European Journal of Forest Research (2025) 144:255–265
https://doi.org/10.1007/s10342-024-01753-2

RESEARCH

Forest management has a mixed effect on understory biomass, but understory species diversity and stand structure are key

Shanshan Chen[1,2] · Shengjun Wu[2] · Jie Yang[1]

Received: 3 January 2023 / Revised: 20 November 2024 / Accepted: 4 December 2024 / Published online: 13 February 2025

Abstract

Comprehending the determinants of change in forest understory biomass (UB) offers a theoretical foundation for sustainable forest management. Our objective was to explore how different forest management practices (forest tending (FT), closing mountains for reforestation (CMRF), and clear-cutting (CC)) affect UB. We surveyed forest stand structure and understory vegetation and measured soil properties. Partial least squares structural equation modeling (PLS-SEM) was applied to explore how forest management, soil properties, stand structure, and understory species diversity influence UB. Our results indicated significant differences in UB under various management conditions, with FT resulting in the highest UB. Stand density, soil organic matter, total nitrogen, and total carbon were negatively correlated with UB, while species diversity was positively correlated with it. The explanatory degree of PLS-SEM results on UB was 61%, and forest management mainly affected UB by influencing stand structure (0.27, insignificant) and understory species diversity (-0.46, significant). Understory species diversity exerts a positive effect on UB, whereas stand structure has a negative effect. Our results highlights the importance of considering both understory species diversity and stand structure in future forest management strategies.

Keywords Forest management types · PLS-SEM · Species richness · Stand structure · Understory biomass

Introduction

Understory vegetation, a vital forest stratum, serves as an essential reservoir for maintaining forest biodiversity and carbon stock (Gilliam 2007; Kumar et al. 2018; Zhang et al. 2016a, b). Understory vegetation possesses a considerable capacity to enhance the carbon pool in the forms of understory vegetation biomass, forest floor, and soils due to its substantially high turnover rate (Landuyt et al. 2019). Additionally, understory vegetation has become an important buffer for reducing carbon emissions and alleviating climate change thanks to its strong capacity for community regeneration and carbon accumulation (Mitchard 2018). Therefore, maintaining sufficient understory vegetation and its biomass should be a key objective in forest ecosystem management.

The crucial role of understory plants in maintaining biodiversity, soil nutrient cycling, and carbon storage has gained increasing attention (Jin et al. 2022; Palmroth et al. 2019; Zhang et al. 2022), prompting a shift in forest management priorities from timber production to forest quality and ecological restoration (Zhou et al. 2016). At present, a primary goal of forest management is to maintain equilibrium between the upper canopy and the understory vegetation biomass. However, most studies have examined the impact of individual management practices on understory species diversity, stand structure, or soil properties (Hart et al. 2008; Li et al. 2020; Trentini et al. 2017; Zhang et al. 2022; Zhou et al. 2016), while the differential impacts of multiple forest management approaches on understory biomass (UB) remain unclear. Furthermore, there is a need for a relatively rigorous and comprehensive evaluation of current

Communicated by Tianjian Cao.

✉ Shengjun Wu
wsj@cigit.ac.cn

[1] CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, China

[2] State Key Laboratory of Water Security for Lake and Watershed, Chongqing Institute of Green and Intelligent Technology, Chinese Academy of Sciences, Chongqing 400714, China

forest management practices to identify optimal strategies that maximize UB.

Typically, forest management practices include clear-cutting, forest tending, thinning, and so on (Baran et al. 2020; Okudaa et al. 2003; Trentini et al. 2017), all of which affect the driving factors of dynamic changes in UB, such as stand structure and species diversity. Thinning or clear-cut harvesting can enhance understory species diversity by improving the full acquisition of available resources by plants (e.g., light, water, and nutrients). However, Baran et al. (2020) reported that forest thinning or clearcut harvesting may reduce species diversity in the understory due to the increased dominance of one or a few species. In contrast, forest tending by cutting and thinning dead wood can improve the complementary utilization of light, water, and nutrients in a limited space and thus improves stand canopy density and UB (Trentini et al. 2017).

Species diversity and stand structure, largely depended on forest management, are also important factors affecting UB (Sigurdsson et al. 2005; Su et al. 2021; Wang et al. 2018). Usually, high species diversity has high resource-use efficiency, suggesting that an increase in species diversity enhances UB (Gao et al. 2021), as different species contribute uniquely to ecosystem function (Barry et al. 2019). As a result of competition for resources such as light, nutrients, space, and water, an increase in stand structural indices will usually be lower than the UB. For example, the increase of stand density (Zangy et al. 2021), canopy closure which is defined as the proportion of sky hemisphere obscured by vegetation when viewed from a single point (Jennings et al. 1999), and diameter at breast hight (DBH) (Zhang et al. 2016a, b) have been shown to decrease UB. There is currently some controversy on the relationship between the stand structure and the UB (Silva Pedro et al. 2015; Thom and Seidl 2016). On one hand, stand structure (such as by reducing canopy closure) increases species diversity in the understory, thereby improving UB (Li et al. 2020). On the other hand, adjustments in stand structure, such as decreasing stand density, can improve light availability and temperature conditions in the understory, as well as promote soil nutrient cycling, all of which support plant growth (Terborgh et al. 2017). Previous studies have shown that forest management is conducive to species diversity increase (Rossman et al. 2018) and biomass accumulation (Wang et al. 2021). Whereas some studies revealed contrasting results on the impact of forest management on species diversity along with the negative (Wang et al. 2021), or neutral effects (Barefoot et al. 2019). Therefore, it is urgent to identify the key factors driving the effects of forest management on UB.

In this study, we divided forest management into three categories according to their nature and human interference level: clear-cutting (CC), forest tending (FT), and closing mountains for reforestation (CMRF). CC refers to the removal of understory vegetation to decrease resource competition between canopy trees and understory plants, and it has the strongest disturbance to the understory vegetation and only reduces stand density. The primary goal of CC is to promote the growth of tree species by reducing competition with understory species for resources. FT, a moderate disturbance, entails the selective removal and thinning of less desirable trees to improve the stand density and enhance both vertical and horizontal forest structure, thereby increasing forest quality and ecological benefits (Liu et al. 2015). CMRF represents a low-impact intervention, where the forest is enclosed, and human interference is prohibited (Liu et al. 2009), with the goal of promoting natural forest recovery and quality. Our objectives were (1) to identify the most beneficial forest management methods for understory biomass retention, and (2) to clarify the underlying mechanisms of how forest management affects UB.

Materials and methods

Study area

The study area, located in Chongqing in the Three Gorges Reservoir area (Fig. 1a), is characterized by a subtropical monsoon climate with high temperatures and abundant rainfall in summer. The average annual temperature and precipitation are 17.13 °C and 1130 mm, respectively.

