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Interactions between deciduous and coniferous litter in decomposition processes: Insights from ATR-FTIR spectroscopy and elemental analyses

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ABSTRACT

Forest litter decomposition is crucial for carbon and nutrient cycling, especially in mixed broadleaf-coniferous forests. Interactions between different litter types can accelerate or inhibit decomposition, depending on species composition, microbial activity, and environmental factors. This study examines how litter samples from oak (*Quercus sp.*), beech (*Fagus sylvatica L.*), and pine (*Pinus sylvestris* L.) decomposes in pure and mixed stands across four European sites. Samples were collected at different decomposition stages (*L*, *F*, and *H* layers) and analysed for total organic carbon, total nitrogen, total phosphorus, and molecular composition using ATR-FTIR spectroscopy. A generalized linear mixed model assessed the influence of species identity, forest type, and pine proportion in mixed stands on decomposition and nutrient dynamics. Our results revealed contrasting effects of litter mixing. Broadleaf litter enhanced pine needle decomposition, particularly in the *H* layer, likely due to facilitation. Conversely, broadleaf litter decomposition, specially oak in the *F* layer, was inhibited in mixed stands. Beech litter degradation remained largely unaffected. ATR-FTIR analysis suggested molecular transformations, with increased aromatic compounds and reduced aliphatic groups, especially in mixed stands, though these spectral interpretations carry some uncertainty. These findings highlight the role of species composition in shaping litter decomposition dynamics. While ATR-FTIR provided useful information on chemical changes during decomposition, its interpretation should be complemented with other approaches to improve confidence in functional inferences. Incorporating species-specific responses can inform forest management strategies aiming to balance nutrient cycling and long-term carbon sequestration.

1. Introduction

Forest litter decomposition is crucial for carbon and nutrient cycling. Interactions between different litter types can accelerate or inhibit decomposition, depending on species composition, microbial activity, and environmental factors (Lal, 2005, Pan et al., 2011). A key process contributing to this storage is the decomposition of plant litter, which influences nutrient cycling, soil formation, and the stabilization of soil organic carbon (SOC) (López-Marcos et al., 2018). The diversity and chemical complexity of litter in species-rich forests are recognized as key drivers of enhanced SOC formation and stabilization (Chen et al., 2020). One key dynamic driving these processes is the priming effect, where the decomposition rate of one type of litter is altered by the presence of another. This interaction can accelerate or decelerate SOC

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mineralization, impacting nutrient availability, soil fertility, and overall ecosystem functioning. (Huys et al., 2022) highlighted that the chemical composition of plant litter significantly influences the dynamics of SOC underlining the importance of considering species-specific litter traits in understanding SOC dynamics and managing carbon stocks in mixed forest ecosystems.

Soil and vegetation are closely interrelated, as soil properties influence vegetation establishment while vegetation, in turn, alters soil characteristics (Getino-Álvarez et al., 2023). The primary sources of soil organic matter (SOM) and nutrients in forests are litter and root decomposition, and their contributions to soil processes are strongly dependent on tree species composition. Tree species influence both the quantity and quality of litterfall, which affects the dynamics of SOM entering the soil (Lucas-Borja et al., 2012, Román Dobarco et al., 2020).

Several factors influencing the decomposition dynamics of mixed litter have been identified (Song et al., 2010): The nutrient composition of plant litter, particularly nitrogen (N) and phosphorus (P), significantly shapes decomposition rates. Positive correlations between high initial N and P concentrations and non-additive effects in mixed litter decomposition have been observed, leading to enhanced decomposition dynamics (Taylor et al., 1989). Additionally, mixed litter enhances the abundance and diversity of decomposers, particularly fungi, by providing varied resources that support diverse and effective decomposer communities (Wardle et al., 2006). Nutrient exchange between litter species also plays a critical role, with fungal hyphae actively transporting nutrients between litter types and enhancing the decomposition of specific components (Schimel and Hättenschwiler, 2007).

Despite extensive research, critical gaps remain in understanding how differences in litter quality influence SOC dynamics under natural field conditions, especially in mixed-species forests where deciduous and coniferous litter coexist (Chen et al., 2020, Liu et al., 2016). Previous studies on the effects of litter mixing have produced inconsistent results, ranging from positive to neutral to negative outcomes (Song et al., 2010). For instance, Taylor et al. (1989) found that adding *Alnus crispa* litter to *Populus tremuloides* increased mass loss, while (Fyles and Fyles, 1993) observed accelerated decomposition of *Pseudotsuga menziesii* when mixed with *Alnus rubra*. Conversely, Prescott et al. (2000) found no significant effects of mixing *Picea glauca, P. menziesii*, *Pinus contorta, P. tremuloides* and *Alnus rubra* litter, while Chapman et al. (1988) reported both positive and negative effects depending on specific litter combinations. One major limitation of many litter-mixing studies is the lack of analysis of individual species within the mixtures. Without separating the litter components after sampling, it is challenging to determine the specific contributions of each species to the overall decomposition process and to evaluate potential synergistic or antagonistic interactions. For example, Zhang et al., (2008)) showed that while the total mass loss in a mixture of *Castanopsis eyrei* leaves and *P. massoniana* needles was like the sum of their individual decompositions, the decomposition of *C. eyrei* was accelerated, whereas that of *P. massoniana* was slowed. These findings highlight the importance of examining the individual dynamics of each species in mixed stands to understand the net effects of litter interactions (Song et al., 2010).

Controlled experiments, such as litter bag studies and laboratory incubations, have advanced our understanding of decomposition processes but often oversimplify the complexity of natural systems (Salamanca et al., 1998, Wardle et al., 2006). Litter bags constrain interactions between litter and the environment, limiting decomposers access and altering microbial activity. Similarly, laboratory conditions fail to capture the full range of biotic and abiotic interactions, such as environmental gradients and temporal changes in decomposition. Field-based studies conducted under natural conditions are therefore essential to reveal the complex interactions that govern decomposition *in situ*.

Fourier Transform Infrared (FTIR) spectroscopy, and particularly the Attenuated Total Reflectance variant (ATR-FTIR), has become an increasingly valuable tool in soil science due to its capacity to characterize soil organic matter (SOM) with minimal sample preparation (Janik et al., 2007; Margenot et al., 2023). Although its use in litter decomposition studies remains limited, ATR-FTIR shows great potential for monitoring functional group transformations during litter breakdown, offering detailed insights into chemical changes that occur throughout the decomposition process (Tatzber et al., 2011; Duboc et al., 2012). This is especially relevant for evaluating how mixtures of deciduous and coniferous litter influence decomposition dynamics in mixed forest stands. However, ATR-FTIR also presents important limitations. The overlapping of absorption bands can hinder the identification of specific functional groups, especially in complex matrices such as decomposing litter. Moreover, ATR-FTIR is only semi-quantitative, providing relative rather than absolute concentrations of compounds, and is sensitive to sample properties like particle size, moisture content, and contact with the ATR crystal—factors that can introduce variability and spectral noise (Tinti et al., 2015; Kassem et al., 2023). Water interference in the mid-infrared region further complicates interpretation and may require specific preprocessing strategies (Zhang et al., 2022). Additionally, some absorption bands are associated with multiple types of compounds (e.g., C═O stretching from carboxylic acids, esters, or amides), adding uncertainty to peak assignments (Tinti et al., 2015). Despite these challenges, when complemented with elemental analysis, ATR-FTIR remains a valuable method for exploring species-specific litter chemistry and for gaining insight into the molecular transformations underpinning decomposition processes in forest ecosystems.

To address these knowledge gaps, this study investigates litter decomposition in pure and mixed forest stands within the same local environment at each site, analysing individual litter components in mixed plots. This approach enables a more precise assessment of species-specific contributions and interactions, particularly in forests where deciduous and coniferous litter coexist. We hypothesize that in mixed broadleaf–conifer forests, litter interactions may influence decomposition dynamics in a litter-type-dependent manner. Additionally, we propose that the influence of litter mixing will vary across decomposition stages, with more noticeable effects occurring in intermediate stages (F layer), and diminishing in later stages (H layer), as litter becomes more decomposed and chemically homogenized. These patterns are expected to be reflected in changes in litter chemistry, as inferred from ATR-FTIR spectral features and supported by elemental analyses (C, N, P).

