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The distribution of carbon stocks between tree woody biomass and soil differs between Scots pine and broadleaved species (beech, oak) in European forests

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Abstract

While the impacts of forest management options on carbon (C) storage are well documented, the way they affect C distribution among ecosystem components remains poorly investigated. Yet, partitioning of total forest C stocks, particularly between aboveground woody biomass and the soil, greatly impacts the stability of C stocks against disturbances in forest ecosystems. This study assessed the impact of species composition and stand density on C storage in aboveground woody biomass (stem + branches), coarse roots, and soil, and their partitioning in pure and mixed forests in Europe. We used 21 triplets (5 beech-oak, 8 pine-beech, 8 pine-oak mixed stands, and their respective monocultures at the same sites) in seven European countries. We computed biomass C stocks from total stand inventories and species-specific allometric equations, and soil organic C data down to 40 cm depth. On average, the broadleaved species stored more C in aboveground woody biomass than soil, while C storage in pine was equally distributed between both components. Stand density had a strong effect on C storage in tree woody biomass but not in the soil. After controlling for stand basal area, the mixed stands had, on average, similar total C stocks (in aboveground woody biomass + coarse roots + soil) to the most performing monocultures. Although species composition and stand density affect total C stocks and its partitioning between aboveground woody biomass and soil, a large part of variability in soil C storage was unrelated to stand characteristics.

Keywords Ecosystem carbon storage · Aboveground carbon storage · Soil organic carbon · Carbon distribution · Tree species identity · Triplet-transects

Introduction

Due to a combination of carbon storage in forest ecosystems and forest-derived products, as well as to carbon substitution (Gustavsson et al. 2017), forests and the forestry sector are considered fundamental to mitigate the impacts of climate change (Bastin et al. 2019; Bowditch et al. 2020; Gustavsson et al. 2017). This leads to the emergence of the Climate-Smart Forestry concept which, among others, implies the implementation of management options for maximizing C storage in forests (Bowditch et al. 2020; Pichancourt et al. 2014). To get a holistic understanding of how forest management could influence ecosystem C storage necessitates the consideration of major forest components, such as coarse roots and aboveground woody biomass and the soils (Liu et al. 2018; Ma et al. 2019), as these together constitute more than 85% of total forest C (Yude et al. 2011). In the context of forest management aimed at enhancing C storage, species composition and stand density are the key variables often targeted for silvicultural manipulations, based on their direct influence on C storage in forests, especially in tree woody biomass (Laganiere et al. 2010; Liu et al. 2018; Mayer et al. 2020). Nevertheless, the effect of species composition and stand density on C storage could be different for above- and belowground woody biomass and the soil (Ruiz-Peinado et al. 2013, 2016), which needs further attention.

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Carbon storage in forest ecosystems depends on the identity of the tree species involved (Ammer 2019; Blaško et al. 2020; Osei et al. 2021) and the environmental context (Ammer 2019; Forrester and Bauhus 2016). Some studies and reviews have examined the impact of species identity on aboveground and belowground woody biomass and/or C storage (e.g. Blaško et al. 2020; Ma et al. 2019) and soil C storage (Dawud et al. 2017; Osei et al. 2021; Vesterdal et al. 2013). Regarding tree components (both aboveground woody biomass and coarse root), C stocks per unit basal area are often used as surrogate for species-specific C storage potential (Torres and Lovett 2013), owing to the strong relationship between tree basal area and tree woody biomass (Forrester and Bauhus 2016; Torres and Lovett 2013). Torres and Lovett (2013) found higher aboveground woody C stocks per unit basal area in oak (*Quercus resinosa*) than pine (*Pinus oocarpa*) at the same site in Mexico, indicating a higher C storage potential of the oak (a broadleaved species) than the pine (a conifer). Similarly, Ma et al. (2019) found that *Populus tremuloides* forest (a broadleaved species) was associated with more root biomass production than neighbouring *Pinus banksiana* (a conifer species) forests in Canada. In the soil, species identity effects on C storage is also categorized broadly into that of broadleaved species and conifers (Boča et al. 2014; Mayer et al. 2020; Vesterdal et al. 2013; Wiesmeier et al. 2013). Reviews by Vesterdal et al. (2013) and Mayer et al. (2020) indicated similar total soil C stocks between conifers and broadleaved species but with a trade-off in C stock between forest floor and mineral layers; where conifers have more C stocks in the forest floor and upper mineral soil layers, while broadleaved species have more C stocks in the mineral sub-soil layers. However, a meta-analysis by Boča et al. (2014) found no differences in C stocks in the mineral soil between conifers and broadleaved species; though conifers had more topsoil C stocks than broadleaved species. As a result, a study with coniferous and broadleaved species covering large environmental gradients is needed to better assess this inconsistency.

Stand density is another key factor that influence C accumulation in both aboveground woody biomass and coarse root biomass (Torres and Lovett 2013), and in the soil (Laganiere et al. 2010; Zielonka et al. 2021). Among silvicultural treatments, Ruiz-Peinado et al. (2013) considers activities that alter stand density (such as regeneration felling and thinning) as those with the greatest impact on stand biomass and consequently the amount of C in the forest. Beyond its general effect, stand density may also be affected by species composition. For monocultures, fully stocked stands of different species can show different C stocks as a result of species-specific self-tolerance and maximum stand density (Pretzsch and Biber 2005; Pretzsch and del Río 2020). When managed, the range of stand BA values typically differs among species, which may also lead to differences in C stocks in the trees (Pretzsch and Biber 2005; Torres and Lovett 2013). In mixed-species stands, mechanisms such as crown complementarity, shade tolerance heterogeneity, divergence in root plasticity, among others, could increase stand density compared to that expected from the monocultures (Ammer 2019; Forrester and Bauhus 2016; Pretzsch and Biber 2016; Pretzsch et al. 2016) and consequently, C stocks. In the soil, stand density could affect C storage by altering litter inputs (Bahru and Ding 2020; Laganiere et al. 2010; Mayer et al. 2020) or forest micro-climatic conditions such as moisture content and temperature (Boča et al. 2014; Ruiz-Peinado et al. 2013). The impact of stand density on soil C storage is, however, not consistent, as positive (Lindner et al., 2010; De Marco et al. 2016), negative (Noh et al. 2013) and neutral effects (Johnson and Curtis 2001; Laganiere et al. 2010; Ruiz-Peinado et al. 2013, 2016) have been reported.

