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Dominant ecological processes and plant functional strategies change during the succession of a subtropical forest

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ABSTRACT

Understanding community assembly process could enhance forest conservation and restoration, while which dominant ecological process drives the community assembly during forest succession is still controversial. In this study, the phylogeny-based and functional trait-based indicators were used to investigate the community assembly processes during forest succession in southern China. 30 dominant species and 33 functional trait indicators related to plant competition, reproduction, and defense strategies, 7 environmental factors related to light availability and soil nutrients, and species richness were selected to explore the dominant ecological processes during succession via Monte Carlo method, structural equation model, multiple linear regression, and one-way ANOVA analysis. Results showed that both the community phylogenetic and functional trait structures changed during succession. Phylogenetic structure clustering and functional trait clustering were evident in early succession. In middle succession, the phylogenetic structure and functional trait structure were randomly dispersed. In middle and later succession, the phylogenetic structure clustering, functional trait clustering, and functional trait evenly dispersed were found. The environmental factors, especially the soil P content, and species richness were found to have significant effects on the community assembly processes during succession. Dominant species in early succession always occupied acquisitive strategies and had high light-use ability and low investment in defense, but dominant species in later succession showed more conservative strategies and exhibited diverse defense strategy, reproductive strategy, and light and nutrient resource-use strategy, apparently in order to adapt changing and more complex environments. The results demonstrate that the relative importance of ecological processes changed during succession. Environmental filtering mainly dominated in early succession, and its strength gradually decreased as succession progressed. Both environmental filtering and competitive exclusion had important effects on community assembly in later succession. The assessment of the relative importance of ecological processes during succession could be biased if only based on one plant functional strategy.

1. Introduction

Forest succession is a dynamic process in community assembly that changes over time under different environmental conditions (Clements, 1916; Bhaskar et al., 2014; Gafta et al., 2016). Ecologists have found that initial colonization conditions, plant ecological strategies, and stochastic processes may lead to various trajectories during succession (Rees et al., 2001; Letcher et al., 2012; Purschke et al., 2013). Understanding community assembly processes during succession could enhance forest conservation and restoration (Guariguata and Ostertag, 2001) and might also enhance the restoration of wastelands caused by industrialization, urbanization, and abandonment of agricultural lands.

Phylogenetic structures and plant functional traits have been recognized as important avenues for understanding the dynamics of

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community assembly. The variations in phylogenetic structures and functional traits along resource-use environmental gradients could explain the differences in community assembly (Gong et al., 2019). Environmental filtering (based on abiotic factors) and interspecific competition (biotic factors) have been reported to play an important role in determining species coexistence in communities (Feng and van Kleunen, 2016). The Environmental filters, as one important assembly rule, could select the species (or individuals) in possession of certain traits in a community, resulting in the phylogenetic clustering of the community. Competitive exclusion has negative density-dependent effects, not only on conspecific individuals but also on closely related relatives, leading to the phylogenetic overdispersion. When the strength of environmental filtering and competition processes are balanced or weak, the phylogenetic structure of a community might be random/dissimilarities (Kembel and Hubbell, 2006). It is predicted that at the beginning of succession, owing to high light intensity and low nutrients, strong environment filtering could initially select good dispersers or fast-growing species from several clades of related species sharing similar functional strategies, the phylogenetic and functional trait structure in this stage might be clustering (Whitfeld et al., 2012) (Fig. 1). Species interactions (competition) at this stage are generally less important (Connell and Slatyer, 1977). When local habitats are modified by early colonists, the functionally similar species (e.g., annuals and heliophytes) could be replaced by other species (e.g., shade-tolerant tall perennials) (Li et al., 2015b). During this process, the early succession might experience continuous species immigration from the regional species pool, resulting in more phylogenetic and functional dissimilarities, i.e., random assembly might be important at the middle successional stage (Anderson, 2007) (Fig. 1). In later succession, due to the loss of large clades of early successional species, the community structure tends to be characterized by clusters of species that are close related and share similar functional traits. With increases in resource heterogeneity during succession, later successional stages may include not only related species with similar functional traits, but also diverse species with different functional traits (Letcher et al., 2012). It is therefore difficult to predict the dominant ecological processes shaping phylogenetic and functional trait community structures in the later successional stage.

Additional data are required regarding community assembly processes during succession (Gafta et al., 2016). Earlier studies mainly focused on temporal changes in species composition, single plant functional trait, or plant functional groups (e.g., Noble and Slayter, 1980; Purschke et al., 2013). These studies, however, often ignored the differences among species, multivariate correlations between functional traits, and the functional differences between functional groups (Villéger et al., 2008), all of which are needed to increase our understanding of community assembly mechanisms. With the growing interest in including phylogenetic information in community ecology research, an increasing number of studies have used both phylogeny-based analysis and functional trait-based analysis to evaluate the extent to which random and deterministic processes drive community assembly (Cianciaruso et al., 2012; Purschke et al., 2013; Li et al., 2015b). In general, if the co-occurring species in plot- or site-level communities are closely related and have similar functional traits (i.e., if the community exhibit phylogenetic structure clustering and functional trait clustering), environmental filtering might be driving the community assembly (Fig. 1, top row). In contrast, if species are not related and their functional traits are evenly dispersed (i.e., their phylogenetic structure and functional traits are evenly dispersed), competitive exclusion and niche differentiation might be driving the community assembly (Fig. 1 middle row) (Webb et al., 2002; Kraft and Ackerly, 2010).

Plant functional traits have been recognized as measurable indicators of acquisitive and conservative strategies of plants, which reflects how plants adopt and influence the biotic and abiotic environment (Balachowski and Volaire, 2018). Understanding which set of functional

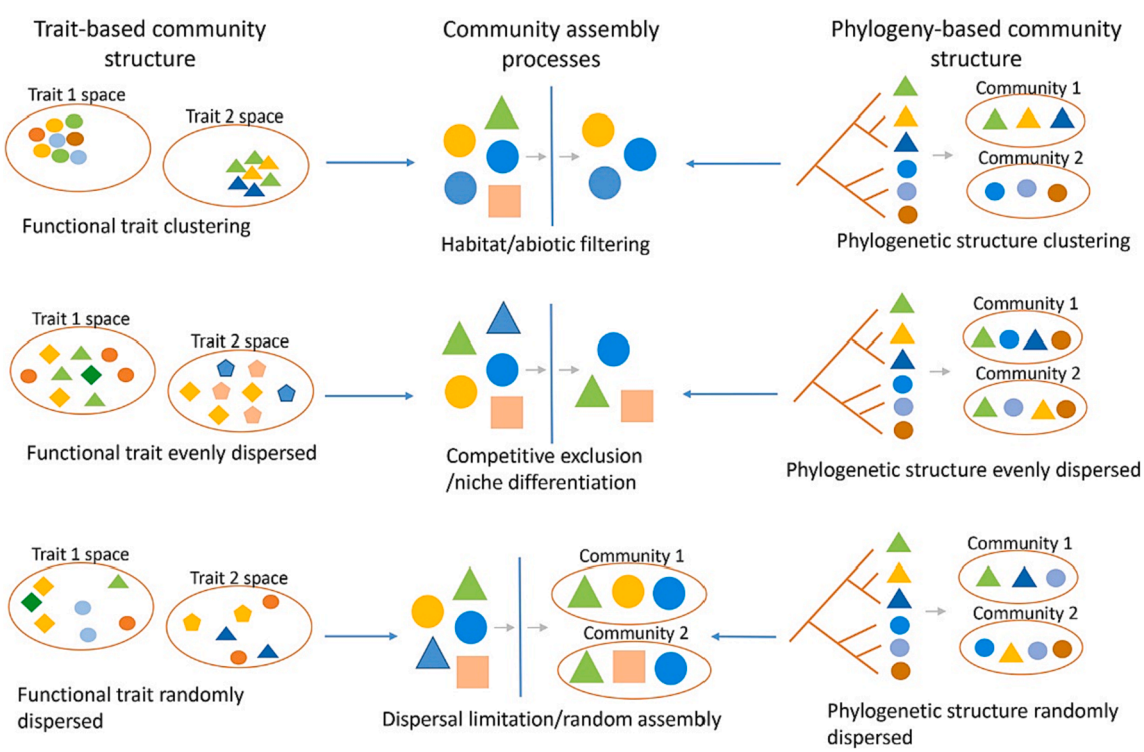

Fig. 1. Conceptual model for predicting relevant ecological processes as related to functional trait-based and phylogeny-based community structure. The same shapes in functional trait-based community structure (on the left) represent species with similar functional traits, and the same shapes in phylogeny-based community structure (on the right) represent closely related species. The same shapes in community assembly processes (in the center) represent the type of species that are used to assess community structure (e.g., the species that are used for phylogeny-based and functional trait-based analyses of community structure). Different colors in the figure represent different species. The blue arrows in the middle row indicate the inference processes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

traits determines the species persistence along a resource-use strategies gradient is important for our understanding of the dynamic process of community assembly in forest succession. In general, at early successional stage, dominant species do not tolerate frequent and intense fires, low soil nutrient and low water availability (Leandro et al., 2018), and always share some specific acquisitive functional strategies. For example, dominant species in early succession tend to invest in achieving high photosynthetic and reproductive rates, but tend to invest low in competitive and in maintaining defense strategies (Han et al., 2019). As light intensity decreases with succession, the dominant species are likely to change from light-demanding, annuals to shade-tolerant perennials, with more investment in competitive and defensive strategies (Han et al., 2019). That is, the functional strategies (i.e., the balance between acquisitive and conservative strategies) of dominant species could change during succession with the changing environmental condition.