2. Material and methods

2.1. Location

This study was conducted across a climatic gradient in Europe to investigate litter decomposition under varying environmental conditions among sites, while maintaining identical environmental conditions within each site for comparisons between pure and mixed stands. The selected sites, depicted in Fig. 1, represent diverse temperate regions.

The study sites are described as follows: 1) Valberzoso Forest (42º53’53’’N, 4º14’32’’W), located in the municipality of Brañosera, in the northern part of the province of Palencia, Spain, within the Montaña Palentina, a mountainous region that forms part of the Cantabrian Mountains; 2) Montgrony Forest (42º15’46’’N, 2º04’18’’E), situated in the municipality of Gombrén, in the province of Girona, Spain, belonging to the Pre-Pyrenean Mountain Range; 3) Schrobenhausen Forest (48º34’51’’N, 11º13’53’’E), located in the district of Neuburg-Schrobenhausen, within the Upper Bavaria region of southern Germany, in the Danube Valley region and the Bavarian Alpine Foreland; and 4) Niepołomice Forest (50º01’34’’N, 20º19’34’’E), situated in Wieliczka County, within the Lesser Poland Voivodeship in southern Poland, lying in the Carpathian Foothills.

Table 1 summarizes the main characteristics of the study sites, including their geographical location, altitude, slope, geological

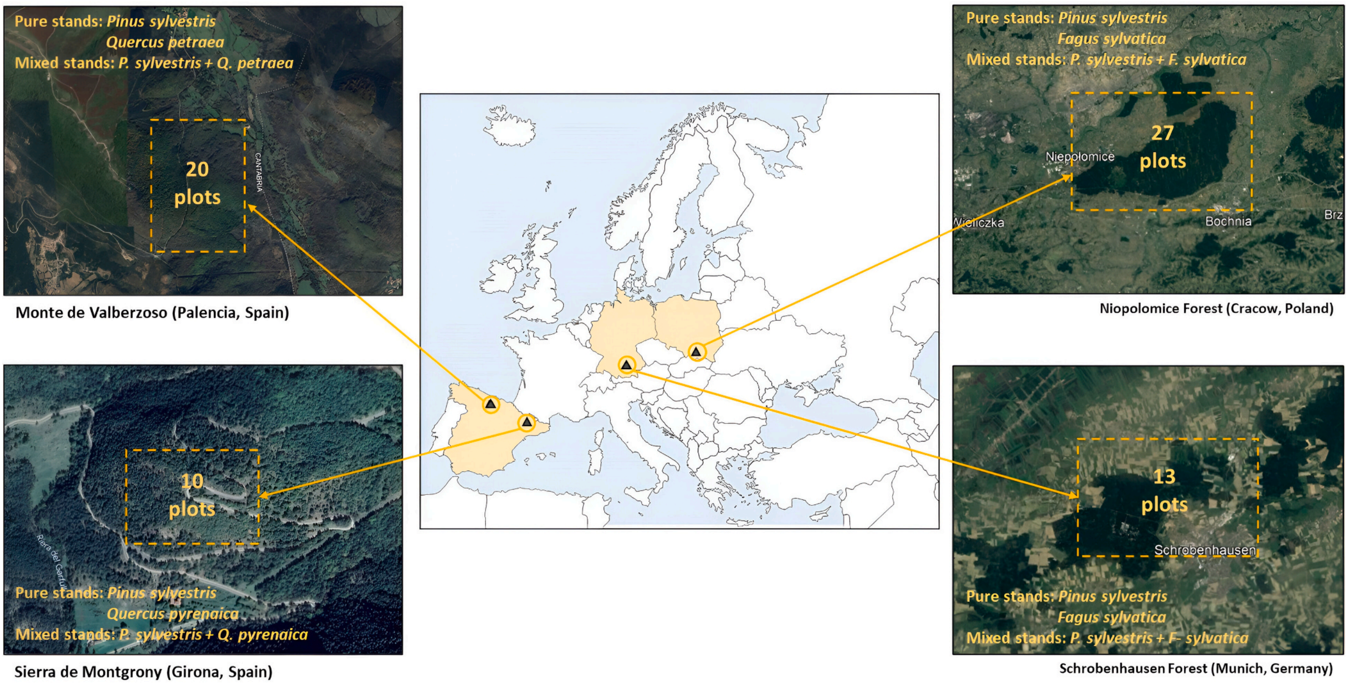

Fig. 1. Study site location: Valberzoso Forest (Palencia. Spain). Montgrony Forest (Girona. Spain), Schrobenhausen Forest (Neuburg-Schrobenhausen, Munich, Germany) and Neopolomice Forest (Wieliczka, Cracow, Poland).

Table 1
Stands characteristics.

Woodland Area	Location	Altitude (m)	Age (years)	Slope (%)	Geology	MAT (°C)	MAP (mm yr^{-1})	Soil Type
Valberzoso Forest	Palencia (Spain)	1151–1219	50	10–17	Sandstones, conglomerates, and lutites	8.7	1150	Umbrisol
Montgrony Forest	Girona (Spain)	1116–1293	50	35–45	Sandstones, loams, and limestone	7.5	951	Regosol
Schrobenhausen Forest	Neuburg-Schrobenhausen (Germany)	250–430	57	< 5	Tertiary sediments, coarse and fine sands	7.5	827	Podsol
Niepolomice Forest	Wieliczka (Poland)	208–213	50–65	< 5	Pleistocene sands	8.4	670	Podsol

*Note: MAT = Mean Annual Temperature; MAP = Mean Annual Precipitation; Soil Types according to World Reference Base for Soil Resources (IUSS Working Group WRB, 2022).

composition, and selected climatic parameters. The studied stands ranged in age from 50 to 65 years, with no silvicultural interventions recorded in the past decade (Błońska et al., 2018, de Streel et al., 2021, Getino-Álvarez et al., 2023).

2.2. *Experimental Design*

The study was conducted in 70 plots: 21 in pure stands of Scots pine (*Pinus sylvestris* L.), 12 in pure stands of beech (*Fagus sylvatica* L.), 9 in pure stands of oak (*Quercus* sp.: *Q. pyrenaica* and *Q. petraea*), 12 in mixed stands of pine + oak, and 16 in mixed stands of pine + beech, both with

Table 2
Main characteristics of the sampled plots.

Woodland Area	Type of mass	N° plots	Tree species	% Psy	D (cm)	BA (m^2 ha^{-1})	n (trees ha^{-1})	TDB (Mg/ha)
Valberzoso Forest	Pure of pine	6	*Pinus. sylvestris*	99–100	15.5–41.2	61.2–93.4	767–1407	5.9–19.3
	Pure of oak	6	*Quercus petraea*	0	8.5–34.5	24.5–64.4	896–2687	7.9–16.8
	Mixed pine+oak	8	*P. sylvestris* + *Q. petraea*	11–90	8.5–36.3	33.5–71.3	768–1792	7.5–18.5
Montgrony Forest	Pure of pine	3	*Pinus sylvestris*	100	13.3–31.8	16.3–44.9	512–896	7.1–10.1
	Pure of oak	3	*Quercus pyrenaica*	0	7.5–21.0	16.1–28.4	1408–1920	4.4–12.5
	Mixed pine+oak	4	*P. Sylvestris* + *Q. pyrenaica*	11–81	7.9–29.8	25.7–36.3	640–1152	4.7–9.8
Schrobenhausen Forest	Pure of pine	4	*Pinus sylvestris*	99–100	21.3–41.0	33.9–63.7	256–640	15.8–18.4
	Pure of beech	4	*Fagus sylvatica*	0	7.7–30.5	24.7–33.1	896–1408	12.2–19.4
	Mixed pine+beech	5	*P. sylvestris* +*F. sylvatica*	8–64	7.5–38.9	22.0–54.5	768–1280	10.5–14.2
Niepolomice Forest	Pure of pine	8	*Pinus sylvestris*	100	15.6–39.5	32.9–72.8	512–1408	3.0–21.1
	Pure of beech	8	*Fagus sylvatica*	0	8.6–39.0	23.6–41.4	384–1024	5.7–15.2
	Mixed pine+beech	11	*P. sylvestris* +*F. sylvatica*	14–87	7.4–40.6	19.8–54.6	512–1280	6.5–25.9

**Note:* %Psy: *Pinus sylvestris* percentage; D: Diameter range at breast height (cm, measured at 1.3 m above the ground) in centimetres; BA: Basal area range per hectare (m^2 ha^{-1}); n: Tree density range (total trees per hectare); TDB: total dry biomass (Above-ground dry biomass range per hectare, Mg ha^{-1}); Mixed plots include a combination of species indicated in the "Tree species" column.

varying proportions of pine in the mixtures. Stand characteristics, including tree species, diameter at breast height, age, spatial location of individual trees, and plot size, were obtained from the EuMiXFOR dataset (COST Action FP 1206 EuMIXFOR), which is publicly available (Getino-Álvarez et al., 2023, Heym et al., 2017). The dataset includes information on a variety of plot types sampled across four study locations. Table 2 provides an overview of the main characteristics of these plots.

