



Climatic water availability modifies tree functional diversity effects on soil organic carbon storage in European forests

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Received: 19 December 2022 / Revised: 18 April 2023 / Accepted: 5 May 2023
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Abstract

Forest stand and environmental factors influence soil organic carbon (SOC) storage, but little is known about their relative impacts in different soil layers. Moreover, how environmental factors modulate the impact of stand factors, particularly species mixing, on SOC storage, is largely unexplored. In this study, conducted in 21 forest triplets (two monocultures of different species and their mixture on the same site) distributed in Europe, we tested the hypothesis that stand factors (functional identity and diversity) have stronger effects on topsoil (FF + 0–10 cm) C storage than environmental factors (climatic water availability, clay + silt content, oxalate-extractable Al–Al_{ox}) but that the opposite occurs in the subsoil (10–40 cm). We also tested the hypothesis that functional diversity improves SOC storage under high climatic water availability, clay + silt contents, and Al_{ox}. We characterized functional identity as the basal area proportion of broadleaved species (beech and/or oak), and functional diversity as the product of broadleaved and conifer (pine) proportions. The results show that functional identity was the main driver of topsoil C storage, while climatic water availability had the largest control on subsoil C storage. Functional diversity decreased topsoil C storage under increasing climatic water availability, but the opposite was observed in the subsoil. Functional diversity effects on topsoil C increased with increasing clay + silt content, while its effects on subsoil C were negative at increasing Al_{ox} content. This suggests that functional diversity effect on SOC storage changes along gradients in environmental factors and the direction of effects depends on soil depth.

Keywords Soil organic carbon · Forest ecosystem services · Triplets · Oxalate-extractable metals · Context-dependency effects · Functional diversity

Introduction

Soil organic C (SOC) storage in forest ecosystems is crucial for global climate mitigating efforts (Bowditch et al. 2020; Mayer et al. 2020) because soils contain more than two-thirds of total forest C stocks (Dixon et al. 1994; Pan et al. 2011). SOC stock is also a key indicator of overall soil quality (Mayer et al. 2020; Wiesmeier et al. 2019). The balance between litter input (above- and belowground) and decomposition determines SOC stocks in forests (Liu et al. 2018). This suggests that scientific investigations into stand parameters that affect the quality and quantity of organic

matter input and the prevailing environmental factors that control decomposition and stabilization of organic matter are worthwhile to improve our understanding of SOC storage in forests (Adhikari et al. 2020; Mayer et al. 2020; Rasmussen et al. 2018). While previous studies have attempted to assess the effect of either stand or abiotic drivers of SOC storage, information about their comparative effects is limited.

Species selection is a crucial management decision to influence SOC storage in forests (Chen et al. 2022; Dawud et al. 2017). According to the mass ratio hypothesis, functional traits of dominant species determine ecosystem functioning (Grime 1998). In line with this, tree species are commonly grouped into broadleaved and conifer functional groups to examine their effects on SOC storage (Augusto et al. 2015; Dawud et al. 2017; Prescott and Vesterdal 2021). SOC-related functional traits of most broadleaved species

Communicated by Agustin Merino.

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are high litter quality (high nutrient content, low contents of high molecular compounds such as lignin, tannin, etc.), high production of fine roots (Mayer et al. 2020; Vesterdal et al. 2013). They are also more associated with microbial communities than most coniferous counterparts (Mayer et al. 2020; Vesterdal et al. 2013). These traits promote fast litter transformation and incorporation into upper mineral soil layers (Prescott and Vesterdal 2021; Vesterdal et al. 2013). Common functional traits of most coniferous forests are low litter quality (nutrient-poor litter with high molecular compounds) and acidic needles. These limit their microbial transformation leading to accumulation of SOC in the forest floor more than broadleaved forests (Dawud et al. 2017; Vesterdal et al. 2013).

Mixing tree species belonging to different functional groups (i.e. functional group diversity) increases the portfolio of functional traits in the forest for delivery of more ecosystem goods, services, and functions, than monocultures (Ratcliffe et al. 2017; Van Der Plas et al. 2016). As a result, more functionally diverse forests are expected to have higher soil C stocks than less diverse forests due to greater productivity and associated litter inputs (Augusto and Boča 2022; Chen et al. 2022; Mayer et al. 2020). The response of SOC storage to tree diversity has been investigated by selected studies (Chen et al. 2022; Dawud et al. 2017; Osei et al. 2021), but was found to be inconsistent due to strong dependence on the environmental context (Chen et al. 2022; Fanin et al. 2021; Ratcliffe et al. 2017). This is in accordance with the general framework that diversity—forest productivity relationships change along environmental gradients (Ammer 2019; Forrester and Bauhus 2016). Yet, the factors underpinning this context-dependency of tree diversity effects are usually elusive (Dawud et al. 2017; Fanin et al. 2021; Osei et al. 2021). This constraints opportunities to scale-up and generalize research outcomes (Fanin et al. 2021; Ratcliffe et al. 2017). Ratcliffe et al. (2017) and Dawud et al. (2017) investigated drivers of context-dependency of species richness effects on SOC in European forests but they only considered up to 10 and 20 cm soil depths, respectively. A similar study by Fanin et al. (2021) sampled up to 100 cm depth but their experiment occurred at a single site in southwestern France. Consequently, patterns of tree diversity effects on soil C storage beyond 20 cm depth along abiotic gradients in Europe remain a significant knowledge gap. By contrast, Chen et al. (2022) provided the drivers of context-dependency of tree diversity effects on SOC up to 55 cm depth in temperate and boreal forests across Canada.

