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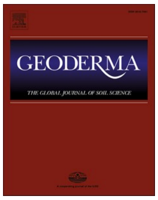

Seasonal effects of altitude and vegetation on litter and organic carbon in deciduous and coniferous forest soils

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ABSTRACT

This study investigated seasonal changes in litter and soil organic carbon contents of deciduous and coniferous forests at two altitudes (500 and 1000 m a.s.l.), which were used as proxies for temperature changes. To this aim, adjacent pine (P500 and P1000) and deciduous forests (downy oak forest at 500 m a.s.l. and beech forest at 1000 m a.s.l., D500 and D1000, respectively) were selected within two areas along the western slope of a calcareous massif of the Apennine chain (central Italy). Periodic sampling was carried out within each site (a total of 19 sampling dates: 6 in autumn, 4 in winter and spring, and 5 in summer), taking each time an aliquot of the upper mineral soil horizon and measuring litter thickness and CO_2 emission from the soil. The samples were then analyzed for their content of organic C, total N, water-soluble organic C and N (WEOC and WEN, respectively), and the natural abundance of ^{13}C and ^{15}N. Soil and litter C and N stocks were calculated. The chemical and isotopic data suggested that organic C and N transformations from litter to the upper mineral soil horizon were controlled not only by temperature but also by the quality (i.e. C:N ratio) of the plant material. In particular, the more the temperature decreased, the more the quality of the organic matter would influence the process. This was clearly showed by the greater ^{13}C fractionation from litter to soil organic matter (SOM) in D1000 than in P1000, which would indicate a higher degree of transformation under the same thermal condition of the plant residues from the deciduous forest, which were characterized by a more balanced C:N ratio than the pine litter. However, while at 500 m altitude a significant SOM ^{13}C fractionation and a parallel increase in soil CO_2 emissions occurred in the warmer seasons, no seasonal $\delta^{13}C$ variation was observed at 1000 m for both forests, despite the different quality of SOM derived from deciduous and coniferous forests. Our findings suggested that organic C and N transformations from litter to the upper soil mineral horizon were greatly controlled by the quality of the plant residues, whereas soil temperature would seem to be the major driver for the seasonal evolution of SOM.

This study, by considering two different vegetation types (deciduous and coniferous), allowed to evaluate the combined interactions between the plant residue quality and temperature in controlling litter and SOM mineralisation/accumulation processes.

1. Introduction

Forests cover about 4 billion hectares globally and, roughly, 25 % of them are located in Europe (Faostat, 2023). Forests are important reservoir of atmospheric carbon (C), where about 44 % is stored as soil organic matter (Pan et al., 2011) and accounts for about half of the total organic C in terrestrial ecosystems. (Mayer et al., 2020). Because of its great storage capacity, soils play a pivotal role in the global C cycle, and slight changes in the soil organic carbon (SOC) dynamic can lead to meaningful alterations in the atmospheric CO_2 concentrations (Morisada et al., 2004; Hoffmann et al., 2014). To date, a growing number of studies have been published investigating the effect of key drivers such as climate, land cover or topography on SOC content and dynamics (e.g., Smith et al., 2018; Adiyah et al., 2022; Saputra et al.,

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2022; Nave et al., 2022). Among them, the altitudinal gradient across relatively small spatial scales has been used to predict the changes in SOC dynamics along large-scale climatic gradients (Choudhury et al., 2016; De Feudis et al., 2016; Nottingham et al., 2019). The forest SOC stocks generally increase with altitude due to the lower decomposition of soil organic matter (SOM) at the colder high-elevation sites (Tashi et al., 2016; De Feudis et al., 2016; Massaccesi et al., 2020). Altitude has a negative effects on primary production, which results in a decline of litterfall (Chimdessa, 2023; Blanco et al., 2006) and a reduction of the rate of SOC mineralisation greater than that of plant biomass production (De Feudis et al., 2016; Choudhury et al., 2016; Cardelli et al., 2019; Kumar et al., 2021). Furthermore, the quality of plant residues is affected by altitude, which causes changes in vegetation and an increase in the proportion of aliphatic compounds, such as waxes and glycerides (Djukic et al., 2010; Yao et al., 2021). These compounds exhibit high resistance to degradation and contribute to SOC stabilisation (Piccolo et al., 1999; Lorenz et al., 2007). Altitude can also affect the quality and proportion of soil organic matter (SOM) pools (De Feudis et al., 2017; De Feudis et al., 2019) which respond to environmental factors according to their different stability (Hakkenberg et al., 2008; Fissore et al., 2009; De Feudis et al., 2019). At least as the climate, also the type of vegetation plays a role in the accumulation of SOC and its degradation by soil microbial community (Vesterdal et al., 2013; Kooch et al., 2017; Józefowska et al., 2017). Indeed, plant species differently influence SOC dynamics due to the quantity and quality of litter input, and direct and indirect interactions with soil particles and soil biota (Reich et al., 2005; Mueller et al., 2012; Frouz et al., 2009, 2013; Prescott and Grayston, 2013; Mayer et al., 2020). Tree species (i.e., broadleaves or conifers) has been recognized as an important driver for amount and transformation processes of SOC, especially in the upper horizons (Augusto et al., 2015; Dawud et al., 2017). For example, the meta–analysis conducted by Rehschuh et al. (2021) showed a higher SOC accumulation under conifer than under beech forest, which was attributed to the different plant productivity, quantity and decomposition rate of both aboveground and root litter (Augusto et al., 2015).

Because of the large amounts of C stored in soils, about 98 Pg C year^{-1}, which is about ten times the carbon emission rate from fossil fuel combustion (IPCC, 2013), is released to the atmosphere mainly in the form of CO_2 through the respiration of roots and soil organisms (Hanson et al., 2000; Bond-Lamberty and Thomson, 2010; Berisso et al., 2013). Although previous studies have reported that soil respiration is mostly driven by soil temperature (Lellei-Kovács et al., 2011) and plant species composition (Badraghi et al., 2021) there is still uncertainty about which abiotic and biotic factors affect soil respiration under field conditions. The occurrence of a positive relationship between soil temperature and CO_2 efflux rate from soil is generally well acknowledged and it is attributed to the enhancement of the activity of roots and soil organisms (microbial communities and soil dwelling organisms) with increasing temperature (Subke et al., 2003). Tree species affect SOC decomposition rates and soil respiration through the release of organic residues, both as litterfall and rhizodepositon (Olsson et al., 2012), which shape the size, activity and structure of the microbial biomass (Paterson, 2003; Paterson et al., 2007; Lorenz and Thiele-Bruhn, 2019; Zheng et al., 2022). However, the results of many studies on the influence of tree species on soil respiration are inconsistent. In fact, while some studies highlighted that broadleaf forests have higher soil respiration rates than coniferous forests (Raich and Tufekcioglu, 2000; Růžek et al., 2021), other studies did not find any difference in soil respiration between temperate deciduous and coniferous species (Subke et al., 2006; Pandey et al., 2023).

All the aforementioned studies on SOC dynamics and soil respiration did not consider the effect of the season. In fact, the environmental factors (e.g., climate, land cover, topography) also govern variation in the intra-annual dynamics of carbon in the forest ecosystems (Kang et al., 2003; Riveros-Iregui et al., 2012; Stielstra et al., 2015). In particular, the differential climatic conditions throughout the seasons take a decisive control on tree physiology (Rasche et al., 2011). For example, the root activity (i.e., respiration and belowground C allocation) is generally higher in spring and autumn (Montagnoli et al., 2019). However, the importance of the season on vegetation is greatly affected by the type of vegetation itself. In temperate climates, deciduous forests are characterized by an active plant biomass production during the spring and summer periods followed by a short period of litterfall in autumn, when plant residues accumulate on the forest floor. Conversely, coniferous forests are characterized by a longer vegetative period resulting in a larger accumulation of litter on soil surface (Vořiškova et al., 2014, Žifčáková et al., 2016). The seasonal changes in plant activity could also affect the soil microbial communities involved in SOC turnover (Koranda et al., 2013), which in turn are directly influenced by seasonal changes in abiotic factors, such as soil temperature (Siles et al., 2016).

