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Tree functional strategies and soil microbial communities regulate forest ecosystem services

Jianqing Wang[1,2] Peter Manning[3] Josep Peñuelas[4,5] Francis Q. Brearley[6] Xiuzhen Shi[1,2] Peng Leng[1,2] Manuel Esteban Lucas-Borja[7] Samiran Banerjee[8] Manuel Delgado-Baquerizo[9] Zhiqun Huang[1,2]

[1]Key Laboratory for Humid Subtropical Eco-Geographical Processes of the Ministry of Education, Institute of Geography, Fujian Normal University, Fuzhou, China

[2]Fujian Provincial Key Laboratory for Subtropical Resources and Environment, School of Geographical Sciences, Fujian Normal University, Fuzhou, China

[3]Department of Biological Sciences, University of Bergen, Bergen, Norway

[4]CREAF, Centre de Recerca Ecològica i Aplicacions Forestals, Cerdanyola del Vallès, Ctalonia, Spain

[5]Global Ecology Unit, CREAF-CSIC-UAB, Bellaterra, Catalonia, Spain

[6]Department of Natural Sciences, Manchester Metropolitan University, Manchester, UK

[7]Higher Technical School of Agricultural and Forestry Engineering, Castilla-La Mancha University, Albacete, Spain

[8]Department of Microbiological Sciences, North Dakota State University, Fargo, North Dakota, USA

[9]Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS), CSIC, Laboratorio de Biodiversidad y Funcionamiento Ecosistémico, Sevilla, Spain

Abstract

1. Forests provide key ecosystem services. However, the role of tree functional strategies and soil microbial communities in supporting multiple ecosystem services remains unclear.
2. To bridge this gap, we conducted a field experiment involving monocultures of 28 tree species with diverse functional traits and their associated soil microbial

communities. We assessed multiple indicators of ecosystem services to gain insights into their interrelationships.

3. Our study revealed strong connections between tree functional traits, soil microbial communities and ecosystem services such as nutrient cycling, water retention and ecosystem productivity. Broadleaved trees had a negative impact on nutrient cycling rates but positively influenced ecosystem productivity compared to coniferous trees. Deciduous trees positively associated with ecosystem water availability compared to evergreen trees. Tree species with resource-acquisitive strategies were associated with faster nutrient cycling rates. Furthermore, trees forming ectomycorrhizal associations increased nutrient cycling and multifunctionality (i.e. multiple ecological functions and services) compared to trees with arbuscular mycorrhizal associations. More importantly, leaf nitrogen content indirectly influenced multifunctionality by affecting the ratio of fungi-bacteria and soil microbial composition.
4. *Synthesis and applications*. This research highlights the role of tree functional strategies and soil microbial community composition in influencing the ecosystem services of subtropical forests, and provides important information on which functional groups may be planted to promote particular bundles of ecosystem services.

Keywords: Biodiversity; ecosystem functioning, resource-use strategies, subtropical forest, soil microbial community, tree functional traits, tree species

1. Introduction

Forests provide a myriad of ecosystem services and functions including numerous wood products, climate regulation, nutrient cycling, water retention, carbon storage, and the maintenance of biodiversity (Brockerhoff *et al.*, 2017; Shi *et al.*, 2021). Prior studies have established that tree species diversity positively influences ecosystem multifunctionality due to the complementary effects of different tree species (Schuldt *et al.*, 2019; Zak *et al.*, 2003). The underlying mechanism typically proposed is that each tree species occupies a unique ecological niche, enabling complementarity and facilitation between them that increases the value or rate of various ecosystem functions (Gamfeldt *et al.*, 2013; Nadrowski *et al.*, 2010). While there is much work on the relation between tree traits and ecosystem function (Baez & Homeier, 2018; Wright *et al.*, 2010), less is known about how the functional strategies of dominant trees relate to multiple ecosystem services simultaneously, to create different 'bundles' or portfolios of ecosystem service supply, and the related concept of multifunctionality, typically measured as simultaneous high levels of multiple ecosystem services (Manning *et al.*, 2018). Further research on this topic is therefore needed to fully understand the underlying mechanisms linking ecosystem multifunctionality to tree species and develop effective forest management strategies to improve ecosystem service provision, e.g. in guiding the restoration of ecosystems under the umbrella of the 2020-2030 United Nations Decade of Restoration (https://www.decadeonrestoration.org/).

Trees vary in their characteristics, such as leaf type (broadleaved vs. coniferous) and leaf phenology (evergreen vs. deciduous), as well as their associations with mycorrhizal fungi in their root systems, which can also influence ecosystem services via their functional differences (e.g. in nutrient acquisition strategies) (Augusto *et al.*, 2015; Tedersoo *et al.*, 2020). Evergreen trees, with their persistent foliage and extended growing periods, play a crucial role in nutrient cycling and water retention by continuously transpiring and absorbing nutrients throughout the year. In contrast, deciduous trees, shedding leaves seasonally, provide periodic resource pulses for soil biota, thereby influencing nutrient cycling and water retention differently, with leaf shedding indicating a seasonal variation in the intensity of influence (Augusto *et al.*, 2015; Macinnis-Ng *et al.*, 2016). As a consequence, evergreen gymnosperms can contribute a greater quantity of nutrients to the soil–plant biogeochemical cycle compared to deciduous angiosperms (Augusto *et al.*, 2015). However, many evergreen gymnosperms also possess 'slow' resource acquisition strategies (Diaz *et al.*, 2016), and so may also be associated with slow functioning rates. Arbuscular mycorrhizal (AM) trees, aided by fungal associations, enhance nutrient uptake and carbon storage, whereas ectomycorrhizal (EM) trees primarily improve inorganic nutrient acquisition and soil microbial activity (Looney *et al.*, 2018; Talbot *et al.*, 2013). Nevertheless, a major uncertainty in understanding tree species-ecosystem function and service relationships is the relative contributions of tree life strategies, and related microbial communities and functional traits, in driving individual and multiple ecosystem functions, and their related services.

Tree species also differ in their strategies for acquiring and allocating resources, with a key axis of functional variation being resource-acquisitive versus resource-conservative strategies (De Deyn *et al.*, 2008; Reich, 2014). In general, ecologists have used resource economics theory to explain trait variation in roots and leaves, which serve as the aboveground and belowground plant organs for resource acquisition through soil nutrient uptake and photosynthesis (Bergmann *et al.*, 2020; Wright *et al.*, 2004). Specific leaf area (SLA), leaf dry matter content (LDMC), leaf N content, specific root length (SRL), and root N content have been widely employed as measures of tree resource-use strategies (Shen *et al.*, 2022; Wan *et al.*, 2022). Furthermore, the influence of tree species on ecosystem functioning is mediated by their effects on free-living soil microbes, which consume and process organic inputs from living organisms. As these microbes control the rates of many ecosystem functions and their related services, incorporating the influence on soil microbial diversity, biomass, and structure can potentially enhance our understanding of ecosystem services (Pommier *et al.*, 2018; Zhou *et al.*, 2020). However, the mechanisms via which soil microbial properties impact forest ecosystem services, and the relative importance of different tree species traits and related microbial community differences in explaining ecosystem service supply remains largely unexplored.

Here, we conducted a field experiment to quantify the roles of tree functional strategies and soil microbial communities in driving the ecosystem services provided by subtropical forest plantations. Based on the relationships described above, we proposed that broadleaved, evergreen, and AM trees would promote ecosystem productivity, nutrient cycling rates, carbon stocks as well as soil health. This is due to the relatively larger and more constant input of resources into the soil–plant nutrient cycle by broadleaved and evergreen tree species, while AM fungi improve resource acquisition by extending hyphae into nutrient-depleted zones beyond the root area (Augusto *et al*., 2015; Phillips *et al*., 2013). Furthermore, given that tree species with resource-acquisitive strategies often exhibit fast growth and photosynthetic rates (Weemstra *et al*., 2021), we thus hypothesized that resource-acquisitive tree species would lead to higher supply rates for multiple ecosystem services linked to biogeochemical cycling. Finally, we proposed that soil microbial communities would mediate the effects of tree species on multiple ecosystem services and functions.

