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# Divergent above- and below-ground biodiversity pathways mediate disturbance impacts on temperate forest multifunctionality

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## Abstract

Biodiversity plays a fundamental role in provisioning and regulating forest ecosystem functions and services. Above-ground (plants) and below-ground (soil microbes) biodiversity could have asynchronous change paces to human-driven land-use impacts. Yet, we know very little how they affect the provision of multiple forest functions related to carbon accumulation, water retention capacity and nutrient cycling simultaneously (i.e. ecosystem multifunctionality; EMF). We used a dataset of 22,000 temperate forest trees from 260 plots within 11 permanent forest sites in Northeastern China, which are recovering from three post-logging disturbances. We assessed the direct and mediating effects of multiple attributes of plant biodiversity (taxonomic, phylogenetic, functional and stand structure) and soil biodiversity (bacteria and fungi) on EMF under the three disturbance levels. We found the highest EMF in highly disturbed rather than undisturbed mature forests. Plant taxonomic, phylogenetic, functional and stand structural diversity had both positive and negative effects on EMF, depending on how the EMF index was quantified, whereas soil microbial diversity exhibited a consistent positive impact. Biodiversity indices explained on average 45% (26%–58%) of the variation in EMF, whereas climate and disturbance together explained on average 7% (0.4%–15%). Our result highlighted that the tremendous effect of biodiversity on EMF, largely overpassing those of both climate and disturbance. While above- ($\beta = 0.02–0.19$) and below-ground ($\beta = 0.16–0.26$) biodiversity had direct positive effects on EMF, their opposite mediating effects ($\beta = -0.22$ vs. $\beta = 0.35$ respectively) played as divergent pathways to human disturbance impacts on EMF. Our study sheds light on the need for integrative frameworks simultaneously considering above- and below-ground attributes to grasp the global picture of biodiversity effects on ecosystem functioning and services. Suitable management interventions could maintain both plant and soil microbial biodiversity, and thus guarantee a long-term functioning and provisioning of ecosystem services in an increasing disturbance frequency world.

**KEYWORDS**
biodiversity, climate, disturbance, ecosystem functioning, functional traits, natural forests, soil microbes

## 1 | INTRODUCTION

Forests harbour much of the terrestrial biodiversity, and provide fundamental functions and services, such as biomass production, nutrient cycling and water retention (Gamfeldt et al., 2013; Pan et al., 2013). However, human-driven disturbances, such as habitat destruction and resource overexploitation, can cause drastic terrestrial biodiversity loss and ecosystem changes (Isbell et al., 2011; Le Provost et al., 2020; Newbold et al., 2016). For example, selective logging, as a widespread anthropogenic disturbance in natural forest ecosystems, can exert critical direct effects on above-ground biomass stock (Dai et al., 2004). Also, selective logging can influence forest biodiversity which includes both above-ground plant diversity and below-ground soil diversity (McGuire et al., 2015), resulting in potentially far-reaching effects on forest ecosystem functioning (Seidl et al., 2017; Sommerfeld et al., 2018).

As the forest recovery proceeds from the post-logging disturbance, subsequent forest biomass recovers when emerging trees grow to occupy the gaps created by the felled trees (de Avila et al., 2018; Saunders et al., 2012). Subsequently, the loss of forest biomass can be compensated if the forests are left to recover, primarily depending on the magnitude of disturbance intensity (Piponiot et al., 2016). Existing theories are producing mixed predictions on how the whole functions of the community changes during secondary succession. For instance, MacArthur's minimization principle suggests that more mature and late-stage communities should become more efficient by minimizing energy wastage, thereby maximizing ecosystem functions (MacArthur, 1984). However, a recent study demonstrated that mid-stage communities could be more effective at utilizing resources (Ghedini et al., 2018). Understanding how biodiversity associated with multiple ecosystem functions (multifunctionality hereafter; EMF, Byrnes et al., 2014) across different levels of ecosystem disturbance is essential to predict the changes in forest services that underpin human well-being in a more managed world (Felipe-Lucia et al., 2018; Zhao et al., 2020).

Most of current studies investigated a lens of human-driven disturbance impacts to focus on either a single or narrow set of biodiversity attributes and ecosystem functions (Le Provost et al., 2020; Newbold et al., 2016). Beyond the number of species (taxonomic diversity; Felipe-Lucia et al., 2018; Gamfeldt et al., 2013), the diversity of phenotypes (functional trait diversity) and of evolutionary lineages (phylogenetic diversity) could represent key biodiversity attributes promoting EMF (Gross et al., 2017; Le Bagousse-Pinguet et al., 2019, 2021; Yuan et al., 2020). These biodiversity attributes could play a key role in promoting EMF either because functionally distinct species promote the overall resource-use efficiency (i.e. the niche complementarity effect) or because of the inclusion of species strongly influencing ecosystem functioning (i.e. the selection effect; Loreau & Hector, 2001; Tilman, 1997). In addition to these biodiversity attributes, the functional identity of dominant species (i.e. the functional trait composition), rather than trait diversity per se, is often viewed as the main driver of ecosystem functioning (Grime, 1998), which can be estimated using the community-weighted mean (CWM) of functional trait values (Prado-Junior et al., 2016; Tobner et al., 2016). Stand structural attributes, such as individual tree size (diameter and/or height) inequality among and within species, could also have key implication for the functioning of forest ecosystems (reviewed by Ali, 2019), by enhancing above-ground light interception and utilization and promoting production efficiency (Gough et al., 2019). Ultimately, below-ground organisms, such as soil microbes, represent a large fraction of unseen terrestrial diversity regulating plant productivity and biogeochemical processes such as nutrient cycling and litter decomposition (Van Der Heijden et al., 2008), which allow the shift of energy and matter between above- and below-ground components of an ecosystem, and alter nutrient supply and the resource partitioning (Delgado-Baquerizo et al., 2020; Wagg et al., 2014; Yuan et al., 2020). Contradictory results have been reported regarding the relative importance of above- and below-ground biodiversity in driving EMF (Delgado-Baquerizo et al., 2016; Jing et al., 2015; Yuan et al., 2020). Because plant taxonomic, phylogenetic, functional, stand structure and soil microbes attributes, do not necessarily relate to each others, they could have contrasting influences on EMF (Le Bagousse-Pinguet et al., 2019, 2021). This largely hampers our ability to improve the understanding of the relationships between biodiversity and ecosystem functioning to formulate sustainable conservation and management policies in the context of global anthropogenic changes (Balvanera et al., 2006; Soliveres et al., 2016).