While the effect of selected forest management options on C storage in separate forest ecosystem components is well documented (Mayer et al. 2020; Torres and Lovett 2013), there is still inadequate information regarding their impacts on several stocks simultaneously, as well as on the resulting distribution between aboveground woody biomass and the soil (Ma et al. 2019). Meanwhile, species composition could alter the distribution of C between above- and belowground woody biomass (Martin-Guay et al. 2020), and between aboveground biomass and the soil (Liu et al. 2018; Ma et al. 2019). Information about the ratio of aboveground woody C to soil C shed light on the consequence of forest management (in terms of species selection, stand density, etc.) for the distribution of C among forest ecosystem components. Distribution of C among forest ecosystem components is also critical to better assess the stability of C stocks to disturbances (Wiesmeier et al. 2013). According to Hisano and Chen (2020), a suit of tree species traits such as high N, P, specific leaf area and wood density increase the rates of biomass accumulation in trees, but they reduced soil C stocks in the organic layer across Canadian forests (Chen et al. 2022). Within the trees, C distribution between aboveground woody biomass and coarse root biomass could be related to the biomass allocation strategies of the species in the forest (Martin-Guay et al. 2020; Niinemets and Valladares 2006).

This study aims to investigate the impact of species composition and stand density on C storage and distribution in aboveground woody biomass (stem + branches), coarse root biomass, and the soil (forest floor + 0–40 cm) ecosystem components of forest triplets distributed in seven countries in Europe. The triplets (two-species mixed stands and their corresponding monocultures at the same site; Osei et al. 2021) were of three types: beech-oak, pine-beech, and pine-oak. Pine (*Pinus sylvestris* L.) is coniferous and shade intolerant. Beech (*Fagus sylvatica* L) and oak (*Quercus petraea (Matt.)* Liebl./*Q. robur* L.) are both broadleaved species but beech is shade tolerant while oak has medium tolerance for shade (Niinemets and Valladares 2006). We selected these ecosystem components (aboveground woody biomass, coarse root biomass, soil) because they are the major C sinks in forests responsible for over 85% of total forest C stocks (Yude et al. 2011). We estimated C stocks in aboveground woody biomass and coarse root biomass using species-specific biomass allometric equations applicable for both monospecific and mixed forest stands in Europe (Forrester et al. 2017). Because we used species-specific allometric equations to investigate C storage in tree woody biomass, we assume additivity is predominant so this study did not assess species mixing effect on C storage in tree woody biomass. For the soil C stocks, we followed procedures described in Osei et al. (2021). Specifically, we tested the hypotheses that:

H1 Broadleaved species (beech, oak) and conifer (pine) have distinct species identity effects on C storage in forests. The broadleaved species have more C stocks per unit basal area than pine in aboveground woody biomass and coarse root biomass. In the total soil layer, the three species have similar C stocks, but pine has more topsoil and lower subsoil C stocks than the broadleaved species.

H2 Total stand density has stronger effect on C storage in aboveground woody biomass and coarse root biomass than in the soil.

Materials and methods

Study design and site characteristics

The study plots were in 21 triplets (i.e. two-species mixed stands and their respective monocultures at the same site; Osei et al. 2021) distributed in seven countries in Europe (Tables S1-S3). This study involved three main triplet types: beech-oak (*Fagus sylvatica* L–*Quercus petraea* (Matt.) Liebl.), pine-beech (*Pinus sylvestris* L.–*Fagus sylvatica* L.), and pine-oak (*Pinus sylvestris* L.–*Quercus robur* L. / *Quercus petraea* (Matt.) Liebl.). The beech-oak triplets were all located in Belgium. For each triplet, the three stands were mostly close to each other, located in similar site conditions, and were of similar ages. Consequently, we did not control for stand age in this study as ANOVA tests provided evidence of overall age similarity among stands within each triplet type (beech-oak: $F = 0.25$, $p = 0.80$; pine-beech: $F = 0.03$, $p = 0.97$; pine-oak: $F = 0.18$, $p = 0.84$). We further confirmed similarity of soil conditions in the three stands of each triplet by particle size analyses on composite soil samples (10–20 cm depth) from the three stands (Osei et al. 2021).

Detailed climatic, topographic, and edaphic characteristics at the triplet sites are reported in Osei et al. (2021). Briefly, mean annual temperature (T, °C) ranged from 8.0 to 10.4 °C at beech-oak sites, 7–10.5 °C at pine-beech sites, and 7.4–10.8 °C at pine-oak sites (Tables S1–S3). Mean annual precipitation (P, mm/year) ranged from 800.0 to 1112.0 mm/year at beech-oak sites, 650.0–1175.0 mm/year at pine-beech sites, and 550.0–881.8 mm/year at pine-oak sites (Tables S1–S3). The soils at the sites were predominantly Cambisols (Osei et al. 2021).

Dendrometric measurements and computation of C stocks in aboveground and coarse root woody biomass.

We conducted total stem diameter (dbh) inventory in each stand (threshold diameter > 7 cm). Using dbh values and the total plot size (in hectares), we calculated basal area (BA, m^2/ha) of trees in stands with sizes ranging from 0.40 to 1.72 ha for beech-oak triplets, 0.01–1.60 ha for pine-beech, and 0.04–0.5 ha for pine-oak triplets. Subsequently, we summarized BA in each stand by species. In cases where few other species occurred amongst the two main species of interest in a given stand, we categorized their total BA as that of "other species". The total BA in each stand for all triplets is reported in supplementary Tables S1-S3. The ranges of stand BA were 22.3–34.1 m^2/ha for beech-oak, 11.3–77.7 m^2/ha for pine-beech, and 14.6–50.8 m^2/ha for pine-oak triplets. There were no overall differences in total BA among stands in pine-beech ($F = 1.50$, $p = 0.26$) and pine-oak ($F = 2.31$, $p = 0.14$) triplets, but BA of the mixed beech-oak stands were higher ($F = 18.22$, $p = 0.001$) than in the respective pure stands. At species level, beech had a BA range of 23.3–72.0 m^2/ha, oak 14.6–36.4 m^2/ha, and pine 11.30–77.7 m^2/ha (Tables S1–S3). To estimate biomass stocks in aboveground woody components (stem + branches) and coarse roots of the main tree species (i.e. pine, beech, oak), we selected species-specific biomass allometric equations (Table S4) from a comprehensive database developed by Forrester et al. (2017). For the few "other species" in some plots, only *Betula pendula/pubescens* had species-specific equations for estimating biomass of both aboveground woody components and coarse root. For the rest, we used generalized equations for coniferous or broadleaved species to estimate biomass in component(s) lacking species-specific equations (Table S4). In selecting the allometric equations, our key criterion was to select equations developed from tree diameter ranges similar to that of our dataset. In addition, we prioritized equations that included dbh and stand basal area (BA, m^2/ha) or trees per hectare (TPH) to capture the potential effect of stand density (Forrester et al. 2017). For a given tree species, the same allometric equation was applied to individuals in pure and mixed stands as done in previous studies (e.g. Blasko et al. 2020; Ma et al. 2019) because there were not available allometric equations for species growing in mixed forests. In each stand, we calculated C stocks in the aboveground woody biomass (stem + branches) and coarse root biomass as follows:

