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Plant Functional Trait Responses to Dolomite and Limestone Karst Forests in Southwest China

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Abstract: Southwest China is distributed with the largest area of limestone and dolomite karst landscapes in the world, and its ecological environment is very fragile; the problem of rock desertification is particularly prominent. Karst lithological differences make habitats and soil heterogeneity more complex, and vegetation has developed certain morphological and physiological structural characteristics to adapt to these special environments, which will most likely lead to differentiation in vegetation functional characteristics, such as seed size, wood density, life type and flowering time, thus affecting the number and growth of seedlings and young trees and the future succession potential of forest stands in karst-vegetation restoration. Therefore, it is important to understand the differences in species composition and the functional characteristics of dolomite and limestone karst forests. Over a 2-year period, we investigated a total of 3170 individuals from 123 species and analyzed the relationship between the species compositions and the functional characteristics of two karst-forest areas with different lithology (i.e., limestone and dolomite karst). It was found that the average number of species with medium-diameter seeds and medium wood density in dolomite plots was obviously greater than the average number of species in limestone plots, but this reached no significant difference. However, with the gradual restoration of each forest, the height and carbon sequestration capacity of the trees began to diverge, with the relative abundance of species with tall trees and high wood density being significantly higher in limestone plots than in dolomite plots. The species richness of evergreen trees was significantly higher in the limestone plots than in the dolomite plots. There was no significant difference in the relative species richness of flowering plants in the two karst-forest areas during spring–summer and winter–spring seasons; however, the species richness of flowering plants in the limestone karst forests was significantly higher than that of flowering plants in the dolomite karst forests during summer and autumn seasons. These significant traits were very closely related to the species richness of the understory plants. Further insight into the temporal aspects of karst-forest succession is needed to grasp how functional traits affect the restorations of different lithological karst forests to their primary states.

Keywords: functional traits; wood density; forest succession; karst; rocky desertification

1. Introduction

China has an approximate karst area of 3.44 million km², which accounts for 15.6% of all of the karst areas in the world [1]. Karst rocky desertification has long been regarded as a major environmental problem that has significantly limited social and economic development in Southwest China and has a powerful influence on the 1.7 million people in the regions [1]. Some of the most typical characteristics of karst areas are well-developed surface and subsurface double-layered karst landscapes and high habitat heterogeneity. Differences in topography, soil, climate and other environmental factors in the region directly affect the vegetation-succession process and tree-species distribution pattern [2]. The

ecology of karst-forest trees is mainly impacted by hydrological, edaphic and topographic factors that exhibit fine spatial heterogeneity [3].

Subtropical evergreen–deciduous broadleaved forests are the dominant forest type in the subtropical region of Southwest China. Their species have obvious morphological and functional traits, which are optimal materials for studying the mechanisms of species coexistence and functional-feature change [4,5]. Tree species have shown nonrandom distributions associated with soil conditions, and these distribution patters have already been verified in a 15 ha plot in Southwest China [6]. Previous papers have shown that deciduous tree species are more common on more gradual slopes in tropical karst forests [7,8], but tall evergreen tree species are common on lower slopes with deeper soils and more moisture [3]. During the process of soil formation, lithology plays an important role in many processes of vegetation succession [9]. For example, soil C and N contents may increase significantly from cropland to forest in dolomite, but they may vary insignificantly among successional periods in limestone [10]. Distribution of dominant tree species is obviously related to total phosphorus, nitrogen and potassium contents in soil [11–13].

Plants tend to respond to external environmental variation by changing their own physiological or morphological structures. In the long-term evolutionary process, habitat heterogeneity enhances the stability of ecosystems by increasing plant-community diversity [14]. Hence, specific morphological and physiological characteristics are developed that are adapted to the habitat, leading to a high diversity of functional traits. However, there are significant differences between dolomite and limestone in terms of karst morphology, degree of rock fracture development, soil thickness and water-holding capacity of weathered crust, which regulate spatial allocation of regional soil and water resources and the geochemical cycling process of nutrients and thus affect vegetation growth and functional-trait variation [15,16]. The numbers of dominant species in the limestone-forest arbor layer and in the shrub layer had no overlap at all, but the number of species pairs was 14 higher than that in the dolomite forest. Forests in pure limestone regions are relatively rich in species of trees and shrubs [17].

Species differences have a significant impact on wood density, which can have several variations between species [18]. For example, coniferous wood is usually loose and soft, while broadleaf wood is mostly dense and hard. Some functional attributions of trees, such as growth rate, age, structure, height, etc., also have an effect on wood density [19]. A study of 12 karst tree species in karst forests found that the wood density of evergreen trees was significantly higher than that of deciduous trees [20,21]. In particular, environmental factors can affect the wood density of plants by changing hydrothermal conditions in karst areas where water and nutrients are highly susceptible to loss. Wood density exhibits uniform distribution in relation to habitat types that range from valleys to peaks. Tree species in karst hilltops with little soil substrate display higher tissue density than that of species grown in valleys that maintain more soil [22].