It follows that when studying which ecological processes drive forest succession, researchers should assess a comprehensive array of functional traits that represent different plant functional strategies. In addition, plant functional strategies (e.g., competition strategy, defense strategy, and reproduction strategy) can often be simultaneously represented by different plant functional traits, which reflect different aspects of the strategies (Marino et al., 2010; Pu et al., 2020). For example, specific leaf area (SLA), light-use efficiency, and maximum plant height (H) can all refer to a plant's competitive ability. However, light-use efficiency could be a better indicator of a competitive strategy in early succession, while SLA and H might be better indicators of a competitive strategy in later succession. To our knowledge, however, few studies have tested the processes of community assembly of forest succession by assessing a broad array of functional traits (Bhaskar et al., 2014; Lohbeck et al., 2014).

Many parts of the monsoon evergreen broadleaved forest, a zonal vegetation type in the subtropical region, have long been disturbed by human activities (Yan et al., 2006), but have also, in some cases, been subject to restoration. The Dinghushan National Nature Reserve, is now composed of several successional stages (communities), including degraded grassland, coniferous forest, mixed coniferous and broadleaved forest, and monsoon evergreen broadleaved forest. Extensive long-term studies of community structures, functions, and dynamics have been conducted in these communities, and plant functional traits have been found to be good predictors of community dynamics (Li et al., 2015a). Although Zhang et al. (2018) found that environmental filtering might be the major ecological process driving the community assembly in the monsoon evergreen broadleaved forest, studies about community assembly process during succession are still rare. In the current research, 33 plant functional trait indicators of 30 dominant species, and 7 environmental factors and species richness in four successional communities were selected to explore the dominant ecological processes during succession. The selected functional trait indicators were related to plant competition, defense, and reproduction strategies. We attempted to answer two questions: (i) Which are the dominant ecological processes driving the succession of the subtropical forest? (ii) How the plant functional strategies change during subtropical forest succession?

2. Materials and methods

2.1. Research site

This study was conducted at the Dinghushan National Nature Reserve, southern China (E 112°32′57″, N 23°9′51″). The reserve has a monsoon climate. The mean annual precipitation is 1788 mm, and approximately 80 % falls from April to September, resulting in a distinct seasonality of precipitation. The mean annual temperature is 21.9 °C, and the coldest month is January (Lu et al., 2018). The soils of these forests are acidic (pH < 4).

The forests are in three typical successional stages, including a coniferous forest (SUC-2, about 60 years old), a mixed coniferous and broadleaved forest (SUC-3, about 100 years old), and an old-growth monsoon evergreen broadleaved forest (SUC-4, about 400 years old) (Yan et al., 2006). The dominant species of each forest were identified as being those with a sum of "importance values (IV)" exceeding 75 % of the total IV (Peng, 1996) (The data was shown in Han et al., 2019) (Fig. 2). During June to August of both 2016 and 2017, functional trait data were collected from five 30 m × 30 m plots in each forest (all plots had similar altitude, slope and aspect).

To compare the communities of the successional forests (SUC-2, SUC-3, and SUC-4) with a pre-forest community (SUC-1), we investigated a nearby grassland community that was about 4 years old; the community had previously consisted of a coniferous forest, which had been degraded by human activities. In 2016, we designated five 5 m × 5 m plots in the grassland. To identify the dominant species in the grassland, we assessed the coverage of each species in the plots; those species with the highest coverage whose combined coverage represented >80 % of the total coverage were identified as dominant species (The data was shown in Han et al., 2019) (Fig. 2). The functional traits of the dominant grassland species were also measured from June to August in both 2016 and 2017.

2.2. Measurement of plant functional traits

2.2.1. Whole-plant traits

Woody density (WD), defined as the dry weight of main stem divided by its volume, was measured using the method of Perez-Harguindeguy et al. (2016). WD was measured for five individuals of each dominant species in each plot in both 2016 and 2017. Following Perez-Harguindeguy et al. (2016), the maximum tree height (H) and crown area (CA) of 20–30 mature trees of each dominant tree species in each forest were determined. It was noted that the WD, H and CA of grass species were not measured. The life form (LF) of each dominant species was defined based on field observations and previous reports (Wu et al., 2003).

2.2.2. Plant reproductive traits

In 2016, plant reproductive traits were assessed for three randomly selected species (female individuals were selected if the species was dioecious) of each dominant species from three individual plots in each successional stage. The flowering and fruiting phenology at a 15d interval in 2016 and 2017 were monitored, so that each year included a total of 24–25 measurement days (Han et al., 2019). We recorded whether there were flowers or fruits on each individual on each measurement day. Mature fruits for most dominant species were also collected in each plot and their 1000-seed dry weight (SW) were determined. The fruit dispersal mode (DM), pollination pattern (PP), and fruit type (FT) were determined based on field observations and previous reports (Wu et al., 2003; Pei, 2011).

The first flowering and fruiting time (FFL and FFR), and the lengths of the flowering and fruiting cycles (LFL and LFR) were selected as the measures of flower and fruit phenology. FFL or FFR was measured as the total number of days from the first day of January to the first flowering or fruiting time divided by 30. LFL or LFR was characterized as the total number of days that the individuals remained in bloom or had fruit divided by 30 (Han et al., 2019).

2.2.3. Leaf structural and chemical traits

A total of 50–100 fully expanded sun-exposed leaves of each individual (3–5 individuals of each dominant species were selected) in each plot were collected between 1 July and 20 August (wet season) each year in 2016 and again in 2017; for the shade-tolerant species in the understory, leaves from the top of the canopy were collected. The leaves were stored in polyethylene bags and transported to the laboratory within 3 h (Perez-Harguindeguy et al., 2016). Leaf thickness (LT) and leaf chlorophyll content per unit area (CHl) of 15–20 leaves were determined with a digital thickness gauge (EXPLOIT, China), and a SPAD-502 Plus

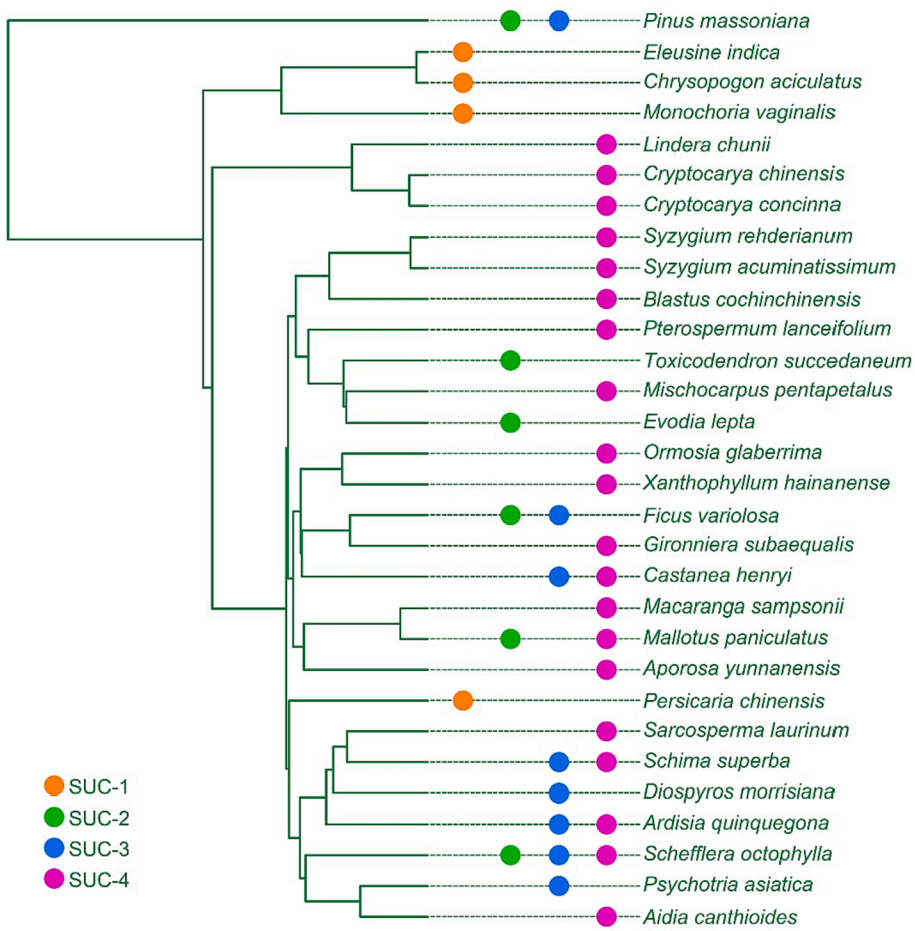

Fig. 2. The dominant species selected for study in each successional stage (SUC-1, SUC-2, SUC-3, and SUC-4) at Dinghushan, China. The solid circles indicate species existing in the successional stage, and different successional stages are indicated by different colors. SUC-1, SUC-2, SUC-3, and SUC-4 refer to grassland, coniferous forest, mixed coniferous broadleaved forest and monsoon evergreen broadleaved forest respectively.

Chlorophyll Meter (Konica Minolta, China), respectively (Rozendaal et al., 2006). Specific leaf area (SLA) was defined as leaf area (excluding the petiole) divided by leaf dry weight (oven-dried at 60 °C for 72 h). Leaf mass per area (LMA) was defined as leaf dry weight divided by leaf area, and leaf dry matter content (LDMC) was defined as the leaf dry weight divided by its fresh weight (Li et al., 2015a). The leaf area was determined with an LI-3000C portable area meter (LI-COR, USA). In addition, leaf stomata density (SD) and stomata size (SS) were measured with a stereo-microscope (JSM-6360LV, Japan) (Chen and Huang, 2013).