Two main factors identified in previous studies as drivers of context-dependency of functional diversity effects on SOC storage are climatic water availability (Chen et al. 2022; Dawud et al. 2017; Fanin et al. 2021; Ratcliffe et al. 2017) and soil texture (Dawud et al. 2017; Ratcliffe et al. 2017). Climatic factors, namely temperature and

precipitation, influence SOC storage via their effects on net primary productivity (NPP) of forest ecosystems that in turn determines above- and below-ground litter input, and also through control on litter decomposition (Adhikari et al. 2020; Rasmussen et al. 2018; Wiesmeier et al. 2019). Local site topography also impacts precipitation, water flow paths, water accumulation and discharge, which altogether determine site moisture regime and consequently SOC storage (Hobley et al. 2015). Nonetheless, their effects are minor at large scales and often conflate with climatic factors (Hobley et al. 2015). Soil texture is considered very important for SOC storage due to the interaction of organic matter with soil mineral surfaces and its role in soil water holding capacity (Basile-Doelsch et al. 2020; Dynarski et al. 2020), which also has consequence for nutrient availability to trees. However, clay content was not a significant driver of SOC in a continental-scale study but rather oxalate-extractable Al, pH, and climate (Rasmussen et al. 2018). Oxides and hydro-oxides of aluminium (Al) and iron (Fe) are indicators of soil surface properties particularly related to sorption capacity in the mineral phase (Ashida et al. 2021; Rasmussen et al. 2018). The direction of tree diversity effects along gradients in these abiotic factors is very difficult to predict (Ammer 2019; Forrester and Bauhus 2016). Previous studies have recorded positive tree diversity effects on forest productivity under both dry, poor site conditions (Lu et al. 2018; Toïgo et al. 2015) and also under humid conditions (Steckel et al. 2019). This emphasizes that positive diversity–productivity relationships are possible under both harsh and favourable site conditions. Therefore, we might expect functional diversity to increase forest litter input to the soil under varied site conditions, but the resulting net effect on SOC stocks would be contingent on the prevailing environmental factors through their impacts on organic matter retention. Accordingly, functional diversity should improve SOC storage when those SOC drivers favour SOM retention over decomposition. In the studies of Fanin et al. (2021) and Ratcliffe et al. (2017), tree diversity had positive effects on SOC stocks with increase in water availability. However, it remains unclear whether this trend is consistent over a large gradient of environmental conditions in Europe and whether the direction of effect varies with soil depth.

In our previous study (Osei et al. 2021) that compared species identity versus mixing effects on SOC, we found that species identity (i.e. beech, oak, pine) was an important driver of SOC, especially in the topsoil layers, and that the mixing effect was more important in deeper layers. Site as a random factor explained a large variability in soil stocks, but we did not investigate the specific factors behind the site effect, how the effect of those factors compares with stand effects, or how site factors could possibly interact with functional diversity. In the same study, we investigated each of the three species combinations (pine–oak, pine–beech,

beech–oak) separately and thus failed to demonstrate the overall effect of functional group (in terms of BA proportions of broadleaved tree species) on SOC storage along the entire gradient of environmental conditions in Europe covered by the study. The objective of this study is to compare the relative importance of stand (functional identity and diversity) versus environmental factors (climate, soil texture, oxalate-extractable Al) for SOC storage in top (forest floor + 0–10 cm) and subsoil layers (10–40 cm), and to unravel the environmental drivers of context-dependency of functional diversity effects on SOC storage.

The forests were in triplets (two monocultures of different species and their mixture on the same site; sp A, sp B, spp A + B) composed of broadleaved–broadleaved (beech–oak) and coniferous–broadleaved (pine–beech; pine–oak) tree species, which were distributed along large gradient of environmental conditions across seven European countries. We characterized functional identity as the basal area (BA) proportion of broadleaved species (beech, oak), while functional diversity was computed as the product of the BA proportions of broadleaved and conifer (pine) species. The SOC stocks were estimated on soil samples from the forest floor (FF) down to 40 cm in 10 cm intervals following procedures described in Osei et al. (2021). We tested the hypotheses that:

(H1) functional identity (in terms of BA proportions of broadleaved tree species) and diversity influence topsoil C storage more than environmental factors, while the opposite occurs in subsoil layers.

(H2) positive effect of functionally diverse forests on SOC storage occurs with increase in climatic water availability, fine soil texture (clay + silt) and oxalate-extractable Al contents.

Materials and methods

Study design and site characteristics

This study was conducted in 21 forest triplets across Europe (Fig. 1). A triplet consisted of two monocultures of different species and their mixture on the same site (sp A, sp B, spp A + B). The three forest stands in each triplet were of similar ages (based on tree cores and forest archives) and had homogenous soil conditions based on texture analyses on soil samples in the 10–20 cm depth. The triplets were of three types: five beech–oak (*Fagus sylvatica* L.–*Quercus petraea* (Matt.) Liebl.), eight pine–beech (*Pinus sylvestris* L.–*Fagus sylvatica* L.), and eight pine–oak (*Pinus sylvestris* L.–*Quercus robur* L./*Quercus petraea* (Matt.) Liebl.). These

tree species are widely distributed in Europe and are very important for forestry. The triplets were located along wide climatic and edaphic gradients in Europe. Briefly, mean annual temperature ranged from 7.0 to 10.8 °C, while mean annual precipitation ranged between 550.0 and 1175.0 mm/year (Table 1). We characterized the combined effect of precipitation (P, mm) and temperature (T, °C) by the de Martonne aridity index (DMI; $P/T + 10$; de Martonne 1926). The DMI represents climatic water availability (hereafter “water availability”). The DMI ranged from humid to very humid (30.8–60.0 mm/°C; de Martonne 1926).

The average clay content across sites was 12.5%, while silt content was 31.5%. The average oxalate-extractable Al (Al_{ox}) content, which was used as surrogate for soil surface mineralogy (due to its capacity for mineral–mineral and organo-mineral associations; Wiesmeier et al. 2019), was 141.3 mg/kg (Table 1). The oxalate-extractable Al was highly variable among sites compared to other environmental variables (Table 1). Further information on study design and site characteristics can be found in Osei et al. (2021).

Computation of stand basal areas and functional group proportions

With a diameter threshold of > 7 cm, we conducted stem diameter (dbh) inventory in every forest stand. We calculated stand basal areas (BA, m²/ha) from tree dbh values and plot sizes (ha). In each stand, we combined the BAs of the two main species of interest in our study design as stand BA. Subsequently, we partitioned the BA of species in a given stand into broadleaved and conifer functional groups. The broadleaf functional group consisted of BA proportion of beech and/or oak, and the conifer functional group was BA proportion of pine. We grouped beech and oak together because they are both broadleaved species and they had similar effect on SOC storage in a previous study from this dataset (Osei et al. 2022). This approach enabled us to investigate the broadleaved functional group effects on SOC at the European scale because each triplet had either beech or oak as a constituent species and the triplets were at different locations across Europe.

