



Original Articles

Strategic differentiation of subcommunities composed of evergreen and deciduous woody species associated with leaf functional traits in the subtropical mixed forest

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ABSTRACT

The joint assembly of evergreen and deciduous tree species, typical karst vegetation of evergreen and deciduous broad-leaved mixed forests through respective subcommunities, play an important role in maintaining biodiversity in subtropical karst regions, and leaf functional traits can strategically specify plant resource utilization. However, it is unclear how these assembled subcommunities of evergreen and deciduous species maintain differentiation strategies. This study surveyed 53 forest plots of 20 m × 20 m dividing 212 adjacent lattices in a typical karst forest. Leaf traits of woody plants were measured regarding the specific leaf area (SLA), leaf dry matter content (LDMC), leaf tissue density (ltd), and leaf C, N, and P contents. The differences between deciduous and evergreen subcommunities were compared using the community-weighted means (CWM). The SLA and LDMC of the deciduous subcommunity were greater than the evergreen subcommunity; meanwhile, the leaf C, C/N and C/P ratios of the evergreen subcommunity were significantly higher than those of the deciduous subcommunity. However, the leaf N, P and N/P ratios of the deciduous subcommunity were significantly enhanced than the evergreen subcommunity. Moreover, both subcommunities showed significant negative correlations between SLA, leaf N and ltd, LDMC, signifying a trade-off of leaf-economic trait in deciduous and evergreen subcommunities. Furthermore, principal component analysis (PCA) on leaf functional traits specified the strategic differentiation mainly located at the side of the resource acquisition with high SLA and leaf N content for the deciduous subcommunity and situated at the side of the resource conservation with high LDMC and ltd for the evergreen subcommunity. In conclusion, the trade-off correlated with leaf functional trait differentiation suggested a resource acquisition strategy for the deciduous subcommunity and a resource conservation strategy for the evergreen subcommunity in the subtropical climate-dominating mixed forest of karst ecosystem.

1. Introduction

A plant community is a complex functional entity formed from mutual adaptation through different plant species assemblies interacting with the environment in a specific area (Bo et al., 2016). Community stability depends on the types of interactions among species in the community and the sensitivity of each species to different

environmental fluctuations (Margalef, 1969; Cohenpb and Charles, 1985). Forest communities are generally composed of rich plant species, such as herbs and woody plants (Rozendaal et al., 2019), or different leaf ecological habit plants, e.g., the deciduous and evergreen species in a natural forest (Ye et al., 2022). The communities with different numbers of species as the same structure were defined as modular subcommunities by Holt and Lawton, (1994). Therefore, these species with

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different structures and functions were grouped into different subcommunities to investigate the complex communities in community function (Bär Lamas et al., 2016). For example, the evergreen and deciduous species in a mixed forest may combine modular subcommunities according to their different leaf habits regarding nutrient return and utilization differences. Different subcommunities share different ecological roles for community stability through the interactions between species of respective subcommunities in a fluctuating environment (Ives et al., 2000). Especially, these subcommunities with different leaf habits typically have distinct leaf morphological and functional traits (Huang et al., 2015), which lead to different resource availability and adaptive strategy to diverse environmental conditions (Kloppel et al., 2000; Yao et al., 2020).

Plant functional traits in morpho-physio-phenological performance are related to the ability to acquire or preserve resources (Violle et al., 2007). Leaf functional traits are critical to exploring the mechanism of resource utilization in plant communities in changing environments (Qin and Shangguan, 2019). Diaz et al., (2004) and Garnier et al., (2006) emphasized that leaf functional traits could reflect the response of plants to environmental changes and regulate the impact of plants on ecosystem processes. The variations of leaf functional traits among plant communities could explain variations in community structure and composition (Ma et al., 2022). However, the mechanism of different subcommunities strategically maintaining community stability is unclear due to the trait variation under environmental fluctuation (Ives et al., 2000). The mass ratio hypothesis suggests that the effect of plant functional traits on ecosystem functions is sturdily governed by the relative contribution to the total biomass or species abundance (Grime, 1998). Therefore, traits of the community-weighted mean (CWM) is the simplest method to measure community-level functions by the relative richness of species and their CWM values at the community level could assess community aggregation properties (Violle et al., 2007) or species behavior (Wright et al., 2010). For example, the higher specific leaf area (SLA) and leaf nitrogen content characteristically designate a community dominated by individuals of fast-growing acquisitive species with higher light-saturated photosynthetic rates (Chelli et al., 2020). Deciduous and evergreen plants with different leaf characteristics are generally found in a forest community, representing multiple coexisting strategies (Ávila-Lovera et al., 2019). However, it remains ambiguous how the evergreen and deciduous subcommunity's adaptive strategy to maintain community stability, especially in mixed forest vegetation, such as the karst evergreen and deciduous broadleaved mixed forest in the karst topography.

The karst landform of southwestern China is one of the largest karst topography in the world, shaped by the dissolution of one or more layers of soluble bedrock (Fan et al., 2011; Zhang et al., 2017). The complex and fragile ecological environment is characterized by soil and water loss, bedrock exposure, rocky terrain desertification, and the shallow and discontinuous soil layer leading to low vegetation coverage (Shen et al., 2020; Li et al., 2022b). The evergreen broadleaved forest is typical zonal vegetation with a complex community structure and high biodiversity due to the subtropical climate condition in southwest China (Feest et al., 2010; Su et al., 2015). However, the dominant vegetation type is the evergreen and deciduous broadleaved mixed forest in the karst ecosystem of southwest China (Peng et al., 2012; Liu et al., 2015; Zhang et al., 2022b). These karst forests strangely differ from the evergreen broadleaved forest developed in non-karst regions of general landforms under the same climatic zone (Liu et al., 2016). Givnish, (2002) and Jin et al., (2018) explored the coexistence of evergreen and deciduous broadleaved trees under the same climatic conditions; they found that plants with different leaf phenology have different leaf shedding frequency, leaf longevity, and leaf functional traits, which affect their resource economic strategies and adaptability for different environmental conditions. Furthermore, the previous study suggests that mixed species forests with species differing in leaf phenology, i.e., evergreen or deciduous species, can increase the diversity and

productivity of the forest community through resource utilization (Lu et al., 2016). Therefore, the evergreen and deciduous broadleaved mixed forest as non-zonal karst vegetation are essential to maintain karst forest ecosystem stability.

The karst vegetation is mainly composed of evergreen mixing deciduous species, and it can modularize evergreen and deciduous subcommunities according to plant leaf habits. However, the mechanism of formational maintenance is unclear in non-zonal karst vegetation. To be exact, how these assembled subcommunities of evergreen and deciduous species strategically differentiate is still unclear. Exactly it is incorrect to attribute it to karst landform, and perhaps an assumption is interesting whether the coexistence of deciduous trees supports the growth and maintenance of evergreen trees in the same climates controlling evergreen broadleaved forests. Therefore, exploring the ecological strategies of evergreen and deciduous subcommunities for resource utilization capacity in the evolution of karst vegetation is necessary. Those species present an acquisitive strategy with high leaf nutrients, high photosynthesis rates and short leaf lifespan, and low dry-mass investment per leaf area. In contrast, those species exhibit a conservative strategy with long leaf lifespan, expensive leaf construction, low nutrients and rates of photosynthesis (Wright et al., 2005; Liu et al., 2022). Generally, deciduous species have shorter leaf life spans than evergreen species (Hikosaka et al., 2021), and deciduous species obtain resources rapidly for maintaining efficient photosynthesis due to ephemeral leaf span compared to evergreen species conserving more biomass for durable leaf photosynthesis, according to Kikuzawa, (1991) and Pringle et al., (2011). Therefore, we hypothesized that the deciduous subcommunity adopts an acquisitive resource strategy and conversely presents a conservative resource strategy for the evergreen subcommunity in karst forests (H1). Moreover, the leaf economic spectrum can explain a fundamental trade-off between distributing plant resources to structural tissues or leaf photosynthetic processes, which mainly operate independently for growth, plant functional type, or biome (Wright et al., 2004). Therefore, we hypothesized that there was a trade-off of leaf functional traits in deciduous and evergreen subcommunities steadily with the leaf economic spectrum (H2). The aim is to explore the strategic difference of subcommunities based on leaf habits in measuring the community traits of karst forest, further significant to understand the vegetation evolution and degraded vegetation restoration.

2. Materials and methods

2.1. Communities survey and leaf collection

Three towns of Xiayun, Gaofeng and Machang of Pingba District, Anshun City, Guizhou Province, China, were selected for community surveys and leaves collections. These areas have typical karst mountains (26°22'~26°28' N, 106°20'~106°26' E; altitude: 963 m ~ 1645.6 m; Fig. 1). It belongs to a subtropical moist monsoon climate. The annual precipitation is approximately 1298 mm with a range of annual average temperature in 14 °C ~ 24 °C. Here, the forest vegetation is typical evergreen and deciduous broadleaved mixed forest as non-zonal vegetation, which plays an important role in maintaining biodiversity and ecological function for the karst mountain environment.

