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Effects of biotic and abiotic factors on ecosystem multifunctionality of plantations

Jiaxin Tian[1], Tian Ni[1], Zheng Miao[1], Yuanshuo Hao[1], Aiyun Ma[1], Lihu Dong[1*] and Fengri Li[1*]

Abstract

Background Mixed forests are better than monoculture forests in biodiversity, stand structure and productivity stability. However, a more comprehensive assessment of the ecosystem functions of monoculture and mixed plantations is lacking. We compared the single functions and ecosystem multifunctionality (EMF) in *Fraxinus mandshurica* and *Larix olgensis* mixed plantations with monoculture plantations in Northeast China and discussed the influences of biodiversity and environmental factors on EMF.

Results The mixed plantations had higher biodiversity and ecological functions. Biodiversity was significantly higher in mixed plantations (such as CWM_{MH}, Shrub.Shannon, Shrub.Richness, Herb.Shannon, Herb.Richness), but environmental factors differed less among the three forest types, and belowground diversity differed significantly only in the Bacterial.Shannon and Fungal.Shannon. Mixed plantations showed significant differences in single ecological functions relative to monoculture plantations, with more pronounced differences between mixed plantations and *Larix olgensis* monoculture plantations. Weighted ecosystem multifunctionality was significantly higher in mixed plantations than in monoculture plantations. EMF was mainly driven by tree diversity, environmental factors, shrub and herb species diversity, and soil microbial alpha diversity, which explained 25.35%, 8.94%, 8.83%, and 7.65% of the variation, respectively.

Conclusions The establishment of mixed plantations can increase the biodiversity of forest stands and improve the ecosystem functions. These results highlight the advantages of multi-species plantations and the necessity of planting them. They are important for the conservation of biodiversity and the sustainable management of plantations.

Keywords Ecosystem multifunctionality, Plantation, Biodiversity, Environmental factor

Introduction

Plantation management is important for global biogeochemical cycles and climate change mitigation due to the rapid growth, high forest turnover, and extensive planted areas (Hua et al. 2022). Since the 1970s, China has promulgated and implemented several forest protection projects (e.g., the Returning Farmland to Forest Program, Three-North Shelter Forest Program, and Natural Forest Protection Program), plenty of plantations have been planted in a short period. The 2019 9th National Forest Resources Inventory indicated a 7.95-million hectare forest plantation area in China, the highest globally (Administration 2019). However, these plantations face some challenges. As a result of the long-term traditional plantation management mode, many plantations with simple structure and single tree species have been formed, resulting in serious problems such as soil acidification and soil fertility decline (Wang et al. 2017). Meanwhile, biodiversity loss has negatively affected

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*Correspondence:
Lihu Dong
lihudong@nefu.edu.cn
Fengri Li
fengrili@nefu.edu.cn
[1] Key Laboratory of Sustainable Forest Ecosystem Management-Ministry of Education, School of Forestry, Northeast Forestry University, Harbin 150040, Heilongjiang, China

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forest productivity and ecosystem services (Gurmesa et al. 2023). Nowadays, researchers have attempted to establish mixed plantations with multiple tree species to improve their biodiversity and ecosystem functions (Sande et al. 2017; Yang et al. 2022). Studies on the multifunctionality of forest ecosystems have traditionally focused more on natural forests with mixed species, while little attention has been paid to the multifunctionality changes in mixed-species plantations (Lwila et al. 2021). Therefore, it is important and necessary to study the changes in ecological functions and ecosystem multifunctionality of mixed plantations to achieve sustainable management (Xu et al. 2021).

Forest ecosystems can provide a variety of ecological functions. Previous studies on plantations have focused on single functions, such as carbon sequestration capacity, timber production, nutrient cycling and productivity (Ma et al. 2007; Dangal et al. 2017; Luo et al. 2019; Carrasco et al. 2022; Wang et al. 2022a; Li et al. 2023b). To data, few studies have comprehensively evaluated the multifunctionality of plantation ecosystems and their influencing factors. As a comprehensive index used to evaluate multiple ecological functions, ecosystem multifunctionality (EMF) is of great significance for comprehensively understanding ecosystem structure and functions. Therefore, it is necessary to consider the ecosystem function of plantations from various perspectives to accurately evaluate the EMF of plantations (Manning et al. 2018; Wang et al. 2022b; Xu et al. 2023). The two mechanisms through which biodiversity influences EMF are selection- and niche-complementarity effects (Mensah et al. 2018; Wang et al. 2021). The niche-complementarity effect stipulates that heightened diversity of species can improve the efficiency of limited space and resource utilization and realize a variety of ecosystem functions (Tilman et al. 1997). However, communities with higher species diversity are more likely to have high-yielding species, which are often the main determinants of ecosystem functions (selection effect) (Huston 1997). Changes in the environment enhance or decrease ecosystem multifunctionality, but greater ecosystem multifunctionality increases resistance to environmental change (Hong et al. 2022; Zhao et al. 2024). Most studies agree that ecosystem functions are stronger in communities with higher biodiversity, including accumulation of soil organic carbon and recycling of nutrients (Inkotte et al. 2022). Uncertainty exists in the driving of EMF by aboveground and belowground biodiversity, as species diversity, stand structural diversity, functional characteristics of dominant species, and soil microbial diversity affect EMF differently, and thus the exploration of the relationship between biodiversity and EMF needs to be further strengthened.

The biodiversity of monoculture forests is limited compared to that of natural forests (Hua et al. 2022). The species diversity is more concentrated in understory vegetation in monoculture forests, and the herb and shrub diversity fulfils a vital role in promoting the EMF (Wei et al. 2021). In addition to aboveground biodiversity (species diversity, structural diversity, functional diversity, and phylogenetic diversity), biodiversity also includes soil microbial diversity (bacterial and fungal alpha diversity) (Soliveres et al. 2016). Soil microbial communities are complex and diverse, which affects the biogeochemical cycle and plays a key role in ecosystem functions (Li et al. 2023a). Likewise, the relationship between microbial diversity and EMF can be positive (Delgado-Baquerizo et al. 2016; Cui et al. 2022), negative (Huang et al. 2024), or neutral (Osburn et al. 2021), depending on the research methods and scale used. Belowground biodiversity is closely related to the soil environment. For example, soil pH strongly influences microbial composition and community structure across soil types and at different spatial scales (Zheng et al. 2019). Additionally, increased soil water content may be associated with higher complexity of plant community structure and EMF, which can also explain EMF changes (Li et al. 2021; Migliavacca et al. 2021). Belowground biodiversity and soil environment are important for evaluating the EMF in plantations because the continuous planting of large areas of monoculture forests affects plantation soil fertility and sustainable management (Zeng et al. 2021; Yang et al. 2022). Therefore, studying only aboveground or belowground diversity may lead to bias in EMF assessments (Delgado-Baquerizo et al. 2020).

