

Rich litter admixture effects on belowground carbon dynamics in temperate forests: From leaf litter input to molecular composition of soil organic matter

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ARTICLE INFO

Keywords:

Forest restoration
Soil acidification
Carbon persistence
Organic matter composition
Pyrolysis-GC/MS
Mesofauna
Litter quality

ABSTRACT

Soil acidification is a common threat to forests in sandy areas of Western Europe, resulting from past land-use and atmospheric deposition. Converting pine monocultures to mixed forests is a management strategy to enhance biodiversity and overall forest resilience that allows to counteract acidification through admixture of tree species with high litter quality. While positive effects of “rich litter” admixture on soil nutrient availability have been evidenced, the implications for soil organic carbon (SOC) dynamics remain poorly understood. Here, we present an in-depth, small-scale study that uniquely combines data on tree composition, forest floor properties, decomposer communities, SOC stocks, carbon fractionation and soil organic matter molecular composition to assess the effects of converting *Pinus sylvestris* monocultures to mixed broadleaved forest. We investigated five twin-plots on sandy soils in Belgium and the Netherlands, each consisting of a pine monoculture and an adjacent mixed forest enriched with broadleaved species producing nutrient-rich litter. We examined how changes in tree composition cascaded through the forest carbon cycle, from tree litter inputs up to SOC at the molecular level. Our findings indicate that admixture of rich-litter species strongly alters soil pH, forest floors and belowground communities. Total soil carbon (C) changes were more subtle, suggesting a longer response time to overstory changes. Nonetheless, despite the limited spatial-scale, a change in belowground processes was clearly observed in the SOC fractions and molecular composition: pine monocultures store proportionally more C in labile fractions and molecular changes indicating a stronger microbial reworking in mixed broadleaved forests, promoting increased C storage in stable fractions over time.

1. Introduction

Establishing resilient forests is critical to mitigate the effects of climate change, adapt to impacts of future environmental disturbances and secure the delivery of a multitude of ecosystem services (Nabuurs et al., 2017). Maintaining healthy forest ecosystems hinges on sustainable nutrient and carbon (C) cycles, yet in North-Western Europe the latter have been increasingly disrupted by the progressive acidification of forest soils. Natural acidification by soil weathering has greatly been accelerated by anthropogenic deposition of sulphur (S) in the past, and

current elevated nitrogen (N) deposition, and magnified by a monotonous choice of overstorey species (Augusto et al., 2002; Ulrich, 1991). Soil acidification severely alters the availability of nutrients and base cations in the forest ecosystem, increases aluminium (Al) toxicity and alters the composition, diversity and functionality of belowground communities (Briones, 2014; Mulder et al., 2005; Wall et al., 2012). This problem is particularly pressing in Pleistocene sandy regions of Belgium, the Netherlands and Germany, where soils have limited buffer capacity and forests are often dominated by Scots pine (*Pinus sylvestris*) monocultures (Desie et al., 2020).

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<https://doi.org/10.1016/j.foreco.2026.123782>

Received 4 February 2026; Received in revised form 30 March 2026; Accepted 1 April 2026

Available online 22 April 2026

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To mitigate forest soil acidification in pine monocultures, various management practices have been proposed and implemented. These include soil amendments to increase pH and base cations, including liming or application of rock dust (Van Der Bauwhede et al., 2024), or altering forest species composition (Desie et al., 2020; Kooch and Bayranvand, 2017; Van Nevel et al., 2014). Desie et al. (2020) showed that sandy soils with a low buffer capacity and high N availability create a ‘window-of-opportunity’ for improving soil health by admixture of tree species with litter rich in base cations, such as small-leaved lime (*Tilia cordata*) and sweet cherry (*Prunus avium*). These species with high litter quality will further be denoted as ‘rich litter’ tree species, as opposed to coniferous tree species, or deciduous species with lower litter quality such as beech or oak (Desie et al., 2020).

The impact of rich litter input on soil pH, soil base saturation, exchangeable soil aluminium, macro-nutrient availability, earthworms communities and tree species vitality on sandy soils is well evidenced (Desie et al., 2020; Schelfhout et al., 2017; Verstraeten et al., 2018). Nonetheless, the potential benefits of rich litter admixture on the broad decomposer community, soil C cycles and soil C persistence remain far less understood (Angst et al., 2022), and cannot be ignored in a time shaped by climate change. And, although the impact of rich-litter admixture on earthworms has been studied, the ecological niches of other soil faunal taxa and their effects on soil material cycles are largely neglected (Briones, 2014; De Wandeler et al., 2016). Previous studies in more loamy soils have linked litter quality to the catabolic diversity of soil communities (Desie et al., 2019; Heděnc et al., 2020), and the relative distribution of C over mineral-associated organic matter (MAOM) and particulate organic matter (POM) fractions, yet it remains unclear if such processes are equally relevant in soils with low mineral reactivity, such as sandy soils (Angst et al., 2023; Cotrufo et al., 2022; Doetterl et al., 2025; Lavalée et al., 2020). Ultimately, there is still substantial scientific uncertainty with respect to the mechanistic process underpinning C stabilisation and destabilisation in forest soils. This is particularly true for less researched conditions, such as sandy or acidic forest soils (Hayes and Swift, 2020; Lehmann et al., 2020), where POM potentially plays a different role in C persistence (Angst et al., 2023). Finally, the molecular composition of soil organic matter (SOM) is often overlooked, even though it can provide valuable and detailed information on the origin and decomposition of organic matter (OM) (Angst et al., 2021; Kögel-Knabner, 2002; Wrightson et al., 2025). Moreover, while many studies document the effect of overstory species on individual soil properties or processes (i.e. a reductionist approach), studies that aim to understand how such effects cascade through the soil ecosystem, and approach soils as complex systems are needed (Angst et al., 2023; Lehmann et al., 2020).

In sum, numerous authors have highlighted that soils are complex systems and that management-induced changes in soil C persistence should be assessed across ecosystem compartments and across different soil depths (Lehmann et al., 2020; Schmidt et al., 2011). However, studies that do so remain limited because of the large amounts of different data that is required for such an approach. Therefore, in this reconnaissance paper we adopt an explicitly small-scale but integrative approach to improve understanding of how conversion of pine monocultures through the admixture of rich-litter tree species cascades through multiple, interconnected compartments of forest ecosystems on sandy soils. By combining complementary analyses across tree composition, forest floor, soil physicochemical properties, soil fauna, soil microbiota, soil C stocks, SOC fractions and SOM molecular composition, we provide a more holistic assessment of C cycle responses to overstory conversion. To this end, five forests were selected in the Pleistocene sandy deposit region (Southern Netherlands, Northern Belgium), representative for temperate zone forests exposed to substantial anthropogenic pressures from soil acidification and N deposition. In each forest, adjacent twin-plots were selected that were either dominated by pine (pine-control), or had a considerable admixture of rich-litter tree species (pine-converted). The following hypotheses will

be tested to support our aim: 1) rich litter admixture reduces forest floor accumulation and soil acidity and improves nutrient availability, 2) soil fauna communities shift from microarthropod-dominated systems toward more earthworm-dominated communities and increased microbial activity, and 3) changes in soil biota and litter quality influence SOC fractions and molecular SOM composition. The molecular composition of the SOM will reflect these altered decomposition pathways and have larger amounts of microbial derived compounds such as N-compounds and smaller amounts of intact plant material such as lignins. By investigating these hypotheses as a connected chain of interactions, even within a limited set of forests, this study captures key interdependencies in forest C dynamics that can inform a more targeted selection of key variables (indicative for changing processes) in larger-scale surveys or monitoring schemes.

2. Materials and methods

2.1. Study area and twin-plot setup

The study area is located in the south of the Netherlands and the northeast of Belgium, situated on the West-European sand belt with sand deposits from the Pleistocene (Beerten et al., 2014; von Doorn et al., 1997). This area has a temperate climate, with a mean annual precipitation of 820 mm and mean annual temperature of 10.9 °C (climate-data.org). Five sites on sandy soils were selected, each using a twin-plot design to control for edaphic context and isolate the effect of overstory tree species composition. At each site, two adjacent forest stands were selected: the typical Scots pine monoculture (*Pinus sylvestris*), common in the Netherlands and Belgium, and a neighbouring stand that was either converted from pine monoculture or is currently undergoing conversion to a mixed forest. The mixed forest stands are characterised by a high admixture of mature rich litter tree species including European lime (*Tilia x europaea*), silver birch (*Betula pendula*), sycamore maple (*Acer pseudoplatanus*), common rowan (*Sorbus aucuparia*) and black cherry (*Prunus serotina*, Table 1). These twin-plots are referred to as “pine-control” and “pine-converted” plots, respectively. A plot of 10 m x 10 m was delineated in each of those twin-plots. In the pine-control plots the average percentage of rich litter species was 22% and of poor litter species 78% of the total basal area (Table 1). In the pine-converted plots, this was the reverse with 73% rich litter species and 27% poor litter species. All soils had sandy textures, with sand contents ranging from 57% to 85%. Soil types were described using an auger until 1 m deep and classified according to the World Reference Base for Soil Resources (IUSS Working Group WRB, 2022). Soil types included Anthrosols, Camisols, Umbrisols and Podzols. Humus types were described according to the Humus Reference Base (Zanella et al., 2012) and varied from mor and moder humus types in the pine-control plots, to moder and mull types in the pine-converted plots (Table 1).

2.2. Sampling and in-field data collection

Tree species were identified and their basal area was determined. Soil samples were taken from both organic and mineral soil layers. The thickness of the forest floor layer (O-layer) was measured by digging out a 10 × 10 cm soil square three times per twin-plot for the fragmented (OF) and humic (OH) layer excluding the litter (OL) layer because it encompasses too much uncontrolled variation (e.g. wind, season). The litter (OL) and organic (OF+OH) layer were subsequently sampled in a 25 × 25 cm plot to determine total forest floor mass (Zanella et al., 2012). For the mineral soil samples, a composite sample of 10 samples per plot was made using a gouge auger (ø30 mm) for the 0–10 cm (topsoil) and 10–20 cm (subsoil) interval, with the mineral soil starting under the forest floor layer. Three replicates were taken for the bulk density using a Kopecky ring, for both 0–10 cm and 10–20 cm.