We randomly selected 53 forest plots for community surveys, which were the size of 20 m × 20 m and further divided into four adjacent lattices of 10 m × 10 m subplots for each plot, thus totally containing 212 subplots. The average distance of plots was 2,018 m when the min and max distance were 50 m and 4,419 m, respectively. All plots are in mid-slope positions, with an average slope gradient of 20°, average soil depth of 25 cm, and average rock bareness of 55 %. All plots were surveyed in the field and were identified the plant species compositions, individual numbers, tree height and the diameter at breast height (DBH) of plants with DBH ≥ 1 cm in height more than 1.3 m, habitat information of slope, position and aspect, etc. Especially, the surveyed forest community could be divided into three vertical layers of trees, shrubs,

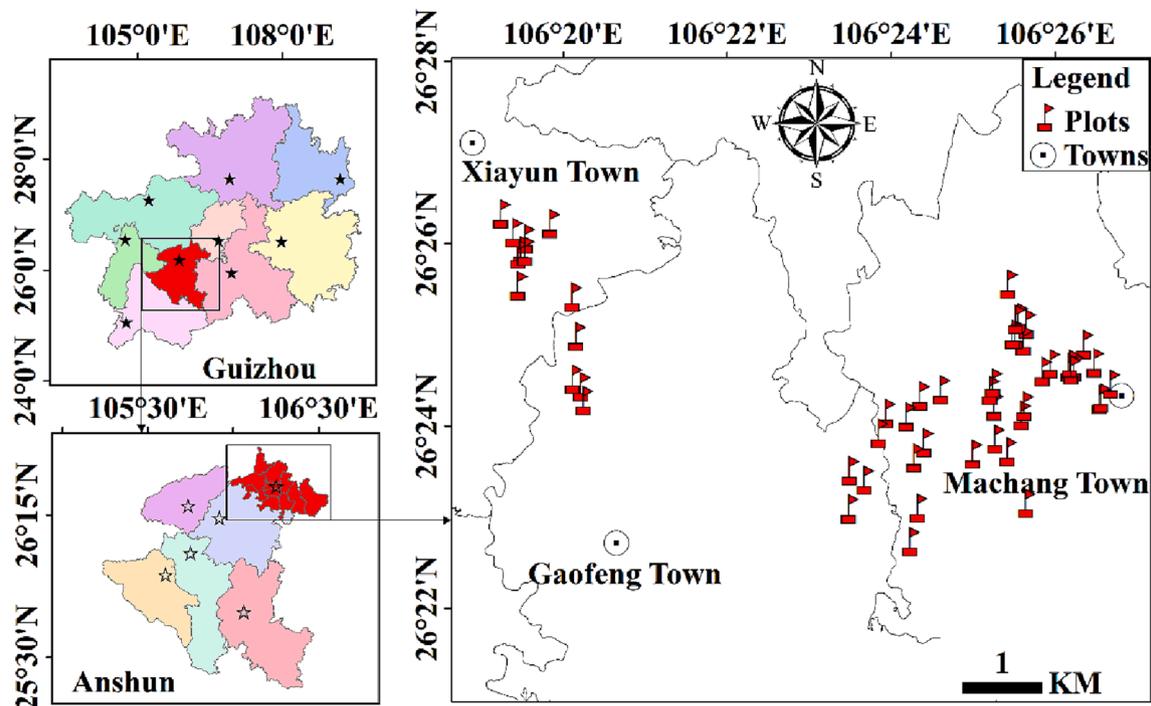


Fig. 1. Field plots location and distribution. In this study, sets of 53 forest plots were used for community surveys within typical karst mountains, those distributed in three towns of Xiayun, Gaofeng, and Machang of Pingba District, Anshun City of Guizhou Province, China, located in $26^{\circ}22' \sim 26^{\circ}28' \text{ N}$, $106^{\circ}20' \sim 106^{\circ}26' \text{ E}$, altitude range from 963 m to 1645.6 m. Additionally, each plot was divided into four adjacent lattices of $10 \text{ m} \times 10 \text{ m}$ as a subplot, and a total of 212 subplots were included in the field surveys.

and herbs according to plant height and species property. In the factual survey process, those woody plants of $\geq 5 \text{ m}$ were recorded into the tree layer dominated by evergreen species of *Itea yunnanensis*, *Quercus phillyraeoides*, *Cinnamomum bodinieri* and *Ligustrum lucidum*, and deciduous species of *Platycarya strobilacea* and *Carpinus pubescens*, otherwise as the shrub layer dominated by evergreen *Myrsine africana*, and deciduous *Carpinus pubescens*, *Rosa cymose*, *Pyracantha fortuneana* and *Coriaria nepalensis*, while herbs were a separate layer under the canopy as the dominant plants including *Cyrtomium fortune*, *Setaria faberii*, *Arthraxon hispidus* and *Ficus tikoua*, etc. These plant species assemble the karst community and share the canopy jointly. A total of 92 woody species was investigated in all plots and all woody plants were broadleaved species. Out of 92 woody species, 41 deciduous species belong to 21 families and 37 genera, and 51 evergreen species belong to 27 families and 37 genera. In particular, the subcommunity analysis of all woody species in one plot was conducted by modularizing the leaf habits concerning the evergreen and deciduous plants. Namely, this work included two subcommunities of evergreen and deciduous species. Additionally, the healthy branches of woody plants were collected through four orientations with the surveyed plots. All branches were kept fresh by wrapping them into a freshness protection package for further measuring leaf functional traits, such as the leaf area (LA), leaf thickness (LT), fresh leaf weight (LFW), and leaf dried weight (LDW). A total of 14,870 functional leaves were obtained from woody plants, including 6,067 evergreen leaves and 8,803 deciduous leaves. All data of individuals and leaf traits of woody species were analyzed for the differences between evergreen and deciduous subcommunities in this study.

2.2. Selection and measurement of leaf traits

In special, nine leaf traits were selected for exploring leaf ecological resource strategy, including the specific leaf area (SLA), the leaf dry matter content (LDMC), the leaf tissue density (ltd), the contents of leaf carbon (C), nitrogen (N) and phosphorus (P) and their stoichiometric ratios of C/N, C/P and N/P. The SLA was explained as a good surrogate

for resource ability related to the carbon and nutrient status in tissues, development of structural and chemical defenses, leaf life span, and nutrient resorption rates (Reich et al., 1992; Bär Lamas et al., 2016). The LDMC was an important predictor of plant resource utilization, acquisition, and availability (Cornelissen et al., 2003). Theoretically, the stoichiometric ratio of leaves C, N, and P can reflect how plants adapt to the growing environmental conditions (Rong et al., 2015). Exactly leaf C and ltd may reveal the resource conservation, physical defense, and resistance to disturbance suggested by Perez-Harguindeguy et al., (2013). Meanwhile, the leaf N and P were closely related to resource acquisition and carbon balance (Wright et al., 2004; Adler et al., 2014), significantly affecting the plant's photosynthetic efficiency (Wright et al., 2004). Therefore, these trait parameters can specify the adaptive resource strategy for varying environments for plant individuals and communities.

In the beginning, all leaves collected from filed plots were scanned for LA by a foliar digital scanning system (WinRHIZO_Pro LA2400). The LT was measured by a vernier caliper of 0.01 mm precision; then a balance of 1:10,000 weighted the LFW; the following were dried for 48 h at 105° C in an oven until constant mass for obtaining the LDW. We used these measured traits to calculate the various traits of SLA, LDMC and ltd by equations of $\text{SLA} = \text{LA}/\text{LDW}$, $\text{LDMC} = \text{LDW}/\text{LFW}$ and $\text{ltd} = \text{LDW}/\text{LA} \times \text{LT}$ in this study. Then dried leaves were milled using a ball mill (Retsch MM400, Germany) to obtain the fine powder for measuring element contents of C, N, and P. Respectively, the leaf C adopted by the potassium dichromate method, leaf N measurement used by Kjeldahl method (BUCHI K-360, Switzerland), and leaf P measurement determined by molybdenum anti colorimetric method. These chemical determination methods were performed according to Zhang, (2011). In addition, the stoichiometric ratio for C/N, C/P, and N/P was calculated, respectively.

2.3. Community-weighted means of leaf traits

Community traits can reflect the turnover in species composition and

the ecological strategies in plant communities across varying environmental gradients (Kandlikar et al., 2022). The community-weighted mean (CWM) of traits is valuable in describing community composition and ecosystem function, according to Muscarella et al., (2017). Lavorel et al., (2008) suggested that the community-weighted mean of traits can be calculated by the relative abundances of species and their traits values. Therefore, CWM was calculated to explore the plant ecological strategies between subcommunities in our study to understand karst vegetation's evolution further. The CWM traits of the deciduous and evergreen subcommunities can be calculated respectively by the following formula as follows:

$$CWM = \sum_{i=1}^n RA \times trait_i$$

Where CWM is the community-weighted means, n is the number of species in respective subcommunities, and RA is the relative abundance of species i to respective subcommunities. $Trait_i$ is the trait value of specie i via measurement.

2.4. Data analysis

The T-test was performed through SPSS software (version 22.0; IBM, Armonk, NY, USA) to compare the CWM traits difference at the community level between two subcommunities, and the boxplot was drawn to visualize these differences. Additionally, the correlation analysis was performed using Principal component analysis (PCA) and Pearson analysis. Further, PCA was used to summarize the resource strategies of evergreen and deciduous subcommunities. All graphs were drawn by Origin software (Pro. 2021 version, Origin Lab, USA).