The flowering time of a plant is the most important stage in its life history. Flowering time is closely linked to nutritional and reproductive growth, and variations in plant flowering can limit or promote plant-species establishment and thus community structure and functional traits [23,24]. The flowering time of perennial plants is one of the most widely used indicators for production studies [25]. In karst regions, the biological processes that lead to flowering might be influenced by weathering of rock derivation from climate variation. A previous study suggested that the mean trend of flowering duration in West China was larger than that in East China, and the extending trends for shrub species were found to be more significant than those for tree species [26]. However, some research suggests that there is no clear conclusion about the effect of environmental changes on floral phenology [27–29].

Currently, many studies focus on climate and soil to influence plant growth, while lithological control of plant growth is often neglected [30–34]. However, tree and shrub species composition and biodiversity under pure limestone and dolomite conditions were significantly different when Maolan karst primary forest was studied [35]. Therefore, for

vegetation restoration projects in different lithologic karst areas, how to select tree species should not only consider plant productivity, survival rate and site conditions but also the future ecological function of these restored forests. For example, a previous study showed that seeds that rely on small animals or wind dispersal were more abundant in planted forests than in mature natural forests [36].

Accordingly, as plant functional traits such as seed type, wood density and flowering time are some of the most widely used indicators for changes in environmental factors, this study aims to evaluate these functional traits and their influence on tree-species richness, composition and distribution in dolomite and limestone karst forests in Southwest China.

2. Materials and Methods

2.1. Study Sites

This study focused on two karst sites: Shibing (26°57′42.4558″ N, 108°14′45.63919″ E) and Liping (109°7′18.15″ N, 25°59′15.08″ E) (Figure 1). These study sites are located about 400 km apart and were classified based on the lithology in the Southwest China karst region, of which the Shibing karst area was dominated by dolomite and Liping dominated by limestone. In these two sites, the representative vegetation was subtropical evergreen deciduous broadleaf or limestone evergreen broadleaf. The dominant tree species in the community are Fagaceae *Quercus fabri* Hance and *Q. acutissima* Carr., Anacardiaceae *Choerospondias axillaris* (Roxb.) B. L. Burtt & A. W. Hill, Theaceae *Schima superba* Gardn. et Champ., Juglandaceae *Platycarya strobilacea* Sieb. et Zucc., etc. In the forest understory, the common species are mainly Lauraceae *Lindera glauca* (Sieb. et Zucc.) Bl., Hamamelidaceae *Loropetalum chinense* (R. Br.) Oliver, Oleaceae *Ligustrum quihoui* Carr., etc.
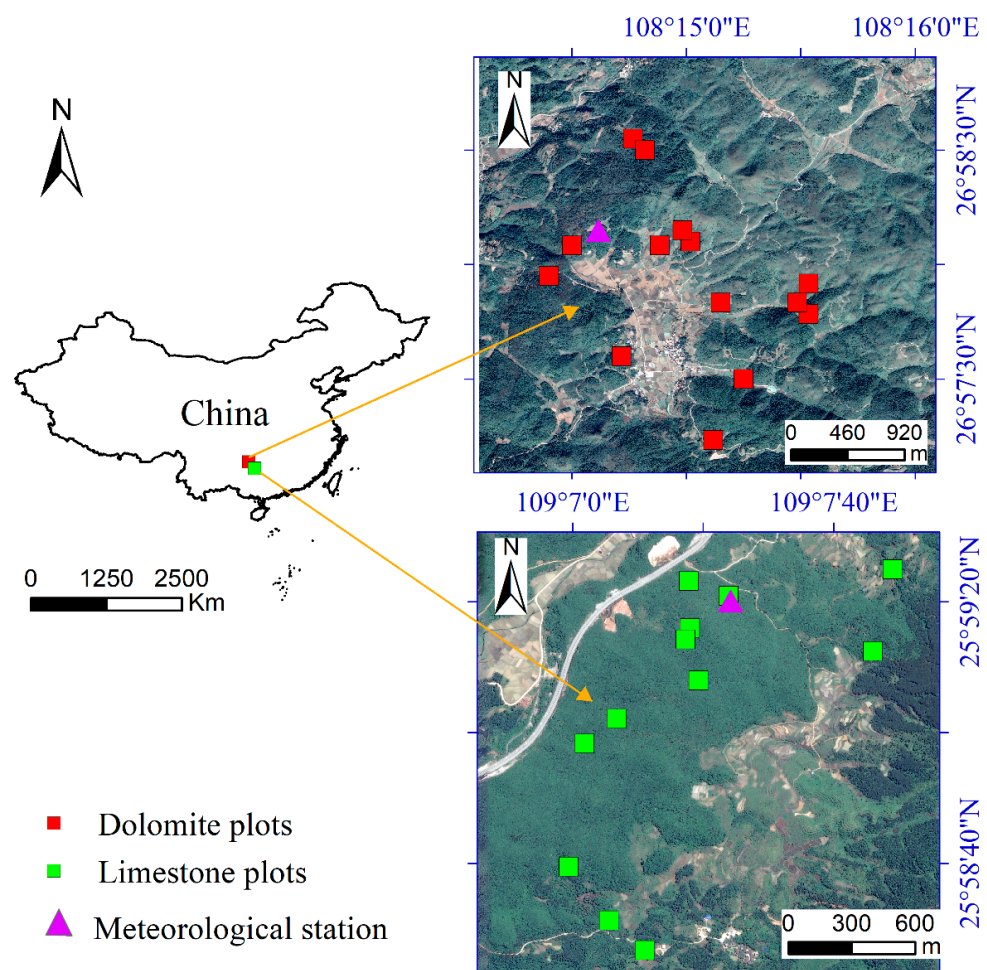

