

Interactions between leaf traits and environmental factors enhance the understanding of leaf habits in a subtropical forest

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Abstract

It is well known that evergreen and deciduous species have different functional traits and utilize different strategies in growth and adaptation to environments, however little work has been done to elucidate whether leaf habit mediate the effect of trait-environment interactions on plant performance. Here we wanted to illuminate whether relative growth rate of deciduous and evergreen species depended on multiple trait-environment interactions. We measured eight leaf traits of 1230 individuals from 25 species and collected topographic factors, edaphic variables and competition index in a subtropic evergreen and deciduous mixed forest. Then we modeled plant relative growth rate with high-order trait-environment interactions for evergreen and deciduous species respectively using generalized linear mixed model and visualized the difference between leaf habits. Results showed that leaf habits were divided by trait PC1 (41.8%) which was related to leaf lifespan and resource acquisition. We found that trait-environment interactions improved growth predictions for both leaf habits but the optimal models for them were different. Moreover, the explanatory power of deciduous species models was always higher than that of evergreens. These results indicated that leaf habits with different life history strategies were reflected by trait-environment interactions. We emphasized the importance of leaf habits in explaining forest productivity and functions, and future research should focus on the effects of leaf habits on other demographic metrics and spatial patterns to solve the coexistence of the two leaf habits in mixed forests.

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ABSTRACT

It is well known that evergreen and deciduous species have different functional traits and utilize different strategies in growth and adaptation to environments, however little work has been done to elucidate whether leaf habit mediate the effect of trait-environment interactions on plant performance. Here we wanted to illuminate whether relative growth rate of deciduous and evergreen species depended on multiple trait-environment interactions. We measured eight leaf traits of 1230 individuals from 25 species and collected topographic factors, edaphic variables and competition index in a subtropic evergreen and deciduous mixed forest. Then we modeled plant relative growth rate with high-order trait-environment interactions for evergreen and deciduous species respectively using generalized linear mixed model and visualized the difference between leaf habits. Results showed that leaf habits were divided by trait PC₁ (41.8%) which was related to leaf lifespan and resource acquisition. We found that trait-environment interactions improved growth predictions for both leaf habits but the optimal models for them were different. Moreover, the explanatory power of deciduous species models was always higher than that of evergreens. These results indicated that leaf habits with different life history strategies were reflected by trait-environment interactions. We emphasized the importance of leaf habits in explaining forest productivity and functions, and future research should focus on the effects of leaf habits

on other demographic metrics and spatial patterns to solve the coexistence of the two leaf habits in mixed forests.

Key words: adaptive value, community dynamics, functional traits, leaf habits, mixed forest, tree demography

1. Introduction

Evergreen and deciduous species evolved in many clades repeatedly (Feng, et al. 2020), reflecting the different directions of leaf economic spectrum, where evergreen species employed resource-conservative strategies and deciduous species were resource-acquisitive (Bai, et al. 2015, Castorena, et al. 2022, Li, et al. 2022, Wright, et al. 2004). Compared to deciduous species, evergreen species have a longer leaf lifespan, thicker leaves, smaller specific leaf area (SLA) (Ruiz-Robledo and Villar 2005, Tomlinson, et al. 2013), lower photosynthetic rates per unit mass (Ackerly, et al. 2002, Antunez, et al. 2001, Reich, et al. 1992), and invest more in structural construction and compounds related to defense (Aerts 1995, Martínez, et al. 2002, Mooney and Gulmon 1982, Sobrado 1991, Villar and Merino 2001, Villar, et al. 2006). A few studies supported that deciduous species grew faster than evergreen species for its high SLA but the difference of growth rate is vague after taking competition and phylogeny into account (Antunez, et al. 2001, Goldberg 1982, Ruiz-Robledo and Villar 2005)

Generally, evergreen species always distribute in wet tropical or warm temperate region, while deciduous species dominate in cool temperate with freezing winter or tropical savannas with seasonal drought (Defries, et al. 2000). However, a combination

of evergreen and deciduous species can be found in some biomes (Reich, et al. 1992, Woodward, et al. 2004), especially in subtropic evergreen forests where many Eastern Asian species can be found (Wu 1980). Recent studies have shown that mixed forests consisting of both evergreen and deciduous species were more productive than the forests containing only one type (Feng, et al. 2022). So how do they coexist to the same conditions? Plant traits can help explain different response of leaf habits to environment (Tomlinson, et al. 2013). A study from savannas where evergreen and deciduous can also co-exist shows that storage allocation differed between leaf habits: deciduous juveniles allocated more non-structure carbohydrates in roots to support leaf regrowth and evergreens invested more in leaves and stems as biomass increased (Tomlinson, et al. 2013). And another reason, they are considered to be favored by different micro environments. For example, evergreen vegetations dominate in nutrient-poor environments (Aerts 1995, Fang, et al. 2017) and canopy gap densify deciduous seedlings in a subtropical forest (Jin, et al. 2018). However, previous studies about the different leaf habits focused on only one aspect, either the functional traits or the environments.