Leaf nitrogen content per unit mass (LN) and leaf phosphorus content per unit mass (LP) were determined using the modified Kjeldahl method, and molybdenum anti-colorimetric method, respectively (Li et al., 2015a). We calculated the LN/LP (N/P) ratio, because it can reflect a limitation of nitrogen or phosphorus (Wright et al., 2005). As an index of water availability at the species level (Warren et al., 2001), leaf stable ^{13}C isotope composition (C13) was determined with an IsoPrime100 (Elemental, USA) stable isotope ratio mass spectrometer.

2.2.4. Leaf defensive traits

For assessment of the defensive traits of young leaves of each dominant species, the presence of a multi-layered epidermis (MLE), trichomes (Tr), and enhanced cuticles (EC) were determined with a stereo-microscope for each plot (Chen and Huang, 2013). The detailed methods were shown in Han et al. (2019).

2.2.5. Leaf physiological traits

Leaf light-capturing strategies were quantified as the maximum CO_2 assimilation rate per unit mass (A_{mass}), the leaf transpiration rate per unit mass (T_{mass}), and the leaf stomatal conductance per unit mass (g_s) (Li et al., 2015a). The leaf respiration rate per unit mass (R_{mass}) and water-use efficiency (WUE) were also determined because of their importance for plant metabolism (Keenan et al., 2013). Between 8:30 am and 12:00 am on a date between 1 July and 20 August in both 2016 and 2017, a LI-COR 6400 Portal Photosynthesis System (LI-COR, USA) was used to measure the following indices per unit leaf area: A_{area}, T_{area}, g_{sa}, and R_{area}; these indexes were measured on 3–5 fully expanded leaves in each successional stage for each dominant species. According to preliminary trials, the light intensity of the photosynthesis-light curve was set at 1600, 1200, 1000, 800, 600, 400, 200, 100, 50, 20, or 0 μmol m^{-2} s^{-1} with a red-blue LED light source; and chamber temperature was set at 25 °C; and the reference CO_2 concentration was set at 400 μmol mol^{-1}. The following indices were calculated: $A_{mass} = A_{area}/LMA$, $T_{mass} = T_{area}/LMA$, $g_s = g_{sa}/LMA$, and $R_{mass} = R_{area}/LMA$ (Osnas et al., 2013). WUE was measured as A_{area}/T_{area} (Gago et al., 2014). The photosynthetic nitrogen-use efficiency (PNUE) and photosynthetic phosphorus-use efficiency (PPUE) were calculated as A_{mass}/LN and A_{mass}/LP, respectively.

2.3. Measurement of environmental factors

Soil randomly cores (5 cm diameter × 20 cm deep) were collected in each plot of all successional stages on a data between 1 July and 20 August in 2016 and 2017; they were combined to from one composite sample and were transported to laboratory within 3 h. The roots and stones of the samples were removed and then were passed through a 2-

mm sieve. Using the indophenol blue method, the soil ammoniacal nitrogen content (NH_4^+-N) of fresh soil samples were determined. The soil total carbon content (TC) was determined using the potassium dichromate method, and soil organic matter (SOM) was calculated as TC × 1.724 (Liu, 1996). The total nitrogen content (TN) and total phosphorus content (TP) of air-dried soil samples were determined using the modified Kjejdahl method and the molybdenum anti-colorimetric method (Liu, 1996). After extraction with 0.1 M $BaCl_2$, soil exchangeable K^+, and Mg^{2+} (E_k, and E_{mg}) were determined with an ICP optical emission spectrometer (Tanabe, Hidenori, Tokyo, Japan) (Wright et al., 2001).

Leaf area index (LAI), as a typical indicator of the light availability under the forest, was measured on a cloudless morning using the LAI-2200C Plant Canopy Analyzer (LI-COR, Inc., Lincoln, NE, USA). LAI was calculated by recording 30 below canopy-points distributed evenly in each plot of all successional stages and 6 above canopy-points outside the communities on a data between 1 July and 20 August in both 2016 and 2017.

2.4. Statistical analysis

Mean functional trait values were used for each species in each successional stage in this study, although consideration of the intraspecific variation in functional traits could be useful (Baraloto et al., 2010). We believe that mean trait values were appropriate for the aims of the current study given the high species turnover rates during succession. Because of the right-skewed distribution of most traits other than the categorical traits, the trait values were firstly standardized using the Z-score and then were normalized by a $\log_{10}$ transformation as needed before further data analysis. The trait data set is available in Table B.

2.4.1. Phylogenetic tree construction

A phylogenetic tree with all dominant species was constructed (Fig. 2). This was done using the function of *phylomatic* in the "branching" package, which is similar to the Phylomatic website (https://www.phylodiversity.net/phylomatic/) (Webb and Donoghue, 2005). Phylogenetic distances among species were estimated based on the phylogenetic hypothesis of "tree zanne 2014" (Zanne et al., 2014), which provided the branch length information needed for this study.

2.4.2. Estimating trait conservatism

Phylogenetic signal of functional trait was calculated using Blomberg's K statistic (Blomberg et al., 2003) with the function *phylosig* (in "phytools" package) under the environment of R 3.4.4 (Revell, 2012). The phylogenetic signal of the K statistic was determined by using a Brownian motion-like model of trait evolution (Kraft and Ackerly, 2010). The 0 value of the K statistic indicates the absence of a phylogenetic signal, and $K = 1$ indicates that the trait distribution perfectly matches a Brownian motion of trait evolution. $K > 1$ indicates stronger similarities among closely related species than expected, and $K < 1$ indicates higher convergence than expected by the evolution model of Brownian motion. The significance of K was evaluated based on the comparison between the observed K value and the distribution of K values obtained by shuffling the species across the tips of the phylogenetic tree 999 times (Kraft and Ackerly, 2010).

2.4.3. Phylogeny-based analysis of community structure

The net relatedness index (NRI) and the nearest taxon index (NTI) were used to assess the phylogenetic community structure for all plots of each site in this study (Webb et al., 2002). The NRI is a standardized index for phylogenetic clustering or evenness, and is based on the mean pairwise phylogenetic distances (MPD) between co-occurring taxa in the community. The NTI is considered another index of phylogenetic relatedness and is often presented with NRI. NTI is based on the mean distance of the most closely related co-occurring taxon (mean nearest taxon distance, MNTD) (Letcher et al., 2012).

The functions *ses.mpd* and *ses.mntd* in the "picante" package were used to construct the null model by shuffling the species labels and maintaining the species richness across the phylogenetic tree (Letcher et al., 2012). All of the dominant species were used when constructing the null model, because they belong to the same species pool (Pei, 2011).

The abundance-weighted method was used to calculate NRI and NTI. The significance of NRI and NTI for each plot was assessed by comparing the observed MPD/MNTD to a null distribution of MPD/MNTD on 999 null communities. Positive values of NRI and NTI indicate that the species in question in a plot are more related than expected (phylogenetic clustering), and negative values indicate that the species in a plot are phylogenetically evenly dispersed (Webb and Donoghue, 2005).

2.4.4. Functional trait-based analysis of community structure

Because functional dendrograms and phylogenetic trees can be calculated by an identical data structure, any index used to assess a phylogenetic tree can also be used for functional trait-based distance matrices (Cianciaruso et al., 2012). As was the case with MPD, the mean pairwise functional distances (MFD) among co-occurring species can be measured (Cianciaruso et al., 2012). To correspond to the NRI, the standardized effect size of MFD (SES.MFD) were also defined as follows:

$$\text{SES.MFD} = \frac{\text{observed(MFD)} - \text{mean(expected(MFD))}}{\text{standard deviation of expected MFD}}$$

The functional trait-based null community was constructed in the same way as the phylogeny-based null community, i.e., by shuffling the species labels and remaining the species richness across the functional dendrogram. The abundance-weighted method was used to calculate SES.MFD. The significance of SES.MFD was assessed by comparing the observed MFD to a null distribution of MFD on 999 null communities. Negative values of MFD indicate functional trait clustering, and positive values indicate functional trait evenly dispersed.

Because the community trait range was sensitive to environmental filtering, and because the standard deviation of nearest neighbor distance along trait axes (SDNN) was sensitive to competitive exclusion, the indices of functional trait range and SDNN were also selected (Kraft et al., 2015). In each plot, the observed abundance-weighted indices were compared to a null distribution generated by creating 999 random communities constructed in the same way as SES.MFD. Plot-level Wilcoxon signed-rank tests were used to assess the significance of the three indices (Kraft and Ackerly, 2010).

2.4.5. Data analysis

One-way analysis of variance (ANOVA) was used to examine the differences in community phylogenetic and functional trait structure from the four successional stages. To identify the effects of environmental factors and biotic factors (species richness) on the phylogenetic and functional trait structure, a structural equation modeling (SEM) and multiple linear regression were used. The structural equation modeling was used to disentangling the relationships between environmental factors, species richness, phylogenetic structure and functional trait structure (Gong et al., 2019). The multiple linear regression was used to assess the relative effects of environmental factors and species richness on the community phylogenetic structure. Before the data analysis, all factors (predicators) were standardized using the Z-score to interpret parameter estimates on a comparable scale (Le Bagousse-Pinguet et al., 2017). The model selection procedure of multiple linear regression was based on the corrected Akaike information criterion (AICc) according to Le Bagousse-Pinguet et al. (2017). The analyses were conducted with the packages "corrgram", "psych", and "multcomp" in the environment of R 3.4.4 (Hothorn et al., 2008; Revelle, 2018; Wright, 2018; R Development Core Team, 2018).