Together, these changes in environmental factors (i,e., temperature and vegetation) might result in differential trends in SOC cycling. Consequently, an investigation of the changes in SOC along an altitudinal gradient and throughout the seasons would be helpful to minimize uncertainty in future soil carbon feedback projections. Therefore, this study aimed to evaluate the changes in litter and soil organic carbon contents over one calendar year in adjacent deciduous and coniferous forests at two altitudes (500 and 1000 m a.s.l.) which were used as proxies of temperature change. We hypothesized that (1) soil temperature drives SOC mineralization/accumulation processes in both forests; (2) deciduous forests promote lower SOC accumulation than coniferous forests; and (3) the driving role of temperature on organic C stored in litter and soil is modulated by vegetation.

2. Materials and methods

2.1. Study sites

Two areas at about 500 and 1000 m a.s.l. were identified along the western slope of Monte Cucco, a calcareous massif of the Apennine chain (central Italy). Within each area, two adjacent forests were chosen, one consisting of a pine (*Pinus nigra* J.F. Arnold) reforestation established in the late 1970s (P500 and P1000, respectively at 500 and 1000 m altitude), and the other of native deciduous species, specifically a mixed forest dominated by downy oak (*Quercus pubescens* Willd.) at 500 m (D500) and a beech (*Fagus sylvatica* L.) forest at 1000 m a.s.l. (D1000). All the deciduous forests were coppices, although they were no longer managed for at least two decades. The soil cover due to litter layer was almost complete and the coverage due to understory ranged from 5 to 30 %, with very limited signs of erosion. The mean annual air temperature and mean annual precipitation at the altitude of 500 and 1000 m range from 13.6 to 10.8 °C and from 1100 mm to about 2000 mm, the latter mainly in form of snow, respectively. The general features of the study areas were reported in Table 1.

2.2. Soil, bulk density determination and soil temperature measurement

The soils of the study areas developed from marly limestone. After a soil survey carried out to minimize the influence due to the unavoidable soil spatial variability, within an area of about 400 m^2 for each altitude and forest type, three profiles were excavated (in total: 3 profiles × 2 forest types × 2 elevations = 12 profiles). The soil morphologies were described per Schoeneberger et al. (2012) (Table S1) and the soils were classified, according to Soil Taxonomy, as Typic Humustepts (Soil Survey Staff, 2022).

The determination of the bulk density of the upper 10-cm soil layer, which comprised the A and sometimes a small portion of the AB horizons, was carried out when the soil profiles were exposed by the core method, using steel cylinders (height: 51 mm; diameter: 50 mm). The samples were collected in duplicate from the upper 10-cm soil layer of each profile and, once in the laboratory, dried at 105 °C to a constant

Table 1
General features of the study sites under deciduous and pine forests at two altitude (500 and 1000 m a.s.l.). Mount Cucco massif, Central Apennines, Italy.

	500 m a.s.l.		1000 m a.s.l.	
	Deciduous forest	Pine forest	Deciduous forest	Pine forest
Coordinates	43°16′57″ N, 12°45′39″ E	43°16′58″ N, 12°45′38″ E	43°23′36″ N, 12°42′31″ E	43°22′53″ N, 12°42′48″ E
Exposure	W-NW	W	W-SW	W-SW
Mean slope	20°	20°	25°	30°
Soil T[a]	12.5 °C		10.0 °C	
MAAT	13.6 °C		10.8 °C	
MAP	1100 mm		2000 mm	
Parent material	Marly limestone with layers of flintstone		Marly limestone with layers of flintstone	
Dominant trees	*Quercus pubescens Willd.* (60 %), *Fraxinus ornus L., Ostrya carpinifolia Scop.*	*Pinus nigra J.F. Arnold* (90 %), *Fraxinus ornus L., Quercus pubescens Willd.*	*Fagus sylvatica L.* (90 %), *Acer campestre L., Quercus cerris L., Prunus avium L.*	*Pinus nigra J.F. Arnold* (80 %), *Acer opalus subsp. obtusatum (Waldst. & Kit. ex Willd.) Gams, Acer pseudoplatanus L., 1753, Sorbus aria (L.) Crantz, Quercus spp.*
Understory	*Brachypodium rupestre (Host) Roem. & Schult, Lonicera caprifolium L, Cotynus cogygria Scop., Citisus sessilifolius L. 1753, Asparagus acutifolius L., Carex flacca Schreb., seedlings.*	*Brachypodium rupestre (Host) Roem. & Schult, Spartium junceum L., seedlings.*	*Aegopodium podagraria L., Arctium lappa L., 1753*	*Brachypodium rupestre (Host) Roem. & Schult, Lonicera xylosteum L., Viola alba subsp. dehnhardtii (Ten.) W. Becker, Daphne laureola L.*
Soil[b]	loamy-skeletal, mixed, mesic, Typic Humustepts	loamy-skeletal, mixed, mesic, Typic Humustepts	loamy, mixed, mesic, Typic Humustepts	loamy-skeletal, mixed, mesic, Typic Humustepts

[a] Soil temperatures were measured (at 10 cm depth) from October 2017 to November 2018.

[b] Soil Survey Staff. Keys to Soil Taxonomy, 13th ed.; USDA—Natural Resources Conservation Service: Washington, DC, USA, 2022.

weight. Bulk density was calculated from the ratio of dried mass to cylinder volume and corrected for rock fragments (fraction larger that 2 mm) content by the following calculation:

$$\mathrm{BD}\ (\mathrm{kg\ dm^{-3}}) = (\mathrm{mt}\ [\mathrm{kg}] - \mathrm{mr}\ [\mathrm{kg}])\ /\ (\mathrm{vt}\ [\mathrm{dm^{-3}}] - \mathrm{vr}\ [\mathrm{dm^{-3}}]),$$

where BD is the bulk density, *mt* and *vt* are respectively the mass and volume of the sample collected by the steel cylinder, and *mr* and *vr* are respectively the mass and volume of rock fragments contained in the sample.

In order to assess the C and N supplied by the deciduous and pine forests at the two altitudes, twelve samples of the litter layer, consisting of both Oi and Oe horizons, were randomly taken from each plot. The Oi horizon consisted of undecomposed or slightly decomposed plant residues (fibric material), while the Oe horizon consisted of partially physically and biochemically altered residues (hemic material) (Soil Survey Staff, 2022). A 40 × 40 cm sampling frame was used to collect the litter layers. Briefly, the sampling frame was placed on the forest floor and all the litter within the frame and down to the soil-litter interface was collected, placed in plastic bags and taken to the laboratory and oven-dried at 105 °C. Further, the bulk density of the litter layer, was estimated by considering the collected mass (105 °C), layer thickness and sampling surface (De Feudis et al., 2022).

With the aim to monitoring the soil temperature at the two altitudes, temperature loggers (iButton DS 1922l-F5#, iButtonLink, USA) were installed in the soil of the study areas at a depth of 10 cm. The soil temperature was recorded daily (averaging four measurements per day) from October 2017 to November 2018.

2.3. *Periodic soil sampling, and litter thickness and CO_2 fluxes measuring*

Over thirteen months (October 2017-November 2018), the three plots within each site were periodically sampled (a total of 19 sampling dates: 6 in autumn, 4 in winter and spring, and 5 in summer) by opening a mini-pit and taking an aliquot of the upper 10-cm mineral soil layer, carefully avoiding collecting any of the overlying organic horizon. Once in the laboratory, the soil samples were air-dried, deprived of the visible roots and sieved through a 2-mm mesh.

In addition, at each plot and for each sampling date, the litter thickness was determined by a ruler and averaging eight randomly distributed measurements, whereas the CO_2 emissions from soil to atmosphere were obtained by using an EGM4 portable analyzer (PP System, USA) equipped with an SRC-1 air circulation chamber and averaging three randomly distributed measurements.

2.4. *Chemical and isotopic analyses*

The C and N contents of the litter were determined after the collected whole samples were ground by a knife mill until they passed through a 1-mm sieve, by using a Thermo Flash 2000 CN elemental analyzer (Thermo Fisher Scientific, USA). The total organic C content (TOC) of the soil samples was assessed by digestion with K-dichromate, heating the suspension at 180 °C for 30 min (Nelson and Sommers, 1996), while the total N content (TN) was determined using a Thermo Flash 2000 CN elemental analyzer (Thermo Fisher Scientific, USA). The content of water-soluble organic C and N (WEOC and WEN, respectively) in the soil samples was determined by soaking an aliquot of each sample in distilled water (solid/liquid ratio of 1:10) and shaking for 12 h with an orbital shaker (140 rpm). The mixture was centrifuged at 1400 g for 10 min and then filtered through Whatman 42 filter paper. The resulting solution was analyzed for its WEOC and WEN content by the elemental analyzer after acidification of the solution with a few drops of concentrated H_3PO_4. The available soil P (P_{av}) was estimated according to Olsen et al. (1954).

