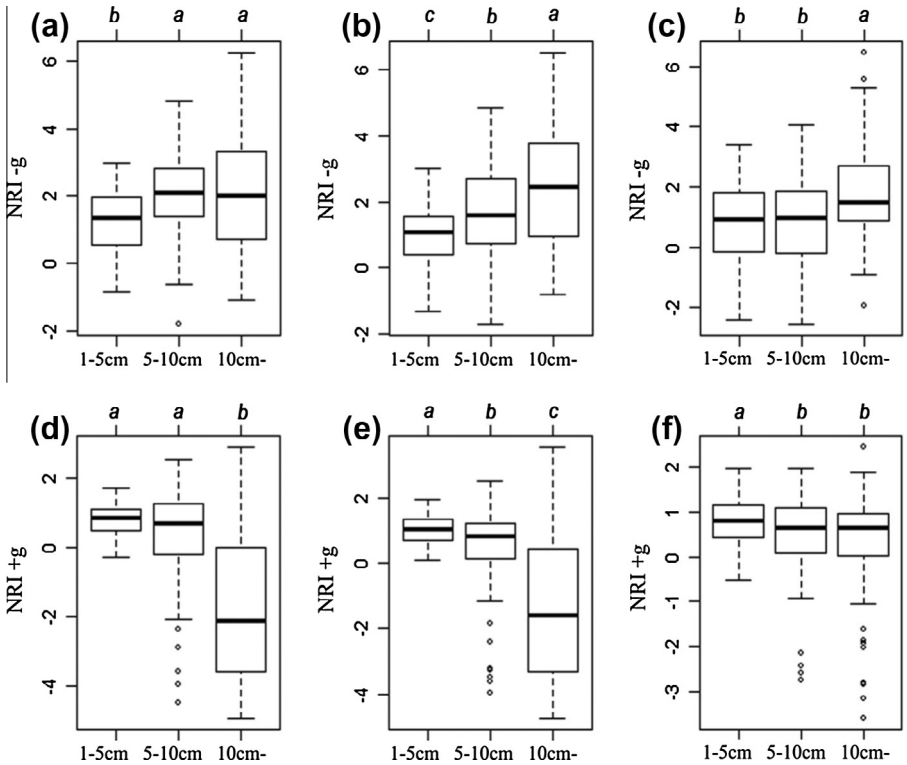

Fig. 2. Phylogenetic community structure (Net Relatedness Index, NRI) when including or excluding gymnosperms species (+g, including gymnosperms species; −g, excluding gymnosperms species) at 20 × 20 m scale in relation to size class for (a, d) twice-cut forest, (b, e) once-cut forest and (c, f) undisturbed forest. Different letters indicate significant differences in mean NRI between size classes ($P < 0.05$). Results at the other two spatial scales are listed in Figs. C.1 and C.2.

Recent studies show that anthropogenic disturbance may shape the phylogenetic and functional community structure of forests and thus potentially their functioning. Random or clustering phylogenetic structure in early succession and strong overdispersed phylogenetic structure in later succession was found during succession in a tropical lowland wet forest stands of Costa Rica

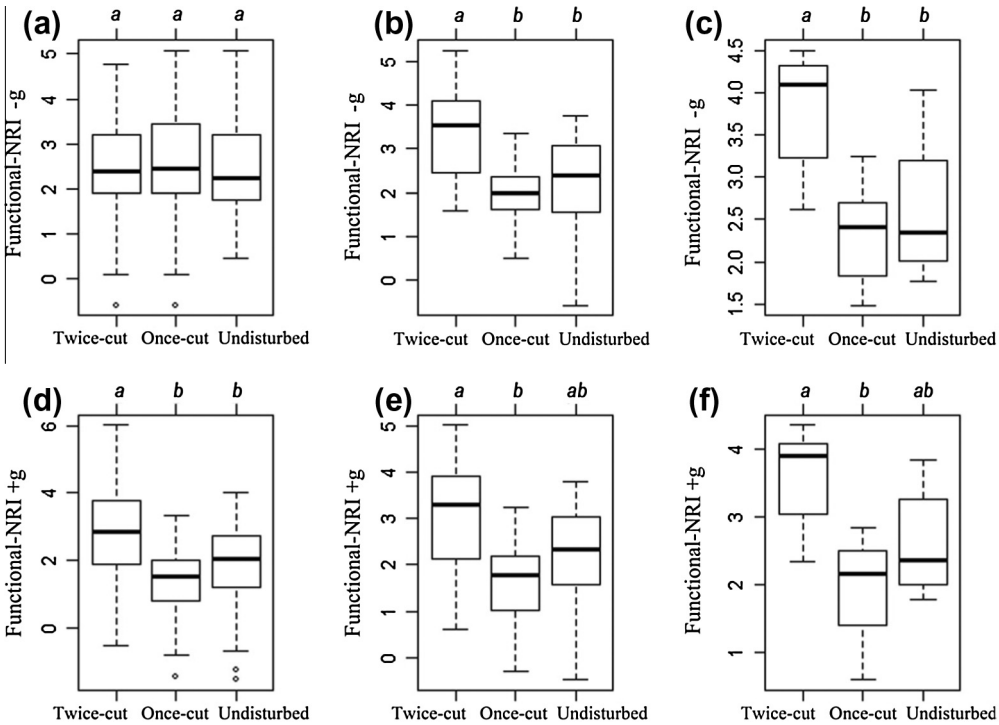

Fig. 3. Multiple traits structure of the three types forests at three spatial scales when including or excluding gymnosperms species (+g, including gymnosperms species; −g, excluding gymnosperms species): (a) and (d) 10 × 10 m scale, (b) and (e) 20 × 20 m scale, and (c) and (f) 50 × 50 m scale. The results are similar at the three spatial scales.