Interactions between traits and environment allow plants have alternative functional design (Worthy, et al. 2020). For example, trees with high SLA tend to have high growth rate in fertile habitats, but grow slowly in nutrient-poor soil (Davies 2001, Liu, et al. 2012). And in recent years, some studies has studied the interactions among multiple traits and multiple environments to explore whether there are multiple optima along environmental gradients (e.g., Laughlin and Messier (2015), Li, et al. (2021), Li,

et al. (2022)), meaning that species with different functional traits can have the same fitness in different environments within the same community and thus can coexist stably, which may provide a new way to explain the coexistence of evergreen and deciduous species.

To confirm this idea, we chose a 25-hectare subtropical forest in China populated by both deciduous and evergreen trees and selected 25 of the most abundant species (16 evergreen and 9 deciduous). We modeled relative growth rate (RGR) by two-way, three-way, and four-way trait-environment interactions for deciduous and evergreen trees to answer the following questions: 1) Do trait-environment interactions improve growth predictions in this plot? We hypothesize that the interactions between environments and functional traits can be used to predict plant performance. 2) Do leaf habits influence the effects of trait-environment interactions on plant fitness? If so, how? We hypothesized that phenotypic performance of leaf habits depends on different trait-environment interactions, and the evergreen and deciduous trees could achieve the similar fitness through the interaction of traits and environment in different environments in the given community.

2. Material and Methods

2.1 Site description

This study was conducted in a 25-ha permanent subtropical forest plot (BDGS, 500 m × 500 m, 29°46'2.46", 110° 5'14.88") in Badagongshan National Nature Reserve, Hunan province, China. This area is part of the Wu Ling Mountains, which is one of

the three species diversity hotspots in China(Wang, et al. 2022). Wu Ling Mountain region is characterized by a typical humid monsoon climate, and the zonal vegetation is evergreen broad-leaved forest. However, the plot's elevation ranges from 1354.7m to 1455.9m, where the low temperature led to deciduous trees. Hence the vegetation in the plot is subtropical evergreen and deciduous broad-leaved mixed forest. Annual mean temperature and precipitation is 11.5 °C and 2105.4 mm, respectively. This area rains up to 176 days each year, resulting in 90% relative humidity.

The BDGS plot was established in 2011 following the standards of the Center for Tropical Forest Science (Condit 1995). The first census was completed in 2011 and over 180,000 free-standing individuals with diameter at breast height (DBH) \geq 1cm belonging to 232 species, 114 genera, and 53 families were tagged, measured, identified, and mapped. This community is dominated by Fagaceae, Ericaceae, Lauraceae, and Theaceae, with deciduous trees forming 59.9% of canopy species. We re-censused the plot in 2016 and 2021 following the same method to record new recruits and newly dead individuals.

2.2 Tree sampling

We chose 25 of the most abundant tree species, including 16 evergreen and 9 deciduous species, to study the differences between leaf habits. Information about sampled individuals was provided in Supporting information. In order to cover all growth phases, individuals were divided into three groups: juveniles (DBH < DBH₉₉^{1/2}), adults (DBH \geq DBH₉₉^{2/3}) and middle-aged (DBH₉₉^{1/2} \leq DBH < DBH₉₉^{2/3})

(Bagchi, et al. 2011). Intra-specific trait variation plays an important role in analysis of leaf habits difference (Vargas, et al. 2021). The importance of plasticity was evident from the many studies that demonstrated the influence of variable phenotypes on plant fitness (Maharjan, et al. 2021, Russo, et al. 2005, Umana and Swenson 2019, Umana, et al. 2018, Zhang, et al. 2017). Thus, we collected 40-58 duplications for each species to cover enough intra-specific variation and sampled a total of 1230 individuals during the growing season (June - September) from 2018 to 2021.

RGR is defined as $(\log(\text{DBH}_1) - \log(\text{DBH}_0)) / \text{interval}$, where DBH_0 and DBH_1 is the measures of DBH taken in 2011 and 2021, respectively, and the interval is the time elapsed (in years) between census dates. Owing to measurement error, RGR values with a difference in DBH measurements greater than 0.75 cm were removed from analysis (Chen, et al. 2016).

2.3 Environmental variables

Abiotic factors included topographic parameters and soil variables. Topographic parameters were measured at the beginning of plot construction including elevation, slope, convexity, and aspect (sinaspect). To characterize the soil, we collected 934 samples (0-10cm depth) selected randomly but evenly across the 25-ha forest plot. The samples were used to analyze seven physicochemical properties, including bulk density (BD, g cm^{-3}), soil carbon-13 (^{13}C), ratios C:N, soil phosphorus content (SPC), soil carbon density (SCD), pH, and temperature (soil T). Detailed sampling and determination process please refer to Li, et al. (2016). We calculated topographic and

soil variables for each 20m*20m quadrat using the *autoKrig* function in the *automap* R package and assigned the quadrat-level average value of the nearest quadrat (20m×20m) to each individual tree.