Earthworms were collected on 3 standardised locations within the forest plots, and sampled within a 0.71 × 0.71 m² plot using mustard

Table 1

Field variables (n = 1 per site). Left pine-control plots, right pine-converted plots. Tree species ordered to size of basal area. *tree species present but do not account for basal area.

		Groote Heide (GH)		Hechtel-Eksel (H)		Kasterlee (K)		Maashorst (M)		Veldhoven (V)	
		<u>Pine-control</u>	<u>Pine-converted</u>	<u>Pine-control</u>	<u>Pine-converted</u>	<u>Pine-control</u>	<u>Pine-converted</u>	<u>Pine-control</u>	<u>Pine-converted</u>	<u>Pine-control</u>	<u>Pine-converted</u>
Soil type		Gleyic Podzol	Gleyic Umbrisol	Podzol	Plaggic Anthrosol	Gleyic Cambisol	Gleyic Cambisol	Cambisol	Anthric Umbrisol	Cambisol	Cambisol
Texture	Clay %	4.21	4.33	3.79	4.45	4.62	2.49	2.45	3.48	3.64	4.03
	Sand %	62.45	57.23	70.31	66.64	75.2	85.6	82.74	69.7	62.56	55.76
Basal area [m ² /ha]	Total	29	29	11.5	12	28.5	37	16	31	26	28.5
	Poor	26	4	3.5	5	26	17	11	8	18	2.5
	Rich	3	25	8	7	2.5	20	5	23	8	26
Humus Type		Eumor	Mesomull	Hemimoder/Eumoder	Oligomull	Hemimor	Dysmoder	Eumor	Hemimoder/Eumoder	Eumoder/Dysmoder	Dysmull/Hemimoder
Tree species/Understory		Pinus sylvestris, Betula pendula, Frangula alnus, Ilex aquifolium, Quercus robur*, Sorbus aucuparia*, Pseudotsuga menziesii*	Acer pseudoplatanus, Salix caprea, Tsuga spp., Fagus sylvatica, Pseudotsuga-menziesii, Fraxinus excelsior, Corylus avellana, Larix spp., Crataegus monogyna*, Carpinus betulus*	Pinus sylvestris, Betula pendula, Ilex aquifolium*, Sorbus aucuparia*, Prunus serotina*, Rubus fruticosus*, Dryopteris dilatate*	Tilia europea., Quercus petraea, Quercus robur, Dryopteris dilatate*, Castanea sativa*	Pinus sylvestris, Quercus robur, Betula pendula, Corylus avellana, Tilia spp., Acer pseudoplatanus*, Quercus rubra*, Sorbus aucuparia*	Pinus sylvestris, Corylus avellana, Tilia europaea, Acer platanoides, Amelanchier lamarckii, Prunus serotina, Carpinus betulus, Ilex aquifolium*, Castanea sativa*, Sorbus aucuparia*, Quercus robur	Pinus sylvestris, Prunus serotina, Pinus sylvestris, Quercus robur	Prunus serotina, Pinus sylvestris, Quercus robur	Pinus sylvestris, Quercus robur, Prunus serotina, Betula pendula, Sorbus aucuparia	Prunus serotina, Pinus sylvestris, Acer pseudoplatanus*, Rubus fruticosus*, Ilex aquifolium*
Average tree age		65	50	50	37	50	50	70	40	60	50
Land use before forest		Heathland (until 1712)		Heathland (until 1777) Agriculture (1979–1990)		Heathland (until 1777)		Heathland (until 1955)		Heathland (until 1927) Extensive agriculture (until 1954)	

powder extraction followed by hand sorting a 30 × 30 × 25 cm soil subset (Valckx et al., 2011). The earthworms were stored in ethanol and determined to species level (Sims and Gerard, 1999; Valckx et al., 2009).

Within each plot, three soil samples of the combined OF, OH and 0–10 cm mineral soil layer were taken for mesofauna extraction, using a Tullgren funnel with 3 mm gauze. The mesofauna were then stored in 70% ethanol and identified (Macfadyen, 1961).

2.3. Laboratory analyses

2.3.1. Soil biota determination

The count and biomass was determined for anecic, endogeic, epigeic and epianecic earthworms. Anecic earthworms were absent. Juvenile worms were classified separately. The identification was done according to Tilling (2014) and Wheater and Read (1996).

2.3.2. Incubation experiment

As a proxy for microbial activity, an incubation experiment was performed (Creamer et al., 2014; Dettmann et al., 2021; Zornoza et al., 2007). Respiration measurements were conducted for the O-layer, 0–10 cm and 10–20 cm mineral soil. The soil samples were sieved through 2 mm and soil moisture was determined. 100 g of dried soil was weighed into jar. Prior to emission measurements, the soil was rewetted until 60% of the total pore volume was filled with water, followed by an incubation for 2 weeks at 25 °C. Next, the jars were closed and CO₂ measurements were done at day 1, 2, 3 and 4 using a PBI Dansensor CheckPoint II. After day 4, the lids were opened and 24 h before the next measurement they were closed again. The CO₂ concentration was measured again on day 8, 11, 15 and day 18.

2.3.3. Soil analyses

Soil samples and bulk density samples were oven dried at 40–45 °C. A subset of the soil samples was homogenised by milling.

Total C and N content was measured by dry combustion with an elemental analyser (Flash 2000, Thermo Fisher Scientific, Waltham, MA, USA, ISO 10694). pH and EC were measured in 1:5 ratio soil:demi water (HI 991000 pH sensor). The cation exchange capacity (CEC) was measured according to the ISO 23470 standardised protocol using an extraction with cobalt hexamine (Co[NH₃]₆Cl₃) on 20 g of soil. The concentration of Co, Ca, K, Na and Mg were measured using Inductively Coupled Plasma-Optical Emission Spectrophotometry (ICP-OES, Varian 720-ES, Varian Inc.). Base saturation (BS) was calculated based on the CEC and base content.

2.3.4. SOC fractions

Mineral soil samples (<2 mm) were used for density fractionation and followed an adaptation of the protocol of Zimmermann et al. (2007). This resulted in three fractions: particulate organic matter (POM), silt and clay (s + c) and sand and stable aggregates (S+A). 150 ml of demi-water was added to 30 g of soil and was disrupted with an intensity of 22 J ml⁻¹ to break down the aggregates, followed by wet-sieving over 63 µm. The fraction < 63 µm was filtered over 45 µm and the fraction > 45 µm was dried (s + c). The fraction > 63 µm was subjected to a density fractionation using a sodium polytungstate (SPT) solution with a density cut-off of 1.8 g cm⁻³. The light fraction was classified as POM, and the heavy fraction was classified as S+A and both fractions were rinsed and filtered with demi water to remove excess SPT. Total C % of the POM, S+A and s + c fractions is measured using a ThermoFisher Scientific elemental analyser (Flash 2000). Relative abundances of the fractions were calculated based on the weight per fraction and the total weight of all fractions combined.

Using the %C analysed for the bulk soil and the different SOC fractions and their relative mass percentage, the relative amount of C in the fraction was calculated based on the % TOC. The POM was assigned to represent the labile fraction of OM and the S+A fraction and s + c fractions are considered a stable fraction (Lehmann et al., 2020).

Dividing the stable over the labile fraction provides a stability factor that was used in the data interpretation to determine the C persistence (Desie et al., 2019).

2.3.5. Pyrolysis-GC/MS

In order to determine the chemical composition of the SOM the bulk topsoil (0–10 cm) samples were analysed using a multi-shot furnace pyrolyzer, coupled to a Thermo Scientific (Milan, Italy) Trace 1300 Gas Chromatograph and an ISQ Mass spectrometer (Milan, Italy). The samples were introduced to a Rxi-1MS fused silica column (Restek, 30 m x 0.25 mm ID x 0.50 µm DF) coated with 100% di-methyl poly-siloxane. Between 1 mg and 2.5 mg soil was used, depending on the soil C%. The pyrolysis temperature was set at 600 °C, and held for 0.10 min. The sample was introduced in the GC with helium as the carrier gas, with a temperature of 50 °C for 1 min, with an increase of 7 °C min⁻¹ until 320 °C is reached and held for 10 min, resulting in a total measurement time of 50 min. The GC was coupled to a Thermo Scientific ISQ 7000 Single Quadrupole MS (Italy) (*m/z*: 40–500; ionization energy: 70 eV), with the injection temperature set at 250 °C (split mode: 1:100). The identification of the pyrolysis products was done based on the retention time and mass spectra (NIST MS search 2.3 library v17). This resulted in a list of 123 identified compounds. Peak integration was checked manually, using the Chromeleon Chromatography Studio software (Thermo Scientific, USA), and identified based on the selection of a quantifying ion and one confirming ion (Table S2, Supp.). For each sample, peak areas of the quantifying ions of all 123 pyrolysis products were summed and set at 100%, resulting in a semi-quantitative relative amount of each individual pyrolysis product. Pyrolysis compounds were grouped according to their structural similarity largely following Brock et al. (2020) and Schellekens et al. (2017) and include aliphatic compounds (Al), benzenes (B), lignins (Lg), N-containing compounds (N), polyaromatic hydrocarbons (PAH), phenols (Ph) and polysaccharides (Ps).

2.4. Statistical analyses

Data analysis and visualisation were done using R studio (v4.3.4.). Pairwise comparison between pine-control and pine-converted plots was done graphically for each site (e.g. Figs. 2–5,8,9, right) and across all sites (e.g. Figs. 2–5,8,9, left) using linear mixed modelling (LMM), with site as a random factor (Variable X ~ conversion + (1 | Site), Table S1 Supp.). These linear models were made for forest floors, physicochemical properties, total carbon and carbon fractions. Residuals of the LMM (fitted–observed responses) were checked for normal distribution. Soil faunal data were evaluated using PERMANOVA (vegan package), with Hellinger transformation on the data (count data), followed by the SIMPER analysis. To account for the spatial variation the PERMANOVA was performed using Site + Conversion. To evaluate and visualise variation in mesofauna and pyrolysis-GC/MS data multivariate analyses (PCA) were executed (Fig. 6 and 10). Due to the large influence of Levoglucosan and Hentriacontane in the pyrolysis-GC/MS data (Fig. S3 Supp.), these compounds have been removed from the analysis to better visualise the trends. This did not affect the conclusions.