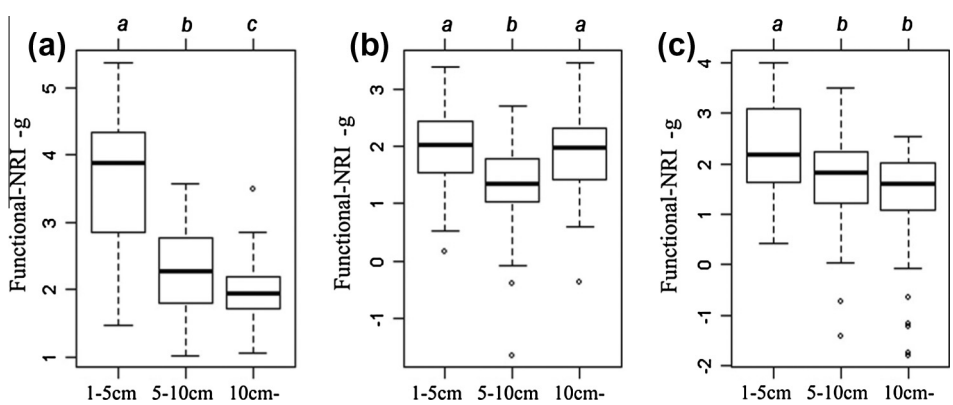

Fig. 4. Size class analysis of multi-trait structure excluding gymnosperms species (−g, excluding gymnosperms species) at 20 × 20 m scale: (a) twice-cut forest, (b) once-cut forest and (c) undisturbed forest. Different letters indicate significant differences in mean NRI between size classes ($P < 0.05$). Results at the other two spatial scales are listed in Figs. C.1 and C.2.

(Letcher, 2010). Phylogenetic clustering increased with increasing disturbance severity in a tropical forest in southern China (Ding et al., 2012), and similar phylogenetic-disturbance relations have been found in tropical forests in New Guinea (Whitfeld et al., 2012) and Costa Rica (Letcher et al., 2012; Norden et al., 2012). Ding et al. (2012) found that response traits, such as dispersal mode, seed mass, physical defense and fruit type, were overdispersed only in highly disturbed lowland forest, while effect traits showed no consistent patterns among saplings, treelets and adult trees. The recovery of disturbed forests and associated dynamics in phylogenetic and functional community structure may have important implications for ecosystem functioning and biodiversity conservation (Ding et al., 2012; Norden et al., 2012).

Given phylogenetic niche conservatism, phylogenetic clustering (where species are more related than expected by chance) may result from deterministic environmental sorting processes, while phylogenetic over-dispersion may be caused by competitive exclusion or facilitation (Kembel and Hubbell, 2006; Valiente-Banuet and Verdú, 2007; Webb, 2000; Webb et al., 2002). A random phylogenetic pattern could be generated by neutral community assembly processes (Hubbell, 2001; Letcher, 2010) or by the combined effects of habitat filtering and competition exclusion in a community. However, with alternative trait-phylogeny relations, e.g., due to the presence of phylogenetically isolated clades (Liu et al., 2013; Losos, 2008), these various community assembly processes may also result in alternative phylogenetic structures. Thus, studies that look at phylogenetic and functional structure jointly are needed to increase our understanding of community assembly and functioning (Kraft and Ackerly, 2010; Swenson and Enquist, 2009).

Here, we assessed how anthropogenic disturbance affects phylogenetic and functional community structure in a subtropical forest in southern China. We also assessed to which extent these effects are dependent on tree size class. Moreover, as tree species

Table 1
Linear modeling of phylogenetic and functional NRI as a function of LDSR (light-demanding species ratio), ILBA (individual-level basal area), and CLBA (community-level basal area) separately in each type of forest and for all forest types combined at 20 × 20 m scale. The adjusted R^2 is given. The subscript of R^2 "phy" and "fun" means phylogenetic and functional structure separately.

Explanatory variable	Forest type	R^2_{phy}	R^2_{fun}
LDSR	Undisturbed	0.021	0.201**
	Once-cut	0.018	0.107**
	Twice-cut	0.058**	0.757**
	Overall	0.012	0.215**
ILBA	Undisturbed	0.001	0.007
	Once-cut	0.097**	0.000
	Twice-cut	0.074**	0.214**
	Overall	0.032**	0.031**
CLBA	Undisturbed	0.107**	0.118**
	Once-cut	0.081**	0.001
	Twice-cut	0.023	0.028
	Overall	0.077**	0.009

** $p < 0.01$.

richness has been found to be well explained by the disturbance indicator, proportion of light-demanding species (LDSR) (Molino and Sabatier, 2001), we also evaluated if it is a significant predictor for phylogenetic and functional structure. These questions are important for forest management in China as only 2% of Chinese forests are intact old-growth forests (Liu, 2006), with most forests having experienced strong anthropogenic disturbances due to past tree harvesting.

2. Materials and methods

2.1. Study sites

The study site is located at Gutianshan National Nature Reserve (GNNR), Zhejiang Province, East China (29°10′19.4″N–29°17′41.4″N, 118°03′49.7″E–118°11′12.2″E) and the reserve is about 81 km^2. Annual mean temperature is 15.3 °C and annual precipitation ranges from 1793 mm to 1960 mm. Subtropical red soil with granite or deeply weathered granite as parent rock is the dominant soil type (Zhang et al., 2011). Subtropical evergreen broad-leaved forest is the typical vegetation in GNNR (Yu et al., 2001) with *Castanopsis eyrei* and *Schima superba* as the dominant species.