The natural abundance of ^{13}C and ^{15}N in soil and litter samples was determined using Continuous Flow-Isotope Ratio Mass Spectrometry (CF-IRMS). Aliquots of samples were weighed into silver capsules, treated with 2 M HCl solution to remove inorganic C, dried at 60 °C, and then combusted in an O_2 stream using an elemental analyzer (Thermo Flash 2000 CN, Thermo Fisher Scientific, USA). The CO_2 and N_2 produced were then analyzed by an isotope ratio mass spectrometer (IRMS, Delta V Advantage, Thermo Fisher Scientific, USA). The obtained values were expressed as $\delta^{13}C$ and $\delta^{15}N$:

$$\delta^{13}C = [(^{13}C/^{12}C_{sample} - {}^{13}C/^{12}C_{standard})/(^{13}C/^{12}C_{standard})] \times 10^3$$

$$\delta^{15}N = [(^{15}N\ /^{14}N_{sample} - {}^{15}N/^{14}N_{standard})/(^{15}N/^{14}N_{standard})] \times 10^3$$

relative to the international reference standard V-PDB (Vienna Pee Dee Belemnite standard) and atmospheric N_2, respectively.

2.5. *Stock calculation*

The C and N stocks of the litter layer of deciduous and pine forests at the two elevations were calculated by multiplying the C and N concentration by bulk density and thickness of the layer, which was measured at each sampling date.

Stocks of organic C and total N accumulated in the upper 10 cm of mineral soil for each elevation and forest type were calculated by multiplying the concentration of C and N by the bulk density and considered thickness (10 cm) using the following formula (De Feudis et al., 2022):

Stock Mg ha^{-1} = E (g kg^{-1}) × BD (kg dm^{-3}) × (1- VG) x S (m) × 10

where E is the element considered (organic C or total N), BD is the bulk density, VG is the content of coarse fragments (fraction greater than 2 mm) expressed in % by volume and evaluated during the soil description, S is the thickness of the horizon considered, 10 is a conversion factor to express the value of the stock in Mg ha^{-1}.

2.6. *Statistical analysis*

With regard to the seasonal soil and litter sampling, the data obtained from the three plots within each site (D500, P500, D1000, P1000) were averaged, so that the replicates corresponded to the number of samplings within each season (6 for autumn, 4 for winter and spring, and 5 for summer).

To test separately 1) the effects of altitude and forest type within each season and 2) the effects of season and forest type within each altitude (500 m and 1000 m a.s.l.), two distinct two-way ANOVAs were performed on the measured variables. As for soil isotopic data, differences between altitude, forest type and season were analyzed simultaneously through a three-way ANOVA. All the statistical analyses were performed using R (R Core Team, 2020). Before performing the ANOVA analysis, the graphical analysis of residuals was used to verify the normality and homoscedasticity of the data which were transformed when necessary. The transformation was selected by the maximum likelihood procedure suggested by Box and Cox (1964), as implemented in the boxcox function of the package MASS (Venables and Ripley, 2002). The multiple comparison test were carried out according to Fisher's Least Significant Difference (FLSD) with a significance level of 0.05. For the graphical representation of the effect of altitude and forest type on some of the measured variables along the seasons, non-metric multidimensional scaling (NMDS) analyses were performed by the R package "vegan" with the dissimilarity matrix calculated by the Gower's distance. In particular the NMDS analysis was run on the following variables: TOC, TN, WEOC, WEN, C:N ratio, P_{av}, $\delta^{13}C$, $\delta^{15}N$, litter thickness and CO_2 efflux. Before performing the NMDS analysis, the data were standardized by subtracting the mean and dividing by the standard deviation.

3. Results

3.1. *Soil temperature, thickness of the litter layers and CO_2 emissions from soils under deciduous and pine forest at 500 m and 1000 m altitude*

In the two study areas, the average annual soil temperature measured at a depth of 10 cm was 12.5 °C at 500 m and 10.0 °C at 1000 m a.s.l., very close to the values of the air temperature at the two altitudes. The minimum soil temperatures were recorded in the winter season, both at 500 m (5.97 °C) and at 1000 m (3.03 °C), while the highest ones were those in summer with values of 19.11 and 17.05 °C at 500 m and 1000 m, respectively (Table 2). In the sites at 1000 m, the soil temperature was always lower than that of the sites at 500 m with the maximum gap (about 3 °C on average) occurring in the winter seasons (Table 2).

Table 2
Seasonal soil temperatures (10 cm depth) at study sites located at 500 m and 1000 m a.s.l. on Mount Cucco massif (Central Apennines, Italy). Standard error is given in parentheses (Fall n = 118; Winter n = 89; Spring n = 91; Summer n = 91). Different letters indicate a significant difference according to Fisher's LSD test ($p < 0.05$).

Altitude	Autumn	Winter	Spring	Summer
	°C			
500 m	12.14 (0.83)^c	5.97 (0.17)^f	12.77 (0.41)^c	19.11 (0.15)^a
1000 m	9.07 (0.34)^e	3.03 (0.15)^g	10.82 (0.45)^d	17.05 (0.15)^b

The thickness of the litter layer showed a general decreasing trend from autumn-winter to spring-summer seasons for both forests and altitudes. Considering the individual seasons, the litter thickness of P500 was higher than that of D500 for all seasons, with the exception of spring where they showed comparable values. At 1000 m the litter thickness of broadleaf and pine forests differed only in winter. Regarding the altitude effect, going from 500 to 1000 m, deciduous forest showed an increase in litter thickness all throughout the year, whereas pine litter have statistically significant positive changes in its thickness only in winter and spring (Table 3).

At both altitude and vegetations, the lowest CO_2 emissions from soil to atmosphere were recorded in the winter season (Table 4). During the cold seasons, at both 500 and 1000 m altitude, CO_2 fluxes from soil did not show significant differences between the two forest ecosystems. Conversely, in spring and summer, when the highest values were recorded at both elevations, CO_2 releases from soil were greater for D500 (0.67 and 0.64 g CO_2 $m^{-2}h^{-1}$, respectively) and for P1000 (0.30 and 0.27 g CO_2 $m^{-2}h^{-1}$, respectively) than for P500 and D1000, respectively.

The CO_2 released from the soil under the deciduous forests diminished with increasing elevation in all seasons, whereas the CO_2 fluxes under pine forests decreased at higher elevation in autumn and winter and did not show any statistically significant changes going from 500 to 1000 m altitude in spring and summer (Table 4).

3.2. *Chemical properties of the litter and soil under deciduous and pine forest at 500 m and 1000 m altitude*

The litter layer of the deciduous forest had a lower C concentration and a higher N concentration than that of the pine forest at both 500 m and 1000 m (Table 5). Consequently, the pine litter had a higher C:N ratio than the deciduous litter at both altitudes. The total soil organic carbon (TOC) did not vary significantly through the seasons with exception of D1000 m where TOC content increased from autumn to winter (Table 6). According to the vegetation type, at 500 m the uppermost soil layer under the deciduous forest always had a 22–30 % higher TOC content than that of the pine forest. Conversely, at 1000 m, the soil under pine forest showed larger TOC contents, except for spring where the values were not statistically different between the two forest types. By comparing the different altitudes within each season, while under pine forest the TOC content was always larger at 1000 m than at 500 m, under the broadleaf forest some differences occurred only in autumn, showing greater TOC concentrations at the lower elevation than at the higher one (Table 6).

The total nitrogen (TN) content reached the highest values in winter and spring in D500, and in winter for the soil under the pine forest (Table 6). Comparing the two types of vegetation within each season, as seen for the TOC, the soil under the deciduous forest showed a decreasing TN concentration with increasing elevation in all seasons, while the opposite occurred for the soil under pine forests.

At 500 m, along the year the soil C:N ratios were the highest in autumn and summer both for deciduous and pine forest, whereas at 1000 m no differences occurred. Comparing the two types of vegetation within each season some differences were found at 1000 m where the soils under beech showed always greater values than those under pine forest. Within each season, while under the deciduous forest the soil C:N ratio had always higher values at 1000 m than at 500 m, under the pine forest there were no significant differences between altitudes, except for the slight increase recorded in winter (Table 6).