Stand and site selection

To analyze the effect of different forest management practices on UB, the criteria for stand selection were as follows: first, the stand was monospecific, and second, only one forest management practice had been implemented within the last two decades. CMFT sites were plantations with even-aged, single-species stands, while FT and CC sites included a few tree species in uneven-aged stands. The CC plots are all afforestation sites where tree seedlings were planted at a density of 2,500 stems per hectare. In contrast, the FT and CMFT plots are natural secondary forests, established through natural regeneration of local tree species. Most ecological management practices were implemented around 2008, with a 2–3 year difference at some sample sites. The dominant tree species at the sampling sites include Chinese fir (*Cunninghamia lanceolata*), Masson pine (*Pinus massoniana*), Japanese larch (*Larix kaempferi*), and cypress (*Cupressus spp.*). To representatively and systematically select sample sites, forest survey data was collected from the local Forestry Bureau, and consultations were held with senior forestry practitioners. Based on these criteria,

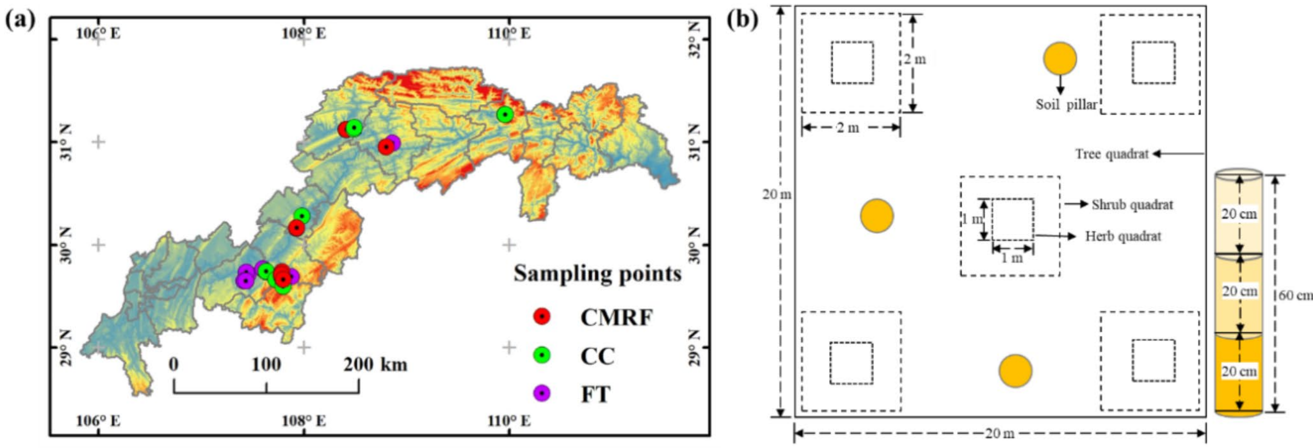

Fig. 1 The sampling sites (**a**) in the study area and diagram of vegetation quadrat survey and soil sampling (**b**)

28 suitable sample sites were selected. The average stand densities for CC, FT, and CMFT plots are 1,800, 1,425, and 1,225 stems per hectare, respectively.

Field measurements and biomass calculations

In each sampled stand, a 20 × 20 m plot was chosen to represent the stand. All plots were situated more than 100 m from forest edges adjacent to farmland and roads. Understory vegetation surveys were conducted in October 2020 and September 2021. The shrub layer refers to any woody plant species between 1.3 and 4.0 m in height (Hart and Chen 2008). The herbaceous layer contained seedlings of trees and shrubs (no more than 1.3 m in height) and all herbaceous vascular plants (Su et al. 2021). Consequently, some species appeared in both the herb and shrub layers. Within each plot, five 2 × 2 m shrub subplots and five 1 × 1 m herb subplots were set according to the plum shape (Fig. 1b), and herb subplots were set within the shrub subplots.

To assess the biomass of the herb and shrub layers, understory plants within each quadrat were harvested by cutting at the groundline and packing separately in labeled cotton gauze bags. The harvested samples were dried at 70 °C to a constant mass and then weighed. UB was calculated as the sum of the biomasses of the shrub and herb layers, with tree seedlings included in the shrub layer biomass.

Understory species diversity and stand structure

Species diversity indices were used to represent understory species diversity. Species richness refers to the total number of species observed in each quadrat, and Shannon's index was chosen to measure understory species diversity. Species diversity indices were calculated using the vegan package in R v.4.0 (Oksanen et al. 2019).

Stand structure variables in this study included stand density, diameter at breast height (DBH), and canopy closure. Stand density, indicating the strength of plant-plant interactions, was defined as the number of individual trees within a quadrat, with trees of DBH $\geq$ 5 cm recorded using a steel measuring ruler. Canopy closure represents the light conditions of the understory vegetation. We applied ocular (visual) estimation to measure the canopy closure, which is an inexpensive and conceptually simple procedure for estimating canopy closure (Paletto and Tosi 2009; Van Hees and Mead 2000). An expert operator assigned a cover index to each tree in a given quadrat, then calculated the average of these cover indices across the sample square, yielding a canopy closure value expressed as a percentage.

Soil properties measurements

For soil sampling within each plot, three sampling points were selected to dig the 0–60 cm soil profile to obtain a mixed sampling (Fig. 1b). All soil samples were naturally air-dried, manually cleaned of small stones and roots, and sieved through a 0.149 mm mesh. To obtain the soil nutrient status at each sampling sites, we measured total carbon, total nitrogen, total potassium, available potassium, total phosphorus, soil pH, soil organic matter, and soil texture. Total carbon and total nitrogen were measured using an elemental analyzer (Vario EL cube, Elementar, Langenselbold, Germany) (Ye et al. 2019). The content of total potassium and available potassium was detected using a flame photometer (PF6410, INESA, China) (Ren et al. 2020). Total phosphorus was measured using an ultraviolet photometer (UV-1750, Shimadzu, Japan) (Ren et al. 2020). Soil pH was measured in a 1:2.5 mixture of soil-water using a Mettler Toledo pH meter after shaking with deionized water. Soil organic matter was measured by the mass loss after hydrolysis in a Muffle furnace at 550 °C (Dean 1974). Soil texture was analyzed using a laser particle analyzer (Mastersizer 3000, Malvern Panalytical, UK).

Statistical analyses

A summary of biomass, understory species diversity, stand structure, and soil properties are provided in Table S1. One-way ANOVA was used to investigate the differences in understory species diversity, stand structure, soil properties, and biomass among FT, CMRF, and CC. Additionally, simple linear regression analysis was applied to assess the relationship between understory species diversity, stand structure, soil properties, and UB. Pearson correlations between variables are presented in Fig. S1.

Variance partitioning analysis was performed using the "varpart" function in the "vegan" package of the R. The pure effect and the shared effect of each factor were visualized using Wayne diagrams.

Partial least squares structural equation modeling (PLS-SEM) was used to evaluate multiple relationships among forest management, soil properties, understory species diversity, stand structure, and UB. PLS-SEM, a type of structural equation modeling, performs effectively with a limited number of observations, given the complexity of the model structure (Hair et al. 2017). We tested PLS-SEM based on the effects of forest management as a categorical variable on the predictors and UB. With this model structure, we also assessed the direct and indirect effects of predictors on response variables using the corresponding mediator(s). Several parameters were used to assess model effectiveness: loading values indicate the contribution of observed variables to latent variables, with higher values representing a stronger contribution; R^2(R-squared) assesses the fit of endogenous variables; with values above 0.3 considered acceptable; goodness of fit (GOF) evaluates overall model performance. Additionally, Dillon-Goldstein's rho (DG. rho) and average variance extracted (AVE) were seleceted to assess model reliability and validity (Liu et al. 2024). The PLS-SEM was performed using the *plspm* package, with all analyses conducted in R. 4.0 (R Core Team 2021).

