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Tree species identity drives soil organic carbon storage more than species mixing in major two-species mixtures (pine, oak, beech) in Europe

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ABSTRACT

Mixed forests are usually associated with higher aboveground carbon storage compared to the corresponding monocultures but information on the impact of tree species mixing on soil organic carbon (SOC) is still limited. Yet, maximizing SOC storage is crucial for ecosystem C sequestration and many other ecosystem services. This study used a triplet approach (ie. two-species mixed stand and respective pure stands at the same site) to assess the impact of tree species identity and mixing on SOC storage in eight pine-oak, eight pine-beech and five beech-oak triplets in Europe. We sampled the forest floor (FF) and 0–40 cm in the mineral soil per 10 cm interval. For each triplet type, we fitted basal area (BA) proportion of one component species (for species identity) and a BA-based plot-level True Shannon Diversity index (for species mixing) as explanatory variables for SOC stocks in linear mixed effects models, which included stone content and plot BA as covariates, and site as a random intercept. Considering the total soil depth (FF + 0–40 cm), species identity effect on SOC stocks was only significant for pine-beech and pine-oak triplets but explained more variability in SOC stocks than species mixing across triplet types. Species mixing effect was not significant for any triplet type in the total soil depth. While species identity consistently drove SOC storage in the topsoil layers across triplet types, species mixing explained more variability in SOC stocks in the deeper soil layers except for pine-oak triplets. The results showed that species identity is a stronger driver of SOC storage than species mixing. While tree species identity effect was strongly related to a conifers *vs* broadleaves signature, the drivers behind mixing effects remained elusive. The results suggest that targeted selection of tree species could better enhance SOC storage in European forests than a mere increase in species richness.

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1. Introduction

Forest soils and associated peat deposits contribute about 70% to the global soil organic carbon (SOC) pool and are thus important sinks in the global carbon cycle (Dixon et al., 1994; Schleuß et al., 2014). Co-benefits of SOC include improvement in soil fertility, water-holding capacity, potential site productivity, and belowground biodiversity (Mayer et al., 2020). It is therefore essential to find appropriate management options to sustain or increase SOC stocks. While tree species selection has already been discussed as a means of sequestering C in soils in past years (Jandl et al., 2007), the impacts of tree species mixing on SOC sequestration remain much less documented (but see Dawud et al., 2016, 2017; López-Marcos et al., 2018). Filling-in this knowledge gap is of special relevance, as the establishment of mixed-species stands is encouraged by many forest policies as a way to provide a wider range of ecosystem services (Ratcliffe et al., 2017) and to increase stability against climate change (Mayer et al., 2020; Ratcliffe et al., 2017), compared to monocultures.

The capacity of forest ecosystems to store SOC depends largely on the identity of tree species (species-specific effects) of which the forest is composed (Hansson et al., 2011, Langenbruch et al., 2012; Vesterdal et al., 2013) and their interaction with soil properties and local climate (Augusto et al., 2015; Verstraeten et al., 2018). Different tree species planted on the same site differ in SOC accumulation rates (Mareschal et al., 2010) due to contrasting litter inputs (Augusto et al., 2015; Díaz-Pinés et al., 2011) and decomposition rates (Hansen et al., 2009). In a *meta*-analysis, Laganiere et al. (2010) found that afforestation with broadleaved tree species increased SOC stocks by 25% on average, compared with 2% with conifers in 2–3 decades. However, SOC stocks at the forest floor are generally greater under conifers such as pine than under broadleaved species like oak and beech (Augusto et al., 2015; Vesterdal et al., 2013). In Denmark, Vesterdal and Raulund-Rasmussen (1998) found forest floor SOC stocks in the order oak < beech < spruce < pine. Greater accumulation of SOC in the forest floors of pine-dominated forests could be attributed to slower decomposition rates that, in turn, is the consequence of high lignin and low N contents in pine litter (Augusto et al., 2015; Berg et al., 2015; Krishna and Mohan, 2017). On the contrary, oak and beech species often have larger mineral SOC stocks than pine (Frouz et al., 2009; Hansson et al., 2011; Vesterdal et al., 2013). This is due to rapidly decomposing leaf litter and greater SOC incorporation and stabilization in mineral horizons (Augusto et al., 2015; Wiesmeier et al., 2013) occasioned by low lignin and high N contents (Krishna and Mohan, 2017). It is also due partly to the more abundant soil macrofauna communities under these broadleaf tree species (Schelfhout et al., 2017). Due to the pronounced effects of litter traits mentioned above, species identity effects on SOC stocks are generally stronger in the forest floor and upper mineral layers compared to deeper (below ~ 20 cm) soil layers (Dawud et al., 2016; López-Marcos et al., 2018).

Though there are exceptions to this pattern, increase in tree diversity is frequently associated with greater aboveground productivity, which leads to improved carbon storage in aboveground tree components (Chen et al., 2018; Hulvey et al., 2013; Liang et al., 2016; Liu et al., 2016). In addition, tree diversity reduces the impact of disturbances (e.g. pests) on carbon storage in living biomass and net primary production (Silva-Pedro et al., 2015). In contrast to its effects on aboveground carbon storage, tree diversity impacts on SOC storage remain much less documented, and appear to be less consistent (Mayer et al., 2020). While consistently positive diversity effects on SOC storage have been found in the subtropics (Chen et al., 2018; Liu et al., 2016), more contrasting effects have been reported in Europe (Błońska et al., 2018; Dawud et al., 2016, 2017; Schleuß et al., 2014). Studying a diversity gradient of 1–5 tree species in asingle site (Białowieża forest, Poland), Dawud et al. (2016) reported selected synergistic diversity effects in the lower mineral soil layers. In another study across major European forest types, the SOC stocks in the topsoil were found to be positively but weakly related to diversity (Dawud et al., 2017). Various mechanisms could drive changes in SOC storage in species diverse forests. For example, mixed stands usually have a more complex stand structure and higher basal area than monocultures (Błońska et al., 2018; Pretzsch, 2014), which could translate into greater aboveground litter input and topsoil carbon accrual in mixed stands than the respective monocultures (Błońska et al., 2018; Laganiere et al., 2010). On the other hand, decomposition and mineralization of aboveground litter in diverse stands is often accelerated by litter diversity (Joly et al., 2017; Li et al., 2017). In the lower mineral soil layers, greater accumulation of SOC under species-diverse stands could result from many possible mechanisms. These include increased root litter and rhizodeposition to mineral soil carbon pool as a result of a more intensive exploitation of soil resources by roots (Brassard et al., 2013) or through the activities of soil macro-organisms such as earthworms stimulated by litter diversity (Chapman and Koch, 2007; Hättenschwiler and Gasser, 2005). Deeper storage of SOC under more diverse forests could also enhance the stability of SOC stocks to disturbances due to better protection against microbial decomposition, particularly in clay-rich soils (Jandl et al., 2007).

The current knowledge suggest that the impact of species diversity on SOC storage in forest ecosystems is smaller and less consistent than the effects of tree species identity or functional group (Dawud et al., 2016, 2017; Mayer et al., 2020). The magnitude and direction of species mixing effects on SOC storage vary according to species involved, climate, or soil type (Ratcliffe et al., 2017). Thus, studies on the impact of tree species composition (species identity and mixing) on SOC storage necessitates numerous replicate studies under a broad range of ecological conditions to produce generalizable conclusions (Mareschal et al., 2010; Vesterdal et al., 2013).