3. Results

3.1. Overstory

Total basal area in the pine-control plots consisted of 76% poor litter quality tree species dominated by *Pinus sylvestris* and 24% rich litter species. In the pine-converted plots 26.5% of the overstory was composed of poor litter quality tree species, and 73.5% of rich litter species (Fig. 2, Table 1).

3.2. Soil and forest floor properties

A significant difference between the control and converted plots was

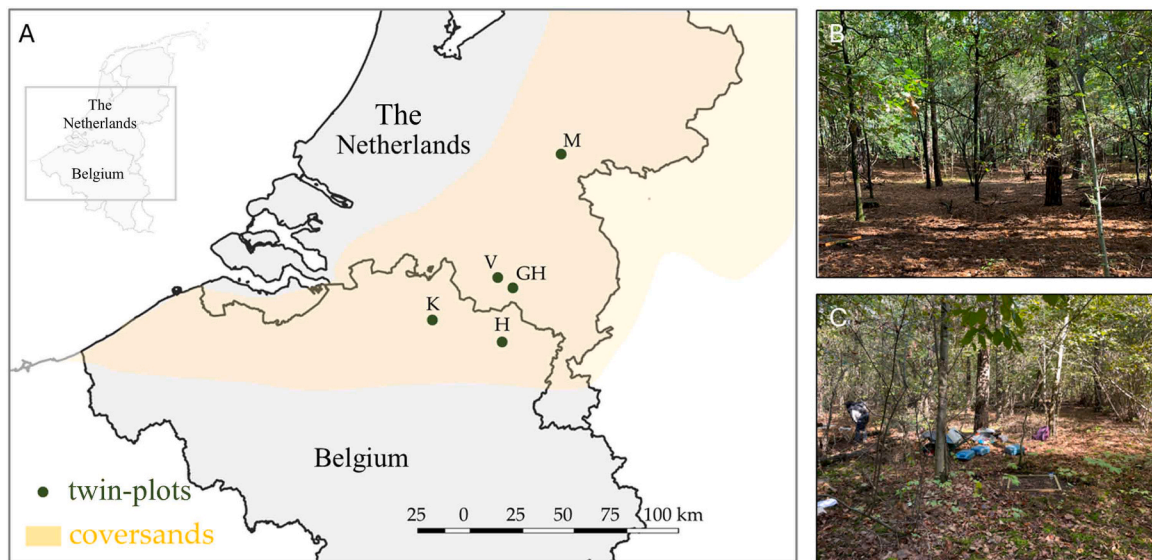


Fig. 1. A: Locations of twin-plots in the Netherlands and Belgium, located on tertiary cover sands (yellow band). GH = Groote Heide, H = Hechtel-Eksel, K = Kasterlee, M = Maashorst, V = Veldhoven. B: Control pine plot in Kasterlee. C: Converted pine plot in Kasterlee.

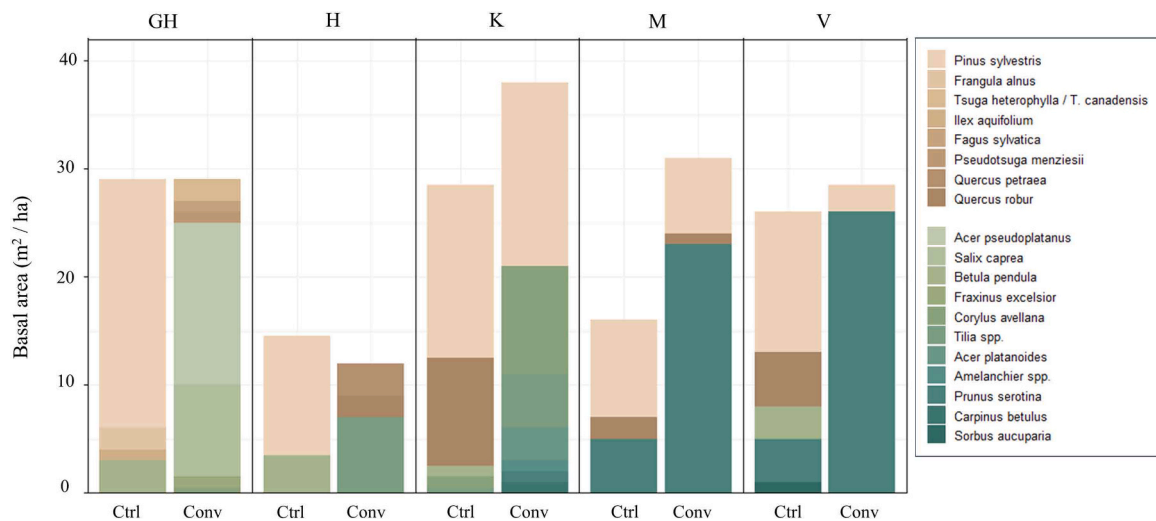


Fig. 2. Overstory tree species composition. Brown represents poor litter quality tree species, green represents rich quality tree species. Expressed in basal area (m²/ha). Abb: GH = Groote Heide, H = Hechtel-Eksel, K = Kasterlee, M = Maashorst and V = Veldhoven, Ctrl = Pine-control and Conv = Pine-converted.

observed in the forest floor, with a mean forest floor thickness of 8.2 cm for the pine-control plots and 4 cm for pine-converted plots ($p < 0.05$) (Table 2; Fig. 3).

The mean pH (water) in the O-layer of the pine-converted plots was higher (5.43) than in the pine-control plots (3.82) (Table 2). In the topsoil and subsoil the pine-converted plots also had a higher mean pH as compared to pine-control plots (4.96 vs 4.51, and 5.18 vs 4.33 respectively). The mixed linear model with site as a random effect showed a significant difference in pH between control and converted in the O-layer ($p < 0.05$), a marginally significant difference ($p = 0.09$) between twin-plots in the topsoil and a significant difference ($p < 0.05$) between twin-plots in the subsoil.

The mean base saturation was also higher in the pine-converted plots than in the pine-control plots (respectively 30.1 vs 19.3 for the topsoil and 18.7 vs 10.0; Table 2). No significant difference in base saturation between the pine-control and pine-converted plots were found in both the topsoil ($p = 0.38$) and the subsoil ($p = 0.28$). However, large differences in base saturation between different forest plots were observed (Fig. 4).

The mean values of CEC in the topsoil for pine-control plots 5.24 $\text{cmol}_c \text{kg}^{-1}$ and for pine-converted plots was 7.29 $\text{cmol}_c \text{kg}^{-1}$, and in the subsoil the mean CEC value was 4.45 $\text{cmol}_c \text{kg}^{-1}$ in pine-control plots and 4.65 $\text{cmol}_c \text{kg}^{-1}$ in pine-converted plots (Table 2). No significant differences were found in CEC between the topsoil ($p = 0.24$) and the subsoil ($p = 0.89$).

No significant difference in the bulk density (Table 2) between the topsoil (pine-control vs pine-converted) ($p = 0.87$) and the subsoil ($p = 0.78$) was found.

3.3. Biota

3.3.1. Soil fauna

The total biomass of earthworms in the pine-converted plots (33.9 g) was markedly higher than in the pine-control plots (15.7 g, Fig. 5), however this difference is not significant ($p = 0.31$). The epigeic earthworms showed a marginally significant higher biomass in the pine-converted plots ($p = 0.09$). Variation among sites is high, especially for epi-anecic earthworms in the pine-converted plots. No earthworms were

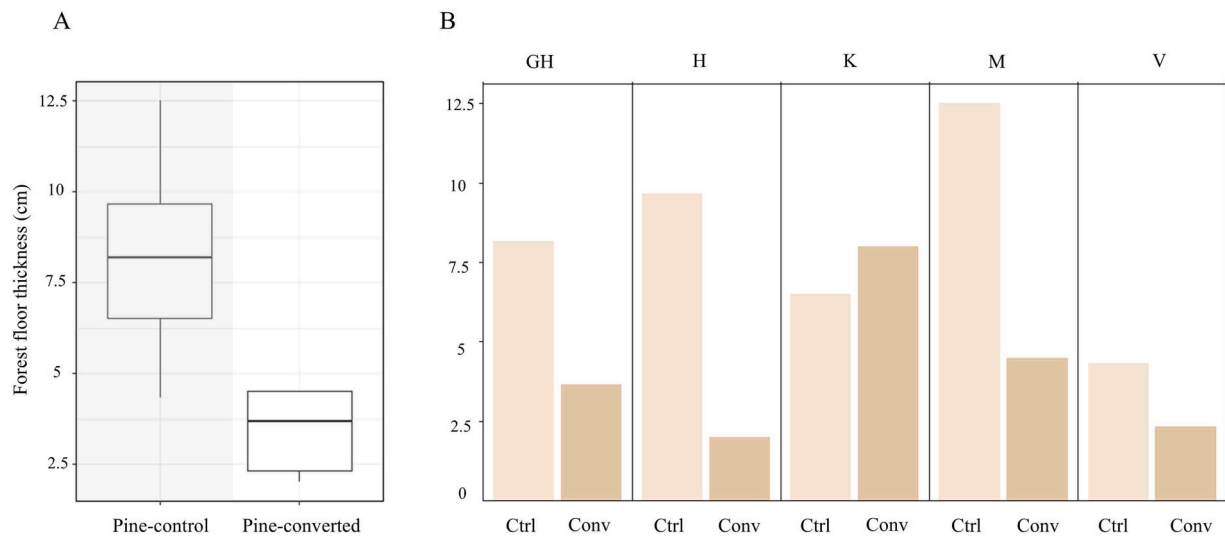


Fig. 3. Forest floor thickness. A shows pooled data in boxplots (mean, quartiles and range) of pine-control and pine-converted plots ($n = 5$). Panel B shows bar plots of the individual values for each plot ($n = 1$). Abb: GH = Groote Heide, H = Hechtel-Eksel, K = Kasterlee, M = Maashorst and V = Veldhoven, Ctrl = Pine-control and Conv = Pine-converted.