Larix olgensis monoculture forests have some problems in the long term, such as the loss of nutrients leading to a decrease in soil fertility and the single species leading to a decrease in biodiversity (Yan et al. 2016). In general, *Fraxinus mandshurica* monoculture forests are more difficult to establish due to the high mortality of seedlings (Wang et al. 2013). Therefore, the establishment of mixed plantations can enhance stand productivity and functions of ecosystems (Li et al. 2020b; Feng et al. 2022). In mixed plantations, the principle of mutualism between two species can promote the growth of both species (Lwila et al. 2021). The roots of *Fraxinus mandshurica* improve soil chemical and microbial properties, thereby increasing soil nutrients (Wang 2002; Yan et al. 2016). This current study analyzed the differences between monoculture forests and mixed plantations and the correlation between their above- and belowground biodiversity, EMF, and environmental factors. Our primary objectives were to: (1) quantitatively assess the ecosystem multifunctionality of monoculture and mixed plantations; (2) identify the differences in environmental

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factors, ecosystem functions, and biodiversity between monoculture and mixed plantations; and (3) clarify the associations between environmental factors, biodiversity, and multifunctionality of the ecosystem. We aim to evaluate three hypotheses: H1: mixed plantations would have higher biodiversity than that of monoculture plantations, especially in terms of shrub-herb and soil microbial alpha diversity; H2: compared to monoculture plantations, mixed plantations would increase ecosystem functions; H3: aboveground biodiversity has a greater impact on ecosystem multifunctionality than belowground biodiversity.

Materials and methods
Site of study
The plantations were established in Shangzhi Forestry Bureau in Shangzhi City, Heilongjiang Province, China (127° 18′ 0″–127° 56′ 12″, 45° 18′ 16″–45° 35′ 55″). The area is a temperate humid continental monsoon climate zone, with a wet summer, dry spring, and icy winter. The mean yearly temperature is 2.8 °C and mean yearly precipitation is 723 mm, mainly occurring from June to August. The soil is a dark brown forest soil type, and the parent material is granite bedrock. Vegetation is categorized as Changbai flora, a typical broad-leaved, coniferous mixed forest in China and natural secondary forest and plantation formed by human disturbance. The main native tree species are *Fraxinus mandshurica*, *Betula platyphylla*, *Pinus koraiensis*, *Larix olgensis*, and *Acer pictum*, etc.

Experimental design
The selected plantations were with same age and same initial spacing (2 m×1.5 m). *Larix olgensis* and *Fraxinus mandshurica* seedlings were planted in row mixtures. Six monoculture *L. olgensis* plantations (PL), three monoculture *F. mandshurica* plantations (PF), and six mixed *L. olgensis*–*F. mandshurica* plantations (LF) were selected to set up plots. The area of each plot was 0.09 ha (Table 1) and three 10 m×10 m tree subplots were established in each plot. Three 2 m×2 m shrub, 1 m×1 m herb, and 0.5 m×0.5 m litter subplots were established in each plot, respectively. The composition and number of trees in

each plot with a diameter at breast height (DBH)≥5 cm was recorded, and their height and DBH were measured. The aboveground biomass (BT) of each tree species in the each plot was estimated according to DBH allometry equations for *Larix olgensis* and *Fraxinus mandshurica* (Xie 2022). Standard sample trees were selected and at least 50 intact leaves were collected for leaf functional trait measurements. The leaf area was scanned using a scanner and calculated using the ImageJ software. The specific area of leaves was calculated as: Specific leaf area=(leaf area/leaf dry weight)×100%. The leaves were placed into an oven and dried at 80 °C to constant weight, and their dry weight was measured.

The species composition, abundance, height, and coverage of shrubs and herbs were investigated. The harvest method was used to obtain all the shrubs, herbs, and litter in the plots, and their fresh weights were measured. In the laboratory, samples were dried at 80 °C to constant weight, and the biomasses of shrubs, herbs, and litter (BS, BH, and BL, respectively) were measured. The contents of N and C in litter were determined utilizing the $K_2Cr_2O_7/H_2SO_4$ oxidation and semimicro-Kjeldahl methods, respectively.

Measurements of soil physicochemical properties, soil enzymes and microbes
Nine sampling sites were evenly distributed in each plot. The 0–10 cm layer of soil was drilled using a soil drill (5 cm in diameter). This soil layer was used because studies have shown that it is the layer most significantly affected by tree species (Augusto et al. 2002). Composite samples were evenly mixed and transported to the laboratory in a sealed bag. After filtering the samples through a 2-mm sieve, they were sub-divided into three components. Soil microbial diversity was analyzed at −80 °C, soil enzyme activity was analyzed at −4 °C, and air-dried samples were utilized to measure the soil chemical and physical characteristics. Soil water content (SWC) and soil bulk density (SBD, g/cm³) were identified through the use of the cutting ring method. Soil pH was measured using a pH meter. Organic C in soil (SOC, g/kg) was determined utilizing the $K_2Cr_2O_7/H_2SO_4$ oxidation approach, and total N (TN) in soil was determined

Table 1 Basic characteristics of the stand types

Stand type	Density (trees/ha)	Altitude (m)	Canopy density	Species	Age (yrs)	Mean DBH (cm)	Mean height (m)
PL	2207±170	369	0.75	L	23	12.16±0.44	13.71±1.14
LF	1861±284	408	0.70	L	22	13.22±0.62	15.00±0.69
				F	22	12.31±0.25	15.36±1.08
PF	1996±223	395	0.75	F	21	10.89±0.51	13.70±0.66

Note: PL, monoculture *Larix olgensis* plantation; LF, mixed *Larix olgensis* –*Fraxinus mandshurica* plantation; PF, monoculture *Fraxinus mandshurica* plantation. L, *Larix olgensis*; F, *Fraxinus mandshurica*.

utilizing the semimicro-Kjeldahl method. Density of organic C in soil (SOD, g/m^2) was calculated using the following formula:

$$SOD = SOC_i \times SBD_i \times H_i \times (1 - G_i)/100 \quad (1)$$

where i represents the layer of soil, H_i indicates depth of soil sample, and G_i represents the proportion (%) of soil consisting of gravel > 2 mm in diameter.