The plots were established with circular shape with 5 m of radius. The location of the circular plots was carried out through a spatial analysis using the geopositioning of individual trees. Voronoi polygons were created based on the Euclidean distance between each neighbour, determining their area of influence within the plot, assigning a relative value of basal area (BA) concerning the containing plot. Once the land was divided by the Euclidean distance between individuals, plots with a 5-meter radius were determined based on the relative BA criterion (each polygon's area relative to the total area), showing different representative mixing percentages. The analysis was performed using QGIS 3.16 (QGIS Development Team, 2017). The location of plots was decided based on three fundamental criteria: (1) avoiding overlap between plots; (2) covering different existing mixing percentages; and (3) each plot encompassed a minimum of 5 trees.

The percentage of species mixture at each plot was calculated as a ratio between the sum of Scots pine influence areas and the total area of the subplot and was expressed as pine percentage. For more information, refer to Getino-Álvarez et al. (2023). Detailed data on circular plots, including the percentage of pine composition, is presented in Table S1 in the supplementary information.

2.3. Soil Profile Description and Classification

To describe and characterize the soil profile at each study site, soil pits were excavated in all three stand types (pure Scots pine, pure broadleaf, and mixed stands), resulting in a total of twelve excavations. In mixed stands, soil pits were in areas considered representative of the overall species composition, typically in transitional zones between the influence areas of both species, based on the spatial distribution of trees and Voronoi polygons. These pits were used to inform the interpretation of soil and decomposition conditions across forest types. However, since soil type did not vary substantially among stand types within each site, the four profiles corresponding to pure Scots pine (Pinus sylvestris L.) stands, common to all study locations, were described and presented in the manuscript. These representative profiles were classified according to the World Reference Base for Soil Resources (IUSS Working Group WRB, 2022).From each mineral horizon, both disturbed and undisturbed soil samples were collected. Disturbed samples were oven-dried at 105 °C for 24 h, weighed (±0.001 g), and used to calculate soil bulk density (BD). Additional soil material was air-dried, disaggregated, and sieved to < 2 mm prior to the determination of physical and chemical properties. The proportion of coarse fragments (CF; > 2 mm) was determined from these samples. Physical properties included particle size distribution, assessed using the pipette method, with subsequent determination of clay, sand, and silt content. Soil colour was assessed on both dry and moist samples. Chemical analyses included pH measured in a 1:2.5 soil-to-water suspension, and cation exchange capacity (CEC), determined following the method described by Bascomb (1964). Total carbonates were quantified by acid–base titration using 1 M HCl and 0.5 M NaOH (Bashour and Sayegh, 2007). Soil organic matter (SOM) was estimated using the Walkley and Black (1934) method, by converting oxidizable organic carbon to organic matter using a factor of 1.724.

2.4. Litter Sampling and Laboratory Processing

Litter samples were collected from the forest floor at three locations within each circular plot, each situated 1 m from the centre. The sampling points were spaced 120° apart and oriented towards North (0°), East-Southeast (120°), and South-Southwest (240°) to account for spatial variability within each plot. At each of the three sampling points, a 25 × 25 cm^2 wooden frame was used to collect the litter. The samples from all three points within a plot were then combined in the field to create a single composite sample per plot. To ensure that only leaf litter was collected for analysis, coarse woody debris (e.g., large branches) was carefully removed from the sampling area before collection. In mixed stands, we followed a microsite-scale approach as recommended by Getino-Álvarez et al. (2023), considering the influence of trees within a 5-meter radius of the plot centre, rather than relying solely on stand-level classification. This approach reduces the risk of mismatching litter origin with species composition and improves the representativeness of local interactions affecting decomposition.

Once collected, the composite litter samples were spread out and air-dried in the laboratory. The material was then separated by litter layer and classified into three fractions: L (fresh litter layer, formed on the forest floor surface and consisting of relatively undecomposed plant material), F (fermented litter layer, including partially decomposed but still recognizable plant residues), and H (humified litter layer, representing highly decomposed organic matter). Litter fractions were oven-dried at 60 °C to constant weight for at least 48 h and then weighed to the nearest 0.01 g to calculate the dry biomass (DM) of each layer per hectare. Total dry biomass (TDB, Mg DM ha^{-1}) was obtained by summing the biomass of the three litter layers (L + F + H). A representative subsample was taken for the subsequent determination of carbon and nitrogen stocks (C stock and N stock).

The remaining material, already separated by layer, was then sorted by tree species (pine, oak, and beech). The presence of pine litter was visually assessed in the L and F layers, where pine needles can be clearly distinguished from broadleaf litter due to their distinct morphological characteristics. No species-level separation was carried out for the H fraction due to the difficulty of distinguishing between species at this advanced stage of decomposition.

In total, 266 litter samples were collected, processed, and analysed: 126 from pure stands (42 stands × 3 samples, one per layer corresponding to the dominant tree species), and 140 from mixed stands (28 stands × 5 samples: two per layer in L and F, one per species, plus one unseparated sample for the H layer). In the H layer, mixtures were further distinguished in mixed stands based on the species present in the stand, resulting in $H_{pine+beech}$ or $H_{pine+oak}$. Samples were finely ground using a Retsch MM301 mill and stored in airtight containers for subsequent chemical and spectroscopic analyses.

Sampling was conducted between July and October in both 2018 and 2019, before the annual leaf fall, to ensure valid comparisons across plots by avoiding seasonal variation in litter decomposition.

2.5. Chemical analysis of the forest floor litter layers

Total carbon (TC) and total nitrogen (TN) of the forest floor litter layers were determined by dry combustion using a LECO CNS928 elemental analyser. While the litter samples generally lacked inorganic carbon, exceptions were observed in the *F* and *H* layers of the Montgrony Forest plots. In this case, organic layers, situated above a calcareous mineral soil, contain carbonates derived from the underlying soil matrix. In these samples total inorganic carbon (TIC) was determined by dissolution of carbonates on excess of HCl, followed by back titration of the remaining acid using NaOH. The endpoint of the titration was determined potentiometrically upon reaching a pH value of 6.5. Total organic carbon (TOC) of these forest floor litter layers was calculated as the difference between TC and total inorganic carbon (TIC). Total organic carbon to total nitrogen ratio (TOC/TN) was calculated. Carbon and nitrogen stocks (C and N stocks) for each litter layer were calculated by multiplying the dry biomass per hectare (DM) of each layer by its corresponding organic C or N concentration. Ash content was determined after calcination in a muffle furnace at 480ºC for 5 h.

Subsequently, ashes were dissolved with an acidic solution ($HCl+HNO_3$), and the concentration of total phosphorus (TP) of the forest floor litter layers was determined using the colorimetric method of vanadomolybdophosphoric acid (Kitson and Mellon, 1944).