Soil sampling and estimation of soil parameters

We placed ten (10) sampling points in each mixed stand and five (5) points each in the corresponding monocultures. At each sampling point, we sampled the forest floor (organic layer above the mineral soil) with 30 cm × 30 cm metal frame. Subsequently, we dug sampling pits in 10 cm interval until 40 cm depth. We estimated total volume (soil + voids + stones) of soil samples in each 10 cm pit by the volume replacement method (Al-Shammary et al. 2018) with glass beads. Samples were air-dried, crushed

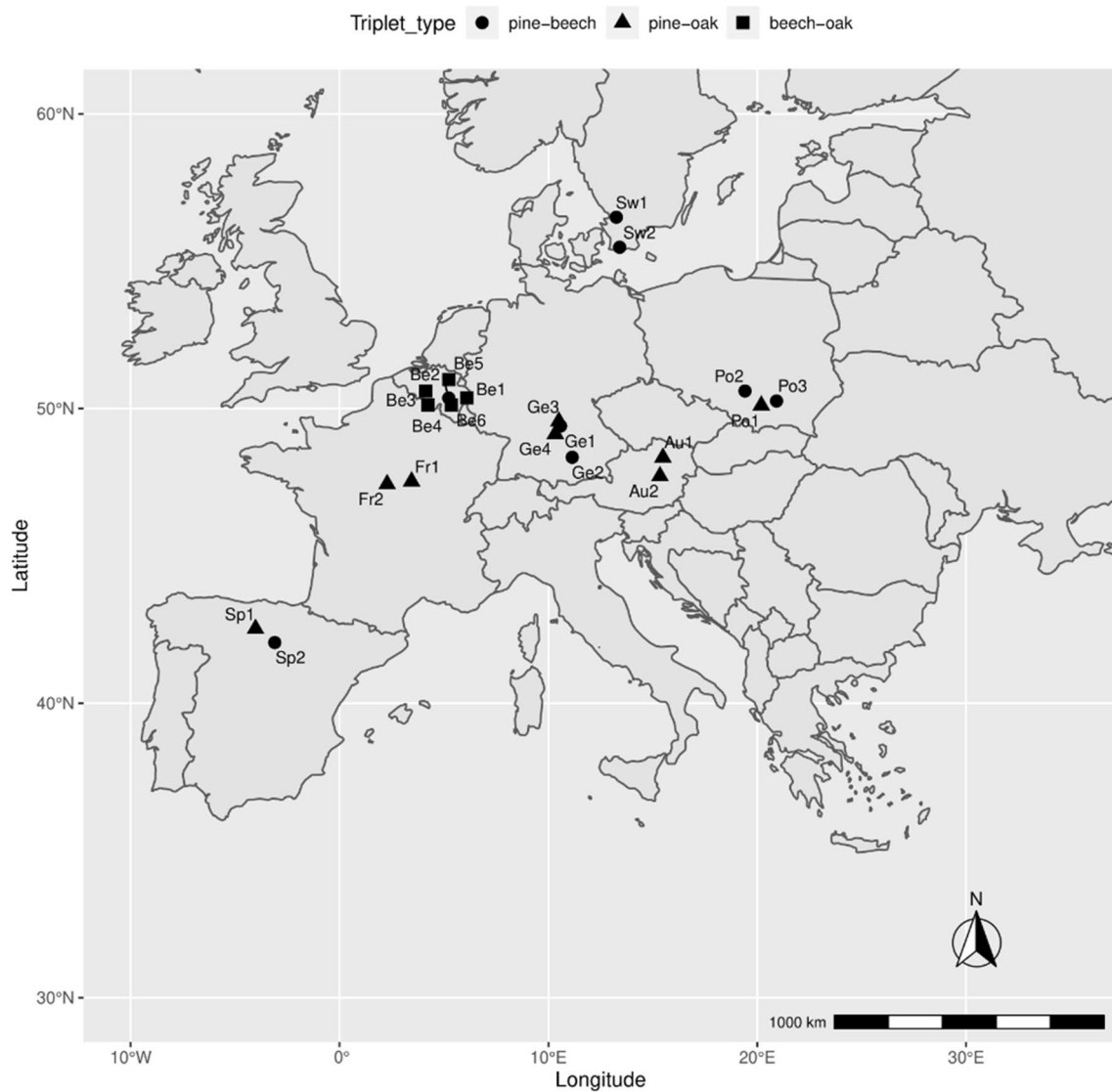


Fig. 1 Map of study sites in seven European countries. Countries were: Au = Austria; Be = Belgium; Fr = France; Ge = Germany; Po = Poland; Sp = Spain; Sw = Sweden

Table 1 Descriptive summary of environmental variables used in this study

Variable	Mean	Range	CV (%)
Mean annual precipitation (P, mm)	794.7	550.0–1175.0	22.1
Mean annual temperature (T, °C)	8.8	7.0–10.8	12.3
de Martonne index (DMI; $P/T + 10$, mm/°C)	42.2	30.8–60.0	21.4
Oxalate-extractable aluminium (Al_{ox} , mg/kg)	141.3	62.3–534.1	88.1
Clay + silt content (%)	44.0	2.5–85.4	57.7

The soil variables were determined on composite samples (1 sample per stand in each triplet) from the 10–20 cm soil depth. CV denotes coefficient of variation, calculated as the ratio of standard deviation to the mean

and then passed through 2 mm sieve to separate fine soil (< 2 mm), coarse roots (> 2 mm), and stones. We picked visible roots in fine soil to reduce their influence on C

contents. We separately weighed all the fine soil and the stone fractions. We determined stone volume by water displacement method. Sub-samples of fine soils were ground

into powder with Vibratory Disc Mill (Retsch RS 200, Germany) for C and N analyses on all samples (totalling 2080) using CN Analyser (FlashEA® 1112, USA). Computation of SOC stocks has been described in Osei et al. (2021). Soil pH, particle size distribution, and oxalate-extractable Al (Al_{ox}) was determined on samples from the 10–20 cm depth. We determined soil pH in deionized water at a ratio of 1:10 using inoLab pH Level 1 (WTW GmbH, Germany). Particle size distribution was determined by sedimentation method following protocol NF X31-107. The Al_{ox} was extracted by 0.2 M ammonium-oxalate at pH 3 according to Blackmore et al. (1981), and the concentration of Al was determined by ICP.