Here, we used a unique dataset of over 22,000 temperate forest trees belonging to 81 species from 260 plots within 11 permanent plots (i.e. sites) to investigate how multiple attributes of above- (i.e. taxonomic, phylogenetic, functional and stand structural diversities) and below-ground (i.e. soil bacteria and soil fungi) biodiversity simultaneously influence forest EMF under post-logging disturbances. We also considered multiple climate factors as potential drivers of biodiversity and EMF. We address the following questions: (1) Do nearly undisturbed mature forests exhibit the highest EMF compared with the other disturbed forests, following the MacArthur's (1984) minimization principle? (2) Do the multiple attributes of temperate forest biodiversity have contrasting effects on EMF as found in drylands ecosystem (Le Bagousse-Pinguet et al., 2019)? and (3) Are the effects of post-logging disturbance on forest EMF equally mediated by above- and below-ground biodiversity pathways? We hypothesize that below-ground biodiversity is less affected by environmental changes compared to above-ground biodiversity, thereby above-ground and below-ground biodiversity are mediating the divergent effects of disturbance on temperate forest EMF.

## 2 | MATERIALS AND METHODS

### 2.1 | Study sites and forest inventories

The study was conducted in temperate forests from the Changbai Mountain (40°54′ to 44°03′N, 124°47′ to 130°09′E), located in Liaoning and Jilin Provinces in Northeastern China (Figure S1a in Appendix S1). The region is characterized by a temperate continental climate with long cold winters and warm summers. Mean annual temperature and precipitation are 2.8°C and 700 mm respectively. The dominant vegetation type is the broad-leaved and Korean pine (*Pinus koraiensis*) mixed forests, with high productivity compared to other forests from the same latitude (Stone, 2006). These forests are also hotspots of diversity and home numerous emblematic, but endangered species such as the Siberian tiger (*Pantha tigris longipilis* L.) and ginseng (*Panax ginseng C.A. May*; Shao et al., 1994). The soils are classified as the Alfisol according to the US soil taxonomy (Yang & Li, 1985). All studied sites have been protected from intensive human disturbance since 1998, as a result of the implementation of a Natural Forest protection. Thus, forests recovering from disturbances include stands with different successional stages in the study area (Chen et al., 2014).

Eleven forest permanent plots (>0.6 ha in size) were established in 2012 and 2013 (see Table S1 for details), and have been re-inventoried after 5 years following a standard field protocol (Yuan et al., 2018). The elevation ranged between 653 and 1020 m a.s.l. Soil pH ranged between 5.4 and 7.1 (Table S1). Within each plot (Figure S1b in Appendix S1), all individual trees with a DBH ≥ 1 cm in contiguous 20 × 20 subplots were tagged, identified and measured following a standard field protocol (Hao et al., 2007). The geographical coordinates of all individual trees were also recorded. A total of 22,766 individuals belonging to 81 species, 46 genera and 26 families were recorded (Yuan et al., 2018).

### 2.2 | Quantifying disturbance intensity and climate variables

The disturbance intensity of each plot was evaluated by counting the number of tree stumps that had been removed in the field using a chainsaw in the 1990s (Kahl & Bauhus, 2014). In addition, the official records of the Local Forestry Bureau, Jilin and Liaoning Provinces were examined to collect the relevant selective logging data. Collectively, plots were primarily classified into three disturbance intensity levels, according to the partial harvesting (e.g. thinning, selective harvesting): relatively low (<10%), medium (10%–20%) and high (20%–30%) disturbance. Plots with a low disturbance level were distributed in the core zone of the Changbai Mountain Nature Reserve (Figure 1), which was established in 1960 and is part of the World Biosphere Reserve Network under the Man and the Biosphere Project in 1980 (Shao et al., 1994). Plots with medium and high disturbance levels were primarily located around the residential area of the village and small town.

We also considered 19 climate variables as potential drivers of EMF, that is, annual mean temperature, mean diurnal range, isothermality, temperature seasonality, a maximum temperature of the warmest month, minimum temperature of the coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality (coefficient of variation), precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter and precipitation of coldest quarter. These climate variables were collectively extracted from the WorldClim database (Hijmans et al., 2005), with records from 1970 to 2000 at a 30-arc second spatial resolution (~1 $km^2$).