Results

Understory biomass, understory species diversity, and stand structure under different forest management

UB, shrub layer biomass, and herb layer biomass showed significant differences among the three treatments (Fig. 2). Under FT, the UB, shrub layer, and herb layer were the highest, with average values of 284.06 g/m^2, 181.37 g/m^2, and 102.69 g/m^2, respectively. In contrast, the lowest UB, shrub layer, and herb layer biomass were observed under CC, with average values of 103.50 g/m^2, 67.12 g/m^2, and 36.37 g/m^2, respectively. For the herb layer, biomass under FT was significantly different from that under CC, whereas was no significant difference between the herb layer biomass of CC and CMRF. Moreover, the shrub layer biomass and UB under the different forest management regimes showed the same regularity as the herb layer biomass. Notably, the shrub layer biomass was higher than the herb layer biomass (Fig. 2b and c).

Understory species diversity was not significantly different under the different forest management regimes (Fig. 3). FT exhibited the highest understory species richness and biomass, followed by CMRF and CC. There were significant differences in stand structure under different forest management regimes, implying that forest management affected stand structure (Fig. 4). Specifically, CC had the highest stand density and canopy closure; FT had the largest DBH; CMRF had the lowest canopy closure and DBH, and FT had the lowest stand density.

Effects of biotic and abiotic factors on understory biomass

Variance partitioning analysis showed that UB was influenced to some extent by environmental factors (Fig. 5). UB was mainly affected by the combined interaction of forest management, stand structure, and species diversity, followed by soil properties, with explanation rates of 19%, 13%, and 8%, respectively.

The PLS-SEM model indicated that all predictor variables together accounted for 61% of the variation in the UB ($R^2=0.61$) (Fig. 6). The GOF value was 0.5, demonstrating an acceptable overall model quality. Stand structure had a significant negative effect on UB with a path coefficient of -0.48 ($P=0.003$), whereas forest management indirectly and positively influenced UB via stand structure (path coefficient: 0.27, $P=0.15$). Soil properties had a direct positive effect on UB (Fig. 6), and forest management had a significant indirect positive impact on it via stand structure (path coefficient: 0.46, $P=0.003$). Meanwhile, understory species diversity strongly affected UB (path coefficient: 0.59, $P<0.001$), while forest management significantly, indirectly, and negatively affected it through species diversity, with a path coefficient of -0.46 (path coefficient: 0.46, $P=0.04$).

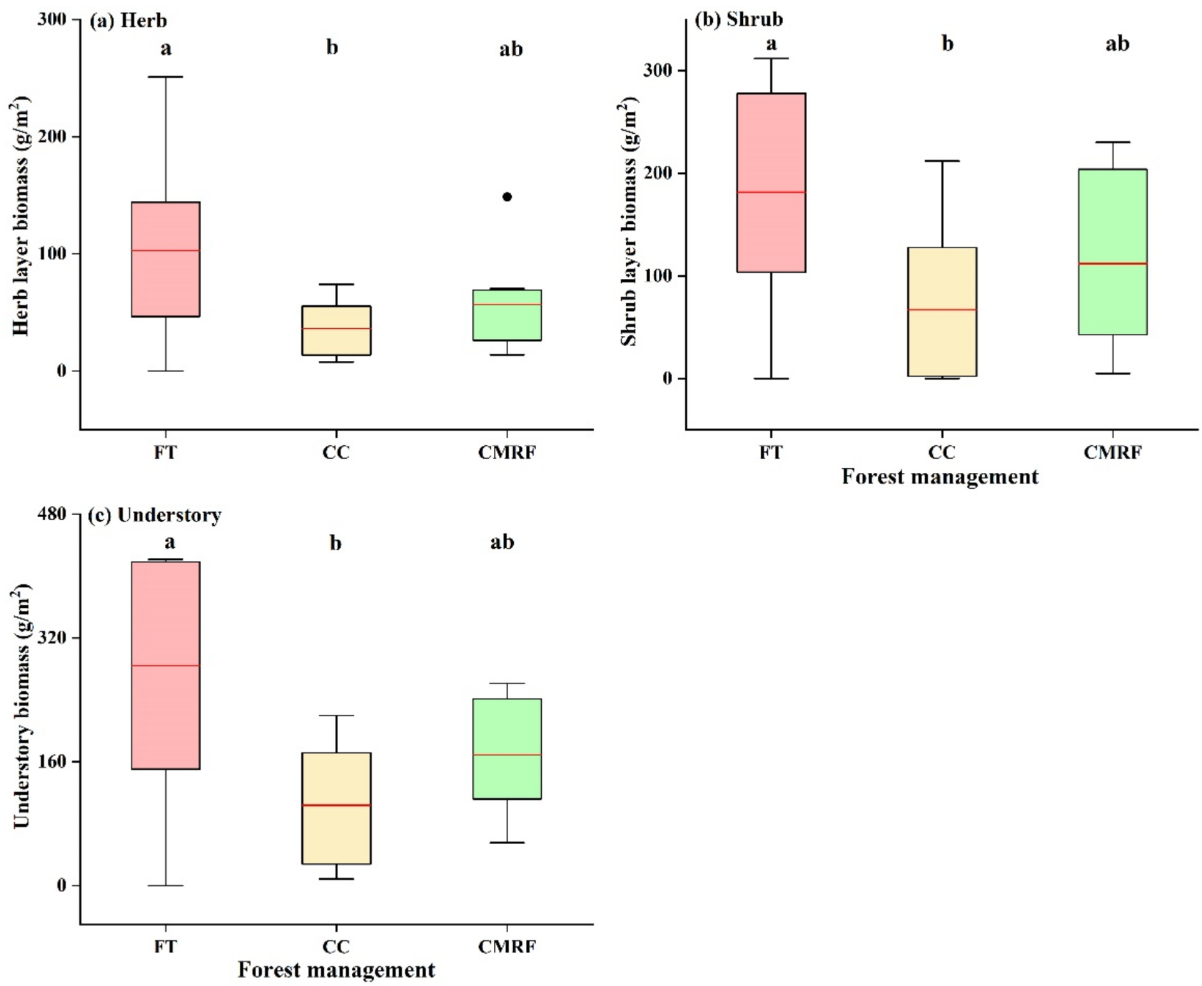

Fig. 2 Differences in understory biomass, shrub biomass, and herb biomass under different forest management practices. Different letters above the boxplots indicate significant differences at the $p < 0.05$ level according to Tukey's post hoc test. FT: Forest tending; CC: Clear-cutting; CMRF: Closure of mountains for reforestation

Discussion

Mixed effects of forest management on understory biomass

Forest management influences understory biomass (UB) in complex ways. First, it directly promotes UB. Additionally, forest management indirectly affects UB through interactions with understory species diversity, stand structure, and soil properties. Specifically, management enhances UB via stand structure and soil properties, but negatively impacts UB through understory species diversity. While species diversity contributes positively to UB, stand structure and soil properties both have negative effects. Furthermore, these components–stand structure, soil properties, and understory species diversity–interact with each other, with forest management playing a critical role in shaping all these factors. Therefore, it was not possible to determine whether the overall effect of forest management on UB was predominantly positive, negative, or neutral. Therefore, we refer to the impact of forest management on UB as a mixed effect.