Statistical analyses

We performed all analyses in R software (R Core Team 2020) and tested significance at 95% confidence level in all cases. First, we used the BA proportion of broadleaved functional group (i.e. % BA of beech and/or oak) as a surrogate for functional group identity (hereafter, “functional identity”) in all stands. Following Kirwan et al. (2009), we computed the product of BA proportions of broadleaved and conifer functional group (i.e. % BA of pine) to characterize functional group diversity (hereafter, “functional diversity”) in all stands. The coefficient associated with this product tested the effects of the interaction between different tree functional groups (i.e. main effect of functional diversity) on SOC storage. This functional diversity measure was maximum in stands with equal BA proportions of broadleaved and conifer species (i.e. $0.5 \times 0.5 = 0.25$) but zero in complete monocultures.

Environmental factors considered for testing hypotheses in this study were climatic water availability, soil texture, and soil surface reactivity (oxalate-extractable— Al_{ox}) based on their key roles in SOC storage reported in previous studies (Adhikari et al. 2020; Rasmussen et al. 2018; Wiesmeier et al. 2019). We excluded soil pH because it can be affected by both overstorey vegetation and environmental factors. However, it will be used as a background information for the interpretation of stand and environmental effects. Because soil fertility, water holding capacity, and C storage are driven by the fine mineral fractions, we selected clay + silt content for the analyses as done in Rasmussen et al. (2018). The preliminary analyses revealed low Pearson correlations (threshold of $r = 0.7$) among the environmental factors (clay + silt, Al_{ox} , DMI). The final mixed effect model for testing our hypotheses was as follows:

$$\begin{aligned} \text{SOC} \sim & \alpha_1 + \alpha_2 \text{ stone content} + \alpha_3 \text{BA} \\ & + \alpha_4 \text{ functional identity} + \alpha_5 \text{ functional diversity (FD)} \\ & + \alpha_6 \text{ DMI} + \alpha_7 \text{ ClaySilt content} + \alpha_8 Al_{ox} + \alpha_9 \text{FD} \\ & \times \text{DMI} + \alpha_{10} \text{FD} \times \text{ClaySilt content} + \alpha_{11} \text{FD} \\ & \times Al_{ox} + e_{(\text{triplet})} + \epsilon \end{aligned} \quad (1)$$

α_1 is the regression coefficient of the intercept, α_2 – α_{11} are the regression coefficients of the fixed effects, $e_{(\text{triplet})}$ is a random parameter associated with site and ϵ is the error term. SOC is the soil organic C stock (in Mg/ha) either in the topsoil (FF+0–10 cm), subsoil (10–40 cm), or the total soil layer (FF+0–40 cm). Stone content (%) was included to account for differing stoniness among stands; BA ($\text{m}^2 \text{ha}^{-1}$) is the total basal area of the main species to account for stand density; functional identity is the BA proportion of broadleaved species (beech and/or oak) in each stand; and functional diversity is the product of broadleaved and conifer (pine) BA proportions. Al_{ox} is oxalate-extractable aluminium (mg/kg); DMI is the de Martonne aridity index calculated from mean annual precipitation and temperature ($\text{mm}/^\circ\text{C}$), high values denote increase in climatic water supply. Clay-Silt is the sum of clay and silt content (%).

We standardized (mean = 0, SD = 1) the explanatory variables in all models to allow independent interpretation of interactions and main effects. We represented significant interactions between functional diversity and environmental factors in the mixed models at the mean (0), mean + SD (1), and mean – SD (–1) in graphical moderation analyses. These levels showed the direction of functional diversity effects on SOC storage at average (0), above average (1), and below average (–1) conditions of the interacting environmental factors. Mixed effects modelling was appropriate for the hierarchical nature of the study design to address spatial correlation among the three stands of a triplet. It also controlled for the effects of other environmental factors not included in our analyses (Zuur et al. 2009). Subsequently, we performed variance partitioning to obtain the percentage of variability in SOC explained by fixed effects, random effects, and residuals. We used *lme4* R package (Bates et al. 2015) for mixed effect modelling with restricted maximum likelihood (REML). We conducted model inspections for normality, collinearity (using variance inflation factors, VIF), and heteroscedasticity with *performance* (Lüdtke et al. 2021) and *ggResidpanel* (Goode and Rey 2022) R packages. The VIFs of parameters in the models were all less than 3.0, which indicated that multicollinearity did not affect our models. We estimated significance of predictors with Satterthwaite's degrees of freedom method in

lmerTest R package (Kuznetsova et al. 2017). We used *partR2* R package (Stoffel et al. 2020) for variance partitioning and performed moderation analyses with *ggeffects* R package (Lüdtke 2018).

Results

Main effects of stand and environmental factors on SOC storage

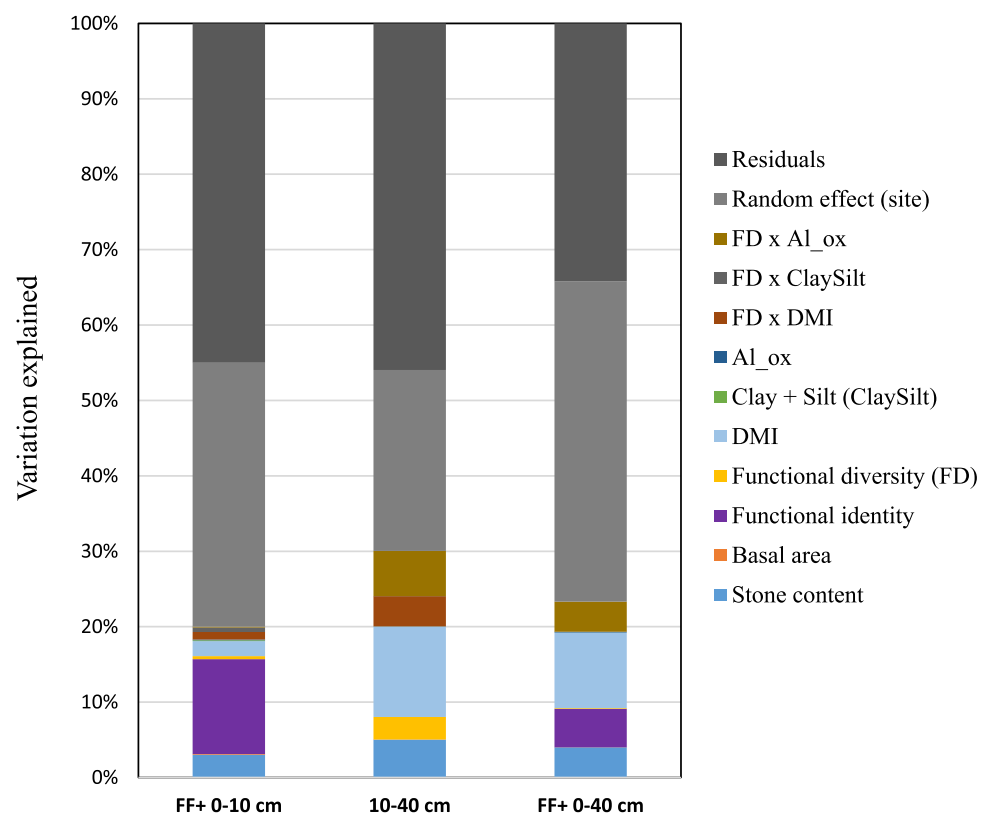
Functional identity was a significant driver of SOC storage in the topsoil (Table 2) and explained about 12.0% of variation in SOC stocks (Fig. 2). Functional diversity