2. Materials and methods

2.1 Experimental description

This study aimed to investigate the relationships between tree species and ecosystem functioning in subtropical forests. The field experiment was conducted in Shanghang, Fujian Province, China (25°07′N, 116°32′E), which has a humid subtropical climate with an average annual precipitation of 1,637 mm and a mean annual temperature of 19.8 °C, based on data from 1971 to 2020. The soil is derived from sandstone and is classified as red soil according to the Chinese Soil Classification System, which corresponds to an Ultisol in the USDA Soil Taxonomy. The basic chemical properties of the topsoil are as follows: pH (H_2O) of 4.53, total organic carbon of 3.40%, total N of 0.16%. The experimental region was previously covered by Chinese fir (*Cunninghamia lanceolata* [Lamb.] Hook; Cupressaceae) plantations. In March 2019, following the clear-cutting of the Chinese fir plantations, a total of 28 common subtropical tree species were planted in monoculture as saplings in 81 randomly selected plots, with 2 to 4 replicates for each tree species (Table 1). The trees were planted at a density of 256 trees per plot, each covering an area of 12 m × 12 m, with approximately 0.75 m spacing between rows. To limit cross-over effects, all plots were separated by a buffer zone of at least 2 m. Of the 28 species, 7 were deciduous and 21 evergreen, 5 were coniferous and 23 broadleaved, and 20 were AM and 8 EM (Table S1).

2.2 Soil sampling and analysis

Soil sampling was conducted in August 2021 when the trees had been growing for 2.5 years. Ten topsoil cores (0-10 cm depth) were randomly collected from the center of the plot, surrounding each tree stem. Cores were extracted using a 3.5 cm diameter auger after carefully removing the litter layer. The collected soil cores were thoroughly mixed to form a composite sample. The 81 soil samples were divided into two portions for subsequent analysis. One was stored at 4 °C for soil physical and chemical analyses, while the other was stored at -20 °C for microbial analysis.

Soil water content (SWC) was measured by oven-drying subsamples at 105 °C for 24 hours. Soil nitrification and mineralization rates were determined by differences in total nitrate N and mineral N concentrations between the beginning and end of a 28-day incubation at 25 °C in an incubator, respectively. The soil carbon (TC) content was analyzed using a CNS Macro Elemental Analyzer (Elementar, Germany).

Soil enzyme activities: β-glucosidase, cellobiohydrolase, acid phosphatase, and N-acetylglucosaminidase, were determined using MUB (4-methylumbelliferone)-linked substrates (Saiya-Cork *et al*., 2002). Soil phospholipid fatty acids analysis (PLFA) was employed to assess the diversity and biomass of soil microbial communities. This technique characterizes microbial populations, including bacteria, fungi, and actinomycetes, by examining fatty acid profiles in the soil samples (Wan *et al*., 2022). Soil microbial composition was then described by principal coordinates analysis (PCoA) of Bray-Curtis distance matrices.

2.3 Plant sampling and functional traits

In 2020, litterfall mass were measured from all individual trees within the experimental plots. Litterfall was collected once a month in each experimental plot using five litter traps (47 cm × 47 cm) for one year. The collected litter was dried at 65 °C for 72 hours to determine its dry weight. The litter's maximum water-holding capacity was evaluated by immersing dry litter in water for 24 hours. In May 2021, leaf samples were collected from at least three representative trees of each species from each plot. The sampling involved selecting one south-facing branch from the canopy, and leaves were carefully collected from this branch ensuring representative samples for analysis. LDMC was calculated by dividing water-saturated fresh leaf mass by the corresponding dry leaf mass. SLA was calculated by dividing the dry weight of the leaf by the corresponding fresh leaf area. Leaf N content was analyzed using finely-ground dry leaf samples (8-10 mg) on a CNS Macro Elemental Analyzer. Root branches with intact terminal branch orders were selected and cut, and 5 g of fresh biomass from first-order roots was collected as the representative sample. Root N content was quantified by analyzing finely-ground dry root samples.

2.4 Ecosystem service indicators

Multiple aspects of ecosystem service provision were captured by using several indicator measures for each to form what we refer to as ecosystem service classes. These aspects were: ecosystem productivity, carbon stocks, nutrient cycling (fast rates equated to high ecosystem service supply), water retention (high water retention considered high service supply), and soil health (high soil activity considered indicative of healthy soil). These capture multiple aspects of ecosystem functioning with strong links to service provision (Table 1). Ecosystem productivity was evaluated using litterfall mass. Nutrient cycling was assessed using soil mineralization rates and nitrification rates. Carbon stocks were represented by soil microbial biomass carbon and dissolved organic carbon, the most rapidly changing pools over the timeframe considered. Soil health was represented by soil enzyme activities. Water retention was indicated by SWC and litter maximum water-holding capacity. Within each service class, standardized ecosystem variables were converted into individual services using the formula: ecosystem services = (species value - minimum value) / (maximum value - minimum value) (Wang *et al.*, 2019). Each transformed ecosystem variable had a minimum value of zero and a maximum value of one. The normalized individual services, averaged across the indicators of each, were then averaged to calculate the overall multifunctionality score (Maestre *et al.*, 2012; Shi *et al.*, 2021). Furthermore, we calculated multifunctionality by equally weighting all ecosystem services and functions to reduce the influence of highly correlated functions (Manning *et al.*, 2018).

2.5 Statistical analyses

All statistical analyses were performed using R 4.0.2 software. The principal coordinates analysis (PCoA) of Bray-Curtis distance matrices was used to evaluate the relative score distribution of individual ecosystem functionality indicators. A PERMANOVA test, performed using the Adonis function from the 'vegan' package in R, was then employed to assess how variation in the main axes of these multiple ecosystem functions differed among different tree species. The tree economics spectrum categorizes tree functional traits (leaf N, LDMC, SLA, root N, SRL) into resource-acquisitive or resource-conservative strategies using principal component analysis (PCA) (Fig. S1) (Roumet *et al.*, 2016; Wright *et al.*, 2004). The impacts of soil microbial communities (fungi and bacteria ratio, diversity, biomass, and composition) and plant functional traits (leaf N, LDMC, SLA, root N, SRL) on these PCA axes of ecosystem functioning were examined using a multiple regression model. Pearson's correlation analysis was conducted to explore the relationships between multiple ecosystem service indicators, tree functional traits and soil microbial communities. The effects of plant functional traits and soil microbial communities on multiple ecosystem services were assessed using a multiple regression model with the 'relaimpo' package in R. Finally, structural equation models (SEMs) were applied to examine the direct and indirect effects of tree functional traits and soil microbial communities on ecosystem multifunctionality using the ‘piecewiseSEM’ package in R (Lefcheck, 2016).

3. Results

3.1 The relationship between tree species and ecosystem services

Distinct patterns were observed in the response of the multiple ecosystem service classes to different tree species (Table S2). *Mytilaria laosensis* exhibited the highest values (standardized value, presented here and hereafter, = 0.79) for ecosystem productivity, while *Taxus wallichiana* and *Cunninghamia lanceolata* had the lowest values. *Osmanthus fragrans* exhibited the lowest soil health (0.07), water retention (0.19), and multifunctionality (0.22). *Phoebe chekiangensis* exhibited the lowest carbon stocks (0.19), while *Magnoliaa maudiae* showed the lowest nutrient cycling values (0.10). *Schima superba* exhibited the highest soil health (0.45), whereas *Sapindus saponaria* showed the highest water retention (0.70). By contrast, *Alnus trabeculosa* displayed the highest carbon stocks (0.61), nutrient cycling (0.84), and multifunctionality (0.50).