Soil enzyme activities, including those of *N*-acetylglucosaminidase (NAG), β-glucosidase (GC), and acid phosphatase (ACP), in the samples were identified using the double-antibody sandwich approach. Solid-phase antibodies were prepared by coating a microporous plate with purified NAG, GC, or ACP antibodies. NAG, GC, or ACP were applied to the coated monoclonal antibody micropores, following which horseradish peroxidase (HRP)-labeled NAG, GC, or ACP antibodies were added to form a complex of antibody-antigen-enzyme-labeled antibodies. Subsequent to comprehensive washing, the 3,3′,5,5′-tetramethylbenzidine (TMB) substrate was included for coloration. TMB color transitions to blue under HRP enzyme catalysis and finally to yellow under acid action. Color depth shows positive relationships to NAG, GC, and ACP activity in the sample. Absorbance (OD) was determined using an instrument for enzyme labeling at 450 nm, and the activity of NAG, GC, or ACP was identified using a standard curve.

Microbial community total DNA was extracted using the E.Z.N.A.® Soil DNA kit (Omega Bio-tek, Norcross, GA, USA). Quality of the extracted DNA was determined using 1% agarose gel electrophoresis, and the concentration and purity of DNA was determined using a NanoDrop2000 spectrophotometer. The primers 338 (5′-ACTCCTACGGGAGGCAGCAG-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′) were applied for PCR amplification of the V3-V4 region of the 16S rRNA gene, and ITS1F (5′-CTTGGTCATTTAGAGGAA GTAA-3′) and ITS2R (5′-GCTGCGTTCTTCATCGAT GC-3′) were utilized. PCR products of the same sample were mixed, following which a 2% agarose fluorometer, purified using an AxyPrep DNAGel Extraction Kit (Axygen Biosciences, Union City, CA, USA) was used for recovery, 2% agarose gel electrophoresis was used for identification, and a Quantus agarose fluorometer (Promega, USA) was used for quantification. The present study utilized a NEXTFLEX Rapid DNA-Seq Kit to construct the library. Shanghai Majorbio Biopharm Technology (Shanghai, China) performed the sequencing using an Illumina MiSeq PE300 platform. Within sequencing, the original sequence was regulated using the Fastp software and spliced using the Flash software. Then, the Uparse software package was used to cluster the sequences by OTUs (operational taxonomic units), and

chimerism was eliminated according to the 97% similarity threshold. Fungi and bacteria were identified based on using the Silva 16S rRNA (v138) and UNITE/QIIME ITS datasets, respectively. The RDP Classifier was utilized to annotate the representative sequences of OTU in the species taxonomy, and the threshold of confidence was set at 0.7. The results of the annotation of species taxonomy were obtained. Alpha diversity was evaluated by diversity and richness indices (Chao1, Shannon–Wiener, and ACE).

Evaluation of biodiversity

As only one or two species were studied, tree diversity was characterized by the weighted average of the DBH coefficient of variation (CV$_D$), specific leaf area (SLA), and maximum tree height (MH). The Simpson diversity (*D*), species richness (*R*), Shannon–Wiener diversity (*H*), and Pielou's evenness indices (*J*) were used to characterize the shrub (abbreviated as S.Simpson, S.Shannon, S.Richness, and S.Pielou, respectively) and herb layer species diversity (abbreviated as H.Simpson, H.Shannon, H.Richness, and H.Pielou, respectively). The Shannon, ACE, and Chao1 indices were used to characterize the soil bacterial (B.Shannon, B.Ace, and B.Chao, respectively) and fungal alpha diversity (F.Shannon, F.Ace, and F.Chao, respectively).

The following equations were used for the calculations:

$$CV_D = SD_D/Mean_D \times 100\% \quad (2)$$

$$CWM = \sum_{i=1}^{n} BA_i \times Trait_i \quad (3)$$

$$R = S \quad (4)$$

$$H = -\sum P_i ln P_i \quad (5)$$

$$D = 1 - \sum P_i^2 \quad (6)$$

$$J = H/lnS \quad (7)$$

where SD_D is standard deviation of DBH, $Mean_D$ is average value of DBH, CWM is community trait of species i, BA_i is relative basal area of species i, $Trait_i$ is trait value of i species, n is the number of species in the community, S is number of species, P_i is the proportion of the number of individuals of species i to the total number of individuals in the community.

Quantification of multifunctionality

The weighted multifunctionality is calculated according to Manning et al. (2018). When calculating the EMF, we

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selected as many different types of functions as possible to represent the overall function of the ecosystem. Eight forest functions related to aboveground and belowground processes were quantified to represent the ecosystem multifunctionality: tree biomass (BT), shrub biomass (BS), herb biomass (BH), litter biomass (BL), *N*-acetyl-glucosaminidase (NAG), β-glucosidase (GC), acid phosphatase (ACP), and soil organic carbon density (SOD). These parameters are closely linked to the productivity, soil carbon storage, and nutrient cycling in forest ecosystems. However, the selected functions may be correlated, and overweighting some functions may lead to deviation. Pearson correlation analysis was performed after standardizing the eight function variables with *Z*-score transformation, and it showed highly correlated variables. (Fig. 1). Therefore, the converted variables were analyzed using hierarchical clustering analysis, and clustering subsets were determined (Fig. 2). Each clustering subset was assigned the same weight (for example, the weight of BH is 1, and the weight of BS, SOD, NAG, GC is 0.25), and the weighted average multifunction index was calculated.