Figure 1. The locations of dolomite and limestone karst-forest plots in Guizhou Province, Southwest China.

Rolling topography is a common feature; elevation ranges from 500 m to 850 m above sea level. The soil types were mainly limestone and dolomite, weathered to form limestone soils. This area is characterized by a typical subtropical monsoon climate (a warm, rainy season and a cool, dry season). Meteorological data (such as air temperature, extreme temperature, precipitation, etc.) were measured with a ground meteorological station in each of our study sites (Figure 1). There was an average annual temperature of 16.3 °C. The annual precipitation was approximately 1182.4 mm, and the mean number of wet days (daily precipitation > 2 mm) was 223 days of each year. The monthly minimum and maximum temperature averaged 1.7 °C (January) and 32.5 °C (July), respectively.

2.2. Plots Survey and Soil Samples

A total of 18 sample plots in the Shibing dolomite karst forests were investigated; 4 of those plots (data not shown) were artificial-pure-forest plots and therefore not included in the analysis. In the Liping limestone karst forests, 12 sample plots were investigated. All sample plots were 20 m × 20 m in size and were randomly selected between 2017 and 2019. The field work was performed in July and August. In each plot, tree species with diameters more than or equal to 3 cm at breast height (DBH) had their diameters recorded to 0.1 cm using a tape and were surveyed as tree species. Woody species that were less than 3 cm DBH and shrubs were surveyed as seedlings or saplings. In these sample plots, all woody plants were systematically recorded to the species, with an exception of a few that were identified to the genus, since it was difficult to identify them to the species in the field without flowers or fruits.

In each of these plots, four soil samples were collected from the four-10 × 10 m-quadrat central area of each plot, and then these four soil samples were mixed to build one composite sample in each plot in this field work. All soil samples were naturally air-dried and sieved with 2 mm mesh for physical and chemical analysis of the soil [37]. The soil organic carbon concentration (SOC) was determined via wet oxidation using the dichromate redox colorimetric method [10]. Total nitrogen (TN) was measured based on the Kjeldahl method. Total phosphorus (TP) was measured using an ultraviolet spectrophotometer according to the Mo-Sb colorimetric method [38]. Total potassium (TK) was measured with a sodium-hydroxide fusion–atomic absorption method.

2.3. Functional Trait Selection

To analyze the responses of the functional traits of dolomite and limestone karst in Southwest China, functional data for our 123 species were compiled from the published literature. Five functional traits were selected for this analysis: (1) Species were categorized based on seed size, using classes, as having small width (width less than or equal to 6 mm), medium width (6–20 mm) or large width (more than or equal to 20 mm); (2) Species were categorized based on wood density, using classes modified from [39], as having low density (less than or equal to 0.4 g/cm^3), medium density (0.4–0.6 g/cm^3) or high density (more than 0.6 g/cm^3); (3) Species were classified into two life forms: deciduous and evergreen; (4) Species flowering times were classified into three categories: March to June, July to September and October to next year's February; (5) Species were classified by their maximum height, using classes modified from [39], as understory trees (height less than 10 m), sub-canopy trees (10–20 m) or canopy trees (height more than 20 m).

2.4. Data Analysis and Statistics

Species richness provides a useful measure of diversity while species-abundance models describe distribution of species abundance. Species richness is correlated with sampling area. A species accumulation curve (SAC) was used to evaluate the adequacy of sampling efforts and to compare the richness between the limestone karst forests and the dolomite karst forests [40]. Species richness was computed as follows (more details can be seen in [7]):

$$S_{obs} = \sum_{i=1}^{H} S_i$$

where S_{obs} represents the number of observed species in the pooled plots and S_i stands for the number of species found in exactly i plots of the empirical sample set, which has a total of H samples [7,8].