### 2.3 | Quantifying above- and below-ground biodiversities

We quantified the taxonomic attributes of above-ground forest diversity using the species richness (S) and Shannon–Wiener diversity indices of tree species ($H_S$). We built up a supertree for all the trees using the online software of Phylomatic (http://www.phylodiversity.net) which includes updated time-calibrated branch length of seed plants and combining multigene molecular and fossil data (Zanne et al., 2014). Based on the obtained phylogenetic tree, we calculated (1) Faith's phylogenetic diversity index ($PD_F$), which quantifies the total length of all branches connecting trees in a given subplot (Faith, 1992), and (2) the phylogenetic species variability (PSV) reflecting how phylogenetic relatedness decreases the variance of a hypothetical neutral trait (Helmus et al., 2007). We also investigated the role of functional identity and diversity on EMF by computing the CWM of trait values and the functional dispersion index (FD) respectively. The two indices were weighted by the species' relative basal area within a subplot. Functional traits included maximum

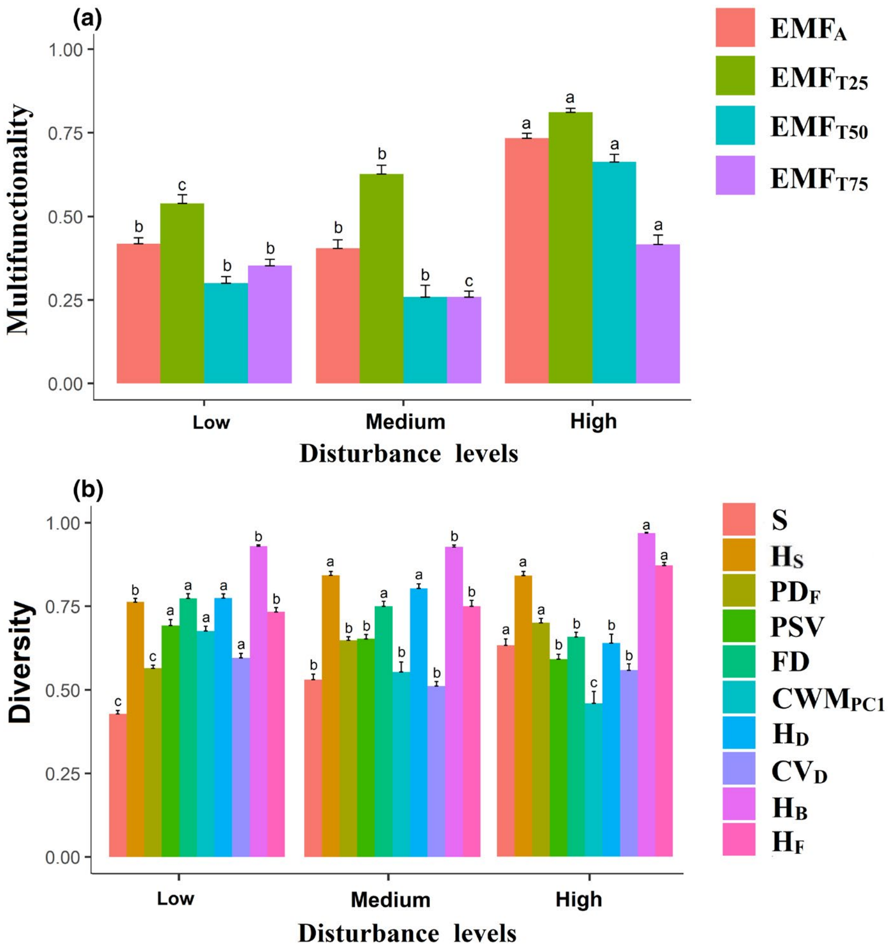

**FIGURE 1** The effect of disturbance intensity on forest ecosystem multifunctionality (a) and above- and below-ground biodiversity (b). Ecosystem multifunctionality includes averaged (EMF$_A$), 25% (EMF$_{T25}$), 50% (EMF$_{T50}$) and 75% threshold levels (EMF$_{T75}$). Above-ground diversity includes species richness (S), Shannon–Wiener diversity of tree species (H$_S$), Faith's phylogenetic diversity (PD$_F$), phylogenetic species variability (PSV), functional dispersion of functional traits (FD), the first PCA axis of the community-weighted mean of six functional traits (CWM$_{PC1}$), Shannon–Wiener diversity of tree size variation (H$_D$) and the coefficient of variation for tree DBH (CV$_D$); the below-ground diversity includes, Shannon–Wiener diversity of soil bacteria (H$_B$), and Shannon–Wiener diversity of fungi (H$_F$). Different lowercase letters within each panel indicate significant ($p < 0.5$) differences between treatment means, after using Tukey's method to correct for multiple comparisons. Error bars represent ±1 SE [Colour figure can be viewed at wileyonlinelibrary.com]

tree height, wood density, leaf phosphorus content (LPC), leaf nitrogen content (LNC), specific leaf area (SLA) and leaf area (LA), which are related to life-history and nutrient and water-use efficiencies (Pérez-Harguindeguy et al., 2013; Appendix S1). We also quantified the stand structural diversity (H$_D$), using the Shannon–Wiener diversity index of tree size variation (i.e. tree DBHs) using 2 cm DBH as a discrete class (Ali et al., 2016). Meanwhile, individual size inequality (CV$_D$) was quantified as the coefficient of variation for tree DBH within each subplot, as a proxy for overall tree size variation. The variability in DBH within natural forests captures the degree of complexity in multilayered stand structure in terms of light capture and use by component species and interacting individuals (reviewed by Ali, 2019).