Table 2 Results of mixed effect models (Eq. 1) showing the effect of functional identity (% BA of beech and/oak; broadleaved species), functional diversity (product of broadleaved and pine BA proportions; FD), de Martonne index (DMI; calculated from mean annual precipitation and temperature), clay + silt content, oxalate-extractable aluminium (Al_{ox}), and interactions of FD with environmental factors on soil organic C stocks (Mg/ha). P-values in bold are significant at 95% confidence level

Parameters	FF+0–10 cm	10–40 cm	FF+0–40 cm
Intercept	55.97 (3.46), < 0.001	38.79 (2.36), < 0.001	95.07 (5.41), < 0.001
Stone content	−5.71 (1.42), < 0.001	−4.40 (1.12), < 0.001	−10.16 (2.02), < 0.001
Stand basal area	−1.85 (1.51), 0.22	0.03 (1.19), 0.98	−1.34 (2.00), 0.50
Functional identity	−9.23 (1.17), < 0.001	−1.31 (0.92), 0.16	−10.26 (1.53), < 0.001
Functional diversity (FD)	−2.36 (1.23), 0.05	2.42 (0.97), 0.01	0.42 (1.61), 0.79
DMI	6.06 (4.47), 0.19	10.68 (3.12), 0.002	17.36 (6.71), 0.01
Clay + silt (ClaySilt)	2.54 (3.55), 0.48	0.05 (2.63), 0.98	2.33 (5.00), 0.64
Al_{ox}	−3.15 (3.12), 0.32	1.19 (2.20), 0.59	−3.51 (4.64), 0.45
FD x DMI	−5.74 (1.70), 0.001	6.00 (1.36), < 0.001	0.74 (2.24), 0.74
FD x ClaySilt	2.90 (1.43), 0.04	−0.88 (1.14), 0.44	2.47 (1.87), 0.19
FD x Al_{ox}	1.17 (1.07), 0.27	−5.18 (0.85), < 0.001	−4.68 (1.40), 0.001

Positive estimate for FD indicates that pine-broadleaved interactions improve SOC storage, and vice-versa. Stand BA and stone content were included as covariates to address contrasted stand density and stoniness among stands. All predictors were standardized (mean=0, SD=1) to allow interpretation of main and interaction effects. Site was fitted as random effect in all models

Fig. 2 Percentage of variation in SOC stocks explained by functional identity (% BA of beech and/or oak; broadleaved species), functional diversity (product of broadleaved species and pine BA proportions; FD), de Martonne index (DMI; calculated from mean annual precipitation and temperature), clay + silt content, oxalate-extractable aluminium (Al_{ox}), and interactions of FD with environmental factors as predictors of soil organic C stocks (Mg/ha) in mixed effect models (Eq. 1 in Sect. 2.4). Stand BA and stone content were included as covariates to address contrasted stand density and stoniness among stands. All predictors were standardized (mean=0, SD=1) to allow computation of variance explained by main and interaction effects independently. Site was fitted as random effect in all models



was marginally significant ($p = 0.05$), and interacted significantly with DMI and clay + silt content. With *ca* 1.0%, contribution of functional diversity to total variability in topsoil C was much lower than that of functional identity (12.0%). In the topsoil, increasing the proportion of broadleaved species in the forest was associated with a reduction in SOC storage (Table 2).

None of the three environmental factors had significant main impact on SOC storage in the topsoil (Table 2). The main effects of environmental factors (DMI, Clay + silt, Al_{ox}) together were responsible for only 2.2% variability in SOC stocks in the topsoil (Fig. 2). In the subsoils, functional diversity was significantly related to SOC storage but not functional identity. Amongst the environmental factors, DMI significantly improved SOC storage in subsoils and explained 12.0% variation, while the other environmental factors were not significant (Table 2; Fig. 2). The percentage of variability in subsoil C storage explained by the stand factors (3.0%) was just a quarter of variability explained by the environmental factors (12.0%; Fig. 2). Considering the total soil layer (FF + 0–40 cm), functional identity but not functional diversity, had significant control on SOC stocks. Among the environmental factors, only climatic water availability had significant (and positive) main effects on SOC storage in the total soil depth.

Interactions between functional diversity and environmental factors

The effect of functional diversity on SOC storage in the topsoil (FF + 10 cm) was dependent on climatic water availability and soil texture (Table 2; Fig. 3a and b). In the subsoils, climatic water availability and Al_{ox} moderated the effect of functional diversity on SOC storage (Table 2). With an increase in climatic water availability, functional diversity effects on SOC storage shifted from negative in the topsoil to positive in the subsoil (Fig. 3a and c).

In the topsoil, increase in functional diversity had slightly negative effect on SOC storage at below average clay + silt content (Fig. 3b). The Al_{ox} content changed the direction of functional diversity effects on subsoil C storage from positive at below average levels to negative with increasing Al_{ox} (Fig. 3d). The variance partitioning demonstrated that the interaction of functional diversity with the three environmental factors explained about 10% of variability in subsoil C storage. This explained variance was 5.9 times the variance accounted for by the interactions in the topsoil C stocks (1.7%; Fig. 2).