Nine 1-ha (100 m × 100 m) plots (Fig. A.1) were randomly selected in the GNNR and divided into three categories according to their disturbance history: twice-cut forest, once-cut forest and undisturbed forest. There were three replicates of each category. Twice-cut forest was clear-cut about 50 years ago and then selectively cut about 20 years ago, while once-cut forest was clear-cut about 50 years ago. Stands in both categories have been undergoing natural recovery since these last anthropogenic disturbances. Undisturbed forest has not experienced tree-felling within the last 100 years and is generally located at the core area of GNNR (Song et al., 2011).

All plots were censused in 2009 when every woody individual with diameter at breast height (DBH) ⩾1 cm was tagged, mapped, identified to species and had its DBH recorded. All species were scored as light-demanding or non-light-demanding mainly according to habitat descriptions in Flora of China (http://www.efloras.org/flora_page.aspx?flora_id=2), supplemented with information based on web searches. Species with habitat information indicating occurrence in open forest, disturbed area and anthropogenic habitats were scored as light-demanding species ($n = 75$) (see Table B.1).

2.2. Phylogenetic tree

Expanding the phylogenetic tree published by Feng et al. (2012) we added another 17 woody species occurring within the GNNR into the new phylogenetic tree using the same method, finally including 173 species, constituting the GNNR species pool used in this study. This phylogenetic tree was constructed by three chloroplast DNA regions (*rbcLa*, *matK* and *trnH-psbA*) following Kress et al. (2009). The process included: (1) extracted total DNA from leaf tissue with the CATB method (Doyle and Doyle, 1987; Khanuja et al., 1999); (2) amplified and sequenced to the three DNA regions using Polymerase Chain Reaction (PCR); (3) compared each sequence from the GenBank using Blast (Altschul et al., 1997); (4) compared the three DNA genes individually using MUSCLE software (Edgar, 2004); (5) matched and built a super matrix with the R package 'Phylotools' (Zhang et al., 2010); (6) set the three division GTR + GAMMA model to the three DNA regions using RAxML software (Stamatakis, 2006); (7) employed the maximum likelihood method to build the phylogenetic tree; (8) confirmed the approval rating of every node by 1000 rapid bootstrap tests; (9) constructed an ultrametric tree using software 'r8s' with non-parametric rate smoothing method (Sanderson, 2003). The angiosperms was set to a minimum age of 131.8 Ma (Morris et al., 2007; Magallón and Castillo, 2009), the eudicot crown group was set to a minimum age of 125 Ma (Smith et al. 2010; Magallón and Castillo, 2009), and the crown group of Pittosporaceae and Araliaceae was set to a minimum age of 40.4 Ma (Wikström et al., 2001; Martínez-Millán, 2010). These three nodes for the angiosperm families were adopted to constrain the node ages here.

2.3. Functional traits

The following functional traits representing important axes of plant adaptive strategies were recorded for each study species: maximum canopy height (MH), specific leaf area, leaf area (LA), leaf phosphorus content (LPC), and leaf nitrogen content (LNC). MH was taken from Flora of China (Editorial Committee of Flora of China, 2004). Leaf samples were collected from the canopy of at least three individuals of each species. Images of leaves were produced by Epson scanner and then leaf area was calculated by ImageJ software (Abramoff et al., 2004). Leaves samples were dried (60 °C and 48 h) until constant weight and the dry weight was recorded to get the SLA. Standard Kjehldahl nitrogen determination method and UV-Spectrometer were used to get the LPC and LNC data. A Principal Component Analysis of the five traits was

done and the species scores were used to construct a distance matrix (Euclidian distance). Based on this distance matrix, a clustering tree (n = 171 spp.) was built using cluster analysis (complete linkage method which finds similar clusters).

2.4. Data analysis

We used the Net Relatedness Index (NRI) to represent the phylogenetic and functional trait structure. The index is calculated as follows:

$$NRI = -1 \times \frac{MPD_{obs} - mean(MPD_{null})}{sd(MPD_{null})}$$

MPD_{obs} is the observed mean pairwise distance of each quadrat; $mean(MPD_{null})$ means the average value of the 999 null communities while $sd(MPD_{null})$ is the standard deviation of mean pairwise distance the 999 null communities. The null communities were generated by randomly shuffling the species names at tips of the phylogenetic or functional tree. Positive *NRI* indicates more clustering of community phylogenetic or functional structure than expected by chance and negative *NRI* indicates more over-dispersion of community phylogenetic or functional structure than expected (Webb et al., 2002).

Each 1-ha plot was divided into quadrats of 10 m × 10 m, 20 m × 20 m and 50 m × 50 m to allow for a multi-scale analysis. As the quadrats were nested in each plot, we used linear mixed effects model to analyze the effects of disturbance regimes on phylogenetic and functional community structure. We added a random effect variable to account for plot-specific effects and the effect of spatial autocorrelation. We then conducted the multiple comparisons to test for differences in community structure among the three types of disturbance history stands or among the three size classes. The linear mixed models were computed using the lmer() function in the 'lme4' package, while the multiple comparisons were conducted by glht() function in 'multcomp' package in R statistical software (R Development Core Team, 2009).

In order to compare the patterns between different DBH size classes, we divided the trees into three DBH size classes (smaller than 5 cm, 5–10 cm and larger than 10 cm). We then used linear mixed effects model to test relationships between NRI and disturbance indicators at the scale of 20 × 20 m scale. r^2 and P values of these linear analysis were computed using 'MuMIn' and 'languageR' packages. We employed three disturbance indicators: community-level basal area (CLBA, the sum of the basal area of all the individuals in a quadrat), individual-level basal area (ILBA, the average of the basal area of all the individuals in a quadrat), and light-demanding species ratio (LDSR, the ratio of light demanding individuals to the total number of individuals in a quadrat). Finally, since the gymnosperms might strongly affect the results of community phylogenetic and functional structure, we also conducted the same analysis after excluding gymnosperm species.