3.2 Impacts of tree functional types on ecosystem services

Tree species were functionally classified according to leaf types and phenology, mycorrhizal types, and resource-use strategies (Fig. 1 and Figs. S2, S4). Our results showed that coniferous, ectomycorrhizal, and resource-acquisitive trees significantly increased the nutrient cycling indicator values by 25.5%, 3.6% and 1.7% ($P < 0.001$), respectively. Deciduous trees significantly increased water retention services by 0.08 % ($P = 0.028$) compared to evergreen trees. Broadleaved trees significantly increased ecosystem productivity services by 283.8% ($P < 0.001$). Ectomycorrhizal trees significantly decreased multifunctionality by 1.0% compared to AM trees ($P = 0.043$). However, the mycorrhizal type, resource-use strategy, leaf type, and phenology had minimal impacts on carbon stocks and soil health (Fig. 1).

The PERMANOVA test conducted on the PCoA ordination revealed a significant divergence in the distribution of multiple ecosystem services, based on both leaf type (*P* = 0.001) and resource-use strategies (*P* = 0.015) but not leaf phenology and mycorrhizal type (Fig. 2).

3.3 Tree functional traits and soil microbial communities as drivers of ecosystem services

The relationship between tree functional traits, soil microbial communities, and ecosystem services was evaluated using multiple regression and correlation analysis (Fig. 3 and Fig. S4). The multiple regression model and correlation analysis revealed that tree functional traits were strongly related to ecosystem services. Specifically, leaf N was significantly and positively related to nutrient cycling services, but negatively related to ecosystem productivity (Fig. S4). Leaf N and SLA emerged as the better predictors of the services of ecosystem productivity (Fig. 3). Root N showed a significant and negative correlation with soil health (Fig. 3 and Fig. S4).

Furthermore, the regression analysis indicated that the ratio of fungi-bacteria emerged as the best predictor of the services of soil health, nutrient cycling, and water retention (Fig. 3). Moreover, the correlation analysis revealed that the ratio of fungi-bacteria was significantly and positively correlated with soil health, water retention, and ecosystem productivity, but was negatively related to nutrient cycling (Fig. S4). Soil microbial biomass showed a significant and positive association with water retention (Fig. S4). Soil microbial composition emerged as the best predictor of ecosystem productivity (Fig. 3). Similarly, water retention, ecosystem productivity, and multifunctionality were significantly associated with soil microbial composition (Fig. S4).

The structural equation model revealed that leaf N significantly decreased the ratio of fungi to bacteria, and that this ratio was significantly associated with soil microbial composition. Soil microbial composition, in turn, significantly affected ecosystem multifunctionality. Overall, the integrated factors accounted for 6% of the variation in ecosystem multifunctionality (Fig. 4).

4. Discussion

4.1 Role of tree functional traits on ecosystem services in subtropical forests

Deciduous tree species were associated with higher ecosystem water retention compared to evergreen species. Deciduous trees shed their leaves during the dry and cold seasons, reducing canopy interception and increasing water infiltration into the soil, which may enhance groundwater recharge and improve water retention (Augusto *et al.*, 2015). By contrast, evergreen trees sustain year-round transpiration, leading to a more consistent but potentially higher water demand (Hasselquist *et al.*, 2010). Therefore, deciduous species likely encourage soil moisture retention and water infiltration, potentially fostering slower and more conservative ecosystem water cycling.

Coniferous trees can be associated with faster nutrient cycling than broadleaved trees (Augusto *et al.*, 2015), and our result demonstrated that coniferous tree species with resource-acquisitive strategies promoted nutrient cycling. This is likely due to the distinct physiological and ecological traits of coniferous trees, such as needle leaves, which were more efficient in nutrient retention and less susceptible to nutrient leaching than broadleaved trees (Franklin *et al.*, 2020). Coniferous trees also typically exhibit higher root nutrient foraging capabilities, which allow for greater uptake of soil nutrients (Park *et al.*, 2008). Additionally, coniferous species tend to allocate more resources to root biomass and associated mycorrhizal networks, which can further accelerate nutrient cycling processes (Ostonen *et al.*, 2011). However, our findings suggest that broadleaved tree species are more effective in promoting ecosystem productivity, likely due to their ability to optimize leaf area and aboveground biomass distribution (Niinemets *et al.*, 2006). The higher leaf area of broadleaved species leads to more efficient resource capture, particularly in terms of light interception, ultimately supporting greater ecosystem productivity (Liu *et al.*, 2016). Broadleaved species also generally exhibit a higher rate of carbon allocation to aboveground biomass, which contributes to greater forest productivity (Chave *et al.*, 2005). Consequently, a trade-off exists between coniferous species enhancing nutrient cycling and broadleaved species boosting productivity, underscoring the need to evaluate the relative importance of these factors in forest management goals.

Our findings indicate that the overall impact of leaf type, leaf phenology, mycorrhizal type, and resource-use strategy on carbon stocks, soil health and ecosystem multifunctionality were marginal (Fig. 1). The limited duration of the two-and-a-half-year study period may have contributed to these weak effects. Ecosystem processes and interactions operate over long-time scales, and the effects of trees on some services may take longer to manifest as the trees mature (Hastings, 2010). A previous study suggests that tree species identity influenced C sequestration rates in forest soils, but these differences were not substantial enough to significantly alter the overall soil carbon pool, even after 30 years (Vesterdal *et al*., 2008). However, short-term experiments such as ours can provide valuable information regarding the ecology of recently established plantations, and indicate the potential direction of future ecosystem services. However, to more comprehensively understand potential impacts, longer-term studies are needed to observe sustained and cumulative effects of tree species on ecosystem services.

4.2 Soil microbial communities and tree functional traits as drivers of forest ecosystem services

Consistent with our hypothesis, soil microbial community structure, specifically the ratio of fungi-bacteria and soil microbial composition, emerged as a key biological factor explaining variation in ecosystem services among tree species (Fig. 3). This is in concordance with other studies that soil functioning is well explained by soil microbial community structure (Zhou *et al*., 2020), rather than soil microbial diversity and biomass. However, it should also be noted that the effects of tree species on soil microbial diversity and biomass may require a longer period to become evident than that of our study (Hastings, 2010).

Soil microbial community structure, in particular the ratio of fungi-bacteria, was associated with several ecosystem services, including soil health, water retention, nutrient cycling and ecosystem productivity. This relationship can be linked to plant resource use strategies, with bacterial dominated systems typified by exploitative plants, rapid growth and tissue turnover and associated rapid soil process rates s (Wardle *et al.*, 2004; Boeddinghaus *et al.*, 2019; Neyret *et al.*, 2024). In contrast, soil fungi dominated systems which have generally slower rates of nutrient cycling (Neyret *et al.*, 2024). However, soil fungi play an important role in the decomposition of complex woody plant material, facilitating soil microbial activity (Talbot *et al.*, 2013), and are recognized for their involvement in plant productivity, especially by acquiring nutrients directly from organic matter via ectomycorrhizal fungal associations, and this may explain their positive association with these aspects of ecosystem functioning in this study.