At 500 m altitude, the available phosphorus (P_{av}) content did not vary significantly over the seasons for the pine forest soil, while slightly

Table 3
Seasonal thickness of the litter layer under deciduous and pine forests at study sites located at 500 m and 1000 m a.s.l., Mount Cucco massif (Central Apennines, Italy). Standard error is given in parentheses (autumn n = 6, winter n = 4, spring n = 4, summer n = 5). Different letters indicate a significant difference according to Fisher's LSD test ($p < 0.05$) within each individual season (lowercase letters) and throughout the sampling period for each individual elevation (uppercase letters).

Altitude	Autumn		Winter		Spring		Summer	
	Deciduous forest cm	Pine forest	Deciduous forest	Pine forest	Deciduous forest	Pine forest	Deciduous forest	Pine forest
500 m	3.7 (0.2)$^{b, BC}$	5.2 (0.2)$^{a, A}$	3.8 (0.3)$^{c, B}$	4.9 (0.23)$^{b, A}$	3.2 (0.2)$^{c, CD}$	3.6 (0.2)$^{bc, BC}$	2.9 (0.2)$^{b, D}$	3.6 (0.2)$^{a, BC}$
1000 m	5.7 (0.2)$^{a, A}$	5.8 (0.3)$^{a, A}$	4.9 (0.23)$^{b, B}$	6.1 (0.4)$^{a, A}$	4.0 (0.2)$^{ab, C}$	4.2 (0.2)$^{a, BC}$	3.6 (0.3)$^{a, C}$	3.4 (0.3)$^{ab, C}$

Table 4
Seasonal carbon dioxide emissions from soils under deciduous and pine forests at study sites located at 500 m and 1000 m a.s.l., Mount Cucco massif (Central Apennines, Italy). Standard error is given in parentheses (autumn n = 6, winter n = 4, spring n = 4, summer n = 5). Different letters indicate a significant difference according to Fisher's LSD test ($p < 0.05$) within each individual season (lowercase letters) and throughout the sampling period for each individual elevation (uppercase letters).

Altitude	Autumn		Winter		Spring		Summer	
	Deciduous forest g CO_2 $m^{-2}h^{-1}$	Pine forest	Deciduous forest	Pine forest	Deciduous forest	Pine forest	Deciduous forest	Pine forest
500 m	0.33 (0.07)$^{a, B}$	0.35 (0.07)$^{a, B}$	0.11 (0.04)$^{a, C}$	0.12 (0.04)$^{a, C}$	0.67 (0.22)$^{a, A}$	0.44 (0.12)$^{ab, AB}$	0.61 (0.07)$^{a, A}$	0.47 (0.08)$^{b, AB}$
1000 m	0.16 (0.05)$^{b, BC}$	0.25 (0.06)$^{ab, AB}$	0.03 (0.01)$^{b, E}$	0.05 (0.01)$^{b, DE}$	0.14 (0.05)$^{c, C}$	0.30 (0.08)$^{b, A}$	0.19 (0.02)$^{c, B}$	0.26 (0.02)$^{bc, A}$

Table 5
Contents of carbon and nitrogen and C/N ratio of the litter layer (Oi/Oe horizons) of the broadleaf and pine forests at 500 and 1000 m a.s.l., Mount Cucco massif (central Apennines, Italy). Within each variable, different letters indicate significant differences according to Fisher's LSD test ($p < 0.05$). Numbers in parentheses are the standard errors (n = 12).

Altitude	Broadleaf forest			Pine forests		
	C g kg^{-1}	N g kg^{-1}	C/N ratio	C g kg^{-1}	N g kg^{-1}	C/N ratio
500 m	417.81 (6.18)^{b}	10.75 (0.52)^{b}	39.71 (0.83)^{b}	474.82 (8.28)^{a}	7.53 (0.19)^{c}	62.88 (2.87)^{a}
1000 m	366.63 (10.49)^{c}	17.56 (0.41)^{a}	20.95 (0.51)^{c}	471.81 (5.92)^{a}	12.17 (1.13)^{b}	43.49 (5.28)^{b}

higher values were recorded in summer and autumn for D500 (Table 6). At 1000 m, the P_{av} concentration in both forest soils increased with respect to the lower altitude, with the highest values recorded in winter and summer for the deciduous forest and in summer for the pine forest. The increase of P_{av} content at 1000 m was most evident for the soil under deciduous forest, where the values (about three to six fold higher than at 500 m) were larger than that of the soil under pine forest in all seasons.

The water extractable organic carbon (WEOC) content of the soils under both vegetation types showed the highest values in winter and no significant difference between the two altitudes, except in autumn for the deciduous forest soil. (Table 7). Comparing the two types of vegetation within each season, the soil under deciduous and pine forests had similar WEOC content at both elevations all along the year, with one only exception in autumn where the D500 showed greater content of soluble organic C than P500. Water extractable nitrogen (WEN) showed the highest values in winter at both altitudes for deciduous and pine forests (Table 7).

3.3. δ^{13}C and δ^{15}N of litter and soil under deciduous and pine forest at 500 m and 1000 m altitude

The litter ^{13}C and ^{15}N isotopic values were similar for both deciduous and pine forests at 500 m altitude, with average values around –28.5 ‰ for δ^{13}C and –4.6 ‰ for δ^{5}N (n = 12; Fig. 1a). Conversely, litter values were markedly different at 1000 m. Pine litter at this altitude was enriched in ^{13}C by + 1.2 ‰ (–27.3 ‰) and ^{15}N by + 1.7 ‰ (–2.9 ‰), but beech litter the was lower in ^{13}C by −0.5 ‰ (–29.0 ‰) but higher in ^{15}N by + 3.9 ‰ for (–0.7 ‰) (Fig. 1a).

Soil δ^{13}C and δ^{15}N values were higher than those of the litter, with the most pronounced differences for ^{13}C in the beech forest at 1000 m and for ^{15}N in both forest types at 500 m (Fig. 1b). Forest soil δ^{13}C signatures between 500 and 1000 m altitude were significantly different (Fig. 1b). The δ^{13}C of the soil at 500 m under the deciduous forest had a small although significant increasing trend going from autumn ($\delta^{13}C =$ –27.1 ‰) to summer ($\delta^{13}C = –26.8$ ‰). This was not the case for the pine where δ^{13}C values were similar along all seasons ($\delta^{13}C \approx –27.0$ ‰). Soil δ^{15}N values at 500 m were higher in the deciduous forest than in the pine forest for most seasons. The highest δ^{15}N values were measured in spring, and were not significantly different in deciduous (1.3 ‰) and pine (1.5 ‰) forests. The lowest δ^{15}N values occurred in autumn under pine and in summer under deciduous wood (–1.6 and –0.9 ‰, respectively) (Fig. 1b).

The δ^{13}C values at 1000 m under both vegetations were larger than at 500 and did not change throughout the year, although they were differentially grouped in Fig. 1b. The deciduous forest soil showed values of δ^{13}C ranging from –26.4 to –26.5 ‰, whereas the soil under pine had values around –26.2 ‰. The natural abundance of soil ^{15}N under pine did not show significant seasonal changes, but under deciduous forest ranged from 3.2 ‰ in autumn to –1.2 ‰ in summer (Fig. 1b).

Table 6

Total organic carbon (TOC) and total nitrogen (TN) contents, C/N ratios, and available phosphorous (P_{av}) contents the soils under deciduous and pine forests at study sites located at 500 m and 1000 m a.s.l., Mount Cucco massif (Central Apennines, Italy). Standard error is given in parentheses (autumn n = 6, winter n = 4, spring n = 4, summer n = 5). Different letters indicate a significant difference according to Fisher's LSD test ($p < 0.05$) within each individual season (lowercase letters) and throughout the sampling period for each individual elevation (uppercase letters).