We selected conspecific neighborhoods crowding index (NCI) as the biotic variable to quantify competition effects relating to intraspecific competition (Equation 1),

$$NCI = \sum_{j=1, m \neq j}^J \frac{DBH_j^2}{d_{mj}^2} \quad (1)$$

where d_{mj} is the distance between focal tree m and its conspecific neighbor j , and J is the number of all conspecific neighborhoods within the study radius. The study radius was always set to 15 m.

2.4 Functional traits

To analyze the difference of leaf habits, we selected eight leaf traits related to leaf economics spectrum (Wright, et al. 2004), including leaf size (LS, cm²), specific leaf area (SLA, m² kg⁻¹), leaf dry matter content (LDMC, mg kg⁻¹), leaf nitrogen content (LNC, mg g⁻¹), leaf phosphorus content (LPC, mg g⁻¹), leaf carbon content (LCC, mg g⁻¹), leaf thickness (LT, mm), leaf chlorophyll content (CHL, SPAD) (Supporting information). We used trimmers to collect mature, healthy, and complete sun leaves for trait measurement. These traits were correlated with resource acquisition and physical defense (Adler, et al. 2014, Sterck, et al. 2011, Visser, et al. 2016, Wright, et al. 2010),

and previous work had shown a strong relationship between SPAD and leaf photosynthesis(Coste, et al. 2010). The details of sampling and determination of the first seven leaf indexes please refer to Zhang, et al. (2020). Average chlorophyll content was determined by measuring the front and back of each leaf 4-5 times with SPAD-502 instrument.

2.5 Data analysis

To test how well life history strategies correlate to functional trait differences between evergreen and deciduous species, we performed principal component analysis (PCA) for eight leaf traits. Analysis of variance (ANOVA) was conducted to compare intra- and inter-species variation.

We modeled RGR with traits, environments, and trait-environment interactions by generalized linear mixed model (GLMM) for two leaf habits to verify the importance and effects of trait-environment interactions. Initial DBH is an important determinant of growth, so we set log-transformed DBH values as a main effect in all models. To exclude spatial autocorrelation, we set quadrats as a random intercept. To avoid variation caused by growth differences due to species identity rather than functional traits, we set species as a random term. All the generalized linear mixed models were grouped into two-way models (Equation 2), three-way models (Equation 3) and four-way models (Equation 4) (Li, et al. 2021). To exclude collineation of variables, we chose LS, traits of PC1, and traits of PC2 as the candidate traits for three group models. T represents any of the eight traits, and T1 and T2 are never from the same PC axis. 17

T1×T2 combinations were analyzed. Consistent with PCA results of environments (Supporting information), we set two orthogonal abiotic variables (soil pH and bulk density) and one biotic variable (NCI) as candidate environment indexes of E, E1, and E2. Each model was evaluated for deciduous and evergreen individuals, resulting in 24 two-way models (Equation 2), 51 three-way models (Equation 3) and 51 four-way models (Equation 4) of each leaf habit (Supporting information). To ensure normality, NCI, all functional traits, and environmental variables (except BD and soil pH) were log-transformed and standardized prior to analysis.

$$RGR \sim T + E + T \times E + (1|species) + (1|quadrats) + \log(DBH) \quad (2)$$

$$RGR \sim T_1 + T_2 + E + T_1 \times E + T_2 \times E + T_1 \times T_2 + T_1 \times T_2 \times E + (1|species) + (1|quadrats) + \log(DBH) \quad (3)$$

$$RGR \sim T_1 + T_2 + E_1 + E_2 + T_1 \times E_1 + T_1 \times E_2 + T_2 \times E_1 + T_2 \times E_2 + T_1 \times T_2 \times E_1 + T_1 \times T_2 \times E_2 + T_1 \times E_1 \times E_2 + T_2 \times E_1 \times E_2 + T_1 \times T_2 \times E_1 \times E_2 + (1|species) + (1|quadrats) + \log(DBH) \quad (4)$$

Where *RGR* is the relative growth rate of individual, T, T₁ and T₂ are functional traits referred in *data analysis*, E, E₁, E₂ represent environment variables referred in *data analysis*.

The coefficient of determination (R²) included marginal r-squared values (R²_m) and conditional r-squared values (R²_c) which were computed using the *r.squaredGLMM* function from the *MuMIn* R package. We excluded models in which corresponding interaction terms were nonsignificant. To analyze the efficacy of using trait-

environment interactions to predict RGR, we conducted variation partitioning analysis (VPA) of four-way models and partitioned R^2_c to evaluate the average proportion of random effects, fixed effects, and two-way, three-way, four-way interactions of fixed effects.

To visualize how RGR varied with trait combinations under specific environment, we chose two three-way models, SLA×LCC×NCI (model 7 in Supporting information) and LS×LDMC×NCI (model 10 in Supporting information), in which the three-way interaction terms were significant for both leaf habits to simulate the relationship between RGR and T1 by fixing extreme value of T2 and NCI. For example, we assumed LCC and NCI in model 7 had the minimum value, and then simulated the relationship between RGR and SLA. Besides, we generate 3D plot to demonstrate the relationship between combinations of traits and RGR against the background of extreme values of E1 and E2 in four-way models (only model 14 and model 34). All analyses were conducted in R v.4.0.1 (R Core Team 2020).