2.6. Spectral measurements of the forest floor litter layers

Forest floor samples were scanned with ATR-FTIR (Nicolet iS50 FT-IR-ATR). The reflectance of the sample was recorded at a resolution of 4 cm^{-1} and 64 scans per spectrum. A background spectrum in air was acquired before samples acquisition. All ATR-FTIR spectra were baseline corrected to remove the slope variation caused by scatter and variation in particle size (Farnet-Da Silva et al., 2017). The relevant peaks were selected using an automated peak-picking command based on local maxima (5 % sensitivity). All spectra were visualized, processed, and analyzed using OMNIC software. This software was used to process spectral data for baseline correction (connecting line method), smoothing (Savitzky–Golay method), and normalization. The peak intensity (by height) was recorded to assess the magnitude of infrared absorption of the selected peaks. Normalization was performed by dividing each peak height by the sum of all peak heights considered in the spectrum, ensuring comparability between samples (Tinti et al., 2015). Tatzber et al. (2010) and Tinti et al. (2015) outlined the bands integrated for the evaluation of the recorded infrared spectra (IR) of organic layers and peaks (see supplementary Table S2), highlighting the molecular vibrations and chemical groups associated with each spectral range.

The main FTIR peaks identified in soil organic matter (SOM) correspond to different functional groups and organic compounds, providing valuable insights into C dynamics, decomposition processes, and organic compounds transformation (Tinti et al., 2015).

The most relevant absorption peaks were found at around 2919 and 2838 cm^{-1} which were assigned to C-H stretches (CH_3 and CH_2) of aliphatic chains. These peaks represent hydrophobic organic-compound functional groups (Chavez-Vergara et al., 2014).

In the carbonyl and amide region (1729–1559 cm^{-1}), the 1729–1711 cm^{-1} band represents C═O stretching (Tatzber et al., 2010 and Tinti et al., 2015). The 1646 cm^{-1} peak reflects C═O stretching of tertiary amides and C–N stretching of unsaturated nitrogen linkages. It also includes amide II vibrations of primary amides (Margenot et al., 2023). The 1614 peak encompasses amide II vibrations in primary amides, carboxylates, and other amides (Rao, 1963).

In the aromatic and aliphatic vibration region (1559–1370 cm^{-1}), the 1559–1512 cm^{-1} band is linked to aromatic skeletal vibrations, amide II, and aromatic C═C bonds (Haberhauer and Gerzabek, 1999, Janik et al., 2007). The 1445 cm^{-1} peak includes CH and NH of amide II, as well as aliphatic C–H deformation (Antil et al., 2005). The 1418 cm^{-1} peak is related to malonic and benzoic acids, amide III vibrations, and carbonates (Rao, 1963). The 1370 cm^{-1} band highlights C–O vibrations of phenolic OH, COO^-, and O–H groups, along with CH_3 bending (Rao, 1963).

The phenolic, carboxylic and sulfonamide region (1317–1154 cm^{-1}) includes the 1317 cm^{-1} band, representing malonic acids, sulfonamides, and aromatic amines (Tatzber et al., 2010). The 1259 cm^{-1} band corresponds to benzoic acids, phenolic groups, and aryl ethers (Rao, 1963, Tatzber et al., 2007). The 1154 cm^{-1} band is associated with aliphatic OH and sulfonamides and the 1233 cm^{-1} band involves C═O and OH vibrations in carboxylic acids, phenols, and acetates (Rao, 1963).

One of the strongest FTIR peaks occurs between 1100 and 1030 cm^{-1} , corresponding to C–O stretching in cellulose, β-anomers, and β-glycosides (Calderón et al., 2011). The 886 cm^{-1} band highlights carbonate contributions (Tatzber et al., 2007).

2.7. Statistical analysis

A generalized linear mixed model (GLMM) was used to analyse the data. An incomplete 2 × 5 factorial design was implemented, including two fixed between-subject factors: forest type (pure or mixed) and litter type (oak, beech, pine, pine-beech, or pine-oak litter). Additionally, a within-subject repeated measures factor was included to account for forest floor litter layer, with three levels (L, F, and H). A 3 × 3 unstructured variance–covariance matrix was specified separately for each forest type to model the correlation structure across litter layers. Sampling site was included as a random effect, with heteroscedastic variances across layers. To better capture within-group variability in mixed stands, the proportion of pine in the litter mixture (pine_share) was incorporated as a continuous covariate. Pine_share was entered into the model prior to forest type, following a Type I sum of squares approach. This ordering was intentional, as we considered the continuous gradient of pine dominance to be a more informative ecological predictor than the categorical forest type classification. This approach allowed us to first assess the effect of pine share across all plots and then evaluate whether forest type still explained additional variability beyond that gradient. For the response variables TOC, TN, and TP, a beta distribution with a logit link function was used. For the stocks of C and N and all derived indices expressed as ratios, a gamma distribution with a log link was applied. Estimated marginal means were computed using the inverse link function based on GLMM results. The normality of marginal and conditional studentized residuals was assessed using the Kolmogorov–Smirnov test.

3. Results

3.1. Soil properties

Some physical and chemical properties of the four soil profiles described from pure Scots pine stands, each representative of the soil conditions at their respective study sites, are presented in Table 3. The Valberzoso Forest soil profile, classified as an Umbrisol, exhibited feature characteristics of this soil group, including sandy loam textures and moderate acidity throughout the profile. The *A* horizon stood out with the highest value of SOM and CEC. As depth increased, BD and the proportion of CF rose, while SOM and CEC decreased, consistent with the limited development and lower fertility typical of the cambic horizon. The absence of carbonates aligned with their acidic, organic-rich nature and strong influence of weathered parent material. The Montgrony Forest soil profile, classified as a Regosol, was characterized by its shallow depth and the strong influence of calcareous parent material. The *A* horizon, a fertile silt loam, was rich in SOM and had a moderately alkaline pH (8.5), driven by the high carbonate content typical of calcareous soils. Despite its alkalinity, there was no evidence of sodicity, and the soil chemistry is dominated by calcium carbonate rather than sodium-based compounds. The Niepolomice Forest and Schrobenhausen Forest soils were classified as Podzols. In the Niepolomice Forest profile, the strongly leached *E* horizon was dominated by sand with negligible amount of SOM, low CEC and pH, consistent with eluviation. Below this, the *Bhs* horizon revealed SOM and iron/aluminum accumulation, resulting in a slight increase of SOM and CEC compared to the overlying *E* horizon. Similarly, the Schrobenhausen Forest profile shows marked horizon differentiation, with an *Ah* horizon rich in SOM underlain by progressively nutrient-poor layers. Both profiles maintained acidic pH levels and lacked carbonates.

3.2. Litter ATR-FTIR Spectra

The ATR-FTIR spectra of forest floor samples revealed distinct absorption peaks that define their spectral profiles. Fig. 2 displays the spectra of litter layers (L, F, and H) from Pine, Oak, and Beech floor litter, showing characteristic peaks. A total of 19 absorption bands were initially identified (Table S2), but only 17 were included in the statistical analysis: A2919, A2838, A1729, A1711, A1614, A1559, A1539, A1512, A1445, A1418, A1370, A1317, A1259, A1233, A1204, A1154, and

Table 3
Physical and chemical properties of the four described soil profiles from pure Scots pine stands.