Nonetheless, existing studies usually consider a large gradient of tree species richness but on a limited number of sites (Błońska et al., 2018; Dawud et al., 2016; Schleuß et al., 2014). Conclusions from such studies usually lack generality to guide forest management at large scales. Additionally, some studies involved species diverse plots without corresponding monoculture plots for all the species in the mixed stand, which does not allow for a proper comparison of SOC storage by tree species in monocultures versus mixtures (Hulvey et al., 2013). This present study addresses these gaps by adopting a triplet transect approach (i.e. two-species mixed stand and respective pure stands at the same site). This method was used to study the impact of species identity and species mixing on SOC storage and distribution in the forest floor and first 40 cm of mineral soil in forests over an unprecedented range of climate, topographic, and soil conditions. Furthermore, this study allows analyses of tree mixtures involving species with varying traits: pine-oak and pine-beech (gymnosperms-angiosperms interactions) and beech-oak (angiosperm-angiosperm interactions). Scots pine (*Pinus sylvestris* L.) is coniferous, shade intolerant, and has low N but lignin-rich needles. Oak (*Quercus petraea* (Matt.) Liebl. / *Q. robur* L.) is deciduous, shade intolerant, has relatively high N and lignin-poor litter. Similarly, beech (*Fagus sylvatica* L.) is deciduous but shade tolerant and has relatively high N and lignin-poor litter. However, beech litter has higher chemical recalcitrance than oak (Jonard et al., 2008; Vesterdal and Raulund-Rasmussen, 1998). All studied species are of major importance for forestry and have a widespread distribution across Europe. The overall aim of the study was to assess the average impact of species identity and species mixing on SOC storage in selected European forests, while accounting for potentially contrasting site effects. We hypothesized that, across all triplet types:

(H1) Effect of tree species identity on SOC stocks is more prominent in topsoil layers than deeper soil layers.

(H2) Effects of tree species mixing on SOC stocks are stronger in deeper soil layers than in the topsoil.

(H3) Overall, species identity is a stronger driver of SOC storage than species mixing in the whole soil depth.

2. Material and methods

2.1. Triplets and site characteristics.

A triplet transect approach (see description and application in Pretzsch et al., 2019) was used to select 21 triplets in seven European countries for soil sampling in mature forest stands (Fig. 1; Table 1). In order to assess potential complementarity between different tree species in relation to soil carbon storage, we selected triplets composed of species with contrasting characteristics. These are pine-beech (*Pinus sylvestris* L. - *Fagus sylvatica* L.), pine-oak (*Pinus sylvestris* L. - *Quercus robur* L / *Quercus petraea* (Matt.) Liebl.) and beech-oak (*Fagus sylvatica* L - *Quercus petraea* (Matt.) Liebl). We selected eight pine-beech, eight pine-oak, and five beech-oak triplets (Fig. 1; Table 1).

The soils at our study sites are all acidic (Tables S1-S3) and were predominantly Cambisols (Table 1). The soil types at the pine-beech sites are mainly Cambisols and Podzols, and that of pine-oak are mainly Cambisols and Planosols. All but one soils at the beech-oak sites are Cambisols. Mean annual temperature (T) ranges from 7.0 to 10.5 °C at pine-beech sites, 7.4 to 10.6 °C at pine-oak sites, and 8.0 to 10.4 °C at beech-oak sites. Mean annual precipitation (P) ranges from 650.0 to 1175.0 mm at pine-beech sites, 550.0 to 881.8 mm at pine-oak sites, and 800.0 to 1112.0 mm at beech-oak sites (Table 1). Contrary to pine-beech and pine-oak sites, all the beech-oak sites are located in Belgium and thus have more limited climatic, topographic, and edaphic gradients (Fig. 1; Table 1). We used results of particle size analyses on composite samples from 10 to 20 cm soil depth to check within-triplet homogeneity of soil conditions for all triplets studied. These detailed site characteristics are reported in supplementary Tables S1-S3.

Complete dendrometric information for triplets in this study are reported in supplementary Tables S4-S6. Briefly, average basal area (BA) at plot level varies from 22.0 to 48.6 m^2ha^{-1} for pine-beech triplets, from 12.4 to 50.1 m^2 ha^{-1} for pine-oak triplets, and from 25.1 to 34.9 m^2ha^{-1} for beech-oak triplets (Table 1). The basal area proportions of pine in mixed plots were within 33.3 – 72.6% for pine-beech triplets (Table S4), and 36.2 – 58.4% for pine-oak triplets (Table S5); the basal area proportions of beech in mixed beech-oak stands ranged between 47.4 and 67.8% (Table S6).

2.2. Sampling approach

For each triplet, 10 sampling points were spread over the mixed stand and 5 sampling points in each monoculture stand (Fig. 1). We placed 10 sampling points in the mixed stands to best cover the range of local basal area proportions of the two species in those stands. For each sampling point, we took the forest floor (organic soil layer above the mineral soil layers) with a 30 cm × 30 cm metal frame and then dug up to 40 cm in the mineral layers in a 10 cm depth increment (ie. forest floor (FF), 0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm; Dawud et al., 2016).

Consequently, 100 potential samples (ie. 5 × 5 + 5 × 5 + 10 × 5) were obtained for each triplet resulting in a total of 2080 samples for the entire study (20 samples from the 20–30 cm and 30–40 cm depths could not be sampled due to waterlogging in Triesdorf and Niepołomice sites). Total volume of mineral soil samples (soil + voids + stones) was estimated in the field by a volume replacement method (Al-Shammary et al., 2018). This method involved a complete refilling of each sampling pit (ca. 10 cm deep × 10 cm wide) with ~ 1 mm glass beads and then measuring the volume of these glass beads in a graduated cylinder.

2.3. Laboratory analyses

At their arrival in the lab, all samples were air-dried for at least 3 months before further treatments. Forest floor samples were first inspected to exclude living materials, roots and branches (>2 cm diameter), fruits, and stones. The remaining materials were first crushed by Retsch SM 300 cutting mill (Retsch GmbH, Germany), and sub-samples were further milled by Foss Cyclotec 1093 (FOSS Analytical, Denmark) into < 2 mm fine material. Mineral samples were crushed by hand and adhering soil on stones (if any) was removed from stones and added to the fine-soil fraction. Each mineral sample was then passed through 2 mm sieve to separate fine soil (<2 mm), coarse roots (>2 mm), and stones. We picked visible fine roots in the residual fine soil with forceps to minimize their influence on C contents. We separately weighed all the fine soil and the stone fractions.

Sub-samples of fine soil were ground with Vibratory Disc Mill (Retsch RS 200, Germany). Subsequently, ~1.5 g of ground sub-samples of each forest floor and mineral samples were oven-dried at 105 °C for 24 h to determine moisture content and total dry weight of samples. We measured pH of samples with both 0.01 M $CaCl_2$ at a ratio of 1:2.5 and deionized water at a ratio of 1:10 using inoLab pH Level 1 (WTW GmbH, Germany) to confirm the absence of carbonates before C analyses. We used a CN Analyzer (FlashEA® 1112, USA) to carry out C and N analyses on all 2080 air-dried samples (both forest floor and mineral) through a flash dynamic combustion method.

Volume of stones in mineral samples was estimated by a water displacement method on 20% of the total number of sampled mineral soil layers per triplet. We then used the estimated stone volume to develop triplet-specific linear regression between stone volume and

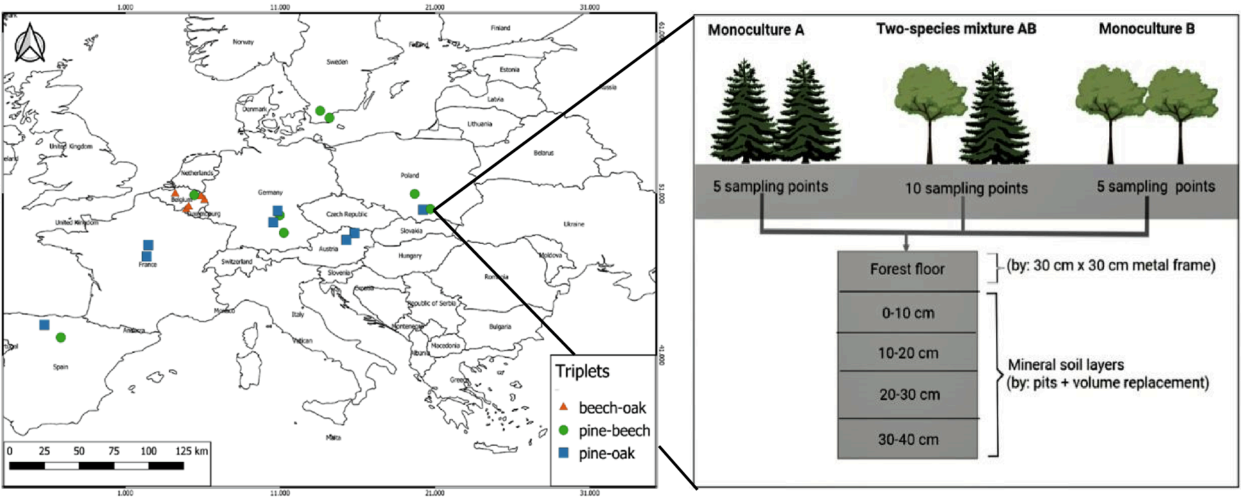

Fig. 1. Location of the 8 pine-oak, 8 pine-beech and 5 beech-oak triplets selected for this study (Left panel). Forest floor and mineral soil sampling in the two monocultures (A, B) and two-species mixed forest (AB) of each triplet (Right panel).