3. Results

3.1 Leaf trait variation of leaf habits

The first two principal coordinate axes of leaf traits explain 63.8% of trait variation in BDGS plot (Fig. 1). PC1 is related to lifespan and resource acquisition, showing SLA, LNC, LPC, CHL and LT and accounts for 41.8% of variation. There is a notable difference between leaf habits along PC1. Evergreen species tend to have thick leaves with high chlorophyll content while deciduous species have thin and large leaves with

high nitrogen and phosphorus content. PC2 shows LDMC and LCC, which are related to physical defense, and accounts for 22% of variation. We also compared trait variations difference between leaf habits. Compared to evergreen leaf habit, deciduous species tend to exhibit more intraspecific trait variation (except LPC and LDMC) and species identity contributed ~80% variation of LS and LDMC (Supporting information).

3.2 Effects of trait-environment interactions in predicting RGR

There were 0 and 3 significant two-way interactions (SLA×NCI, LCC×NCI, LCC× pH) for deciduous and evergreen species two-way models, respectively (Supporting information). For three-way models, there were 10 and 7 significant three-way interactions for deciduous and evergreen species, respectively. Two of the three-way models (SLA×LCC×NCI and LS×LDMC×NCI) were significant for both leaf habits (Supporting information). There were 5 and 6 significant four-way interactions for deciduous and evergreen species, respectively, however, there was no identical significant model for two leaf habits (Supporting information). Compared to evergreen species, R^2 , specially R^2_c , was higher for deciduous leaf habit in every model. The average of R^2_c increased slightly with the interaction order for evergreen species (ranging from 0.247 to 0.267) and deciduous species (ranging from 0.366 to 0.397) (Supporting information).

According to the VPA of four-way models, two-way interactions explained an average of 13.3% of fixed effects in deciduous models but almost zero for evergreen models. Plant size contributed 41.9% and 38.1% of R^2_c in deciduous and evergreen

models, respectively. Traits, environments and their interactions contributed average 26.9% of R^2_c in deciduous models and explained an average of 11.8% of R^2_c in evergreen models (Fig. 2, Supporting information).

3.3 Functional alternative designs of different leaf habits

In the two three-way models which were significant for both leaf habits, SLA×LCC×NCI model, and LS×LDMC×NCI model, the relationships between environments and RGR were complicated under different trait combinations. In the SLA×LCC×NCI model, the patterns of RGR-environments were exactly the opposite for the two leaf habits. For example, in the trait combination with minimum SLA and minimum LCC, RGR decreased with NCI for deciduous species (Fig. 3A, red line) but increased with NCI for evergreen species (Fig. 3B, red line). The other three combinations of SLA and LCC got the similar results, with the patterns completely opposite for the two leaf habits (Fig. 3A and B). However, in the LS×LDMC×NCI model, the relationship between RGR and NCI were consistent for deciduous and evergreen species (Fig. 4).

All significant four-way models were different between deciduous and evergreen species, especially in the environmental factors. For example, soil pH was only significant in deciduous models while BD, reflecting soil texture, was only significant in evergreen models (Supporting information). Even within the same leaf habit, in the 3D plot of the significant four-way models, surface consisting of trait combinations and RGR do not always monotonically change, which means there can be multiple trait

combinations lead to similar performance under specific context (Fig. 5 and Supporting information).

4. Discussion

The demographic rates of individual plants are affected by functional traits (Iida, et al. 2014, Paine, et al. 2015, Wright, et al. 2010). However, the dynamics of the local plant community are not only dependent on the functional traits of the species, but also subject to the environmental conditions within the community (Chave, et al. 2009, Muller-Landau 2010). Hence, studying the effects of environments on the relationship between plant functional traits and demographic rates is a necessary part of elucidate the growth-survival trade-off strategy of forest community species.

Focusing on interactions between community-weighted functional traits, soil properties and survival probability, using two way interactions including one functional trait and one environmental factor, it was found that SLA had adaptive values along a soil fertility gradient for herbaceous plants (Laughlin, et al. 2018). Then, Worthy, et al. (2020) and Li, et al. (2021) used high order interactions (three way interactions including trait×trait×environment and four way interactions including trait×trait×environment×environment) to model the survival and growth, and both of them found multiple trait combinations leading to multiple performance peaks. Here, we also demonstrated the importance of high-order interactions in explaining growth variation. The proportion of R^2_c explained by trait-environment interactions in our study is higher than the proportion of Li, et al. (2021), which study in a broadleaf evergreen

forest in South China), possibly due to the high intraspecific trait variation and environmental heterogeneity in our plot. Intraspecific variations observed for all the traits in this study (except LDMC) and the coefficient of variance (CV) of soil pH in our study were both slightly larger than that found by Li, et al. (2021). Even so, the proportion of significant relationships was still low. One possible explanation for the low percentage of significant models is that some environment-trait interactions may influence other demographic variables. For example, chlorophyll content is positively correlated to survival (Poorter and Bongers 2006) and SLA is related to seedling establishment (Zirbel and Brudvig 2020).