Positive effects of understory species diversity on understory biomass

Understory species diversity did not differ significantly across different forest management practices. FT had the highest understory species richness and biomass, followed by CMRF and CC (Fig. 2). Previous studies have shown that thinning increases understory plant diversity in both shrub and herb layers (Hart 2008; Wang et al. 2021). FT

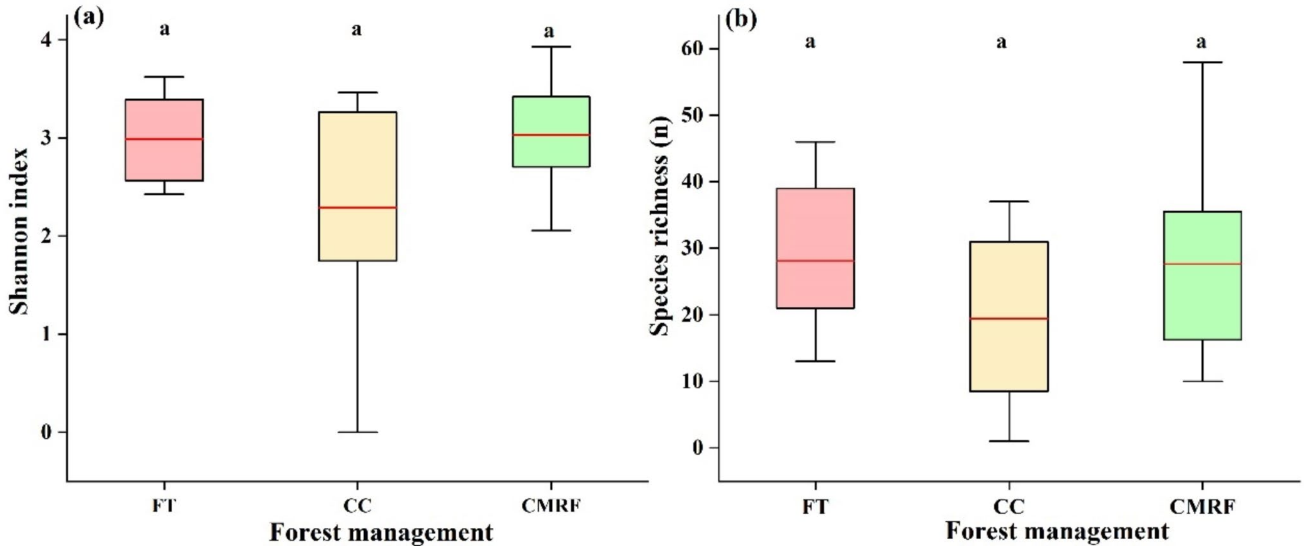

Fig. 3 Differences in Shannon index and species richness under different forest management. Different letters above the boxplots indicate significant differences at the $p < 0.05$ level according to Tukey's post hoc test

reduces canopy cover through tree pruning, which improves the microclimate (such as light, water, and soil nutrient availability), and influences resource availability and heterogeneity, promoting an increase in understory species diversity. Improvements in understory light and temperature are beneficial for plant growth and increase the number of individual plants. Therefore, the number and biomass of individual plants tended to increase. Studies have also indicated that forest management can increase species diversity in understory herb layers (Su et al. 2021). Diversity in both the shrub and herb layers greatly improved after FT in the southern humid domain (Li et al. 2020). Compared to FT, understory plant diversity is lower in CC due to the high density of plantations, high canopy closure, and low branch height, which lead to limited understory light, restricting the growth of shrubs and herbs. In addition, plot-scale diversity is influenced by the regional species pool, and the CC plots were originally wasteland or cultivated land. Consequently, the seed bank in CC is less abundant than in FT and CMRF.

We found that species richness was positively correlated with UB under different forest management regimes (Fig. S2). The FT plots exhibited the highest understory species richness and higher UB (Fig. 3). FT enhances herbaceous biomass growth by reducing canopy closure, improving the understory light condition, and promoting the growth of understory herbs, and shrubs (Tinya and Ódor 2016; Trentini et al. 2017). This increase may be attributed to the clearing of shrubs and standing dead trees, as well as thinning in the FT woodlands, which creates a canopy gap effect. Ren et al. (2021) showed that canopy gap disturbance can decrease plant competition for resources, promoting complementary utilization of resources and the effect of niche complementarity on productivity through increased understory species diversity. For example, the dynamics of herb and shrub diversity in FT or thinning are not exactly the same (Fig. 3; Yılmaz et al. 2018). A shrub layer with a high density can result in low herb species diversity as a result of the shade effect (Fig. S5; Li et al. 2020), whereas it could potentially enhance herb species richness by improving soil nutrient availability and light heterogeneity as the shrub layer expands (Yu et al. 2022).

Across all three forest management practices, greater species diversity was generally linked to increased biomass in the herbaceous, shrub, and understory layers. However, this association did not hold for the herbaceous layer in plantation forests (Figs. 2 and 3; Fig. S5). This phenomenon can be explained by several ecological mechanisms. One is niche complementarity, where reduced interspecific competition allows species to use available resources more efficiently. Another is interspecific facilitation, where some species modify the environment in ways that enhance the growth or survival of others. Additionally, the selection effect (or sampling effect) suggests that as species richness increases, the probability of including highly productive species with unique functional traits also rises (Fox et al. 2005; Loreau and Hector 2001). This, in turn, increases the likelihood of positive interactions, such as complementarity and facilitation, and leads to improved ecosystem functioning (Forrester 2014; Fridley 2001; Ruiz-Benito et al. 2014). Shrub and herbaceous species can efficiently utilize resources through niche complementarity due to their distinct niches, thereby enhancing species diversity. Additionally, different species occupy various niches, maximizing biomass through resource partitioning (Liu et al. 2023). This