To evaluate the soil fungal and bacterial diversities, we randomly selected two sampling points from the four midpoints between the central point and corners in each 20 × 20 m subplot in August 2018 (Figure S1c). Five soil cores (3.8 cm diameter, 10 cm deep) at each sampling point were collected, pooled and brought to the laboratory for analyses. Each soil sample was further divided into two parts: one for soil microbial diversity measurements (i.e. bacteria and fungi), and the other for soil nutrient analyses after removing roots and stones and air-dried for 24 h. All obtained values were averaged to represent mean soil microbial diversity per subplot. For the calculations of Shannon–Wiener diversity indices of soil fungi and bacteria, samples were rarified to 3000 sequences for bacteria and 2,200 sequences for fungi per soil sample. A summary of diversity variables is provided in Table S1 in Appendix S1. More details about the measurements of plant functional traits and soil microbes are provided in Appendix S2.

## 2.4 | Quantifying ecosystem multifunctionality (EMF)

We quantified the EMF of the studied forests using nine key functions, that is, (1) coarse woody productivity (CWP), (2) above-ground biomass of wild edible plants (AGB$_W$), (3) soil organic carbon density (SOD), (4) litter layer biomass (B$_L$), (5) water holding capacity of litter layer (WHC$_L$), (6) water holding capacity of the soil (WHC$_S$), (7) soil available nitrogen (AN), (8) soil available phosphorus (AP) and (9) soil available potassium (AK; Table S1 in Appendix S1). More specifically, CWP is a good proxy for net primary production and carbon sequestration rate in a forest. AGB$_W$ is an important forest function that supports human welfare such as providing food and fibre. Soil is the largest organic carbon reservoir in the terrestrial biosphere, and plays a critical role in the global carbon cycle. B$_L$ is an effective indicator of litter production, and is also an important food source and habitat for soil fauna (Trogisch et al., 2017). As the sources of three main rivers, the Changbai area has been categorized as one of the Chinese key ecology function areas for water conservation (Yu et al., 2015), and thus, $WHC_L$ and $WHC_L$ could represent the water conservation capacity of the forest floor. AN, AP and AK constitute a surrogate for available nutrient pools (Garland et al., 2020).

Coarse woody productivity (Mg $ha^{-1}$ $yr^{-1}$) was estimated by summing biomass growth and recruitment rates, which was calculated as the increment of stems alive in the last and first inventories, and the biomass of stems recruited into DBH ≥1 cm between the first and last forest inventories respectively (Yuan et al., 2019). For the quantification of the above-ground biomass of wild edible plants, we first recognized medicinal and edible shrub species according to the Flora Reipublicae Popularis Sinicae (Hong & Blackmore, 2015), and then the mean above-ground biomass stock (Mg $ha^{-1}$) of wild edible plants was quantified using specific species allometric models (He et al., 2011). Soil organic carbon density (kg $m^{-2}$) of the 0–10 cm layer was calculated based on the formula $C_d = (1 - \theta_i) \times \rho_i \times 0.58 \times c_i$, where $\theta_i$ is gravel (>2 mm) content at sample location $i$ (%),$\rho_i$ is soil bulk density in the surface layer (g $cm^3$) and $c_i$ is organic matter content in the $i$th soil sample (g $kg^{-1}$).

Litter biomass (Mg $hm^{-2}$) was determined through the collection of the intact litter layer above soil mineral horizons with a hand spade, after removing the surface dried twigs and herbs. The water holding capacity (WHC, Mg $hm^{-2}$) of litters and soils was determined using full drainage methods (Naeth et al., 1991). Soil N (g $kg^{-1}$) was determined following the Kjeldahl method. Soil P (g $kg^{-1}$) was measured by molybdate colorimetry, after digestion in $H_2SO_4$–$HClO_4$. Total K (g $kg^{-1}$) was derived using atomic absorption spectrometry. Available N was alkali digested and was detected using hydrochloric acid titration method, whereas available P was extracted following the method of Mehlich 1 (Nelson et al., 1953). Soil available K was obtained with detection by atomic absorption spectrometry (AAS). Please see detailed measurement approaches in Appendix S2.

All individual functions were *z*-scored (standardized deviates) and averaged to calculate the averaged forest EMF index ($EMF_A$; Byrnes et al., 2014). We also evaluated whether multiple functions are simultaneously performing at a high level using the multiple threshold approach, which calculates the number of functions that reach a given threshold (i.e. the per cent of the maximum value of each of the functions measured in the dataset). This maximum is defined as the mean of the five highest values for each function observed across all study plots. We used multifunctionality-threshold values of 25% ($EMF_{T25}$), 50% ($EMF_{T50}$) and 75% ($EMF_{T75}$).

## 2.5 | Statistical analyses

We first conducted a principal component analysis (PCA) to reduce the multicollinearity in CWM indices and climate variables, separately. The result indicated that the first axis of PCA on CWM indices ($CWM_{PC1}$) explained 56.9% of the total variation in CWM variables, mainly reflecting taller trees (high CWM of height) but lower CWM of SLA and LNC (i.e. conservative strategy). The first axis of PCA on climate variables ($Clim_{PC1}$) accounted for 67.1% of the variation representing increasing temperature and precipitation gradients (Table S2).