3. Results

3.1. Effect of disturbance regimes on forest phylogenetic structure

We found that gymnosperms strongly influenced phylogenetic community structure and its link to disturbance, as well as the relationship between phylogenetic community structure and size class (Figs. 1 and 2). With gymnosperm included, tree assemblages in disturbed plots, i.e., twice cut and once cut plots, and considering stems larger than 10 cm (especially in the disturbed plots) were more phylogenetically overdispersed than when considering only angiosperms.

For angiosperms, there was a trend towards less phylogenetic clumping with increasing time since disturbance, i.e., phylogenetic structure was more overdispersed in undisturbed forest (Fig. 1), albeit the pattern was non-significant. Clustering furthermore increased with increasing size in plots with any of the three disturbance histories (Fig. 2). This pattern might be consistent with the pattern in Fig. 1 if interpreted as representing a successional sequence. The patterns at the other two spatial scales were similar (Figs. C.1 and C.2).

3.2. Effect of disturbance regimes on forest functional structure

Gymnosperms, however, did not similarly affect multi-trait functional structure or its relationship to disturbance history (Fig. 3). We henceforth only report the angiosperm-only results for functional structure. Multi-trait functional structure was generally clustered and there was a trend towards decreasing clustering with time since disturbance, similar to the phylogenetic pattern for angiosperms.

The size class results furthermore showed that functional clustering tended to decrease with increasing size under all disturbance regimes, except for once-cut forest without gymnosperms (Fig. 4), which was a divergent pattern compared with phylogenetic structure. Patterns at the other two spatial scales were similar (Figs. D.1 and D.2).

3.3. Relationships to disturbance indicators

As have described above (Figs. 1 and 3), gymnosperms affected phylogenetic, but not functional structure, so we here only reported the results considering only angiosperms. Generally, functional structure was better predicted by disturbance indicators than phylogenetic structure (Table 1, Fig. E.1), with LDSR better than CLBA and ILBA in explaining both phylogenetic and functional structure, especially for functional structure (Table 1). Moreover, LDSR was found to be positively correlated with phylogenetic NRI, but negatively correlated with functional NRI (Fig. E.1).

4. Discussion

Integrative analyses of community phylogenetic and functional structure may provide better understanding of how disturbance and successional dynamics shape plant communities (Ding et al., 2012; Letcher, 2010; Letcher et al., 2012; Norden et al., 2012; Whitfeld et al., 2012). This is well illustrated by the present study where we find non-random patterns in phylogenetic and functional community structure along successional gradients in a subtropical Chinese forest at all three spatial scales. Our results also highlight that functional community structure is better linked to proportion of light demanding species than phylogenetic community structure.

Phylogenetic structure showed strongly divergent relationships to disturbance history depending on whether or not gymnosperms were included in the analyses. Similar sensitivity to inclusion of specific outlying clades has also been reported in other studies (Letcher et al., 2012). Three gymnosperm species occur in the study plots, among which *Pinus massoniana* and *Cunninghamia lanceolata* are the most abundant and are widely found in the earliest phases of the succession (Cheng et al., 2011; Tang et al., 2010). As a result the relative abundance of gymnosperms is 0.027 in twice-cut forest and 0.043 in once-cut forest, but only 0.009 in undisturbed forest. Reflecting this, with gymnosperms included the two types of disturbed stands tended to have overdispersed phylogenetic community structure and especially so among the large-sized stems, which would represent the first generation of trees

recruited after last disturbance (Fig. 1). However, importantly gymnosperms did not cause divergent patterns in functional structure (Fig. 3).

Considering only angiosperms, there was a non-significant trend towards decreasingly clustered phylogenetic structure with increasing time since disturbance (Fig. 1) and later recruitment since disturbance, as indicated by decreasing stem size (Fig. 2). Considering the relationship to the disturbance indicators, there were strong relationships to LDSR and in agreement with the other results angiosperm phylogenetic clustering generally increased with an increasing proportion of light-demanding species present (Fig. 10, Table 1). These patterns are all consistent with previous studies of successional trends in phylogenetic community structure in tropical forests and other plant communities (Brunbjerg et al., 2012; Ding et al., 2012; Whitfeld et al., 2012). This decreasing clustering could reflect disturbance filtering on conserved traits, but increasing negative interactions among closely related species during succession could also contribute, i.e., competitive exclusion via phylogenetic limiting similarity (Violle et al., 2011) or an increasingly role of negative interactions among congeners via host-specialized pest and pathogens (Peters, 2003).

The changes in functional community structure over succession were partly consistent with the angiosperm-based phylogenetic patterns, suggesting that the latter were indeed linked to filtering on the studied traits. Notably, multi-trait functional community structure tended to become less clustered with increasing time since disturbance (Fig. 3). Considering the stem size classes, the strongest multi-trait clustering was surprisingly found in the smallest size class, i.e., the generation with the longest time since disturbance (Fig. 4). These results may reflect that species in the undisturbed plots and small stem communities tend to be mainly dominated by short-statured species, understory treelet and shrub species, (e.g., *Rhododendron ovatum*, *Rhododendron latoucheae*, *Camellia fraterna* and *Eurya muricata* were among the dominant species in undisturbed forest; *Loropetalum chinensis*, *R. ovatum*, *E. muricata*, *C. fraterna* and *Vaccinium carlesii* dominated in small stem communities), i.e., causing reduced variation in maximum stem height (Tables F.1 and F.2). Considering the relationship of functional trait structure to the disturbance indicators, there were