Contrary to our initial hypothesis, EM tree species showed greater nutrient cycling and multifunctionality than AM tree species (Fig. 3 and Fig. S4), although AM fungi are known to improve plant nutrient uptake and cycling by extending their hyphae beyond the nutrient-depleted zones surrounding the roots (Phillips *et al.*, 2013). This unexpected outcome may stem from specific soil conditions favoring EM-associated processes in our study. EM fungi are adept at decomposing organic compounds, enabling them to mobilize a broader spectrum of nutrients locked within the soil organic matter, especially in relatively high soil organic matter content (Read *et al.*, 2003). Indeed, the soil organic matter content was maintained at a relatively high level, averaging approximately 5.6% in the present study. This enhanced ability facilitates more efficient nutrient uptake and cycling, thereby supporting multifunctionality. By contrast, AM fungi primarily rely on inorganic nutrients, making them less efficient in nutrient acquisition under such conditions (Willis *et al.*, 2013). Consequently, the high soil organic matter content in the present experiment likely benefits EM tree species, enabling them to more effectively exploit the available nutrient pools and contribute services of nutrient cycling and multifunctionality.

There is mounting evidence to suggest that tree resource-use strategies are important factors influencing ecosystem functioning, and thus ecosystem services, in forest ecosystems (Augusto & Boca, 2022; Zak *et al*., 2003). Trees with resource-acquisitive strategies can gain competitive advantages in productive environments, where they out-compete conservative species, and efficiently absorb and allocate nutrients to enhance ecosystem nutrient cycling and plant growth rates (Weemstra *et al*., 2021). This could promote multiple ecosystem services (Fig. 1). Among the tree functional traits, leaf N content emerged as the best predictor of the nutrient cycling indicators (Fig. 3). This supports the idea that leaf N content plays a pivotal role in driving multiple ecosystem functions (Hodgson *et al*., 2011). It is well established that leaf and root functional traits reflecting plant economics and resource-use strategies, influence plant performance and multiple ecological functions (Pierce *et al*., 2017; Weemstra *et al*., 2021), with species exhibiting high leaf N content signifying resource-acquisitive strategies that promote efficient nutrient cycling (Hodgson *et al*., 2011). In our data this is further supported by the positive association between leaf N concentrations and nutrient cycling (Fig. S4), indicating that greater leaf N is correlated with higher nutrient demands, leading to enhanced nutrient uptake and changes in soil nutrient dynamics (Ng *et al*., 2019). Furthermore, leaf N is significantly associated with soil microbial community structure (Fig. S4). It is worth noting that leaf N content indirectly influenced multifunctionality by affecting the ratio of fungi-bacteria and soil microbial composition (Fig. 4).

4.3 Implications for conservation and restoration in subtropical forest

In combating climate change and land degradation, it is crucial to establish the link between subtropical tree species and ecosystem services, particularly in terms of carbon sequestration and biodiversity support (Lewis *et al*., 2019). However, in China the prevalence of juvenile forest cover and the pronounced coniferization of subtropical forests are thought to have significantly diminished the provision of ecosystem services (Wang *et al*., 2022). Selecting appropriate tree species that support biodiversity and ecosystem services is a vital strategy for restoring forest ecosystems (Thomas *et al*., 2014; Fremout *et al*., 2022). Through the intentional selection of tree species with desirable traits, restoration has the potential to enhance ecosystem services in forests, and to rehabilitate crucial natural environments (Nunes *et al*., 2022). For example, by strategically planting EM species to promote nutrient cycling and multifunctionality, as it is measured here, and by planting deciduous trees to water retention (e.g. in more arid environments), we can enhance the overall health and sustainability of forest ecosystems, benefiting both the natural environment and society.

Our research also provides valuable guidance for ecosystem restoration efforts within the United Nations framework for the 2020-2030 decade on restoration. Currently, forest restoration plans must enhance ecosystem services to ensure the sustainable development of human society. Based this goal and on our results, we propose three concepts to improve forest restoration strategies. 1) Expand the restoration areas of dominant tree species in subtropical regions based on their relationship with desired ecosystem services. 2) Establish a planting resource repository (e.g. an online database or app) that provides information on species nutrient resource use strategies, and relates tree functional traits to ecosystem services, thus providing information for managers to optimize forest ecosystem service performance. 3) Consider the role of soil microorganisms in maintaining forest ecosystem services, as the support of ecosystem multifunctionality by soil microbial diversity has now been widely documented (Pommier *et al*., 2018; Shi *et al*., 2021; Wang *et al*., 2024; Zhou *et al*., 2020). Achieving these goals would also benefit from information about which services are desired and prioritized (measurable in social surveys) (Peter *et al*., 2022) and measurement of a wider range of ecosystem services to better reflect true multifunctionality, e.g. biodiversity benefits and cultural value (Manning *et al*., 2018; Neyret *et al*., 2023).

In summary, these insights into the relationships between tree species and ecosystem functions can inform the management of forest ecosystems, especially in cases where specific services are desired. Future studies incorporating longer-term observations, mixtures of tree species and broader spatial scales (van der Plas *et al*., 2016a, b) could further enhance our understanding of these intricate interactions and their implications for ecosystem multifunctionality.

5. Conclusion

Our study revealed that tree species have distinct and significant effects on various ecosystem services. Broadleaved tree species enhanced ecosystem productivity but slowed nutrient cycling, while deciduous trees contributed positively to water retention. Trees associated with ectomycorrhizal fungi promoted nutrient cycling and multifunctionality. Soil microbial communities, particularly the ratio of fungi-bacteria, and microbial composition were more closely associated with ecosystem functions and overall multifunctionality than microbial diversity and biomass. Furthermore, our findings highlight the crucial role of resource-use strategies in shaping ecosystem multifunctionality. Specifically, tree species with higher leaf N content showed greater nutrient cycling, indicating that tree species adopting a resource-acquisitive strategy play a key role in influencing ecosystem services.

Data Availability Statement

The data and R scripts supporting the findings of this study are available in the supplementary materials.

References

Augusto L, Boca A. (2022) Tree functional traits, forest biomass, and tree species diversity interact with site properties to drive forest soil carbon. *Nature Communications* 13, 1097.

Augusto L, De Schrijver A, Vesterdal L, Smolander A, Prescott C, Ranger J. (2015) Influences of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate and boreal forests. *Biological Reviews* 90, 444-466.

Baez S, Homeier J. (2018) Functional traits determine tree growth and ecosystem productivity of a tropical montane forest: Insights from a long-term nutrient manipulation experiment. *Global Change Biology* 24, 399-409.

Bergmann J, Weigelt A, van Der Plas F, Laughlin DC, Kuyper TW, Guerrero-Ramirez N, Valverde-Barrantes OJ, Bruelheide H, Freschet GT, Iversen CM, Kattge J, Luke McCormack M, Meier IC, Rillig MC, Roumet C, Semchenko M, Sweeney CJ, Ruijven J, York LM, Mommer L. (2020) The fungal collaboration gradient dominates the root economics space in plants. *Science Advances* 6, eaba3756.

Boeddinghaus RS, Marhan S, Berner D, Boch S, Fischer M, Hölzel N, Kattge J, Klaus VH, Kleinebecker T, Oelmann Y, Prati D, Schäfer D, Schöning I, Schrumpf M, Sorkau E, Kandeler E, Manning P. (2019) Plant functional trait shifts explain concurrent changes in the structure and function of grassland soil microbial communities. *Journal of Ecology* 107, 197-2210.

Brockerhoff EG, Barbaro L, Castagneyrol B, Forrester DI, Gardiner B, González-Olabarria JR, Lyver PO, Meurisse N, Oxbrough A, Taki H, Thompson ID, van der Plas F, Jactel H. (2017) Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodiversity and Conservation* 26, 3005-3035.

Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, Fölster H, Fromard F, Higuchi N, Kira T, Lescure JP, Nelson BW, Ogawa H, Puig H, Riéra B, Yamakura T. (2005). Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145, 87-99.

De Deyn GB, Cornelissen JH, Bardgett RD. (2008) Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters* 11, 516-531.