$$\mathrm{AGC} = \left(\sum \mathrm{AGB}/1000 \right) * (1/\text{plot size}) * 0.5 \tag{1}$$

$$\mathrm{RTC} = \left(\sum \mathrm{RTB}/1000 \right) * (1/\text{plot size}) * 0.5 \tag{2}$$

where AGC = C stocks in aboveground woody biomass (Mg/ha), AGB = dry weight biomass of aboveground wood (Kg), RTC = C stocks in coarse root biomass (Mg/ha), RTB = dry weight biomass of coarse roots (Kg), Plot size = area of plot (hectares, ha), 1000 = factor to convert aboveground wood and root dry weight biomass from Kg to Mg, 0.5 = factor to estimate C stocks as half of dry weight biomass per ha (Penman et al. 2003).

Characterization of soil C stocks

Procedures for soil sampling, analyses, and computation of C stocks are described in Osei et al. (2021). Briefly, we placed 10 sampling points in mixed forest stands and 5 points in each corresponding monoculture. At each sampling point, we sampled the forest floor with a 30 cm × 30 cm metal frame. In the mineral layers, we sampled 10 cm depth intervals down to 40 cm by pit excavation method (*ca.* 10 cm wide × 10 cm deep). To estimate total volume of mineral soil samples (soil + voids + stones), we completely refilled each pit with ~ 1 mm glass beads and then measured the volume of glass beads that occupied each pit in a graduated cylinder. The soil samples were air-dried and sieved with 2 mm mesh to separate fine soil (< 2 mm) from roots (> 2 mm) and stones. Visible roots in the fine soil portions were picked with forceps to reduce their influence on soil C estimates. For each triplet with stones, we used water displacement method in the laboratory to estimate volume of stones in 20% of the mineral soil samples and developed triplet-specific relationship between stone mass and volume to estimate the volume of the rest. After determining stone volume, we discarded all the stones and roots that we separated from the soil, because potential C storage in these fractions was outside the scope of this study. The estimated volume of stones in a given sample was expressed as a percentage of total volume of that sample. We oven-dried ~ 1.5 g of sub-samples at 105 °C for 24 h to determine moisture content and total dry weight of samples. Further sub-samples of fine soil were ground with Vibratory Disc Mill (Retsch RS 200, Germany) and carried out carbon and nitrogen analyses on portions of the ground samples with a CN Analyzer (FlashEA® 1112, USA).

Statistical analyses

The statistical analyses were performed to first characterize species-specific impact on C storage in aboveground woody biomass (stem + branches), coarse root biomass, and soil in monospecific stands across triplet types. Subsequently, we assessed the impact of stand density and species composition on C storage and distribution in the afore-mentioned forest ecosystem components. This approach allowed us to infer C storage and distribution patterns in mixed stands from the species' behaviour in monospecific stands, as we expected additivity to be dominant. We chose mixed effects modelling due to the hierarchical nature of the sample design to address spatial correlation among the three stands of a triplet, and to account for the influence of confounding environmental factors (Zuur et al. 2009).

Species identity effect on C storage in the different components

To examine whether species-specific effects on C storage differ from one ecosystem component to another (H1), we pooled all the pure stands across triplet types together. For aboveground wood and coarse root components, we extracted species-specific BA of the three main species (oak, beech, pine) and their corresponding C stocks (aboveground woody C and coarse root C) estimated in each monospecific stand. Afterwards, we fitted the BAs of the three species as explanatory variables for aboveground woody C and coarse root C stocks in a mixed effect model. This was to determine how a unit change in BA of each species affect C storage in tree components.

$$\mathrm{y} \sim \text{beech BA} + \text{oak BA} + \text{pine BA} + e_{(\text{triplet})} + \varepsilon \tag{3}$$

where y refers to the species-specific aboveground woody C (Mg/ha) or coarse root C (Mg/ha). The beech BA, oak BA, and pine BA were species-specific basal area (m^2/ha) in pure stands. $e_{(\text{triplet})}$ is the random parameter associated with triplet, and ε is the error term. Regarding the soil component, we investigated species identity effects on soil C storage in the forest floor (FF), individual mineral soils layers, and whole soil profile; the FF and 0–10 cm were considered as topsoil, whereas the 10–20 cm and 20–40 cm layers were assigned to sub-soil. We used the model below:

$$\text{Soil C} \sim \text{species} + \text{stand BA} + \text{stone content} + e_{(\text{triplet})} + \varepsilon \tag{4}$$

Species was a categorical variable with three levels (beech, oak, pine). Stand BA was the total basal area (m^2/ha) in a given pure stand to account for differing stand densities. Stone content refers to the percent stone volume of the total soil volume at a given soil layer (except forest floor) to control for differing stoniness in stands. $e_{(\text{triplet})}$ is the random parameter associated with triplet, and ε is the error term.

Effect of stand density and species composition on C storage and distribution

In order to separate general stand density effects from species composition effects, we fitted mixed-effect models with stand BA and species composition as fixed effects and triplet as random effects. This controlled for confounding effects of one parameter on the other, as the two (stand BA and species composition) are usually related (Forrester and Bauhus 2016; Pretzsch and Biber 2016). Species composition was a categorical variable with three levels for each triplet type (i.e. two pure stands and their mixed stand). For each triplet type, the effects of species composition on C storage and distribution were examined by controlling for stand BA due to differences in stand density among the forests (Forrester and Bauhus 2016; Pretzsch and Biber 2016). For each triplet type, we used the model structure below to assess the impact of stand density and species composition on aboveground woody C, coarse roots C, total C (aboveground + roots + soil), as well as aboveground woody C: soil C ratio and coarse root C: aboveground woody C ratio.

$$\text{y} \sim \text{stand BA} + \text{species composition} + e_{(\text{triplet})} + \varepsilon \tag{5}$$

where y refers to the response variables, namely aboveground woody C (Mg/ha), coarse root C (Mg/ha), and total C stocks (aboveground + root + soil; Mg/ha), aboveground woody C: soil C ratio (unitless) and root C: aboveground woody C ratio (unitless). Stand BA and species composition are as explained above. $e_{\ (\text{triplet})}$ is the random parameter associated with triplet and ε is the error term. Concerning the impact of stand density and species composition on soil C in total soil layer (FF + 0–40 cm), we modified model (5) above by including stone content as an additional fixed covariate to address differences in stoniness among stands:

$$\text{Soil C} \sim \text{stand BA} + \text{species composition} + \text{stone content} + e_{(\text{triplet})} + \varepsilon \tag{6}$$