3. Results

3.1. CWM of leaf phenotypic traits differences between evergreen and deciduous subcommunities

The SLA and LDMC of the deciduous subcommunity were significantly higher than the evergreen subcommunity (Fig. 2a-b), predicting that higher SLA and LDMC of deciduous subcommunity enable them to maximize light capture and be more efficient at defense in the karst mixed forests. In contrast, the evergreen subcommunity's ltd was slightly greater than the deciduous subcommunity (Fig. 2c). It showed that the evergreen subcommunity tends to invest in leaf structure for defense compared to the deciduous subcommunity. Overall, the results suggested that the deciduous subcommunity prefers resource acquisition by increasing SLA, while the evergreen subcommunity favors resource conservation by decreasing SLA and increasing ltd in strategy.

3.2. CWM of leaf stoichiometric trait differences between evergreen and deciduous subcommunities

The leaf C, C/N and C/P ratios of the evergreen subcommunity were significantly higher than deciduous subcommunity (Fig. 3a; Fig. 3d-e), representing that the evergreen subcommunity had a strong life defense strategy and higher investment profit to N and P for carbon assimilation. In contrast, the leaf N, P, and N/P ratio of the deciduous subcommunity were significantly greater than the evergreen subcommunity (Fig. 3b-c; Fig. 3f), signifying that the deciduous subcommunity via falling leaves had a greater ability to acquire fast and transform nutrient resources than the evergreen subcommunity in nutrient-deficit soil of karst forests. Additionally, the lower nutrients of N and P of the evergreen subcommunity probably show the conservation of nutritional resources in leaf tissue for maintaining evergreen leaves. Meanwhile, the leaf N/P ratio of 21.25 for the deciduous subcommunity was significantly higher than the N/P ratio of 19.15 for the evergreen subcommunity (Fig. 3f), demonstrating that evergreen and deciduous plants were equally limited by soil phosphorus due to their N/P ratios are more than the value of 16.0. However, the P limitation of the deciduous subcommunity was higher than the evergreen subcommunity according to these results. Overall, all the results again show that the evergreen subcommunity gains more C through investing in a small number of N and P, tending to be a resource conservation strategy. Conversely, the deciduous subcommunity tends to have a fast acquisition resources strategy in N and P.

3.3. Correlation among leaf functional traits of CWM in respective to subcommunity

PCA revealed the relationship across leaf functional traits for deciduous and evergreen subcommunities (Fig. 4). On the one hand, the variations of CWM traits of deciduous subcommunity were summarized by 40.6 % at PC1 and 30.0 % at PC2 axis, respectively (Fig. 4a). The first PCA showed that the SLA was significantly negatively correlated with leaf C, C/N ratio, LDMC and ltd, and significantly positively correlated with leaf N and N/P ratio; leaf N was significantly negatively correlated with leaf C, C/N ratio and LDMC, and significantly positively correlated with SLA and leaf P; the LDMC was significantly negatively correlated with leaf N, N/P ratio and SLA, and significantly positively correlated with C/N ratio and ltd; the ltd was significantly negatively correlated with SLA, and significantly positively correlated with LDMC (Fig. 4a; Fig. 5a). On the other hand, the variations of CWM traits of evergreen subcommunity were explained by 40.9 % at PC1 and 26.0 % at PC2 axis, respectively (Fig. 4b). The second PCA showed that the SLA was significantly negatively correlated with leaf C, C/N ratio, LDMC and ltd, and significantly positively correlated with leaf N and P; leaf N was significantly negatively correlated with C/N ratio, C/P ratio and LDMC,

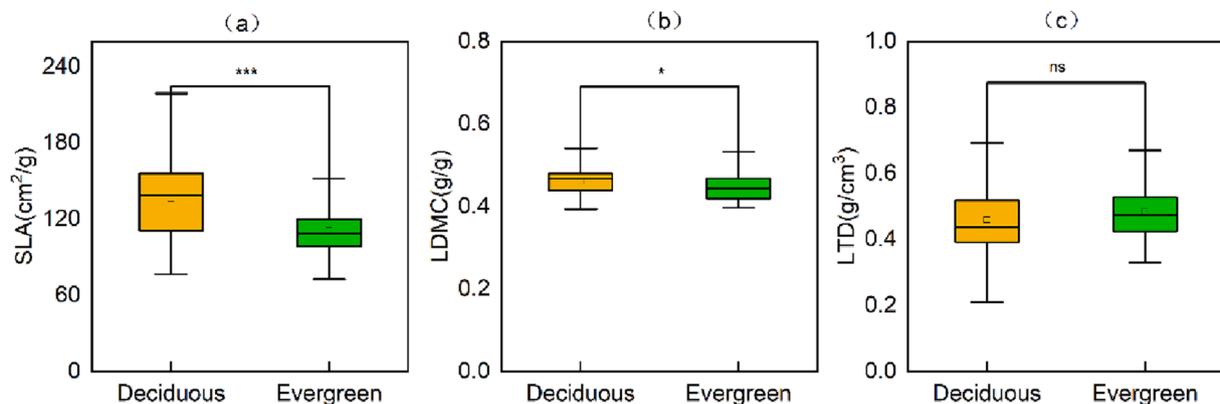


Fig. 2. Trait differences in leaf phenotype on the specific leaf area, leaf dry matter content and leaf tissue density between deciduous and evergreen subcommunities in karst mixed forests. *, **, and *** specify a significant difference between deciduous and evergreen subcommunities by T-test at $p \leq 0.05$, $p \leq 0.01$, and $p \leq 0.001$, respectively; ns indicates non-significant differences.

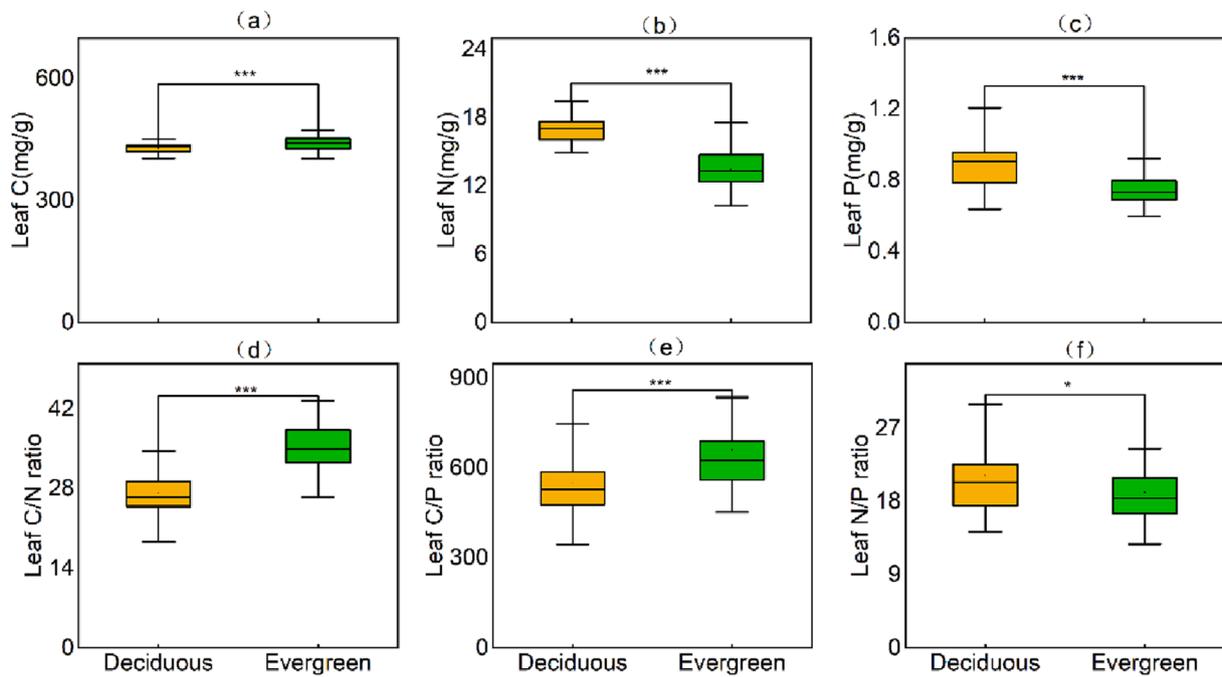


Fig. 3. The differences in leaf carbon, nitrogen, phosphorus content, and the stoichiometric ratio between deciduous and evergreen subcommunities in the karst mixed forests. For the explanation of *, **, and ***, see Fig. 2.