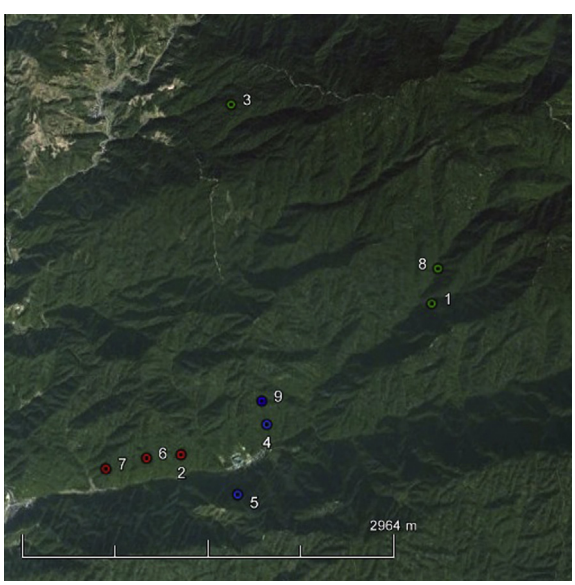

Fig. A.1. Map showing the nine 1-ha plots. Plot 2, 6 and 7 in red are twice-cut forest; plot 4, 5 and 9 in blue are once-cut forest; plot 1, 3, 8 in green are undisturbed forest. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table B.1
Light-demanding species list in secondary subtropical forest of nine 1-ha plots.

Species name	Family
Ailanthus altissima	*Simaroubaceae*
Alangium kurzii	*Alangiaceae*
Alniphyllum fortunei	*Styracaceae*
Antidesma japonicum	*Euphorbiaceae*
Aralia chinensis	*Araliaceae*
Broussonetia kazinoki	*Moraceae*
Carpinus viminea	*Betulaceae*
Castanopsis eyrei	*Fagaceae*
Chimonanthus salicifolius	*Calycanthaceae*
Cinnamomum camphora	*Lauraceae*
Corylopsis glandulifera var.hypoglauca	*Hamamelidaceae*
Cunninghamia lanceolata	*Taxodiaceae*
Cyclocarya Paliurus	*Juglandaceae*
Dalbergia hupeana	*Fabaceae*
Dendrobenthamia japonica	*Cornaceae*
Diospyros glaucifolia	*Ebenaceae*
Diplospora dubia	*Rubiaceae*
Ehretia acuminata	*Boraginaceae*
Euonymus centidens	*Celastraceae*
Euonymus myrianthus	*Celastraceae*
Euonymus oblongifolius	*Celastraceae*
Euscaphis japonica	*Staphyleaceae*
Gardenia jasminoides	*Rubiaceae*
Glochidion puberum	*Euphorbiaceae*
Idesia polycarpa	*Flacourtiaceae*
Ilex chinensis	*Aquifoliaceae*
Ilex elmerrilliana	*Aquifoliaceae*
Ilex ficoidea	*Aquifoliaceae*
Ilex latifolia	*Aquifoliaceae*
Ilex micrococca	*Aquifoliaceae*
Ilex pubescens	*Aquifoliaceae*
Ilex rotunda	*Aquifoliaceae*
Ilex triflora	*Aquifoliaceae*
Lindera aggregata	*Lauraceae*
Lindera glauca	*Lauraceae*
Liquidambar formosana	*Hamamelidaceae*
Litsea cubeba	*Lauraceae*
Litsea elongata	*Lauraceae*
Lithocarpus glaber	*Fagaceae*
Loropetalum chinense	*Hamamelidaceae*
Lyonia ovalifolia	*Ericaceae*
Maclura cochinchinensis	*Moraceae*
Machilus pauhoi	*Lauraceae*
Magnolia officinalis	*Magnoliaceae*
Mahonia bealei	*Berberidaceae*
Neolitsea aurata	*Lauraceae*
Nyssa sinensis	*Nyssaceae*
Photinia parvifolia	*Rosaceae*
Phyllanthus glaucus	*Euphorbiaceae*
Pieris formosa	*Ericaceae*
Pinus massoniana	*Pinaceae*
Platycarya strobilacea	*Juglandaceae*
Quercus phillyraeoides	*Fagaceae*
Quercus serrata var.brevipetiolata	*Fagaceae*
Reevesia pycnantha	*Sterculiaceae*
Rhododendron mariesii	*Apiaceae*
Rhododendron simsii	*Apiaceae*
Rubus chingii	*Rosaceae*
Sapium japonicum	*Euphorbiaceae*
Sassafras tzumu	*Lauraceae*
Sinoadina racemosa	*Rubiaceae*
Sloanea sinensis	*Elaeocarpaceae*
Sorbus folgneri	*Rosaceae*
Stachyurus chinensis	*Stachyuraceae*
Styrax suberifolius	*Styracaceae*
Syzygium buxifolium	*Myrtaceae*
Tilia endochrysea	*Tiliaceae*
Tilia japonica	*Tiliaceae*
Trema cannabina var.dielsiana	*Cannabaceae*
Uncaria rhynchophylla	*Rubiaceae*
Vaccinium bracteatum	*Ericaceae*
Vaccinium mandarinorum	*Ericaceae*
Vernicia montana	*Euphorbiaceae*
Viburnum sempervirens	*Adoxaceae*
Wikstroemia monnula	*Thymelaeaceae*

particularly strong relationships to LDSR, with generally decreasing trait clustering with increasing proportion of light-demanding species present (Fig. E.1, Table 1). As above, this may reflect the high abundance of short-statured species in less recently disturbed plots. Moreover, the stronger explanatory power of disturbance indicators for functional structure than phylogenetic structure may indicate that functional structure was more easily shaped by local disturbance, which was in line with recently studies (Feng et al., 2013; Purschke et al., 2013).