Horizon	Depth (cm)	Colour dry	Colour moist	CF (%)	Sand (%)	Silt (%)	Clay (%)	Textural Class	BD (g cm^{-3})	pH	SOM (%)	CEC (cmol$_c$ kg^{-1})	CaCO$_3$ (%)
Valberzoso Forest													
A	0–22	7.5YR 4/2	10YR 2/2	0.5	63.1	22.1	14.8	Sandy Loam	0.96	5.5	3.9	24.2	0.0
B	22–43	7.5YR 4/2	10YR 3/3	0.7	70.4	14.4	15.2	Sandy Loam	1.47	6.0	2.4	18.3	0.0
C	43–72	7.5YR 5/6	7.5YR 5/6	14.9	65.5	18.4	16.1	Sandy Loam	1.57	6.4	0.5	14.6	0.0
Montgrony Forest													
A	0–22	10YR 5/2	10YR 3/2	14.7	18.9	55	26.1	Silt Loam	1.01	7.8	4.0	20.7	31.4
B	22–39	10YR 5/3	10YR 4/2	1.2	36.2	41.4	22.3	Loam	1.54	8.5	1.6	13.5	38.1
C_k	39–47	10YR 5/4	10YR 4/4	20.2	22.6	41.9	35.5	Clay Loam	1.67	8.3	1.3	16.4	20.5
Niepolomice Forest													
A_h	0–10	10YR 2/2	10YR 2/1	1.8	87.2	7.8	5.0	Loamy Sand	1.41	3.5	7.2	33.9	0.0
E	10–41	10YR 7/1	10YR 6/2	1.2	94.0	3.5	2.5	Sand	1.83	4.5	0.0	7.4	0.0
B_{hs}	41–60	10YR 3/4	10YR 3/2	25.1	79.1	12.9	8.1	Loamy Sand	1.62	3.9	1.7	29.4	0.0
Schrobenhausen Forest													
A_h	0–3	10YR 4/1	10YR 3/1	2.0	90.4	5.6	4.1	Sand	1.11	3.6	8.8	30.9	0.0
A	3–14	10YR 5/3	10YR 4/2	5.3	87.7	5.3	7.0	Loamy Sand	1.25	4.0	1.9	18.6	0.0
B_s	14–66	10YR 6/4	10YR 5/6	4.7	90.5	3.7	5.7	Sand	1.56	4.5	0.2	7.9	0.0
C	66–115	10YR 6/4	2.5Y 6/3	2.1	92.8	3.2	4.0	Sand	1.50	4.5	0.01	10.0	0.0

**Note:* Depth: soil horizon depth; CF: coarse fraction (>2 mm); Sand/Silt/Clay: sand/silt/clay content; BD: bulk density; pH: pH value (measured in water 1/2.5); SOM: soil organic matter content; CEC: cation exchange capacity.

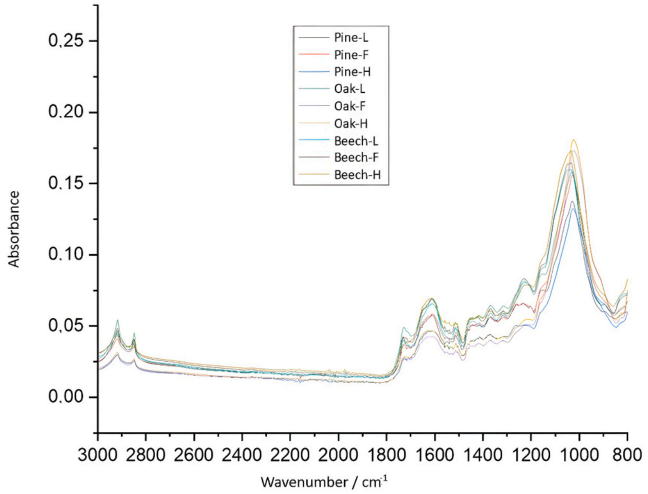

Fig. 2. ATR-FTIR Spectra of Forest Floor Samples.

A1031. Two bands were excluded due to their inconsistent presence across samples: the band at 886 cm^{-1} (A886) was only detected in samples containing carbonates, which were not consistently present in all litter types, and the band at 1646 cm^{-1} was absent in pine litter. To ensure robust and comparable results among species, the statistical analysis focused exclusively on the 17 bands that were consistently observed across all litter types.

3.3. Effects of pine share and forest type on forest floor litter elemental concentrations and stocks

In the GLMM, the continuous covariate *pine_share* was entered into the model prior to the categorical factors, allowing its effect to be evaluated before adjusting for forest type and its interactions. Table 4 summarizes the statistical significance of the effects of the continuous covariate *pine_share*, as well as the two-way and three-way interactions involving forest type, on nutrient concentrations (TOC, TN, TP), the TOC/TN ratio, and C and N stocks (C stock and N stock, respectively). *Pine_share* showed significant positive effects on TOC and the TOC/TN ratio, while no significant effects were detected for TN, TP, or C and N stocks.

After accounting for the variability explained by *pine_share*, several significant interaction effects involving forest type were detected. These included two-way and three-way combinations with litter type and litter layer. The interaction *forest* × *litter* × *layer* was significant for TOC, TN, TP, and both carbon and nitrogen stocks. For the TOC/TN ratio, the three-way interaction was not significant; however, both *forest* × *litter* and *forest* × *layer* interactions were significant. The concentrations and significant differences in TOC, TN, TP, and the TOC/TN ratio in oak, beech, and pine litter across the different soil litter layers (L, F, and H), as well as between pure and mixed stands for each layer and litter type, are shown in Fig. 3. Similarly, the data and significant differences related to C and N stocks are presented in Fig. 4

As can be seen in Fig. 3, across all three litter types, in both pure and mixed stands, a general decline in TOC and an increasing trend in TN and TP values were observed as decomposition advanced.

Significant differences between pure and mixed stands were mainly reflected in TOC, particularly in oak and pine litter. In oak litter, mixed stands showed significantly higher TOC and TN in the F layer, but no

Table 4
Statistical significance (*p*-values) for the continuous covariate *pine_share* and for two-way and three-way interactions involving the categorical factor *forest type*, in relation to total organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), the TOC/TN ratio, and nutrient stocks (C stock and N stock).

FACTORS	pine_share	pine_share (sign)	Forest*Litter*Layer	Forest*Layer	Forest*Litter	Forest
TOC	< 0.0001 (***)	+	< 0.0001 (***)	0.0004 (***)	0.0334 (*)	0.0269 (*)
TN	0.8924 ns	ns	0.0342 (*)	< 0.0001 (***)	< 0.0001 (***)	0.5861 ns
TP	0.1045 ns	ns	0.0454 (*)	0.0011 (**)	0.0026 (**)	0.2600 ns
TOC/TN	0.0093 (**)	+	0.8394 ns	< 0.0001 (***)	< 0.0001 (***)	0.9215 ns
C stock	0.0720 ns	ns	< 0.0001 (***)	0.0002 (***)	< 0.0001 (***)	< 0.0001 (***)
N stock	0.2613 ns	ns	< 0.0001 (***)	< 0.0001 (***)	< 0.0001 (***)	< 0.0001 (***)

Note: The sign (+) indicates a positive relationship between *pine_share* and the response variable. Asterisks denote significance levels: $p < 0.05$ (*), *p < 0.01 (**), p < 0.001 (***)*. “ns” indicates non-significant results ($p \geq 0.05$).