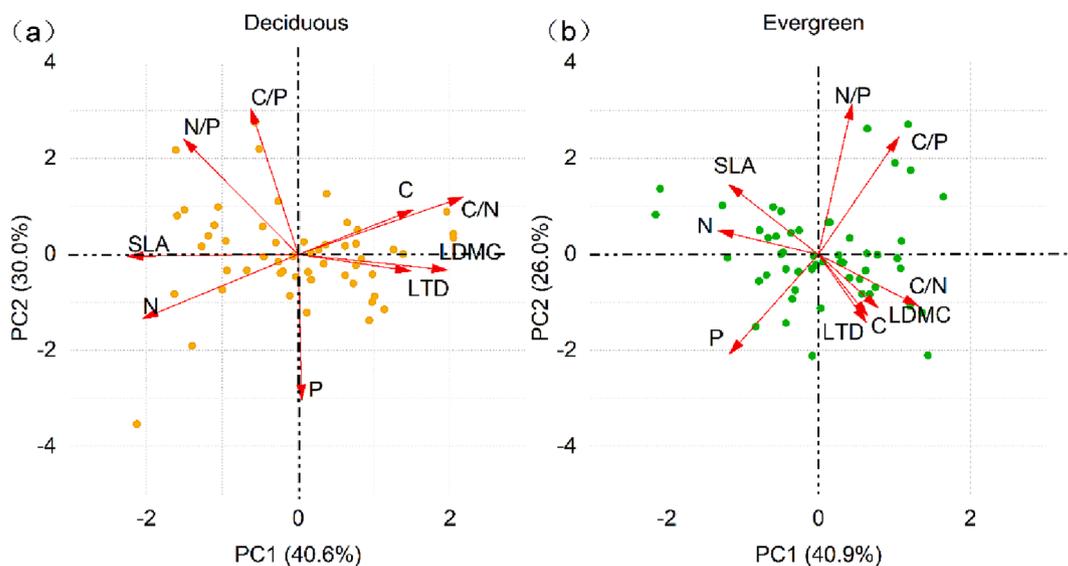


Fig. 4. The principal component analyses (PCA) for leaf functional trait correlations in the karst mixed forest’s respective deciduous and evergreen subcommunities. Yellow dots showed the deciduous subcommunity distribution at the PCA axis (a), and blue dots showed the evergreen subcommunity distribution at the PCA axis (b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and significantly positively correlated with SLA and leaf P; the LDMC was significantly negatively correlated with leaf N and SLA, and significantly positively correlated with leaf C, C/N ratio and ltd; the ltd was significantly negatively correlated with SLA, and significantly positively correlated with leaf C and LDMC (Fig. 4b; Fig. 5b). Overall, both deciduous and evergreen subcommunities showed significant negative correlations between SLA, leaf N and ltd, LDMC, specifying a leaf economic spectrum trade-off between the two subcommunities.

3.4. PCA analysis for leaf functional traits on CWM in evergreen and deciduous subcommunities

The variations of leaf functional traits of CWM of both

subcommunities were described by 41.3 % at PC1 and 26.9 % at PC2 axis, respectively. The PC1 axis mainly reflected the changes in SLA, LDMC, ltd, and leaf N (Fig. 6a). The deciduous subcommunity was mainly located on the high SLA and leaf N side of the resource acquisition, and the evergreen subcommunity was mainly located on the high LDMC and ltd side of the resource conservation (Fig. 6a). The resource acquisition strategy was correlated to a high leaf P and N/P ratio. The resource conservation strategy was correlated to the high leaf C and C/N ratio (Fig. 6a). It showed the main functional trade-off among subcommunities with different leaf habits in the karst mixed forest. Overall, the deciduous subcommunity with high SLA and leaf N had an acquisitive strategy. In contrast, the evergreen subcommunity with high LDMC and ltd had a conservative strategy.

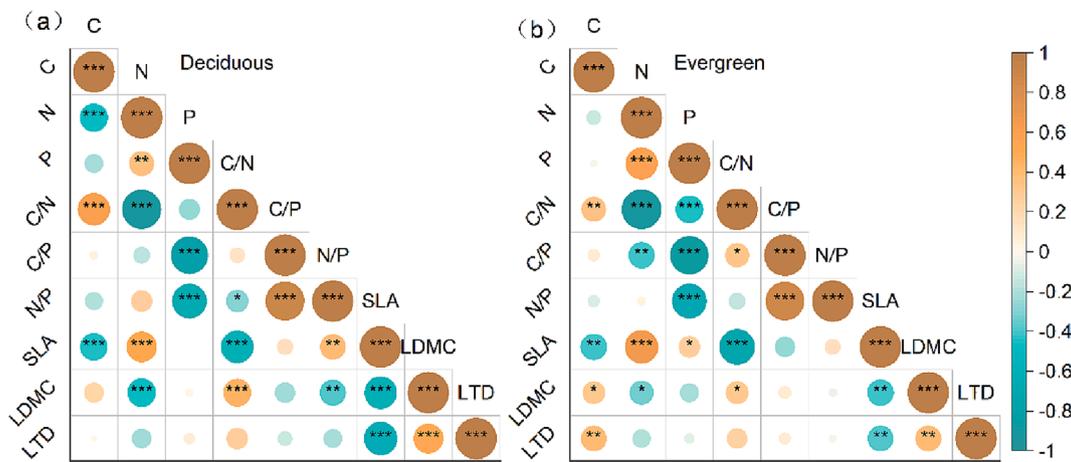


Fig. 5. Pearson correlation analyses for leaf functional traits separately for deciduous and evergreen subcommunities in subtropical karst mixed forests. For the explanation of *, **, and ***, see Fig. 2.

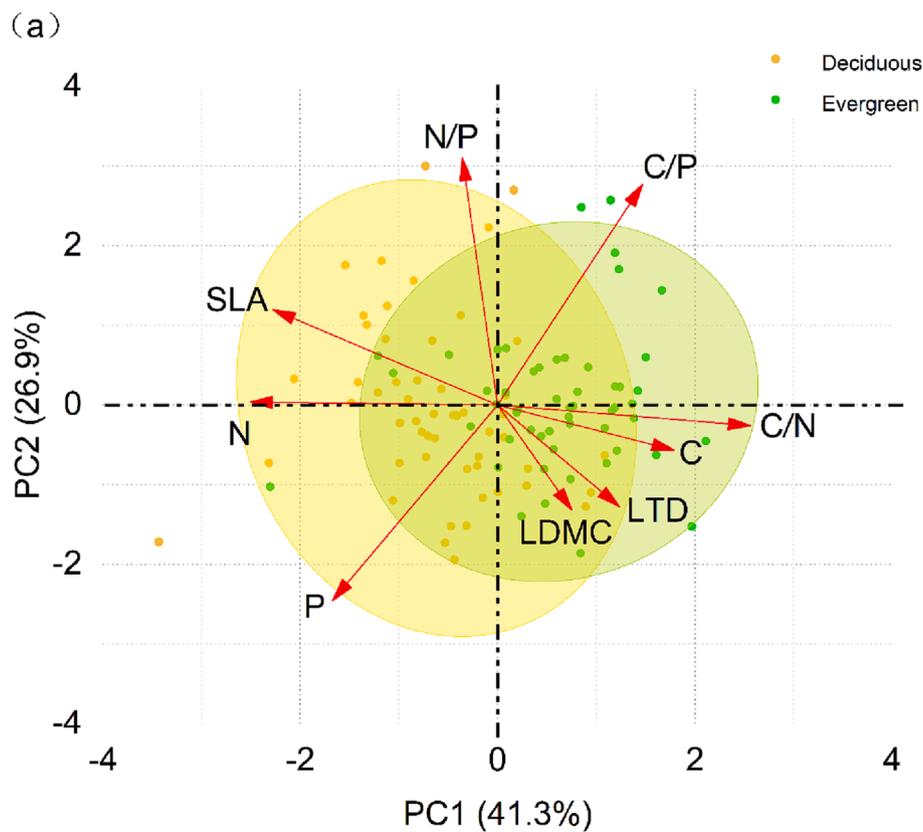


Fig. 6. PCA for leaf functional trait deviation in the strategy of the deciduous and evergreen subcommunities in karst mixed forests. For the explanation of yellow dots and blue dots, see Fig. 5. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Leaf traits differentiation by functional leaf habits in both evergreen and deciduous subcommunities

In this study, the evergreen subcommunity had lower SLA, LDMC, leaf N, P, and the ratio of N/P with higher leaf C and ratios of C/N and C/P when compared with the deciduous subcommunity, but ltd was not significant between two subcommunities (Figs. 2-3). On the one hand, leaf functional traits can reflect plant functional strategies (Jiang et al., 2016) to adapt environments for survival (Zhang et al., 2017). Here, the evergreen subcommunity had lower SLA due to the longer-lived leaves

of the evergreen species requiring more biomass investment in structural integrity and defense against disturbances (Zhang et al., 2017). However, the deciduous subcommunity with higher SLA can quickly obtain light leading to high photosynthetic rates and faster growth rates (Fonseca et al., 2000), which maximizes resource capture during a limited growing season in a low-resource environment (Poorter et al., 2009). On the other hand, the smaller SLA can reduce foliar transpiration and improve resource use efficiency, which is beneficial for adaptation to nutrient-poor habitats (Fu et al., 2019), which supports the evergreen subcommunity had a higher resource use efficiency according to our results. Moreover, Ávila-Lovera et al., (2019) suggested that the sclerophyllous-thicker leaves could well-protect plants against

structural damage. Also, plant leaves with high leaf C, LDMC, ltd and low N and P aimed to defend tissue damage in leaf structure (Chabot and Hicks, 1982; Dirzo and Boege, 2008; Freschet et al., 2010), part consisting with our results that the evergreen subcommunity had significantly higher the leaf C and lower leaf N and P than the deciduous subcommunity (Fig. 3a-c). It indicated that the evergreen subcommunity tends to leaf structural defense and leaf protection in resource strategy.