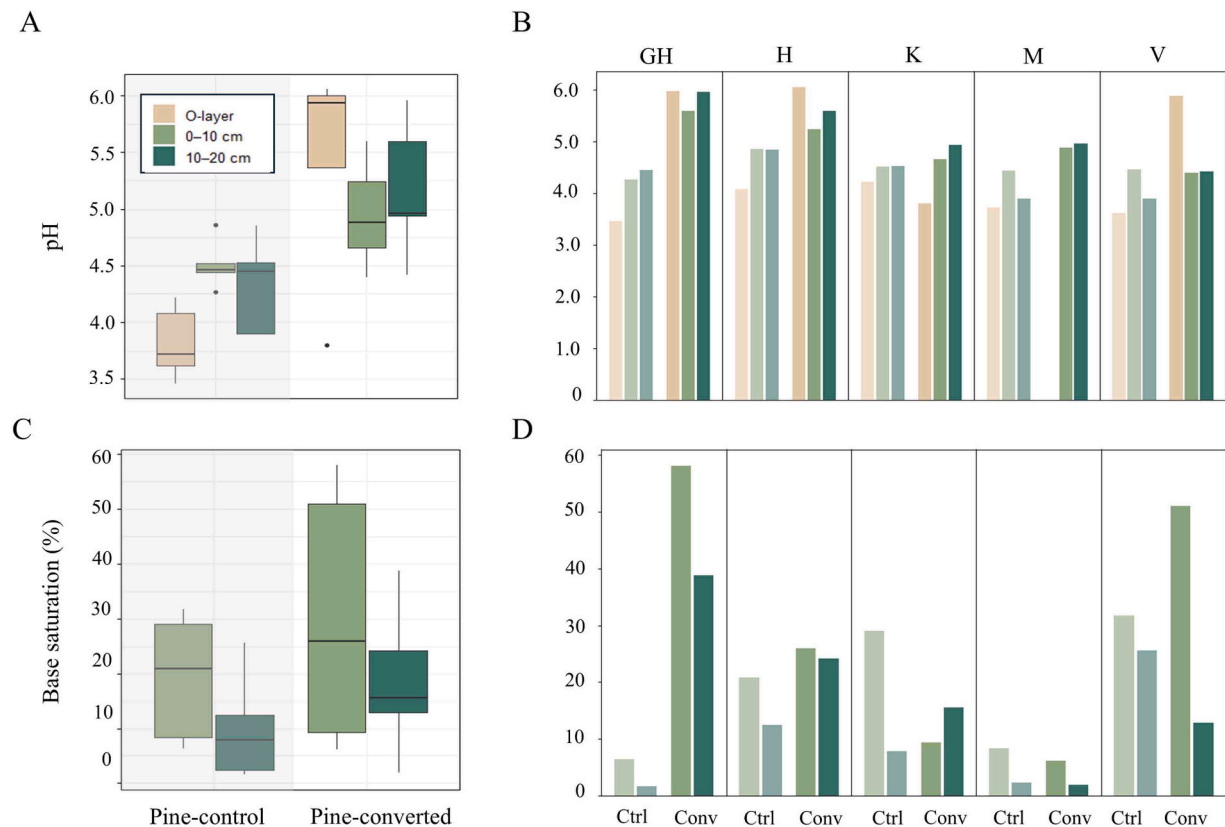


Fig. 4. pH water (top) and base saturation (%) (bottom) of the organic layer (light beige), 0–10 cm (mid green) and 10–20 cm mineral soil (dark green) showing differences between pine-control (grey box - left) and pine-converted plots (white box - right). Panels A and C illustrate the pooled data in boxplots (median, quartiles and range) whereas panels B and D show bar plots of the individual values for each plot. Abb: GH = Groote Heide, H = Hechtel-Eksel, K = Kasterlee, M = Maashorst, V = Veldhoven, Ctrl = Pine-control and Conv = Pine-converted.

found in both the converted and pine-control plots of the Maashorst, and in Groote Heide pine-control.

The mesofauna species abundance (Fig. 5) was corrected for the forest floor thickness and expressed as the amount per volume showing the relative abundance per volume. Mesofauna species abundance per area can be found in Supp. Fig. S1. A PERMANOVA showed a significant

difference in mesofauna community composition between pine-control and pine-converted plots ($p = 0.033$), with no significant effect of site ($p = 0.151$). In terms of volume, there was a slightly higher abundance of mesofauna in converted plots compared to control plots, though not significant ($p = 0.4$), whereas if abundance is expressed per surface area the reverse significant difference was found ($p = 0.01$). In the pine-

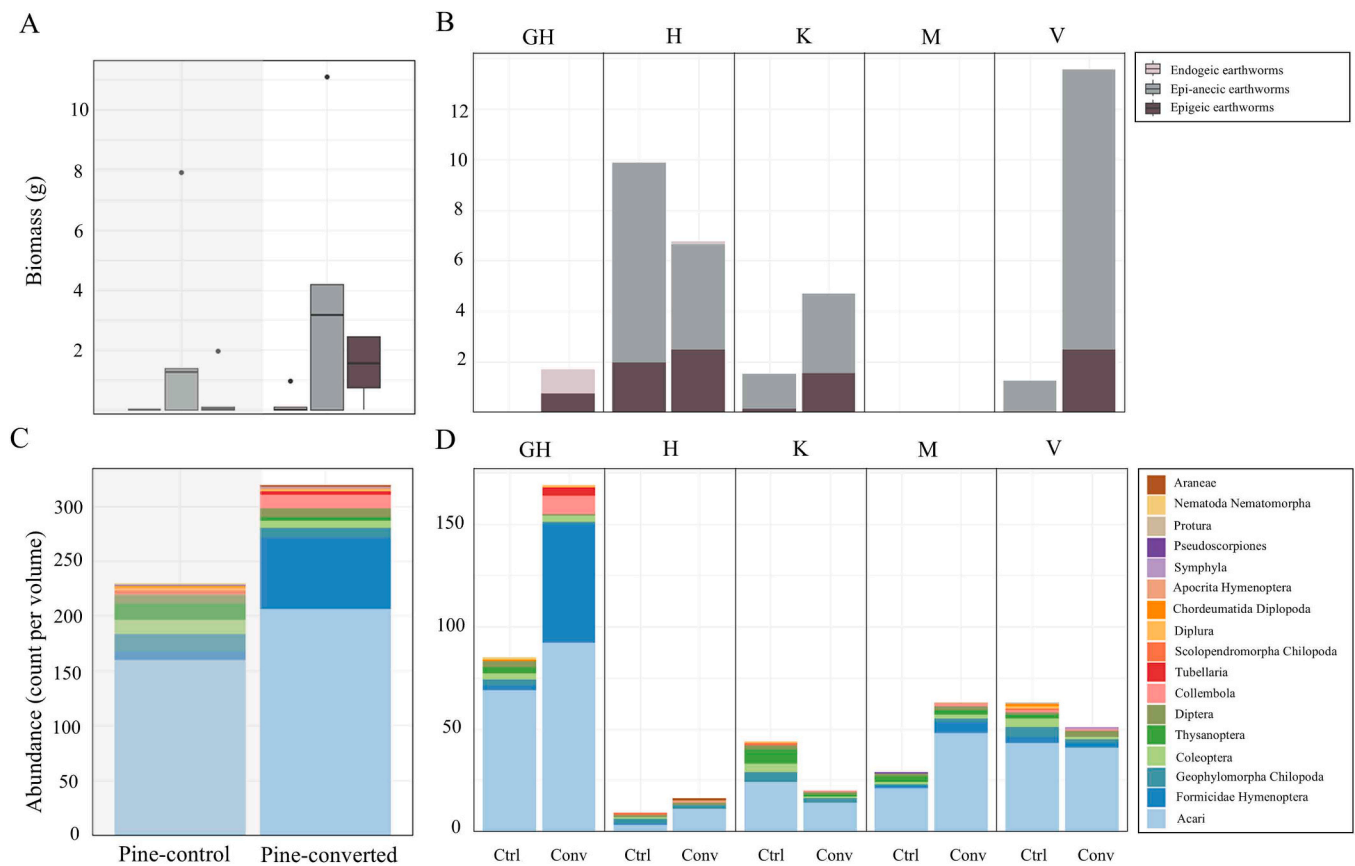


Fig. 5. Earthworm biomass (top) and mesofauna abundance (bottom). Panel A shows pooled data in boxplots (median, quartiles and range) of the earthworm biomass grouped in ecological groups ($n = 15$). Panel B and D show bar plots of the individual earthworm biomass (B) and mesofauna abundance (D) per plot ($n = 3$). Mesofauna per volume is used, which is corrected for the humus thickness. Panel C shows the pooled total abundance of mesofauna. Abb: GH = Groote Heide, H = Hechtel-Eksel, K = Kasterlee, M = Maashorst and V = Veldhoven, Ctrl = Pine-control and Conv = Pine-converted.

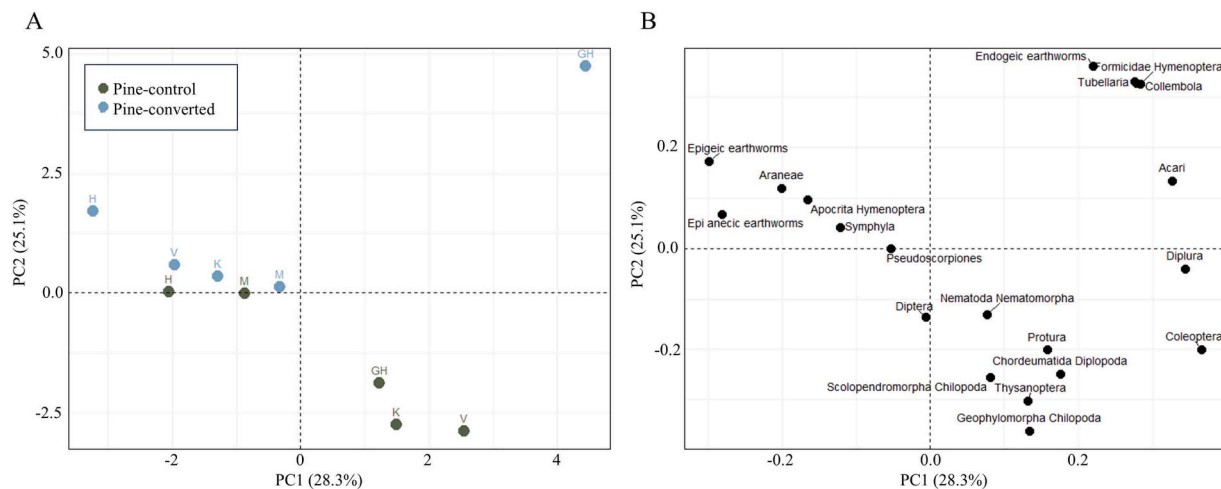


Fig. 6. Principle component analysis of the mesofauna and earthworms counts in pine-control (dark grey) and pine-converted plots (light blue). A. Scores of PCA. B. Loadings of PCA. Abb: GH = Groote Heide, H = Hechtel-Eksel, K = Kasterlee, M = Maashorst, V = Veldhoven.