3. Results

3.1. The effects of environmental factors and species richness on community assembly

3.1.1. Relationships among environmental factors, species richness, and community phylogenetic and functional trait structure

SEMs showed that the environmental factors (TP, TN, and $NH4^{+}$-N) have a direct impact on species richness and NRI, and at the same time, richness also has a direct impact on NRI (Figs. 3, 4). Both environmental factors and richness have strong effect on NRI according to the standardized effects from SEM (Figs. 3, 4). The $H_{SES.FD}$ was not only directly affected by TN, and $NH4^{+}$-N and NRI, but also indirectly affected by richness and environmental factors through NRI (Fig. 3a, c, e). Among them, the NRI and environmental factors had a great impact on $H_{SES.FD}$ than richness based on the standardized effects from SEM (Fig. 3b, d, f). Both environmental factors (TN, TP) and richness had direct and indirect effects on $SLA_{SES.FD}$ (Fig. 4a, b, c). In addition to NRI, TN, and $NH4^{+}$-N, the richness also has a strong effect on $SLA_{SES.FD}$ (Fig. 4f).

3.1.2. The relative effects of environmental factors and richness on community phylogenetic structure

According to the variance decomposition analysis of the multiple linear regression models (Fig. 5), environmental factors could explain >80 % of the variance of NRI and NTI along the successional gradient, especially the TP, which could explain 46 % and 43 % of the variance of the NRI and NTI, respectively. In addition, richness also has a significant effect on NRI and NTI, which could explain approximately 19 % and 9 % of the variance in NRI and NTI, respectively (Fig. 5).

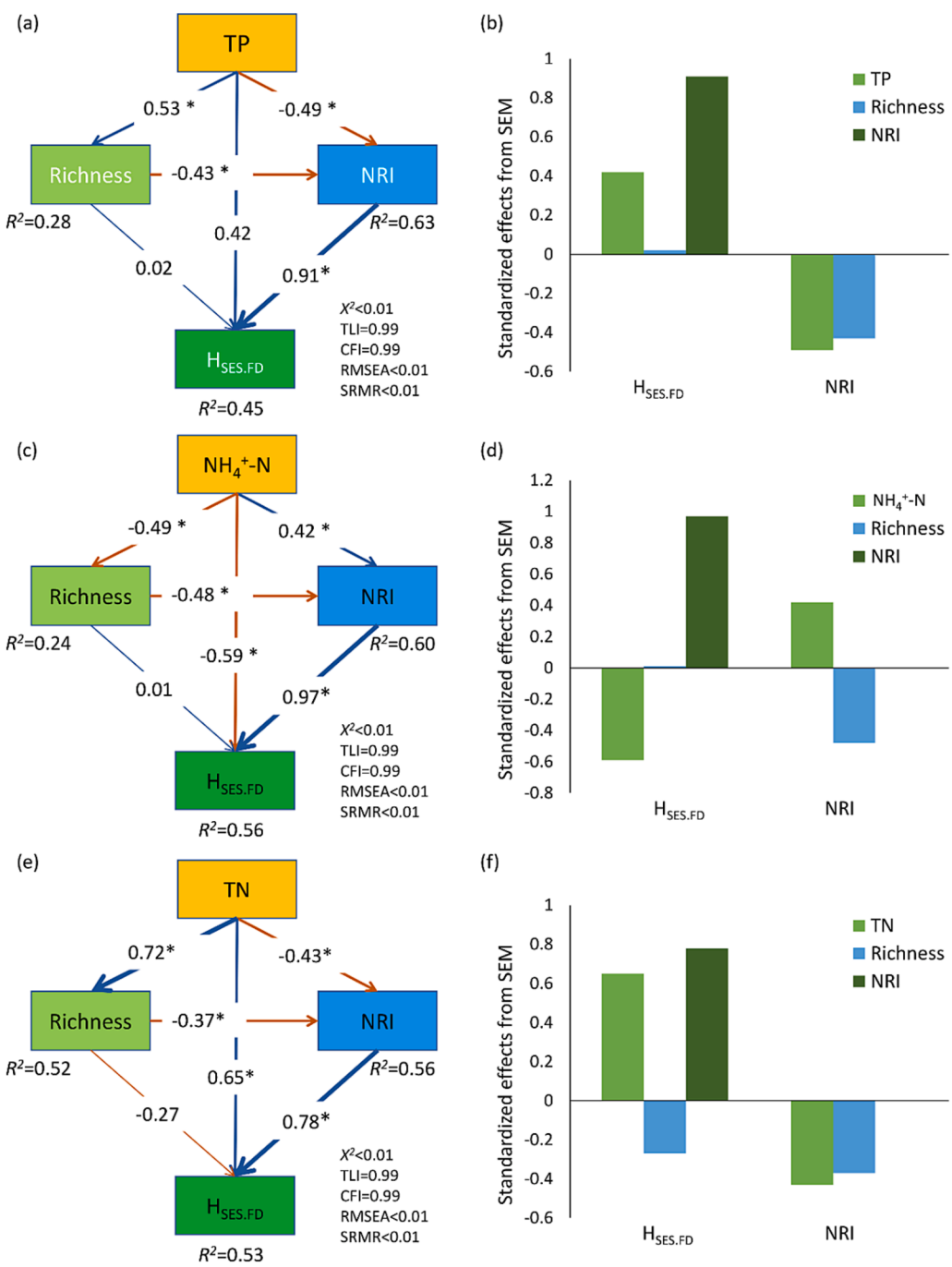

Fig. 3. Structural equation model for the relationships between environmental factors, species richness, NRI and $H_{SES.FD}$. Single-headed arrows indicate the hypothesized direction of causation. The blue and orange arrows indicate positive and negative relationships, respectively. Values along all paths indicate the standardized regression coefficients, and significance indicated as follows: *P < 0.05. Arrow width is proportional to the strength of the relationship. R^2 refers to the proportion of variance explained by the relationship. (b, d, f) represent the standardized total effects derived from the corresponding structural equation model. $H_{SES.\ FD}$ refers to the standardized effect size of the functional distance of maximum height from the null model approach; NRI refers to the net relatedness index; $NH4^{+}$-N refers to soil ammoniacal nitrogen content; TN refers to soil total nitrogen content; and TP refers to soil total phosphorus content. TLI, CFI, RMSEA, and SRMR refer to the Tucker-Lewis index, comparative fit index, root mean square error approximation, and the standardized root mean square residual, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