We tested the effects of disturbance on EMF and individual functions separately, as well as on above- (i.e. taxonomic, phylogenetic, functional and stand structure) and below-ground (i.e. soil bacterial and fungal diversity) diversity indices using two-way ANOVA models. A post-hoc Tukey's test was used to assess the significant differences among disturbance levels.

We used multiple linear regression models to evaluate the effects of the multiple predictors considered on EMF. However, before conducting regression analysis, we removed the highly correlated predictors (i.e. $r > 0.7$), such as $H_S$ and PD, $H_D$ and $CV_D$, to avoid multicollinearity issues (see Figure S2). Hence, nine variables including five above-ground diversity indices ($H_S$, $PD_F$, FD, $CV_D$ and $CWM_{PC1}$), two below-ground diversity indices ($H_B$ and $H_F$), one composite climate variable ($Clim_{PC1}$) and disturbance levels were included into the multiple regression models for predicting EMF. The disturbance levels were treated as an ordinal categorical variable (i.e. a regular numeric variable) and were coded as 1 (low), 2 (medium) and 3 (high). Since all predictors and response variables were standardized after min–max normalization, an analogue of the variance decomposition analysis was applied to obtain the relative importance of each predictor on a comparable scale, which can be simply calculated as the ratio between its standardized regression coefficient and the sum of all coefficients, and expressed in % (Le Bagousse-Pinguet et al., 2019). The obtained relative importance of predictors was grouped into five identifiable variance fractions: (i) above-ground diversity, (ii) below-ground diversity, (iii) climate, (iv) disturbance levels and (v) unexplained variance. Furthermore, we tested all possible combinations of two-way interaction effects for disturbance, climate and biodiversity (above- and below-ground) on EMF, of which indicated that most of the interaction effects were not significant and hence, less important (Figure S3).

Finally, we used a piecewise structural equation modelling (pSEM) to investigate direct and biodiversity-mediated effects of disturbance intensities on the averaged EMF index, EMF thresholds and individual ecosystem functions. We used site (i.e. 11 plots) as a random factor in pSEM. Since we had multiple candidate variables to use in pSEM, we included those variables of above- and below-ground diversity in final pSEM which had the highest standardized effect on EMF in multiple linear regression models. Also, we tested several pSEMs based on all possible combinations of above- and below-ground biodiversity attributes to further evaluate the best-fitted model. The model fit of pSEM was assessed using the Fisher's C statistic, that is, the model was considered to have an adequate fit to the data when the model had a Fisher's C statistic with $p > 0.05$ (Shipley, 2009). The conditional ($R^2_c$) and marginal $R^2$ ($R^2_m$) were calculated for each of the dependent variables (Nakagawa & Schielzeth, 2013).

We computed the *Pearson* correlations between pairs of individual functions and their relationships with $EMF_A$, aiming to assess the synergies (positive) or trade-offs (negative) between forest functions. All data analyses were conducted in R 3.6.0 (R Development Core Team, 2019). Phylogenetic and functional diversity indices were calculated using the *picante* (Kembel et al., 2010) and *FD* packages (Laliberte & Legendre, 2010) respectively. EMF indices were calculated using the *multifunc* package (Byrnes, 2014). Multiple linear mixed models and pSEM analyses were performed in *nlme* (Pinheiro et al., 2017) and *piecewise SEM* (Lefcheck, 2016) packages respectively.

## 3 | RESULTS

Highly disturbed plots exhibited the highest EMF, even at higher thresholds (Figure 1a). In addition, five of the nine individual functions (i.e. SOD, $WHC_S$, AN, AP and AK) measured in highly disturbed plots were significantly higher than in low disturbed plots. In contrast, $AGB_W$ was higher in low disturbed plots, whereas CWP, $B_L$ and $WHC_L$ did not show significant differences among the three levels of disturbance (Figure S4). As such, plant species richness (S), Shannon–Wiener diversity ($H_S$), Faith's phylogenetic diversity ($PD_F$) and soil microbe diversity ($H_B$ and $H_F$) were higher in highly disturbed plots, whereas functional trait diversity (FD) and identity ($CWM_{PC1}$) and stand structural attributes ($H_D$ and $CV_D$) were higher in low disturbed plots (Figure 1b).

The multiple linear regressions models explained 68%, 56%, 58% and 26% of the variations in $EMF_A$, $EMF_{T25}$, $EMF_{T50}$ and $EMF_{T75}$ respectively (Figure 2). The biodiversity indices explained 45% on average (26~58%) of the variations in EMF, while climate and disturbance together explained on average 7% (0.4%–15%). The cumulative above- and below-ground diversity accounted for about 26.0% (17.5%–39.4%) and 18.9% (8.1%–28.8%) of the variations in EMF respectively. Individual tree size variation ($CV_D$) and soil bacterial diversity ($H_B$) were selected as the best predictors of above- and below-ground diversity, explaining up to 11.3% (4.6%–19.7%) and 6.0% (2.0%–9.9%) of the accounted variance respectively (Figure 2). Since there was no significant relationship between composite climate factors ($Clim_{PC1}$) and EMF, and hence, we did not include $Clim_{PC1}$ in the pSEM analysis (Figure 2).