Discussion

Contrasting effects of stand vs abiotic factors on SOC storage over soil depth

The findings that forest stand factors, particularly functional identity, have stronger control on topsoil (forest floor + 0–10 cm depth) C storage than environmental factors as well as the reverse pattern in the subsoil agrees with our expectation (H1). This lends support to previous findings that different regulatory mechanisms control C accumulation in top versus subsoil layers (Chen et al. 2022; Mayer et al. 2020). In effect, our previous findings of strong species effect on topsoil C, though of varying magnitude in each of the three triplet types (Osei et al. 2021), also prevail at the European scale when the entire dataset is combined. This implies that the functional group of tree species in a forest is more important for forest floor and upper mineral soil C accrual than the environmental factors in this study. This finding contradicts Dawud et al. (2017) who found that site factors explained more variability (~60%) in SOC in the same soil layer (forest floor + 0–10 cm) than functional identity (~20%) in European forests. Dawud et al. (2017) indicated that strong functional group effects on topsoil C storage reflect litter chemistry, associated soil biota, and root dynamics. Broadleaved forests like beech and oak usually have relatively higher foliar and root litter quality (indicated by high N and P concentrations, low lignin/N ratios, etc.) than most coniferous forests (Chen et al. 2022; Krishna and Mohan 2017). Similarly, broadleaved litter often has higher pH values than pine, which reduces soil acidity and spur microbial transformation (Krishna and Mohan 2017; Mayer et al. 2020). Likewise, tree functional groups have distinctive signatures on the identity, abundance, and diversity of soil biota (Prescott and Vesterdal 2021). On average, broadleaved species often support more soil biota than most coniferous species (Prescott and Vesterdal 2021; Vesterdal et al. 2013). According to Prescott and Vesterdal (2021), broadleaved species like beech and oak promote earthworms, bacteria, and mull forest floor forms. These species have decomposition pathways dominated by microbial transformations, macrofaunal detritivorous transformation, and bioturbation by earthworms (Prescott and Vesterdal 2021). The acidic nature of the soils in this study (pH 3.8–4.7) may, however, limit these biotic processes. The afore-mentioned traits of broadleaved species that support faster litter decomposition explain the negative main effects of functional identity (in terms of beech and/or oak proportion) on topsoil C storage (Table 2; Augusto and Boča 2022) and further highlight the consequence of tree species change for SOC storage. In Bavaria, Germany, replacement of spruce and Scots pine by beech led to a 38–45% decrease in forest floor C

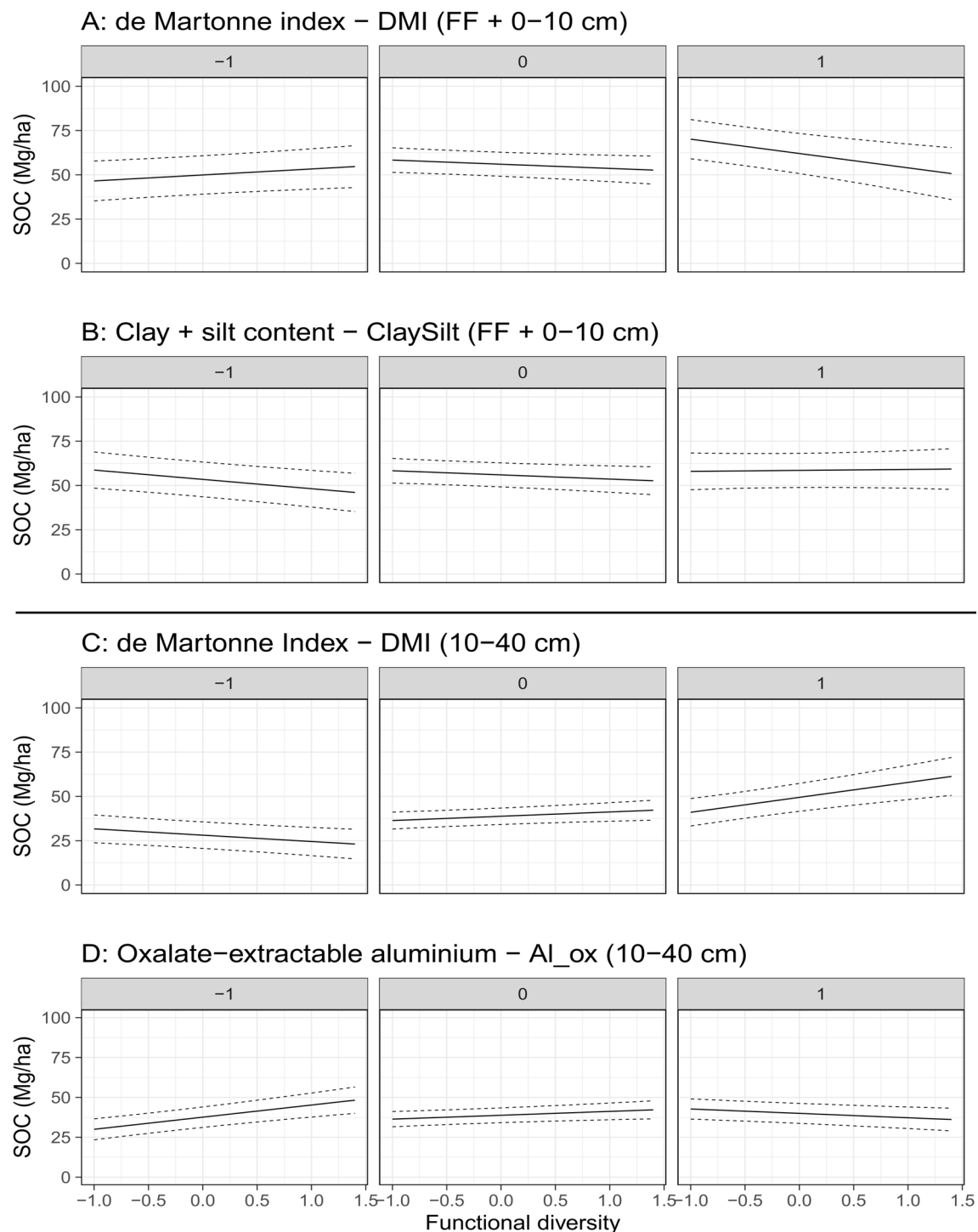


Fig. 3 Significant interactive effects of functional diversity and environmental factors on soil organic C (SOC; Mg/ha) in the topsoil (A: de Martonne index – DMI, B: clay + silt content – ClaySilt) and in the subsoil (C: de Martonne Index – DMI, D: Oxalate-extractable aluminium – Al_{ox}). The figure shows the direction of functional diver-

sity effects on SOC at below average (mean-SD = -1), average (0), and above average (mean+SD = 1) values of the environmental factors, when all other covariates are held constant at their mean values in mixed effect models (Eq. 1 in Sect. 2.4). See Table 2 for full statistical results

stocks but no changes occurred in the mineral soil (Prietz and Bachmann 2012). Similarly, Matos et al. (2010) found that admixture of oak (*Quercus petraea*) in pure stands of