Qi, et al. (2021) found that mass-based leaf photosynthetic rate was positively correlated to the growth of evergreens but not to deciduous species, showing that the functional traits determining the performance of evergreen and deciduous species may be different. We also found empirical evidence of functional alternative designs of different leaf habits, which illustrated the adaptation strategies of evergreen and deciduous trees to the given environment were different. On one hand, evergreen and deciduous species may favor different environments within the community. In our plot, deciduous species favor the areas with high soil pH while evergreen species dominate in nutrient-poor environments (Supporting information). The result is consistent with Fang, et al. (2017). Plants growing in favorable conditions tend to invest more in growth (Davies 2001, Liu, et al. 2016). On the other hand, they may have different strategies to adapt the environments. We can see from the results that the best trait combinations for evergreen species did not always result in the best outcomes for

deciduous species in the same environment, especially for SLA and LCC. Under low competition pressure, deciduous individuals with low SLA and low LCC have similar RGR with evergreen trees with high SLA and low LCC (Fig .3). A study of temperate forest showed that evergreen species spend most time in structure construction while deciduous species get the peak of leaf mass area soon after sprout (Ye, et al. 2022), which indicated that deciduous species are “opportunistic” which tend to favor quick resource turnover before the bad seasons, while evergreen species invest more resources in conservation and defense to get through the unfavorable seasons (Bai, et al. 2015, Muledi, et al. 2020). The difference of leaf traits and shifts of trait-rate relationship along environments between leaf habits may partially explain why many previous studies found limited correlation between functional traits and growth rate (Paine, et al. 2015, Rosas, et al. 2021), because there are complicated trait-environment interactions in a mixed forest (Feng, et al. 2022, Vargas, et al. 2021).

Many studies have found there are density-sensitive properties in the functional traits of species, so the density-dependent effect will affect the coexistence and dynamics of species with different functional traits (Bagchi, et al. 2011, Johnson, et al. 2012, Lasky, et al. 2014). Density may have different effects on different species. For example, species with large seed and dense wood have high ability to tolerate conspecific negative density dependence (Kunstler, et al. 2016, Lebrija-Trejos, et al. 2016). There were some studies discovering that deciduous seedlings suffered higher intense competition than evergreen species in subtropical forests (Lu, et al. 2015, Wang, et al. 2019). In this study, the only environmental factor which got significant

interactions with functional traits for both leaf habits in three-way interactions was NCI, showing the importance of biological factors in explaining the relationship between functional traits and community performance (Lasky, et al. 2014). We have to take density effects into account when study the relationship between the density sensitive traits and growth in the future.

5. Conclusions

Our study investigated the influence of leaf habits on trait-environment interactions and plant performance in a mixed forest and provided a new insight into community assembly. The deciduous and evergreen species, coexisting in the subtropical forest, differed greatly in their functional traits and the interactions with environments. This study improved our knowledge of leaf habits by illuminating how different trait-environment interactions affected individual fitness of deciduous and evergreen species. Future research should focus on other demographic metrics (*e.g.*, survival or regeneration) and more functional traits directly related to leaf habits difference (*e.g.*, leaf lifespan) individually.

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Figure legends

Fig.1 Principal component analysis (PCA) summarizing the variability of eight leaf traits across individual deciduous and evergreen trees. The first two PCA axes are shown with the percentage of explained variance in brackets. The colored ellipses delimit 95% confidence regions. All functional traits were log transformed and standardized. Trait abbreviations: specific leaf area (SLA), leaf size (LS), leaf dry matter content (LDMC), leaf carbon concentration (LCC), leaf nitrogen concentration (LNC), leaf phosphorus concentration (LPC), relative chlorophyll content (CHL), leaf thickness (LT).

Fig.2 Variation partitioning analysis of four-way models for deciduous and evergreen species. a, c: average proportion of random effects and fixed effects for deciduous and evergreen species, respectively; b, d: average variance decomposition of fixed effects for deciduous and evergreen species, respectively.

Fig.3 Relationship between relative growth rate (RGR) and conspecific neighborhoods crowding index (NCI) against specific leaf area (SLA) and leaf carbon concentration (LCC). We fixed extreme values of SLA and LCC to simulate the relationship between NCI and RGR. There are four extreme functional trait combinations: minimum values for both SLA and LCC (the red line); minimum SLA and maximum LCC (the green line); maximum values for both SLA and LCC (the blue line); maximum SLA and minimum LCC (the yellow line). Subplot A is for deciduous species and subplot B is

for evergreen species.

Fig.4 Relationship between relative growth rate (RGR) and conspecific neighborhoods crowding index (NCI) against the combination of leaf size (LS) and leaf dry matter content (LDMC). We fixed the extreme values of LS and LDMC to simulate the relationship between NCI and RGR. There are four extreme functional trait combinations: minimum values for both LS and LDMC (the grey line); minimum LS and maximum LDMC (the black line); maximum values for both LS and LDMC (the pink line) and maximum LS and minimum LDMC (the orange line). Subplot A represents deciduous species, and subplot B represents evergreen species.