Díaz S, Kattge J, Cornelissen JH, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Prentice IC, Garnier E, Bönisch G, Westoby M, Poorter H, Reich PB, Moles AT, Dickie J, Gillison AN, Zanne AE, Chave J, Wright SJ, Sheremet'ev SN, Jactel H, Baraloto C, Cerabolini B, Pierce S, Shipley B, Kirkup D, Casanoves F, Joswig JS, Günther A, Falczuk V, Rüger N, Mahecha MD, Gorné LD. (2016). The global spectrum of plant form and function. *Nature* 529(7585), 167-171.

Franklin HM, Chen C, Carroll AR, Saeck E, Fisher P, Burford MA. (2020). Leaf litter of two riparian tree species has contrasting effects on nutrients leaching from soil during large rainfall events. *Plant and Soil* 457, 389-406.

Fremout T, Thomas E, Taedoumg H, Briers S, Gutiérrez-Miranda CE, Alcázar-Caicedo C, Lindau A, Kpoumie HM, Vinceti B, Kettle C, Ekué M, Atkinson R, Jalonen R, Gaisberger R, Elliott S, Brechbühler E, Ceccarelli V, Krishnan S, Vacik H, Wiederkehr-Guerra G, Salgado-Negret B, González MA, Ramírez W, Moscoso-Higuita LG, Vásquez Á, Cerrón J, Maycock C, Muys B. (2022) Diversity for Restoration (D4R): Guiding the selection of tree species and seed sources for climate-resilient restoration of tropical forest landscapes. *Journal of Applied Ecology* 59, 664-679.

Gamfeldt L, Snall T, Bagchi R, Jonsson M, Gustafsson L, Kjellander P, Ruiz-Jaen MC, Froberg M, Stendahl J, Philipson CD, Mikusinski G, Andersson E, Westerlund B, Andren H, Moberg F, Moen J, Bengtsson J. (2013) Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications* 4, 1340.

Hasselquist NJ, Allen MF, Santiago LS. (2010) Water relations of evergreen and drought-deciduous trees along a seasonally dry tropical forest chronosequence. *Oecologia* 164, 881-890.

Hastings A. (2010). Timescales, dynamics, and ecological understanding. *Ecology* 91, 3471-3480.

Hodgson JG, Montserrat-Marti G, Charles M, Jones G, Wilson P, Shipley B, Sharafi M, Cerabolini BE, Cornelissen JH, Band SR, Bogard A, Castro-Diez P, Guerrero-Campo J, Palmer C, Perez-Rontome MC, Carter G, Hynd A, Romo-Diez A, de Torres Espuny L, Royo Pla F. (2011) Is leaf dry matter content a better predictor of soil fertility than specific leaf area? *Annals of Botany* 108, 1337-1345.

Lefcheck JS. (2016) piecewiseSEM, piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution* 7, 573–579.

Lewis SL, Wheeler CE, Mitchard ET, Koch A. (2019) Restoring natural forests is the best way to remove atmospheric carbon. *Nature* 568, 25-28.

Liu Y, Dawson W, Prati D, Haeuser E, Feng Y, van Kleunen M. (2016). Does greater specific leaf area plasticity help plants to maintain a high performance when shaded?. *Annals of Botany* 118(7), 1329-1336.

Looney BP, Meidl P, Piatek MJ, Miettinen O, Martin FM, Matheny PB, Labbe JL. (2018) Russulaceae: a new genomic dataset to study ecosystem function and evolutionary diversification of ectomycorrhizal fungi with their tree associates. *New Phytologist* 218, 54-65.

Maestre FT, Quero JL, Gotelli NJ, Escudero A, Ochoa V, Delgado-Baquerizo M, Garcia-Gomez M, Bowker MA, Soliveres S, Escolar C, Garcia-Palacios P, Berdugo M, Valencia E, Gozalo B, Gallardo A, Aguilera L, Arredondo T, Blones J, Boeken B, Bran D, Conceicao AA, Cabrera O, Chaieb M, Derak M, Eldridge DJ, Espinosa CI, Florentino A, Gaitan J, Gatica MG, Ghiloufi W, Gomez-Gonzalez S, Gutierrez JR, Hernandez RM, Huang X, Huber-Sannwald E, Jankju M, Miriti M, Monerris J, Mau RL, Morici E, Naseri K, Ospina A, Polo V, Prina A, Pucheta E, Ramirez-Collantes DA, Romao R, Tighe M, Torres-Diaz C, Val J, Veiga JP, Wang D, Zaady E. (2012) Plant species richness and ecosystem multifunctionality in global drylands. *Science* 335, 214-218.

Macinnis-Ng CM, Zeppel MJ, Palmer AR, Eamus D. (2016) Seasonal variations in tree water use and physiology correlate with soil salinity and soil water content in remnant woodlands on saline soils. *Journal of Arid Environments* 129, 102-110.

Manning P, Van Der Plas F, Soliveres S, Allan E, Maestre FT, Mace G, Whittingham MJ, Fischer M. (2018) Redefining ecosystem multifunctionality. *Nature Ecology & Evolution*, 2(3), 427-436.

Nadrowski K, Wirth C, Scherer-Lorenzen M. (2010) Is forest diversity driving ecosystem function and service? *Current Opinion in Environmental Sustainability* 2, 75-79.

Neyret M, Le Provost G, Boesing AL, Schneider FD, Baulechner D, Bergmann J, Vries F, Fiore-Donno AM, Geisen S, Goldmann K, Merges A, Saifutdinov RA, Simons NK, Tobias JA, Zaitsev AS, Gossner MM, Jung K, Kandeler E, Krauss J, Penone C, Schloter M, Schulz S, Staab M, Wolters V, Apostolakis A, Birkhofer K, Boch S, Boeddinghaus RS, Bolliger R, Bonkowski M, Buscot F, Dumack K, Fischer M, Gan HY, Heinze J, Hölzel N, John K, Klaus VH, Kleinebecker T, Marhan S, Müller J, Renner SC, Rillig MC, Schenk NV, Schöning I, Schrumpf M, Seibold S, Socher SA, Solly EF, Teuscher M, Kleunen M, Wubet T, Manning P. (2024). A slow-fast trait continuum at the whole community level in relation to land-use intensification. *Nature Communications* 15(1), 1251.

Neyret M, Peter S, Le Provost G, Boch S, Boesing AL, Bullock JM, Hölzel N, Klaus VH, Kleinebecker T, Krauss J, Müller J, Müller S, Ammer C, Buscot F, Ehbrecht M, Fischer M, Goldmann K, Jung K, Mehring M, Müller T, Renner SC, Schall P, Scherer-Lorenzen M, Westphal C, Wubet T, Manning P (2023). Landscape management strategies for multifunctionality and social equity. *Nature Sustainability* 6(4), 391-403.

Niinemets Ü, Portsmuth A, Tobias M. (2006). Leaf size modifies support biomass distribution among stems, petioles and mid-ribs in temperate plants. *New Phytologist* 171(1), 91-104.

Nunes S, Gastauer M, Cavalcante RB, Ramos SJ, Caldeira JrCF, Silva D, Rodrigues RR, Salomão R, Oliveira M, Souza-Filho PW, Siqueira JO. (2020) Challenges and opportunities for large-scale reforestation in the Eastern Amazon using native species. *Forest Ecology and Management* 466, 118120.

Ostonen I, Helmisaari HS, Borken W, Tedersoo L, Kukumägi M, Bahram M, Lindroos AJ, Nöjd P, Uri V, Merilä P, Asi E, Lõhmus K. (2011) Fine root foraging strategies in Norway spruce forests across a European climate gradient. *Global Change Biology* 17(12), 3620-3632.