We used *lme4* R package (Bates et al. 2015) for mixed-effect modelling. We tested compliance of all models with homoscedasticity, residual normality, and absence of multicollinearity with *performance* R package (Lüdecke et al. 2021). Model parameters were estimated using restricted maximum likelihood (REML). We tested significance of predictors (at 95% confidence level) in all models using Satterthwaite's degrees of freedom method in *lmerTest* R package (Kuznetsova et al. 2017). Whenever species composition was significant in the models, post-hoc analyses were performed with *multcomp* R package (Hothorn et al. 2008). Marginal effects of species composition (i.e. predicted mean and 95% confidence intervals at fixed mean values of other covariate(s)) were illustrated with *ggeffects* R package (Lüdecke 2018). The percentage of variance explained by fixed (R^2m) and combined fixed plus random effects (R^2c) was computed by *MuMIn* R package (Barton 2020). We further partitioned the R^2m values among the fixed effects by *partR2* R package (Stoffel et al. 2020).

Results

Species identity effects on C storage in different forest components

Looking at tree species identity effects across triplet types, the C stocks per unit BA (Mg C/m^2 BA) in the aboveground woody biomass were significantly different ($p < 0.001$) among the species in the order pine < oak < beech (pine: 3.41, oak: 4.52, beech: 5.41). In the coarse root biomass, the C stocks per unit BA were comparable for the two broadleaved species but pine had 63.0% of the value for beech (Table 1). In the soil, species identity effects were detected in the forest floor (FF), upper mineral (0–10 cm), and the total soil layer (FF + 0–40 cm) (Fig. 1, Table S5). Pine had more C stocks in the topsoil layers (FF, 0–10 cm) than the

Table 1 Effect of species-specific basal area (BA, m^2/ha) on C stocks in aboveground woody biomass (stem + branches) and coarse root biomass of pure stands across triplet types based on Eq. 3 ("Species identity effect on C storage in the different components" section). Estimates for a given species show C stocks per unit BA. R^2m shows variation by fixed effects and R^2c shows variation by fixed plus random effects (i.e. triplet)

Ecosystem component	R^2m (R^2c)	Species	Estimate	S.E	95% C.I	*p*-value
Aboveground (Mg/ha)	0.90 (0.91)	Beech	5.41	0.20	5.00–5.83	< 0.001
		Oak	4.52	0.25	4.02–5.02	< 0.001
		Pine	3.41	0.14	3.13–3.69	< 0.001
Coarse root (Mg/ha)	0.88 (0.91)	Beech	0.65	0.02	0.60–0.70	< 0.001
		Oak	0.64	0.03	0.57–0.70	< 0.001
		Pine	0.41	0.01	0.37–0.45	< 0.001

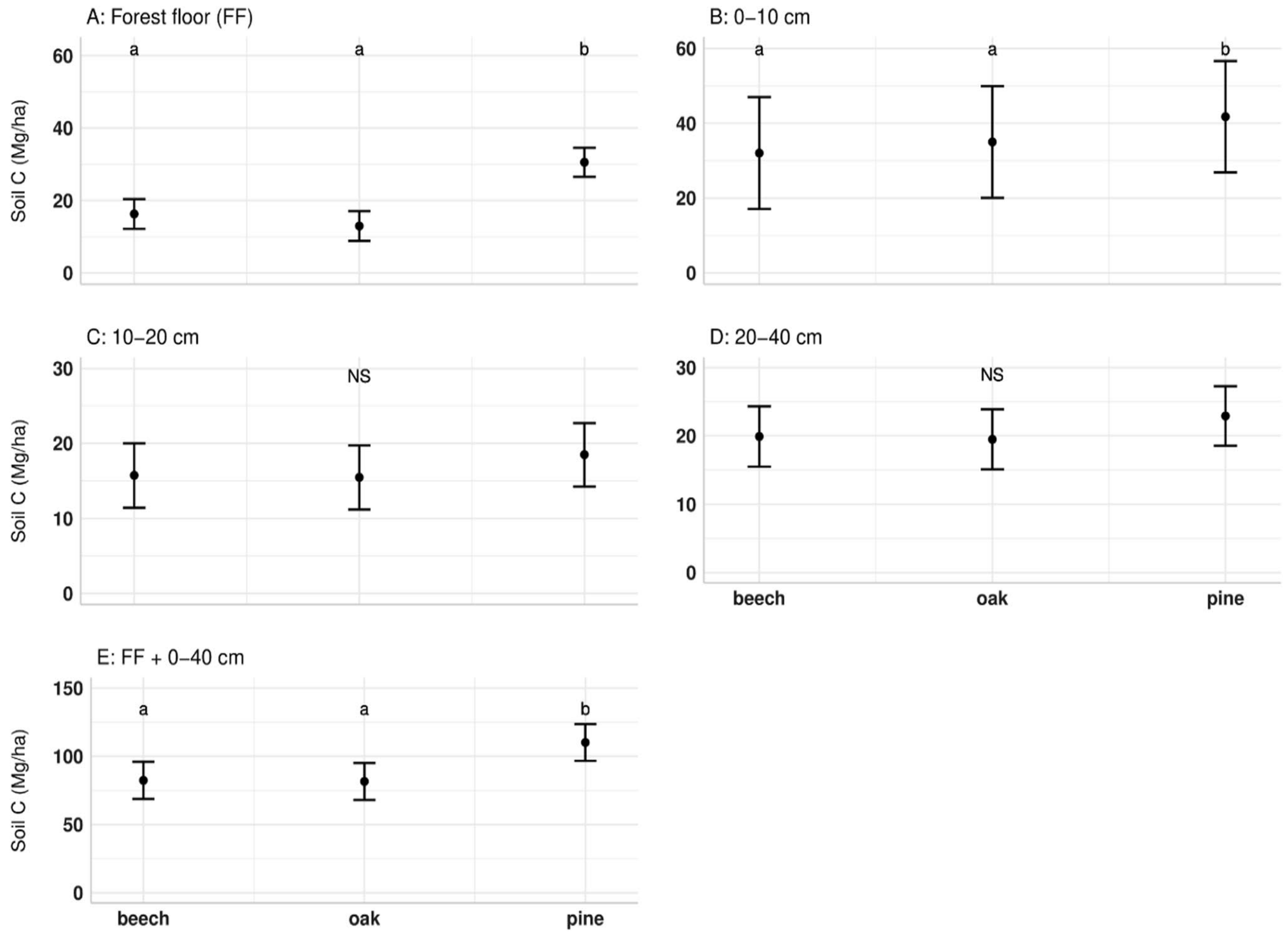

Fig. 1 Influence of tree species identity (beech, oak, pine) on soil C stocks (Mg/ha) in selected soil depths based on mixed effect model (Eq. 4, "Species identity effect on C storage in the different components" section) with species as fixed effect (stand basal area and stone content as covariates) and triplet as random effect. For a given soil depth, species without common letters are significantly different ($p < 0.05$) after controlling for stand BA and stone content; NS shows no significant difference among species. The means and their confidence intervals illustrate the predicted values for each species when the covariates (basal area, stone content) are held constant at their overall means. Full results are available in supplementary Table S5