Observed species richness and its standard deviation were calculated with EstimateS ver. 9.1 for Windows (accessed on 1 September 2022 at: https://www.robertkcolwell.org/pages/1407-estimates) and 100 random iterations from the data [7,8]. Species abundance was computed across a summation of total species percentage cover in each sample site.

A negative binominal GLM (log link), with seed size, wood density, life form, flower time and tree height as fixed effects, was carried out to reflect the significant functional traits associated with species abundance [39]. To explain species-abundance variation in dolomite and limestone karst both between and within functional trait groups, estimated marginal means were carried out for each functional group. Comparisons of the mean abundance in groups for each functional trait were calculated using sequential Bonferroni pairwise tests. To compare the differences between dolomite and limestone karst forests, relative abundances of understory woody species (including shrubs, seedlings and saplings) with different functional trait groups (seed size, wood density, life form, blooming stage and tree height) were calculated using Mann–Whitney U tests [39]. Mann–Whitney U tests were also employed for the effects of lithology (i.e., karst dolomite and karst limestone) on soil properties. SPSS 25.0 (SPSS Inc., Chicago, IL, USA) and OriginPro 2018 (Originlab Inc., Northampton, MA, USA) for Windows were used to perform statistical analysis and draw figures, respectively.

3. Results

3.1. Species Diversity and Soil Characteristics

Between 2018 and 2019, 3170 individuals from 123 tree species were identified in dolomite and limestone karst forests. For all classes, species accumulation curves (SACs) showed that community species richness was sufficiently captured within the scope of the investigation and hence was sufficient enough to estimate community richness related to the number of sampling plots (Figure 2). However, the species abundance of the two karst forest areas was extremely uneven (Figure 3), with the 12 and 10 most abundant species, respectively, comprising more than 60 percent of all of the individual plants in the dolomite and limestone karst forests, respectively (the 20 most abundant tree species can be seen in Supplementary Materials Tables S1 and S2). Hence, the majority of species had low abundances across the two karst forest areas, with the 40 and 52 least abundant species combined contributing only 10 percent of the dolomite and limestone karst forests, which showed that the average abundances at the individual scale were relatively uniform, with negligible influence. However, it is worth noting that the response of the species richness of the total, tree-species and understory plants differed significantly between the dolomite and limestone karst forest areas ($p < 0.01$).
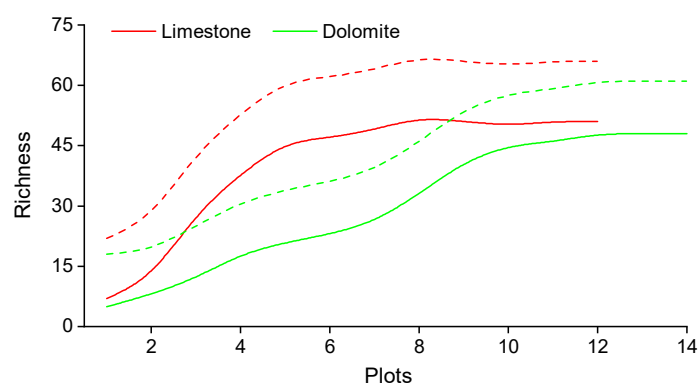

Figure 2. Species accumulation curves (SACs) relating total species richness to dolomite and limestone karst-forest sampling-plot treatment. The solid line represents the SAC and the dashed line represents one positive standard deviation.
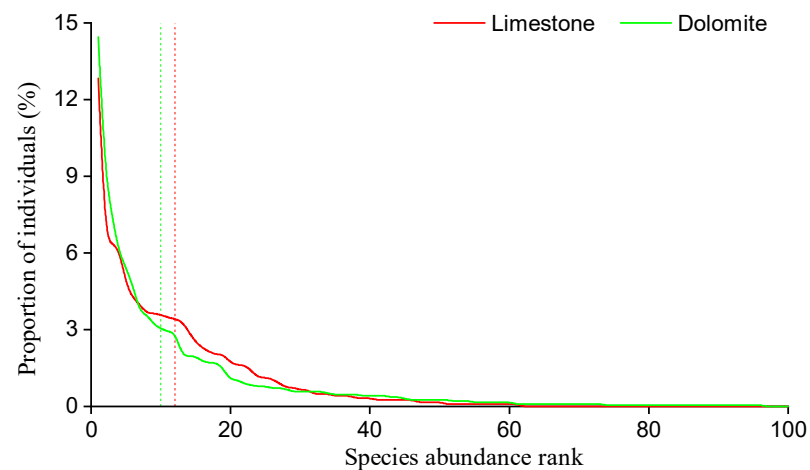
Figure 3. A rank–abundance curve of all tree species (124 species, 36 common species) studied in dolomite (n = 96 species) and limestone (n = 61 species) karst forests in Southwest China from 2017 to 2019. The most abundantly planted species account for >60% of plants and are displayed with the dashed line. The 20 most abundant tree species can be found in the Supplementary Materials.