Park BB, Yanai RD, Fahey TJ, Bailey SW, Siccama TG, Shanley JB, Cleavitt NL. (2008). Fine root dynamics and forest production across a calcium gradient in northern hardwood and conifer ecosystems. *Ecosystems* 11, 325-341.

Peter S, Le Provost G, Mehring M, Müller T, Manning P. (2022). Cultural worldviews consistently explain bundles of ecosystem service prioritisation across rural Germany. *People and Nature* 4(1), 218-230.

Phillips RP, Brzostek E, Midgley MG. (2013) The mycorrhizal-associated nutrient economy: a new framework for predicting carbon–nutrient couplings in temperate forests. *New Phytologist* 199(1), 41-51.

Pierce S, Negreiros D, Cerabolini BE, Kattge J, Díaz S, Kleyer M, Shipley B, Wright SJ, Soudzilovskaia NA, Onipchenko VG, van Bodegom PM, Frenette-Dussault C, Weiher E, Pinho BX, Cornelissen JHC, Grime JP, Thompson K, Hunt R, Wilson PJ, Buffa G, Nyakunga OC, Reich PB, Caccianiga M, Mangili F, Ceriani RM, Luzzaro A, Brusa G, Siefert A, Barbosa, NPU, Chapin III FS, Cornwell WK, Fang J, Fernandes GW, Garnier E, Stradic SL, Peñuelas J, Melo FPL, Slaviero A, Tabarelli M, Tampucci D. (2017) A global method for calculating plant CSR ecological strategies applied across biomes world-wide. *Functional Ecology* 31, 444-457.

Pommier T, Cantarel AA, Grigulis K, Lavorel S, Legay N, Baxendale C, Bardgett RD, Bahn M, Poly F, Clément JC. (2018) The added value of including key microbial traits to determine nitrogen-related ecosystem services in managed grasslands. *Journal of Applied Ecology* 55, 49-58.

Read DJ, Perez-Moreno J. (2003) Mycorrhizas and nutrient cycling in ecosystems–a journey towards relevance?. *New phytologist* 157(3), 475-492.

Reich PB. (2014) The world-wide ‘fast–slow’plant economics spectrum: a traits manifesto. *Journal of Ecology* 102, 275-301.

Roumet C, Birouste M, Picon-Cochard C, Ghestem M, Osman N, Vrignon-Brenas S, Cao KF, Stokes A. (2016) Root structure–function relationships in 74 species: evidence of a root economics spectrum related to carbon economy. *New Phytologist* 210, 815-826.

Saiya-Cork K, Sinsabaugh R, Zak D. (2002) The effects of long term nitrogen deposition on extracellular enzyme activity in an Acer saccharum forest soil. *Soil Biology and Biochemistry* 34, 1309-1315.

Schuldt A, Ebeling A, Kunz M, Staab M, Guimarães-Steinicke C, Bachmann D, Buchmann N, Durka W, Fichtner A, Fornoff F. (2019) Multiple plant diversity components drive consumer communities across ecosystems. *Nature Communications* 10, 1460.

Shen Y, Umaña MN, Li W, Fang M, Chen Y, Lu H, Yu S. (2022) Linking soil nutrients and traits to seedling growth: A test of the plant economics spectrum. *Forest Ecology and Management* 505, 119941.

Shi X, Wang J, Lucas-Borja ME, Wang Z, Li X, Huang Z. (2021) Microbial diversity regulates ecosystem multifunctionality during natural secondary succession. *Journal of Applied Ecology* 58, 2833-2842.

Talbot JM, Bruns TD, Smith DP, Branco S, Glassman SI, Erlandson S, Vilgalys R, Peay KG. (2013)

Independent roles of ectomycorrhizal and saprotrophic communities in soil organic matter decomposition. *Soil Biology and Biochemistry* 57, 282-291.

Tedersoo L, Bahram M, Zobel M. (2020) How mycorrhizal associations drive plant population and community biology. *Science* 367(6480), eaba1223.

Thomas E, Jalonen R, Loo J, Boshier D, Gallo L, Cavers S, Bordács S, Smith P, Bozzano M. (2014) Genetic considerations in ecosystem restoration using native tree species. *Forest Ecology and Management* 333, 66-75.

van Der Plas F, Manning P, Allan E, Scherer-Lorenzen M, Verheyen K, Wirth C, Zavala MA, Hector A, Ampoorter E, Baeten L, Barbaro L, Bauhus K, Benavides R, Benneter A, Berthold F, Bonal D, Bouriaud O, Bruelheide H, Bussotti F, Carnol M, Castagneyrol B, Charbonnier Y, Coomes D, Coppi A, Bastias CC, Dawud SM, Wandeler HD, Domisch T, Finér L, Gessler A, Granier A, Grossiord C, Guyot V, Hättenschwiler S, Jactel H, Jaroszewicz B, Joly FX, Jucker T, Koricheva J, Milligan H, Müller S, Muys B, Nguyen D, Pollastrini M, Raulund-Rasmussen K, Selvi F, Stenlid J, Valladares F, Vesterdal L, Zielínski D, Fischer M. (2016a) Jack-of-all-trades effects drive biodiversity–ecosystem multifunctionality relationships in European forests. *Nature Communications* 7, 11109.

van Der Plas F, Manning P, Soliveres S, Allan E, Scherer-Lorenzen M, Verheyen K, Wirth C, Zavala MA, Ampoorter E, Baeten L, Barbaro L, Bauhus J, Benavides R, Benneter A, Bonal D, Bouriaud O, Bruelheide H, Bussotti F, Carnol M, Castagneyrol B, Charbonnier Y, Coomes DA, Coppi A, Bastias CC, Dawud SM, Wandeler HD, Domisch T, Finér L, Gessler A, Granier A, Grossiord C, Guyot V, Hättenschwiler S, Jactel H, Jaroszewicz B, Joly F, Jucker T, Koricheva J, Milligan H, Mueller S, Muys B, Nguyen D, Pollastrini M, Ratcliffe S, Raulund-Rasmussen K, Selvi F, Stenlid J, Valladares F, Vesterdal L, Zielínski D, Fischer M. (2016b) Biotic homogenization can decrease landscape-scale forest multifunctionality. *Proceedings of the National Academy of Sciences* 113(13), 3557-3562.

Vesterdal L, Schmidt IK, Callesen I, Nilsson LO, Gundersen P. (2008) Carbon and nitrogen in forest floor and mineral soil under six common European tree species. *Forest Ecology and Management* 255(1), 35-48.

Wan X, Yu Z, Wang M, Zhang Y, Huang Z. (2022) Litter and root traits control soil microbial composition and enzyme activities in 28 common subtropical tree species. *Journal of Ecology* 110, 3012-3022.

Wang L, Delgado-Baquerizo M, Wang D, Isbell F, Liu J, Feng C, Liu J, Zhong Z, Zhu H, Yuan X, Chang Q, Liu C. (2019) Diversifying livestock promotes multidiversity and multifunctionality in managed grasslands. *Proceedings of the National Academy of Sciences* 116(13), 6187-6192.

Wang J, Shi X, Lucas-Borja ME, Lam SK, Wang Z, Huang Z. (2022) Plants, soil properties and microbes directly and positively drive ecosystem multifunctionality in a plantation chronosequence. *Land Degradation & Development* 33(16), 3049-3057.

Wang J, Peñuelas J, Shi X, Liu Y, Delgado Baquerizo M, Mao J, Zhang G, Liu C, Pan G (2024). Soil microbial biodiversity supports the delivery of multiple ecosystem functions under elevated CO_2 and warming. *Communications Earth & Environment* 5(1), 615.

Wardle DA, Bardgett RD, Klironomos JN, Setala H, Van Der Putten WH, Wall DH. (2004) Ecological linkages between aboveground and belowground biota. *Science* 304, 1629-1633.