Fig.5 The 3D visualization of deciduous RGR responding to interactions of LS×LCC against four backgrounds (consisting of soil pH and NCI). The surface consists of growth rate, LS and LCC. a, b, c, d correspond to four contexts: maximum values for both soil pH and NCI; minimum values for both soil pH and NCI; maximum soil pH and minimum NCI; minimum soil pH and maximum NCI. LS: leaf size; LCC: leaf carbon concentration; NCI: conspecific neighborhoods crowding index.

Fig.1

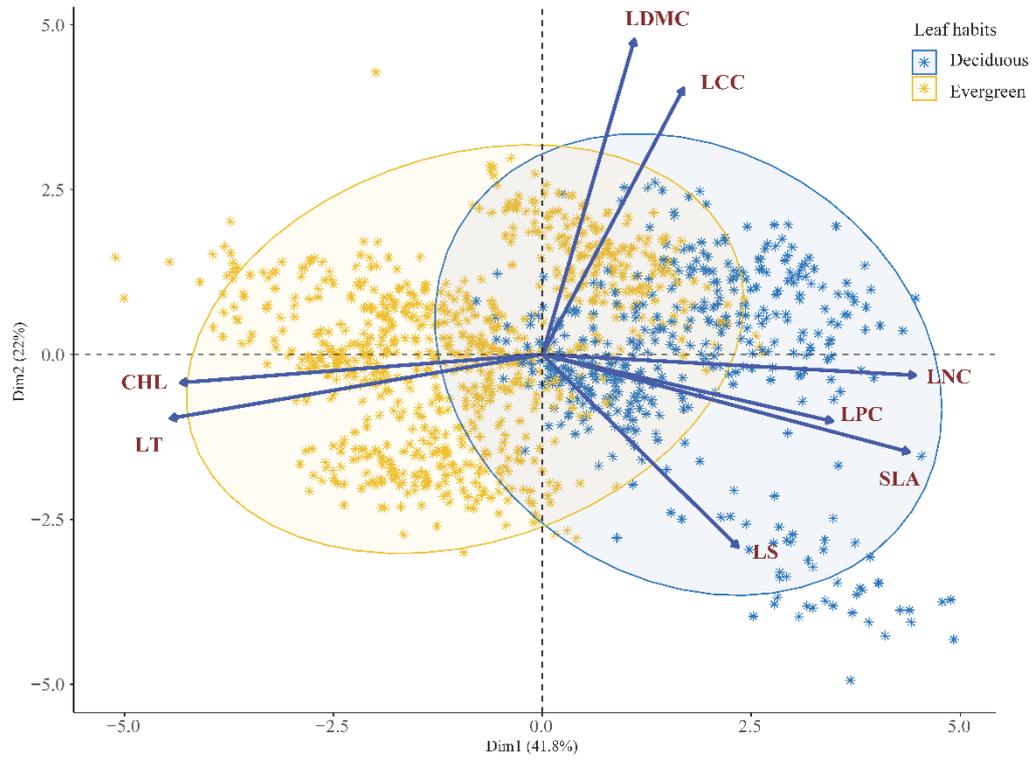


Fig. 2