Scots pine led to a reduction in SOC stocks in the topsoil. Counter-intuitively, this quick transformation of broadleaved litter in the topsoil by decomposers is a strategic pathway

for stabilization of organic matter in the soil (Augusto and Boča 2022; Kallenbach et al. 2016; Prescott and Vesterdal 2021). This is because soil microbes transform organic matter into novel compounds that have high residence time and are preferentially sorbed onto soil mineral surfaces (Kallenbach et al. 2016; Prescott and Vesterdal 2021). On the other hand, pine forests have recalcitrant and acidic litter less favourable for microbial transformation, and that results in C accumulation in topsoil layers (Dawud et al. 2017; Krishna and Mohan 2017; Mayer et al. 2020). The strong effect of functional identity (in terms of beech and/or oak proportion) on topsoil C in this study implies that the dominant tree functional group in a forest controls topsoil C storage per the ‘mass ratio hypothesis’ (Grime 1998). However, our findings should not be generalized for all broadleaved and coniferous species as their effect on SOC storage could be different from those tree species studied herein (Augusto et al. 2015; Cools et al. 2014).

In contrast to the topsoil layers, environmental factors (principally climatic water availability) had major control on subsoil C storage as expected (H1). This represents a shift from a species composition-driven C storage in the topsoil to an abiotic-driven C storage in the subsoil. This finding is not so surprising given that the footprint of tree species on SOC storage is in general much lower or even absent in deeper soil layers (Dawud et al. 2017; Gray et al. 2016). The stronger impact of climatic water availability on subsoil C storage than the topsoil contradicts findings by Gray et al. (2016) and Hobley et al. (2015) that climatic influence on SOC storage decreases with depth (up to 30 cm). Emerging understanding that fine roots and their associated microorganisms are the major sources of stable SOC in forest ecosystems (Dynarski et al. 2020; Gross and Harrison 2019; Hobley et al. 2015; Prescott and Vesterdal 2021) implies that abiotic factors that impact root productivity and soil biota are crucial for SOC storage. In this respect, the positive effect of climatic water availability on subsoil C stocks could be explained by its positive impact on fine root productivity (Freschet et al. 2017) and microbial community dynamics (Serna-Chavez et al. 2013) as well as their subsequent transformations into SOM. Augusto and Boča (2022) indicate that favourable environmental conditions for biological activity, such as water availability, enable soil biocoenosis to transform even recalcitrant necromass. Soil texture (i.e. clay + silt content) was not a significant main driver of SOC in this study, which confirms findings of Rasmussen et al. (2018). They found that other abiotic parameters such as climate are better predictors of SOC storage and stabilization than texture at large spatial scales (Rasmussen et al. 2018). This is because similar-sized clay and silt particles usually have different mineral constituents (phyllosilicates, oxyhydroxides and aluminosilicates, organo-metal complexes), which differ in their surface area, reactivity, solubility, and

sorptive capacity (Rasmussen et al. 2018; Wiesmeier et al. 2019). Similarly, Al_{ox} did not have main effects on SOC storage although its positive effect on SOC storage has been reported in several studies (e.g. Poeplau et al. 2021; Rasmussen et al. 2018; Wiesmeier et al. 2019). It has also been cited as a principal driver of SOC storage and stabilization in acidic forest soils like those in this study (Eusterhues et al. 2005; Rasmussen et al. 2018). The likely explanation for its non-significant effect in this study could be that Al_{ox} is more associated with the highly processed SOC fraction as organo-mineral and organo-metallic complexes (Eusterhues et al. 2005) than the total SOC stocks up to 40 cm depth, which is composed of organic matter fractions at varying degrees of decomposition. Another plausible explanation could be that humid conditions intensify weathering of parent material that favour the formation of Al–SOM complexes (Doetterl et al. 2015; Rasmussen et al. 2018) so the strong effects of climatic water availability observed in this study probably masks Al_{ox} effects. The total variability in SOC explained by the fixed effects in our model is comparable to values reported by other studies (Chen et al. 2022; Dawud et al. 2017). In Chen et al. (2022), for example, which included interactions of functional identity and diversity with abiotic factors, the total variability in SOC explained by fixed effects ranged between 18 and 37% for the various soil depths. Although we concede we could improve total SOC variability explained with the inclusion of functional identity—abiotic factors interactions (Chen et al. 2022; Dawud et al. 2017) and the interactions among the abiotic factors (Rasmussen et al. 2018), these were not the focus of this study.

Functional diversity effects on SOC storage change along environmental gradients.

Expectation of positive effect of functional diversity on SOC stocks with increase in climatic water availability, clay + silt content, and oxalate-extractable Al was only partially supported. Climatic water availability interacted with functional diversity in both top- and subsoil (Fig. 3). This confirms findings by Ratcliffe et al. (2017) that water availability is a major driver of context-dependency of tree diversity–ecosystem functioning relationships. A key finding of this study is that higher functional diversity had negative effects on topsoil C storage with increase in climatic water availability but shifted to positive in the subsoil (Fig. 3a and c). Our results for the topsoil are in close agreement with those reported by Chen et al. (2022) for the temperate forest biome, where the effect of functional diversity also shifted from negative at high climatic water availability to positive at decreasing climatic water availability. Mixing broadleaved species with conifers (like pine) would usually improve forest productivity