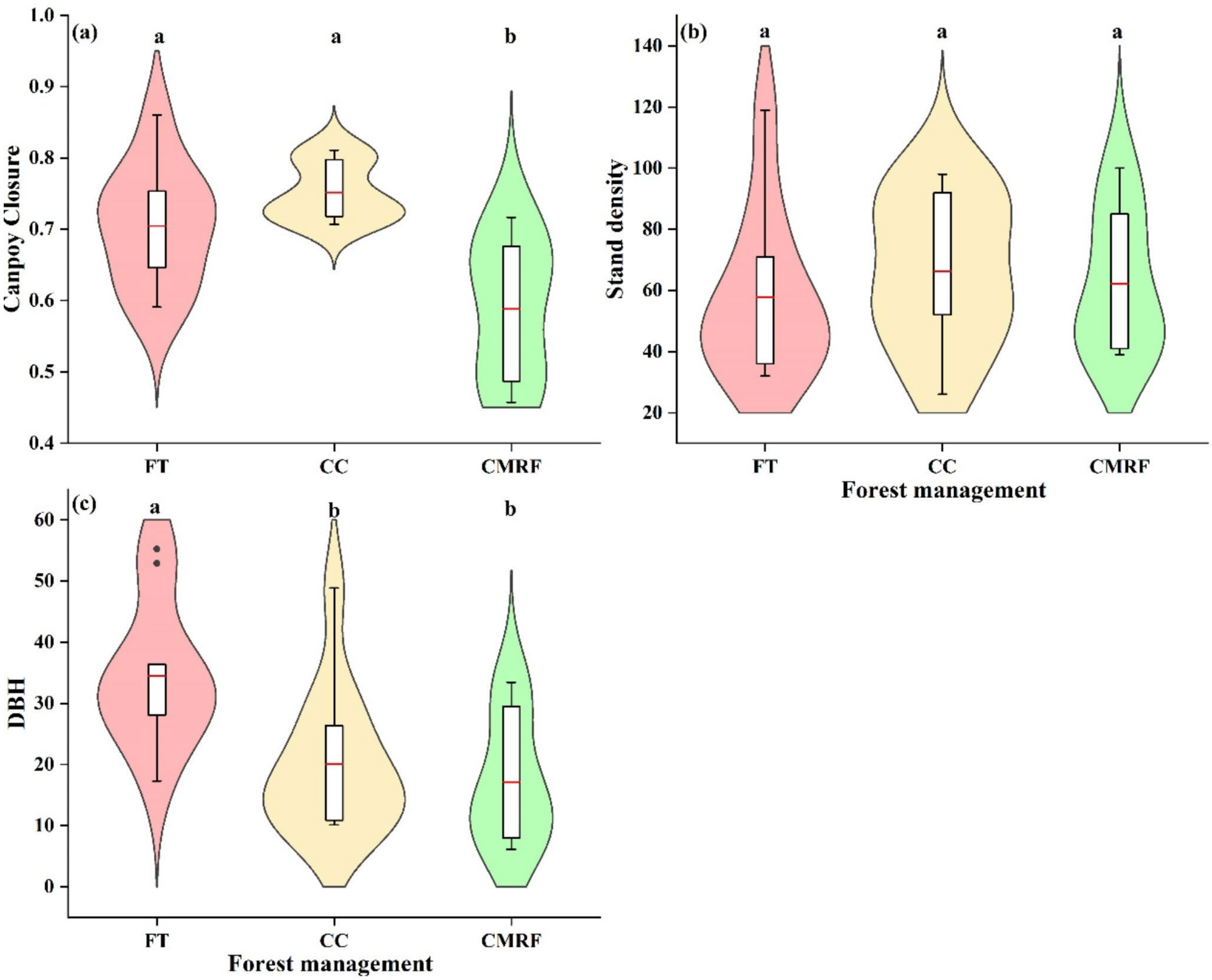

Fig. 4 Differences in stand structure under different forest management. Different letters above the boxplots indicate significant differences at the $p < 0.05$ level according to Tukey's post hoc test

further indicates that species utilize resources such as light, nutrients, and water in different ways, reducing resource competition and enhancing overall community productivity (Zhang et al. 2016a, b). Moreover, understory resources heterogeneity, influenced by canopy trees, may promote niche complementarity (Wei et al. 2021a, b), becoming the primary mechanism driving the understory diversity-productivity relationship.

Negative effects of stand structure on understory biomass

As many studies have stated, UB is powerfully impacted by the overstory structure (Ensslin et al. 2015; Wei et al. 2021a, b). We found a negative relationship between the UB and canopy closure (Fig. S3). Sigurdsson et al. (2005) also reached the same conclusion for larch and birch forest stands. Conversely, Suchar and Crookston (2010) reported no significant relationship between canopy closure and UB. Wei et al. (2021a, b) showed that small variations in canopy closure could increase biomass by approximately 40% in native plantations. These discrepancies may stem from differences in the canopy closure across studies; research suggests that an optimal canopy closure of 0.6–0.7 is recommended to maintain a potentially higher UB (Ahmad et al. 2018, 2019). Apparently, the effects of the overstory structure on UB varied across studies and contexts. In our study, the understory light availability declined as stand density and canopy closure increased, leading some plants to gradually wither and die due to limited growth. After thinning, the light environment improved considerably, allowing understory plants to grow significantly faster.

Understory vegetation is affected by stand structure due to changes in resource availability. We observed a positive

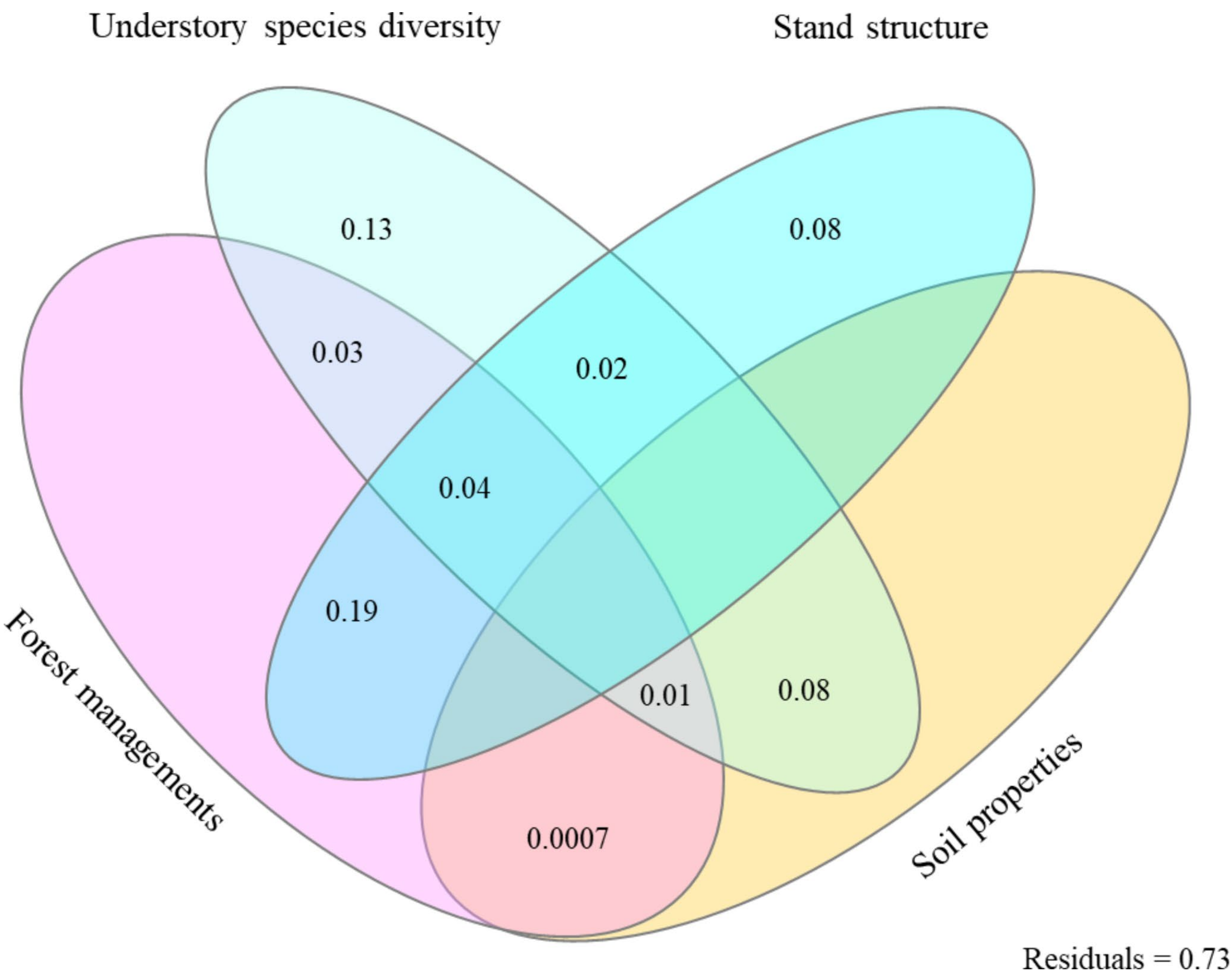

Fig. 5 Variation in understory biomass by forest management, species diversity, soil properties, and stand structure. (Values < 0 not shown)