The tested pSEM models showed that disturbance had significant positive direct effects on EMF ($\beta$ = 0.27–0.54), irrespective of the EMF threshold considered (Figure 3). However, our models also showed opposite indirect effects of disturbances on EMF, highlighting the occurrence of contrasting biodiversity-mediated pathways. While both above- ($\beta$ = 0.02–0.19) and below-ground ($\beta$ = 0.16–0.26) diversity attributes had direct positive effects on EMF, their mediating effects were in partial contrast, that is, negative for above-ground diversity and positive for below-ground diversity. Furthermore, the negative mediating effect ($\beta$ = −0.22) of above-ground diversity on EMF increased with higher thresholds ($\beta$ = 0.02–0.19), highlighting a stronger negative pathway occurring when functions performed at higher rates (Figure 3). In order to complement the results from the main pSEMs (Figure 3), the correlation between forest functions is provided in Figure S5, whereas pSEMs for tested individual forest functions are provided in Figure S6.

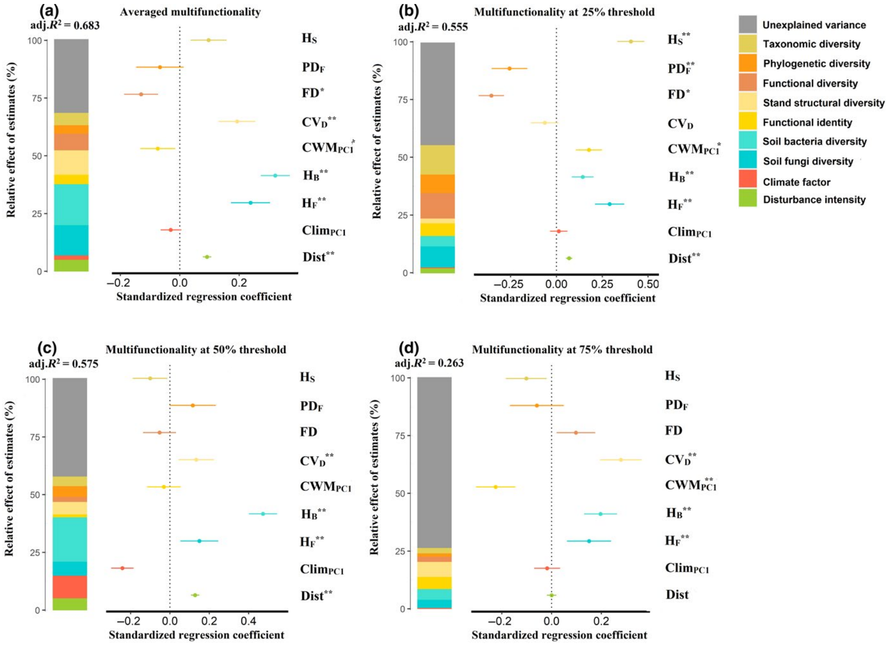

FIGURE 2 Effects of post-logging disturbances, climate and above- and below-ground biodiversity on averaged ecosystem multifunctionality (a), 25% threshold-based (b), 50% threshold-based (c) and 75% threshold-based ecosystem multifunctionality (d). Standardized regression coefficients of model predictors, the associated 95% confidence intervals and the relative importance of each factor (expressed as the percentage of explained variance) are shown. The adj.$R^2$ of the models and the *p*-value of each predictor is given as: **p* < 0.05, ***p* < 0.01. Dist, the disturbance levels; $Clim_{PC1}$, the first axis of 19 climate variables, whereas other abbreviations are explained in Figure 1 [Colour figure can be viewed at wileyonlinelibrary.com]