(Brassard et al. 2013; Ma et al. 2019; Steckel et al. 2019), with an expected increase in litterfall inputs (Dawud et al. 2017; Vesterdal and et al. 2013). Water availability would then modulate SOC accumulation through its impact on the decomposition process, leading to an accelerated litter decomposition at high DMI values, while limited water availability would inherently constraint the decomposition process at drier sites despite any improvement in litter quality and quantity (Chen et al. 2022; Ratcliffe et al. 2017). In that context, the opposite interactive effect between water availability and functional diversity in the subsoil compared to the topsoil could possibly reflect a difference in carbon transfer between the topsoil and the lower soil layers. This operates via higher integration of litter inputs by the decomposer community into the SOM pool under improved water availability than under dry conditions. However, the low pH values prevailing at our sites (pH 3.8–4.7) should limit the extent of organic matter transfer by biological activity in situations of both high and low climatic water availability. Alternatively, water availability could also modulate the impact of functional diversity on competition, leading to a higher competition reduction in more constrained situations in line with the Stress Gradient Hypothesis (Bertness and Callaway 1994). High water availability would therefore enhance competition for soil resources (Steckel et al. 2019) resulting in a shift of fine root production down to deeper soil layers (Brassard et al. 2013; Ma et al. 2019). This would end in a more efficient exploitation of the soil volume in the mixed stands than the monocultures (Bolte and Villanueva 2006; Finér et al. 2017), with attendant addition of fine root litter to the soil matrix (Dawud et al. 2016; Leuschner et al. 2001; Ma and Chen 2016). Such root productivity also enhances supply of root exudates to soil microbial communities, which are major components of subsoil C pools (Dynarski et al. 2020; Kallenbach et al. 2016; Prescott and Vesterdal 2021). Note that such possible shift of fine root production in functionally diverse forests from topsoil to subsoils with increase in climatic water availability could also explain the positive effects of functional diversity on subsoil C as well as the opposite trend in the topsoil (Fig. 3).

Soil texture influenced functional diversity-SOC stock relationship in the topsoil but not in the subsoil (Fig. 3). This agrees with biodiversity–ecosystem functioning study in six European countries by Ratcliffe et al. (2017) that found soil texture as a driver of context dependency of species richness effects on topsoil C cycling. In agreement with the second hypothesis (H2), higher functional diversity had positive effect on C stocks in the topsoil with increasing clay + silt content (i.e. decrease in sand content; Fig. 3b). We posit that soils with low clay and silt content (coarse-textured soils) usually have low sorptive capacity

to bind root litter inputs resulting from root inputs as opposed to fine-textured soils (Poeplau et al. 2021; Wiesmeier et al. 2019). Functional diversity also improved subsoil C storage under decreasing Al_{ox} content, in contrast with our expectations. (H2; Fig. 3d). This outcome could be due to enhanced fine root productivity, exploration, and litter inputs in the subsoil matrix in response to high phosphorous (P) availability (Ma and Chen 2016) under low Al_{ox} contents (Pena and Torrent 1990) because P is the most limiting nutrient in most European forests (Pena and Torrent 1990; Talkner et al. 2016). This is premised on the fact that oxides of Al are the primary adsorbents of P (Pena and Torrent 1990; Sibanda and Young 1986) so P becomes available for plant uptake in soils with low Al_{ox} contents (Pena and Torrent 1990), yet not in all cases (Sibanda and Young 1986).

Conclusion

This study found that functional identity (broadleaved–oak/ beech vs coniferous–pine) was a significant driver of topsoil C storage with functional diversity being marginally significant; they together explained 13.0% variability in SOC storage. In the same soil depth, none of the environmental factors was significant (in terms of main effects), but climatic water availability and clay + silt content had significant interactions with functional diversity. In the subsoil, functional identity was not significant but functional diversity was significant (explained 3.0% variability) and had significant interactions with climatic water availability and Al_{ox} . The results indicate that the dominant functional group in the forest shapes C storage in the topsoil (FF+0–10 cm) but not the environmental factors studied, and thus that site conditions may have limited direct impact on topsoil C storage in European forests. This result implies that future changes in forest species composition due to climate change (Ammer 2019) will potentially impact SOC storage in the topsoil more than the subsoil. Additionally, functionally diverse forestry is a promising management tool for climate mitigation due to its potential to enhance deeper SOC storage and stabilization. Climatic water availability was the only environmental factor that had significant main effect on SOC stocks in the subsoil (accounting for 12.0% variability) and the total soil depth. It also had significant interactions with functional diversity in both top and subsoils. This supports earlier studies that climatic water availability is a major driver of context-dependency of tree diversity effects on SOC storage. As the drivers (and direction) of context-dependency of functional diversity effects on SOC storage were dependent on the soil depth under consideration, our results imply that the direction of functional diversity effects on SOC storage along environmental gradients remains difficult to forecast. Additional studies would therefore be needed to increase

our understanding of the interactive effects of climate and soil drivers with functional diversity. Beyond statistical approaches, more process-based research would be necessary to disentangle the impact of the different environmental drivers on the various C sources and sinks, as well as on stabilization of SOM, under forests covering a range of functional diversity.

Acknowledgements We are grateful to Benjamin Willems and Karine Henin for assisting with soil sampling and laboratory analyses, respectively. We thank the anonymous reviewers for their constructive comments that really improved this manuscript.

Authors' contributions RO was involved in Conceptualization, Investigation, Formal analysis, Writing—original draft, Writing—review & editing. HT contributed to Methodology, Writing—review & editing. MdR, HP, MP, AN, YN, BM, ML, NK, MH, LD, J-TC, CC, KB, FB, Catherine Collet and RR-P were involved in Writing—review & editing. QP contributed to Conceptualization, Methodology, Resources, Funding acquisition, Project administration, Writing—review & editing, Supervision.

Funding The European Union and the National Fund for Scientific Research (Fonds de la recherche scientifique) of Belgium supported this research as part the ERA-Net SUMFOREST project REFORM—Mixed species forest management. Lowering risk, increasing resilience (www.reform-mixing.eu). The lead author was further supported by Université catholique de Louvain for covid-19-related delays of his PhD project. Some of the triplets were selected, established and measured with funding from the EuMIXFOR FP1206 Cost Action project. The Polish State Forests Enterprise also supported one of the Polish co-authors (Grant No: OR.271.3.15.2017). The Orléans site, OPTMix was installed thanks to ONF (National Forest Service, France), belongs to research infrastructure ANAEE-F; it is also included in the SOERE TEMPO, ZAL (LTSER Zone Atelier Loire) and the GIS Coop network.

Availability of data and material (data transparency) The datasets analysed during the current study are available at: <https://doi.org/10.5061/dryad.2v6wvpzs3>

Code availability (software application or custom code) Not applicable.

Declarations

Conflicts of interest The authors declare no conflict of interest.

Ethics approval (include appropriate approvals or waivers) Not applicable.

Consent to participate (include appropriate statements) Not applicable.

Consent for publication (include appropriate statements) All authors gave their informed consent to this publication and its content.

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