Table 1
Selected characteristics of pine-beech, pine-oak, and beech-oak triplets. Triplets are ordered alphabetically by country and then by triplet name.

Type	Country	Triplet name	Location (LAT, LON)	Climate (T, P)	Alt.	BA	Soil Type	SOC stocks (FF, TOTAL)	Stones (%)
Pine-beech	Bel	St. Hubert	50°01′N, 05°27′E	10.5, 1175.0	544.0	22.0	Cambisol	18.14 ± 8.28, 112.8 ± 19.6	20.0 ± 8.0
	Ger	Bamberg	49°53′N, 10°58′E	8.0, 650.0	250.0	40.3	Cambisol	32.7 ± 15.5, 77.7 ± 21.1	0.0
	Ger	Steigerwald	49°47′N, 10°38′E	10.0, 675.0	370.0	44.6	Cambisol	23.1 ± 13.2, 70.0 ± 20.1	0.0
	Pol	Niepołomice	50°01′N 20°14′E	8.2, 650.0	210.0	30.3	Podzol	41.4 ± 22.4, 127.0 ± 38.7	0.0
	Pol	Zagnańsk	50°59′N, 20°41′E	7.8, 662.0	383.0	38.3	Cambisol	10.4 ± 4.5, 59.4 ± 16.7	8.0 ± 5.3
	Spa	Vallejimeno	42°06′N, 03°10′W	8.9, 860.0	1293.0	47.0	Leptosol	19.2 ± 9.8, 80.1 ± 15.4	36.0 ± 10.2
	Swe	Kivik	55°42′N, 14°11′E	7.0, 800.0	25.0	48.6	Cambisol	17.4 ± 10.7, 76.7 ± 14.2	0.0
	Swe	Tyringe	56°08′N, 13°35′E	8.0, 700.0	120.0	33.0	Podzol	24.5 ± 14.1, 110.2 ± 33.9	11.0 ± 9.9
Pine-oak	Aus	Kuhberg	48°35′N, 15°48′E	7.4, 550.0	450.0	32.5	Cambisol	15.6 ± 9.4, 61.0 ± 19.9	31.0 ± 9.7
	Aus	Wilhemdorf	48°33′N, 15°48′E	8.0, 555.6	450.0	31.5	Cambisol	12.2 ± 5.2, 64.4 ± 17.9	35.0 ± 12.7
	Fra	Orleans (HD)	47°49′N, 2°29′E	10.8, 729.0	107.0	16.2	Planosol	27.3 ± 12.9, 102.7 ± 28.7	11.8 ± 11
	Fra	Orleans (LD)	47°49′N, 2°29′E	10.8, 729.0	107.0	12.4	Planosol	30.5 ± 17.5, 104.8 ± 22.5	14.8 ± 8.5
	Ger	Baunach	49°56′N, 10°50′E	9.4, 728.6	331.6	42.0	Cambisol	36.4 ± 16.7, 101.5 ± 24.0	3.0 ± 11.2
	Ger	Triesdorf	49°14′N, 10°33′E	8.8, 734.2	468.3	36.1	Stagnosol	17.0 ± 9.6, 55.9 ± 13.4	0.0
	Pol	Niepołomice	50°02′N, 20°19′E	8.2, 650.0	216.0	35.2	Podzol	29.8 ± 21.6, 101.1 ± 36.8	5.0 ± 7.8
	Spa	Barruelo	42°53′N, 04°14′W	9.3, 881.8	1188.0	50.1	Cambisol	13.4 ± 6.2, 106.3 ± 28.0	0.0
Beech-oak	Bel	Baileux	50°01′N, 04°23′E	8.7, 1081.0	300.0	25.5	Cambisol	9.3 ± 2.8, 114.1 ± 24.8	24.0 ± 5.3
	Bel	Buggenhout	51°00′N, 04°13′E	10.4, 800.0	20.0	28.2	Luvisol	31.8 ± 13.7, 117.7 ± 20.6	0.0
	Bel	Eupen	50°36′N, 06°06′E	8.5, 1112.0	440.0	28.7	Cambisol	17.2 ± 7.9, 112.6 ± 28.3	27.5 ± 10.2
	Bel	Grune	50°09′N, 05°24′E	8.0, 1001.0	420.0	25.1	Cambisol	12.7 ± 7.5, 99.8 ± 16.1	25.9 ± 10.4
	Bel	La Roche	50°11′N, 05°35′E	8.5, 967.0	450.0	34.9	Cambisol	15.3 ± 10.7, 117.7 ± 21.2	33.0 ± 11.5

LAT: latitude; LON: longitude; T: mean annual temperature (°C); P: annual precipitation (mm/year); Alt.: altitude (m); BA: mean plots basal area (m^2/ha) – cf. Tables S4-S6 for plot-level information; SOC-FF: forest floor C stock ($\bar{x}$ ±SD, Mg C/ha); SOC-TOTAL: C stock in FF + 0–40 cm ($\bar{x}$ ±SD, Mg C/ha); Stones: % stones on a volumetric basis in FF + 0–40 cm ($\bar{x}$ ±SD, %); HD: high stand density; LD: low stand density triplet. Soil type classification is based on World Reference Base for Soil Resources (IUSS Working Group WRB 2015). Country codes: Aus (Austria), Bel (Belgium), Fra (France), Ger (Germany), Pol (Poland), Spa (Spain), Swe (Sweden).

stone mass to predict volume of stones in the remaining samples. Volume of stones in a given sample was expressed as a percentage of total volume of that sample.

2.4. Computations of SOC stocks and explanatory variables.

Calculations of SOC stocks followed procedures proposed by Poeplau et al. (2017) as follows:

SOC stocks (Mg C ha^{-1}) = Organic carbon content (%) × fine soil stock (FSS, Mg ha^{-1})

$$\text{For forest floor layers, FSS } \left(\text{Mg ha}^{-1}\right) = \frac{\text{dry weight of forest floor (g)}}{\text{sampling surface (i.e. 30 cm} \times \text{30 cm)}} \times 100$$

$$\text{For mineral soil layers, FSS } \left(\text{Mgha}^{-1}\right) = \frac{\text{dry weight of fine soil (g)}}{\text{total volume of excavation (cm}^3\text{)}} \times \text{depth (10 cm)} \times 100$$

Based on the complete tree diameter inventory, we calculated total basal area (BA, m^2 ha^{-1}) of the two tree species of interest in each plot (plot BA). For pine-oak and pine-beech triplet types, we calculated basal area proportion of pine in each plot (i.e. % BA pine) as a surrogate for species identity; basal area proportion of beech was used for beech-oak triplets. We characterized tree species mixing effect by the Shannon–Wiener index (Shannon, 1948). This index allowed us to characterize mixing effects by taking into account varying basal area proportions of component species in each plot. The expression used was as follows:

$$\text{Shannon–Wiener index (SWx)} = -\sum_{i=1}^{n} \text{Pix} \times \ln(\text{Pix}) \quad \text{where: Pix} = \frac{\text{basal area proportion of species i in plot x}}{\text{total basal area in plot x}}$$

Afterwards, we converted SWx to effective number of species (i.e. True Shannon Diversity) by an exponential function, i.e. exp (SWx), as proposed by Jost (2006). As this study involved species pairs, the maximum value of True Shannon Diversity possible in a plot was two and the minimum value was one for a complete monoculture.