Statistical analyses

Differences in ecosystem functional, environmental, and diversity variables between monoculture and mixed plantations were assessed using ANOVA (one-way analysis of variance). Logarithmic conversion is performed for data that does not obey the normal distribution. Correlations among variables were assessed using Pearson's correlation analysis. Principal component
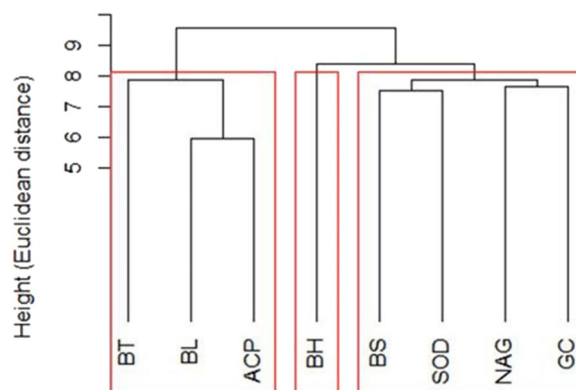

Fig. 2 Cluster analysis of ecosystem functions. Explanations of all abbreviations are the same as Fig. 1

analysis (PCA) was used to reduce the dimensions of shrub and herb species diversity and soil microbial alpha diversity, and the first two principal components with the highest interpretation were retained as comprehensive indicators of shrub and herb species diversity (SH1, SH2) and soil microbial alpha diversity (BF1, BF2). Among them, SH1 and SH2 explained 46.6% and 31.4% of the total variance, and BF1 and BF2 explained 68.7% and 20.5% of the total variance, respectively. Univariate linear regression was utilized to analyze the association between EMF and various factors. Multiple linear regression was applied to analyze the effects of environmental and diversity variables on EMF, and variation partitioning analysis (VPA) was applied to identify the explanation rate of various variables to ecosystem multifunctionality. Statistical analysis was carried out and drawings were made using the R4.2.2 software.

Results

Environmental and diversity characteristics

The SWC and $C:N_L$ of PF were significantly higher than those of LF and PL. The pH of PL was significantly lower than that of LF and PL. The $C:N_S$ and CWM_{SLA} were not significantly different among the different plantations. The CWM_{MH} of LF was significantly higher than that of PF and PL. The CV_D of PL was significantly higher than LF and PF.

The S.Shannon, S.Richness, H.Shannon, H.Richness of LF were significantly higher than PF and PL. The S.Pielou, H.Simpson were not significantly different among the different plantations.

The B.Ace, B.Chao, F.Ace, F.Chao were not significantly different among the different plantations. The B.Shannon of LF and PF was significantly higher than
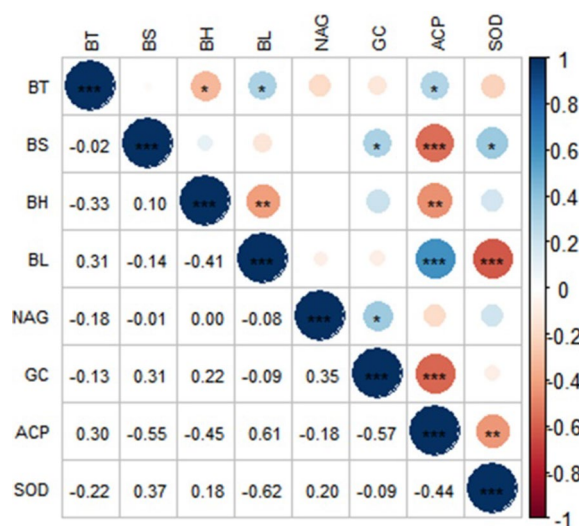

Fig. 1 Pearson correlation analysis of ecosystem functions. BT: tree biomass, BS: shrub biomass, BH: herb biomass, BL: litter biomass, NAG: *N*-acetylglucosaminidase, GC: β-glucosidase, ACP: acid phosphatase, SOD: soil organic carbon density

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Table 2 Environmental and diversity factors of different stand types

	LF	PF	PL
Environmental factor			
SWC (%)	28 ± 5b	34 ± 1a	30 ± 4b
pH	6.19 ± 0.10a	6.14 ± 0.16a	5.81 ± 0.36b
C:N$_S$	10.64 ± 0.61a	10.79 ± 0.19a	10.69 ± 0.43a
C:N$_L$	29.91 ± 6.79b	41.94 ± 5.24a	32.26 ± 7.58b
Tree species diversity			
CWM$_{SLA}$ (cm^2/g)	185.28 ± 30.27a	173.92 ± 37.53a	166.53 ± 33.80a
CWM$_{MH}$ (m)	18.69 ± 0.76a	17.38 ± 0.41b	17.59 ± 1.05b
CV$_D$ (%)	21.29 ± 4.01b	23.74 ± 5.37b	27.50 ± 4.45a
Shrub and herb species diversity			
S.Shannon	1.57 ± 0.29a	1.22 ± 0.47b	0.82 ± 0.42c
S.Simpson	0.72 ± 0.10a	0.61 ± 0.18ab	0.48 ± 0.21b
S.Pielou	0.81 ± 0.10a	0.75 ± 0.12a	0.77 ± 0.28a
S.Richness	7.11 ± 1.63a	5.50 ± 2.18b	3.11 ± 1.52c
H.Shannon	0.99 ± 0.58a	0.35 ± 0.18b	0.68 ± 0.41b
H.Simpson	0.46 ± 0.27a	0.17 ± 0.09a	0.41 ± 0.25a
H.Pielou	0.58 ± 0.26ab	0.34 ± 0.11b	0.70 ± 0.36a
H.Richness	5.06 ± 2.25a	1.88 ± 1.05b	1.83 ± 1.12b
Soil microorganism alpha diversity			
B.Shannon	6.35 ± 0.11a	6.29 ± 0.10a	6.09 ± 0.30b
B.Ace	3456.35 ± 227.16a	3322.31 ± 64.18a	3050.55 ± 282.82a
B.Chao	3342.56 ± 143.99a	3241.36 ± 143.99a	2996.07 ± 287.11a
F.Shannon	4.99 ± 0.13a	4.80 ± 0.12b	4.71 ± 0.26a
F.Ace	1266.87 ± 213.17a	1260.25 ± 202.69a	1164.71 ± 225.30a
F.Chao	1290.25 ± 213.17a	1266.67 ± 196.86a	1158.94 ± 218.29a