Differences in soil nutrient contents, including total nitrogen (TN), total phosphorous (TP), total potassium (TK) and soil organic carbon (SOC) content, for the two karst forest areas are shown in Figure 4. In the dolomite and limestone karst plots, the soil pH values were 6.8 and 5.7, respectively (data not shown). In the secondary dolomite karst forests, the TN, the TP and the SOC in the soil were 18.2%, 220.0% and 57.5% higher than those in the secondary limestone karst forests, but the TK in the soil was 16% lower compared to that in the limestone plots (data not shown). However, there was no significant difference in the TN in the karst soil between the dolomite and limestone plots.
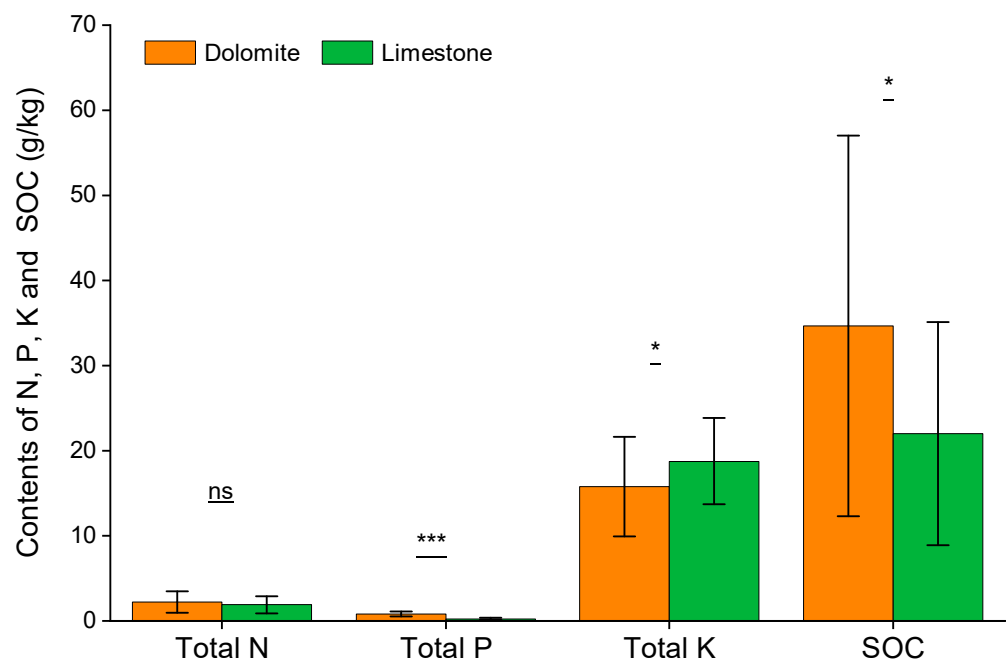

Figure 4. A comparison of total nitrogen (TN), total phosphorous (TP), total potassium (TK) and soil organic carbon (SOC) contents in soil from dolomite and limestone plots in Southwest China. Mann–Whitney U tests were used to examine differences in content of nitrogen, phosphorous, potassium and soil organic carbon in soil from 18 dolomite plots and 12 limestone plots. Each bar represents content mean ± standard deviation of the mean. The asterisks "***" and "*" represent the significance levels of 0.001 and 0.05, respectively, and "ns" represents nonsignificant levels.

3.2. Functional Trait Representation

Comparison of the composition of the individuals in the two karst-forest areas showed that woody species with small and large seeds had significantly higher abundances in the limestone karst forests than in the dolomite karst forests, but reached no statistical significance (Figure 5). Inversely, medium-seeded species abundance was obviously higher in the dolomite karst plots than in the limestone karst plots and reached a extremely significant difference.
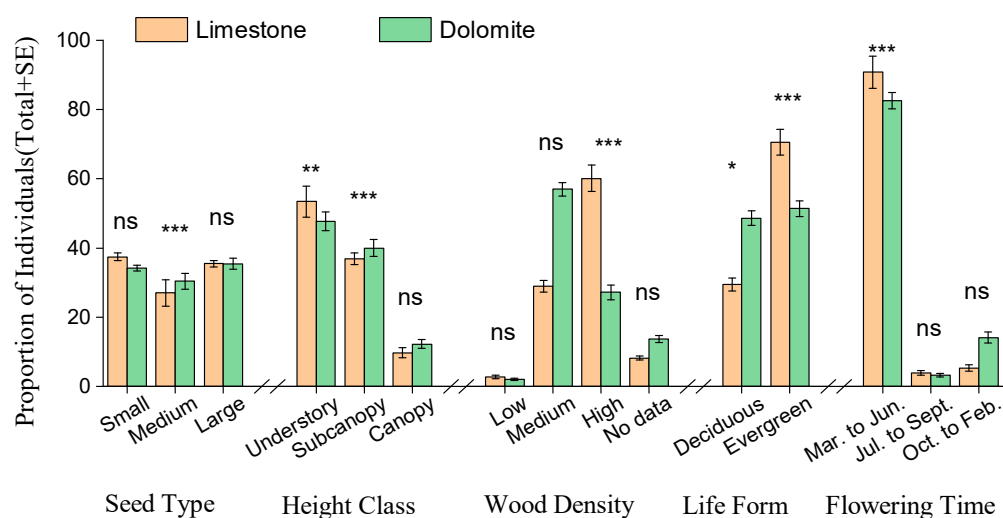