2.5. Statistical analyses

The purpose of our analyses was to assess the average impact of species identity and mixing on SOC stocks across a range of site conditions. The species identity effect was quantified through the slope relating SOC storage to either % pine (for pine-oak and pine-beech triplets) or % beech (for beech-oak triplets). A significant slope means simple additive effects are at play as change in SOC storage is linearly related to the BA proportions of each species in the stand; when significant, the sign and magnitude of the coefficient also reveal how the two species compare in terms of SOC storage. The mixing effect was quantified through the Shannon Diversity index. For two-species mixtures, this index reaches its maximum value for a 50:50 mixture. When significant, a positive parameter value means SOC storage in the mixed stands is higher than expected based on the pure stands; a negative parameter value means lower storage in the mixed stands compared to expectations based on the pure stands. We focused on the FF, 0–10 cm, 10–40 cm, FF + 0–40 cm as they represent, respectively, the organic layer (FF), the organo-mineral layer (0–10 cm), the mineral layer (10–40 cm), and the total soil layer (FF + 0–40 cm). This allowed us to test how identity and mixing effects change across the soil profile, while limiting the risks associated with over-testing. We also computed FF / FF + 0–40 cm ratio, as an indicator of SOC distribution in the soil depth.

For each triplet type, we fitted species identity and species mixing as fixed effects, and site (i.e. location of three plots that make up a triplet) as a random intercept in linear mixed-effect models with *lme4* R package (Bates et al., 2015) for the afore-mentioned soil layers and combinations. We included stone content (except for FF layer) and plot BA in models as covariates to account for influence on SOC stocks by contrasting stoniness (Poeplau et al., 2017) and stand density (Mayer et al., 2020) among plots, respectively. Fitting site as a random effect allows for the control of non-independence by constraining three plots at a given site (i.e. a triplet) to have a common intercept (Zuur et al., 2009). This approach also allows us to test species identity and mixing effects on SOC while accounting for influence by site factors. As effects of site factors (soil, climate, topography) on SOC were not the objective of this study, we treated site as a random intercept in our analyses. The expression used was as follows:

$$\mathrm{SOC} \sim a_0 + a_1 \text{stone content} + a_2 \text{plot BA} + a_3 \text{species identity} + a_4 \text{species mixing} + e_{(site)} + \varepsilon \quad (1)$$

Where a_0, a_1, a_2, a_3, a_4 are regression coefficients of the intercept, stone content, plot basal area, species identity, and species mixing, respectively. $e_{(site)}$ is the random parameter associated with site and ε is the error term.

Likelihood ratio tests did not support the inclusion of random slopes for any of the fixed covariates. We tested models' compliance with homoscedasticity and residual normality with *performance* R package (Lüdecke et al., 2020). We tested multicollinearity among explanatory variables by calculating variance inflation factors (VIFs) with *car* R package (Fox and Weisberg, 2019). Considering that VIFs values were lower than 3 (VIFs < 3) show that multicollinearity did not affect models' estimates (Zuur et al., 2010). We estimated model parameters using restricted maximum likelihood (REML) and tested significance of predictors using t-tests with Satterthwaite's degrees of freedom method in *lmerTest* R package (Kuznetsova et al., 2017). We calculated percentage of variance explained by fixed (R^2m) and combined fixed plus random effects (R^2c) using *performance* R package (Lüdecke et al., 2020). To assess the relative importance of species identity and mixing effects, we further partitioned the variance in SOC by the fixed effects, random effects, and residuals using *BaylorEdPsych* R package (Beaujean, 2012). We tested significance at 95% confidence level in all analyses.

3. Results

3.1. Overview of SOC storage in the three triplet types.

Here, we provide an overview of SOC stocks at plot level for the three triplet types in this study. Detailed SOC stocks in the selected soil layers (FF, 0–10 cm, 10–40 cm, FF + 0–40 cm) per plot for individual triplets are given in supplementary Tables S7-S9. Subsequent statistical comparisons of SOC stocks among plots for the selected soil layers of the three triplet types are available in supplementary Table S10, and illustrated in Fig. 2.

There was a consistent trend of SOC stocks at plot level for pine-beech triplets (beech < pine-beech < pine) and pine-oak triplets (oak < pine-oak < pine) in the FF + 0–40 cm soil layer (Fig. 2A & 2B; Table S10). Briefly, the average SOC in the FF + 0–40 cm soil layer of pine-beech triplets was beech (77.1 Mg C ha^{-1}; range: 37.6–120.2 Mg C ha^{-1}) < pine-beech (90.3 Mg C ha^{-1}; range: 63.6–134.4 Mg C ha^{-1}) < pine (99.4 Mg C ha^{-1}; range: 65.9–143.4 Mg C ha^{-1}). Similarly for pine-oak triplets at the same soil layer, the average SOC in pine plots (103.8 Mg C ha^{-1}; range: 63.5–140.1 Mg C ha^{-1}) was 1.4 fold higher than oak (73.3 Mg C ha^{-1}; range: 46.0–100.2 Mg C ha^{-1}), and 1.2 fold higher than the mixed pine-oak plots (86.0 Mg C ha^{-1}; range: 56.6–106.3 Mg C ha^{-1}; Table S10). Contrary to the above, SOC stocks in the FF + 0–40 cm layer of beech-oak triplets were not significantly different among plots (beech-oak plots: 115.6 Mg C ha^{-1}, range: 102.7–124.3 Mg C ha^{-1}; beech plots: 108.6 Mg C ha^{-1}, range: 97.6–120.8 Mg C ha^{-1}; and oak plots: 109.8 Mg C ha^{-1}, range: 85.2–127.2 Mg C ha^{-1}; Fig. 2C, Table S10).

For the two coniferous-deciduous triplets, a similar trend as for the total soil profile was observed in the forest floor with pure deciduous < mixed < pure coniferous (Fig. 2A & 2B). SOC stocks were significantly higher under pure pine compared to the pure deciduous stands in the 0–10 cm layer for both triplet types, as well as in the 10–40 cm layer for the pine-oak triplets. In the beech-oak triplets (Fig. 2C; Table S10), the SOC stocks in the forest floor were significantly higher under beech than under oak, with intermediate values under the mixed stands. For the mineral soil layers, SOC storage in the 0–10 cm soil layer was higher under the mixed stand compared to the pure stands; there was no significant compositional effect in the 10–40 cm layer, as for the entire soil depth.

3.2. Impact of species identity on SOC stocks.

We observed significant species identity effects on SOC stocks in the total soil depth of pine-beech and pine-oak triplets, but not in beech-oak triplets (Figs. 3–5; Tables S11-S13). However, species identity effects on SOC stocks in the forest floor were consistently significant across triplet types. Notably, species identity significantly influenced the proportion of total SOC accumulated in the forest floor (i.e. FF/FF + 0–40 cm) of all triplet types (Tables S11-S13). Similar to the observed trend in the total soil depth, species identity significantly influenced SOC stocks in the organo-mineral layer (0–10 cm) of pine-beech and pine-oak triplets, but not beech-oak. In the mineral soil layer (10–40 cm), species identity only significantly influenced SOC stocks in the pine-oak triplets (Fig. 4; Table S12).

3.3. Impact of species mixing on SOC stocks.

Tree species mixing did not significantly influence SOC stocks in the total soil depth of any triplet type (Figs. 3–5; Tables S11-S13). Similarly, we did not observe any significant mixing effects on SOC stocks in the forest floor of any of the triplet types. There was a significant positive effect of species mixing on SOC stocks in the organo-mineral layer of beech-oak triplets (Fig. 5C; Table S13). Conversely, we found no evidence of species mixing effects on SOC stocks in the organo-mineral soil layer of pine-beech and pine-oak triplets. (Figs. 3 and 4; Tables S11-S12). While a positive mixing effect was found in the mineral soil layer of pine-beech triplets, mixing had no impact on SOC stocks in the same layer of pine-oak and beech-oak triplets (Figs. 3–5; Tables S11-S13).