broadleaved species, but C stocks in the subsequent deeper layers were similar for all species. In the total soil layer (FF + 0–40 cm), the average C stocks under pine was 1.3-fold higher than under the broadleaved species.

Effect of stand density and species composition on C storage and distribution

The effects of stand density on C storage were analysed after controlling for species composition in the models, and vice versa, due to their interdependence. Stand density, expressed as basal area per ha, proved to be a significant driver of C stocks in aboveground woody biomass and the coarse root biomass as well as the total C stocks for all triplet types (Table S6). It explained > 88.0% variability in aboveground woody C stocks and not less than 79.0% in coarse root biomass C storage across triplet types (Table S6). By contrast, stand density had no significant effect on SOC storage in the whole soil profile and explained only < 3.0% of total variability (Table S6). On the other hand, stand density had positive effects on the ratio of aboveground woody C to soil C for all triplet types (Table S7), whereas its effect on the coarse root to aboveground woody C ratio was restricted to the pine-beech triplet and was negative (Table S7; Fig. S8).

For the three triplet types, the effect of species composition on C storage after controlling for BA differed between components, and this impact was triplet type dependent (Fig. 2; Table S6). Starting with the tree components, the mixed beech-oak stands had 1.2 fold more C stocks in the coarse root biomass than beech, and 1.6 times of oak pure stands; similar C stocks were observed in aboveground woody biomass. While there was no species composition

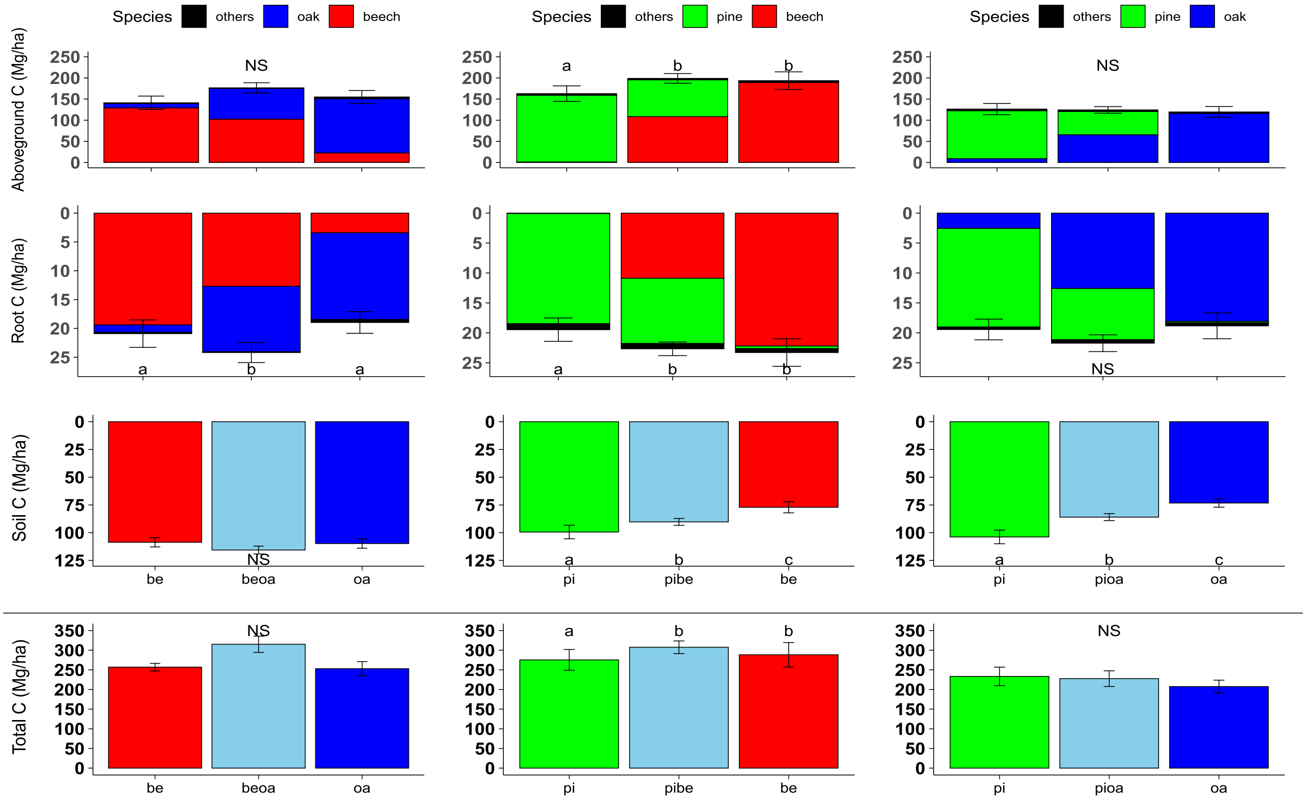

Fig. 2 Impact of species composition on observed C stocks (mean ± S.E; Mg/ha) in the aboveground woody biomass (stem + branches), coarse roots, soil (forest floor + 0–40 cm), and total (aboveground + roots + soil) ecosystem components in beech-oak, pine-beech, and pine-oak triplets. Significant differences were based on mixed effects model 5 (for aboveground and coarse root C) and model 6 (for soil C). The models had species composition, stand basal area, and stone content (only for soil C models) as fixed effects and triplet as random effect. Species "others" refers to species other than the main species of the triplet. For a given triplet, stands without common letters for a particular ecosystem component were significantly different ($p < 0.05$) after controlling for stand BA in the models; NS shows no significant differences among stands. Full results of models are available in supplementary Table S6

effect for the pine-oak triplets, the pine monocultures from the pine-beech triplets accumulated lower C stocks in both the coarse root biomass and aboveground woody biomass compared to the other two stands. With the exception of the coarse roots in the beech-oak triplet, the C storage in mixed stands did not differ from the monocultures with the highest C accumulation after accounting for BA effects. Considering the soil component, the effect of species composition was only significant in the two deciduous-coniferous triplets. All stands differed from each other, and C storage in the mixed stands (pibe, pioa) was intermediate with respect to the corresponding monocultures.