	Altitude	Autumn		Winter		Spring		Summer	
		Deciduous forest	Pine forest	Deciduous forest	Pine forest	Deciduous forest	Pine forest	Deciduous forest	Pine forest
TOC (g kg^{-1})	500 m	96.38 (7,39)$^{ab,\ A}$	75.34 (3.98)$^{c,\ B}$	104.39 (5,62)$^{b,\ A}$	73.38 (1,44)$^{c,\ B}$	94.93 (4,71)$^{b,\ A}$	68.53 (2.44)$^{c,\ B}$	94.48 (2,05)$^{b,\ A}$	70.00 (3.00)$^{c,\ B}$
	1000 m	81.38 (7.49)$^{c,\ D}$	113.37 (6.46)$^{a,\ AB}$	97.69 (0,40)$^{b,\ C}$	121.12 (2.06)$^{a,\ A}$	98,17 (0.51)$^{b,\ BC}$	113.96 (4.71)$^{a,\ AB}$	99.46 (1,68)$^{b,\ BC}$	125.80 (3.81)$^{a,\ A}$
TN (g kg^{-1})	500 m	7.79 (0.47)$^{a,\ BC}$	5.19 (0.12)$^{b,\ E}$	9.71 (0.37)$^{a,\ A}$	6.87 (0.54)$^{b,\ C}$	8.88 (1,81)$^{a,\ AB}$	5.97 (0.73)$^{ab,\ DE}$	6.93 (0.17)$^{b,\ C}$	5.48 (0.19)$^{c,\ DE}$
	1000 m	3.81 (0.17)$^{c,\ E}$	7.34 (0.32)$^{a,\ C}$	5.18 (0.57)$^{c,\ D}$	9.68 (0.38)$^{a,\ A}$	4.76 (0.42)$^{b,\ DE}$	7.71 (0.50)$^{a,\ BC}$	4.40 (0.12)$^{d,\ DE}$	8.25 (0.23)$^{a,\ B}$
C/N	500 m	12.42 (0.74)$^{c,\ BC}$	14.55 (0.79)$^{bc,\ A}$	10.82 (0.84)$^{c,\ C}$	10.88 (0.85)$^{c,\ C}$	11.52 (1,39)$^{c,\ BC}$	11.80 (0.89)$^{c,\ BC}$	13.65 (0.34)$^{c,\ AB}$	12.81 (0.53)$^{c,\ AB}$
	1000 m	21.52 (2.01)$^{a,\ A}$	15.55 (0.93)$^{b,\ B}$	19.60 (2.24)$^{a,\ A}$	12.55 (0.32)$^{b,\ B}$	21.59 (2.16)$^{a,\ A}$	14.93 (0.95)$^{b,\ B}$	22.66 (0.73)$^{a,\ A}$	15.26 (0.42)$^{b,\ B}$
P_{av} (mg kg^{-1})	500 m	14.04 (1.31)$^{c,\ AB}$	10.26 (0.81)$^{d,\ D}$	12.88 (0.86)$^{c,\ C}$	11.15 (1.30)$^{c,\ CD}$	13.79 (1.15)$^{b,\ BC}$	9.65 (0.91)$^{c,\ D}$	14.48 (0.68)$^{c,\ A}$	11.13 (0.40)$^{d,\ CD}$
	1000 m	46.81 (0.72)$^{a,\ B}$	17.15 (0.89)$^{b,\ D}$	57.69 (4.03)$^{a,\ A}$	15.30 (1.17)$^{b,\ DE}$	45.30 (5.01)$^{a,\ B}$	13.09 (0.93)$^{b,\ DE}$	54.29 (2.11)$^{a,\ A}$	30.43 (3.41)$^{b,\ C}$

Table 7

Water extractable organic carbon (WEOC), water extractable nitrogen (WEN), contents of the soils under deciduous and pine forests at study sites located at 500 m and 1000 m a.s.l., Mount Cucco massif (Central Apennines, Italy). Standard error is given in parentheses (autumn n = 6, winter n = 4, spring n = 4, summer n = 5). Different letters indicate a significant difference according to Fisher's LSD test ($p < 0.05$) within each individual season (lowercase letters) and throughout the sampling period for each individual elevation (uppercase letters).

	Altitude	Autumn		Winter		Spring		Summer	
		Deciduous forest mg kg^{-1}	Pine forest	Deciduous forest	Pine forest	Deciduous forest	Pine forest	Deciduous forest	Pine forest
WEOC	500 m	120.81 (22.29)$^{a,\ C}$	76.90 (5.72)$^{b,\ DE}$	272.27 (55.70)$^{a,\ A}$	209.65 (33.78)$^{a,\ AB}$	110.08 (11.84)$^{a,\ CD}$	79.84 (5.83)$^{b,\ D}$	179.0 (14.39)$^{a,\ BC}$	90.37 (2.69)$^{ab,\ D}$
	1000 m	80.20 (4.35)$^{b,\ CE}$	75.27 (5.79)$^{b,\ DE}$	207.92 (6.08)$^{a,\ A}$	172.24 (19.82)$^{a,\ B}$	113.35 (6.47)$^{a,\ BC}$	85.28 (7.70)$^{ab,\ E}$	93.14 (4.600)$^{ab,\ BD}$	65.57 (3.63)$^{b,\ E}$
WEN	500 m	25.89 (2.93)$^{a,\ C}$	15.61 (1.83)$^{b,\ D}$	106.99 (17.38)$^{a,\ A}$	69.49 (6.08)$^{b,\ B}$	23.45 (1.42)$^{b,\ C}$	11.68 (1.03)$^{c,\ E}$	19.47 (1.01)$^{b,\ CD}$	11.53 (0.95)$^{c,\ E}$
	1000 m	29.21 (1.96)$^{a,\ C}$	26.20 (3.94)$^{a,\ CD}$	111.91 (27.72)$^{a,\ A}$	76.03 (7.66)$^{b,\ A}$	37.32 (1.64)$^{a,\ B}$	20.40 (2.73)$^{b,\ D}$	37.37 (3.61)$^{a,\ B}$	21.40 (1.48)$^{b,\ D}$

3.4. Organic C and total N stocks in litter and soil under deciduous and pine forest at 500 m and 1000 m altitude

The organic C and total N stocks of the litter layer were larger at 1000 than at 500 m for both forest types (Tables 8, 9). At both elevations pine litter showed always the largest C stocks (Table 8). The litter from the deciduous forests had similar C stocks all throughout the year, except in summer where the lowest values were found at both 500 and 1000 m. The soil TOC stock showed larger values under deciduous than under pine forests both at 500 m and 1000 m (Table 8) and it did not vary throughout the year in the two forest type, except for a slightly lower value recorded in autumn for the deciduous forest soil at 1000 m. The litter TN stocks at 500 m altitude, were always greater for the pine forest, whereas at 1000 m this occurred only for autumn and winter (Table 9). The soils of deciduous forest showed a higher TN stock than pine soils in all the seasons at 500 m and only in spring and summer at 1000 m.

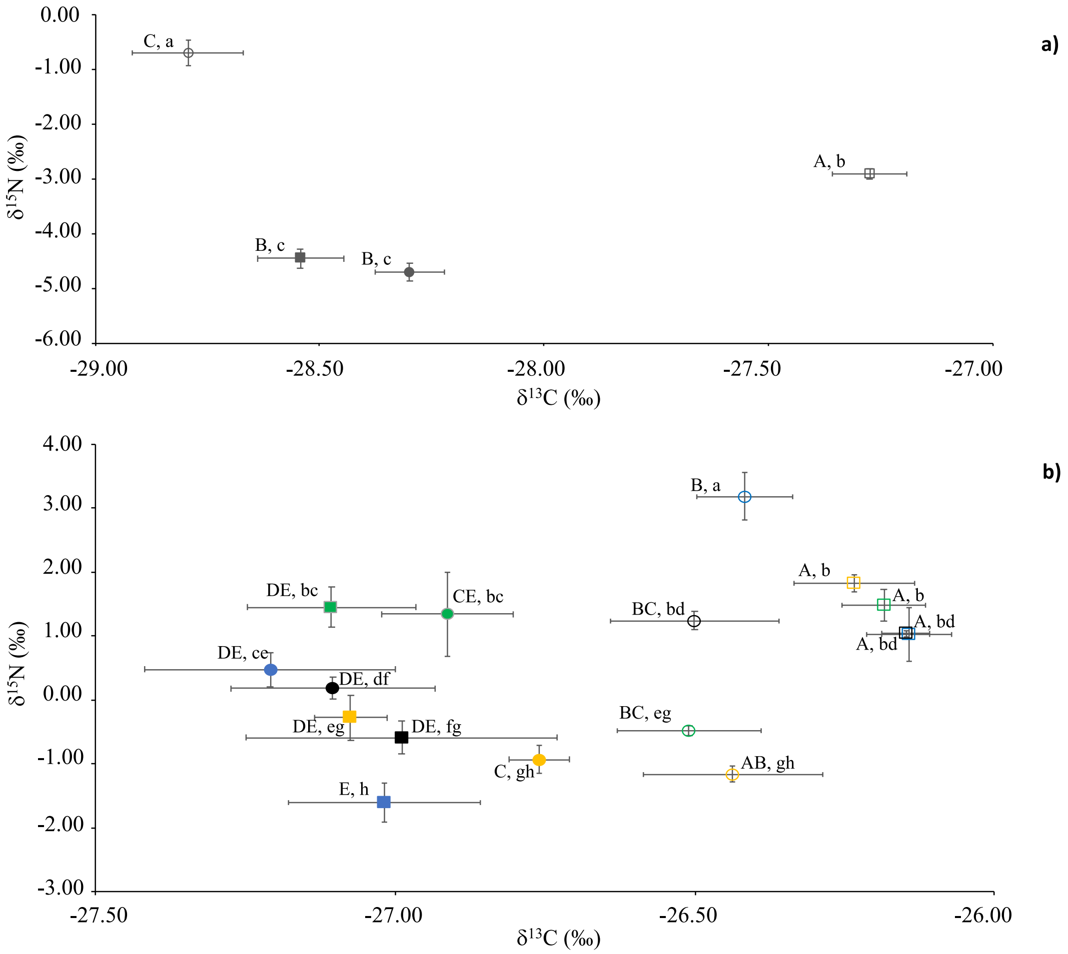
3.5. Non-Metric multidimensional scaling (NMDS) analyses