converted plot of Groote Heide a relative large abundance of mesofauna was found, mainly due to the high amounts of Formicidae Hymenoptera and Acari present. In Kasterlee the mesofauna abundance was higher in the pine-control plots with more Diptera, Thysanoptera and Coleoptera. More Formicidae hymenoptera as well as Acari were found in the pine-converted plot of the Maashorst compared to the pine-control plot. Pseudoscorpiones were only present in the pine-control plot in

Maashorst. The mesofauna taxonomic richness per area in the pine-control plots ranged between 11 and 13 (median = 11), and for the pine-converted plots this ranged between 5 and 12 (median of 10, $p = 0.21$). The mean Shannon diversity index (based on taxonomic groups) of the pine-control plots was 1.34 and for the pine-converted plots it was 1.05. When corrected for the forest floor thickness and expressed as count per volume, the taxonomic richness in the pine-

Table 2

Physico-chemical data for each plot. (n = 1 per site). On the left the values are shown for pine-control plots, and on the right for pine-converted plots.

		<i>Pine-control</i>						<i>Pine-converted</i>					
		Groote Heide (NL)	Hechtel-Eksel (BE)	Kasterlee (BE)	Maashorst (NL)	Veldhoven (NL)	Mean	Groote Heide (NL)	Hechtel-Eksel (BE)	Kasterlee (BE)	Maashorst (NL)	Veldhoven (NL)	Mean
Bulk Density [g/cm ³]	0–10 cm	0.90	0.90	1.05	1.25	1.25	1.07	1.05	1.40	1.10	1.05	0.85	1.09
	10–20 cm	0.80	1.25	1.45	1.25	1.40	1.23	1.30	1.45	1.05	1.10	1.05	1.19
Humus thickness [cm]	OL	1.0	3.0	1.0	1.3	0.8	1.4	1.3	1.0	1.2	1.0	1.0	1.1
	OF	7.2	6.3	1.3	11.2	2.5	5.7	2.3	1.0	3.3	2.5	1.0	2.0
pH [H ₂ O]	OH	0.0	0.3	4.2	0.0	1.0	1.1	0.0	0.0	3.5	1.0	0.3	1.0
	O	3.5	4.1	4.2	4.4	3.6	4.0	6.0	6.1	3.8	- ^a	5.9	5.5
	0–10 cm	4.3	4.9	4.5	4.4	4.5	4.5	5.6	5.2	4.7	4.9	4.4	5.0
	10–20 cm	4.5	4.9	4.5	3.4	3.9	4.3	6.0	5.6	4.9	5.0	4.4	5.2
BS %	0–10 cm	6.4	20.9	29.0	8.4	31.8	19.3	58.0	26.0	9.4	6.2	51.0	30.1
	10–20 cm	1.6	12.4	7.8	2.4	25.6	10.0	38.8	24.2	15.5	1.9	12.9	18.7
CEC	0–10 cm	5.73	6.71	3.99	4.20	5.56	5.24	6.48	5.56	12.51	3.56	8.34	7.29
	10–20 cm	5.97	4.54	4.32	5.94	1.50	4.45	8.85	2.36	1.73	4.61	5.68	4.65
Total C%	O	48.88	32.44	49.88	47.29	38.64	43.43	13.60	21.07	47.9	- ^a	39.62	30.55
	0–10 cm	4.59	4.59	1.62	3.43	2.57	3.36	2.21	1.58	1.50	2.40	4.41	2.42
Total N%	10–20 cm	1.96	1.95	< 0 ^b	3.55	2.20	1.93	1.25	0.64	< 0 ^b	2.52	1.42	1.17
	O	1.44	0.86	1.57	1.78	1.66	1.46	0.54	0.64	1.57	NA	1.38	1.03
	0–10 cm	0.17	< 0 ^b	0.06	< 0 ^b	0.09	0.11	0.12	0.12	0.05	0.12	0.17	0.12
	10–20 cm	< 0 ^b	0.14	< 0 ^b	0.13	0.07	0.11	< 0 ^b	< 0 ^b	< 0 ^b	0.12	0.08	0.1
OM fractions Topsoil (0–10 cm) ^c	POM%	0.3 / 2.6	1.2 / 14.3	0.8 / 16.7	0.6 / 7.5	0.5 / 7.6	0.7 / 9.7	0.3 / 4.8	0.4 / 8.4	0.4 / 15.7	0.3 / 4.9	0.8 / 4.4	0.4 / 7.6
	S+A%	79.7 / 58.9	78.7 / 45.8	91.2 / 37.0	93.4 / 30.2	77.8 / 51.9	84.2 / 44.8	81.1 / 52.4	81.1 / 32.0	94.8 / 41.3	92.0 / 36.7	85.8 / 75.3	86.9 / 47.5
	s + c%	20.0 / 38.4	20.1 / 39.8	8.0 / 46.3	6.1 / 62.3	21.6 / 40.5	15.2 / 45.5	18.7 / 42.8	18.5 / 59.6	4.8 / 43.0	7.7 / 58.4	13.5 / 20.3	12.6 / 44.8
	POM%	0.1 / 1.5	0.4 / 10.3	0.1 / 9.6	0.3 / 4.7	0.2 / 4.9	0.2 / 5.3	0.1 / 4.5	0.1 / 3.6	0.1 / 5.5	0.2 / 4.0	0.1 / 0.9	0.1 / 3.7
OM fractions Subsoil (10–20 cm) ^c	S+A%	77.9 / 43.4	79.8 / 26.5	94.2 / 12.5	94.1 / 36.7	80.7 / 48.3	85.3 / 33.5	76.0 / 28.9	81.6 / 23.1	95.4 / 36.7	91.6 / 21.8	75.1 / 36.0	83.9 / 29.3
	s + c%	21.9 / 55.1	19.8 / 63.2	5.8 / 77.9	5.6 / 63.6	19.2 / 46.8	14.5 / 61.3	23.9 / 66.6	18.4 / 73.3	4.5 / 57.8	8.1 / 74.2	24.8 / 63.1	15.9 / 67.0

^a No O-horizon present^b Measurement below detection limit^c First value shows the relative abundance in weight, second value the % C in the fraction of the TOC.

control plots ranged between 6 and 11 (median = 7) and in the pine-converted plots between 5 and 8 (median = 7, $p = 0.56$) and the mean Shannon diversity index of the pine-control plots was 1.25 and for the pine-converted plots 1.01 (Table S2, Supp.). The SIMPER analysis showed that *Acari* contributed most to the observed differences (~59.5%), although with high within-group variability ($p = 0.886$). *Scolopendromorpha* were present only in pine-control plots and absent in rich ones ($p = 0.066$), suggesting a potential indicator of litter quality.

A principle component analysis applied to the mesofauna dataset (PCA; Fig. 6) explains 53.4% of variance with 28.3% and 25.1% for PC1 and PC2, respectively. Most pine-converted plots are situated in the second quadrant, with negative scores on PC1 and positive scores on PC2 (Fig. 6A), indicating a higher relative abundance of epigeic and epianecic earthworms and spiders (Fig. 6B). The converted stand at GH is an outlier, due to high abundance of Formicidae Hymenoptera, Turbellaria, Collembola and endogeic earthworms. Pine-control plots typically have more negative scores on PC2, indicating a relatively lower abundance of ants and earthworms and higher abundance of centipedes and millipedes, especially for Groote Heide (GH), Kasterlee (K) and Veldhoven (V; Fig. 5 & 6). Species with low abundance cluster together in the fourth quadrant with positive scores on PC1 and negative scores on PC2, and seem not directly influenced by forest type.

3.3.2. Soil microbes

Soil respiration was measured as a proxy for soil microbial activity (Fig. 7). The average respiration of the pine-control plots in the O-layer was $15.35 \mu\text{g C day}^{-1}$ (se = 2.58), with a mean cumulative respiration on day 18 of $234.8 \mu\text{g C g}^{-1}$ soil. The average respiration of the O-layer in the pine-converted plots was 23.33 (se = 3.3) $\mu\text{g C g}^{-1}$ soil per day with a mean cumulative respiration of $350.8 \mu\text{g C g}^{-1}$ soil on day 18. Although not significant, a trend in elevated respiration in the pine-converted plots is observed on day 18 ($p = 0.17$) compared to the pine-control plots in the O-layer. The topsoil (0–10 cm) had an average of 7.67 (se = 1.35) $\mu\text{g C day}^{-1}$ for the pine-control plots and an average of $9.98 \mu\text{g C day}^{-1}$ (se = 2.2) for the pine-converted plots. The pine-converted plots had marginally significantly higher cumulative respiration at day 18 ($p = 0.06$) in the topsoil. In the subsoil layers (10–20 cm), the average respiration in the pine-control plots was $4.14 \mu\text{g C day}^{-1}$ (se = 0.19) and the average respiration in the pine-converted plots was $3.84 \mu\text{g C day}^{-1}$ (se = 0.34). In the subsoil layers

the cumulative respiration only marginally increased with time and no influence of litter type was found ($p = 0.78$).

3.4. Soil carbon stocks and stability factor

No significant difference in total %C in the O-layer between the pine-control and pine-converted plots was found ($p = 0.16$, Table 2). In the topsoil a marginally significant difference ($p = 0.09$) between the pine-control and pine-converted plots was found. In the subsoil this difference between pine-control and pine-converted was not significant ($p = 0.19$). No significant difference between the pine-control and pine-converted plots were found of the total %N in the O-layer ($p = 0.12$), in the topsoil ($p = 0.8$) and in the subsoil ($p = 0.7$, Table 2).