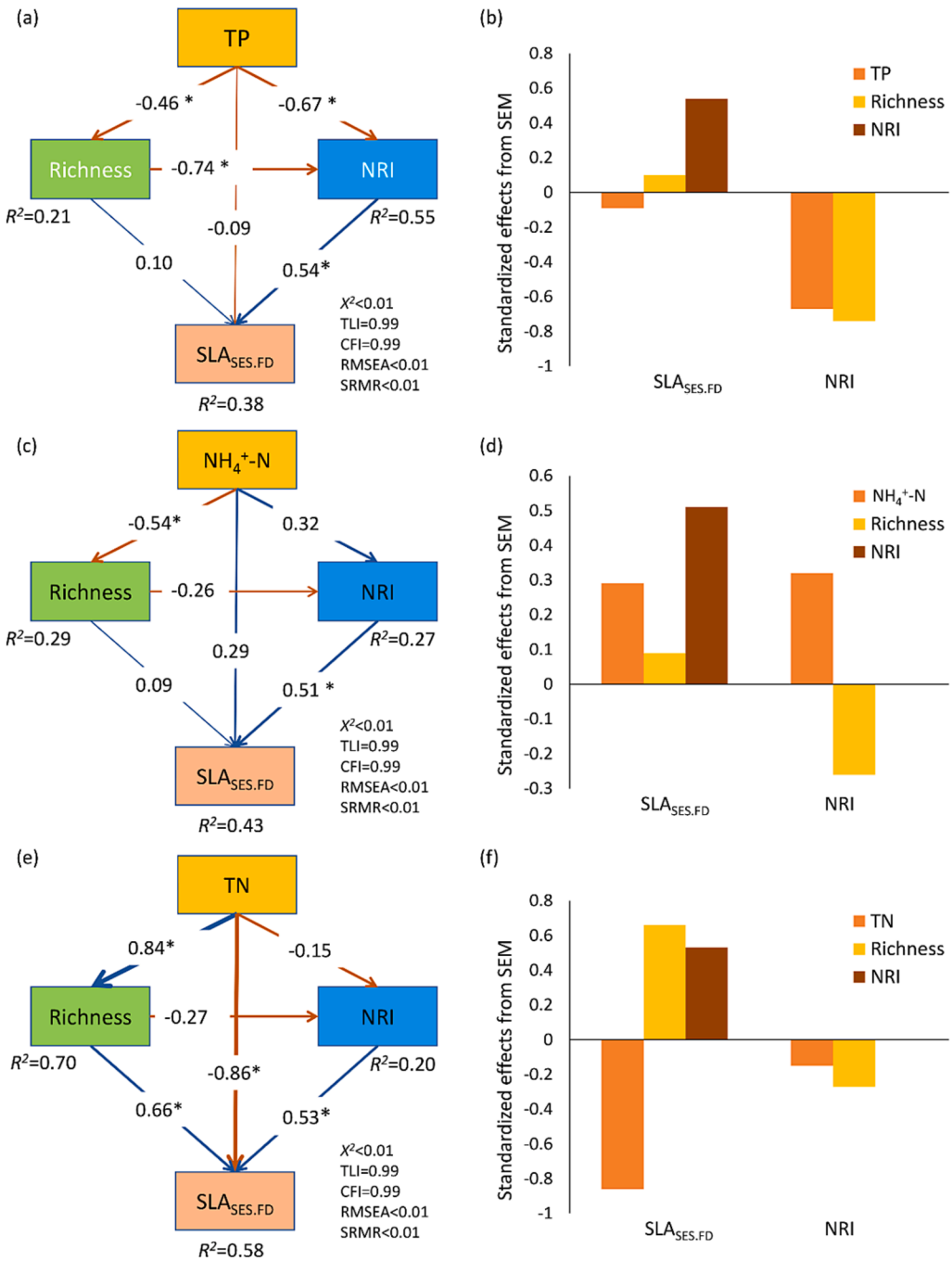

Fig. 4. Structural equation model for the relationships between environmental factors, species richness, NRI and $SLA_{SES.FD}$. Single-headed arrows indicate the hypothesized direction of causation. The blue and orange arrows indicate positive and negative relationships, respectively. Values along all paths indicate the standardized regression coefficients, and significance indicated as follows: *P < 0.05. Arrow width is proportional to the strength of the relationship. R^2 refers to the proportion of variance explained by the relationship. (b, d, f) represent the standardized total effects derived from the corresponding structural equation model. $SLA_{SES.\ FD}$ refers to the standardized effect size of the functional distance of maximum height from the null model approach; NRI refers to the net relatedness index; $NH4^+$-N refers to soil ammoniacal nitrogen content; TN refers to soil total nitrogen content; and TP refers to soil total phosphorus content. TLI, CFI, RMSEA, and SRMR refer to the Tucker-Lewis index, comparative fit index, root mean square error approximation, and the standardized root mean square residual, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Phylogeny-based community structure

NRI and NTI were significantly different among the four successional stages (Fig. 6). The mean values of NRI and NTI from SUC-2 and SUC-3 were greater than zero, unlike the mean values of them in SUC-1 and SUC-4. Significant phylogenetic clustering was found in at least two plots in SUC-1 and SUC-4 (Table A.1), and phylogenetic structure randomly dispersed was found in SUC-2 and SUC-3 (Table A.1; Fig. 7).

3.3. Functional trait-based community structure

3.3.1. Trait conservatism

Most of the 33 functional traits exhibited an intermediate level of trait conservatism with K values ranging from 0.2 for WUE to 0.89 for LT (Table. 1). About half of the functional traits were more conserved than predicted by the Brownian motion model ($P < 0.05$; Table. 1). The conserved traits included the leaf physiological traits, chemical traits and structural traits, and also a few whole-plant traits and reproductive traits. C13, CHl, MLE, SLA, and LMA were significantly more conservative than predicted by the Brownian motion model ($K > 1$; $P < 0.05$; Table. 1).

3.3.2. SES.MFD, range and SDNN

In the SES.MFD analysis, for plant reproductive traits, FFL clustering and LFR clustering were found only in SUC-1 and SUC-2, respectively (Fig. 8a). For the whole-plant traits, significant clustering of WD, CA, H, and LF was found in SUC-4, and LF clustering was found in SUC-1 (Fig. 8b). Most clustering of leaf chemical trait was found in SUC-1, SUC-3, and SUC-4 (Fig. 8c). Most leaf physiological traits exhibited clustering in SUC-4, and the T_{mass} was also clustering in SUC-1 (Fig. 8e).

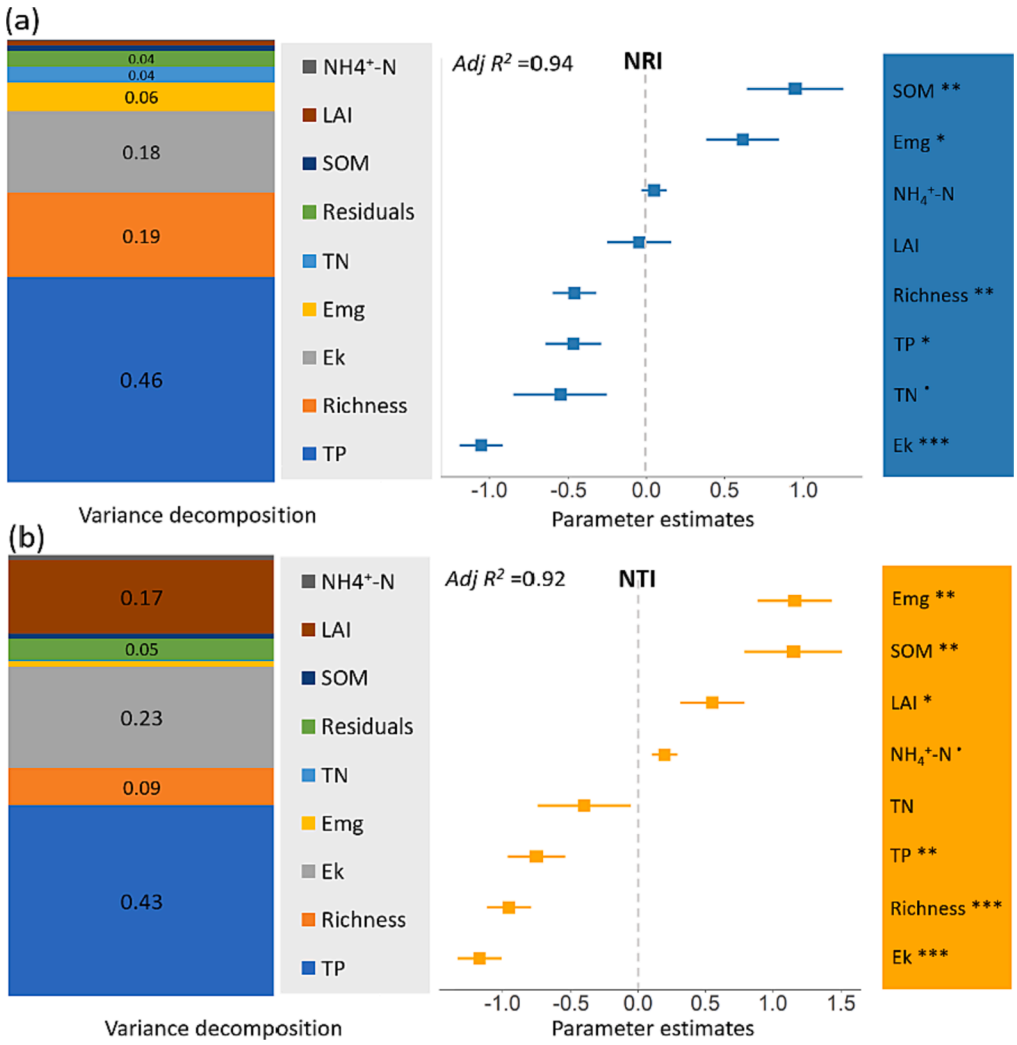

Fig. 5. Effects of multiple environmental factors and richness on the NRI (a) and NTI (b). NH4$^+$-N, SOM, TN, E_{mg}, E_k, TP refer to soil NH_4^+-N, organic matter, total N, exchangeable Mg^+, exchangeable K^+, total P content, respectively. LAI refers to leaf area index. Significance indicated as follows: * <0.05, **<0.01, and ***<0.001.

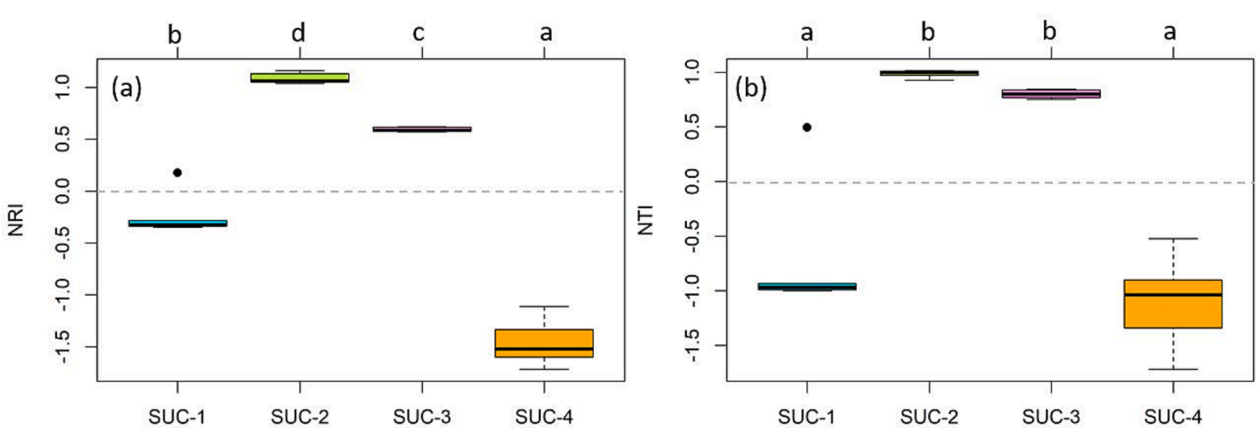

Fig. 6. Comparisons of community phylogenetic structure in four successional stages. (a) and (b) show phylogenetic community structure as indicated by the net relatedness index (NRI) and the nearest taxon index (NTI), respectively. SUC-1, SUC-2, SUC-3, and SUC-4 represent grassland, coniferous forest, mixed coniferous broadleaved forest, and monsoon evergreen broadleaved forest, respectively. Each box shows the interquartile range and median; whiskers indicate the 10th and 90th percentiles. Post hoc differences ($P < 0.05$) in the indices among the four successional stages are indicated by the lowercase letters at the top of each panel.