Concerning the three forest-structural disturbance indicators used, Whitfeld et al. (2012) also used CLBA as a proxy of forest age and found it had a positive relationship with mean pairwise phylogenetic distance (MPD), i.e., phylogenetic diversity. Here, we, however, found that CLBA as well as the other basal area measure ILBA mostly had less power in explaining phylogenetic and functional community structure than LDSR. Molino and Sabatier (2001) likewise suggested that LDSR was a better indicator of disturbance intensity because it more directly reflects the amount of light reaching the forest floor. Alternatively, it may also better capture the plot disturbance history by directly representing the species' light requirements.

To sum up, past human disturbance affects forest structure in Gutianshan, both by general disturbance-related effects and by specifically promoting the establishment of certain gymnosperm species. The latter has strong effects on successional patterns in phylogenetic community structure, but much less so on functional structure. This finding underscores the need to carefully consider the impact of phylogenetic outlier clades on patterns in phylogenetic community structure. Disregarding the gymnosperms, disturbance in this subtropical forest tended to lead to increasing phylogenetic clustering similar to what has been found in other plant communities. A similar tendency for functional clustering along disturbance gradient was also found. In contrast, phylogenetic and functional structure show divergent patterns when compared against size classes and disturbance indicators (notably relative abundance of light-demanding species). The reported findings exemplify how human disturbance may strong shape the phylogenetic and functional structure of forest tree communities, with potential consequences for their functioning and their resilience to further anthropogenic disturbances.

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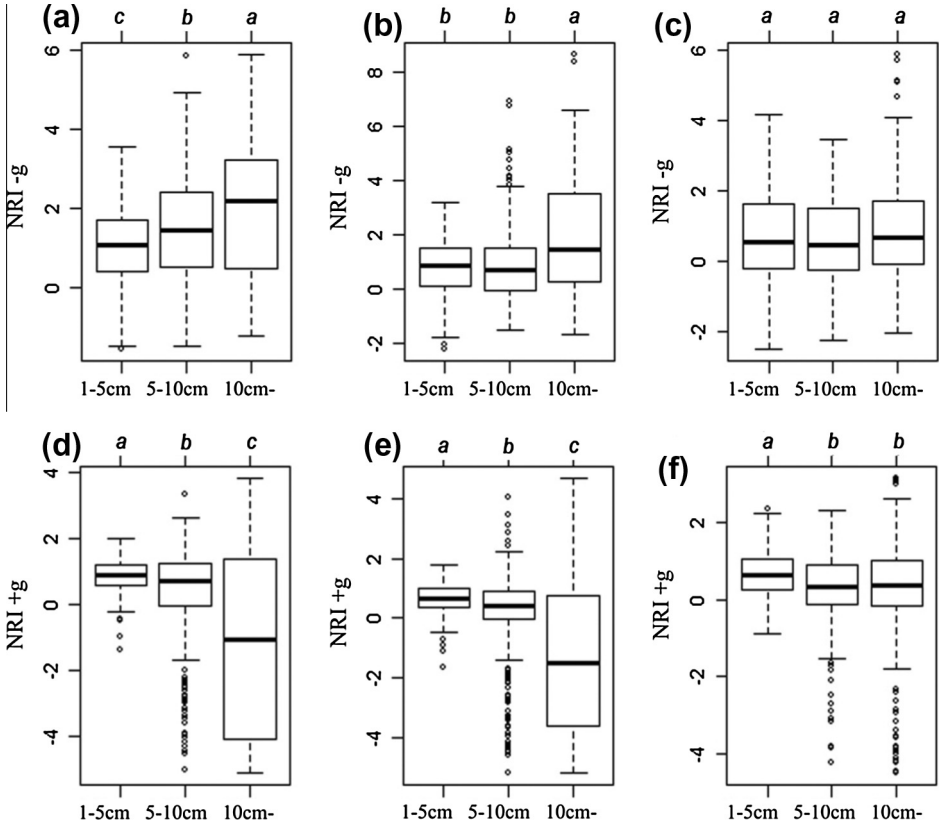

Fig. C.1. Size class analysis of phylogenetic structure at 10 × 10 m scale: (a) and (d) twice-cut forest, (b) and (e) once-cut forest and (c) and (f) undisturbed forest when including or excluding gymnosperms species (+g, including gymnosperms species; −g, excluding gymnosperms species). Different letters indicate significant differences in mean NRI between size classes ($P < 0.05$).