The mean C stock in the O-layer in the pine-control plots was $145.2 \text{ ton ha}^{-1}$ and the mean C stock in the pine-converted plots was 53.4 ton ha^{-1} , and this difference is marginally significant ($p = 0.06$). The mean C stock in the topsoil in the pine-control plots was 26.8 ton ha^{-1} and in the pine-converted plots 24.1 ton ha^{-1} and not significantly different ($p = 0.6$). In the subsoil this is 29 ton ha^{-1} in the pine-control plots and 17.2 ton ha^{-1} in the pine-converted plots and not significantly different ($p = 0.2$).

The stability factor did not show significant differences between pine-control and pine-converted plots in the topsoil ($p = 0.87$) and the subsoil ($p = 0.22$), nor did it significantly change with depth. When evaluating the different C fractions, only topsoil C stored as POM differed in between twin-plots: pine-control plots have significantly more topsoil C stored as POM than pine-converted plots ($p < 0.05$). No significant differences between control and converted plots were found for topsoil S+A and s + c fractions or for the subsoil. The distribution of carbon over different factors did change with depth: regardless of conversion, topsoil layers have more C stored in POM fractions whereas subsoil layers have more C stored in S+A and s + c fractions (Fig. 8).

3.5. Molecular composition

The relative abundances of groups of pyrolysis products for the different locations are presented in Fig. 9. The pine-control plots showed a larger heterogeneity in molecular composition over the different locations than the pine-converted plots, especially in aliphatic compounds, where the latter were more homogenous (Fig. 9). The relative

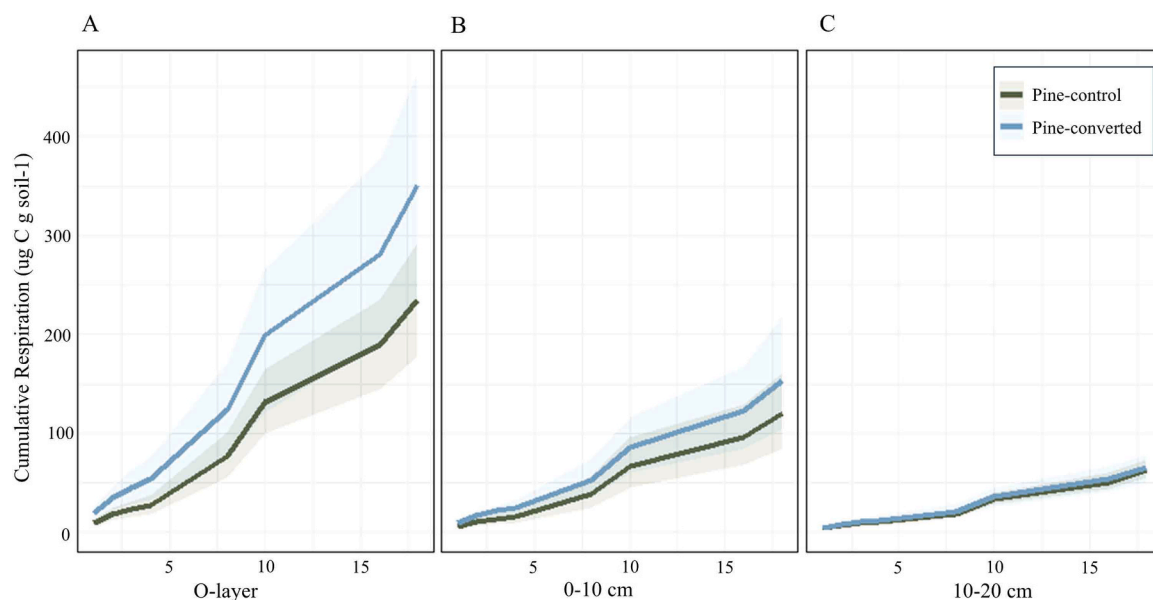


Fig. 7. Cumulative respiration [$\mu\text{g C g}^{-1}$ soil] of the organic layer (A - left), 0–10 cm (B - middle) and 10–20 cm (C - right) of the mineral soil over 18 days. Bold lines represent averages of respectively pine-control (dark grey) and pine-converted plots (light blue). Shaded area represents the 95% confidence interval.

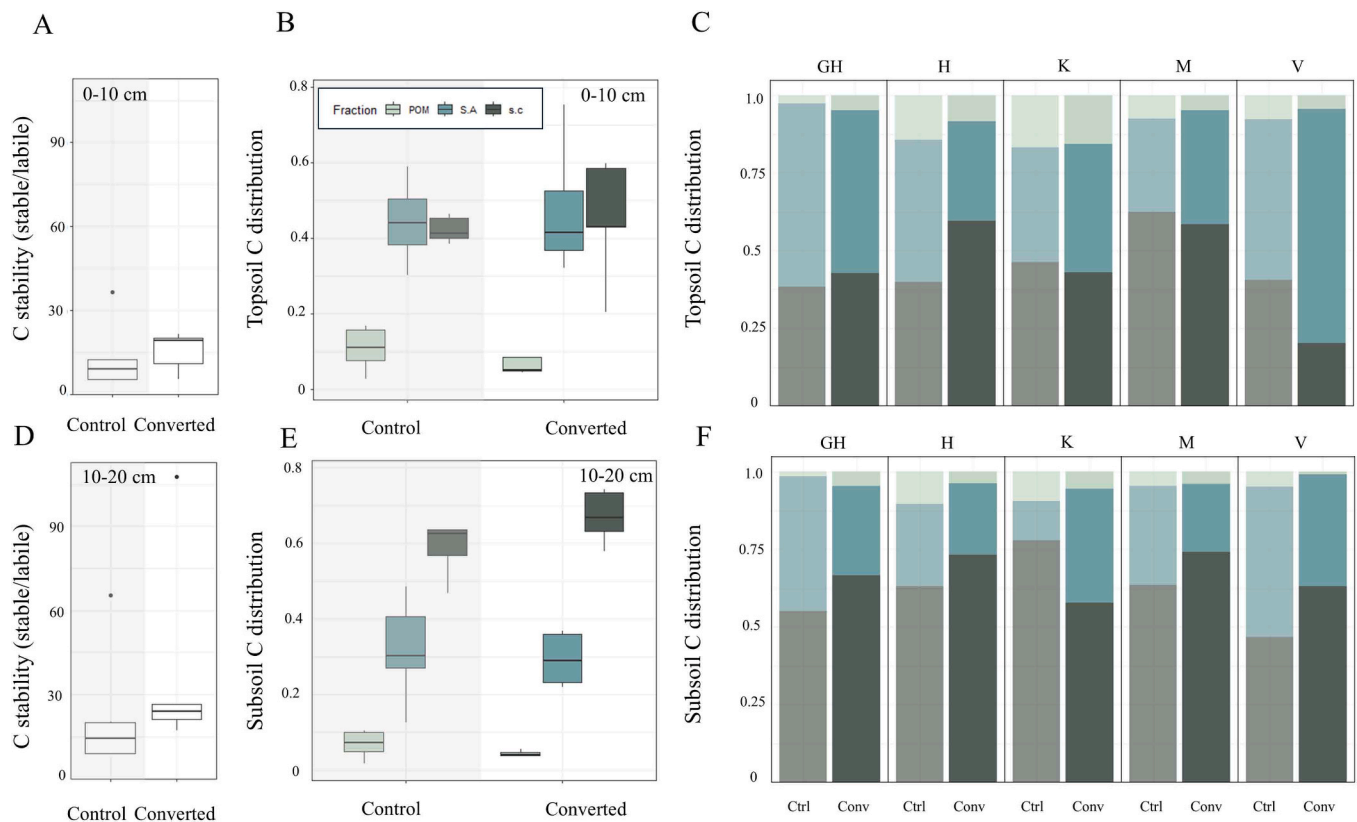


Fig. 8. Stability of C (left, A+D), Proportion of C in the SOC fractions (middle, B+E) and TOC and its distribution in the different twin-plots (right, C+F) for pine-control and pine-converted plots for topsoil (0–10 cm) (top) and subsoil (10–20 cm) (bottom) layers. Carbon fractions are, divided in particulate organic matter (POM, light green), sand and stable aggregates (S+A, green) and silt and clay (s + c, dark green) and are expressed as % of the total soil C. The carbon stability factor is calculated based on the division of carbon in stable (S+A+s + c) and labile (POM) fractions. Abb: GH = Groote Heide, H = Hechtel-Eksel, K = Kasterlee, M = Maashorst and V = Veldhoven, Ctrl = Pine-control and Conv = Pine-converted.

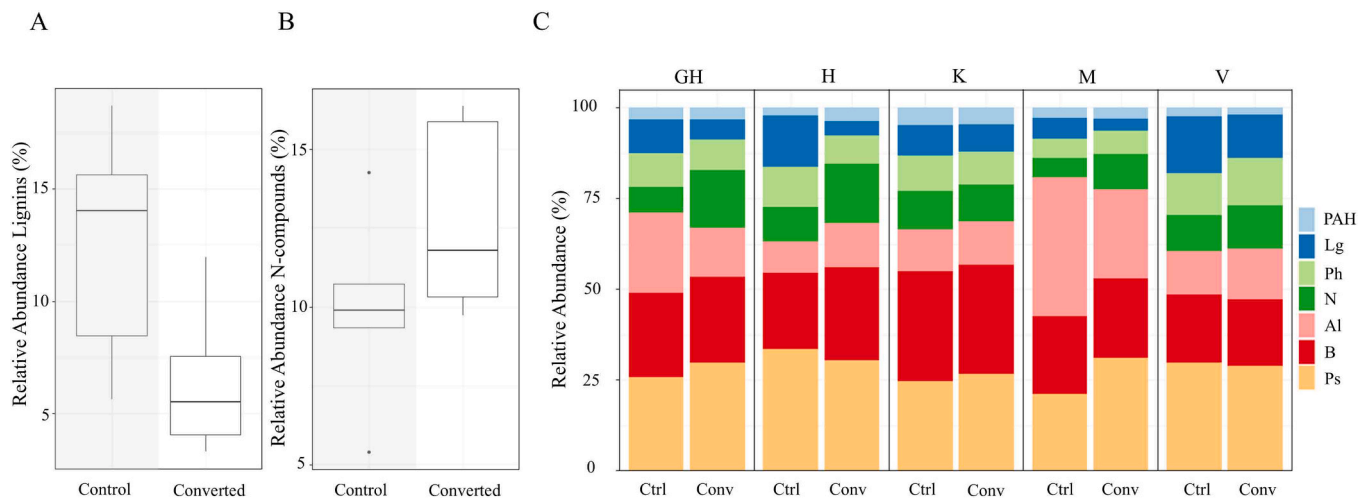


Fig. 9. Relative abundance of groups of pyrolysis products in topsoil (0–10 cm) bulk sample. A and B. Pooled relative abundance of Lignins (A) and N-compounds (B) shown in boxplots (median, quartiles and range). Panels C and D shows bar plots of the relative abundance of pyrolysis products for each plot. Abb: GH = Groote Heide, H = Hechtel-Eksel, K = Kasterlee, M = Maashorst, V = Veldhoven, Ctrl = Pine-control and Conv = Pine-converted. Chemical groups: Al = Aliphatic compounds, B = Benzenes, Lg = Lignins, N = Nitrogen containing compounds, PAH = Polyaromatic hydrocarbons, Ph = Phenols, Ps = Polysaccharides.

abundance of lignin components showed a strong trend (marginally significant, $p = 0.06$) towards being higher in pine-control plots than in the pine-converted plots. In the pine-converted plots the relative abundance of N-containing compounds showed a strong trend (marginally significant, $p = 0.06$) of being higher than in the pine-control plots.