In the functional trait range analysis, clustering of CA, LMA, A_{mass}, and PPNE was found in SUC-4, and clustering of LFL, LDMC and LP was found in SUC-3 (Fig. A.1; Table E, F). Clustering of LFL and SW was found in SUC-2, and clustering of EC, LT, and LMA clustering was found in SUC-1 (Fig. A.1; Table E, F).

In the SDNN analysis, significantly even dispersal was found for only

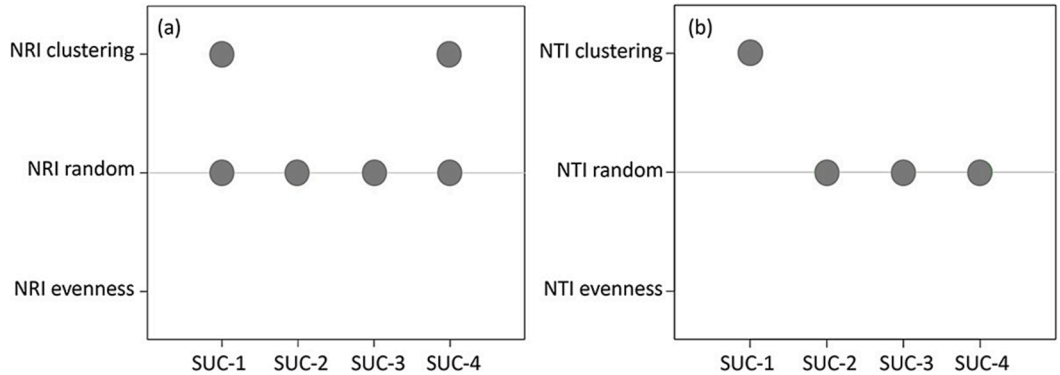

Fig. 7. Summary of the assessments of phylogenetic community structure at the plot-level. Solid circles indicate that clustering, random dispersal, and evenly dispersal of phylogenetic community structure was found in at least two plots in each successional stage. (a) and (b) show phylogenetic community structure as indicated by the net relatedness index (NRI) and the nearest taxon index (NTI), respectively. SUC-1, SUC-2, SUC-3, and SUC-4 represent grassland, coniferous forest, mixed coniferous broadleaved forest, and monsoon evergreen broadleaved forest, respectively.

Table 1
Conservation analyses of the 33 plant functional traits using the *K* statistic.

Plant functional traits	*K*	*P*	Plant functional traits	*K*	*P*
Whole-plant traits			**Leaf defensive traits**		
Woody density (WD)	0.48	0.15	Enhanced cuticle (EC)	0.39	0.29
Crown area (CA)	0.36	0.44	Trichome (Tr)	0.53	0.16
Maximum height (H)	0.39	0.34	Leaf multi-layer epidermis (MLE)	**1.27**	**0.01**
Life form (LF)	**0.76**	**0.02**	**Leaf structural traits**		
Plant reproductive traits			Leaf thickness (LT)	**0.89**	**0.02**
First flowering time (FFL)	0.43	0.11	Specific leaf area (SLA)	**1.95**	**<0.01**
Length of flowering cycle (LFL)	0.37	0.45	Leaf mass per area (LMA)	**1.97**	**<0.01**
First fruiting time (FFR)	0.53	0.08	Leaf dry matter content (LDMC)	0.37	0.24
Length of fruiting cycle (LFR)	0.46	0.18	Stoma density (SD)	0.44	0.48
Thousand seeds weight (SW)	0.45	0.18	Stoma size (SS)	0.43	0.49
Fruit dispersal mode (DM)	0.38	0.38	**Leaf physiological traits**		
Pollination pattern (PP)	0.33	0.55	Leaf respiration rate per mass (R_{mass})	**0.77**	**0.01**
Fruit type (FT)	**0.57**	**0.04**	Leaf photosynthesis rate per mass (A_{mass})	**0.69**	**0.03**
Leaf chemical traits			Leaf stomatal conductance per mass (g_s)	**0.63**	**0.02**
Leaf Isotope ^{13}C content (C13)	**1.42**	**<0.05**	Leaf transpiration rate per mass (T_{mass})	**0.82**	**0.01**
Leaf chlorophyll content (CHl)	**1.34**	**<0.01**	Leaf photosynthetic N use efficiency (PNUE)	**0.81**	**0.01**
Leaf P content (LP)	**0.6**	**0.04**	Leaf photosynthetic P use efficiency (PPUE)	**0.63**	**0.03**
Leaf N/P ratio (N/P)	**0.77**	**<0.01**	Leaf water use efficiency (WUE)	0.2	0.84
Leaf N content (LN)	0.28	0.56			

Notes: $K = 1$ indicates that the observed functional trait distribution matches the Brownian motion model of functional trait evolution across the phylogenetic tree built by all the dominant species in Dinghushan, China. $K < 1$ indicates that the observed functional trait distribution is greater convergent than Brownian model; while $K > 1$ indicates that the functional trait is more conservative (strong phylogenetic signal) than expected. *P* value refers to the Wilcoxon signed-ranks test of the null hypothesis that where the observed *K* value is distributed in the null expectation distribution. The null expectation distribution is determined by shuffling the functional traits across the tips of the phylogenetic tree 999 times. Boldface type indicates the significance level $P < 0.05$.

10 functional traits (Fig. A.2). LT, SLA, C13, LP, A_{mass}, g_s, PNUE, and PPUE was evenly dispersed in SUC-4 (Fig. A.2; Table G). C13 was evenly dispersed in SUC-2 (Fig. A.2a), and T_{mass} and PNUE were evenly dispersed in SUC-1 (Fig. A.2b).

3.3.3. *Comparisons of functional trait diversities among four successional stages*

Except for C13, the SDNNs and ranges of functional traits changed during succession (Figs. 9, 10; Table A.2, H). The range of H tended to be higher in SUC-3 than in other successional stages, and the SDNN decreased during succession (Fig. 9a, b). The range of WD did not change during succession, but its SDNN was highest in SUC-3 (Fig. 9e, f). Among reproductive traits, the range of FFL decreased during succession, while its SDNN tended to increase (Fig. 9g, h). The changes of other phenological traits were similar to those for FFL (Table H). The range of SW increased initially and then decreased during succession, while its SDNN was lower in SUC-4 than in SUC-2 or SUC-3 (Fig. 9i, j).

The range of EC was lowest in SUC-1, and its SDNN was highest in SUC-3 (Fig. 9c, d). The range of SLA decreased with succession, while its SDNN initially increased and then decreased (Fig. 9k, l). The ranges of LN, LP, A_{mass}, and PPUE decreased during succession (Fig. 10), and the ranges of other leaf physiological traits had similar trends during succession (Table H). The SDNNs of LP, A_{mass}, and PPUE tended to decrease during succession (Fig. 10).

4. Discussions

Species dominance is mainly determined by the adaptation of species to the local environments and by the biotic interactions, and the ecosystem function is largely driven by the characteristics of the dominant species (Smith and Knapp, 2003). Consistent with Lohbeck et al. (2014), the rationale behind this study was that ecological processes (e.g., habitat filtering and competitive exclusion) have significant effects on the dominance of species, such that the dominant species at different successional stages could indirectly help in determining the dominate community assembly processes; that determination might be biased, however, if the rare species are not considered.

4.1. *The dominant ecological processes change during succession according to the community phylogenetic and functional trait structure*

Most functional traits in this study were found to be more phylogenetically conserved than predicted by the Brownian motion model, and about half of them had a significant phylogenetic signal (Table 1). These findings indicate that the phylogeny-based analysis could be used to explore the community assembly processes.