The higher leaf C indicated a strong defense life strategy (Rong et al., 2015) and higher carbon fixation capacity (Bai et al., 2015) for evergreen plants, contrarily the low efficiency in C preservation due to frequently renewed for deciduous plants with lower leaf C (Aerts and Chapin, 1999). The deciduous subcommunity had higher leaf N and P than the evergreen subcommunity (Fig. 3b-c), supporting that the evergreen subcommunity was resource conservation and the deciduous subcommunity was resource acquisition in karst habitats with low P and N supply according to studies of Westoby et al., (2002), Tomlinson et al., (2013) and Givnish, (2002). In addition, The evergreen subcommunity had higher leaf C/N and C/P ratios than the deciduous subcommunity (Fig. 3d-e), indicating a higher nutrient utilization efficiency (Small, 1972; Edwards et al., 2014; Rong et al., 2015). Koerselman and Arthur, (1996) suggest that the N/P ratio of the plants directly indicated the type of nutrient limitation, through the N/P ratio < 14 generally indicating N-limitation while a ratio greater than 16 suggesting the P-limitation, the range of 14 and 16 showing both limitations of N and P. Our result found that the leaf N/P ratios in both subcommunities were greater than 16 (Fig. 3f), showing that plant growth was mainly limited by phosphorus in karst soil supported by Sun et al., (2022). Wang et al., (2017) suggested that differences in leaf functional traits of plants with different leaf habits lead to different strategies, especially in resource acquisition and utilization for deciduous and evergreen subcommunities in the infertile karst habitats. Overall, the deciduous subcommunity had high SLA and leaf nutrient contents presenting an acquisitive strategy; in contrast, the evergreen subcommunity had expensive leaf construction with low SLA and low nutrient contents exhibiting a conservative strategy supported the H1 in our results according to Wright et al., (2005).

4.2. The strategy trade-off and strategy differentiation associated with leaf functional traits

Liu et al., (2017) found that leaf functional traits did not vary independently in integrated performance, and any particular trait was constrained by its functional linkages with other traits, consisting our result presentation of positive or negative correlations in SLA, leaf N and LDMC, ltd of both subcommunities (Figs. 4-5). For example, plants with longer leaf life devoting more resources to the leaf structural construction inevitably reduced the resource for maintaining photosynthesis and respiration (Wright et al., 2004; Ordoñez et al., 2009). Exactly as some plants have a strategy of lower SLA and larger ltd (Zhang et al., 2022a), explained by Li et al., (2021) as the maintenance of leaf function or delaying leaf death under adverse conditions. However, Schulze et al., (1994) quarreled that higher SLA indicated a stronger photosynthetic capacity and faster nutrient cycling, as the expense of ltd in leaf structure suggested by Diaz et al., (2004) and Wright et al., (2004). Overall, these studies indicated that plant leaves have greater SLA and leaf N and P for higher photosynthetic capacity at a lower leaf structural investment, such as lower ltd, which could be explained as the trade-off between resource acquisition and resource conservation, according to Reich, (2014). Therefore, the coordination of these key leaf economic traits in our study indicated a trade-off between resource acquisition and resource conservation in both subcommunities, which was consistent with H2.

The trade-off between leaf functional traits inferring rapid resource acquisition and the conservation of resources (Freschet et al., 2010) could be explained by the leaf economic spectrum, which ranks plants

on a specific ecological axis, one side of the leaf ecological axis with large SLA, leaf N, P represent the fast-return strategy; another side with large LDMC, ltd, and leaf C represent the slow-return strategy (Wright et al., 2004; Li et al., 2022a). These studies support our results of the deciduous subcommunity mainly located on the side of the resource acquisition, and the evergreen subcommunity was mainly located on the side of the resource conservation (Fig. 6a). Furthermore, our results were consistent with the previous studies within plant communities about resource acquisition and conservation strategies of evergreen and deciduous plants (Yao et al., 2020; Zhang et al., 2021; Ye et al., 2022). Overall, plants with different leaf habits obtained an optimal trade-off between resource capture and conservation in our study. Simultaneously, the differentiation of plant resource strategies could facilitate niche differentiation (Alvarez Yepiz et al., 2017) and reduced competition intensity (McEwan et al., 2011), which provides an opportunity for the stable coexistence of plants, and improves the resource use efficiency supported by Hikosaka et al., (2021) as well as the biodiversity maintenance (Liu et al., 2017) in resource-poor karst habitat. Overall, the strategy trade-offs and strategy differentiation associated with leaf functional traits in evergreen and deciduous subcommunities provides insight into explaining the coexistence of species and further understanding vegetation evolution in the mixed forests of the karst ecosystem in this study.

4.3. A framework on leaf functional trait differentiation and strategy trade-off to subcommunities of deciduous and evergreen species

These karst forests remarkably differ from the evergreen broadleaved forest developed in non-karst regions of general landforms in the same climatic zone in southwest China (Liu et al., 2016). Therefore, according to our results, we raised a conceptual framework on leaf functional trait differentiation and strategy trade-off to subcommunities of deciduous and evergreen species in karst mixed forests (Fig. 7), according to Wright et al., (2004), Rong et al., (2015), Lohbeck et al., (2015), Collins et al., (2016), Song et al., (2019). It exhibits the trait differentiation of the assembled subcommunities of evergreen and deciduous species in comparing SLA, LDMC, ltd, leaf contents of C, N and P, and their stoichiometric ratios. The significance of the conceptual framework is well to understand that the high or low trait differentiation indicates the resource acquisition and return for deciduous trees or conservation for evergreen trees in a trade-off strategy in the unique karst ecosystem. Possibly deciduous trees aim to provide a fast resource transformation to maintain demands for evergreen trees in the karst ecosystem. As our study, vegetation types are not only dominated by climate, but also closely related to specific habitat conditions in species adaptive distribution attributing to habitat conditions. Further, it is well in future understanding that the vegetation evolution to explain deciduous trees coexisting with evergreen trees in forming karst mixed forest.

5. Conclusion

Our study demonstrated that there were significant differences in CWM of leaf functional traits between deciduous and evergreen subcommunities; meanwhile, the SLA, LDMC, leaf N, P contents, and N/P ratios of the deciduous subcommunity were significantly higher, whereas leaf C and C/N, C/P ratios were significantly lower than the evergreen subcommunity. In addition, PCA on leaf functional traits for both subcommunities showed strategy differentiation; the deciduous subcommunity was mainly located on the side of resource acquisition, and the evergreen subcommunity was mainly located on the side of resource conservation. It directed that plants with different leaf habits obtained the best trade-off between resource capture and conservation. The significance is to explain species coexistence and further understand vegetation evolution. In conclusion, strategy trade-off from the leaf trait differentiation associated with leaf habits presents fast resource acquisition for the deciduous subcommunity and resource conservation for

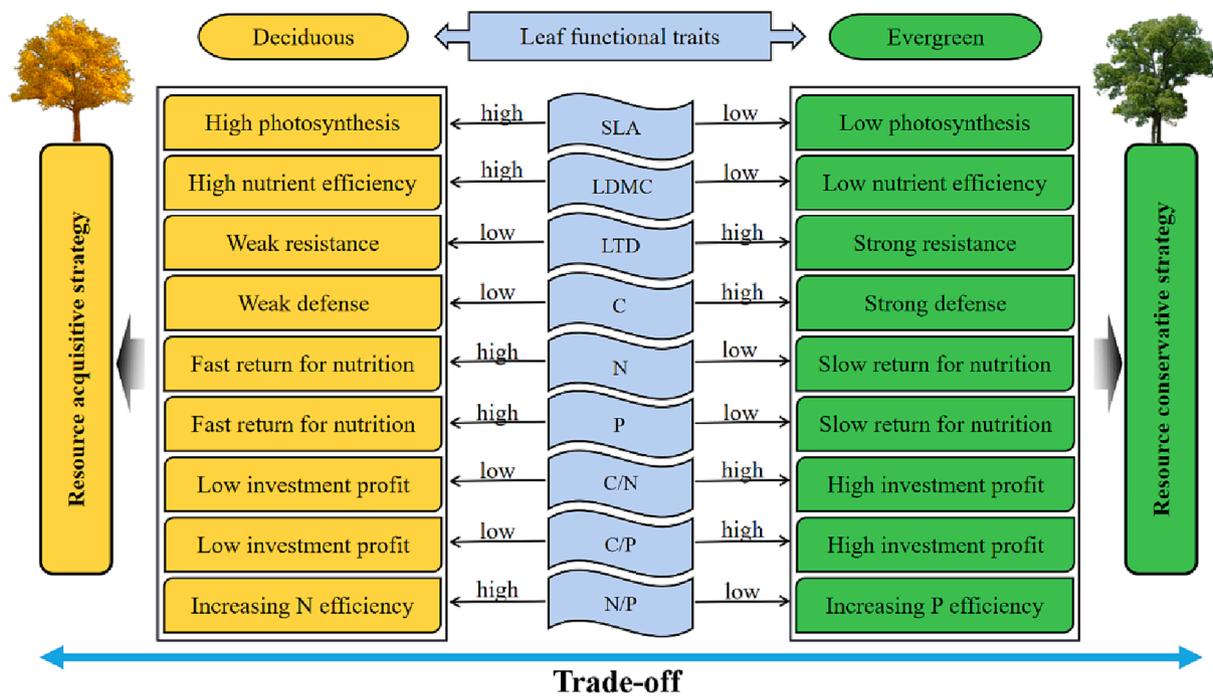


Fig. 7. The conceptual model for leaf functional trait differentiation and strategy trade-off to subcommunities of deciduous and evergreen species in karst mixed forests. The raised conceptual model referred to documents synthetically from Wright et al., (2004), Rong et al., (2015), Lohbeck et al., (2015), Collins et al., (2016), Song et al., (2019). Therefore, the conceptual model proposed according to our results of trait differentiation of the assembled subcommunities of evergreen and deciduous species. The high or low trait differentiation indicates the resource acquisition and returns for deciduous trees or conservation for evergreen trees in a trade-off strategy in the unique karst ecosystem.

the evergreen subcommunity in the mixed forest dominated by the subtropical climate in the karst ecosystem.