A principal component analysis (PCA) visualises the relative spread

of the pyrolysis products (Fig. 10 A). The PCA explained 71% of the total variation. Most pine-converted plots grouped together with negative scores on PC1, with Veldhoven (V) as an exception. When comparing to the loadings plot (Fig. 10B), this infers a high relative abundance of low molecular weight (LMW) polysaccharides, N-containing compounds and benzenes, as opposed to lignins and levosugars. The pine-control plots

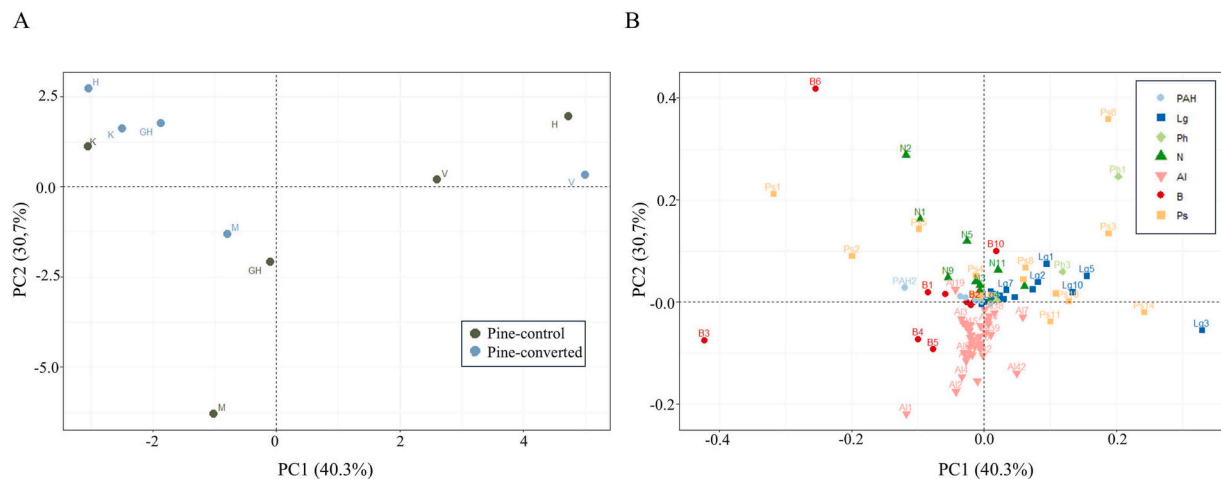


Fig. 10. Projection of PC1 and PC2 of a principle component analysis applied to the pyrolysis products (excl. Hentriacontane and Levoglucosan) of bulk soil in topsoil samples (Table S4 Supp.). Left shows scores of PCA, right shows loadings of PCA. GH = Groote Heide, H = Hechtel-Eksel, K = Kasterlee, M = Maashorst, V = Veldhoven. Chemical groups: Al = Aliphatic compounds, B = Benzenes, Lg = Lignins, N = Nitrogen containing compounds, PAH = Polyaromatic hydrocarbons, Ph = Phenols, Ps = Polysaccharides.

show more variation, with strongly positive scores on PC1 for Veldhoven (V) and Hechtel-Eksel (H), and negative scores on PC2 for Maashorst (M) and Groote Heide (GH) indicative for a higher relative abundance of aliphatic compounds. Kasterlee (K) and Veldhoven (V) differ from the general trend.

4. Discussion

4.1. Scope of the research

Our reconnaissance study integrates a wide spectrum of carbon-related compartments, spanning inputs (forest tree species composition and litter quality) through decomposer communities to actual soil organic C outcomes, including stocks, fractions, and molecular composition, over different soil depths. Despite the limited scope of five sites and ten plots and a relatively short time since conversion (< 50 years), we could infer a consistent shift in processes, with different compartments and soil depths reacting to the change in overstory species at different intensities, thereby supporting our hypothesis. Hence, we demonstrated that the contrast between pine monocultures and converted forests with rich litter admixture goes beyond soil acidity and chemistry (pH and BS, Fig. 4), and affects soil community composition (Figs. 5, 6) and SOC and SOM dynamics (Fig. 7–10). While the observed hypotheses have been discussed in literature (Angst et al., 2023; Desie et al., 2021) and individual relationships have been tested in more extensive datasets (Schelfhout et al., 2017; Verstraeten et al., 2018), the full and complex chain from inputs to C fractionation and molecular composition has rarely been evaluated empirically. This study therefore provides a first, small-scale pilot assessment, highlighting patterns that merit further mechanistic investigation in larger, more detailed studies.

The sites included in this study were selected in close collaboration with local forest managers and are well known by the authors, ensuring both practical relevance and a representative overview of the region. Selected sites reflect different sandy soil types formed in Pleistocene sandy deposits (ranging from Podzols to Anthrosols), yet all characterised by low acid buffering capacity and located close to a pedogenic threshold in acidity (Desie et al., 2021). Moreover, all plots are low in total C stocks (< 5% TOC in 0–10 cm), representative of forests in the region (De Vos et al., 2015), which we consider excellent to study subtle influences of tree species and legacy. Selected forests reflect real-world interventions, spanning species-poor pine monocultures and mixed broadleaved forests with diverse species composition (Fig. 2). From a design perspective, it is important to note that all pine-converted plots

were mixed forests and all pine-control plots were monocultures (with minor admixture in shrub layers, if any), inherently confounding tree species identity and diversity. Nevertheless, this arrangement directly mirrors in-situ restoration measures implemented by local forest agencies, which aim to convert pine monocultures to mixed broadleaved forests including economically and ecologically important species, such as pedunculate oak, alongside rich litter species to mitigate acidification processes (Desie et al., 2020; Desie et al., 2020). In our exploratory study we deliberately selected a diverse range of rich litter tree species: *Tilia cordata*, *Acer pseudoplatanus*, *Prunus serotina*, *Corylus avellana*, *Carpinus betulus*, and more (Table 1), reflecting the variation present in the region.

4.2. Decomposer communities and forest floor

Our results indicate that earthworms abundance and diversity are promoted by the mixed overstory composition including rich litter tree species (Fig. 5), corresponding to previous studies (De Wandeler et al., 2016; Desie et al., 2020; Reich et al., 2005; Schelfhout et al., 2017). The higher abundance of burrowing (endogeic and epi-anecic) earthworm species and their preference for Ca rich leaf material results in thinner forest floor layers through their bioturbating activity (Fig. 3; Desie, et al., 2020; Jones et al., 2010; Schelfhout et al., 2017). In contrast, mesofauna abundance per area (Fig. S1. Supp.) was higher in pine-control plots, corresponding to the thicker forest floors providing more habitat (Ganault et al., 2021). Accordingly, also the taxonomic richness of the mesofauna community is higher in the pine monoculture plots. When expressed per volume (Fig. 5) this trend is no longer apparent, illustrating the impact of habitat availability. This highlights the feedback loop that earthworms, as ecosystem engineers, exert on the forest floor (more earthworms, less accumulation, more nutrients, higher pH, more earthworms) (Desie, Van Meerbeek, et al., 2020), whereas the engineering impact of mesofauna is less pronounced. Nonetheless, the more abundant and richer mesofauna community in terms of taxonomic diversity in pine monocultures (Table S3. Supp.) with more habitat for predating species (i.e. centipedes and millipedes; Fig. 6) suggests that for belowground biodiversity conservation a balance between broadleaved (rich litter) and pine overstories should be sought. The Formicidae (Hymenoptera) abundance in the converted forest plots in Groote Heide is strikingly higher than in the other plots, suggesting that this sample was taken in close proximity of an ant colony, that are typically spatially patchy.

Overall, we can confirm our hypothesis that pine conversion with

rich litter tree species leads to more earthworm dominated soil communities. This implies that soil communities in rich litter dominated mixed forests could lead to more bioturbation and thus potentially C stabilisation (vide infra). In terms of microbial activity, respiration was higher in the O-layer and topsoil (0–10 cm) of converted (mixed) forest plots than in the control pine monocultures (Fig. 7). Although this difference was not significant it aligns with a faster turnover of OM in broadleaved forests suggested in literature (Desie et al., 2020) and supported by a higher proportion of microbially altered components in the SOM, mainly N-compounds and LMW polysaccharides, and a lower accumulation of POM (Fig. 7–10, see also 4.3.). This may indicate a shift from a slower fungal dominated decomposition in the pine-control plots, to a faster bacterial decomposition in the pine-converted plots (Hammel, 1997).

4.3. Soil chemistry, C stocks and persistence

The effect of rich litter tree species shows a significant effect on soil pH as also described in literature (Van Nevel et al., 2014). Yet, contrary to what has been described for finer-textured soils in literature (Desie et al., 2020), base saturation did not significantly increase and was highly variable in our study. As it remained below or near the critical threshold of 30% for all plots, except for the converted plots at GH and V, this indicates that, in terms of soil acidification, they are still recovering and not (yet) in a base dominated soil process domain (sensu Desie et al., 2021). Furthermore, the overall availability of bases in these systems may be too low to be remediated by a change of overstory species alone (Fig. 2) (Desie et al., 2020).