Figure 5. A comparison of the representation of functional traits in tree species (DBH $\geq$ 3 cm) from dolomite and limestone plots in Southwest China. Mann–Whitney U tests were used to examine proportion data of tree species from 14 dolomite- and 12 limestone-karst-forest plots. Each bar represents total proportion of individuals $\pm$ standard error of the mean. The asterisks "***", "**" and "*" represent the significance levels of 0.001, 0.01 and 0.05, respectively, and "ns" represents nonsignificant levels.

To assess the community structure and the carbon sink potential of the two karst forest areas, the proportions of all individuals from different tree-height classes and wood-density-classed species were also compared. There were significant differences in the relative abundances of the understory- and canopy-class species between the limestone karst and dolomite karst forests, but no significant difference was found in all of the subcanopy. Similarly, the relative abundances of low- and high-wood-density species were significantly different between the dolomite-dominated karst and limestone-dominated karst forest areas, but those of medium wood density species were not.

To explore the vegetation-landscape and nectariferous-plant differences of the two karst regions, the representations of species from different life forms and the flowering times from the limestone and dolomite karst forests were recorded and compared (Figure 5). In the two karst regions, the mean abundance of deciduous species had no significant difference, but the proportion of individuals from deciduous species was obviously higher in the dolomite-karst-forest plots than in the limestone-karst-forest plots. However, the average abundance of evergreen species was significantly higher in the limestone karst forests than in the dolomite karst forests. Therefore, the kart forests dominated by limestone looked greener than the karst forests dominated by dolomite in winter.

It is worth noting that many plant species bloom from March to June in the two karst regions, but there was no significant difference. From July to September, the mean abundance of flowering plants was extremely higher in the limestone-dominated karst forests than in the dolomite-dominated karst forests.

3.3. Functional Trait Abundance

For both limestone and dolomite karst secondary forest seedling and sapling species, high class, flowering time, wood density and seed size were significantly associated with abundance (Figure 6), but there was no statistically significant relationship between life form (i.e., evergreen and deciduous species) and mean abundance (Figure 6d,i). Understory and subcanopy species showed higher mean abundance than those of canopy species in both the limestone- and dolomite-dominated karst secondary forests, but the canopy species in the dolomite karst forests had higher abundance than those canopy species in the limestone karst forests (Figure 6a,f). Woody species with a blooming stage from March to June had a higher average abundance than species with a blooming stage from July to next February, but the abundance for species with a blooming stage from October to next February in the dolomite karst forests was obviously higher than that in the limestone karst forests (Figure 6b,g). Interestingly, species with high wood density in limestone karst forests had the highest mean abundance, but species with low wood density had the lowest abundance in the two karst regions. Medium-seed-size seedling species had a higher average abundance than that of low- and large-seed-size species in the two areas (Figure 6e,j). In the two karst regions, the average abundance in the limestone karst forests was generally slightly higher than in the dolomite karst forests.
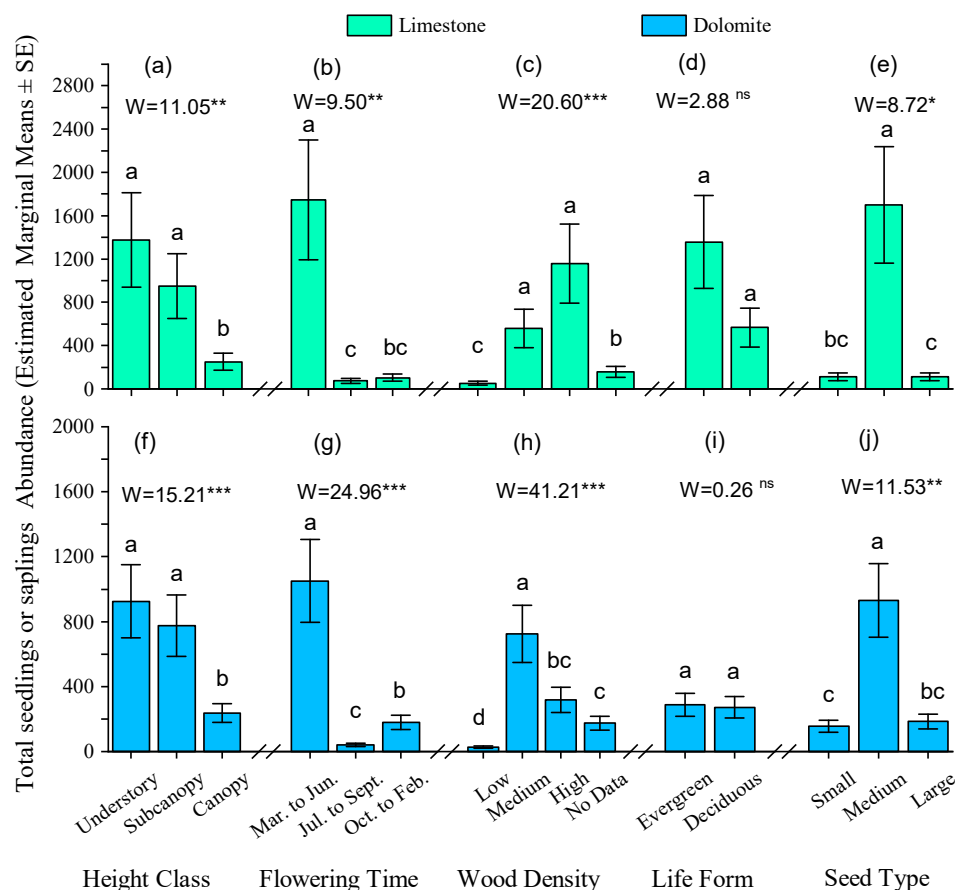