CRediT authorship contribution statement

Wang Li: Investigation, Formal analysis, Data curation, Writing-original draft. **Yuejun He:** Supervision, Conceptualization, Funding acquisition, Writing - review & editing, Investigation, Formal analysis. **Muhammad Umer:** Writing - review & editing. **Yun Guo:** Investigation, Formal analysis, Funding acquisition. **Qiyu Tan:** Investigation, Data curation. **Liling Kang:** Investigation, Data curation. **Zhengyuan Fang:** Investigation. **Kaiping Shen:** Investigation, Validation. **Tingting Xia:** Investigation, Validation. **Pan Wu:** Resources. **Yuan Liu:** Validation, Visualization. **Lipeng Zang:** Investigation, Formal analysis. **Qingfu Liu:** Investigation, Formal analysis. **Yan Zhao:** Visualization. **Hongchun Chen:** Investigation, Visualization. **Ying Zhao:** Investigation, Visualization.

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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References

- Adler, P. B., Salguero Gomez, R., Compagnoni, A., Hsu, J. S., Ray Mukherjee, J., Mbeau Ache, C., and Franco, M., 2014. Functional traits explain variation in plant life history strategies (vol 111, pg 740, 2014). *Proceedings of the national academy of sciences of the united 111* (27), 10019-10019. <https://doi.org/10.1073/pnas.1410430111>.
- Aerts, R., and Chapin, F. S., 1999. The Mineral Nutrition of Wild Plants Revisited: A Re-evaluation of Processes and Patterns. Pages 1-67 in A. H. Fitter and D. G. Raffaelli, editors. *Advances in Ecological Research*. Academic Press. [https://doi.org/10.1016/S0065-2504\(08\)60016-1](https://doi.org/10.1016/S0065-2504(08)60016-1).
- Alvarez Yepiz, J.C., Burquez, A., Martinez Yrizar, A., Teece, M., Yezpe, E.A., Dovicak, M., 2017. Resource partitioning by evergreen and deciduous species in a tropical dry forest. *Oecologia* 183 (2), 607-618. <https://doi.org/10.1007/s00442-016-3790-3>.
- Ávila-Lovera, E., Urlich, R., Coronel, I., Tezara, W., 2019. Seasonal gas exchange and resource-use efficiency in evergreen versus deciduous species from a tropical dry forest. *Tree Physiol.* 39 (9), 1561-1571. <https://doi.org/10.1093/treephys/tpz060>.
- Bai, K., He, C., Wan, X., and Jiang, D., 2015. Leaf economics of evergreen and deciduous tree species along an elevational gradient in a subtropical mountain. *AoB Plants* 7 (2015), plv064. Doi: 10.1093/aobpla/plv064.
- Bär Lamas, M.I., Carrera, A.L., Bertiller, M.B., 2016. Meaningful traits for grouping plant species across arid ecosystems. *J. Plant Res.* 129 (3), 449-461. <https://doi.org/10.1007/s10265-016-0803-6>.
- Bo, J., Jianhua, W., Jin, S., Xianrong, Z., 2016. Characters and species diversity of *Torreya fargesii* Franch. community in the Jinfo Mountains. *J. Land. Res.* 8 (2), 71. <https://doi.org/10.16785/j.issn>.
- Chabot, B. F., Hicks, D. J., 1982. The Ecology of Leaf Life Spans. *Annual Review of Ecology and Systematics* 13 (1), 229-259. Doi: annurev.es.13.110182.001305.
- Chelli, S., Ottaviani, G., Campetella, G., Canullo, R., 2020. Community weighted mean trait data of Italian forest understories. *Data Brief* 28 (2020), 104947. <https://doi.org/10.1016/j.dib.2019.104947>.
- Cohenpb, J.E., Charles, M.N., 1985. When will a large complex system be stable? *J. Theor. Biol* 113 (1985), 153-156. [https://doi.org/10.1016/S0022-5193\(85\)80081-3](https://doi.org/10.1016/S0022-5193(85)80081-3).
- Collins, C.G., Wright, S.J., Wurzbarger, N., 2016. Root and leaf traits reflect distinct resource acquisition strategies in tropical lianas and trees. *Oecologia* 180 (4), 1037-1047. <https://doi.org/10.1007/s00442-015-3410-7>.
- Cornelissen, J., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D., Reich, P., Ter Steege, H., Morgan, H., Van Der Heijden, M., 2003. A handbook of protocols for