The lack of response in C stocks and percentages is in line with the current understanding in literature, i.e. that it typically takes much longer before changes become apparent (Cordaro et al., 2025; Mayer et al., 2020) (Fig. 8). The significantly thicker forest floors in pine monocultures (Fig. 3) and significantly higher relative amount of C in the POM fractions are indicative of a slowed C cycle with more bypass and less microbial alteration of the material (more POM) (Angst et al., 2023; Cotrufo et al., 2022). This is supported by the respiration data (Figs. 7 and 8, Fig. S2. Supp. and Section 4.2.), and in either a higher amount of unaltered plant inputs (mainly lignins and levosugars; Fig. 9 and 10) or a higher bypass of aliphatic components (Vancampenhout et al., 2009b; Zhu et al., 2020). Vice versa, the lower amounts of POM and higher respiration in pine-converted plots indicate an increased decomposition and transformation, reflected also in a higher relative abundance of microbially altered compounds (LMW polysaccharides and N compounds, Fig. 9 and 10).

We hypothesised that under mixed broadleaved forest, subsoil C stocks increase due to more bioturbation (corresponding with the earthworm dominated community) (Vesterdal et al., 2013), however we do not find significant differences in C stocks in subsoil layers in our study. This could be a consequence of the limited time since conversion from pine monoculture (most of the mixed broadleaved forests we sampled are not older than 50 years) or the fact that despite a higher abundance of earthworms in converted plots, they were epigeic and epi-anecic species (Vesterdal et al., 2013). This would also indicate that in terms of soil acidification they are still recovering and not (yet) in a base dominated soil process domain (sensu Desie et al., 2021). Although this short period is enough to impact topsoil layers and soil communities (and molecular composition, see Section 4.4.), this is not sufficient to alter total C percentages and stocks as those typically respond slow to restoration (Cordaro et al., 2025).

4.4. Soil OM molecular composition

Contrary to total C stocks or percentages, a shift in soil C decomposition dynamics upon conversion is clearly evidenced in the molecular composition of the organic matter (Fig. 9). The converted plots show a relative accumulation of LMW polysaccharide pyrolysis products and N-

containing compounds are that are associated with higher microbial alteration (negative scores on PC1; Vancampenhout et al., 2009) as opposed to the more intact plant fragments (levosugars and lignins; Schellekens et al., 2009) that have more positive scores on PC1. This is in line with a higher microbial respiration upon conversion (Section 4.2, Fig. 7) (Prescott and Vesterdal, 2021). For the pine-control plots, the molecular composition is more variable, indicative for two contrasting potential mechanisms. Although both are consistent with a slower decomposition, as also evidenced in the respiration (Fig. 7) and accumulation of POM (Fig. 8) (Lavalée et al., 2020; Schellekens et al., 2015), they vary in the nature of the components that remain in the soil. Two of the pine-control plots (in Veldhoven and Hechtel-Eksel) showed higher relative abundances of lignin products, which together with the levosugars (high positive scores on PC1) represent lignocellulose from (relatively intact) plant materials. The abundant understory of grasses and brambles (*Robus fruticosus*) could likewise contribute to a high input of lignocellulose, as also evidenced in the higher relative abundance of 4-vinylphenol (Lg3), an important derivative of grass lignin and considered an indicator for grass-derived organic matter.

Plots in Groote Heide and Maashorst show a contrasting trajectory, with an accumulation of aliphatic compounds rather than lignocelluloses in the SOM—components that are abundant in the cuticular waxes of pine needles (Nierop et al., 2006; Stabentheiner et al., 2004). However, their selective accumulation in the relative absence of lignocellulose compounds represents not merely an accumulation of plant material, but a selective bypass of energy-low, nutrient-poor molecules by specialist communities in coniferous forests with very strong edaphic constraints, such as high aluminum toxicity or very low base saturation (Vancampenhout et al., 2010; Zhu et al., 2020), as was also evidenced in Groote Heide and Maashorst (Table 2). In literature, this phenomenon has also been linked to legacy effects of former heathlands (Vancampenhout et al., 2010; Brock et al., 2019; von Oheimb et al., 2008), which is also the case for Groote Heide and Maashorst, which are forests planted on former heathland about 70 years ago (Fig. 10).

Finally, two plots divert even further from the general trend: a high contribution of microbially altered SOC similar to the pine-converted plots was found in the pine-control plot of Kasterlee, which may be due to a higher share of pedunculate oak (*Quercus robur*) relative to Scots pine (*Pinus silvestris*): although oak litter is still considered poorly decomposable as compared to other broadleaved species, its litter still has a higher base content (Desie, Vancampenhout, Nyssen, et al., 2020) and can lead to a higher microbial alteration in the soil as compared to pine (Vancampenhout et al., 2010). The higher base saturation observed at the Kasterlee control plot, close to the threshold of 30% (Chadwick and Chorover, 2001), may also be related to a higher weatherable reserve in the marine sands of Poederlee, occurring at variable depth below the cover sands at that location (Louwye et al., 2020). A second exception was the pine-converted plot of Veldhoven, showing high abundances of lignocelluloses and exceptionally high amounts of levoglucosan (Fig. S3. Supp.). A potential explanation may be the dominance of *Prunus serotina* in that forests stand, as its plant tissues may contain high amounts of this compound (Fine et al., 2004).

The different dynamics in the soil molecules of pine-control plots on former heathland (accumulation of aliphatic compounds; Maashorst and Groote Heide), as compared to plots with abundant undergrowth (Hechtel-Eksel and Veldhoven) as well as the deviant composition at Kasterlee and Veldhoven, highlight that SOC dynamics depend on more than overstory litter quality alone, and can be highly context dependent (Vancampenhout et al., 2010; Zhu et al., 2020). For example, not all sandy soils are the same: there is a large variation in soil profiles for the same texture (Table 1, e.g. from Podzol to Anthrosol) and therefore outcomes in terms of C sequestration. Accordingly, the potential for forest managers to alter belowground ecosystem functioning can differ significantly. In conclusion, land-use legacy, edaphic conditions, understory characteristics or specific tree species traits are important to take into account besides litter quality when evaluating C cycling and

the impact of forest management.

4.5. Implications of the emerging patterns for forest management

In only one generation of converting pine monocultures to mixed rich litter forest our reconnaissance study already illustrates distinct effects on soil belowground functioning and a shift in C sequestration mechanisms. As hypothesised, admixing rich litter species counteracted soil acidification, leading to a more diverse earthworm community. However, in terms of mesofauna abundance and diversity and conservation, it seems better to strive for a good mix of litter quality inputs (ranging from coniferous to poor litter oak and beech to rich litter from lime and cherry). In practice this means maintaining pine trees on some locations and converting to mixed forests on other, balancing conservation efforts with optimised nutrient cycling and other functions (Desie, Vancampenhout, Nyssen, et al., 2020). Until recently, *Prunus serotina* was considered an undesirable tree species in forests on sandy soils. Since eradication of this tree species has proven impossible in most cases, forest managers started to consider it as part of the forest flora (Nyssen et al., 2024) embracing it for its positive impact on ecosystem functioning (Desie et al., 2023).

Moreover, while the C stocks did not differ, this exploratory research indicates that C cycles are different (evidenced in the differences in respiration, total soil C, SOC fractions and in the molecular data) and appear to move towards more deeper and stable incorporation of C (less C stored in POM). This is beneficial in terms of climate change mitigation as well as climate change adaptation (increased water storage related to improved aggregation, bioturbation and C incorporation).

5. Conclusion

Comparisons between pine monocultures and converted forests on sandy soils revealed higher soil pH in converted stands, likely reflecting the mitigation of soil acidification through the input of rich litter high in base-cations from admixed tree species. Earthworm biomass and microbial activity also increased in converted mixed forests. Despite these effects on soil chemical and biological properties, total SOC stocks showed little change, suggesting that total SOC stocks respond more slowly to changing litter quality. Carbon stability was not significantly affected, however there was a trend towards increased decomposition of POM in the pine-converted plots, supported by increased microbial respiration and altered molecular composition of SOM. Assessing SOM at the molecular level via pyrolysis-GC/MS proved valuable to detect subtle changes in carbon dynamics and provides insight in potential legacy effects of previous land-uses. Overall, this small-scale, yet in-depth, explorative study was able to identify emerging patterns in the carbon dynamics, providing a foundation for future studies exploring specific mechanisms in greater detail. This study showed that the effects of introducing rich litter species as a restoration measure on carbon dynamics are context-dependent, influenced by legacy effects and soil biota. In conclusion, pine monocultures store proportionally more C in labile fractions (POM), while mixed broadleaved forests enhance C storage in stable fractions through e.g. stronger microbial reworking.

CRediT authorship contribution statement

S.E. Nijdam: Writing – original draft, Formal analysis, Investigation. **K. Vancampenhout:** Writing – review & editing, Supervision. **B. Jansen:** Writing – review & editing, Supervision. **E. Morriën:** Writing – review & editing, Supervision. **J. Schellekens:** Writing – review & editing. **B. Leenders:** Investigation. **J. Simons:** Investigation. **L. Van den Berg:** Writing – review & editing. **M. de Graaf:** Writing – review & editing. **B. Nyssen:** Conceptualization. **B. Muys:** Conceptualization, Writing – review & editing. **E. Desie:** Conceptualization, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Sascha Nijdam reports financial support was provided by Research Foundation Flanders. Ellen Desie reports financial support was provided by Province of North Brabant. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank the assistance of the technicians at the KU Leuven and at UvA-IBED. Also, we appreciate the help of MSc graduates Yariisa Driesen and Kato Van Criekeing during sampling and lab analysis. We also thank the Bosgroep-Zuid Nederland for their support and plot selection. This research was funded by Provincie Noord-Brabant in the Netherlands (LFG leefgebieden project) and by FWO (1292824N & G060721N).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2026.123782](https://doi.org/10.1016/j.foreco.2026.123782).

Data availability

Data will be made available on request.

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