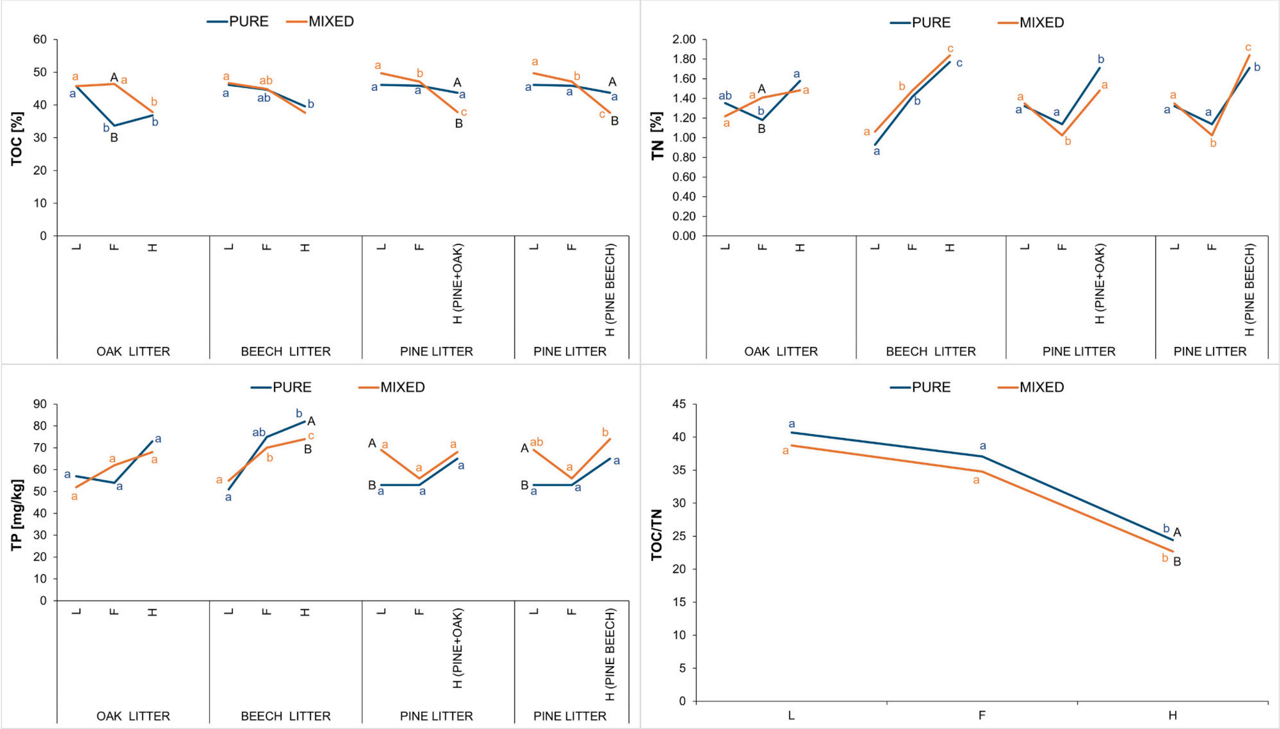

Fig. 3. Total Organic Carbon (TOC [%]), Total Nitrogen (TN [%]), Total Phosphorus (TP [mg/kg]) and TOC/TN ratio in oak, beech and pine litter across the layers (*L*, *F*, and *H*) in pure and mixed forest stands. Different letters indicate significant differences between layers within each species (lowercase letters) and between forest types within each litter layer (uppercase letters; in this case, letters are only added when the differences are significant).

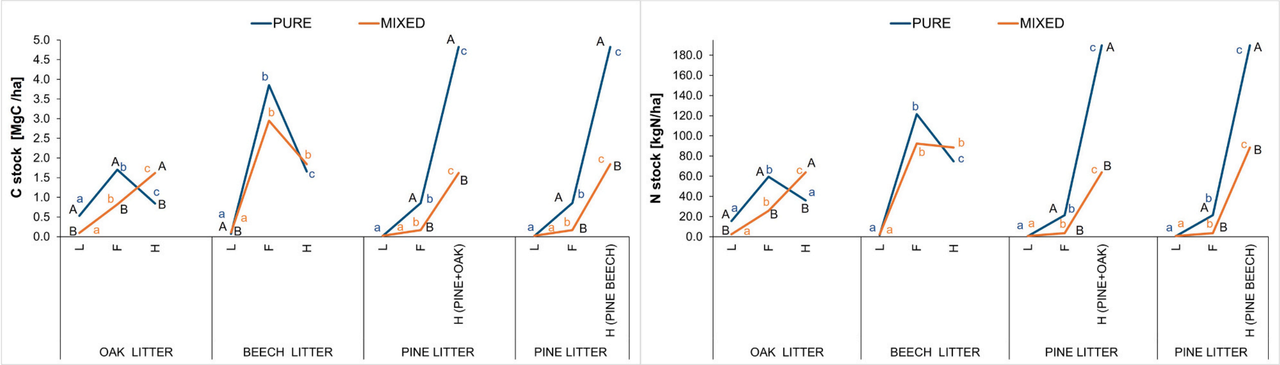

Fig. 4. Carbon and Nitrogen stock (MgC/ha and kgN/ha, respectively) in oak, beech and pine litter across the layers (*L*, *F*, and *H*) in pure and mixed forest stands. Different letters indicate significant differences between layers within each species (lowercase letters) and between forest types within each litter layer (uppercase letters; in this case, letters are only added when the differences are significant).

differences were observed in the H layer. In pine litter, significantly higher TOC was found only in the L layer. In contrast, beech litter showed significant differences only for TP in the H layer. Overall, among the variables studied, TP was the least sensitive to the effect of stand composition.

Significant differences in C and N stocks between pure and mixed stands were observed depending on tree species and litter layer. In oak litter, C and N stocks were significantly higher in pure stands in the L and F layers, while in the H layer they were significantly higher in mixed stands. In pine litter, both C and N stocks were significantly lower in mixed stands compared to pure stands in the F and H layers. No significant differences were found in the L layer. In beech litter, significant differences in C and N stocks were observed in the L layer, with higher values in mixed stands. No significant differences were found in the F or H layers.

3.4. *Effects of pine share and forest type on forest floor litter ATR-FTIR spectral features*

The statistical analysis of ATR-FTIR peak intensities revealed significant associations between the continuous covariate *pine_share* and several spectral absorption peaks. Table 5 shows the statistical significance of the effects of *pine_share*, as well as two-way and three-way interactions involving forest type, on the intensity of ATR-FTIR absorption peaks corresponding to specific wavenumbers. The direction of the relationship with *pine_share* (positive "+" or negative "-") is also indicated when significant. Positive relationships with *pine_share* were detected for 11 out of the 17 peaks identified, specifically at A1204, A1233, A1259, A1317, A1370, A1445, A1614, A1711, A1729, A2838, and A2919. In contrast, negative associations were observed at A1031, A1154, A1418, and A1559. No significant effect of *pine_share* was found for peaks at A1512 and A1539. In addition to the main effect of

Table 5
Statistical significance (*p*-values) for the continuous covariate *pine_share* and for two-way and three-way interactions involving the categorical factor *forest type*, in relation to absorption peaks identified by ATR-FTIR spectroscopy. Each row corresponds to a specific wavenumber (cm^{-1}) associated with a peak in the forest floor litter spectrum.

Wavenumber (cm^{-1})	pine_share	pine_share (sign)	Forest*Litter*Layer	Forest*Layer	Forest*Litter	Forest
A1031	< 0.0001(***)	-	< 0.0001(***)	< 0.0001(***)	0.0013 (**)	0.0221 (*)
A1154	< 0.0001(***)	-	0.0037 (**)	0.1987 ns	0.1435 ns	0.0002 (***)
A1204	< 0.0001(***)	+	0.2891 ns	< 0.0001(***)	0.1983 ns	0.0277 (*)
A1233	0.0212 (*)	+	0.0004 (***)	< 0.0001(***)	0.2268 ns	0.1695 ns
A1259	< 0.0001(***)	+	0.0011 (**)	0.0002 (***)	0.0029 (**)	0.3262 ns
A1317	< 0.0001(***)	+	0.0064 (**)	< 0.0001(***)	< 0.0001(***)	0.0650 ns
A1370	< 0.0001(***)	+	0.0006 (***)	0.0011 (**)	0.0004 (***)	0.3593 ns
A1418	< 0.0001(***)	-	0.9628 ns	< 0.0001(***)	0.2510 ns	0.0459 (*)
A1445	< 0.0001(***)	+	0.0019 (**)	0.0003 (***)	0.0125 (*)	0.7569 ns
A1512	0.4659 ns	ns	0.1756 ns	< 0.0001(***)	0.0040 (**)	0.1882 ns
A1539	0.1626 ns	ns	0.1660 ns	< 0.0001(***)	0.0012 (**)	0.0242 (*)
A1559	0.0075 (**)	-	0.0096 (**)	< 0.0001(***)	< .0006 (***)	0.0172 (*)
A1614	0.0040 (**)	+	0.3940 ns	< 0.0001(***)	0.7380 ns	0.4725 ns
A1711	0.0055 (**)	+	0.0043 (**)	0.0166 (*)	0.0644 ns	0.0443 (*)
A1729	< 0.0001(***)	+	0.0114 (**)	< 0.0001(***)	0.1199 ns	0.7527 ns
A2838	< 0.0001(***)	+	0.0014 (**)	< 0.0001(***)	0.0185 (*)	0.6084 ns
A2919	< 0.0001(***)	+	0.0002 (***)	< 0.0001(***)	0.0344 (*)	0.2738 ns

Note: The sign (+) indicates a positive relationship between *pine_share* and the response variable. Asterisks denote significance levels: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***). “ns” indicates non-significant results ($p \geq 0.05$).

pine_share, several wavenumbers showed significant two-way and three-way interactions involving forest type, litter type, and forest floor layer (see Table 5 for full details). These results indicate that both pine dominance and forest structural context contributed to the observed variability in litter chemical composition as captured by FTIR spectroscopy.