The data are shown as average ± standard errors. The differing letters of one row represent significant differences between different stand types ($p < 0.05$). The data are shown as average ± standard error. The differing letters of one line represent a significant difference between different plantation types ($p < 0.05$). LF: Mixed *F. mandshurica* and *L. olgensis* plantation; PF: monoculture *F. mandshurica* plantation; PL: monoculture *L. olgensis* plantation; SWC: Soil water content; C:N$_S$: ratio of C to N in soil; C:N$_L$: ratio of C to N in litter; CWM$_{SLA}$: average community-weighted specific area of leaves; CWM$_{MH}$: average community-weighted maximum height; CV$_D$: DBH coefficient of variation; S.Shannon: Shrub Shannon–Wiener index; S.Simpson: Shrub Simpson index; S. Pielou: Shrub Pielou index; S.Richness: Shrub Species Richness; H.Shannon: Herb Shannon–Wiener index; H.Simpson: Herb Simpson index; H. Pielou: Herb Pielou index; H.Richness: Herb Species Richness; B.Shannon: Bacterial Shannon–Wiener index; B.Ace: Bacterial Ace index; B.Chao: Bacterial Chao index; F.Shannon: Fungal Shannon–Wiener index; F.Ace: Fungal Ace index; F.Chao: Fungal Chao index

PL. The F.Shannon of LF was significantly higher than that of PF and PL (Table 2).

Single and multiple ecosystem functions

The single-function value of the mixed plantations mostly exceeded that of the monoculture plantations. For example, the BT, BH, BS, and GC in LF significantly exceeded that in PF and PL ($p < 0.05$; Fig. 3). BL and ACP in PL significantly exceeded PF and LF, and SOD was significantly higher in PF than in PL and LF ($p < 0.05$; Fig. 3). For NAG, there were no differences among the three stand types. To better integrate the eight single ecosystem functions and evaluate EMF, the weighted average method was used. The results showed that LF resulted in significantly increased weighted multifunctionality ($p < 0.05$, Fig. 3).

Predictors of weighted ecosystem multifunctionality

The relationship among the functions of a single ecosystem, its diversity, and environmental factors is complex. In the present study, the results of the bivariate relationship analysis between multifunctionality, diversity, and environmental factors showed multifunctionality had a positive correlation with SWC, CWM$_{MH}$, C:N$_S$, SH1, and SH2, among which a significant correlation occurred only with SH1, as well as a negative correlation with pH, CWM$_{SLA}$, CV$_D$, C:N$_L$, BF1, and BF2, among which a significant relationship occurred with CWM$_{SLA}$, CV$_D$, and BF2 (Fig. 4).

VPA and multiple linear regression were used to analyze the effects of biodiversity and environmental factors on ecosystem multifunctionality. Our results showed that EMF was negatively correlated with pH, CWM$_{SLA}$, CV$_D$, C:N$_L$, and BF2 (Fig. 5) and positively correlated with SH1. However, it had no significant correlations with the other variables.

On average, 50.8% of the observed total variation was explained, with EMF driven mainly by tree diversity, environmental factors, shrub and herb species diversity, and soil microbial alpha diversity, which explained 25.35%, 8.94%, 8.83%, and 7.65% of the variation, respectively (Fig. 5). Among these, CWM$_{SLA}$ and CV$_D$ were significantly negatively related to EMF, the diversity of soil microbes was negatively related to EMF, shrub and herb species diversity was positively related to EMF, and C:N$_L$ and pH were negatively related to EMF.