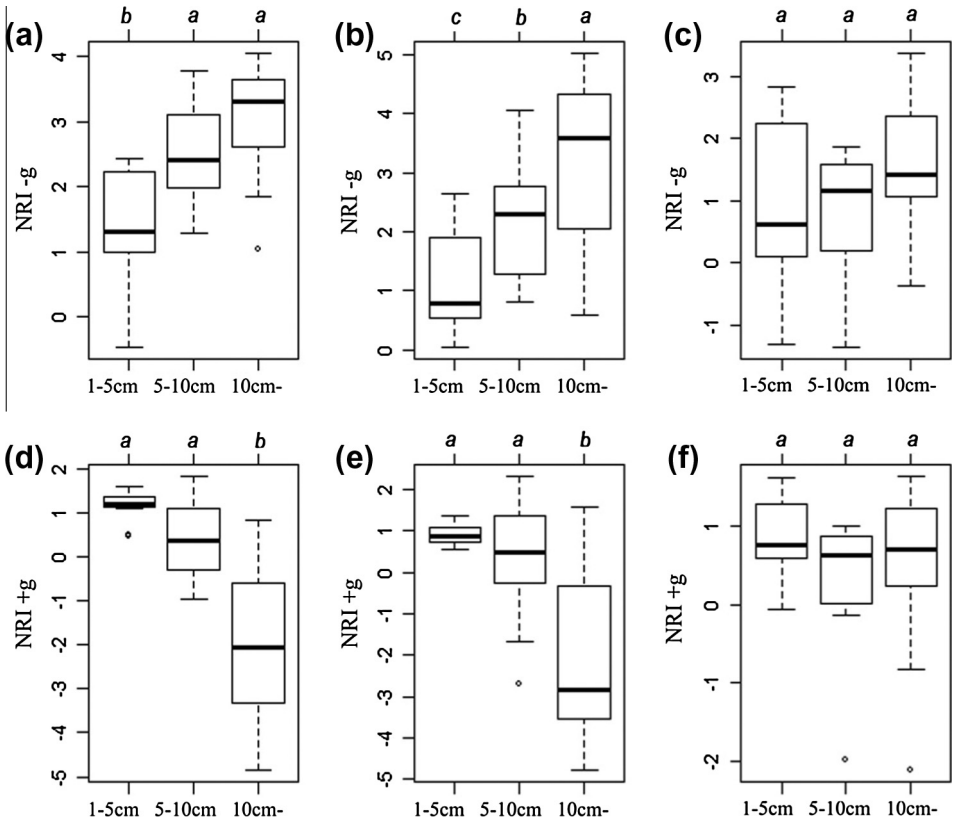

Fig. C.2. Size class analysis of phylogenetic structure with or without gymnosperm species at 50 × 50 m scale: (a) and (d) twice-cut forest, (b) and (e) once-cut forest and (c) and (f) undisturbed forest. Different letters indicate significant differences in mean NRI between size classes ($P < 0.05$).

Appendix A

Map showing the nine 1-ha plots (see Fig. A.1).

Appendix B

Light-demanding species list in secondary subtropical forest of nine 1-ha plots (see Table B.1).

Appendix C

Size class analysis of phylogenetic structure with or without gymnosperm species at different scales (see Figs. C.1 and C.2).

Appendix D

Size class analysis of multi-trait structure without gymnosperm species at different scales (see Figs. D.1 and D.2).

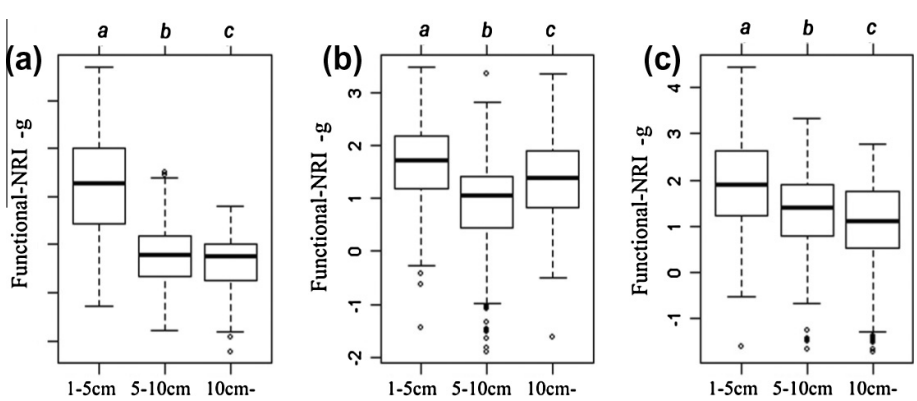

Fig. D.1. Size class analysis of multi-trait structure when excluding gymnosperms species (−g, excluding gymnosperms species) at the 10 × 10 m scale: (a) twice-cut forest, (b) once-cut forest and (c) undisturbed forest. Different letters indicate significant differences in mean NRI between size classes ($P < 0.05$).

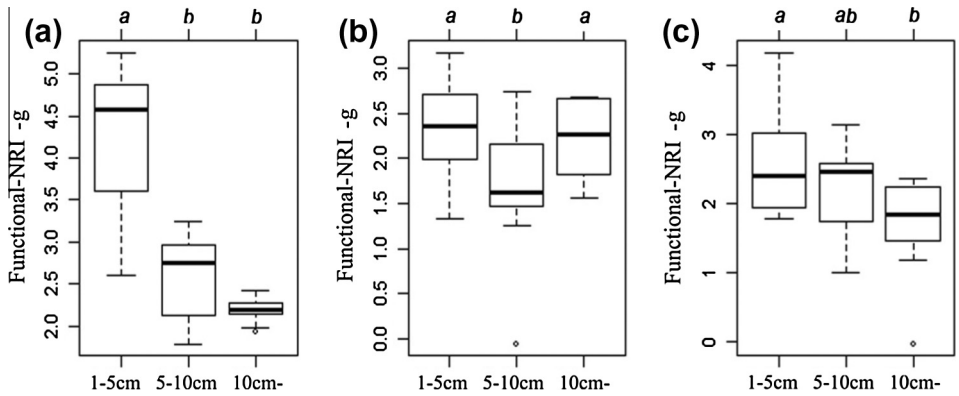

Fig. D.2. Size class analysis of multi-trait structure when excluding gymnosperms species (−g, excluding gymnosperms species) at the 50 × 50 m scale: (a) and (d) twice-cut forest, (b) and (e) once-cut forest and (c) and (f) undisturbed forest. Different letters indicate significant differences in mean NRI between size classes ($P < 0.05$).