The NMDS analyses showed different behaviour between the soils under deciduous and pine forests and between the two altitudes across the four seasons (Fig. 2). For pine forest soils, the most pronounced dissimilarity between the two elevations was evident in the summer season (Fig. 2d), which appeared to be primarily driven by total organic carbon (TOC), and the natural abundance of ^{13}C and ^{15}N. For the soils under deciduous forests at 500 and 1000 m, the NMDS plots suggested a marked dissimilarity in all the seasons, and particularly in summer (Fig. 2a, 2b, 2c, and 2d). This dissimilarity was mainly driven by WEN, P_{av}, C:N ratio and CO_2 fluxes. At 500 m, the ellipses representing the two vegetation types overlapped in all seasons, whereas at 1000 m the ellipses were always well separated.

4. Discussion

4.1. Seasonal trends in litter thickness and TOC and TN content

Forest floor thickness showed the highest values in autumn and winter seasons. This was due to both the litterfall occurring in autumn (Jasińska et al., 2020; Farooq et al., 2022; Rawlik et al., 2023) and the lower seasonal temperatures limiting litter decomposition (Faber et al., 2018). However, while there was no change in litter thickness between autumn and winter for D500, P500 and P1000, there was a decrease for D1000. This decrease could be attributed to the quality of plant residues in D1000 (beech forest), which among the four sites has the lowest and most-balanced C:N ratio (20.95) enhancing forest floor degradation (Faber et al., 2018), even in the cold seasons. Conversely, during the spring and summer seasons, the type of the plant residues did not seem



LEGEND: circles: deciduous forests; squares: pine forests. Solid simbols: 500 m a.s.l.; empty symbols: 1000 m a.s.l.
blue: autumn, black: winter, green: spring; yellow: summer. Litter layer: grey symbols (in the plot A).

Fig. 1. Isotopic signatures ($\delta^{15}N$ and $\delta^{13}C$) of litter layer (a) and soil (b) under deciduous and pine forests at study sites located at 500 m and 1000 m a.s.l.. Mount Cucco massif (Central Apennines. Italy). The bars are the standard errors (litter: n = 12; soil: autumn n = 6, winter n = 4, spring n = 4, summer n = 5). For litter layer and soil, different letters (uppercase for $\delta^{13}C$ and lowercase for $\delta^{15}N$) indicate a significant difference according to Fisher's LSD test ($p < 0.05$). For symbols, see figure legend.

Table 8
Seasonal carbon stocks of litter layer (Oi/Oe horizons) and soil (upper 10 cm) under deciduous and pine forests at study sites located at 500 m and 1000 m a.s.l.. Mount Cucco massif (Central Apennines. Italy). Standard error is given in parentheses (autumn n = 6, winter n = 4, spring n = 4, summer n = 5). For litter layer and soil, different letters indicate a significant difference according to Fisher's LSD test ($p < 0.05$), within each season (lowercase letters) and throughout the sampling period for each altitude (uppercase letters).

Altitude	Autumn		Winter		Spring		Summer	
	Deciduous forest Mg ha^{-1}	Pine forest	Deciduous forest	Pine forest	Deciduous forest	Pine forest	Deciduous forest	Pine Forest
Litter layer								
500 m	3.60 (0.29)$^{c, B}$	9.32 (0.48)$^{b, A}$	3.78 (0.16)$^{d, B}$	9.08 (0.34)$^{b, A}$	3.55 (0.13)$^{c, B}$	7.84 (0.61)$^{b, A}$	2.94 (0.28)$^{c, C}$	6.63 (0.58)$^{b, A}$
1000 m	9.13 (0.61)$^{b, BC}$	19.20 (1.48)$^{a, A}$	7.66 (0.02)$^{c, CD}$	18.40 (0.23)$^{a, A}$	7.46 (0.38)$^{b, CD}$	15.76 (1.54)$^{a, A}$	5.92 (0.85)$^{b, D}$	11.65 (1.52)$^{a, B}$
Soil								
500 m	59. 74 (4.55)$^{b, A}$	46.04 (5,14)$^{c, B}$	64.36 (3.38)$^{b, A}$	44.90 (0.88)$^{c, B}$	58.79 (2.96)$^{b, A}$	41.97 (1.50)$^{c, B}$	58.45 (1,22)$^{b, A}$	42.87 (1.94)$^{c, B}$
1000 m	74.28 (6.86)$^{a, B}$	56.92 (3.11)$^{b, C}$	89.31 (0.30)$^{a, A}$	60.89 (0.87)$^{b, C}$	89.49 (0.52)$^{a, A}$	57.00 (2.32)$^{b, C}$	83.38 (2.88)$^{a, A}$	62.96 (1.85)$^{b, C}$

to have any influence on the degradation of the forest floor. Indeed, litter thickness decreased in all the sites suggesting a high impact of the warm temperatures on degradation processes. Similarly, the P1000 had a thicker litter layer than the P500 in winter and spring but not in summer and autumn. This could be due both to the warm summer temperatures and to the lower C:N ratio of the P1000 litter compared to P500, which

Table 9

Seasonal nitrogen stocks of litter layer (Oi/Oe horizons) and soil (upper 10 cm) under deciduous and pine forests at study sites located at 500 m and 1000 m a.s.l.. Mount Cucco massif (Central Apennines. Italy). Standard error is given in parentheses (autumn n = 6, winter n = 4, spring n = 4, summer n = 5). For litter layer and soil, different letters indicate a significant difference according to Fisher's LSD test ($p < 0.05$), within each season (lowercase letters) and throughout the sampling period for each altitude (uppercase letters).