relationship between UB and DBH (Fig. S3c). Ali et al. (2019) showed that DBH and UB forests were positively correlated in a natural subtropical forest. The structure of overstory trees imposes competitive limitations on understory vegetation, enhancing understory plant growth by altering the availability of light, heat, soil moisture, and space for shrub and herbaceous plants (Barbier et al. 2008; Wei et al. 2020). However, some studies have shown that UB is not always related to stand structure (Chen et al. 2020; Jin and Bao 2014). For example, low UB may depend more on factors such as forest management, natural disturbance, or soil conditions, which also influence light, heat, and nutrient availability and may be less responsive to stand structure.

Effects of soil properties on understory biomass

The UB is influenced by species richness and stand structure. Additionally, soil factors also affect UB (Ali et al. 2019; Guo et al. 2021; Zhang et al. 2015). Total P, N, C, available K, and soil texture all showed negative correlations with UB (Fig. S4). This negative relationship between soil properties and UB may be associated with the fact that most species have adapted to habitats with low nutrients content (Poorter et al. 2015). In contrast to our findings, Yamashita et al. (2004) showed that soil N availability enhanced aboveground biomass in two coniferous plantations. Similarly, high soil fertility can lead to nutritional imbalances or even vegetation mortality, which can negatively impact the biomass of tree propagation (Bordin et al. 2019). We also found a weak positive correlation between SOM and UB, indicating that SOM may be the limiting factor for understory plant growth in the forests of the Three Gorges Reservoir. Therefore, the relationship between soil nutrients and UB may depend on the overall soil fertility (Baraloto et al. 2011).

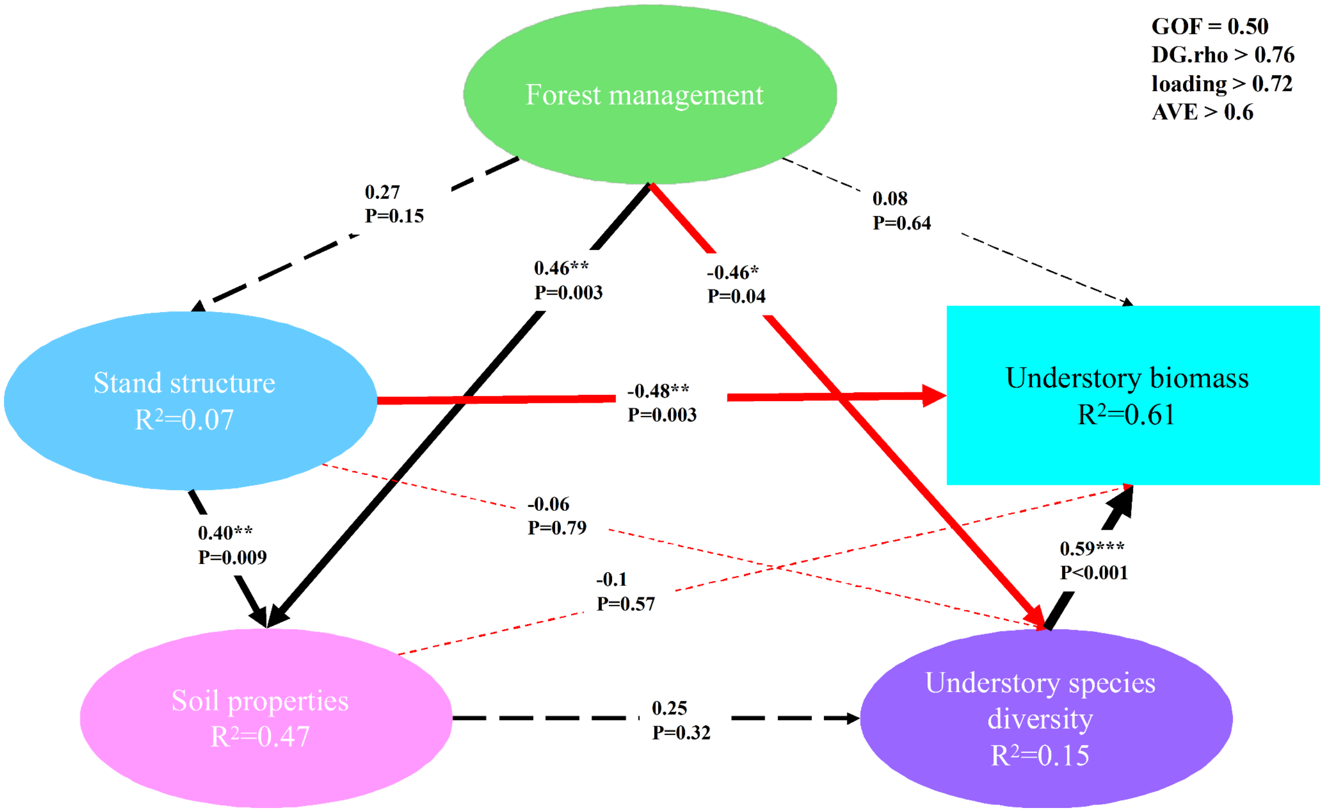

Fig. 6 Partial least-squares path model relating understory biomass to soil properties, stand structure, species diversity, and forest management, with relative contributions. Solid black arrows denote positive whereas red arrows denote negative direct effects. Dotted arrows represent non-significant effects. Line width shows the magnitude of the direct effect, and numbers represent standardized path coefficients. Asterisk indicates significance test level (*$p<0.05$; **$p<0.01$; ***$p<0.001$). R^2 values represent the explained variance of response variables. GOF = goodness of fit, DG.rho = Dillon-Goldstein's rho, AVE = average variance extracted

Conclusion

Our study shows that different forest management regimes drastically influence the forest UB. The PLS-SEM model reveals that the influence of forest management on UB has mixed effects and is mainly indirect by affecting the stand structure and understory species diversity. These findings further emphasize the importance of stand structure, a factor that has been previously overlooked. Furthermore, our results highlight that species diversity is the primary element affecting UB, indicating that niche complementarity is the dominant mechanism driving changes in UB.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10342-024-01753-2.

Acknowledgements We thank Mr.Songlin Zhang, Mr.Cunfeng Zhao, Mr.Zhaofei Wen for help during fieldwork. We are grateful to the Forestry Bureaus of Fuling, Fengdu, Kaizhou, Yunyang, Zhongxian, and Wushan for their help in our sampling efforts. We also thank the anonymous reviewers for their helpful comments on an early version of the manuscript. This work is jointly supported by the National Natural Science Foundation of China (Grant No.42371071), the Three Gorges' follow-up scientific research project from Chongqing Municipal Bureau of Water Resources (NO. 5000002021BF40001).