Across all three litter types, in both pure and mixed stands, a general decline in peak intensities was observed as decomposition advanced, particularly at wavenumbers A1204, A1233, A1259, A1317, A1370, A1445, A1711, A1729, A2838, and A2919 (Conversely, A1031, A1154, A1418, A1512, A1539, and A1559 showed an increasing trend in peak values throughout the decomposition process.

When comparing pure and mixed stands, significant differences in litter spectral bands were detected, depending on the species, the litter layer (L, F, or H), and the wavenumber considered. In oak litter, the most consistent differences were found in the F layer, with highly significant values ($p < 0.001$) across most of the analysed wavenumbers. Specifically, peaks at A1233, A1259, A1317, A1370, A1445, A1711, A1729, A2838, and A2919 were significantly higher in mixed stands (with *Pinus* litter) compared to pure oak stands, whereas peaks at A1031 and A1154 were significantly lower. In the H layer, significant differences were also observed, though less consistently. No significant differences were detected in the L layer.

For beech litter, comparisons between pure and mixed stands revealed a more conservative pattern, with few significant differences. In the L layer, significant differences were observed for A1154 and A1317 at a low significance level ($p < 0.05$), and for A1559 with a highly significant value ($p < 0.0001$). In the H layer, only A1711 showed a significant difference ($p < 0.01$), while no significant changes were detected in the F layer.

In Pine litter, the comparison between pure and mixed stands revealed significant differences for most of the wavenumbers analysed, particularly in the H layer. More precisely, for H layers peak intensities at A1233, A1259, A1317, A1370, A1445, A1711, A1729, and A2838 were significantly lower in the presence of deciduous litter compared to pure pine stands, but conversely, for A1031 and A1154, peak values were higher in mixed stands. Some differences were also detected in the L layer (A1031, A1729, A2838, and A2919) and in the F layer (A1154, A1317, and A1559), although these were less consistent and of lower statistical significance.

4. Discussion

4.1. *Transformation of forest floor Litter: Chemical and Molecular Changes Across Decomposition Stages*

Our results showed that TOC, TN, and the TOC/TN ratio in fresh litter varied significantly among species; however, these differences disappeared as litter underwent further transformation, particularly in the *F* and *H* layers. This pattern aligned with the *Chemical Convergence Hypothesis* in forest floor litter decomposition, which proposes that, despite initial differences in litter chemistry among species, decomposition processes lead to a progressive homogenization of organic compounds over time (Ayres et al., 2009). As labile compounds were rapidly degraded, microbial processing dominated, resulting in the accumulation of more recalcitrant and stable compounds, such as lignin derivatives and parahumic substances (Homann, 2012).

TOC/TN ratios tended to decrease along the decomposition gradient from L to H layers, showing significantly lower values in the H layer compared to the L and F layers, consistent with progressive carbon mineralization (Berg and McClaugherty, 2008). These patterns were observed in both pure and mixed stands. Notably, TOC/TN was significantly lower in the H layer of mixed stands compared to pure stands, suggesting that the effect of species mixture on C and N dynamics becomes more pronounced at advanced stages of litter decomposition. As decomposition progressed through the F and H layers, microbial activity and enzymatic processes promoted C mineralization and CO_2 release (Prescott et al., 2000), leading to a gradual decline in TOC. The lack of significant changes in TN and TP suggested that C dynamics were more sensitive to stand composition than N or P cycling.

Additional processes such as fragmentation, leaching, and microbial assimilation further contributed to the decline in TOC as litter transitioned through decomposition stages (Cotrufo et al., 2013). The *H* layer, representing the most advanced stage of decomposition, was dominated by highly processed, stabilized organic compounds, where increased microbial processing and humification resulted in a lower TOC content than in the *L* layer (Berg and McClaugherty, 2008). The accumulation of microbial-derived compounds and parahumic substances further altered the C composition, favouring recalcitrant forms over easily degradable C sources (Schmidt et al., 2011).

Molecular composition changes during decomposition were confirmed through ATR-FTIR analyses. The increase in aromatic peaks (A1512 cm^{-1}), associated with lignin and tannins (Tatzber et al., 2010, Tinti et al., 2015), suggested enhanced condensation and stabilization of aromatic compounds in advanced decomposition stages. Concurrently, signals corresponding to alkyl and methylene groups (A2838 cm^{-1} and A2919 cm^{-1}), indicative of lipids and waxes (Tatzber et al., 2010, Tinti et al., 2015), generally decreased as humification progressed, reflecting microbial degradation of labile components. Although no differences in aromaticity were observed among stand types in fresh litter (*L* layer) or in the most humified litter (*H* layer), variations in the *F* layer suggested that litter mixtures influenced microbial community activity, affecting the molecular composition of forest floor litter. For example, pine litter increased aromaticity in the *F* layer of pine-broadleaf mixed stands, whereas broadleaf litter mixed with pine needles had the opposite effect. These shifts highlighted the complex interactions between litter and microbes at the molecular scale (Song et al., 2010). The decrease in TOC content in the *F* and *H* layers did not indicate a regression in humification, but rather the progressive decomposition and mineralization of labile C compounds, leading to a net loss of TOC. However, as confirmed by our FTIR analysis, this process was accompanied by an increase in recalcitrant and aromatic compounds, consistent with the pre-humification process. Therefore, while TOC decreased overall, the remaining C pool became more chemically stable over time. It is important to note that, while ATR-FTIR provided valuable insights into chemical changes, it did not offer direct evidence of decomposition rates or microbial processes. These findings would benefit from complementary analyses (e.g. enzymatic activity, microbial community composition) to support the molecular-level patterns inferred here.

In addition to species composition, differences in site conditions such as altitude, latitude, and climate may influence decomposition rates. While our design controls for local variability, environmental gradients across the study sites may shape broader decomposition patterns and modulate the strength of species interaction effects in mixed forests.

4.2. *Effect of Pine Litter Presence on the Decomposition of Broadleaf Litter*

Our results indicated that the presence of pine litter delayed the decomposition of oak litter, particularly in the *F* layer of mixed oak-pine forests. This effect was evidenced by the higher TOC concentrations, the increase in peaks associated with aliphatic compounds (A2838 cm^{-1}, A2919 cm^{-1}) and C═O stretch (A1711 cm^{-1}, A1729 cm^{-1}), along with the decrease in the A1031 cm^{-1} peak, corresponding to polysaccharides, cellulose, hemicellulose, and soluble carbohydrates (Tatzber et al., 2010). Thai et al. (2024) reported that C═O functional groups in SOM became more pronounced with depth, reflecting progressive organic matter stabilization. This trend was linked to chemical transformations such as the oxidation of lignin-derived compounds and polyphenols, which contributed to the formation of more stable C pools in forest soils. The decline of the 1031 cm^{-1} peak indicated the enzymatic breakdown of polysaccharides, a process associated with C loss from more labile sources and the eventual accumulation of structurally complex organic residues. This pattern was consistent with the humification theory, which described the transformation of organic matter into more stable forms, in part through interactions with mineral surfaces. Zech et al. (1996) associated litter decomposition with an increase in aliphatic compounds (alkyl groups) and carboxyl groups, alongside a decrease in O-alkyl groups, observations that aligned with the findings of Tatzber et al. (2011) and the compositional changes reported by Thai et al. (2024). Moreover, our results showed that the effects of species mixture on C and N stocks varied with litter layer in oak stands. In pure oak stands, C and N stocks were significantly higher in the L and F layers, while in mixed stands, higher values were observed in the H layer. This shift may reflect a redistribution of organic matter and nutrients toward deeper layers under the influence of pine litter input.