Figure 6. A comparison of the relative abundances of seedlings or saplings (all woody plants or shrubs DBH ≤ 3 cm) and their functional traits, (**a**,**f**) tree height class, (**b**,**g**) flowering time, (**c**,**h**) wood density, (**d**,**i**) life form and (**e**,**j**) seed type, from dolomite and limestone plots in Southwest China. Estimated marginal means among groups were computed from abundance data from the two karst sites using a negative binomial GLM (log link) with the Wald chi-square Stata (W). Each bar represents estimated marginal mean ± standard error of the mean. Bars with different letters stand for significant differences based on Bonferroni pairwise tests. The asterisks "***", "**" and "*" represent the significance levels of 0.001, 0.01 and 0.05, respectively, and "ns" represents nonsignificant levels.

4. Discussion

In this study, we described the vegetation of karst forests with different lithologies and analyzed their functional diversity and compositions. These differences are, without question, associated with lithological character across regions in conjunction with local forest-stand disturbance history (e.g., natural forests to secondary forests after firewood gathering for livelihood) [41]. In our study area, the functional trait responses to the dolomite and limestone karst forests showed statistical differences because many species exhibit distributions in relation to special topographic positions. Early logging may directly or indirectly influence regional species biodiversity in forested karst landscapes [42], especially in the understories. This is why total seedlings or saplings were higher than total individuals due to logging in the two karst forest areas. Interestingly, litter production is closely associated with the tree species that are most strongly driven by structural attributes and stand biodiversity [43]. Therefore, secondary forest stands dominated by deciduous tree species can accumulate large amounts of litter over a short term, which in turn will promote niche differentiation and thus increase the biodiversity in the lower locations of the karst areas, where moisture is easily preserved.

Trees with smaller species abundance and higher aggregation have stronger density dependence [44]. Evergreen plants in karst areas usually adopt a conservative water-use strategy with larger wood density and lower water-conduction and photosynthesis rates, but have higher water-use efficiency and stronger abilities to maintain expansion and resist cavitation embolism. Hence, the physiological functions of the leaves and branches can be maintained under water deficit conditions [45,46].

However, deciduous plants tend to adopt a risky water-use strategy with small wood density and large xylem ducts, resulting in high hydraulic conductivity and photosynthetic capacity to compensate for the loss of carbon in the dry season through rapid growth in the rainy season [47,48].

In present study, the species richness of the two karst forest areas differed significantly as wood density increased with higher tree height. There are two possible reasons for this difference: one is that trees actively increase their wood densities to adapt to increased pressure on their trunks as they grow, and the other is that as the trees grow, the trunks are subjected to greater pressure, which causes tree cells to become more compact and some gaps to be filled by compression, so the trees passively increase their wood density. As such, some young trees may need more light and rainfall to reach the canopy in a short period of time through rapid growth, so differences in nutrient content inevitably lead to differences in seedling-species richness; however, as trees grow, especially when they reach medium height, either wood density is not sensitive enough to hydrothermal conditions or environmental factors are not the dominant factors in wood-density changes, so the tree-species individuals of the two karst forest areas had no significant difference. Thus, in limestone karst forests, where the number of individuals of evergreen species is dominant, the heights of the largest trees (i.e., the canopy) and the species richness of high wood density are both significantly higher than in dolomite karst forests.