Author contributions Shanshan Chen: Conceptualization; sampling; data curation; methodology; writing-original draft; writing-editing and review. Shengjun Wu: Conceptualization; writing-review; funding acquistion; supervision. Jie Yang: Writing-review.

Declarations

Competing interests The authors declare no competing interests.

References

Ahmad B, Wang YH, Hao J, Liu YH, Bohnett E, Zhang KB (2018) Optimizing stand structure for trade-offs between overstory timber production and understory plant diversity: a case-study of a larch plantation in northwest China. Land Degrad Dev 29:2998–3008

Ahmad B, Wang YH, Hao J, Liu YH, Bohnett E, Zhang KB (2019) Optimizing stand structure for tradeoffs between overstory and understory vegetation biomass in a larch plantation of Liupan Mountains, Northwest China. Ecol Manage 443:43–50

Ali A, Lin SL, He JK, Kong FM, Yu JH, Jiang HS (2019) Climate and soils determine aboveground biomass indirectly via species diversity and stand structural complexity in tropical forests. Ecol Manage 432:823–831

Baraloto C, Rabaud S, Molto Q, Blanc L, Fortunel C, HÉRault B, DÁVila N, Mesones I, Rios M, Valderrama E, Fine PVA (2011) Disentangling stand and environmental correlates of aboveground biomass in amazonian forests. Glob Chang Biol 17:2677–2688

Baran J, Pielech R, Kauzal P, Kukla W, Bodziarczyk J (2020) Influence of forest management on stand structure in ravine forests. Ecol Manage 463:118018

Barefoot CR, Willson KG, Hart JL, Schweitzer CJ, Dey DC (2019) Effects of thinning and prescribed fire frequency on ground flora in mixed Pinus-hardwood stands. Ecol Manage 432:729–740

Barbier S, Gosselin F, Balandier P (2008) Influence of tree species on understory vegetation diversity and mechanisms involved-A critical review for temperate and boreal forests. Ecol Manage 254:1–15

Barry KE, Mommer L, van Ruijven J, Wirth C, Wright AJ, Bai Y, Connolly J, De Deyn GB, de Kroon H, Isbell F, Milcu A, Roscher C, Scherer-Lorenzen M, Schmid B, Weigelt A (2019) The future of complementarity: disentangling causes from consequences. Trends Ecol Evol 34:167–180

Bordin KM, Müller SC, Collins B (2019) Drivers of subtropical forest dynamics: the role of functional traits, forest structure and soil variables. J Veg Sci 30:1164–1174

Chen HH, Zhu X, Zhu GY, Liu FH (2020) Effects of stand structure on understory biomass of the Quercus spp secondary forests in Hunan Province, China. Chin J Appl Ecol 31:349–356

Dean WE (1974) Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. J Sediment Res 44:242–248

Ensslin A, Rutten G, Pommer U, Zimmermann R, Hemp A, Fischer M (2015) Effects of elevation and land use on the biomass of trees, shrubs and herbs at Mount Kilimanjaro. Ecosphere 6:1–15

Forrester FI (2014) The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. Ecol Manage 312:282–292

Fox JW (2005) Interpreting the 'selection effect' of biodiversity on ecosystem function. Ecol Lett 8:846–856

Fridley JD (2001) The influence of species diversity on ecosystem productivity: how, where, and why? Oikos 93:514–526

Gao WQ, Lei XD, Gao DL, Li YT (2021) Mass-ratio and complementarity effects simultaneously drive aboveground biomass in temperate Quercus forests through stand structure. Ecol Evol 11:16806–16816

Gilliam FS (2007) The ecological significance of the herbaceous layer in temperate forest ecosystems. Bioscience 57:845–858

Guo Y, Du X, Chen H, Zheng G, Zhang X, Wang Q (2021) Influence of shale gas development on core forests in the subtropical karst region in southwestern China. Sci Total Environ 771:145287

Hair JF, Hult GTM, Ringle CM, Sarstedt M, Thiele KO (2017) Mirror, mirror on the wall: a comparative evaluation of composite-based structural equation modeling methods. J Acad Mark Sci 45:616–632

Hart SA, Chen HYH (2008) Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest. Ecol Monogr 78:123–140

Kumar P, Chen HYH, Thomas SC, Shahi C (2018) Linking resource availability and heterogeneity to understorey species diversity through succession in boreal forest of Canada. J Ecol 106:1266–1276

Jennings SB, Brown ND, Sheil D (1999) Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. Forestry 72:59–74

Jin YQ, Bao WK (2014) Relationships of the understory biomass with stand structure across the Sichuan cypress plantation forests in Sichuan Basin, China. Acta Ecol Sin 34:5849–5859

Jin Y, Liu C, Qian SS, Luo Y, Zhou R, Tang J, Bao W (2022) Large-scale patterns of understory biomass and its allocation across China's forests. Sci Total Environ 804:150169

Landuyt D, De Lombaerde ED, Perring MP, Hertzog LR, Ampoorter E, Maes SL, Frenne PD, Ma SY, Proesmans W, Blondeel H, Sercu BK, Wang B, Wasof S, Verheyen K (2019) The functional role of temperate forest understorey vegetation in a changing world. Glob Chang Biol 25:3625–3641

Li X, Li Y, Zhang J, Peng S, Chen Y, Cao Y (2020) The effects of forest thinning on understory diversity in China: a meta-analysis. Land Degrad Dev 31:1225–1240

Liu LS, Dai LM, Wen YG, Wang HA (2015) A review on forest ecosystem management towards ecosystem services: status, challenges, and future perspectives. Acta Ecol Sin 35:1–9 (In Chinese)

Liu Q, Turlings TCJ, Li Y (2023) Can herbivores sharing the same host plant be mutualists? Trends Ecol Evol 38:509–511

Liu SR, Shi ZM, Ma JM, Zhao CM, Zhang YD, Liu XL (2009) Ecological strategies for Restoration and Reconstruction of degraded natural forests on the Upper reaches of the Yangtze River. Scientia Silvae Sinicae 45:120–124 (In Chinese)

Liu Z, Ma R, Zhu D, Konstantinidis, Zhu Y, Zhang S (2024) Organic fertilization co-selects genetically linked antibiotic and metal (loid) resistance genes in global soil microbiome. Nat Commun 15:5168

Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76

Mitchard ET (2018) The tropical forest carbon cycle and climate change. Nature 559:527–534

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2019) Vegan: community ecology package. https://cran.r-project.org/package=vegan

Okudaa T, Suzukia M, Adachib N, Quahc ES, Husseinc NA, Manokaran N (2003) Effect of selective logging on canopy and stand structure and tree species composition in a lowland dipterocarp forest in peninsular Malaysia. Ecol Manage 175:297–320

Paletto A, Tosi V (2009) Forest canopy cover and canopy closure: comparison of assessment techniques. Eur J Res 128:265–272

Palmroth S, Bach LH, Lindh M, Kolari P, Nordin A, Palmqvist K (2019) Nitrogen supply and other controls of carbon uptake of understory vegetation in a boreal Picea abies forest. Agri Meteorol 276–277:107620