3.4. Relative impact of species identity and mixing on SOC stocks.

The relative impact of tree species identity and mixing on SOC stocks was dependent on triplet type and the soil layer under consideration. For the total soil depth, species identity explained more variability in SOC stocks than species mixing across triplet types, yet the contribution of

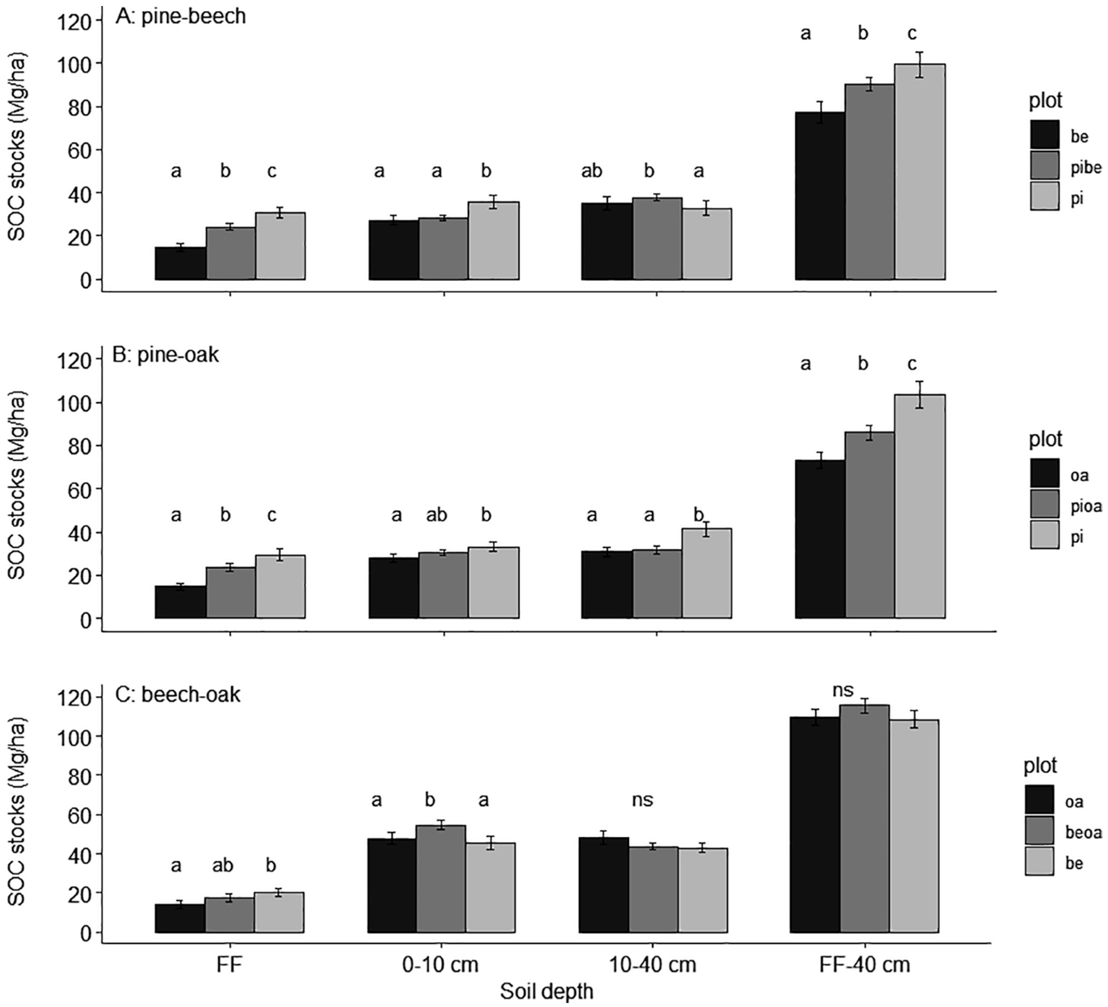

Fig. 2. Comparison of soil organic C stocks (mean ± S.E.) in the total soil profile (FF + 0–40 cm), forest floor (FF), 0–10 cm, and 10–40 cm soil depths of monospecific and mixed plots for each triplet type. For a given soil depth, plots without common letters are significantly different at $P < 0.05$ (Tukey post-hoc test); "ns" means the no-intercept mixed effect model using 'Plot' as a fixed effect and 'Site' as a random factor was not significant at $P < 0.05$. We have reported detailed statistical comparisons in supplementary Table S10.

either of these factors was nearly zero in the beech-oak triplets (Fig. 6; Table S14). Similarly, the overriding impact of species identity over species mixing on SOC stocks in the total soil depth was observed in the forest floor of all triplet types. We found divergent impact of species identity and species mixing on SOC stocks in the organo-mineral layer among triplet types. Specifically, species mixing explained much more variability in SOC stocks than species identity only in two cases: in the organo-mineral layer (0–10 cm) of beech-oak triplets, and in the mineral layer (10–40 cm) of the pine-beech triplets. Species mixing accounted for nearly 3% variability in mineral soil SOC stocks in pine-beech triplets compared with ~ 1% for species identity (Fig. 6; Table S14). There was also the same trend for mineral layer of beech-oak triplets, yet to a much lower extent. Species identity was more important than mixing in all other cases, including all soil layers of pine-oak triplets.

4. Discussion

4.1. Tree species identity strongly influences topsoil SOC storage.

Observation of pronounced species identity effects on SOC stocks at the superficial soil layers (FF, 0–10 cm of pine-beech and pine-oak triplets; FF of beech-oak triplets) is in line with the first hypothesis (H1) that effect of tree species identity on SOC stocks is more prominent in topsoil layers than deeper soil layers. This finding is consistent with some previous studies (Dawud et al., 2016; López-Marcos et al., 2018), and was attributed to foliar litter influence. Cornelissen et al. (2004) and Pérez-Harguindeguy et al. (2000) suggest that functional traits of tree species persist in their litter and modulate decomposition processes in a form of 'afterlife' effect. Indeed, litter of pine needles is characterized by high lignin and relatively low N contents, and these characteristics slow decomposition rates (Berg, 2000; Fassnacht and Gower, 1999). This could explain the observed stronger species identity (in terms basal area proportion of pine) on SOC stocks at the forest floor and upper-mineral layer in pine-oak and pine-beech triplets. In agreement with our results, Dawud et al. (2016) also reported species identity effects (in terms of conifer proportion) on SOC stocks and C/N ratios at the forest floors. In the beech-oak triplets, species identity (in terms of basal area proportion of beech) was significant at the forest floor but not in the organo-mineral 0–10 cm layer. Though the difference in litter recalcitrance between those two broadleaved tree species is more limited than between broadleaved and coniferous (Vesterdal et al., 2013), oak litter is known to decompose faster than beech in acidic soils (Jonard et al., 2008). The faster foliar litter turnover and subsequent incorporation into upper mineral layers under broadleaf species like oak and beech (Berg and McClaugherty, 2003; Leuschner et al., 2001) is also reflected by the mean proportions of carbon stocks at the forest floor (i.e. percentage FF carbon stocks of the total FF + 0–40 cm). These were much lower in the beech-oak (15.2%) compared to the pine-beech (26.2%) and pine-oak