Discussion

Environmental and diversity characteristics

In Northeast China, *Larix olgensis* is often chosen to be mixed with *Fraxinus mandshurica* to improve stand stability and achieve more forest ecosystem functions. Our
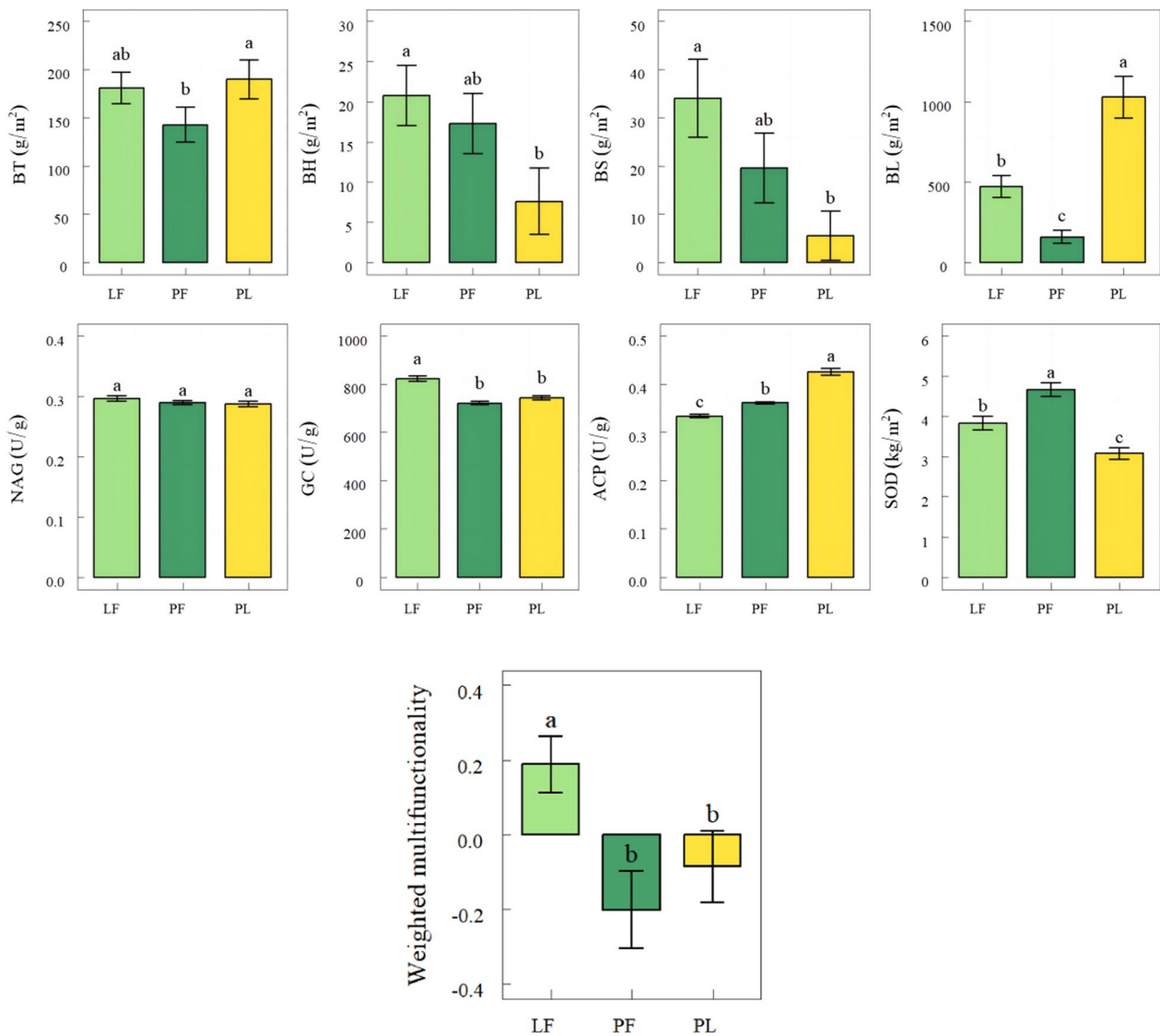
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Fig.3 Eight ecosystem functions of different plantation types and weighted multifunctionality of the different types of plantation. Data are shown as average ± standard error. The differing letters represent significant difference between different stand types ($p < 0.05$). BT: biomass of trees; BH: biomass of herbs; BS: biomass of shrubs; BL: biomass of litter; NAG: *N*-acetylglucosaminidase; GC: *β*-glucosidase; ACP: Acid phosphatase; SOD: Soil organic carbon density

study showed that mixed plantations are superior to monoculture forests in species diversity and soil nutrients, supporting the findings of studies on other forest ecosystems showing that the establishment of mixed plantations can improve the quality of monoculture forests (Williams et al. 2017; Huang et al. 2018; Yang et al. 2023). Furthermore, our results showed that the aboveground and belowground diversities of mixed plantations exceeded those of monoculture forests. These results partially supported our hypothesis H1. The results are similar to some previous studies. For example, Randriamananjara et al. (2023) compared the understory

vegetation of hybrid poplar and spruce monocultures and mixed plantations in the northern forest region of southern Quebec. It was found that the mixture of hybrid poplar and spruce could maximize the diversity of understory vegetation, because the mixed plantation was beneficial to the establishment of some understory vegetation species. Changes in biodiversity are mainly related to the complementary niche effects (Huang et al. 2018). Specifically, forests with complex structures increase the utilization of light and space resources by trees and promote niche complementarity of species in the forest (Gough et al. 2019; LaRue et al. 2019).
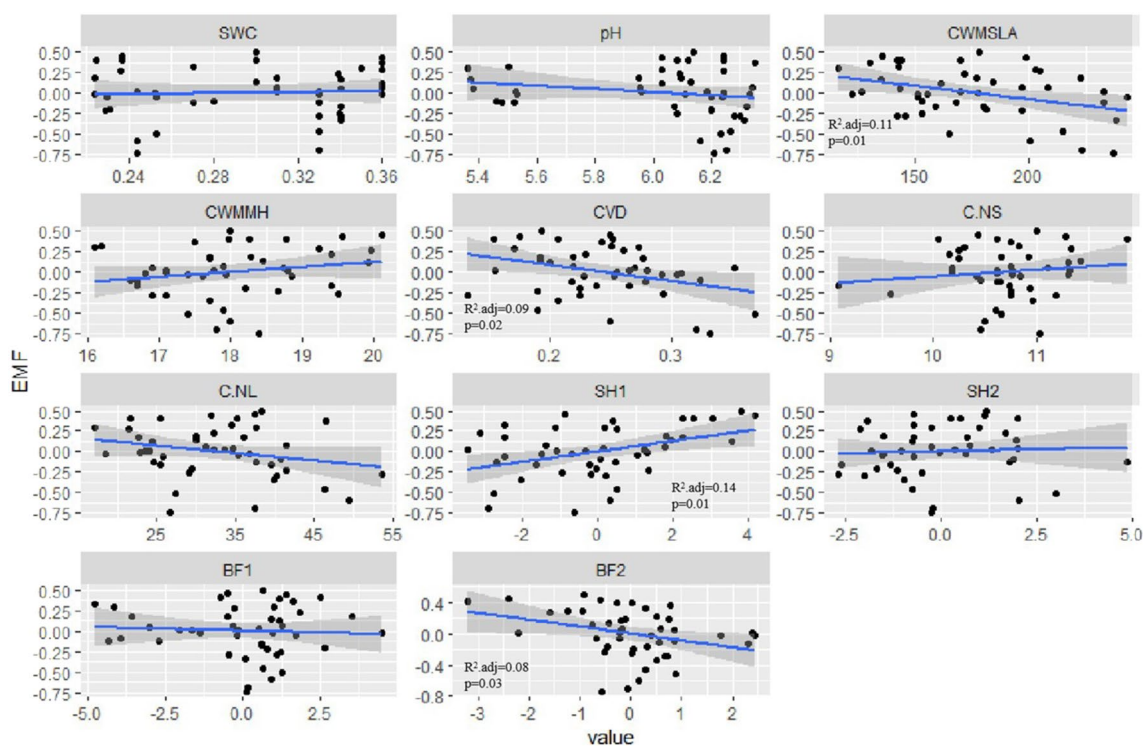
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Fig. 4 Relationships between forest ecosystem multifunctionality (*Z*-scores) and environmental factors (SWC: soil water content, C:N$_S$: ratio of C to N in soil, C:N$_L$: ratio of C to N in litter, pH: Soil pH), biodiversity (CWM$_{SLA}$: average community-weighted specific leaf area, CWM$_{MH}$: average community-weighted maximum height, CV$_D$: DBH coefficient of variation, SH1, SH2: Two principal components of shrub and herb species diversity, BF1, BF2: Two principal components of soil microbial alpha diversity)