Weemstra M, Zambrano J, Allen D, Umaña MN. (2021) Tree growth increases through opposing above-ground and below-ground resource strategies. *Journal of Ecology* 109, 3502-3512.

Willis A, Rodrigues BF, Harris PJ. (2013). The ecology of arbuscular mycorrhizal fungi. *Critical Reviews in Plant Sciences* 32(1), 1-20.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R. (2004) The worldwide leaf economics spectrum. *Nature* 428(6985), 821-827.

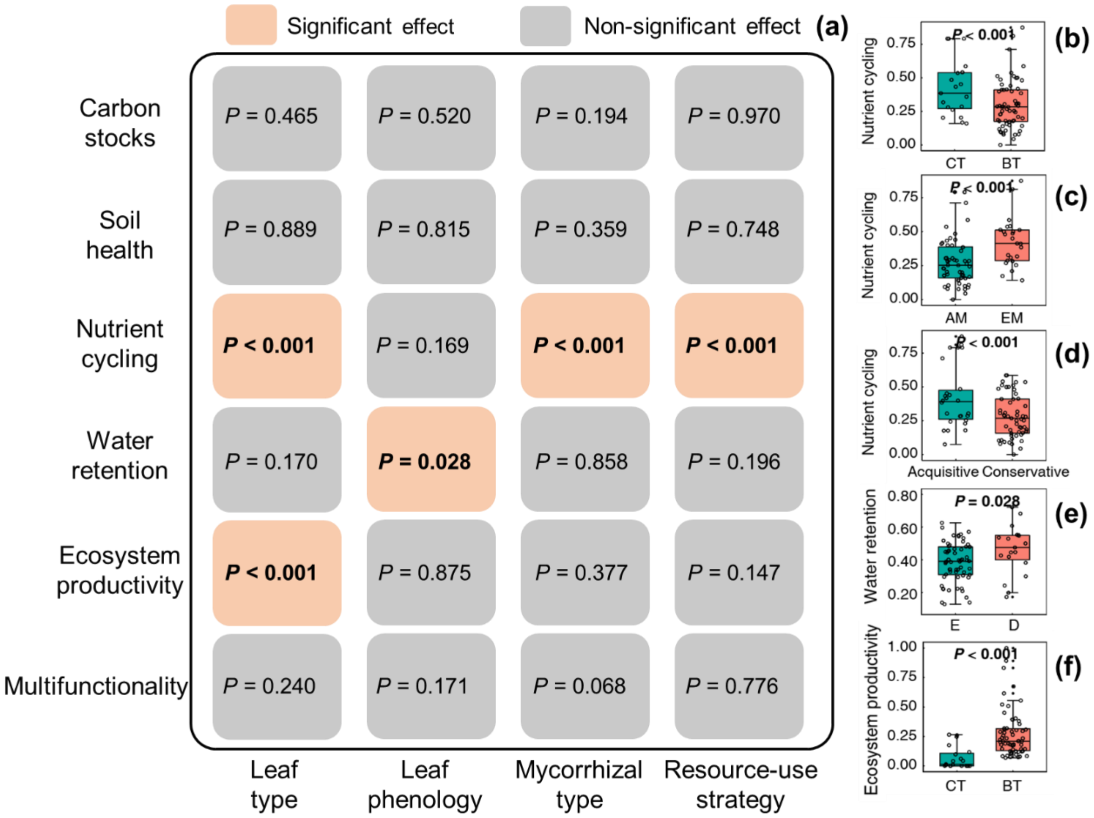
Wright SJ, Kitajima K, Kraft NJ, Reich PB, Wright IJ, Bunker DE, Condit R, Dalling JW, Davies SJ, Díaz S, Engelbrecht BMJ, Harms KE, Hubbell SP, Marks CO, Ruiz-Jaen MC, Salvador CM, Zanne AE. (2010) Functional traits and the growth–mortality trade-off in tropical trees. *Ecology* 91, 3664-3674.

Zak DR, Holmes WE, White DC, Peacock AD, Tilman D. (2003) Plant diversity, soil microbial communities, and ecosystem function: are there any links? *Ecology* 84, 2042-2050.

Zhou Z, Wang C, Luo Y. (2020) Meta-analysis of the impacts of global change factors on soil microbial diversity and functionality. *Nature Communications* 11, 3072.

Table 1 Ecosystem properties used as indicators to examine subtropical tree species effects on multiple ecosystem services

Ecosystem service classes	Ecosystem variables used as indicators
Carbon stocks	Soil microbial biomass carbon, dissolved organic carbon
Soil health	Enzyme activities: β-glucosidase, cellobiohydrolase, N-acetylglucosaminidase, acid phosphatase
Nutrient cycling	Soil nitrification rates, N mineralization rates
Water retention	Soil water content, litter maximum water-holding capacity
Ecosystem productivity	Litterfall mass



	Leaf type	Leaf phenology	Mycorrhizal type	Resource-use strategy
Carbon stocks	*P* = 0.465	*P* = 0.520	*P* = 0.194	*P* = 0.970
Soil health	*P* = 0.889	*P* = 0.815	*P* = 0.359	*P* = 0.748
Nutrient cycling	***P* < 0.001**	*P* = 0.169	***P* < 0.001**	***P* < 0.001**
Water retention	*P* = 0.170	***P* = 0.028**	*P* = 0.858	*P* = 0.196
Ecosystem productivity	***P* < 0.001**	*P* = 0.875	*P* = 0.377	*P* = 0.147
Multifunctionality	*P* = 0.240	*P* = 0.171	*P* = 0.068	*P* = 0.776

Fig. 1 Heatmap illustrating the effect of tree functional traits on ecosystem services in a subtropical tree experiment (a), based on Fig. S2. Boxplots illustrating significant effects of tree functional traits on nutrient cycling (b-d), water retention (e), and ecosystem productivity (f). CT, coniferous; BT, broadleaved; E, evergreen; D, deciduous; AM, arbuscular mycorrhizal; EM, ectomycorrhizal. Gray blocks indicate non-significant effects. Orange blocks indicate significant effects. Bold fonts indicate significant differences at $P < 0.05$. The black solid lines represent mean values, the lower and upper edges indicate the 25th and 75th percentiles, the bars show the 5th and 95th percentiles and each dot corresponds to a data point within the dataset.