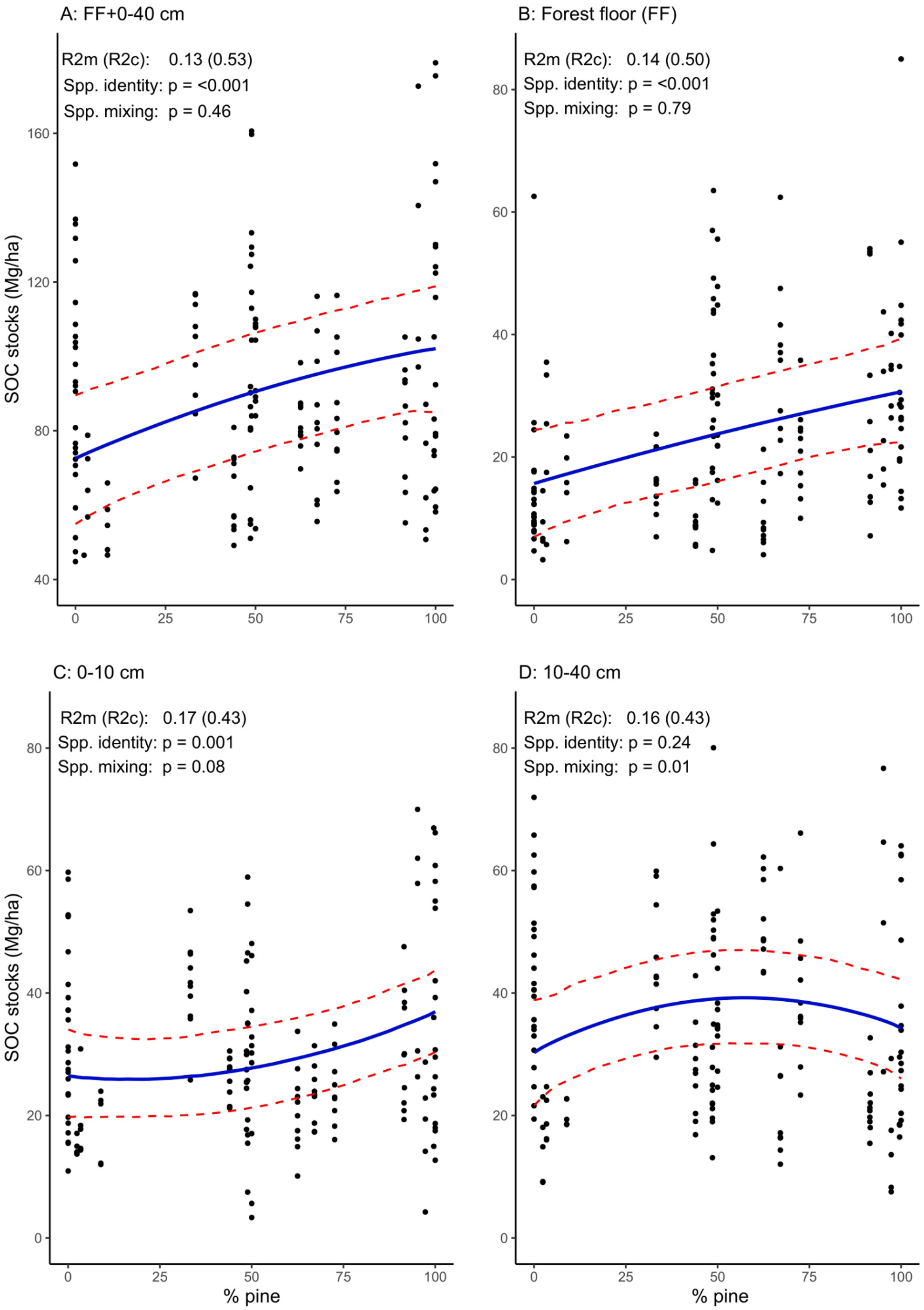

Fig. 3. Black/filled dots are observed soil organic carbon stocks (SOC stocks) against share of pine (% pine) in the total soil profile (FF+0-40 cm), forest floor (FF), organo-mineral layer (0-10 cm), and mineral soil layer (10-40 cm) in the 8 pine-beech triplets. Solid lines show modelled SOC stocks (with 95% confidence interval in dotted lines) based on model (eq. 1) with plot basal area and stone content kept constant (fixed at overall average values). R^2m shows percentage of variance by fixed effects and R^2c shows percentage of variance by fixed plus random effects. P-values are given for the Species identity and Species mixing effects. All parameter estimates are provided in supplementary Table S11.

triplets (25.6%). In contrast to the upper soil layers, species identity effects were limited in the mineral soil layers, except under the pine-oak triplets. Tree species traits influence initial decomposition rates in topsoil layers (Schmidt et al., 2011) but micro-environmental conditions take precedence over species traits on subsoil SOC dynamics as the interactions between SOC and the mineral soil matrix increase with depth (Krishna and Mohan, 2017; Schmidt et al., 2011). Along the same line, Boča et al. (2014) indicate that SOC stocks in the mineral soil layers are stable and less sensitive to changes in the overstory vegetation.

4.2. *Mixing effects on deep SOC are limited to pine-beech triplets.*

Species mixing significantly influenced SOC storage in the deeper soil layers (10–40 cm) of only pine-beech triplets. Thus, our hypothesis that species mixing drives SOC storage in deeper soil layers across triplet types (H2) is not fully supported. Stronger species mixing effects on SOC stocks at the deeper soil layers of pine-beech agrees with Dawud et al. (2016), who found that tree species diversity explained more variability in carbon stocks at the 20–40 cm mineral layer. In this study, significant synergistic mixture effects at the mineral layer of pine-beech triplets could be due to belowground niche complementarity via vertical stratification of fine roots of pine and beech (Brassard et al., 2013). Beech often roots deeply when admixed with coniferous species (Andivia et al., 2016; Bolte and Villanueva, 2006; Curt and Prevosto, 2003; Rothe and Binkley, 2001). This perhaps resulted in a more intensive exploitation of the soil layers that led to higher production of root litter and exudates for

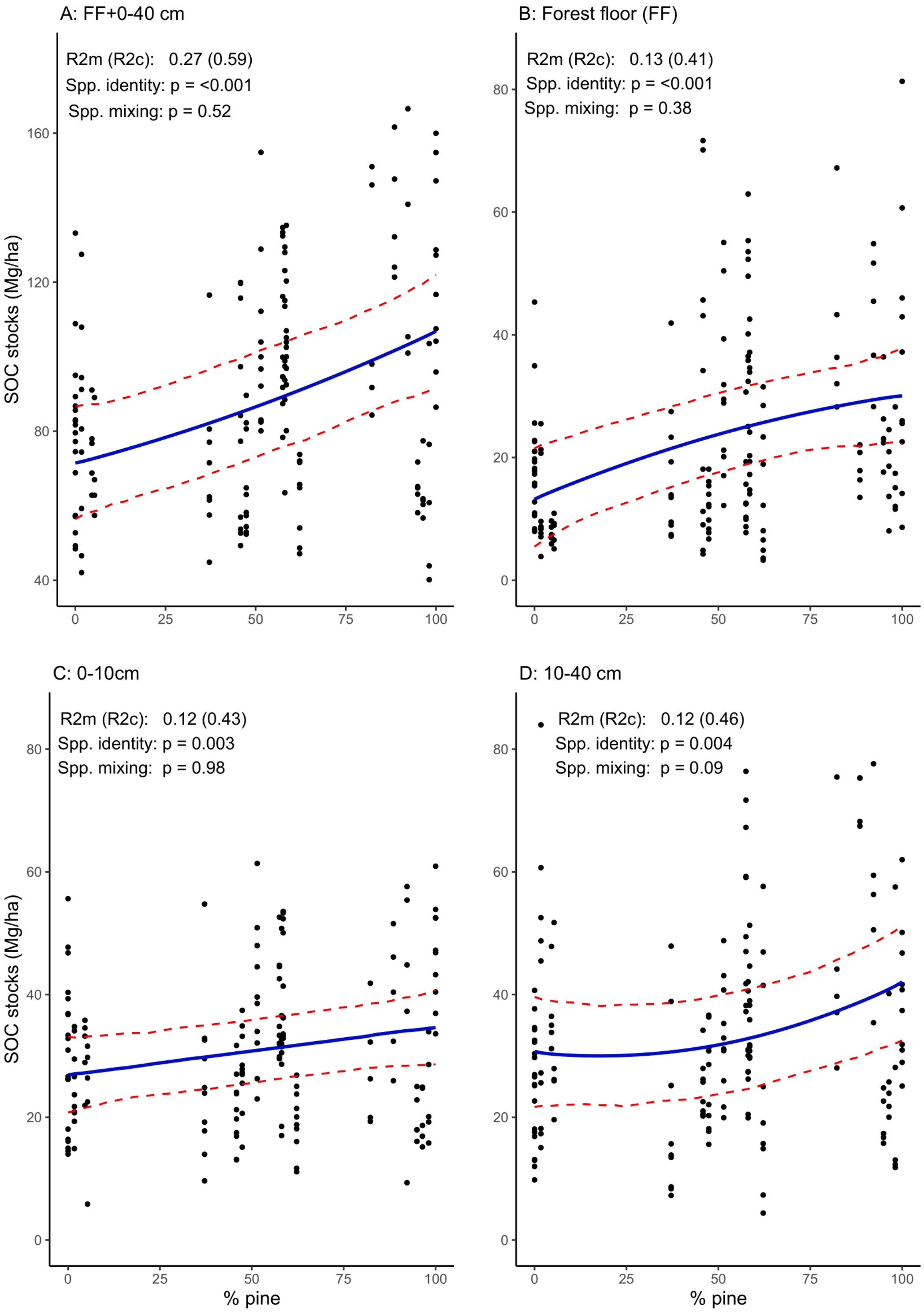

Fig. 4. Black/filled dots are observed soil organic carbon stocks (SOC stocks) against share of pine (% pine) in the total soil profile (FF+0-40 cm), forest floor (FF), organo-mineral layer (0-10 cm), and mineral soil layer (10-40 cm) in the 8 pine-oak triplets. Solid lines show modelled SOC stocks (with 95% confidence interval in dotted lines) based on model (eq. 1) with plot basal area and stone content kept constant (fixed at overall average values). R2m shows percentage of variance by fixed effects and R2c shows percentage of variance by fixed plus random effects. P-values are given for the Species identity and Species mixing effects. All parameter estimates are provided in supplementary Table S12