Mixed plantations promote higher diversity and richness by providing a heterogeneous undergrowth environment that affects microbial community structure (Chen et al. 2019). Soil microbial diversity (fungal and bacterial alpha diversity) of the mixed plantations exceeded that of the monoculture plantations, but only the Shannon indices of bacteria and fungi significantly exceeded those of the monoculture plantations. No significant differences were noted in the remaining microbial diversity indices. Ding et al. (2023) found no significant differences in the soil bacteria alpha diversity when studying changes in soil microbial communities in monoculture *Cunninghamia lanceolata* plantations and mixed plantations. Previous results showed that differences in the soil microbial community were related to soil carbon and nitrogen cycling (Pereira et al. 2019). Rivest et al. (2019) studied the effect of tree diversity on soil microbial diversity in Quebec and show that trees are not a strong driving force of soil biodiversity, as soil characteristics such as pH and total nitrogen are more important than vegetation in shaping soil microbial community composition. Soil microbes play important roles in soil N and C cycles (Zhang et al. 2019b). Mixture of tree species may enhance soil bacterial community stability by increasing bacterial

phylogenetic diversity (Zhang et al. 2019a). The soil pH of the mixed plantations significantly exceeded that of the monoculture plantations, consistent with the results of previous studies (Ding et al. 2023; Xu et al. 2023). Litter is a key factor affecting soil nutrients (Liu et al. 2023). After litter decomposition, plant residues with high nitrogen enter the soil, which inhibits nitrifying bacteria activity and promotes the ammonization of mineral nitrogen, thus increasing the pH (Xu et al. 2006). The CWM$_{MH}$ of the mixed plantations significantly exceeded monoculture plantations, and crown stratification was the key factor in niche separation, which led to the complementary utilization of resources and ensured species coexistence. Tree species with elevated CWM$_{SLA}$ usually show strategies of resource acquisition, and their leaves have higher resource acquisition and growth rates, higher water and nutrient use efficiencies, and characteristic values related to productivity (Qin and Shangguan 2019).

Single and multiple ecosystem functions

When compared to monoculture plantations, the single functions of mixed plantations were greatly improved, with BH, BS, and GC being significantly greater, but the BL of mixed plantations is not significantly higher than
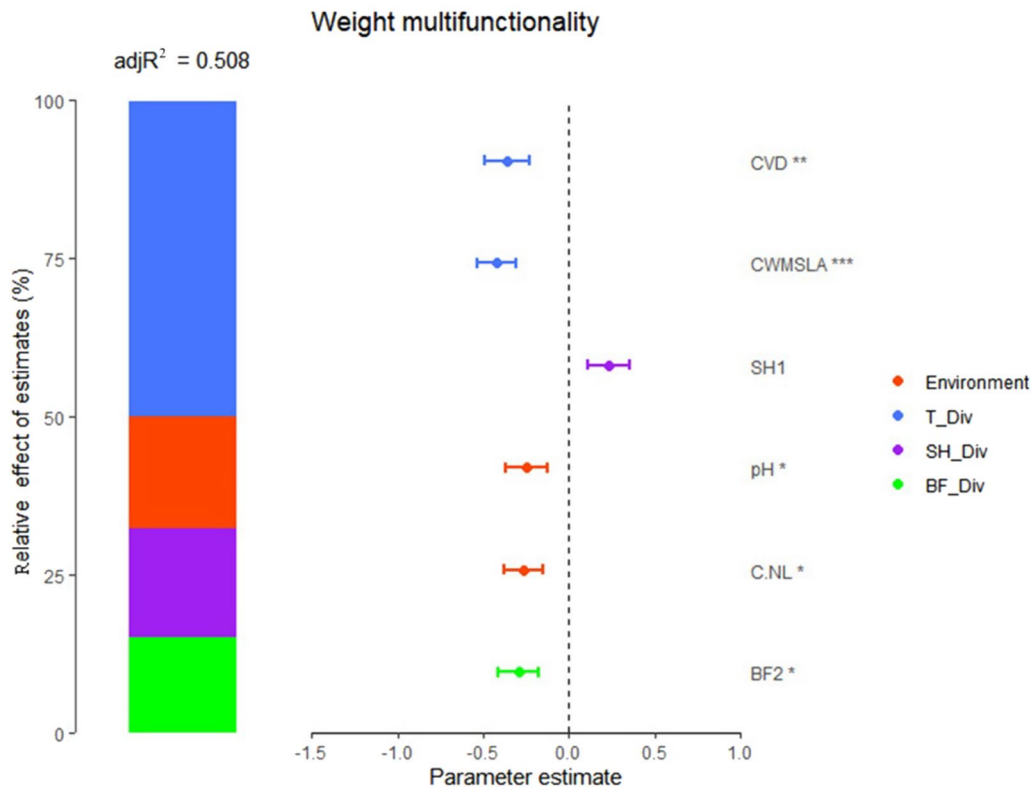
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Fig. 5 Influences of diversity and environmental factors on ecosystem functions. The figure shows the average parameter estimates of model predictors (normalized regression coefficients), relevant 95% confidence intervals, and proportional importance of each factor shown as the % of variance explained. After model adjustment, the R^2 and p values of each predictor were *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