Altitude	Autumn		Winter		Spring			Summer
	Deciduous forest Mg ha^{-1}	Pine forest	Deciduous forest	Pine forest	Deciduous forest	Pine forest	Deciduous forest	Pine Forest
Litter layer								
500	0.09 (0.01)^{c,DE}	0.15 (0.01)^{b,A}	0.10 (0.00)^{d,DE}	0.14 (0.01)^{c,AB}	0.09 (0.00)^{c,DE}	0.12 (0.01)^{b,BC}	0.08 (0.00)^{b,E}	0.11 (0.01)^{b,CD}
1000	0.44 (0.03)$^{a, B}$	0.50 (0.04)$^{a, A}$	0.37 (0.02)$^{b, BC}$	0.48 (0.01)^{a,A}	0.36 (0.02)^{a,BC}	0.41 (0.04)^{a,B}	0.28 (0.03)$^{a, C}$	0.30 (0.04)^{a,C}
Soil								
500	4.71 (0.31)$^{a, BC}$	3.18 (0.13)$^{bc, E}$	6.05 (0.42)$^{a, A}$	4.19 (0.33)$^{b, CD}$	5.53 (1.05)$^{a, AB}$	3.63 (0.43)$^{b, DE}$	4.27 (0.11)$^{a, CD}$	3.36 (0.11)$^{b, E}$
1000	3.50 (0.12)$^{b, BC}$	3.10 (0.08)$^{c, C}$	4.73 (0.33)$^{b, A}$	4.15 (0.15)$^{b, AB}$	4.34 (0.22)$^{ab, A}$	3.26 (0.13)$^{b, C}$	4.27 (0.47)$^{a, A}$	3.48 (0.10)$^{b, BC}$

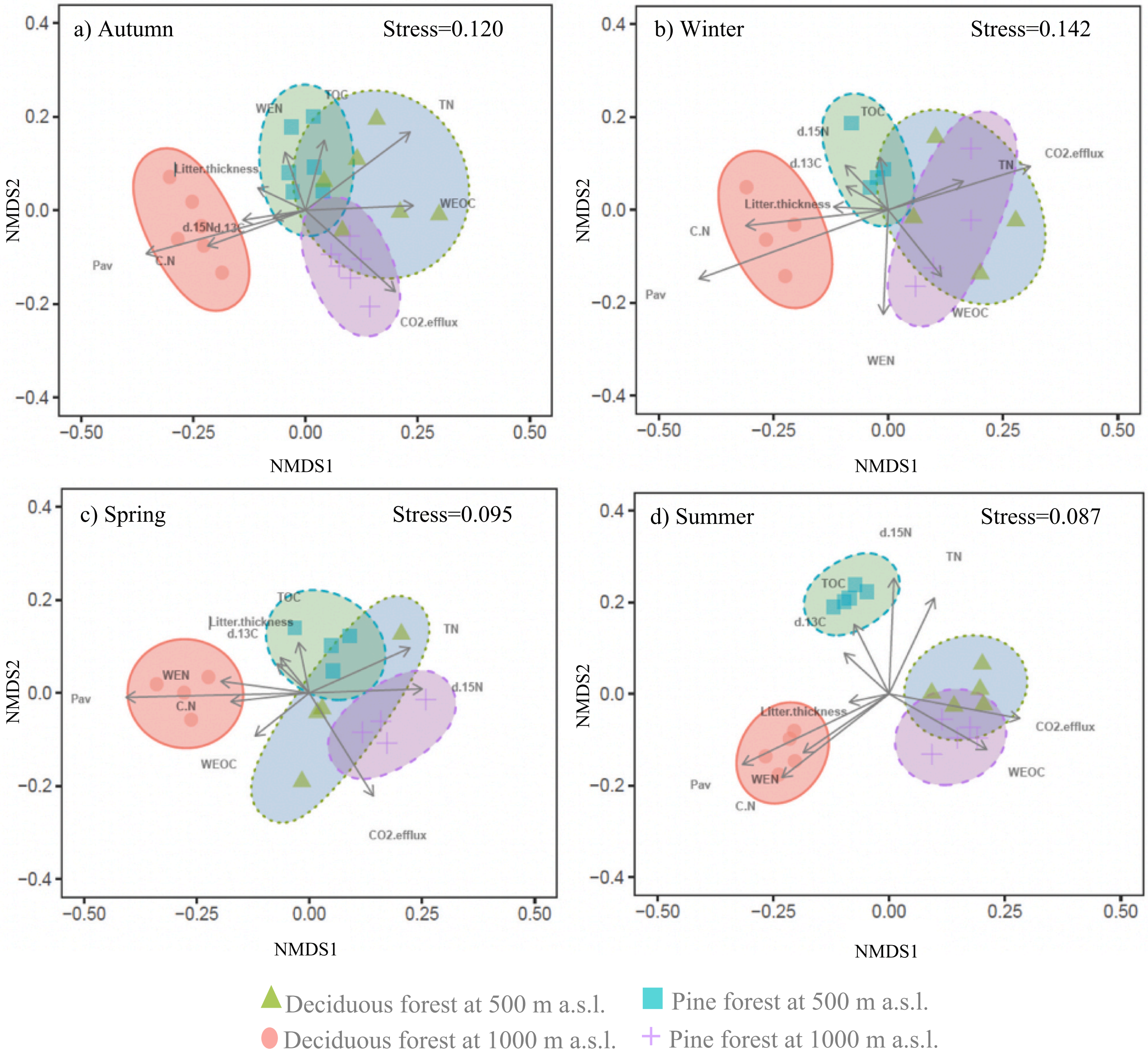


Fig. 2. Non-metric multidimensional scaling (NMDS) analysis performed for each season for soils under deciduous and pine forests at 500 m and 1000 m a.s.l.., Mount Cucco massif (central Apennines, Italy). Circle lines in each NMDS plot are 95 % confidence ellipses.

would favour relatively intensive litter decomposition even at high altitudes (Faber et al., 2018). With regard to the C:N ratio of the forest floor, our findings contrast with those of previous studies (e.g., Hultine and Marshall, 2000; Niu et al., 2021) that reported a decreasing N content in plant tissues with altitude. The higher N content of the pine forest floor at 1000 m compared to 500 m might be attributed to the larger soil TN content (Table 6), and therefore, greater N availability for plants at 1000 m altitude (Warren and Whitehead, 1988).

Generally, soil TOC content did not show seasonal differences within the same forest type at each altitude due to its stability to short–term temperature changes (Moinet et al., 2020; Rocci et al., 2021). The only increase in TOC was observed from autumn to winter in D1000, which was attributed to the degradation of the litter layer and subsequent accumulation of organic matter in the mineral soil (Prescott and Vesterdal, 2021; Zhang et al., 2023). This was possibly due to the mild autumn temperature and the already mentioned C:N ratio of the beech litter and, parallelly, the low temperature in winter that limited SOM degradation (Tables 2, 4, 5). However, although the decomposition of the forest floor is functional for the organic C enrichment of the A horizon, there were no changes in the soil TOC content even in spring and summer, when the litter thickness decreased due to intense decomposition. This could be the result of a balance between the increase of the mineralization rates during the warmer seasons (as evidenced by the increase of CO_2 fluxes, Table 4) and the C input received following litter degradation, which being mostly comprised of soluble and particulate organic matter is sensitive to temperature changes and easily degradable (Benbi et al., 2014; De Feudis et al., 2019; Lugato et al., 2021). Soil TOC contents at 1000 m elevation were generally higher than those at 500 m, which was to be expected given the lower temperatures (Praeg et al., 2020; Massaccesi et al., 2020). Thereby confirming that, in contrast to short-term temperature variations (i.e., seasonal temperature variations), stable differences in thermal conditions (i.e., those related to elevation) have a great influence on soil TOC content.

Comparing the vegetation types, deciduous forests had a higher TOC content than under pine only at lower elevations. This, although both D500 and D1000 litters had a C:N ratios which should have favoured their degradation and subsequent incorporation into the underlying mineral soil (Prescott and Vesterdal, 2021) at both elevations. The lower amount of soil TOC of D1000 than of P1000 was therefore attributed, other than the possible different productivity between broadleaves and conifers (Augusto et al. 2015), to the lower C concentration of D1000 (beech) litter (Table 5). The latter, despite its better degradability, would have released a lower amount of C per unit mass than that resulting from the degradation of the pine litter, although this latter was more recalcitrant. Another possible reason for the low TOC concentration at D1000 could also be the acidic pH of the soil (Table S2), which, by lowering the surface charge of minerals (Fissore et al., 2008), would reduce organo-mineral interactions and thus SOM stabilization (Massaccesi et al., 2020).