increased accumulation of soil carbon in the 10–40 cm depth under mixed pine-beech stands compared to the corresponding pure stands (Brassard et al., 2013; Dawud et al., 2016). Such root-derived carbon inputs are often more stable than foliar litter-derived carbon in forest ecosystems (Sokol et al., 2019a, 2019b). Aside root dynamics, earthworm communities could engineer increased input flux of new or partly decomposed forest floor materials into deeper soil layers of mixed pine-beech stands. Activities of earthworm communities could be stimulated by litter diversity (Hättenschwiler and Gasser, 2005) or increased soil pH through deposition of comparatively calcium-richer beech litter on forest floors, which neutralizes the acidifying effects of pine foliar litter (Berger et al., 2006; Błońska et al., 2018). However, our topsoil pH values largely fall within 3.5–4.5 range (Table S1), which considerably limits earthworm activities (Curry, 1998). Absence of root complementarity between pine and oak could explain the lack of mixing effects on SOC stocks in the mineral soil layers of pine-oak triplets. In the French pine-oak triplets, Bello et al. (2019) did not find evidence of physical complementarity in fine root distribution in mixed pine-oak stand. In the same study, fine root density did not differ between mixed and pure stands of pine and oak. They concluded that inter-

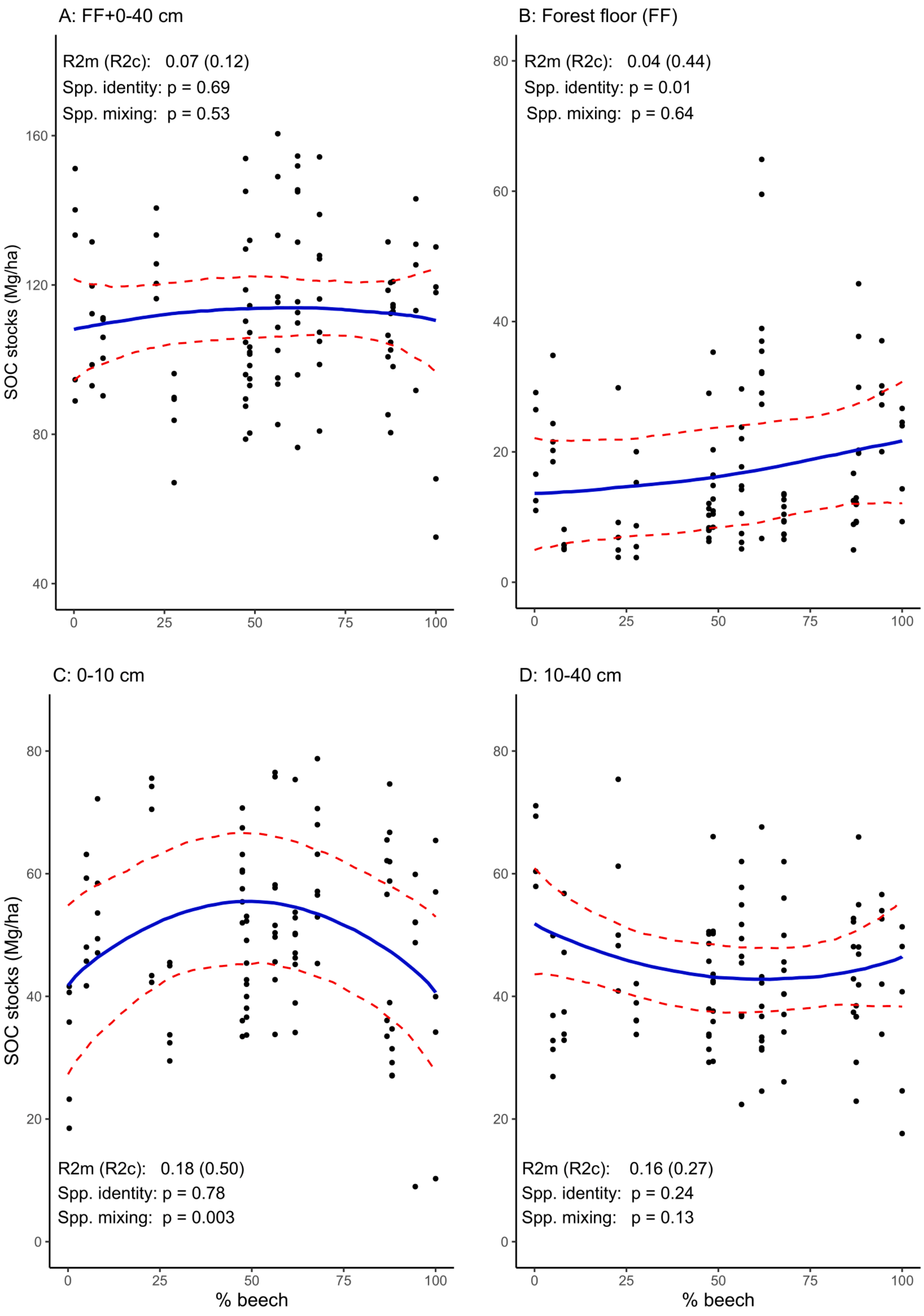

Fig. 5. Black/filled dots are observed soil organic carbon stocks (SOC stocks) against share of pine (% pine) in the total soil profile (FF+0-40 cm), forest floor (FF), organo-mineral layer (0-10 cm), and mineral soil layer (10-40 cm) in the 5 beech-oak triplets. Solid lines show modelled SOC stocks (with 95% confidence interval in dotted lines) based on model (eq. 1) with plot basal area and stone content kept constant (fixed at overall average values). R^{2}m shows percentage of variance by fixed effects and R^{2}c shows percentage of variance by fixed plus random effects. P-values are given for the Species identity and Species mixing effects. All parameter estimates are provided in supplementary Table S13.

specific competition between oak and pine may be similar to intra-specific competition in pure stands (Bello et al., 2019; Curt and Prevosto, 2003).

Contrary to our second hypothesis, we observed significant mixing effects in the organo-mineral layer of beech-oak triplets, instead of deeper soil layers. Though foliar litter input is not expected to differ between the mixed beech-oak and the respective pure stands (Jonard et al., 2008), tree species richness has been reported to induce strong intraspecific variability of beech (*Fagus sylvatica*) leaf traits (Forey et al., 2016). Specifically, lignin content of beech leaves was on average 11.2% in mixed beech-oak stands compared with 9.7% in pure beech stands (Forey et al., 2016). These species richness-induced alterations in foliar chemistry could enhance litter recalcitrance and slow down the decomposition processes. This could translate into higher SOC accumulation in the mixed stands compared with pure oak and beech stands, as observed in the organo-mineral layers of beech-oak triplets. On the other hand, fine root dynamics could also explain the observed synergistic mixture effects on SOC in the organo-mineral layer of beech-oak triplets. We postulate that faster turnover of often nitrogen-rich foliar litter of beech and oak species (Krishna and Mohan, 2017; Pérez-