The relationship between rock type and vegetation has been recognized for a long time. Some previous studies from South Spain have shown that ridges in dolomite areas, especially on the southern slopes or when rocks are very fragmented, are more likely to grow vegetation, but other aspects of the functional characteristics of vegetation are not significantly different from those of limestone areas [49]. This is mainly because dolomite soil maintains lower soil moisture and higher magnesium content [50], and the proportion of local drought-tolerant plants is higher [49,51], which is very similar to the phenomenon we observed in this work.

A survey of tree species in a permanent 25-hectare limestone-karst-forest plot in the Mulun National Natural Reserve showed that of the 93 species recorded in the species-rich subtropical karst forest, the smaller the species richness was and the higher the aggregation was, the stronger the density dependence was. The density dependence of evergreen species is stronger than that of deciduous and understory species [44]. Moreover, tree size

(including tree height and DBH) is one of the important driving factors that affects tree survival and is closely related to tree mortality [52]. No matter what kind of plants grow on a lithology, even closely related species often have ecological differences in community composition and functional traits [53]. Many functional traits, such as tree species diversity, tree size and life form, can significantly affect the seasonal productivity of a stand [43]. For example, dominance of deciduous tree species may lead to slow litter decomposition in karst habitats, which would provide favorable conditions for good adaptation to harsh habitats [54]. In line with our study, the richness of deciduous tree species in dolomite areas was significantly higher than that in limestone areas, providing stable nutrient support for the transition from seedlings or saplings to big trees.

In the humid subtropical karst region, natural secondary forests have a different growing-season length than that of planted forests because they present greater adaptation to hydraulic and edaphic characteristics [55]. Some studies have also shown that environmental factors such as annual rainfall, temperature and pH play a more pronounced effect on the functional traits of plants than the plants themselves play [56]. In soil, TP, SOC and pH were remarkably higher in the dolomite karst areas than in the limestone karst areas. Our results are consistent with the report in Shibing [34]. Development of shrubs or seedlings plays a critical role in the ecological-restoration stages of dolomite regions [34]. In dolomite karst forests, SOC and TN continuously increase with natural succession progresses [38]. As such, the rate of soil formation has an important influence on vegetation growth, and dolomite weathers faster than limestone; the difference between their weathering rates can also have different effects on the functional traits of plants.

Plant functional biodiversity not only significantly increases soil carbon, nitrogen, potassium, calcium, magnesium and cation exchange, but also plant nitrogen, potassium, calcium and magnesium, indicating a positive feedback relationship between plant diversity, plant productivity and soil fertility [33]. Therefore, stand characteristics (e.g., individuals per area) and environmental factors (e.g., lithology and soil nutrient contents) can significantly impact forest functional diversity, such as forest biomass or carbon storage [57]. It was further found that the higher the functional plant diversity was, the greater the nutrient accumulation in the ecosystem was, mainly because of the trade-off between different functional types of plants in terms of their ability to promote soil fertility.

5. Conclusions

Differences in functional characteristics of plants (seed type, wood density, tree height, life form, flowering period) in response to dolomite and limestone karst secondary natural forests were studied. In the limestone karst forests, tree species with small seeds or higher wood density, evergreens and trees that flower from March to June were substantially abundant compared to those of the dolomite karst forests. In analysis of the dolomite and limestone karst secondary forests, the species richness of the functional traits of the main tree species was significantly different. In addition, there were significant differences in species richness of other functional traits between the two karst forest areas, except for life form (evergreen or deciduous). The species richness of tall trees and high wood density in the limestone karst forests was significantly higher than that in the dolomite karst forests, which indicates that limestone karst forests have higher biomass and carbon storage at the current successional stage. However, the number of species with medium wood density, large seeds and flowering seedlings in autumn and winter in the dolomite karst secondary forests was significantly higher than that in the limestone karst forests. The number of species of seedlings and saplings with high wood density, evergreen life forms and medium-sized seeds in the limestone karst secondary forests was significantly higher than that in dolomite karst forests, indicating that limestone karst forests have great carbon-sequestration potential for future succession processes, and the appearance of these forests will be greener in winter and autumn. These findings can provide a critical reference for recovery of tree functional diversity in rock-desertification-restoration plantings. As such, vegetation restoration in dolomite karst areas is more suitable for selection of plants with

medium wood density and that flower in autumn and winter to cultivate more nectariferous plants, but in limestone karst areas, it is more suitable to select tall trees and species with high wood density to increase forest carbon storage. In summary, the differences in the responses of these functional traits to the two different karst forest areas may be closely related to the growth and survival statuses of seedlings and saplings during succession and the nutrient contents of different lithological soils; this requires long-term follow-up observation and further research.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f13122187/s1, Table S1: The 20 most abundant tree species investigated in Liping limestone karst plots in Southwest China. M_DBH represents mean diameter at breast height; M_TH represents mean tree height. Table S2: The 20 most abundant tree species investigated in Shibing dolomite karst plots in Southwest China. M_DBH represents mean diameter at breast height; M_TH represents mean tree height.

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