Poorter L, van der Sande MT, Thompson J, Arets E J M M, Alarcón A, Álvarez-Sánchez J, Ascarrunz N, Balvanera P, Barajas-Guzmán G, Boit A, Bongers F, Carvalho FA, Casanoves F, Cornejo-Tenorio G, Costa FRC, de Castilho CV, Duivenvoorden JF, Dutrieux LP, Enquist BJ, Fernández-Méndez F, Finegan B, Gormley LHL, Healey JR, Hoosbeek MR, Ibarra-Manríquez G, Junqueira AB, Levis C, Licona JC, Lisboa LS, Magnusson WE, Martínez-Ramos M, Martínez-Yrizar A, Martorano LG, Maskell LC, Mazzei L, Meave JA, Mora F, Muñoz R, Nytch C, Pansonato MP, Parr TW, Paz H, Pérez-García EA, Rentería LY, Rodríguez-Velazquez J, Rozendaal DMA, Ruschel AR, Sakschewski B, Salgado-Negret B, Schietti J, Simões M, Sinclair FL, Souza PF, Souza FC, Stropp J, ter Steege H, Swenson NG, Thonicke K, Toledo M, Uriarte M, van der Hout P, Walker P, Zamora N (2015) Peña-Claros M Diversity enhances carbon storage in tropical forests. Global Ecol Biogeogr 24:1314–1328

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Ren YG, Ma MH, Liu Y, Zhu K, Yi YM, Wang XX, Wu SJ, Huang P (2020) Physicochemical determinants in stabilizing soil aggregates along a hydrological stree gradient on reservoir riparian habitats: implications to soil restoration. Ecol Eng 143:105664

Ren S, Ali A, Liu H, Yuan Z, Yang Q, Shen G, Zhou S, Wang X (2021) Response of community diversity and productivity to canopy gap disturbance in subtropical forests. Ecol Manage 502:119740

Rossman AK, Halpern CB, Harrod RJ, Urgenson LS, Peterson DW, Bakker JD (2018) Benefits of thinning and burning for understory diversity vary with spatial scale and time since treatment. Ecol Manage 419–420:58–78

Ruiz-Benito P, Gómez-Aparicio L, Paquette A, Messier C, Kattge J, Zavala MA (2014) Diversity increases carbon storage and tree productivity in Spanish forests. Global Ecol Biogeogr 23:311–322

Sigurdsson BD, Magnusson B, Elmarsdottir A, Bjarnadottir B (2005) Biomass and composition of understory vegetation and the forest floor carbon stock across siberian larch and mountain birch chronosequences in Iceland. Ann Sci 62:881–888

Silva Pedro M, Rammer W, Seidl R (2015) A disturbance-induced increase in tree species diversity facilitates forest productivity. Landsc Ecol 31:989–1004

Su X, Li S, Wan X, Huang Z, Liu B, Fu S, Kumar P, Chen H, Y H (2021) Understory vegetation dynamics of Chinese fir plantations and natural secondary forests in subtropical China. Ecol Manage 483:118750

Suchar VA, Crookston NL (2010) Understory cover and biomass indices predictions for forest ecosystems of the Northwestern United States. Ecol Indic 10:602–609

Terborgh J, Huanca Nuñez N, Alvarez Loayza P, Cornejo Valverde F (2017) Gaps contribute tree diversity to a tropical floodplain forest. Ecology 98:2895–2903

Thom D, Seidl R (2016) Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. Biol Rev Camb Philos Soc 91:760–781

Tinya F, Ódor P (2016) Congruence of the spatial pattern of light and understory vegetation in an old-growth, temperate mixed forest. Ecol Manage 381:84–92

Trentini CP, Campanello PI, Villagra M, Ritter L, Ares A, Goldstein G (2017) Thinning of loblolly pine plantations in subtropical Argentina: impact on microclimate and understory vegetation. Ecol Manage 384:236–247

Van Hees WWS, Mead BR (2000) Ocular estimates of understory vegetation structure in a closed Picea glaucal/Betula papyrifera forest. J Veg Sci 11:195–200

Wang G, Sun Y, Zhou M, Guan N, Wang Y, Jiang R, Liu Z, Wu M, Xia F (2021) Effect of thinning intensity on understory herbaceous diversity and biomass in mixed coniferous and broad-leaved forests of Changbai Mountain. Ecosyst 8:53

Wang H, Zhang M, Nan H (2018) Abiotic and biotic drivers of species diversity in understory layers of cold temperate coniferous forests in North China. J Res 30:2213–2225

Wei L, Archaux F, Hulin F, Bilger I, Gosselin F (2020) Stand attributes or soil micro-environment exert greater influence than management type on understory plant diversity in even-aged oak high forests. Ecol Manage 460:117897

Wei L, Gosselin F, Rao X, Lin Y, Wang J, Jian S, Ren H (2021a) Overstory and niche attributes drive understory biomass production in three types of subtropical plantations. Ecol Manage 482:118894

Wei L, Thiffault N, Barrette M, Fenton NJ, Bergeron Y (2021b) Can understory functional traits predict post-harvest forest productivity in boreal ecosystems? Ecol Manage 495:119375

Yamashita T, Kasuya N, Nishimura S, Takeda H (2004) Comparison of two coniferous plantations in central Japan with respect to forest productivity, growth phenology and soil nitrogen dynamics. Ecol Manage 200:215–226

Ye F, Ma MH, Wu SJ, Jiang Y, Zhu GB, Zhang H, Wang Y (2019) Soil properties and distribution in the riparian zone: the effects of fluctuations in water and anthropogenic disturbances. Eur J Soil Sci 70:664–673

Yılmaz OY, Yılmaz H, Akyüz YF (2018) Effects of the overstory on the diversity of the herb and shrub layers of anatolian black pine forests. Eur J Res 137:433–445

Yu JT, Zhang XN, Xu CY, Hao MH, Choe C, He HJ (2022) Thinning can increase shrub diversity and decrease herb diversity by regulating light and soil environments. Front Plant Sci 13:948648

Zangy E, Kigel J, Cohen S, Moshe Y, Ashkenazi M, Fragman-Sapir O, Osem Y (2021) Understory plant diversity under variable overstory cover in Mediterranean forests at different spatial scales. Ecol Manage 494:119319

Zhang S, Yang X, Li D, Li S, Chen Z, Wu J (2022) A meta-analysis of understory plant removal impacts on soil properties in forest ecosystems. Geoderma 426:116116

Zhang Y, Chen HYH, Coomes D (2015) Individual size inequality links forest diversity and above-ground biomass. J Ecol 103:1245–1252

Zhang Y, Chen HYH, Taylor AR (2016a) Aboveground biomass of understory vegetation has a negligible or negative association with overstoreytree species diversity in natural forest. Global Ecol Biogeogr 25:141–150

Zhang Y, Chen HYH, Taylor AR (2016b) Positive species diversity and above-ground biomass relationships are ubiquitous across forest strata despite interference from overstorey trees. Funct Ecol 31:419–426

Zhou LL, Cai LP, He ZM, Wang RW, Wu PF, Ma XQ (2016) Thinning increases understory diversity and biomass, and improves soil properties without decreasing growth of Chinese fir in southern China. Environ Sci Pollut R 23:24135–24150