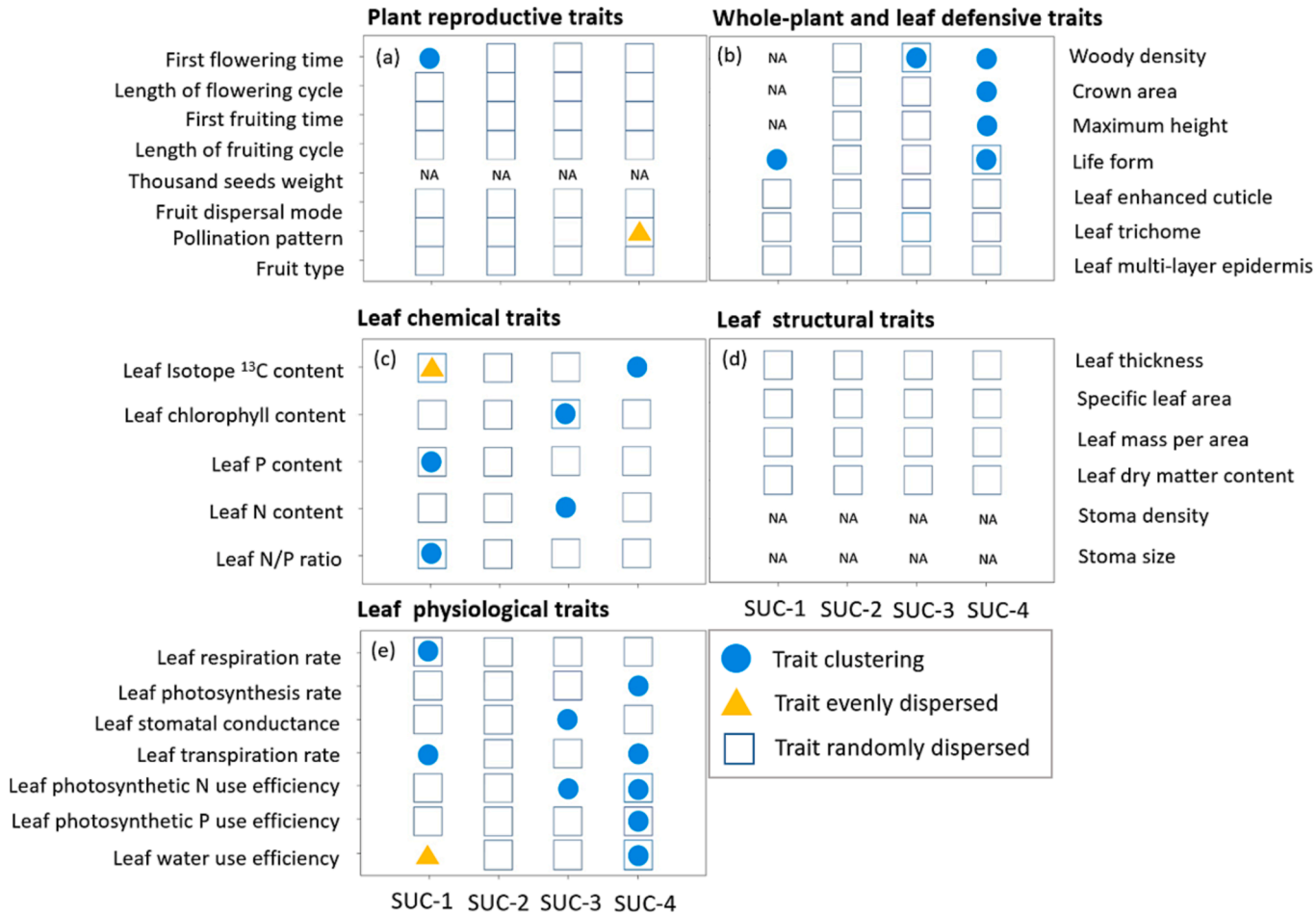

Fig. 8. Summary of functional trait-based analyses of community structure using SES.MFD in plot-level. SES.MFD refers to the standardized effect size of the mean pairwise functional distance (MFD). Circles, triangles, and squares indicate that functional traits were clustered, evenly dispersed, and randomly dispersed, respectively, in at least two plots in each succession. NA indicates that the data were not collected or were missing. The significance level was set as $P < 0.05$ and $P > 0.95$ to detect potential functional trait community structure, although doing so may increase the probability of I error. SUC-1, SUC-2, SUC-3, and SUC-4 represent grassland, coniferous forest, mixed coniferous broadleaved forest, and monsoon evergreen broadleaved forest, respectively.

In this study, the convergent functional trait $H_{SES.FD}$ and the conservative functional trait $SLA_{SES.FD}$ were all found to be directly affected by the environmental factors (TP, NH_4^+-N, TN) and indirectly affected by the species richness through NRI from the SEM analysis (Figs. 3, 4). Meanwhile, the community phylogenetic structure NRI and NTI were also significantly affected by the environmental factors and species richness (Fig. 5), indicating that both environmental filtering and species interaction (competition) have a significantly impact on the processes of community assembly during succession. Among them, the environmental filtering might be more important than competition exclusion, because the environmental factors (especially TP) could explain more variance in NRI and NTI during the subtropical forest succession (Fig. 5). Such results were similar to the study of Pinho et al. (2017) that soil fertility was a key assembly force leading to functional trait convergence and plant assemblages along a tropical forest succession. Additionally, Piwczyński et al. (2016) and Gong et al. (2019) also reported that the environmental filtering were major drivers of community phylogenetic diversity in an understory community.

Across the four successional stages, the dominant species tended to exhibit a high level of phylogenetic clustering in SUC-1 (Table A.1, Fig. 6), meanwhile, the R_{mass}, T_{mass}, FFL, SW, and LP were also found clustering in SUC-1 (Fig. 8), indicating that environmental filtering plays an important role in the early successional stage (Fig. 1). According to our survey, the dominant species in SUC-1 were herbaceous and mainly in the Poaceae family (Fig. 2), which were relatively close compared to the regional species pool and other successional stages, supporting the hypothesis that closely related species are always selected by environmental factors in early succession (Chazdon et al., 2011).

Although we found that both environmental factors and richness have an important impact on community assembly during succession, the phylogenetic structure randomly dispersed (Fig. 7) and plenty of various functional trait structure randomly dispersed (Fig. 8) were found in the middle succession (i.e., SUC-2, SUC-3), indicating that environmental filtering and competitive exclusion might be weak for the community assembly of the middle successional stage. This is consistent with stochastic niche theory, which predicts that with the environmental modification by grass species in early succession, the community might become more suitable for woody species (Tilman, 2004). As a consequence, when woody species enter a modified community through immigration from a regional species pool, community assembly can be largely neutral such that each species has an equal chance to colonize (Emerson and Gillespie, 2008). Under this scenario, dispersal ability and environmental heterogeneity should be involved in the process of community assembly.

Based on the findings of phylogenetic clustering (Fig. 7) and WD, CA, H, LF, A_{mass}, T_{mass}, LNUE, LPUE and WUE clustering in SUC-4 (Fig. 8), our results indicated that environmental filtering was also a major diver in the process of community assembly in later successional stage (i.e., SUC-4), which differs from the findings of many previous studies (Letcher et al., 2012; Purschke et al., 2013). Li et al. (2015b) found that

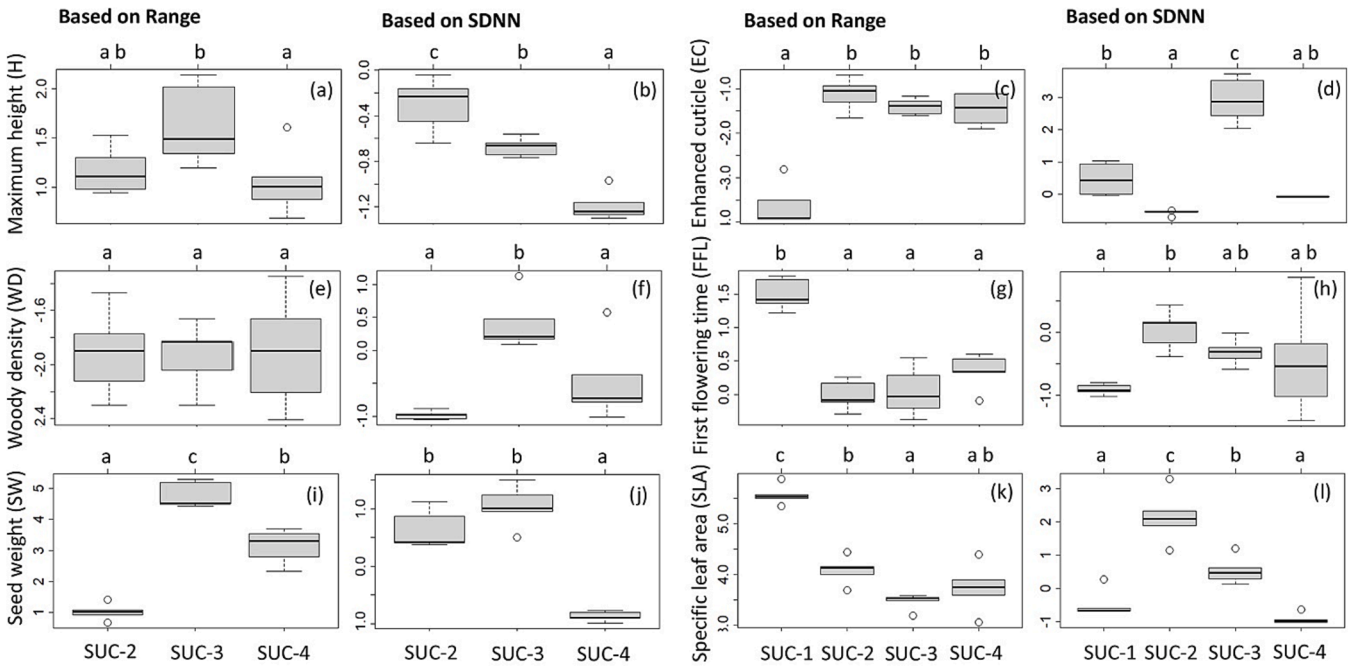

Fig. 9. Comparisons of some whole-plant, reproductive, leaf defensive and structural traits among successional stages based on range and SDNN. SUC-1, SUC-2, SUC-3, and SUC-4 represent grassland, coniferous forest, mixed coniferous broadleaved forest, and monsoon evergreen broadleaved forest, respectively. Each box shows the interquartile range and median; whiskers indicate the 10th and 90th percentiles. Post hoc differences ($P < 0.05$) among the successional stages are indicated by lowercase letters at the top of each panel.

the phylogenetic and functional distances between local extinctions and residents are not associated over time during succession, suggesting that the loss of species distantly related to the resident species might drive communities to be more clustered than over dispersed. The reduced dominance of gymnosperms and herbs in SUC-4 in this study could partially explain the finding of phylogenetic structure clustering in later succession. A relevant question is whether environmental filtering or competitive exclusion is responsible for such declines in dominance. According to Mayfield and Levine (2010), competitive exclusion should eliminate more closely related taxa when the competitive ability of these taxa is lower than that of residents in local communities. The competitive ability (e.g., tree height) of gymnosperms and herbs of SUC-1 was apparently lower than that of shade-tolerant species in the later succession. We infer that competitive exclusion might be one reason for the phylogenetic clustering in later succession. Our results also support the view that community phylogenetic patterns do not enable researchers to readily separate the effects of habitat filtering from the effects of competitive exclusion in later succession (Mayfield and Levine, 2010).