4.2. Seasonal trends in CO_2 emissions and $\delta^{13}C$ and $\delta^{15}N$ of litter and SOM

The generally larger CO_2 fluxes at 500 m than at 1000 m altitude all over the year for both forest types would indicate temperature to be the major driver of SOM mineralization (Laganière et al., 2012; Wang et al., 2010). However, we are aware that soil respiration includes both autotrophic and heterotrophic respiration (e.g., Valente et al., 2021). Therefore the CO_2 effluxes, especially those of the warmer seasons, must be partially attributed to root activity (Schindlbacher et al., 2009). During winter, the combination of the lowest soil temperature and CO_2 efflux together with the highest WEOC concentrations, the most readily available C source for soil microbial community (Bowen et al., 2009; Bolan et al., 2011), highlighted that low soil temperatures hindered organic carbon mineralization in all considered forests. During the warmer seasons, when a larger soil respiration occurred in all sites, D500 showed a great increase of CO_2 emissions from soil. In this case, although an increase in CO_2 emissions occurred across all forests and we could not generally distinguish between autotrophic and heterotrophic sources of respiration, the significant $\delta^{13}C$ increase of SOM (Fig. 1b) at D500 suggested a strong acceleration of the mineralisation processes (Soldatova et al., 2024). This acceleration at D500 was likely promoted by suitable temperature conditions and SOM quality. The significant increase of $\delta^{13}C$ occurred at D500 from autumn to spring and summer, and absent at P500 (Fig. 1b), pointed to a greater SOM mineralisation under the deciduous than the pine forest (Lorenz and Thiele-Bruhn, 2019). However, such accelerated SOM mineralisation at D500 can be also partly explained by the higher soil moisture in deciduous forests compared to pine forests at 500 m across all seasons (see Table S3). Soil moisture is key to regulating microbial activity and SOM mineralisation by supporting higher enzyme activities and enhancing substrate availability (Singh et al., 2021). At 1000 m of altitude, the absence of any seasonal $\delta^{13}C$ variation for both forests, despite the different quality of SOM derived from beech and pine, would confirm the strong impact of temperature on mineralization processes (Kirschbaum, 1995). The intense decrease of $\delta^{15}N$ values throughout the year at D1000 soil has been mostly attributed to the input of fresh N-rich material coming from the beech litter (Fang et al., 2011).

It is interesting to observe that $\delta^{13}C$ values of pine forest were very much higher at 1000 m than at 500 m for both litter and soil. However, shifts of $\delta^{13}C$ in conifer leaves are consistently found over altitudinal gradients (Körner et al., 1988, Marshall and Zhang, 1994; Sparks and Ehleringer, 1997). This higher $\delta^{13}C$ of litter at 1000 m might be due, among other abiotic factors, to the lower mean air temperatures and air pressure (Marshall and Zhang, 1994; Panek and Waring, 1995) preventing photosynthetic C isotope discrimination and thus favour a consequent higher accumulation of ^{13}C in plant tissues (Hultine and Marshall, 2000). The shift of the litter $\delta^{13}C$, from about −28.5 ‰ at 500 m to −27.3 ‰ at 1000 m altitude of pine forest was in line with the increasing rate of the isotopic signature with altitude (2.68 ‰ km^{-1}) reported for *Pinus contorta* by Hultine and Marshall (2000). If we consider the isotopic C fractionation as a mineralisation intensity index (Liebmann et al., 2020), then similar ^{13}C enrichment occurring for D500 and P500 between litter and SOM (from about –28.5 ‰ to about –27.0 ‰) would imply a comparable degradation rates in the two ecosystems. Conversely, this did not occur at 1000 m altitude where the ‰ positive delta between the $\delta^{13}C$ of litter and SOM was about 2.5 ‰ for D1000 and only 1.0 ‰ for P1000. This greater isotopic fractionation occurring for D1000 would suggest a higher degree of transformation from litter to SOM that, under the same thermal condition, must be primarily attributed to the quality of the plant residues (Berg and McClaugherty, 2014; Giudice and Lindo, 2017; Massaccesi et al., 2020; Prescott and Vesterdal, 2021). In particular, the low C:N ratio of D1000 litter, which promotes biochemical N transformations by microbial community (Marty et al., 2019), could be the trigger factor for the rapid mineralisation of organic carbon despite the low temperature at high altitude. Further, as in forest soil the organic matter is the major source of available P (Bueis et al., 2019), enhanced bio-cycling of plant residues at D1000 might also explain the largest available soil P content under beech. This hypothesis was also consistent with the results of the NMDS analysis (Fig. 2), which showed that the differences between deciduous and pine forest soils were more pronounced at higher elevations. This suggested that, as temperature decreased, the vegetation type was the main driver of SOM cycling. Indeed, the dissimilarity of D1000 from P1000, which was greatest in summer, was mainly driven by P_{av} content and C:N ratio in the soil under the deciduous forest.

The ^{15}N natural abundance, unlike ^{13}C, showed seasonal changes in most of the investigated forests likely due to its known high sensitivity to changes in N–limited environments (Marty et al., 2019; Saenger et al., 2024) and intensive forest N recycling (Soldatova et al., 2024). Indeed, although soil ^{15}N is generally considered a poor tracer of N source inputs due to the simultaneous occurrence of multiple transformations, fluxes, inputs and outputs (Robinson, 2001), it provides a single indicator of overall ecosystem N functioning, with higher ^{15}N values indicating a more open N cycling ecosystem. Specifically, at 500 m of altitude, both forest soils showed an increase of δ^{15}N from winter to spring due to the SOM mineralization promoted by the growing temperatures (Gurmesa et al., 2021). The following decrease in the subsequent summer season was likely due to the incorporation of fresh N coming from the litter layer which had a lower δ^{15}N value than that of the soil N.

4.3. C and N stocks in litter and soil

The organic C and N stocks in litter showed higher values at 1000 than at 500 m a.s.l. independently by forest type. In accordance with earlier studies (e.g., Garten and Hanson, 2006; Prietzel and Christophel, 2014), the higher stocks at higher altitude were caused by strongly influence of temperature on organic matter degradation rather than on plant primary production (Bangroo et al., 2017). The larger organic C and N stocks of litter in coniferous than in deciduous forests at both altitudes can be attributed to the lower litter quality (high C:N ratio) of the former compared to the latter which prevented its degradation (Prescott et al., 2000; Růžek et al., 2021). Soil organic C stocks showed similar trends to those observed for the litter. This would suggest, as hypothesized, that both temperature and SOM quality influence soil C storage processes. However, at 1000 m the SOC stock was higher in D1000 than in P1000, which appeared to contrast with the SOC concentration values. Similarly, while the soil N content had higher values in P1000 than in D1000, the soil N stock did not show differences between the two forest types. These contrasting results was attributed to the very high skeleton content of the soil under pine (Table S1) also highlighting the importance to take into consideration the volume occupied by rock fragments for the estimation of soil nutrient stocks (De Feudis et al., 2022).

5. Conclusions

This study, which considered adjacent deciduous and coniferous forests at two altitudes (500 and 1000 m a.s.l.), showed that litter and SOM accumulation/degradation is controlled not only by temperature but also by the quality of plant-derived materials. This was clearly showed by the greater ^{13}C fractionation from litter to SOM in D1000 than in P1000 (with a mineralisation intensity index of 2.5 ‰ and 1.0 ‰, respectively), which would indicate a higher degree of transformation under the same thermal condition of the plant residues from the deciduous forest, which were characterized by a more balanced C:N ratio than the pine litter. However, while at 500 m altitude a significant SOM ^{13}C fractionation and a parallel increase in soil CO_2 emissions occurred in the warmer seasons, no seasonal δ^{13}C variation was observed at 1000 m for both forests, despite the different quality of SOM derived from deciduous and coniferous forests. Hence, our seasonally measured isotopic signatures have drawn a picture where organic C and N transformations from litter to the upper soil mineral horizon were greatly controlled by the quality of the plant residues, whereas soil temperature would seem to be the major driver for the seasonal evolution of SOM.

Regarding the C stocks in deciduous and conifer forests at 500 and 1000 m altitude, the pine forests had higher litter C stocks than the deciduous one at both altitudes, but the opposite occurred for the soil C stocks. The larger soil C stocks under the deciduous forest than under the pine forest, despite the lower soil C concentration of the former, at least at higher elevation, was due to the high skeleton content of the pine soils emphasizing the importance of an accurate soil morphological analysis and the consideration of the skeleton volume for a correct estimation of soil nutrient stocks.

This study carried out along an altitudinal sequence, using the altitude as a proxy for temperature change and considering two different types of vegetation (deciduous and coniferous), allowed to evaluate the combined interactions between the quality of plant residues and temperature in controlling litter and SOM mineralization/accumulation processes.

CRediT authorship contribution statement

M. De Feudis: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **L. Massaccesi:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **C. Poesio:** Writing – original draft, Investigation, Formal analysis, Data curation. **L. Vittori Antisari:** Writing – review & editing, Resources, Conceptualization. **R. Bol:** Writing – review & editing, Data curation, Conceptualization. **A. Agnelli:** Writing – review & editing, Writing – original draft, Validation, Supervision, Investigation, Data curation, Conceptualization.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2025.117382.

Data availability

Data will be made available on request.

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