Looking at the combined aboveground wood (stem + branches), coarse root, and soil (forest floor + 0–40 cm) ecosystem components, species composition effect on C stocks was only observed in the pine-beech triplet. The pine monoculture had a lower total C stock than the other two stands (Fig. 2; Table S6) and had 89.5% of the total C in mixed pine-beech stand. The mixed stands were at least equivalent to the best performing monocultures in all triplet types for total C storage when BA effect was accounted for. Regarding distribution of C among forest components, all stands across triplet types had significantly more C stocks in the aboveground woody biomass than in the soil, except the pine monocultures (Fig. 3, Table S7). In the beech-oak triplets, aboveground woody C-to-soil C ratios were similar for all stands (mean [95% C.I]: be = 1.37 [1.18–1.55], beoa = 1.24 [1.02–1.45], oa = 1.30 [1.13–1.48]). In the coniferous-broadleaved triplets, the ratio between aboveground woody C and soil C stocks tended to decrease towards pine stands (Fig. 3). While all stands differed from each other in the pine-oak triplets (pi = 1.12 [0.77–1.46], pioa = 1.50 [1.16–1.84], oa = 1.85 [1.50–2.20]), only the beech monoculture significantly differed from the two other stands in the pine-beech triplets (pi = 1.63 [0.99–2.27], pibe = 2.21 [1.58–2.84], be = 3.35 [2.70–3.99]) and was > 2 times the value of pine. The average root-to-shoot ratio (i.e. coarse root C: aboveground woody C) across all stands and triplet types was 0.14. The ratio was similar for all stands in beech-oak and pine-oak triplets; in the pine-beech triplets, it

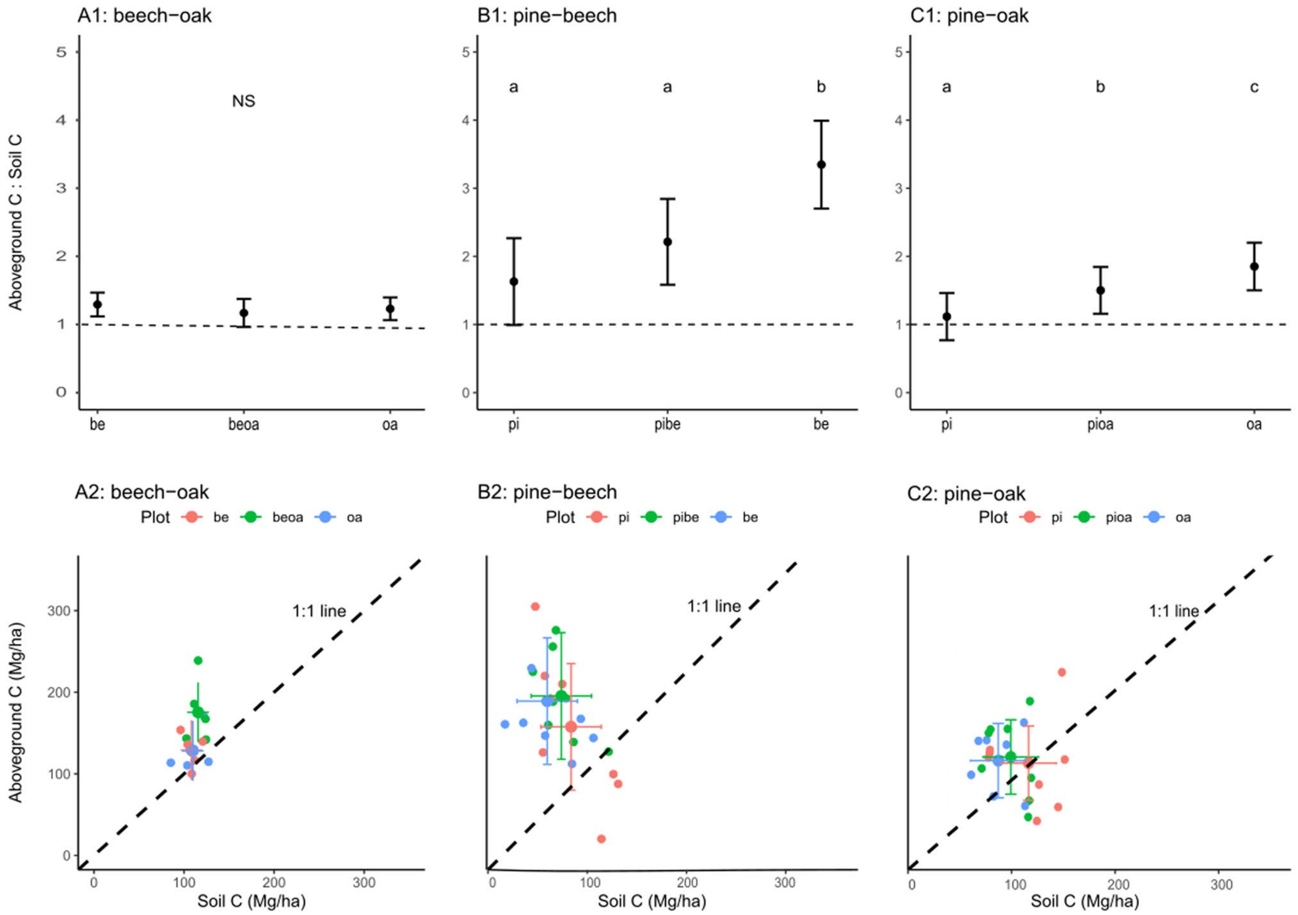

Fig. 3 Panel A1-C1 shows the impact of species composition on the ratio of aboveground woody C (stem + branches) to soil C for each triplet type based on mixed effect models with species composition and basal area (BA) as fixed effects and triplet as random effect (Eq. 5). For a given triplet type, stands without common letters are significantly different ($p < 0.05$) after controlling for BA in the models; NS denotes no significant difference among stands. Full results are available in supplementary Table S7. Means and 95% confidence intervals illustrate predicted values at fixed BA. Confidence intervals above one (i.e. dotted horizontal line) depicts significantly more C in aboveground woody biomass than in soil. Panel A2-C2 shows the relationship between soil C (FF + 0–40 cm) and aboveground woody C. The bidirectional error bars show the mean and standard deviation of raw values in each stand

was higher in the pine monoculture compared to the mixed and pure beech stands (Table S7, Fig. S8).