that of any monoculture plantations. This result positively supports our hypothesis H2. Studies have shown that *Eucalyptus* monoculture plantations in Brazil have a limited ability to provide ecosystem functions and biodiversity conservation (Bellink and Verburg 2023). The biomass and biodiversity of understory vegetation in mixed forests are greater than those in monoculture forests, while the biomass of the trees remains comparable, possibly because of the relatively weak interactions among tree species in young forests. However, as forest stands mature, interactions between species and canopy strengthen, resulting in significant differences in stand biomass (Grossiord et al. 2013). Different tree species compositions will result in varying degrees of canopy structure complexity. Forest structural diversity can increase species diversity and aboveground biomass accumulation by optimizing the allocation of interspecific resources and increasing the capacity of vegetation to obtain and utilize light (Yuan et al. 2020). Niche complementary effects are produced among multiple species and promote the utilization of resources and improve stand productivity. In the present study, the single belowground function of the mixed plantations changed. For example, for enzymes participating in soil nitrogen,

phosphorus, and carbon cycles, except for NAG, the GC of the mixed plantations significantly exceeded the monoculture plantations, whereas the ACP of the mixed plantations was significantly lower than that of the monoculture plantations. SOD in PF significantly exceeded LF and PL. This may be because of the indecomposable needles in the litter of mixed plantations, making it harder to decompose than the litter of PF (Guo et al. 2021). Also, in mixed plantations, the roots of different species may occupy different soil layers over time, resulting in more efficient use of soil nutrients and water resources (Li et al. 2020a).

The averaging method is the main method used to evaluate the ecosystem functions and can analyze changes in single ecosystem functions (Maestre et al. 2012; Byrnes et al. 2014; Chen et al. 2020). Here, weighted multifunctionality demonstrated that the EMF of the mixed plantations significantly exceeded the monoculture plantations. This was consistent with most previous studies showing in relation to monoculture plantations, mixed plantations can provide more ecosystem functions (Xu et al. 2021). However, not all mixed plantations can enhance the EMF; this depends on the tree species (Li et al. 2022b). The mixture of two coniferous species (Norway spruce

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and Scots pine) did not exhibit significant mixing effects (Blaško et al. 2020). This indicates that selecting appropriate mixtures of tree species is crucial for enhancing the EMF. Compared to *L. olgensis* monoculture plantations, *F. mandshurica* monoculture plantations have higher soil nutrient contents and biodiversity. Our study showed that the establishment of *L. olgensis–F. mandshurica* mixed plantations can improve the ecosystem's ecological functions, which should be considered in the establishment of mixed plantations in the future.

Predictors of weighted ecosystem multifunctionality

Improving the EMF is the key objective in establishing a mixed plantation. In different ecosystems, the driving factors of EMF differ, and maintaining a higher level of EMF requires multiple driving factors. We analyzed the importance of biodiversity and environmental factors in driving the EMF in monoculture and mixed plantations. The results showed that EMF was most strongly affected by tree diversity, followed by environmental factors, soil microbial alpha diversity, and shrub and herb species diversity, consistent with our hypothesis H3. Generally, high trophic level diversity is a key driver of forest ecosystems (Schuldt et al. 2018; Luo et al. 2022). In plantations, tree species composition is relatively simple, and species diversity is concentrated in the understory vegetation layer. We found that niche complementary effects and mass ratio hypothesis have a synergistic effect on the EMF (Xu et al. 2023). In environments with limited resources, gradually-growing conservative species (such as those with a small specific leaf area and elevated content of leaf dry matter) determine the high biomass of stands and promote the ecological function of forests (Ali and Yan 2017). However, not only can species diversity affect the EMF, but the relationship between them is more complex, which can promote ecosystem functions by promoting environmental change and biodiversity (Hong et al. 2022). The $C:N_L$ ratio reflects the litter decomposition rate and drives the changes in soil nutrients (Zhang et al. 2019b). Changes in soil pH determine the diversity of soil microorganisms, which is negatively correlated with EMF (Li et al. 2020b). They are also key indicators that affect the EMF (Ouyang et al. 2023). Fungal alpha diversity is more important than bacterial alpha diversity in maintaining EMF (Ouyang et al. 2023; Wang et al. 2023). This may be related to the increase in fungal diversity, which not only accelerates litter decomposition but also leads to an increase in saprophytic and pathogenic fungi, thus affecting forest growth (Li et al. 2022a). Also, maximum height is an important index of light capture ability and interspecific competition. The positive correlation between the CWM_{MH}

and EMF suggested that the selection effect plays an important role in increasing the EMF of monoculture and mixed plantations (Ouyang et al. 2023). The relatively high complexity of stand structures can improve the efficient use of resources and space, especially the biodiversity and productivity of species in the forest, because it affects light availability and absorption (Ali 2019). Notably, EMF is often driven by both biological and abiotic factors; thus, it is worth exploring to comprehensively consider the joint effects of aboveground and belowground biodiversity and environmental factors (Zhang 2023). In addition, weighing more forest functions rather than just considering wood production would be more beneficial for EMF during plantation planting and management (Yuan et al. 2020).

Conclusions

In this study, we found that mixed plantations have higher understory biodiversity. In addition, mixed plantations can effectively alleviate the problem of soil acidification present in monoculture *Larix olgensis* plantations, accelerate litter decomposition rates, and improve soil nutrient contents. The establishment of mixed plantations can increase the biodiversity of forest stands and improve the ecosystem function. Biodiversity is the main reason for the multifunctionality of ecosystems. These results show the advantages of multi-species mixed plantation and the necessity of planting. In contrast to monoculture plantations, the establishment of mixed plantations can improve the ecological functions of forest ecosystems and enhance stand stability, which is important for forests to cope with climate change. Therefore, suitable mixed tree species should be selected when establishing plantations. When assessing the effects of tree species mixtures, the influence of both aboveground and belowground biodiversity and environmental factors on enhancing EMF should be considered.

Author contributions
Jiaxin Tian: Validation, writing—original draft. Tian Ni: Investigation, conceptualization. Zheng Miao: Methodology, Investigation. Yuanshuo Hao: Formal analysis, investigation. Aiyun Ma: Investigation, writing—original draft. Lihu Dong: Conceptualization, supervision, writing—review and editing, funding acquisition. Fengri Li: Supervision, writing—review and editing, funding acquisition.

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Availability of data and materials
Data are available upon reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
All authors agreed and approved the manuscript for publication in Ecological Processes.

Competing interests
The authors declare that they have no competing interest.

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