The presence of pine litter in mixed stands can modulate decomposition dynamics through a combination of chemical, microbial, and structural factors (Bradford et al., 2016). Our results are consistent with this framework, suggesting that the delayed decomposition of oak litter may be influenced by the chemical composition of pine litter, rather than by climatic variability. However, this interpretation should be considered with caution, given the methodological limitations discussed earlier.

Nutrient availability is a key regulator of decomposition (Berg and McClaugherty, 2008). High TOC/TN ratios, low P content and recalcitrant compounds significantly slow decomposition (Bueis et al., 2018, Schimel and Hättenschwiler, 2007). Our study confirmed this, as the presence of pine litter, with its high TOC/TN ratio and initially low P content, likely created a nutrient-poor environment that restricted oak litter decomposition, consistent with Cheetri et al. (2012). Over time, microbial nutrient immobilization and biochemical accumulation increase P and N concentrations, facilitating decomposition, as observed in Spanish forest ecosystems (Martín et al., 1997). Beyond nutrient limitations, pine litter contains phenolic compounds, resins, and terpenes that chemically inhibit microbial activity, enzyme production, and lignin degradation, further slowing oak litter decomposition (Schimel and Hättenschwiler, 2007). This inhibition is well-documented, as phenolic compounds interfere with lignin degradation in oak leaves (Bueis et al., 2018), reinforcing our observations. In addition to chemical constraints, the physical structure of pine litter might further impede oak litter decomposition. Pine needles form dense mats that limit oxygen exchange and water infiltration, creating unfavourable microbial conditions (Lyu et al., 2019). Although some studies suggest pine needles increase moisture retention and facilitate decomposition (Song et al., 2010), our findings indicated that restrictive layering effects outweighed any potential benefits by impeding microbial colonization. These changes in nutrient stocks may further indicate that the chemical and microbial effects of pine litter not only slowed initial decomposition but also altered the vertical allocation of organic matter in broadleaf litter layers. Finally, microbial community composition influenced decomposition dynamics. In mixed stands, pine litter might have favoured microbial communities adapted to coniferous substrates, suppressing those essential for oak litter breakdown (Lin et al., 2021). While we did not analyse microbial community shifts in detail, future studies using high-throughput sequencing or PLFA analysis could provide further insights into microbial responses to litter mixing and their role in nutrient cycling.

4.3. *Effect of Broadleaf Litter Presence on Pine Litter Decomposition*

Our results indicated that the presence of broadleaf litter significantly enhanced the decomposition of pine needles, as evidenced by significantly lower TOC, TOC/TN ratios, and wavenumber peak values at A1233, A1259, A1317, A1370, and A1445 in the *H* layer of mixed oak–pine and beech–pine forests compared to pure pine stands. FTIR analysis of decomposing litter suggested that the chemical composition of pine litter in mixed forests changes more rapidly than in pure pine stands, potentially indicating an accelerated biochemical transformation. According to Thai et al. (2024), the reduction of these spectral peaks is associated with the degradation of ether-linked structures, phenolic compounds, and aliphatic C groups, which are characteristic of pine-derived organic matter. This suggested that broadleaf litter enhanced microbial activity and enzymatic degradation, facilitating the breakdown of recalcitrant C structures and increasing organic matter turnover in mixed stands. However, as FTIR provided indirect evidence of molecular changes through bond vibrations, caution is needed in interpreting these spectral shifts as definitive indicators of decomposition processes. These chemical patterns should be validated with complementary biochemical or microbiological data in future studies. Another possible explanation is nutrient transfer effects, where litter with higher N and P concentrations accelerated the decomposition of nutrient-poor litter (Kuzyakov et al., 2000, Liu et al., 2022, Seastedt, 1984). The high TOC/TN ratio and recalcitrant nature of pine needles typically limited microbial activity, leading to slower decomposition in pure pine forests (Prescott et al., 2000). However, under litter mixture conditions, broadleaf species may have compensated for these limitations by enhancing enzymatic activity and microbial processing of recalcitrant compounds (Song et al., 2010). These findings are supported by the patterns observed in carbon and nitrogen stocks. In pine litter, both C and N stocks were significantly lower in the F and H layers of mixed stands compared to pure stands. This provides additional evidence that the presence of broadleaf litter may enhance the decomposition of pine litter during intermediate and advanced stages.

4.4. Implications for Sustainable Forest Management

Our findings suggest that species composition may influence litter decomposition dynamics, particularly in mixed stands where coniferous and broadleaf species coexist. Mixed-species forests are known to enhance productivity through niche complementarity and facilitation effects (Bravo et al., 2019, Bravo-Oviedo et al., 2014, Pretzsch, 2009). The contrasting effects observed in litter mixtures, enhanced decomposition of pine needles and delayed decomposition of some broadleaf species, underscored the relevance of species-specific interactions for nutrient cycling and soil C dynamics. While most litter is mineralized and released as CO_2, a small fraction is incorporated into the soil, potentially contributing to the formation of humic substances and long-term SOM stabilization (Huys et al., 2022, Gallardo et al., 2011). Silvicultural planning should consider these interactions to optimize decomposition, nutrient availability, and soil structure. Adjusting species composition and stand density could improve ecosystem resilience, and incorporating species-specific decomposition patterns might support the development of ecologically balanced and functionally stable mixed forests (del Río et al., 2021, Liu et al., 2022).

Beyond species-specific effects on litter chemistry and nutrient release, this study also contributes methodologically by combining mid-infrared (ATR-FTIR) spectroscopy with elemental analyses to characterise forest floor litter in both pure and mixed stands. While the interpretation of ATR-FTIR spectra entails uncertainties, especially in the identification of specific functional groups, this integrative approach offers complementary insights into species-specific litter transformations. The joint use of molecular and elemental data enhances our understanding of how litter composition may influence soil organic matter dynamics and stabilization in mixed-species forest ecosystems.

5. Conclusions

This study suggests that species composition may influence litter decomposition dynamics in mixed forests, with interactions that appear to be litter-type specific. In our conditions, broadleaf litter inputs seemed to enhance pine needle decomposition in advanced stages, while potentially slowing the decomposition of the broadleaf litter itself when compared to pure stands. Oak litter appeared particularly sensitive to the presence of pine needles during intermediate decomposition (F layer), whereas patterns observed in the later stages (H layer) were less consistent and should be interpreted cautiously, given the advanced decomposition state and the difficulty in attributing litter origin. In contrast, beech litter decomposition showed little evidence of inhibition by pine needles, which may indicate a higher microbial tolerance to conifer-derived material. The apparent stimulation of pine litter decomposition in the H layer when broadleaf litter was present could be related to enhanced nutrient availability or microbial activity, although these interpretations remain tentative. Overall, our findings highlight the potential for species interactions to shape decomposition processes in mixed stands, while also underscoring the need for complementary microbiological or enzymatic analyses to better understand the underlying mechanisms.

Statements and declarations

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CRediT authorship contribution statement

Turrión M. Belén: Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Valentín Pando:** Writing – review & editing, Formal analysis, Data curation. **Francisco Lafuente:** Writing – review & editing, Validation, Methodology, Investigation, Conceptualization. **Ruth C. Martín-Sanz:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Formal analysis, Data curation. **Marina Getino-Álvarez:** Writing – review & editing, Validation, Methodology, Funding acquisition, Formal analysis.

Authors' Contributions

MGA carried out field and laboratory work. FLA and RCMS supported MGA with the laboratory analysis. VPF carried out the statistical analysis. MBTN wrote the manuscript and prepared figures. MBTN, RCMS, MGA and FLA discussed the results and wrote the discussion. RCMS edited and submitted the manuscript. RCMS has been the correspondence author. MBTN coordinated the research project.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: M.-Belen Turrion reports financial support was provided by Spanish Ministry of Economy and Competitiveness. Marina Getino-Alvarez reports financial support was provided by Spanish Ministry of Economy and Competitiveness. Marina Getino-Alvarez reports financial support was provided by European Union Horizon 2020 - Marie Sklodowska-Curie grant No 778322. Ruth C. Martin-Sanz reports financial support was provided by European Regional Development Fund and Junta de Castilla y León. 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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123038.

Data availability

Data will be made available on request.

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