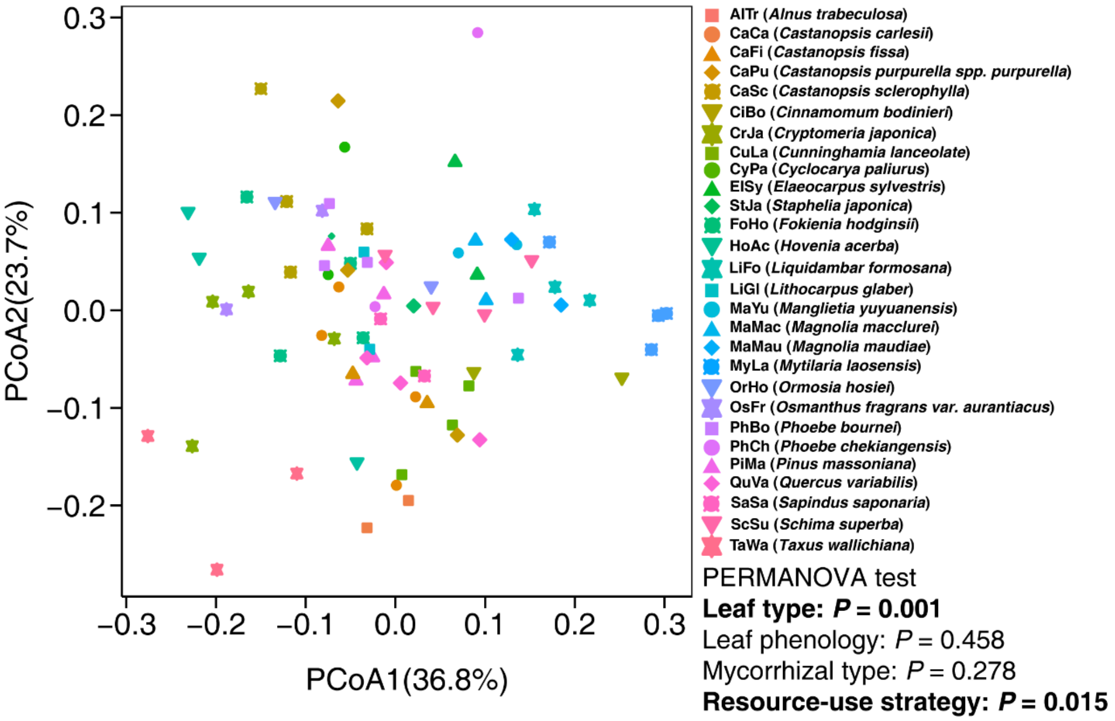


Fig. 2 The structure of multiple ecosystem functional indexes by PCoA analysis under different tree species to examine subtropical tree species effects on multiple ecosystem functions. Bold fonts indicate significant differences at $P < 0.05$.

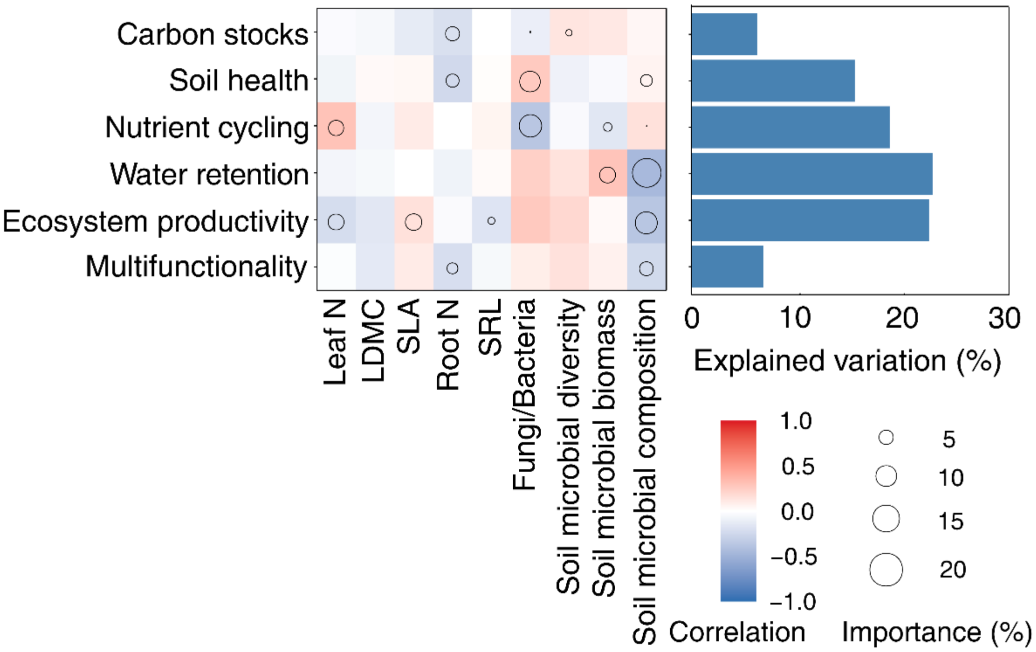


Fig. 3 The effect of tree functional traits and soil microbial communities on ecosystem services to examine subtropical tree species effects on multiple ecosystem services. The red in the heatmap indicates a positive correlation between ecosystem services and tree functional traits and soil microbial communities, while the blue represents a negative correlation. The size of the circles in the heatmap reflects the contribution of tree functional traits and soil microbial communities to ecosystem services, with the bar charts displaying the cumulative contributions. LDMC, leaf dry matter content; SLA, specific leaf area, SRL, specific root length.

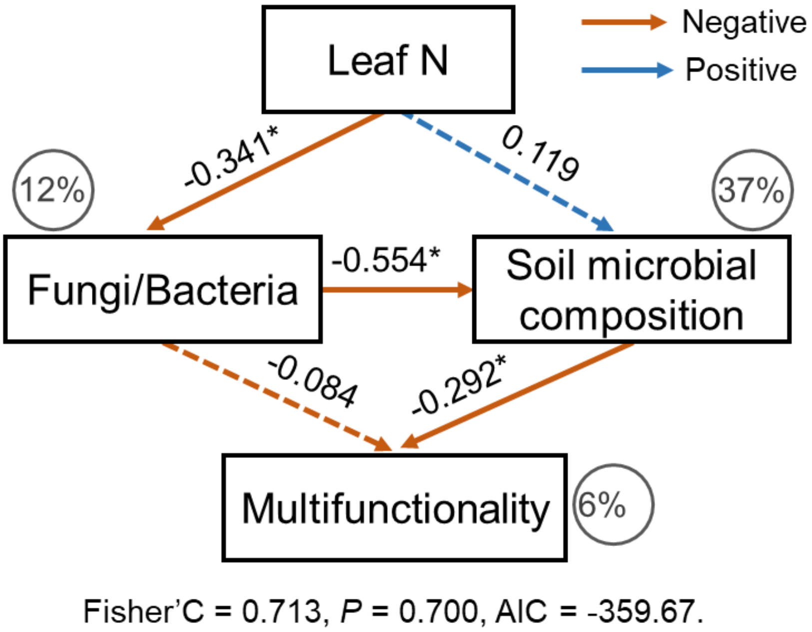


Fig. 4 Structural equation modeling indicating the direct and indirect effects of tree functional traits and soil microbial communities on subtropical ecosystem multifunctionality. The numbers beside the arrows are corresponding standardized path coefficients (*$P < 0.05$). The brown, blue, and dashed lines indicate negative, positive, and non-significant effects, respectively. The percentage of variance for the explained variables is indicated below the corresponding variable.

Supplement material online

Table S1 Tree species used in an experiment to examine subtropical tree species effects on multiple ecosystem services.

Table S2 Changes in ecosystem function indices under different subtropical tree species.

Fig. S1 Principal component analysis (PCA) of tree traits under different subtropical tree species. SRL, specific root length; LDMC, leaf dry matter content; SLA, specific leaf area.

Fig. S2 Effect of tree functional traits on ecosystem services including carbon stocks (a), soil health (b), nutrient cycling (c), water retention (d), ecosystem productivity (e), and multifunctionality (f), in a subtropical ecosystem function experiment. CT, coniferous; BT, broadleaved; E, evergreen; D, deciduous; AM, arbuscular mycorrhizal; EM, ectomycorrhizal. The black solid lines represent mean values, the lower and upper edges indicate the 25th and 75th percentiles, the bars show the 5th and 95th percentiles and each dot corresponds to a data point within the dataset. Bold fonts indicate significant differences at $P < 0.05$.

Fig. S3 Random forest analyses evaluating the effect of tree functional traits on ecosystem services including carbon stocks (a), soil health (b), nutrient cycling (c), water retention (d), ecosystem productivity (e), and multifunctionality (f), in a subtropical ecosystem function experiment. LDMC, leaf dry matter content; SLA, specific leaf area, SRL, specific root length. * indicate significant differences at $P < 0.05$.

Fig. S4 Pearson correlation among ecosystem services, plant functional traits, and soil microbial communities among 28 tree species in the present study. Bold fonts indicate significant differences at $P < 0.05$.