- standardised and easy measurement of plant functional traits worldwide. *Austral. J. Botany* 51 (4), 335–380. <https://doi.org/10.1071/BT02124>.
- Diaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez Harguindeguy, N., Pérez Rontomé, M.C., Shirvany, F.A., Vendramini, F., Yazdani, S., Abbas Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres Espuny, L., Falczuk, V., Guerrero Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P., Zak, M.R., 2004. The plant traits that drive ecosystems: Evidence from three continents. *J. Veg. Sci.* 15 (3), 295–304. <https://doi.org/10.1111/j.1654-1103.2004.tb02266.x>.
- Dirzo, R., Boege, K., 2008. Patterns of herbivory and defense in tropical dry and rain forests. *Tropical forest community ecology* 63–78.
- Edwards, E.J., Chatelet, D.S., Sack, L., Donoghue, M.J., 2014. Leaf life span and the leaf economic spectrum in the context of whole plant architecture. *J. Ecol.* 102 (2), 328–336. <https://doi.org/10.1111/1365-2745.12209>.
- Fan, D.Y., Jie, S.L., Liu, C.C., Zhang, X.Y., Xu, X.W., Zhang, S.R., Xie, Z.Q., 2011. The trade-off between safety and efficiency in hydraulic architecture in 31 woody species in a karst area. *Tree Physiol.* 31 (8), 865–877. <https://doi.org/10.1093/treephys/tpr076>.
- Feest, A., Aldred, T.D., Jedamzik, K., 2010. Biodiversity quality: A paradigm for biodiversity. *Ecol. Indicators* 10 (6), 1077–1082. <https://doi.org/10.1016/j.ecolind.2010.04.002>.
- Fonseca, C.R., Overton, J.M., Collins, B., Westoby, M., 2000. Shifts in trait-combinations along rainfall and phosphorus gradients. *Journal of Ecology* 88 (6), 964–977. <https://doi.org/10.1046/j.1365-2745.2000.00506.x>.
- Freschet, G.T., Cornelissen, J.H.C., Van Logtestijn, R.S.P., Aerts, R., 2010. Evidence of the ‘plant economics spectrum’ in a subarctic flora. *J. Ecol.* 98 (2), 362–373. <https://doi.org/10.1111/j.1365-2745.2009.01615.x>.
- Fu, P.L., Zhu, S.D., Zhang, J.L., Finnegan, P.M., Jiang, Y.J., Lin, H., Fan, Z.X., Cao, K.F., 2019. The contrasting leaf functional traits between a karst forest and a nearby non-karst forest in south-west China. *Funct. Plant Biol.* 46 (10), 907–915. <https://doi.org/10.1071/FP19103>.
- Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Lepš, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V.P., Queded, H., Quétiér, F., Robson, M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M., Theau, J.-P., Thébault, A., Vile, D., Zarovali, M.P., 2006. Assessing the Effects of Land-use Change on Plant Traits, Communities and Ecosystem Functioning in Grasslands: A Standardized Methodology and Lessons from an Application to 11 European Sites. *Ann. Bot.* 99 (5), 967–985. <https://doi.org/10.1093/aob/mcl215>.
- Givnish, T.J., 2002. Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. *Silva fennica* 36 (3), 703–743. <https://doi.org/10.14214/sf.535>.
- Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86 (6), 902–910. <https://doi.org/10.1046/j.1365-2745.1998.00306.x>.
- Hikosaka, K., Kurokawa, H., Arai, T., Takayanagi, S., Tanaka, H.O., Nagano, S., Nakashizuka, T., 2021. Intraspecific variations in leaf traits, productivity and resource use efficiencies in the dominant species of subalpine evergreen coniferous and deciduous broad-leaved forests along the altitudinal gradient. *J. Ecol.* 109 (4), 1804–1818. <https://doi.org/10.1111/1365-2745.13603>.
- Holt, R.D., Lawton, J., 1994. The ecological consequences of shared natural enemies. *Annu. Rev. Ecol. Syst.* 25 (1994), 495–520. <https://doi.org/10.1146/annurev.es.25.110194.002431>.
- Y. Huang X. Ai L. Yao R. Zang Y. Ding J. Huang G. Feng J. Liu Changes in the Diversity of Evergreen and Deciduous Species During Natural Recovery Following Clear-Cutting in a Subtropical Evergreen-Deciduous Broadleaved Mixed Forest of Central China *Trop. Conserv. Sci.* 8 4 2015 1033 1052 <https://doi.org/10.1177/194008291500800413>.
- Ives, A.R., Klug, J.L., Gross, K., 2000. Stability and species richness in complex communities. *Ecol. Lett.* 3 (5), 399–411. <https://doi.org/10.1046/j.1461-0248.2000.00144.x>.
- Y. Jiang X. Chen J. Ma S. Liang J. Huang R. Liu Y. Pan Interspecific and Intraspecific Variation in Functional Traits of Subtropical Evergreen and Deciduous Broadleaved Mixed Forests in Karst Topography, Guilin Southwest China. *Trop. Conserv. Sci.* 9 4 2016 1940082916680211 <https://doi.org/10.1177/1940082916680211>.
- Jin, Y., Russo, S.E., Yu, M., 2018. Effects of light and topography on regeneration and coexistence of evergreen and deciduous tree species in a Chinese subtropical forest. *J. Ecol.* 106 (4), 1634–1645. <https://doi.org/10.1111/1365-2745.12911>.
- Kandlikar, G.S., Kleinhesselink, A.R., Kraft, N.J., 2022. Functional traits predict species responses to environmental variation in a California grassland annual plant community. *J. Ecol.* 110 (4), 833–844. <https://doi.org/10.1111/1365-2745.13845>.
- Kikuzawa, K., 1991. A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. *Am. Nat.* 138 (5), 1250–1263. <https://doi.org/10.1086/285281>.
- Kloeppel, B.D., Gower, S.T., Vogel, J.G., Reich, P.B., 2000. Leaf-level resource use for evergreen and deciduous conifers along a resource availability gradient. *Funct. Ecol.* 14 (3), 281–292. <https://doi.org/10.1046/j.1365-2435.2000.00439.x>.
- Koerselman, W., Arthur, F.M.M., 1996. The Vegetation N:P Ratio: a New Tool to Detect the Nature of Nutrient Limitation. *J. Appl. Ecol.* 33 (6), 1441–1450. <https://doi.org/10.2307/2404783>.
- Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrrough, J., Berman, S., Quétiér, F., Thébault, A., Bonis, A., 2008. Assessing functional diversity in the field – methodology matters! *Funct. Ecol.* 22 (1), 134–147. <https://doi.org/10.1111/j.1365-2435.2007.01339.x>.
- Li, J., Chen, X., Niklas, K.J., Sun, J., Wang, Z., Zhong, Q., Hu, D., Cheng, D., 2022a. A whole-plant economics spectrum including bark functional traits for 59 subtropical woody plant species. *J. Ecol.* 110 (1), 248–261. <https://doi.org/10.1111/1365-2745.13800>.
- Li, S., Gou, W., Wang, H., White, J.F., Wu, G., Su, P., 2021. Trade-Off Relationships of Leaf Functional Traits of *Lycium ruthenicum* in Response to Soil Properties in the Lower Reaches of Heihe River, Northwest China. *Diversity* 13 (9), 453. <https://doi.org/10.3390/d13090453>.
- Li, Q., Umer, M., Guo, Y., Shen, K., Xia, T., Xu, X., Han, X., Ren, W., Sun, Y., Wu, B., Liu, X., He, Y., 2022b. Karst Soil Patch Heterogeneity with Gravel Promotes Plant Root Development and Nutrient Utilization Associated with Arbuscular Mycorrhizal Fungi. *Agronomy* 12 (5), 1063. <https://doi.org/10.3390/agronomy12051063>.
- Liu, H., Li, Y., Ren, F., Lin, L., Zhu, W., He, J.S., Niu, K., 2017. Trait-abundance relation in response to nutrient addition in a Tibetan alpine meadow: The importance of species trade-off in resource conservation and acquisition. *Ecol. Evol.* 7 (24), 10575–10581. <https://doi.org/10.1002/ece3.3439>.
- Liu, C., Liu, Y., Guo, K., Zhao, H., Qiao, X., Wang, S., Zhang, L., Cai, X., 2016. Mixing litter from deciduous and evergreen trees enhances decomposition in a subtropical karst forest in southwestern China. *Soil Biol. Biochem.* 101 (2016), 44–54. <https://doi.org/10.1016/j.soilbio.2016.07.004>.
- Liu, J.T., Wang, X.Y., Liu, L., Wu, X.F., Xia, Z.C., Guo, Q.X., 2022. Rhizosphere soil bacterial communities and nitrogen cycling affected by deciduous and evergreen tree species. *Ecol. Evol.* 12 (7), e9103.
- Liu, S., Zhang, W., Wang, K., Pan, F., Yang, S., Shu, S., 2015. Factors controlling accumulation of soil organic carbon along vegetation succession in a typical karst region in Southwest China. *Sci. Total Environ.* 521–522 (2015), 52–58. <https://doi.org/10.1016/j.scitotenv.2015.03.074>.
- Lohbeck, M., Lebrija-Trejos, E., Martínez-Ramos, M., Meave, J.A., Poorter, L., Bongers, F., 2015. Functional trait strategies of trees in dry and wet tropical forests are similar but differ in their consequences for succession. *PLoS One* 10 (4), e0123741.
- Lu, H., Mohren, G.M.J., den Ouden, J., Goudiaby, V., Sterck, F.J., 2016. Overyielding of temperate mixed forests occurs in evergreen-deciduous but not in deciduous-deciduous species mixtures over time in the Netherlands. *For. Ecol. Manage.* 376 (2016), 321–332. <https://doi.org/10.1016/j.foreco.2016.06.032>.
- Ma, F., Zuo, Z., Yang, L., Li, D., Wang, H., Li, F., Fan, S., Liu, C., Yu, D., 2022. The effect of trait-based diversity on productivity results mainly from intraspecific trait variability in the macrophyte community. *Freshw. Biol.* 67 (7), 1137–1149. <https://doi.org/10.1111/fwb.13906>.
- Margalef, R., 1969. Diversity and stability: a practical proposal and a model of interdependence. *22* (1969), 25–37.
- McEwan, R.W., Lin, Y.C., Sun, I.F., Hsieh, C.F., Su, S.H., Chang, L.W., Song, G.Z.M., Wang, H.H., Hwang, J.L., Lin, K.C., 2011. Topographic and biotic regulation of aboveground carbon storage in subtropical broad-leaved forests of Taiwan. *For. Ecol. Manage.* 262 (9), 1817–1825. <https://doi.org/10.1016/j.foreco.2011.07.028>.
- Muscarella, R., Lohbeck, M., Martínez-Ramos, M., Poorter, L., Enrique Rodríguez-Velázquez, J., van Breugel, M., Bongers, F., 2017. Demographic drivers of functional composition dynamics. *Ecology* 98 (11), 2743–2750. <https://doi.org/10.1002/ecy.1990>.
- Ordoñez, J.C., Van Bodegom, P.M., Witte, J.P.M., Wright, I.J., Reich, P.B., Aerts, R., 2009. A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Glob. Ecol. Biogeogr.* 18 (2), 137–149. <https://doi.org/10.1111/j.1466-8238.2008.00441.x>.
- Peng, W.X., Song, T.Q., Zeng, F.P., Wang, K.L., Du, H., Lu, S.Y., 2012. Relationships between woody plants and environmental factors in karst mixed evergreen-deciduous broadleaf forest, southwest China. *J. Food Agric. Environ.* 10 (1), 890–896. <https://doi.org/10.1016/j.jfoec.2020.118367>.
- Perez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguierry, P., Bret-Harte, M., Cornwell, W., Craine, J., Gurvich, D., 2013. New handbook for standardised measurement of plant functional traits worldwide. *Aust. Bot.* 167–234. <https://doi.org/10.1071/BT12225.CO>.
- Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J., Villar, R., 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytol.* 182 (3), 565–588. <https://doi.org/10.1111/j.1469-8137.2009.02830.x>.
- Pringle, E.G., Adams, R.I., Broadbent, E., Busby, P.E., Donatti, C.I., Kurten, E.L., Renton, K., Dirzo, R., 2011. Distinct Leaf-trait Syndromes of Evergreen and Deciduous Trees in a Seasonally Dry Tropical Forest. *Biotropica* 43 (3), 299–308. <https://doi.org/10.1111/j.1744-7429.2010.00697.x>.
- Qin, J., Shangguan, Z., 2019. Effects of forest types on leaf functional traits and their interrelationships of *Pinus massoniana* coniferous and broad-leaved mixed forests in the subtropical mountain. Southeastern China. *Ecol. Evol.* 9 (12), 6922–6932. <https://doi.org/10.1002/ece3.5259>.
- Reich, P.B., 2014. The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto. *J. Ecol.* 102 (2), 275–301. <https://doi.org/10.1111/1365-2745.12211>.
- Reich, P.B., Walters, M.B., Ellsworth, D.S., 1992. Leaf Life-Span in Relation to Leaf, Plant, and Stand Characteristics among Diverse Ecosystems. *Ecol. Monogr.* 62 (3), 365–392. <https://doi.org/10.2307/2937116>.
- Rong, Q., Liu, J., Cai, Y., Lu, Z., Zhao, Z., Yue, W., and Xia, J., 2015. Leaf carbon, nitrogen and phosphorus stoichiometry of *Tamarix chinensis* Lour. in the Laizhou Bay coastal wetland, China. *Ecological Engineering* 76 (2015), 57–65. <https://doi.org/10.1016/j.ecoleng.2014.03.002>.
- Rozendaal, D. M. A., Bongers, F., Aide, T. M., Alvarez Dávila, E., Ascarrunz, N., Balvanera, P., Becknell, J. M., Bentos, T. V., Brancalion, P. H. S., Cabral, G. A. L., Calvo Rodríguez, S., Chave, J., César, R. G., Chazdon, R. L., Condit, R., Dalling, J.