An even dispersal of A_{mass}, g_s, PNUE, and PPUE were found in SUC-4 (Fig. A.2), indicating that competitive exclusion might be one driver of functional diversity in later succession. In general, greater tree height makes species more competitive in closed-canopy environments (Purschke et al., 2013). In the current study, the SDNN of H was lower in SUC-4 than in the other stages (Fig. 9b), indicating that competitive exclusion based on H was more important in later than in earlier stages. We therefore infer that the clustering of H in later succession (Fig. 8c) might be caused by strong competitive exclusion. The photosynthesis related traits (i.e., A_{mass}, g_s, PNUE, and PPUE) were also found to be clustered in the middle or later succession (i.e., SUC-3, and SUC-4; Fig. 8, A.1, A.2), further indicating the importance of environmental filtering in later succession (Wright et al., 2005). The range and SDNN of the photosynthetic traits were lower in SUC-4 than in SUC-1 (Fig. 10; Table H), suggesting that both environmental filtering and competitive exclusion were stronger in later than in early succession. Thus, the specific competitive strategies of dominant species in later succession could be the results of the comprehensive effects of both environmental filtering and competitive exclusion.

Based on the even dispersal of LP in SUC-4 and the lower value of LP in SUC-4 than in SUC-1 (Table B), we infer that competitive exclusion is important for the P nutrient utilization in later succession. That the range and SDNN of LP were lower in SUC-4 than in the other successional stages (Fig. 10c, d) indicated that the strength of environmental filtering and competitive exclusion for LP are both higher in later succession. Soil P content therefore should be a limiting factor for the community assembly in later succession. The clustering of LP in SUC-1, SUC-3, and SUC-4 indicated the importance of soil P in most successional stages, which was also supported by the SEMs analysis and multiple linear regression analysis (Figs. 3, 4, 5). This is consistent with the conclusion that soil P is a key factor limiting the community development in subtropical region of China (Lu et al., 2018).

4.2. The functional strategies of dominant species changed during succession

Almost leaf physiological traits (e.g., A_{mass}, T_{mass}, PNUE, and PPUE) related to plant competitive strategy were found clustered in SUC-1 (Fig. 8, A.1). Meanwhile, seed weight (SW) and first flowering time (FFL) (as parts of plant reproductive strategy), enhanced cuticle (EC) and leaf thickness (LT) (as part of plant defensive strategy) were also found clustered in SUC-1 (or SUC-2), indicating the important role of environmental filtering in early successional stages. Dinnage (2009) found that past agricultural activities, such as ploughing, are likely to act as an environment filter that selects species with high growth rates, high disturbance-tolerances, and small abundant seeds. According to our previous study (Han et al., 2019), the early successional species in our study site always occupied the acquisitive functional strategies, e.g., high A_{mass}, preferred high light, large numbers of seeds, low leaf thickness etc., which make them more adaptable in the grassland before forest succession began.

We found that EC and LT (as part of plant defensive strategy), and pollination pattern (PP) (as part of plant reproductive strategy) were evenly dispersed in SUC-3 and SCU-4 (Fig. 8, A.1, A.2), indicating that

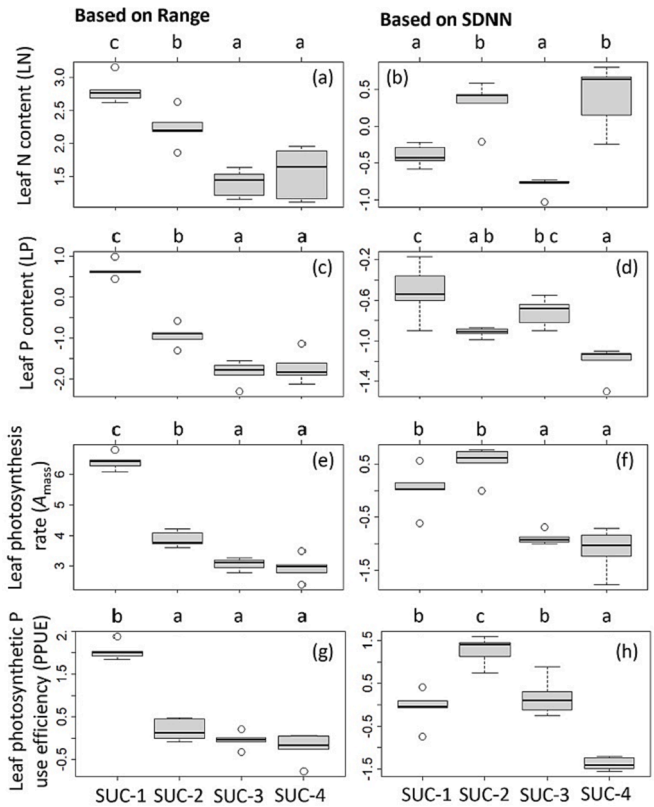

Fig. 10. Comparisons of some leaf chemical and physiological traits among successional stages based on range and SDNN (the standard deviation of nearest neighbor distance along trait axes). All functional traits were abundance-weighted and $\log_{10}$ transformed before analysis. SUC-1, SUC-2, SUC-3, and SUC-4 represent grassland, coniferous forest, mixed coniferous broadleaved forest, and monsoon evergreen broadleaved forest, respectively. Each box shows the interquartile range and median; whiskers indicate the 10th and 90th percentiles. Post hoc differences ($P < 0.05$) among the successional stages are indicated by lowercase letters at the top of each panel.

competitive exclusion was important in later succession. In early succession, the acquisitive herbaceous species lacked thick cuticles and leaves, suggesting that the early residents invest less in defense than the later shade-tolerant woody species (Table B) (Han et al., 2019). In middle to later successional stages, the even dispersal of leaf defensive traits could be caused by strong competitive exclusion, making the defensive strategy of dominant species more diverse in middle to later succession (Fig. 9d). According to our previous study (Han et al., 2019), more and more conservative species with high LT, high EC, insect pollination, and low $R_{mass,}$ appeared in the later successional stages. Our findings regrading plant defensive strategy agree with the theoretical prediction that the relative importance of the processes generating biodiversity after disturbance change over time (Leibold et al., 2004). It is reasonable that the PP was evenly dispersed in later succession, because highly competitive exclusion might have caused the species to find more pollinators to help pollination in later succession (Thompson and Willson, 1979).

4.3. Differences in predictions between phylogeny-based analysis vs Functional trait-based analysis

We found that the information that environmental filtering plays a role in subtropical forest succession, captured by the SEMs, multiple linear regression analysis, phylogeny-based analysis, and functional trait-based analysis. Although the SEMs and multiple linear regression analysis has reported the important effect of richness during succession, only the functional trait-based analysis detected the processes underlying competitive exclusion in SUC-4. The insensitivity of the phylogeny-based analysis to ecological processes has also been reported in some previous studies (e.g., Kraft et al., 2015; Li et al., 2015b).

There are at least two possible explanations for the prediction differences between phylogeny-based and functional trait-based analysis. First, a phylogenetic relationship does not always reflect ecological similarity among species, but it does if the functional strategies are phylogenetically conserved (Purschke et al., 2013). In the current study, conserved plant functional traits (e.g., A_{mass}, T_{mass}, PNUE, and PPUE) showed both clustering and even dispersal in early and later succession, but only clustering was consistent with the results of the phylogeny-based analysis. Considering the regional species pool including gymnosperm and non-woody species, the phylogeny-based analysis might capture more community assembly information if the dissimilarities among species are not large (e.g., as is the case for dissimilarities among angiosperms, but not between angiosperms and gymnosperms). Second, the dominant plant functional strategies often change during succession (Connell and Slatyer, 1977; Letcher et al., 2012). As a consequence, the phylogeny-based analysis cannot detect all of the important ecological processes when the strategies are not convergent. For example, many reproductive traits, and leaf defensive traits did not exhibit significant phylogenetic convergence in this study, but they did reveal some significant ecological processes in the functional trait-based analysis.

5. Conclusions

We combined the analyses of phylogenetic and functional trait community structure during succession to investigate the temporal dynamics of the community assembly process. Deterministic processes (i.e., environmental filtering and competition exclusion) have important effects on community assembly during subtropical forest succession as demonstrated by the following: 1) both environmental filter and competition have an important effect on the process of community assembly during succession. 2) initial community development after disturbance was mainly driven by the environmental filtering; 3) the strength of environmental filtering gradually decreased, while random assembly dominated as succession proceeded; and 4) species coexistence in later succession might be the result of both environmental filtering and competitive exclusion.

Analysis of the 33 functional trait indicators related to plant competition, defense, and reproduction strategies suggested that 1) the species in early succession occupied resource-acquisitive strategy and had high light-use abilities and low defensive abilities, and that 2) more and more conservative species appeared in later successional stage, and the competitive strategy, defensive strategy, and reproductive strategy of the dominant species became diverse. Additionally, functional trait-based indicators might be better than phylogeny-based indicators for revealing ecological processes along successional gradients. The assessment of the relative importance of ecological processes during succession might be biased if only based on one plant functional strategy.

CRediT authorship contribution statement

Taotao Han: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft. **Hai Ren:** Conceptualization, Methodology. **Dafeng Hui:** Writing – review & editing. **Yanpeng Zhu:** Writing – review & editing. **Hongfang Lu:** Writing – review & editing. **Qinfeng Guo:** Writing – review & editing. **Jun Wang:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.109885.

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