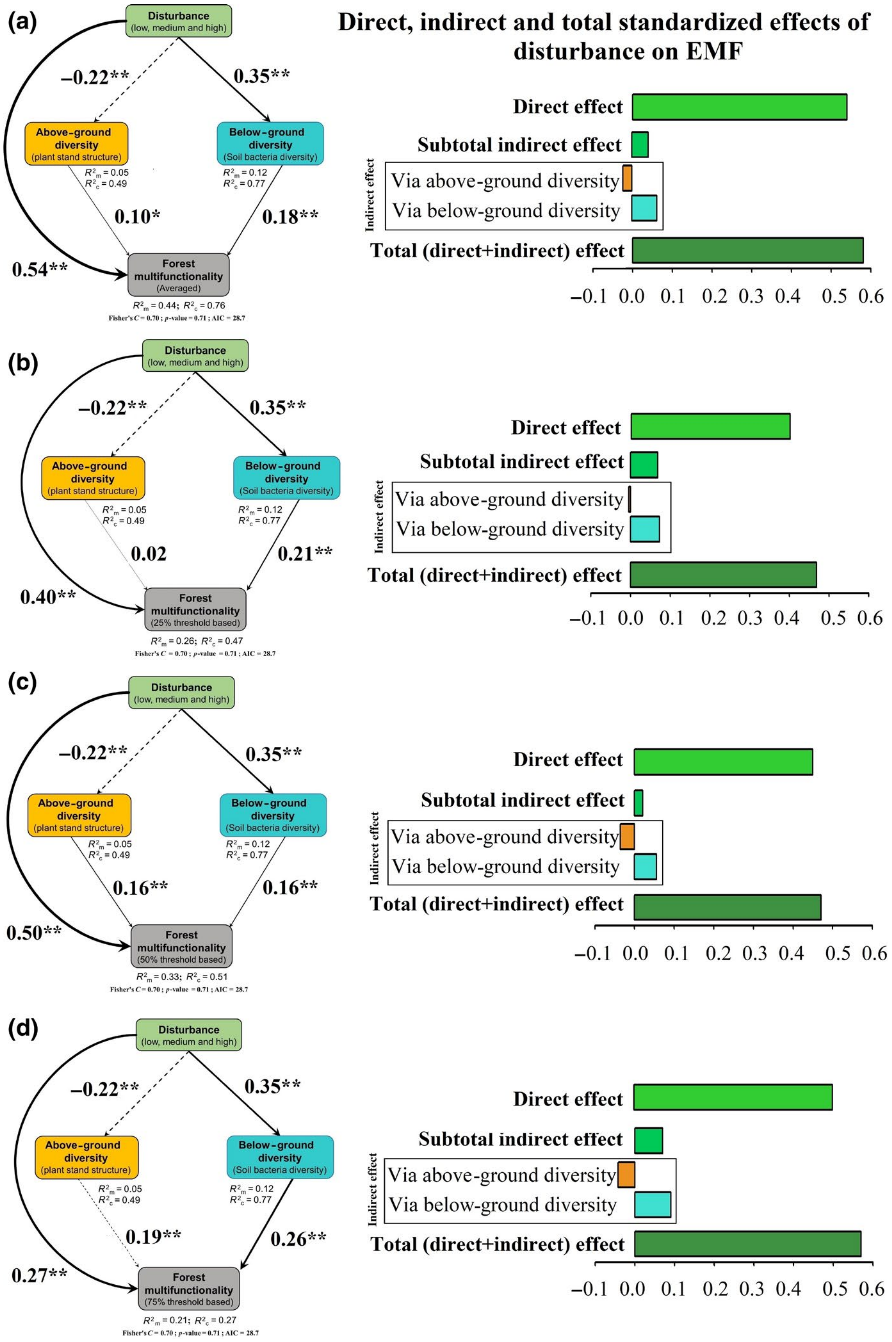

FIGURE 3 Results from the piecewise structural equation models (pSEMs) exploring the direct and indirect effects of disturbance levels on forest multifunctionality at averaged (a) and three threshold levels (b–d) via above-ground diversity and below-ground diversity. Numbers adjacent to arrows are indicative of the effect size of the relationship. Continuous and dashed arrows indicate positive and negative relationships respectively. For all relations, standardized regression coefficients and significance are given (*<0.05, **<0.01). The width of the arrows is proportional to the strength of path coefficients. $R^2$ denotes the proportion of variance explained and model-fit statistics for each pSEM are given [Colour figure can be viewed at wileyonlinelibrary.com]

## 4 | DISCUSSION

Our study offers an integrative framework aimed at exploring how multiple attributes of above-ground (taxonomic, phylogenetic, functional and stand structure) and below-ground (soil bacterial and fungal diversities) biodiversities simultaneously influence the EMF of temperate forests recovering from post-logging disturbances. The effects of biodiversity on EMF were twofold higher than those of both climate and disturbances together, expanding to previous findings on individual function such as productivity to EMF (Duffy et al., 2017). However, our results also show evidence for divergent above- and below-ground biodiversity pathways in mediating disturbance impacts on EMF. Hence, this study highlights the necessity of considering the multi-dimensional role of biodiversity to better grasp its complex effects on the functioning of terrestrial ecosystems in a changing world.

Higher EMF was found in disturbed forests rather than relatively undisturbed mature forests. Our result thus departs from the MacArthur's (1970) minimization principle, suggesting that more mature and late-stage communities should become more efficient by minimizing energy wastage and thus maximizing ecosystem functioning. Rather, our result reminds the recent study of who observed that mid-stage communities could be more efficient at utilizing resources (Ghedini et al., 2018). Specifically, forest canopy removal by sawlogs and timber harvesting indeed could result in tree density and forest biomass decline (Yuan et al., 2018), but our finding shows that relatively high disturbed forests could promote EMF by increasing soil carbon storage, nutrient availability and water retention capability, and hence, supporting the notion that suitable forest practice such as thining could achieve the best combination of high wood yield and nutrients reserves (Schwaiger et al., 2019; Thornley & Cannell, 2000). For example, recent synthesis has shown that forest thinning management practice could increase soil carbon stocks in China (Gong et al., 2021). One possible mechanistic explanation could be that timber harvest can reduce the species competition for limited resources such as light and nutrients, thereby increasing the primary productivity through enhancing the growth of remaining trees (de Avila et al., 2018; Saunders et al., 2012). There was no significant difference in woody production among the three levels of disturbance, implying that subsequent forest biomass recovers when emerging trees grow to occupy the gaps created by the felled trees, and hence, the loss of forest biomass can be compensated if the forests are left to recover, primarily depending on the magnitude of disturbance intensity (Piponiot et al., 2016). Meanwhile, forest thinning can lead more light and precipitation to reach the floor, which in turn may increase the biodegradation of litters and roots by stimulating the activities of microorganisms and soil enzymes, thus accumulating available nutrients pools and SOC stock (Huang et al., 2020; Simonin et al., 2007). Another possible explanation for greater soil carbon stock and WHC in the disturbed forest maybe that faster rates of surface water runoff and sediment transport to lower sites, associating with a decrease in the proportion of sand and increase in clay and soil bulk density in the soil of logged forests compared with the intact forests (Eaton et al., 2021). Collectively, compared with the relative pristine or unmanaged stands, the soil physicochemical properties, such as organic matter and available nitrogen, maximal water retention and total porosity, of natural mixed stands with low and medium management intensities were significantly increased after 10 years of restoration strategy (Wu et al., 2008).