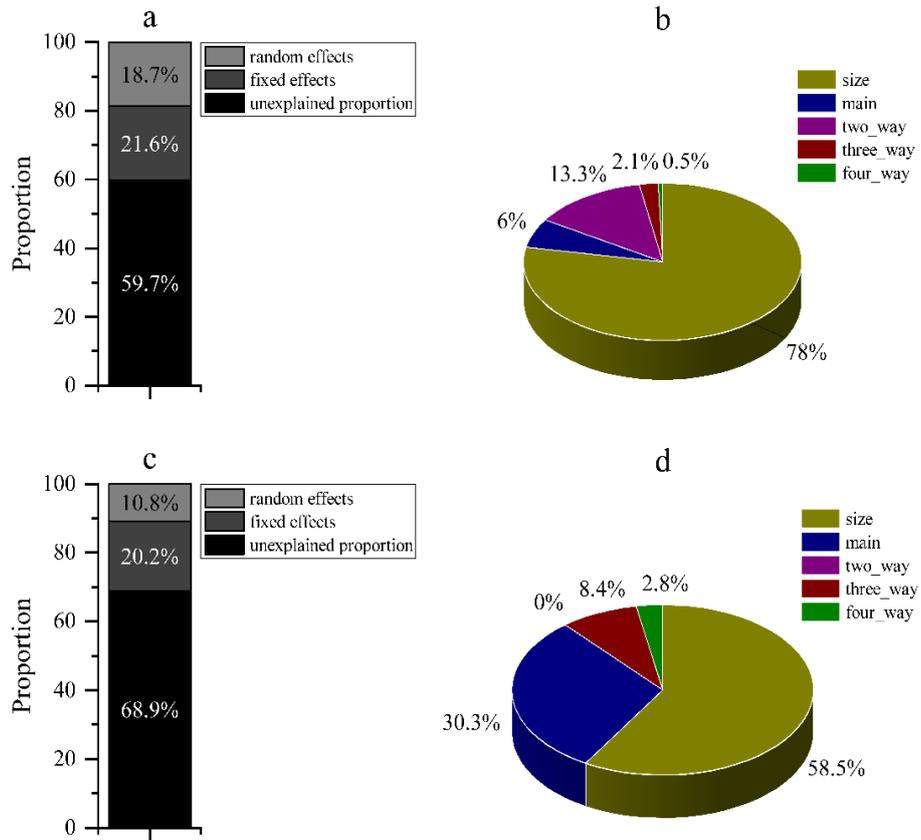


Fig. 3

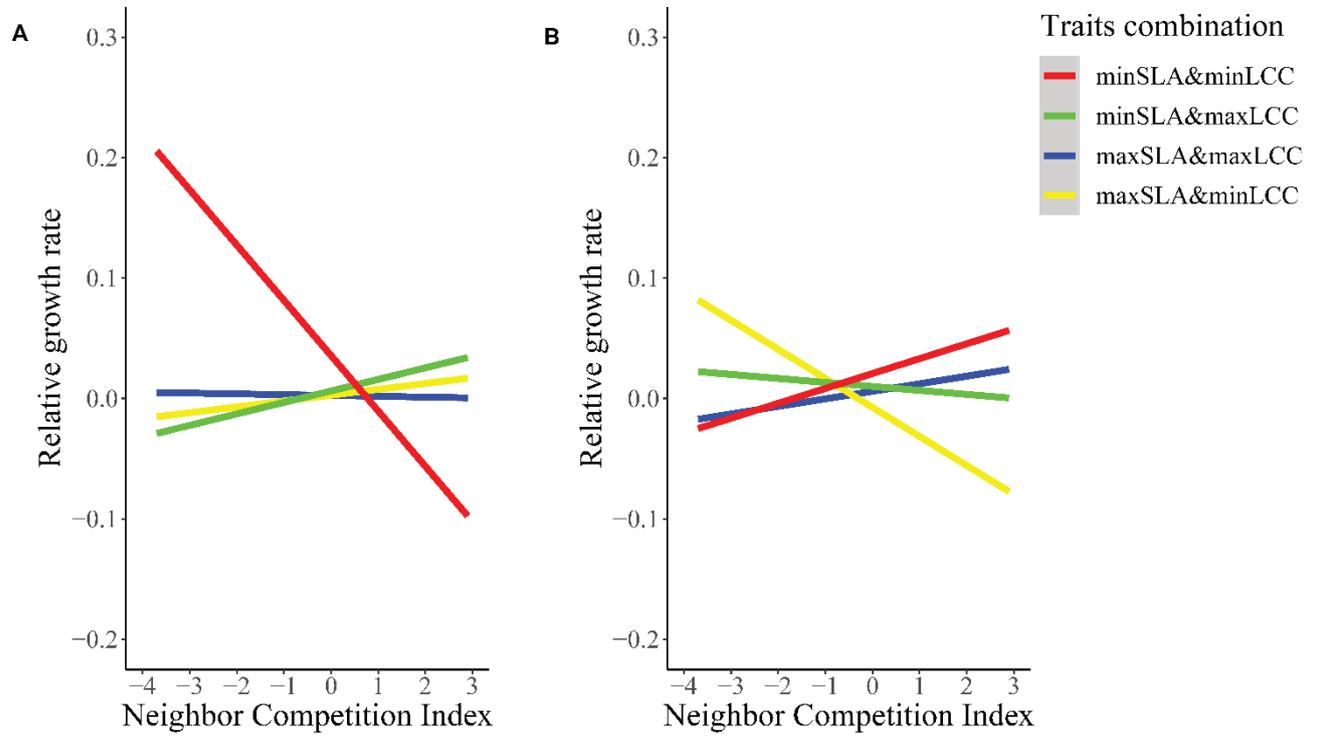


Fig.4

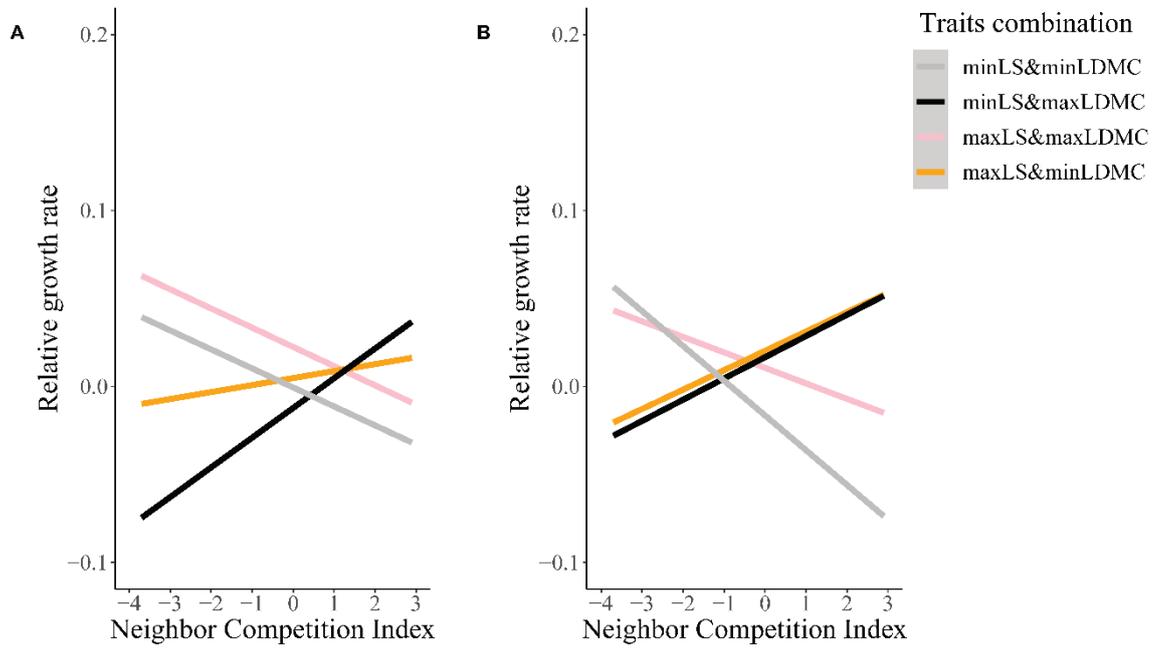
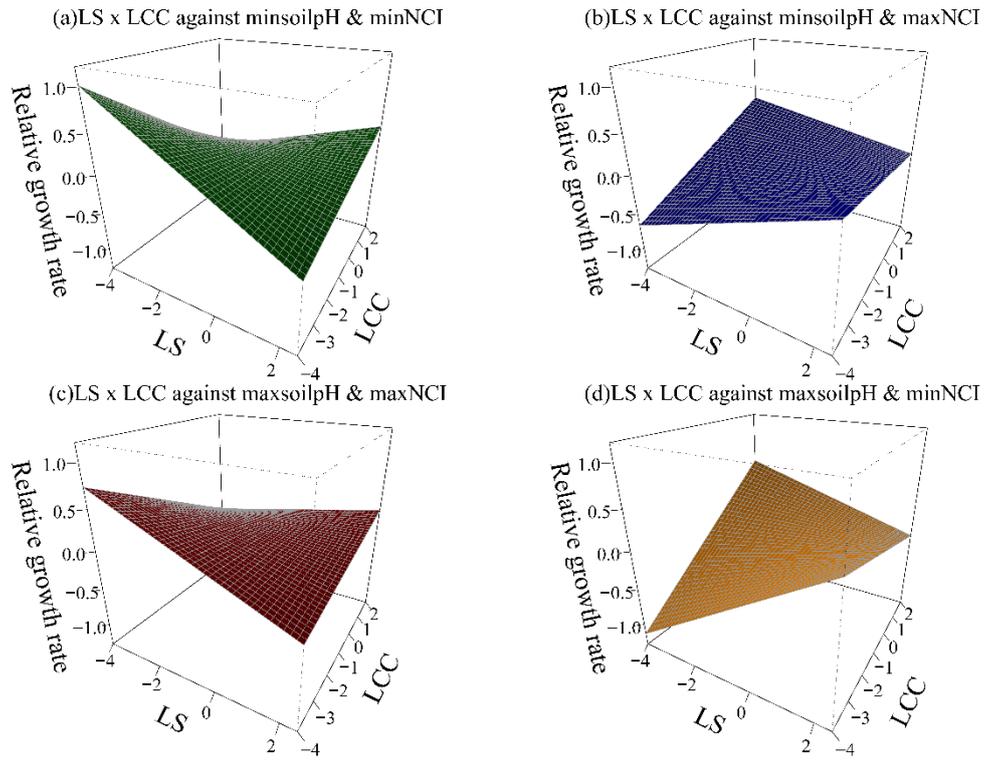


Fig.5



Supporting information

Table S1: Brief information of all the sampled species.

Table S2: Information of eight leaf traits.

Table S3: Results of two-way GLMM models.

Table S4: Results of three-way GLMM models.

Table S5: Results of four-way GLMM models.

Table S6: Results of the variation partitioning of R^2_c for evergreen and deciduous four-way models.

Figure S1: Principal component analysis (PCA) of seven soil physicochemical properties.

Figure S2: Variance decomposition among eight leaf traits, including interspecific variation, intraspecific variation, and unexplained variation.

Figure S3: The 3D visualization of evergreen RGR responding to interactions of LDMC×LT against four backgrounds (consisting of BD and NCI).

Figure S4: The correlation plot between the ratio of evergreen basal area and deciduous basal area and edaphic variables in quadrat level.