Discussion

Broadleaved species (beech, oak) and pine have different impact on C storage in tree woody biomass and the soil.

Applying existing tree-level biomass equations to stands of contrasting diameter distributions, densities, and tree species composition in these European-wide triplet-transects allowed us to highlight and discuss some of the generic factors behind the differences in C accumulation per unit BA among tree species. First we found that broadleaved species (beech, oak) were associated with higher C stocks per unit BA in the aboveground woody biomass and coarse roots than pine as expected (H1). This is similar to findings by Ma et al. (2021) and Torres and Lovett (2013). Higher C stocks in tree woody biomass per unit BA of the broadleaved species than pine in this study could be attributed to high mean specific wood densities of beech (*Fagus sylvatica*) and oak (*Quercus robur/petraea*) compared with pine (Forrester et al. 2017; Pretzsch et al. 2018; Torres and Lovett 2013). Forrester et al. (2017) also add that species with high specific wood density (such as the broadleaved species in this study) are less competitive and therefore allocate more C per unit BA to stems in response to inter- and intra-specific competitions than species with low specific wood density such as pine. For the broadleaved species, the aboveground woody C storage per unit BA was higher for beech than for oak, while coarse root C storage per unit BA was similar for both species (Table 1). This implies that two forest stands with similar basal area share of beech and oak could have comparable root C stocks but higher aboveground woody C stocks in beech than oak under '*ceteris paribus*' conditions. Those tree species effects are consistent with the patterns in Fig. 2 in that the significant difference in C accumulation between the monocultures are limited to pine and beech which have the most contrasting C stocks per BA unit for both aboveground woody biomass and coarse roots components. Moreover, species-specific values for C stock per unit BA in the pure stands could also be related to species-specific differences in self-tolerance and maximum stand density (Pretzsch and del Río 2020; Pretzsch and Biber 2005). The highest C stock per unit BA in the aboveground woody biomass of beech species could be related to its low self-tolerance and high space-consuming strategy via dynamic lateral crown extensions, compared to pine and oak (Pretzsch and Biber 2005).

Comparing the three species for soil C storage, species identity effect was detected in the forest floor, upper mineral soil layer (0–10 cm), and the total soil layer (FF + 0–40 cm). There were more total soil C stocks (FF + 0–40 cm) under pine than the broadleaved species, which rejects our hypothesis of similar total soil C stocks among the three species (H1). Indeed, our expectation of more topsoil C stocks under pine than the broadleaved species was fulfilled. Topsoil C accumulation under pine in this study supports previous studies (e.g. Dawud et al. 2016) and reviews (Boča et al. 2014; Mayer et al. 2020; Vesterdal et al. 2013). Forest floor and upper mineral C accumulation under pine relative to broadleaved species could be explained by slow litter decomposition occasioned by its high lignin/N ratio and low pH (Vesterdal et al. 2013). In this study, broadleaved species did not accumulate more C stocks in the subsoils than pine as hypothesized and also suggested in previously reviews (Vesterdal et al. 2013; Wiesmeier et al. 2013). We posit that high soil acidity at the study sites (Osei et al. 2021) might have inhibited processes known to stimulate C storage in mineral soils under broadleaved species. These include litter degradation by relatively high microbial communities, addition of microbial necromass to mineral soil C pool, and downward litter transfer by endogeic and anecic earthworms (Prescott and Vesterdal 2021; Vesterdal et al. 2013). Another explanation could be an accumulation of fine roots of the broadleaved species in the topsoil layers to forage nutrients released from their high quality litter (Leuschner et al. 2001) instead of the "usual" mineral sub-soil layers (Wiesmeier et al. 2013). Under broadleaved species, fine roots can contribute more than half of the subsoil C pool (Mayer et al. 2020; Vesterdal et al. 2013). The species-specific effects related above supports patterns depicted in Fig. 2 for SOC stocks in the FF + 0–40 cm of the monocultures. The intermediate SOC values observed for the mixed-species stands compared to the monocultures across all triplet types suggested a simple additive effect was at play (Osei et al. 2021). Overall, the contribution of tree species identity to variability in SOC storage (Table S5) was relatively lower than for C storage in aboveground woody biomass (Table 1). This suggests that additional factors control soil C storage (Prescott and Vesterdal 2021; Vesterdal et al. 2013), especially in the mineral soil layers where random effects were much greater than fixed effects (Table S5). These additional drivers of SOC stocks could be climate, soil texture, soil mineralogy, etc. (Wiesmeier et al. 2013; 2019), but this requires further investigation for validation.

Total stand density impacts C storage in tree woody biomass more than the soil.

Though the range of basal area in the current study may be limited compared to thinning experiments (Ruiz-Peinado et al. 2013; 2016), our results can be considered robust because we show how stand density effects on C stocks in tree woody biomass can be different from its effects on soil C stocks under the same stands. The strong influence of BA on C storage in tree biomass at stand level is consistent with previous studies (Ruiz-Peinado et al. 2013, 2016; Torres and Lovett, 2013). For example, stands with low total BA such as pine stand at St. Hubert (Belgium) indeed had low C stocks in aboveground and coarse root woody biomass compared with pine stands with high total BA at Bamberg in Germany (Table S2). Therefore, the total biomass C stocks in a given forest stand are contingent on C stock per unit BA of the constituent species, which is little affected by stand density, and the total BA. Due to the strong relationship between BA and biomass C stocks, BA is often used to estimate stand level C stocks (Burrows et al. 2000; De Marco et al. 2016; Wijedasa et al. 2021) since it integrates both the number and size of trees and it is easily measurable (Burrows et al. 2000). In some cases, inclusion of stand height (as quadratic or arithmetic mean height; top height) further increases the accuracy of biomass predictions (Zhao et al. 2015). In reality, the impact of stand density in shaping stand-level C storage in tree components is complex as it involves several levels. At the individual tree level, stand-level BA may alter the carbon stored in tree biomass of similar diameter. For example, all allometric equations that were used to estimate individual aboveground woody C stocks included a BA variable (Table S4), yet the sign of the associated coefficient differed between beech and pine on one hand, and oak on the other hand. For beech and pine, increasing stand BA (i.e. competition) resulted in increasing aboveground woody C storage, possibly due to C allocation to height growth over radial increment (Pretzsch et al. 2016; Zeide and VanderSchaaf 2002). The opposite trend was observed for oak, likely due to negative impact of competition on lateral crown expansion (Xue et al. 2012). Finally, in addition to total stand-level

BA effects, species composition also impacts C storage as the relationship between stand BA and C storage is species-dependent; in this respect, C storage in mixed stands may also tightly depend on the share of species in total BA for a given stand-level BA values.