Stand structural diversity was the main above-ground biodiversity attribute to promote EMF, particularly at higher multifunctionality thresholds. This result confirms the key role of stand structure for forest EMF, as previously shown for individual functions (e.g. productivity; Ali et al., 2016; Gough et al., 2020). Forests with complex stand structure attribute such as higher tree size variations, mainly reflecting the degree of heterogeneity in vegetation density, could sustain higher EMF likely through optimizing space, resources and understorey microclimatic conditions (Hardiman et al., 2013; Jucker et al., 2015). As the individual size inequality (i.e. $CV_D$) increases, niche differentiation among and plasticity within trees probably augment heterogeneity in branch and leaf density and morphology, resulting in more efficient light intercept and utilize across a range of light conditions (Ali, 2019; Yachi & Loreau, 2007). For instance, our analysis also indicates that more complex communities could lead to faster growth and biomass accumulation of shrub species (Figure S5b).

Considering multiple above-ground biodiversity attributes showed contrasted responses to post-logging disturbance, ultimately leading to positive, neutral and negative effects on EMF (Le Bagousse-Pinguet et al., 2019). Although timber harvesting could cause a reduction in stand structural diversity due to large stems removal, it could promote species diversity by creating forest gaps in which higher light resources might be available for saplings or colonizing seedlings (Molino & Sabatier, 2001). After a disturbance, large canopy gaps provoke great variations in light availability at the forest floor and, on soil temperature and water conditions (Laigle et al., 2021), and could promote higher tree species diversity through the niche partitioning of more greatly contrasting and frequently created resources and/or density effect (Sipe & Bazzaz, 1995). These gaps are expected to be occupied by early-successional, light-demanding species (Poorter & Bongers, 2006). Generally, forest gaps are also expected to be primarily filled by the inclusion of by chance species rather than by best-adapted species because of the stochastic availability of gaps and limited recruitment of juveniles leading to slow competitive exclusion and enable the coexistence of more plant species (Brokaw & Busing, 2000). Interestingly, our results show that the disturbance-induced increase in species richness does not lead to higher functional trait diversity, implying the high functional redundancy in the above-ground species composition. Therefore, ignoring the contrasting effects of land-use impacts on a variety of biodiversity attributes, such as taxonomic, phylogenetic, functional and stand structural diversity, will likely bias our ability to predict the functional consequences of biodiversity decline (Le Bagousse-Pinguet et al., 2019).

In contrast to the above-ground biodiversity attributes considered, high soil bacterial diversity consistently promoted EMF irrespective of the EMF threshold considered, while soil diversity is often viewed to drive EMF mainly at low thresholds (Delgado-Baquerizo et al., 2016; Wagg et al., 2014). Soil bacteria diversity is the main driver for maintaining EMF in many terrestrial ecosystems (Delgado-Baquerizo et al., 2016; Wagg et al., 2014; Wang et al., 2019; Yuan et al., 2020) through maintaining key ecological processes such as nutrient cycling and decomposition (Delgado-Baquerizo et al., 2020; Van Der Heijden et al., 2008). A recent global survey and microcosm experiment revealed that the positive impact of soil biodiversity on EMF can be maintained across biomes after accounting for important ecosystem factors such as climate and plant attributes (Delgado-Baquerizo et al., 2020). The soil bacterial groups have long been recognized to be involved in the early recovery of soil carbon and nitrogen processes(Moore & de Ruiter, 1991), including the degradation of less complex organic carbon, nitrogen fixation and ammonium oxidation that are crucial in managed, young, or recently damaged soils (Eaton et al., 2012; Pajares & Bohannan, 2016). It has been shown that an increase in the abundance of bacteria for nitrogen fixation and ammonium oxidation due to the high demand for nitrogen needed for vegetation and soil ecosystems recovering from disturbances (Nasto et al., 2014).

## 5 | CONCLUSIONS

Our study provides observational evidence that post-logging disturbances (from low to high level) could enhance forest multifunctionality and below-ground biodiversity, while simultaneously declining above-ground biodiversity. While certain attributes of above-ground plant diversity can reduce EMF, above-ground stand structural and soil microbial diversity attributes appear as important biodiversity facets to promote forest EMF. Hence, managing forest ecosystems to maximize above-ground biodiversity, such as higher species richness, may not necessarily maximize a particular subset of functions. In other words, ecosystem service provisioning cannot be solely replaced by the protection of a high above-ground stand diversity (Felipe-Lucia et al., 2018; Meyer et al., 2018). This study underlines that maintaining multifunctional forests through a suitable level of management or disturbance intensity may allow for higher biodiversity and ecosystem services on which human beings are dependent. Hence, we argue that the inclusion of soil biodiversity and disturbance levels should be considered as decisive components of the management decision-making policies (Delgado-Baquerizo et al., 2020; Huang et al., 2020).

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## CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

## AUTHOR CONTRIBUTIONS

ZY, AA, XW and YLB-P conceived the idea. ZY, FD, SL, AS, WZ, JY, FL, SF, ZH and XW conducted the study and collected the data. ZY analysed the data and wrote the first draft with great support from AA and YLB-L, after which all authors contributed substantially to revision.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.d51c5b030.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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