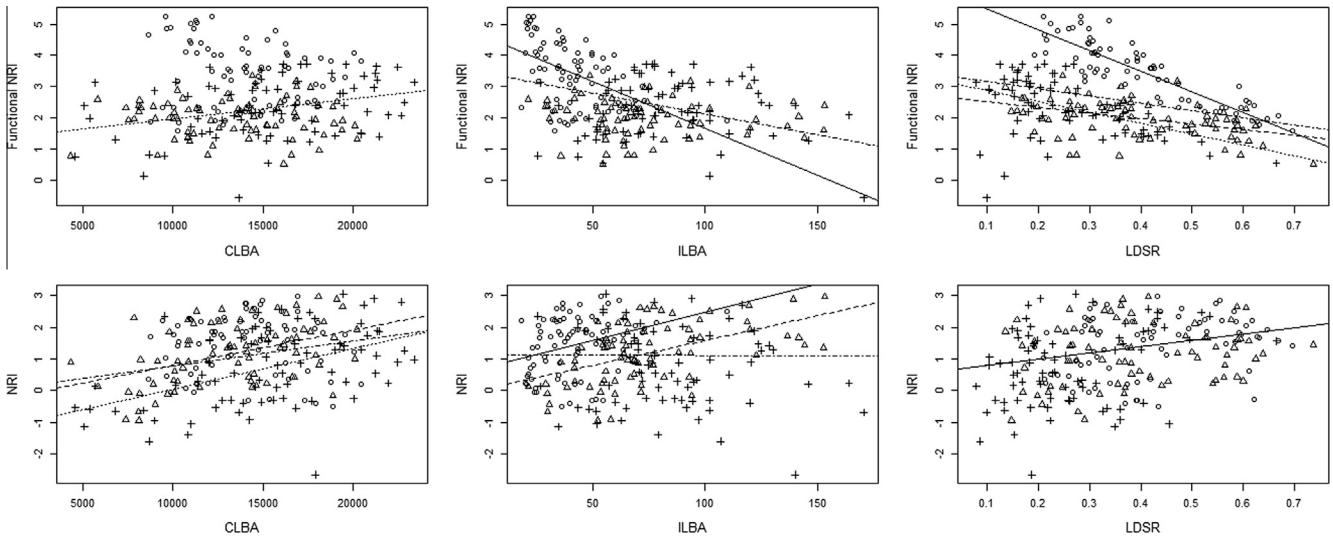

Fig. E.1. The linear relationship between phylogenetic NRI, Functional NRI and community-level basal area (CLBA), individual-level basal area (ILBA), and light-demanding species ratio (LDSR) at 20 × 20 m scale in different types of forests excluding gymnosperms species. Disturbance regime: circle, twice-cut forest; triangle, once-cut forest; cross, undisturbed forest. Lines are only shown for significant ($P < 0.05$) relationships. Solid line for twice-cut forest; dashed line for once-cut forest; dotted line for undisturbed forest and dot-dash line for all forests. See Table 1 for the statistical results. Results at other scales are not listed.

Table F.1
Maximum height of the 15 most abundant species in undisturbed and twice-cut stands.

Undisturbed		Twice-cut	
Species	Max height (m)	Species	Max height (m)
Castanopsis eyrei	20	*Castanopsis eyrei*	20
Rhododendron ovatum	6	*Vaccinium carlesii*	6
Rhododendron latoucheae	5	*Lithocarpus glaber*	15
Camellia fraterna	5	*Loropetalum chinense*	3
Eurya muricata	6	*Adinandra millettii*	16
Camellia chekiangoleosa	6	*Rhododendron ovatum*	6
Distylium myricoides	6.5	*Syzygium buxifolium*	5
Eurya rubiginosa	3.5	*Rhododendron latoucheae*	5
Schima superba	25	*Castanopsis carlesii*	20
Neolitsea aurata	14	*Toxicodendron succedaneum*	10
Symplocos anomala	7	*Neolitsea aurata*	14
Cinnamomum subavenium	20	*Eurya muricata*	6
Rhaphiolepis indica	4	*Schima superba*	25
Cleyera japonica	10	*Cyclobalanopsis glauca*	20
Corylopsis glandulifera	3	*Itea omeiensis*	10
Mean	9.4	Mean	12.07
SD	6.98	SD	6.99

Table F.2
Max height of the 15 most abundant species in small stem and large stem communities.

Small stem		Large stem	
Species	Max height (m)	Species	Max height (m)
Loropetalum chinense	3	*Castanopsis eyrei*	20
Rhododendron ovatum	6	*Schima superba*	25
Eurya muricata	6	*Castanopsis carlesii*	20
Camellia fraterna	5	*Lithocarpus glaber*	15
Vaccinium carlesii	6	*Cyclobalanopsis glauca*	20
Castanopsis eyrei	20	*Quercus serrata*	25
Rhododendron latoucheae	5	*Daphniphyllum oldhamii*	10
Adinandra millettii	16	*Myrica rubra*	15
Lithocarpus glaber	15	*Machilus thunbergii*	20
Itea omeiensis	10	*Distylium myricoides*	6.5
Neolitsea aurata	14	*Loropetalum chinense*	3
Rhaphiolepis indica	4	*Toxicodendron succedaneum*	10
Eurya rubiginosa	3.5	*Castanopsis fargesii*	30
Syzygium buxifolium	5	*Elaeocarpus chinensis*	7
Machilus grijsii	5	*Elaeocarpus decipiens*	15
Mean	8.23	Mean	16.1
SD	5.38	SD	7.73

Appendix E

The linear relationship between phylogenetic NRI, Functional NRI and disturbance indicators (see Fig. E.1).

Appendix F

Maximum height of the 15 abundant species in different types of forest (see Tables F.1 and F.2).

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