While stands with low total BA always resulted in low stand-level C stocks in tree woody biomass, SOC stocks were independent of total stand BA. The negligible effects of BA on soil C relative to tree woody C across triplet types agree with our hypothesis (H1) and previous studies (Cécillon et al. 2017; Laganiere et al. 2010; Ruiz-Peinado et al. 2013) but contradict others (González et al. 2012; De Marco et al. 2016; Zielonka et al. 2021). Inconsistent results for BA effects on soil C could be because the balance between litter input and decomposition processes governs soil C storage (Liu et al. 2018; Vesterdal et al. 2013). While stand density could regulate litter input to the soil layers (Laganiere et al. 2010; Mayer et al. 2020) via canopy leaf area index (Bahru and Ding 2020), climate and soil factors, as well as litter quality, play leading roles in the output or decomposition process (Boča et al. 2014; Wiesmeier et al. 2019). In long-term thinning experiments with maritime pine and Scots pine in Spain, Ruiz-Peinado et al. (2013; 2016) found no differences in soil C stocks among thinning treatments, although C stocks in aboveground woody biomass were significantly reduced in moderately and heavily thinned plots, compared with unthinned plots. This present study suggests that intensive thinning and other forest management activities that substantially change stand density will have more cascade effects on C stocks in tree woody biomass than in the soil.

Species composition influences total C storage and distribution between aboveground woody biomass and the soil.

We analysed species composition effects on C storage and distribution by controlling for stand BA in all models due to their interdependence. Beyond looking at overyielding, it is interesting to evaluate the effect of species composition on C stocks and distribution in mixed and pure stands by direct comparison. The effects of species composition on total C storage (in aboveground wood + coarse roots + soil) were restricted to the pine-beech triplet (Fig. 2). The lower total C accumulation in pure pine compared to the other two stands for that specific triplet can be explained by the much lower C stocks in tree woody biomass per unit BA for pine compared to beech (Table 1), which are not compensated for by the higher soil C storage associated with pine (Fig. 1, Table S5). The similarities in total C stocks between mixed stands and the most performing monocultures of all triplet types show that mixed species forestry will not compromise total C storage (Blaško et al. 2020; Ma et al. 2019). In addition to their neutral or beneficial effects on C storage, mixed-species forests provide a larger range of ecosystem services (Gamfeldt et al. 2013) and may be associated with a higher stability or resilience (Yachi and Loreau 1999) although the latter effect is largely context-dependent. As can be inferred from the previous sections, the ratio between aboveground woody C and soil C (Fig. 3) is largely determined by the total stand BA and species-specific C stocks per unit BA of the component species on one hand, and the species-identity effects on soil C storage on the other hand. This reinforces findings from previous studies that species characteristics in forest stands can disproportionately promote C storage in specific forest components (Ma et al. 2019; Poorter et al. 2012). For the broadleaved stands across all triplets, this resulted in the ratio (aboveground woody C to soil C) being always greater than one; for the pine monocultures, this ratio was not significantly different from one. Therefore, increasing the proportion of broadleaved species in pine stands tended to increase the ratio of aboveground woody C to soil C. This resulted in either an increase (pine-beech) or no change (pine-oak) in total C storage. These findings suggest that inclusion of pine in broadleaved species forests is a trade-off of tree biomass C storage for high soil C storage, and vice versa. This corroborates findings from Chen et al. (2022) and Hisano and Chen (2020), who found that traits usually associated with broadleaved species (high N, P, wood density, etc.) resulted in increased tree biomass accumulation but a reduced soil C stocks. However, soil C stocks under pine was mainly concentrated in the topsoil layers, which are prone to human disturbance, forest fires and rising temperatures (Wiesmeier et al. 2013).

Limitations of the study.

We did not use stand and site specific allometric equations to estimate woody biomass in tree components, but rather relied on generalized species-specific biomass allometric equations developed for a wide range of stands in Europe (Forrester et al. 2017). As a result, we were not able to account for the possible effects of site conditions on biomass estimates of the tree components, yet the triplet approach allowed to control for possible confounding site factors between related stands (Hulvey et al. 2013). Therefore, our results for C storage in tree woody biomass should be considered as average patterns in Europe. We also used allometric equations developed from pure stands to estimate biomass of trees in mixed stands, although changes in tree allometry (del Río et al. 2019) and in biomass allocation between above- and belowground (Ma et al. 2019; Martin-Guay et al. 2020) are possible in mixed stands. Changes in allometry is a disruption of the relationships among tree components described by allometric equations, which could reduce accuracy of biomass estimates for one component from another. Similarly, deviation of a species' biomass allocation between above- and belowground components in mixed stands could potentially lead to over- or under-estimation of biomass values. However, all biomass equations for the main species included either stand basal area (BA) or trees per ha (TPH). This should limit the impact of differences in stand density on biomass estimates arising from differing stand compositions.

Conclusion

Using a triplet-design approach, we were able to provide a general framework to understand how stand density and species selection, impact total C storage as well as the distribution of C among ecosystem components. Our expectation of more C stocks in tree woody biomass of the broadleaved species (beech, oak) than pine was fulfilled. However, pine drove C accumulation in the total soil layer more than the broadleaved species, which was contrary to expectation. This shows that species choice has implication on C storage and partitioning among forest ecosystem components. The dichotomy between C storage patterns in pine and the studied broadleaved species (beech, oak) shows that forest managers need detailed information regarding the effects of specific tree species on C storage in different ecosystem components to implement climate-smart forestry. We found that total stand density exerts strong control on C storage in above- and belowground woody biomass but not in the soil, which confirmed our hypothesis. This finding emphasises that C stocks in soils are better insured than C stocks in tree woody biomass against losses by silvicultural practices and/or disasters that considerably reduce forest stocking. The total C stocks (aboveground + coarse roots + soil) in the mixed stands was at least equivalent to the most performing monocultures in all triplet types after controlling for stand BA. This suggests that at sites where the studied species pairs could grow together, mixed species forestry could guarantee total C storage equivalent to the best performing monocultures, while providing more ecosystem services (Gamfeldt et al. 2013) and ecological resilience than the monoculture counterparts (Yachi and Loreau 1999). Further research is needed to examine C storage in forests composed of a larger range of tree species and to particularly document species mixing effects taking into account the potential impact of mixing on tree allometry and C allocation among tree components. We also recommend investigations into the additional sources of variation associated with C storage in soils.

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Data availability The datasets analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflicts of interest The authors declare no conflict of interest.

Consent for publication All authors gave their informed consent to this publication and its content.

Consent to participate Not applicable.

Code availability Not applicable.

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