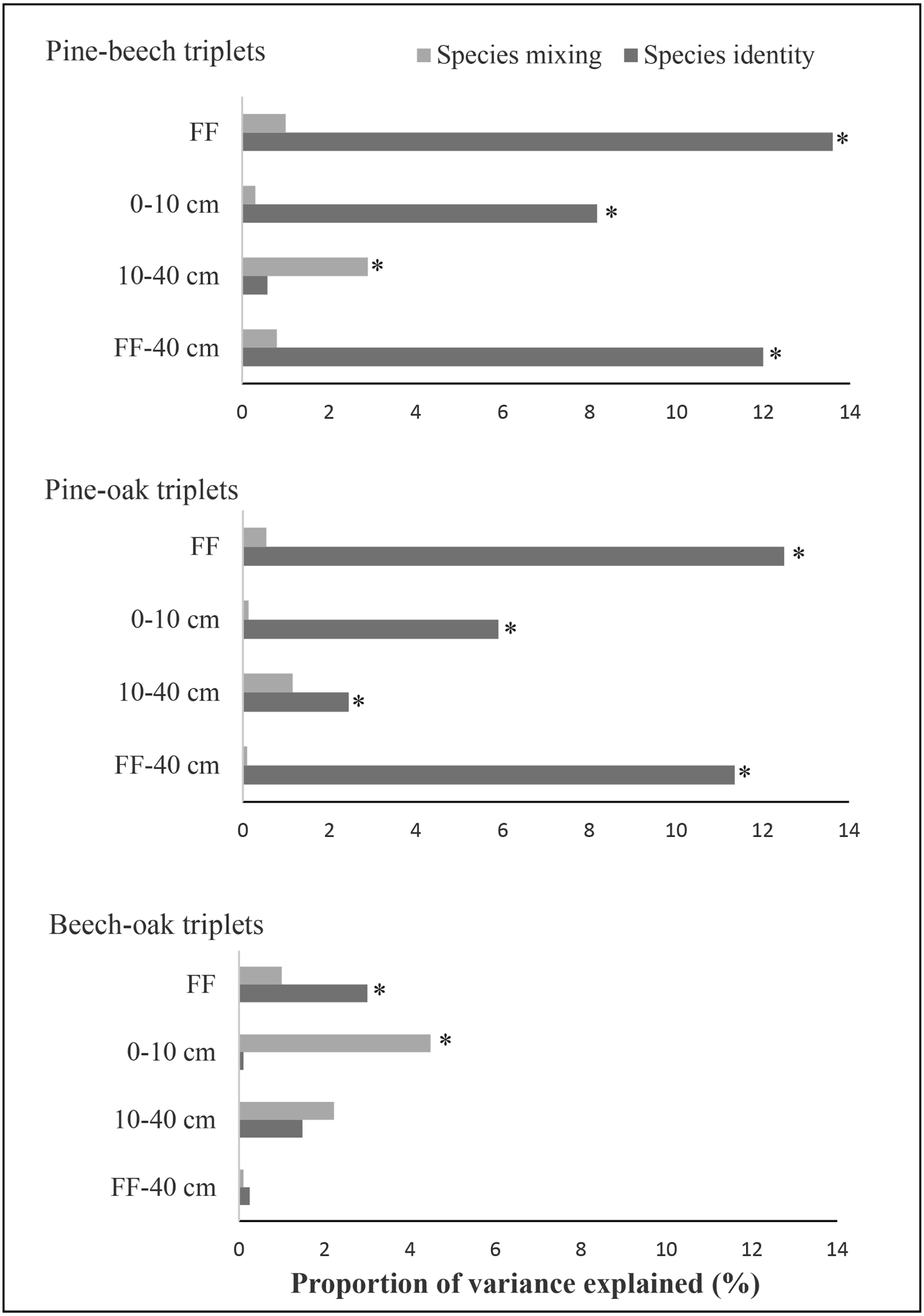

Fig. 6. Proportion of variability in SOC stocks explained by species identity (% basal area of pine for pine-beech and pine-oak triplets; % basal area of beech for beech-oak triplets) and species mixing (True Shannon Diversity index at plot level) in the forest floor (FF), organo-mineral layer (0–10 cm), mineral layer (10–40 cm), and total soil layer (FF + 0–40 cm) in pine-beech, pine-oak, and beech-oak triplets. The models (eq. (1)) included stone content and plot basal area as covariates, and site as random intercept. Bars with asterisks (*) denote a significant effect at P-value < 0.05. A full variance partitioning is given in supplementary Table S14.

Harguindeguy et al., 2000) led to N release into the organo-mineral layers. In response, beech and oak could activate fine root production to forage the released N, thereby increasing root litter input, rhizodeposition, and their associated microbial biomass to carbon pools in the organo-mineral layer of the mixed beech-oak stands more than the respective pure stands (Leuschner et al., 2001). This possible coexistence of fine roots of beech and oak in the organo-mineral layer is in agreement with the reported absence of vertical root stratification in beech-oak mixtures (Leuschner et al., 2001; Smith et al., 2013). We conclude that mixture effects on deeper SOC storage is not unidirectional and is largely contingent on the interplay of root dynamics of the interacting species, their associated soil biota, and the prevailing physicochemical environment.

4.3. *Species identity is a stronger driver of SOC stocks than mixing across triplet types.*

In this study, species identity explained more variability in total SOC stocks than species mixing across triplet types. Hence, our hypothesis that species identity is superior to species mixing in driving total SOC storage (H3) is confirmed. However, the relative impact of tree species identity and mixing on SOC stocks in the selected soil layers was not consistent across triplet types. While species identity was a more important driver of SOC storage than species mixing in all soil layers of pine-oak triplets, species mixing influenced SOC storage more than species identity in 10–40 cm layer of pine-beech and 0–10 cm layer of beech-oak triplets (Fig. 6; Tables S11- S14). These contrasting observations among triplet types further highlights the importance of tree species identity in forest management approaches aimed at increasing SOC stocks (Błońska et al., 2018; Dawud et al., 2017; López-Marcos et al., 2018). In southwestern China, Liu et al. (2016) found that mixed conifer-broadleaf forest and an evergreen broadleaf forest at the same site were similar in diversity indices but had contrasting carbon stocks and this was attributed to dissimilar species compositions. Makkonen et al. (2012) also found differences in decomposition among litter mixtures with equal numbers of species but with different functional group compositions, and recommended trait-based approaches to modelling carbon cycles. Strikingly, we observed a trade-off between significant species identity and species mixing effects on SOC stocks in the selected soil layers amongst all triplet types. Simply put, whenever species mixing was significant at a given soil layer, species identity was always insignificant at the same layer, and vice-versa (Figs. 3–5; Tables S11-S13), consistent with findings of Dawud et al. (2016). The mechanisms underlying this phenomenon remain elusive but it could be an outcome of the magnitude of complementarity between the admixed species in a given soil layer. That is, high complementarity between the admixed species suppresses the dominance of individual species traits in controlling SOC storage, and vice-versa.

4.4. *Conclusions*

This study supports the growing number of studies confirming that species identity is a stronger driver of soil carbon storage than species mixing. While the tree species identity effect is strongly related to a conifers *vs* broadleaves signature, the drivers behind mixing effects remain elusive. Additionally, species identity consistently drives accumulation of soil carbon in the forest floor while species mixing is more important in deeper soil layers, at least in pine-beech and beech-oak triplets. In sites where pine and beech may grow together, mixed forest management with both species could be a promising strategy for a long-term carbon storage owing to the significant increase in soil carbon accumulation in the subsoil layers of mixed pine-beech stands. Considering the wide gradient of edaphic, topographic, and climatic conditions covered by pine-oak and pine-beech triplets, the findings thereof are robust and reflect large scale patterns of soil carbon storage in the studied forest tree species and their mixtures. With regards to SOC storage in beech-oak mixtures, a broader scale study would be needed to generalize our findings. We recommend further investigations into the impact of environmental factors and their interaction with species and mixtures on soil carbon storage. Our results also underline the need for the establishment of more controlled and standardized long-term experiments across Europe to test the specific above and/or below ground mechanisms of mixing effects. Besides carbon stocks, there is also a need to further investigate the impact of species identity and diversity on stability of SOC.

CRediT authorship contribution statement

Richard Osei: Conceptualization, Investigation, Formal analysis, Writing - original draft, Writing - review & editing. **Hugues Titeux:** Conceptualization, Methodology, Writing - review & editing, Supervision. **Kamil Bielak:** Writing - review & editing. **Felipe Bravo:** Writing - review & editing. **Catherine Collet:** Writing - review & editing. **Corentin Cools:** . **Jean-Thomas Cornelis:** Writing - review & editing. **Michael Heym:** Writing - review & editing. **Nathalie Korboulewsky:** Writing - review & editing. **Magnus Löf:** Writing - review & editing. **Bart Muys:** Writing - review & editing. **Yasmina Najib:** . **Arne Nothdurft:** Writing - review & editing. **Maciej Pach:** Writing - review & editing. **Hans Pretzsch:** Writing - review & editing. **Miren del Rio:** Writing - review & editing. **Ricardo Ruiz-Peinado:** Writing - review & editing. **Quentin Ponette:** Conceptualization, Methodology, Resources, Funding acquisition, Project administration, Writing - review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118752.

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