- S., de Almeida Cortez, J. S., de Jong, B., de Oliveira, A., Denslow, J. S., Dent, D. H., DeWalt, S. J., Dupuy, J. M., Durán, S. M., Dutrieux, L. P., Espírito Santo, M. M., Fandino, M. C., Fernandes, G. W., Finegan, B., García, H., Gonzalez, N., Moser, V. G., Hall, J. S., Hernández Stefanoni, J. L., Hubbell, S., Jakovac, C. C., Hernández, A. J., Junqueira, A. B., Kennard, D., Larpin, D., Letcher, S. G., Licona, J. C., Lebrija Trejos, E., Marin Spiotta, E., Martínez Ramos, M., Massoca, P. E. S., Meave, J. A., Mesquita, R. C. G., Mora, F., Müller, S. C., Muñoz, R., de Oliveira Neto, S. N., Norden, N., Nunes, Y. R. F., Ochoa Gaona, S., Ortiz Malavassi, E., Ostertag, R., Peña Claros, M., Pérez García, E. A., Piotto, D., Powers, J. S., Aguilar Cano, J., Rodríguez Buritica, S., Rodríguez Velázquez, J., Romero Romero, M. A., Ruíz, J., Sanchez Azofeifa, A., de Almeida, A. S., Silver, W. L., Schwartz, N. B., Thomas, W. W., Toledo, M., Uriarte, M., de Sá Sampaio, E. V., van Breugel, M., van der Wal, H., Martins, S. V., Veloso, M. D. M., Vester, H. F. M., Vicentini, A., Vieira, I. C. G., Villa, P., Williamson, G. B., Zanini, K. J., Zimmerman, J., and Poorter, L., 2019. Biodiversity recovery of Neotropical secondary forests. *Sci. Adv.* 5 (3), eaau3114. Doi: 10.1126/sciadv.aau3114.
- Schulze, E.-D., Kelliher, F.M., Körner, C., Lloyd, J., Leuning, R., 1994. Relationships among Maximum Stomatal Conductance, Ecosystem Surface Conductance, Carbon Assimilation Rate, and Plant Nitrogen Nutrition: A Global Ecology Scaling Exercise. *Annu. Rev. Ecol. Syst.* 25 (1), 629–662. <https://doi.org/10.1146/annurev.es.25.110194.003213>.
- Shen, K., Cornelissen, J.H.C., Wang, Y., Wu, C., He, Y., Ou, J., Tan, Q., Xia, T., Kang, L., Guo, Y., 2020. AM fungi alleviate phosphorus limitation and enhance nutrient competitiveness of invasive plants via mycorrhizal networks in karst areas. *Front. Ecol. Evol.* 8 (2020), 125. <https://doi.org/10.3389/fevo.2020.00125>.
- Small, E., 1972. Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. *Can. J. Bot.* 50 (11), 2227–2233. <https://doi.org/10.1139/b72-289>.
- Song, G., Wang, J., Han, T., Wang, Q., Ren, H., Zhu, H., Wen, X., Hui, D., 2019. Changes in plant functional traits and their relationships with environmental factors along an urban-rural gradient in Guangzhou, China. *Ecological Indicators* 106 (2019), 105558. <https://doi.org/10.1016/j.ecolind.2019.105558>.
- Su, W.-H., Shi, Z., Zhou, R., Zhao, Y.-J., Zhang, G.-F., 2015. The role of fire in the Central Yunnan Plateau ecosystem, southwestern China. *Forest Ecol Manag* 356 (2015), 22–30. <https://doi.org/10.1016/j.foreco.2015.05.015>.
- Sun, Y., Umer, M., Wu, P., Guo, Y., Ren, W., Han, X., Li, Q., Wu, B., Shen, K., Xia, T., Zang, L., Wang, S., He, Y., 2022. Indigenous microorganisms offset the benefits of growth and nutrition regulated by inoculated arbuscular mycorrhizal fungi for four pioneer herbs in karst soil. *PLoS One* 17 (4), e0266526. <https://doi.org/10.1371/journal.pone.0266526>.
- Tomlinson, K.W., Poorter, L., Sterck, F.J., Borghetti, F., Ward, D., de Bie, S., van Langevelde, F., 2013. Leaf adaptations of evergreen and deciduous trees of semi-arid and humid savannas on three continents. *J. Ecol.* 101 (2), 430–440. <https://doi.org/10.1111/1365-2745.12056>.
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! *Oikos* 116 (5), 882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>.
- Wang, C., Zhou, J., Xiao, H., Liu, J., Wang, L., 2017. Variations in leaf functional traits among plant species grouped by growth and leaf types in Zhenjiang, China. *J. Forestry Res.* 28 (2), 241–248. <https://doi.org/10.1007/s11676-016-0290-6>.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., Wright, I.J., 2002. Plant Ecological Strategies: Some Leading Dimensions of Variation Between Species. *Annu. Rev. Ecol. Systemat.* 33 (1), 125–159. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150452>.
- Wright, S.J., Kitajima, K., Kraft, N.J., Reich, P.B., Wright, I.J., Bunker, D.E., Condit, R., Dalling, J.W., Davies, S.J., Díaz, S., 2010. Functional traits and the growth–mortality trade-off in tropical trees. *Ecology* 91 (12), 3664–3674. <https://doi.org/10.1890/09-2335.1>.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H., Diemer, M., 2004. The worldwide leaf economics spectrum. *Nature* 428 (6985), 821–827. <https://doi.org/10.1038/nature02403>.
- Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Garnier, E., Hikosaka, K., Lamont, B.B., Lee, W., Oleksyn, J., Osada, N., Poorter, H., Villar, R., Warton, D.I., Westoby, M., 2005. Assessing the generality of global leaf trait relationships. *New Phytol.* 166 (2), 485–496. <https://doi.org/10.1111/j.1469-8137.2005.01349.x>.
- Yao, L., Ding, Y., Yao, L., Ai, X., Zang, R., 2020. Trait Gradient Analysis for Evergreen and Deciduous Species in a Subtropical Forest. *Forests* 11 (4), 364. <https://doi.org/10.3390/f11040364>.
- Ye, Y., Kitayama, K., Onoda, Y., 2022. A cost–benefit analysis of leaf carbon economy with consideration of seasonal changes in leaf traits for sympatric deciduous and evergreen congeners: implications for their coexistence. *New Phytol.* 234 (3), 1047–1058. <https://doi.org/10.1111/nph.18022>.
- Zhang, S., Bai, X., Zhao, C., Tan, Q., Luo, G., Cao, Y., Deng, Y., Li, Q., Li, C., Wu, L., Wang, J., Chen, F., Xi, H., Ran, C., Liu, M., 2022b. Limitations of soil moisture and formation rate on vegetation growth in karst areas. *Sci. Total Environ.* 810 (2022), 151209. <https://doi.org/10.1016/j.scitotenv.2021.151209>.
- Zhang, C., Qi, X., Wang, K., Zhang, M., Yue, Y., 2017. The application of geospatial techniques in monitoring karst vegetation recovery in southwest China: A review. *Progr. Phys. Geogr.: Earth and Environment* 41 (4), 450–477. <https://doi.org/10.1177/0309133317714246>.
- Zhang, H., Yang, Q., Zhou, D., Xu, W., Gao, J., Wang, Z., 2021. How evergreen and deciduous trees coexist during secondary forest succession: Insights into forest restoration mechanisms in Chinese subtropical forest. *Glob. Ecol. Conserv.* 25 (2021), e01418.
- Zhang, C., Zeng, F., Zeng, Z., Du, H., Su, L., Zhang, L., Lu, M., Zhang, H., 2022a. Impact of Selected Environmental Factors on Variation in Leaf and Branch Traits on Endangered Karst Woody Plants of Southwest China. *Forests* 13 (7), 1080. <https://doi.org/10.3390/f13071080>.
- Zhang, Y., 2011. Physicochemical analysis of soil, water and plant. *China Forestry Publishing House* 638 (2011), 222–232.